The dynamics of habitat use in the salmonid genera *Coregonus* and *Salvelinus*: ontogenetic niche shifts and polymorphism

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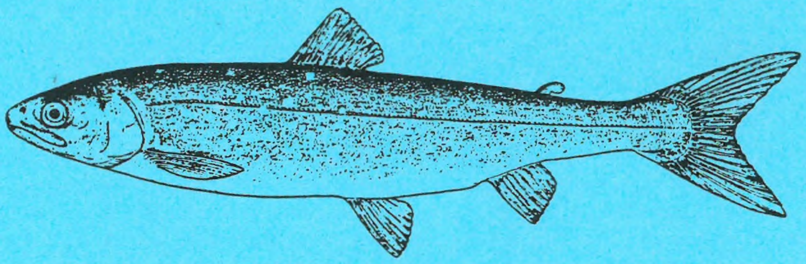
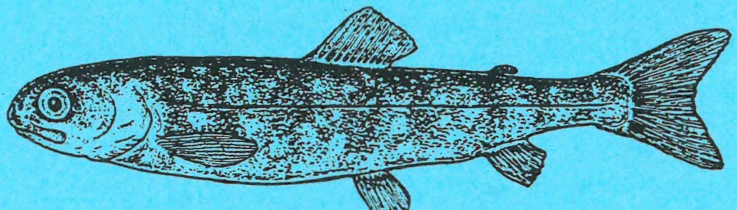
Odd Terje Sandlund





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CONTENTS

PREFACE

This work was carried out while I was employed by the Directorate for Nature Management (DN) (1978 - 81), the Norwegian Society for Rural Development (SNV) (1981 - 89), and, since 1989, the Norwegian Institute for Nature Research (NINA).

First and foremost, I am indebted to my friends and colleagues, Bror Jonsson and Tor Næsje. Bror has been a pillar of support since I started as an undergraduate student in the Voss project, through the various twists and turns of my professional career, until we again are colleagues at NINA. Tor Næsje started as my student at the Mjøsa project, and soon became the kind of supportive colleague who makes the life of a socially inclined scientist worth living.

In addition, I would particularly like to express my gratitude to a few persons whom I have been working with during the process ending with this thesis. During the Mjøsa years, I had a very fruitful cooperation with Gösta Kjellberg of the Norwegian Institute of Water Research (NIVA). My senior colleague in DN, Per Aass, provided useful advice and productive discussions. In SNV, director Kristian Kaus and my section leaders Kåre Ulvund and Anne Siri Brandrud enabled me to participate in research activities in Femund and Thingvallavatn, although strictly speaking I was employed in a management project. In 1983 I was invited by Pétur M. Jónasson to take part in the Thingvallavatn project, and I want to thank him sincerely for his inspiring enthusiasm and for his fund-raising abilities.

My sincere gratitude is also extended to all my other co-authors and the people who have assisted during field work at Mjøsa, Osensjøen, Femund and Thingvallavatn, and in the laboratory work through the years.

Last, but not least, my wife Vera and the "kids" Ragnhild and Kjetil, have accepted living with a "my-work-is-my-hobby" husband and father for many years. I am extremely grateful for their patience and support.

INTRODUCTION

In the present papers, I have studied the role of ontogenetic niche shifts and polymorphism in the formation of the ecological niche of whitefish *Coregonus lavaretus* and vendace *Coregonus albula* in three large lakes in Norway, and Arctic charr *Salvelinus alpinus* in one large lake in Iceland. I have investigated the habitat use of these species and analyzed how they adapt to the temporally and spatially variable environments of northern lakes.

The environment

The biota of northern temperate lakes are characterized by a strong seasonality imposed by the climate. During winter, the ice cover and low water temperatures usually results in low abundances of available invertebrate prey. In addition, the low water temperatures cause low metabolic rates and food uptake in the fish (e.g Brett and Higgs 1970, Elliott 1972, Weatherley 1976, Brett 1979). Higher abundances of available prey are found in spring, summer and autumn. Maximum number of available zoobenthos is often observed in spring and summer, when insects with aquatic larval stages emerge (e.g. Brinkhurst 1974, Aagard 1978, Brittain 1978). Maximum densities of crustacean zooplankton, on the other hand, are commonly seen in late summer and autumn (e.g. Larsson et al. 1978, Adalsteinsson 1979, Langeland and Reinertsen 1982). This seasonality will obviously influence the ecology of fishes in the lakes (Fretwell 1972).

For zoogeographic reasons, few fish species are present in Norwegian and Icelandic freshwaters (Huitfeldt-Kaas 1918). The natural colonization occurred during the last deglaciation about 10,000 years ago. On the Scandinavian peninsula and in Iceland the postglacial land uplift and the salinity of the Baltic and the North Sea created immigration barriers soon after deglaciation. The resulting low diversity of the freshwater fish fauna is clearly seen when the natural fauna of Scandinavian lakes is compared to the fish fauna of the lakes of eastern North America with similar temperature and production regimes (e.g. Scott and Crossman 1973). Postglacial immigration of freshwater fish in eastern North America was not stopped by impassable barriers (Lagler et al. 1977), and consequently the diversity in these lakes are higher.

The species

The salmonid genera *Salvelinus* and *Coregonus*, represented by the species Arctic charr, whitefish, and vendace, are widespread in the species-poor lakes of Scandinavia and Iceland. There has been considerable debate over the taxonomic status of the three species. The morphological and ecological variability between and within populations of whitefish and Arctic charr led to the suggestion that there are five whitefish species (Svärdson 1979) and three Arctic charr species (Nyman 1972, Nyman et al. 1981). Due to differences in spawning time in some sympatric vendace populations, Svärdson (1979, 1988) claimed that there are two vendace species in Scandinavia. These authors assumed that speciation had occurred in geographically isolated localities to the south and east during glaciation, and that the forms immigrating to Scandinavia after deglaciation already were established species.

On the other hand, a number of investigators have maintained that Arctic charr, whitefish and vendace each is one variable species (Reisinger 1953, Dryagin et al. 1969). This is supported by several recent genetic analysis and rearing experiments (Ferguson et al. 1978, Andersson et al. 1983, Hindar et al. 1986, Nordeng 1983, Vuorinen et al. 1981, 1986) which have provided quite conclusive evidence that Arctic charr, whitefish and vendace in northwestern Europe each are one species, which may occur in polymorphic populations. The results also indicate that the diversification in salmonids has occurred within the localities (Ryman et al. 1979, Ferguson 1981, Vuorinen et al. 1981, Hindar et al. 1986).

The lake communities and niche width

The niche width of fish species in low-diversity lake communities may be considered in the light of island biology. Generally, on islands the number of species will increase through immigration until a level when the rate of immigration equals the rate of extinction, and the number of species is stabilized (MacArthur and Wilson 1967, MacArthur 1972). In general, the maximum number of species depends on the area of the island, but island communities normally contain fewer species than comparable mainland systems (Diamond 1973, Connor and McCoy 1979). The low level of interspecific competition on islands leads to an expanded niche which may induce increased variation in morphology (Selander 1966, van Valen 1968), behaviour (Diamond 1978, Feinsinger and Swarm 1982) and genetic structure (Shugart and Blaylock 1973, Steiner 1980). In addition to a wider niche, the wide array of resources available has often led to adaptive radiation into polymorphic populations or, given sufficient time, speciation (Diamond 1978, Avise 1990).

Scandinavian-Icelandic lakes may be considered islands which at some early point in the colonization process have been screened off from further influx of species. The consequence is an even lower number of fish species than should be expected from the lake surface areas (equivalent to island size). Thus, each fish species in the low-diversity lake communities have an opportunity to utilize a wide variety of resources. However, as lake ecosystems in the previously glaciated areas are relatively young (< 10,000 yrs), diversification has not proceeded into speciation, as observed in older lake systems like Lake Baikal, USSR (Smith and Todd 1984) and the great lakes of East Africa (Fryer and Iles 1972, Greenwood 1984, Meyer et al. 1990). In cases where morphs become reproductively isolated, the instability of northern lakes may in most cases cause isolation to break down before diversification proceeds to species level.

According to Christiansen and Fenchel (1977) the ecological niche of animal populations has three main dimensions: time, habitat (space) and diet (resource). In fish communities, between- and within-species segregation is often found to be by habitat and diet (Werner et al. 1977, Mittelbach 1984). Many investigations have indicated that niche overlap between groups of animals is mainly reduced through a segregation by habitat (Schoener 1974, Werner et al. 1977). In large lakes, the habitat available to fish is clearly three-dimensional. Thus, groups may be segregated horizontally, i.e. they may live benthically or pelagically, or vertically by living in different depths along the bottom profile or in the pelagic zone.

The niche width of a population is defined by three components (Christiansen and Fenchel 1977): the **within-phenotype component** (WPC), the **between-phenotype component** (BPC), and the **age structure component** (ASC). Total niche width may be expressed as WPC + BPC + ASC (Vrijenhoek et al. 1987).

The **within-phenotype component** is the variance of each individual in the utilization of resources or in its response to environmental factors, and includes e.g. the seasonal variation in habitat use and diet by an individual fish.

The **between-phenotype component** is the variation in resource use between different individuals within the population. In a polymorphic population, this includes both the differences in resource use among individuals of the same morph and differences between morphs.

The **age structure component** is the age-specific variation in use of resources, including ontogenetic niche shifts (Polis 1984). Thus, an accurate description of the total niche width of a fish population may be reached by defining the niche parameters habitat use and diet of all ontogenetic stages (size groups) and morphs of a population.

The ontogenetic niche

According to foraging theory, individuals will take the prey that give the higher relative energy return (Charnov 1976, Pyke et al. 1977, Stephens and Krebs 1986). In general, this means that the prey size tends to increase as predator size increases. Compared to most terrestrial animals, fishes are characterized by indeterminate and flexible growth, i.e. the onset of sexual maturity does not mean the end of growth as long as there is sufficient food. The growth rate is largely determined by the quality and quantity of food. As the fish grow they are able to take increasingly larger prey without losing the ability to take small prey (Wilson 1975, Werner and Gilliam 1984). The most profitable feeding patch is determined by a combination of prey type and prey abundance, and the fish choose feeding habitat according to the optimal energy returns (Werner et al. 1981, 1983a). The fish occupying the richest patch should thus grow faster and larger than those feeding under poorer conditions.

In presence of predators, the choice of feeding habitat is modified by risk of predation, which decreases with increasing body size (Werner et al. 1983b, Power 1984, Milinski 1986). Small fish are restricted in their habitat use by the presence of predators (Mittelbach 1984, Gilliam and Fraser 1987, Schlosser 1987). As the body size increases, the fish will gradually be less vulnerable to predation, and more profitable foraging patches may be invaded in spite of higher predator frequencies (Werner and Hall 1976, Cerri and Fraser 1983, Power 1984, Mittelbach 1986, Abrahams and Dill 1989). The balance between foraging profitability and predation risk may often change rather abruptly as the fish reach some threshold size not vulnerable to predation (Werner and Hall 1976, 1988, Osenberg et al. 1988). Experiments have shown that the fish are able to at least partly evaluate profitability and predation risk in different feeding patches, and selecting the one offering the greatest expected increase in fitness per unit of time (Dill 1987, Holbrook and Schmitt 1988). There appears to be an element of learning in the process of judging the profitability of habitats (Werner et al. 1981, Persson 1990), so that there will be a time lag between increase in available resources and the ability of the fish to exploit this increase.

The habitat use of species is also influenced by competitors (Grant and Grant 1982, Werner 1986, Bergman 1990). Several Swedish investigations (summarized by Nilsson 1967, 1978), have indicated, based on gut contents, that salmonid species are using habitats differently depending on which other species are present. In terms of dominance related to utilization of pelagic zooplankton, the salmonids brown trout (*Salmo trutta*), Arctic charr, whitefish, and vendace formed a dominance hierarchy, with vendace as the most efficient zooplanktivore (Svärdson 1976).

Polymorphism

The "niche-variation hypotheses" (van Valen 1965) predicts increased differences between individuals when interspecific competition is low, i.e. the between-phenotype component of niche width increases. Polymorphism extends the individual differences into a directed divergence into "vacant" niches that create bi- or multimodality in morphological and ecological population parameters. In fact, it has been assumed as a precondition for the emergence and existence of polymorphism that there is "vacant" niche space available for the various modes of the population (Pimm 1979, Turner and Grosse 1980, Hindar and Jonsson 1982, Wilson and Turelli 1986). Maintaining stable polymorphism require stable niches, which allow morphological and behavioural specialization to develop (Vrijenhoek et al. 1987). For the population to develop bi- or multimodality in characters, the niche space must contain adaptive peaks, which render intermediate morphs less fit (Rosenzweig 1978, Turner and Grosse 1980). Polymorphism in fishes has been shown in a number of characters. It may, as in e.g. salmonids and centrarchids, occur in body size and coloration at sexual maturity, as well as sexual behaviour (Dominey 1980, Gross 1982, 1985, Jonsson and Hindar 1982, Jonsson 1989). In many groups of fish, polymorphism has been shown in trophic characters like dentition, gillraker number, and mouth position (Roberts 1974, Sage and Selander 1975, Turner and Grosse 1980, Kornfield et al. 1982, Lavin and McPhail 1987, Gardner et al. 1988). The morphological differences have been shown to result in differential efficiency in food uptake (Layzer and Clady 1987, Ehlinger 1990).

Polymorphism in fishes may be environmentally induced in a single cohort by e.g. differential feeding conditions during early development (DeAngelis and Coutant 1982, Huston and DeAngelis 1987, Meyer 1987). This phenotypic plasticity appears to occur in many salmonid populations, where divergent forms may be genetically identical (Andersson et al. 1983, Nordeng 1983, Hindar et al. 1986, Ståhl and Hindar 1988).

Assortative mating (isogamy) may subsequently contribute to some degree of reproductive separation between the morphs (Jonsson and Hindar 1982, McKaye et al. 1984). Many salmonid species have been shown to evolve genetically distinct local populations, which are maintained by a reproductive homing behaviour, as in e.g. brown trout (Stuart 1953, 1957), Arctic charr (Frost 1965), and whitefish (Kirkpatrick and Selander 1979). When the various spawning localities provide different environments for the offspring, the various spawning demes may easily develop into morphs which are recognized within the species population.

The problem

As outlined above, the wide array of resources available to fish in the low-diversity communities of large lakes in Scandinavia and Iceland may be utilized through various strategies: large variation in body size, ontogenetic niche shifts and adaptive radiation resulting in trophic polymorphism.

Based on this, the following questions are studied in the present papers:

1 What are the roles of: a) ontogenetic niche shifts and b) polymorphism in the formation of the total niche width of populations of Arctic charr, whitefish and vendace?

2 Do polymorphic populations of charr and whitefish have a more extended niche in terms of habitat use than monomorphic populations of the same species?

The papers are listed below.

LIST OF PAPERS

Paper I Sandlund, O.T., T.F. Næsje, L. Klyve and T. Lindem 1985. The vertical distribution of fish species in Lake Mjøsa, Norway, as shown by gill net catches and echo sounder. **Rep. Inst. Freshwat. Res. Drottningholm 62:** 136 - 149.

Paper II Næsje, T.F, O.T. Sandlund and B. Jonsson 1986. Habitat use and growth of age-0 whitefish, *Coregonus lavaretus*, and cisco, *C. albula*. **Env. Biol. Fish. 15:** 309 - 314.

Paper III Sandlund, O.T., T.F. Næsje and B. Jonsson. Ontogenetic changes in habitat use by whitefish, *Coregonus lavaretus*. **Env. Biol. Fish.** in press.

Paper IV	Næsje, T.F., B. Jonsson, O.T. Sandlund and G. Kjellberg. Habitat switch and niche overlap in coregonid fishes: effects of zooplankton abundance. **Can. J. Fish. Aquat. Sci.** in press.
Paper V	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.
Paper VI	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.
Paper VII	Sandlund, O.T. Ecology of two vendace, *Coregonus albula*, populations separated in 1895. **Manuscript submitted for publication.**
Paper VIII	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.
Paper IX	Sandlund, O.T., K. Gunnarson, P.M. Jónasson, B. Jonsson, T. Lindem, K.P. Magnússon, H.J. Malmquist, H. Sigurjónsdóttir, S. Skúlason and S.S. Snorrason 1991. The arctic charr *Salvelinus alpinus* in Thingvallavatn. **OIKOS in press.**

SYNOPSIS OF RESULTS

Ontogenetic niche shifts

Papers I, II, III, IV, VIII, and IX show that both vendace, whitefish and Arctic charr perform ontogenetic niche shifts. All species start their lives in the benthic zone and turn to utilizing the pelagic zone at a later age.

In vendace, the whole cohort performs a niche shift to the pelagic zone during the first summer (Paper II), and continue living in this zone feeding mainly on zooplankton for the rest of the life span (Paper IV and VII). Even in the littoral zone, however, the diet of age-0 vendace is dominated by crustacean zooplankton (Paper II). Thus, the niche of vendace is narrow, and the specialist nature of the species is reflected in its pelagic zooplanktivore life in a variety of localities (Paper IV, V, VII). The observed fluctuating or regularly oscillating year class strengths in vendace populations

(Paper VI) are probably due to the narrow niche of the species, restricted both in the diet and habitat dimension, creating strong intra-specific interactions.

The generalist nature of Arctic charr and whitefish is indicated by their variable diet and habitat use within and between lakes. The two species resemble each other in their patterns of ontogenetic niche shifts. Populations of both species maintain a basis in the epibenthic habitat, where all size groups of the population usually are present (Paper III, VIII, IX). Among certain size groups, some fish perform a seasonal habitat shift to the pelagic zone when zooplankton abundance is high. In Mjøsa whitefish, the habitat shift occurs just prior to sexual maturity at a size of 25 cm (Paper III and IV). In Femund whitefish, the habitat shift occurs at a size of between 20 - 25 cm (Paper VIII), and is mainly performed by the most slow-growing morph, which matures sexually from a body length of 25 cm onwards. In both lakes the habitat shift involves few fish larger than 35 cm, and only a part of the 25 - 35 cm length group. The change in habitat may therefore be termed niche expansion rather than niche shift. In Mjøsa, the niche of whitefish larger than 35 cm is restricted to feeding in the deep benthic zone on one particular prey item (*Pallasea quadrispinosa*). In Femund, large whitefish utilize the shallow benthic zone (Paper VIII, Sandlund and Næsje 1986).

The ontogenetic development of the niches differs among the Arctic charr morphs in Thingvallavatn (Paper IX). All morphs start their lives in the littoral zone, feeding mainly on chironomid larvae. The benthic morphs remain in the littoral zone, but their diet includes an increasing proportion of the snail *Lymnaea peregra*. Thus, there is a rather moderate niche change in the benthic morphs (SB- and LB-charr). The pelagic morphs, on the other hand, expand their habitat to include both the profundal and the pelagic zone, and their diet includes both zoobenthos and zooplankton, from an age of a few months onwards. The large pelagic morph (LP-charr) performs one additional diet shift, into a diet dominated by fish (*Gasterosteus aculeatus*). In this system, the pelagic morphs (PL- and PI-charr) exhibit generalists' niches, whereas the benthic morphs (SB- and LB-charr) are more specialized.

The dominance of pelagic prey in the diet of pelagic whitefish (Paper II and III) and Arctic charr (Paper IX), indicates that the individual fish stay for a prolonged period in the pelagic zone. This observed pattern of niche shifts generates the hypothesis that the individuals performing the niche shift are morphologically and behaviourally better adapted to a pelagic life than the individuals remaining in the benthic habitat.

Polymorphism

Superficially, the occurrence of polymorphism in whitefish and Arctic charr populations does not seem to increase total population niche width. For instance, the Mjøsa whitefish (Papers I - V) utilize all main habitats (littoral, profundal, pelagic) and all prey types and sizes commonly taken by whitefish, during its lifetime. The Femund whitefish, which according to gillraker number consists of three morphs (Paper VIII), appears to use the same habitats. However, a closer analysis of the niche of each ontogenetic stage reveals differences between mono- and polymorphic stocks. E.g., the niche of juveniles is wider in polymorphic than in monomorphic whitefish populations. In Femund, juveniles were caught in the benthic zone at all depths down to 60 m (Paper VIII, Sandlund and Næsje 1986), indicating a wider habitat than among juveniles of the monomorphic Mjøsa stock, which are restricted to the littoral zone (Paper II, III).

In the Thingvallavatn charr, the variation in habitat use and diet among the morphs, already from age-0, leads to a very wide total niche for this population (Paper IX). Within virtually all size and age groups of fish there are both pelagic and benthic fish. The diet of all size groups between approximately 7 - 22 cm varies from crustacean zooplankton through insects to snails. The diet of fish larger than 22 cm also includes fish.

The observations on head morphology and gillraker number of the pelagic versus the benthic morphotypes in Thingvallavatn (Paper IX) support the notion that sympatric morphs are morphologically specialized to feed on different prey types in different environments. Trophic specialization makes each fish more efficient in utilizing its special resource. A condition for the occurrence of trophic specialization, however, is that there are stable resource bases available. In Thingvallavatn these bases of available resources largely consists of the snail *Lymnea peregra* in the benthic zone, the crustacean zooplankton and the emerging and hatching chironomids in the pelagic zone, and the sticklebacks in the epibenthic zone. The nearly complete absence of competitors has allowed for a trophical diversification and specialization in the Arctic charr population.

In Femund, the number of competitors is also relatively low, and the whitefish has diversified into morphs differing in trophical morphology (Paper VIII). The three morphs have been denoted according to their spawning sites: deepwater (D-), river (R-), and shallow water (S-) whitefish. In this case the morph with the lowest number of gillrakers, i. e. the D-whitefish (28 gillrakers), utilize the pelagic zone during the period of maximum zooplankton abundance. The morphs with the denser gillraker sieves (R-whitefish, 35 gillrakers; S-whitefish, 43 gillrakers) mainly stay in the benthic habitat. This may indicate that the connection between zooplanktivory and the number of gillrakers is not as simple as has been believed (Nikolsky 1963, Lindsey 1981, but see O'Brien 1987). The zooplankton size selection by vendace and whitefish in Mjøsa shown in Paper V also indicate a more complex connection between gillraker morphology and zooplanktivory than is often believed.

It may be hypothesized that some of the differences between whitefish morphs in Femund emerge because the morphs spawn in widely different environments (Paper VIII). The hatching larvae will consequently experience different physical environments and probably different types and abundances of prey. The fact that D-whitefish has a slower growth rate and a smaller asymptotic size than the two other morphs might indicate that fish of the different morphs experience different environments for a prolonged period of time. Thus, other selection pressures of more vital importance than zooplanktivore efficiency in subadult or adult life may cause the gillraker divergence among the whitefish morphs in Femund.

Polymorphism and fish community structure

In temperate lakes, most invertebrate prey available to fish occur in a seasonal manner (Paper III, IV, IX), so that each fish to some degree has to shift from one prey type to another. In Mjøsa, there are in all habitats some species that are trophically more specialized than whitefish (Paper I). Thus, the possible use by whitefish of each habitat is probably restricted. Generalists like whitefish are able to balance this drawback by shifting between prey types and habitats both seasonally and through life (Paper II, III, IV), and no trophic specialization will occur in terms of e.g. polymorphism.

Paper I shows that the habitat of monomorphic whitefish overlap with several of the other dominant species in Mjøsa. In the littoral zone, both perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*) are numerous. Ruffe (*Acerina cernua*) has a benthic habitat that overlaps with the benthic whitefish population, and smelt (*Osmerus eperlanus*) has both a benthic and pelagic habitat, which is similar to that of whitefish. Thus, an extensive coexistence with many species appears not to restrict the habitat dimension of the age-structure component of the niche of the whitefish. The niches of polymorphic stocks are, however, expanded by means of the between-phenotype component.

The polymorphic stocks of whitefish (Paper VIII) and Arctic charr (Paper IX) treated in my investigations are both found in localities with low fish fauna diversity and diverse feeding and spawning habitats.

CONCLUSIONS

1. Vendace, whitefish and Arctic charr expand their resource use through ontogenetic niche shifts (Paper II, III, IV, VIII, IX).
2. Both whitefish and Arctic charr utilize the benthic resources throughout the year and in all age groups, and they are seasonally utilizing the pelagic food resource; both species are trophic generalists (Paper III, IV, IX).
3. Vendace occupy the same habitat and feed on the same food items from an age of a few months onwards; the species is a trophic specialist (Paper IV, VI, VII).
4. Through trophic polymorphism, Arctic charr and whitefish are able to specialize on different food items and habitats, thus exploiting the resource base more efficiently (Paper VIII, IX).
5. Although often correlated to degree of zooplanktivory, gillraker number is not a sufficient morphological parameter for judging the efficiency of a morph or a species as a zooplanktivore (Paper V, VIII).
6. Trophic polymorphism occurs mainly in large and diverse lakes with a relatively low number of fish species, i.e. many stable habitats and no effective competitors (Paper VIII, IX).
7. In lakes with many, more specialized competitors, whitefish is able to utilize various resource types through ontogentic and seasonal habitat shifts (Paper I, II, III).

References

Aagaard, K. 1984. The chironomids of Lake Målsjøen. A phenological, diversity, and production study. - Norw. J. Ent. 25: 21 - 37.

Abrahams, M.V. and L.M. Dill 1989. A determination of the energetic equivalence of the risk of predation. - Ecology 70: 999-1007.

Adalsteinsson, H. 1979. Zooplankton and its relation to available food in Lake Myvatn. - Oikos 32: 162 - 194.

Andersson, L., N. Ryman and G. Ståhl 1983. Protein loci in the Arctic charr, *Salvelinus alpinus* L.: Electrophoretic expression and genetic variability patterns. - J. Fish Biol. 23: 75 - 94.

Avise, J.C. 1990. Flocks of African fishes. - Nature 347: 512 - 513.

Bergman, E. 1990. Effects of roach *Rutilus rutilus* on two percids, *Perca fluviatilis* and *Gymnocephalus cernua*: importance of species interactions for diet shifts. - Oikos 57: 241 - 249.

Brett, J.R. 1979. Environmental factors and growth. - pp. 599 - 675 in: W.S. Hoar, D.J. Randall and J.R. Brett (eds.) Fish physiology. Bioenergetics and growth. Academic Press Inc., New York.

Brett, J.R. and D.A. Higgs 1970. Effects of temperature on the rate of gastric digestion in fingerling sockeye salmon, *Oncorhynchus nerka*. - J. Fish. Res. Board Can. 27: 1767 - 1779.

Brinkhurst, R.O. 1974. The benthos of lakes. - The MacMillan Press Ltd., London.

Brittain, J.E. 1978. The Ephemeroptera of Øvre Heimdalsvatn. - Holarct. Ecol. 1: 239 - 254.

Cerri, R.D. and D.F. Fraser 1983. Predation risk in foraging minnows: balancing conflicting demands. - Am. Nat. 121: 552 - 561.

Charnov, E.L. 1976. Optimal foraging theory: the marginal value theorem. - Theor. Pop. Biol. 9: 129-136.

Christiansen, F.B. and T.M. Fenchel 1977. Theories of populations in biological communities. - Springer-Verlag, New York.

Connor, E.F. and E.D. McCoy 1979. The statistics and biology of the species-area relationship. - Am. Nat. 113: 791 - 833.

DeAngelis, D.L. and C.C. Coutant 1982. Genesis of bimodal size distributions in species cohorts. - Trans. Am. Fish. Soc. 111: 384 - 388.

Diamond, J.M. 1973. The distributional ecology of New Guinea birds. - Science 179: 759 - 769.

Diamond, J.M. 1978. Niche shifts and the rediscovery of interspecific competition. - Am. Sci. 66: 322 - 331.

Dill, L.M. 1987. Animal decision making and its ecological consequences: The future of aquatic ecology. - Can. J. Zool. 65: 803 - 811.

Dominey, W.J. 1980. Female mimicry in male bluegill sunfish - a genetic polymorphism? - Nature 284: 546 - 548.

Dryagin, P.A., P.L. Pirozhnikov and V.V. Pokrovskiy 1969. Polymorphism among whitefishes (Coregoninae), its biological significance and economic importance. - J. Ichthyol. 9: 9 - 17.

Ehlinger, T.J. 1990. Habitat choice and phenotype-limited feeding efficiency in bluegill: individual differences and trophic polymorphism. - Ecology 71: 886 - 896.

Elliott, J.M. 1972. Rates of gastric evacuation in brown trout, *Salmo trutta* L. - Freshw. Biol. 2: 1 - 18.

Feinsinger, P. and L. Swarm 1982. Ecological release, seasonal variation in food supply and the hummingbird *Amazila tobaci* on Trinidad and Tobago. - Ecology 63: 1574 - 1587.

Ferguson, A. 1981. Systematics of Irish charr as indicated by electrophoretic analysis of tissue proteins. - Biochem. System. Ecol. 9: 225 - 232.

Ferguson, A., K.-J.M. Himberg and G. Svärdson 1978. Systematics of the Irish pollan (*Coregonus pollan* Thompson): an electrophoretic comparison with other holarctic Coregoninae. - J. Fish Biol. 12: 221 - 233.

Fretwell, S.D. 1972. Populations in a seasonal environment. - Princeton Univ. Press, Princeton, New Jersey.

Frost, W.E. 1965. Breeding habits of Windermere charr, *Salvelinus willughbi* Günther and their bearing on speciation of these fish. - Proc. R. Soc. (B) 163: 232 - 284.

Fryer, G. and T.D. Iles 1972. The cichlid fishes of the Great Lakes of Africa. - Oliver and Boyd, Edinburgh.

Gardner, A.S., A.F. Walker and R.B. Greer 1988. Morphometric analysis of two ecologically distinct forms of Arctic charr, *Salvelinus alpinus* (L.), in Loch Rannoch, Scotland. - J. Fish Biol. 32: 901 - 910.

Gilliam, J.F., and D.F. Fraser 1987. Habitat selection under predation hazard: test of a model with foraging minnows. - Ecology 68: 1856-1862.

Grant, B.R. and P.R. Grant 1982. Niche shifts and competition in Darwin's finches: *Geospiza conirostris* and congeners. - Evolution 36: 637 - 657.

Greenwood, P.H. 1984. African cichlids and evolutionary theories. - pp. 141 - 154 in: A.A. Echelle and I. Kornfield (eds.) Evolution of fish species flocks. University of Maine at Orono Press, Orono, Maine.

Gross, M.R. 1982. Sneakers, satellites and parentals: polymorphic mating strategies in North American sunfishes. - Z. Tierpsychol. 60: 1 - 26.

Gross, M.R. 1985. Disruptive selection for alternative life histories in salmon. - Nature 313: 47 - 48.

Hindar, K. and B. Jonsson 1982. Habitat and food segregation of dwarf and normal Arctic charr (*Salvelinus alpinus*) from Vangsvatnet Lake, western Norway. - Can. J. Fish. Aquat. Sci. 39: 1030-1045.

Hindar, K., N. Ryman and G. Ståhl 1986. Genetic differentiation among local populations and morphotypes of Arctic charr, *Salvelinus alpinus*. - Biol. J. Linn. Soc. 27: 269 - 285.

Holbrook, S.J. and R.J. Schmitt 1988. The combined effects of predation risk and food reward on patch selection. - Ecology 69: 125 - 134.

Huitfeldt-Kaas, H. 1918. Ferskvandsfiskenes utbredelse og indvandring i Norge med et tillæg om krebsen. - Centraltrykkeriet, Kristiania.

Huston, M.A. and D.L. DeAngelis 1987. Size bimodality in monospecific population: a critical review of potential mechanisms. - Am. Nat. 129: 678 - 707.

Jonsson, B. 1989. Life history and habitat use of Norwegian brown trout (*Salmo trutta*). - Freshwat. Biol. 21: 71 - 86.

Jonsson, B. and K. Hindar 1982. Reproductive strategy of dwarf and normal Arctic charr (*Salvelinus alpinus*) from Vangsvatnet Lake, Western Norway. - Can. J. Fish. Aquat. Sci. 39: 1404 - 1413.

Kirkpatrick, M. and R.K. Selander 1979. Genetics of speciation in lake whitefishes in the Allegash basin. - Evolution 33: 478 - 485.

Kornfield, I., D.C. Smith, P.S. Gagnon and J.N. Taylor 1982. The cichlid fishes of Cuatro Ciénegas, Mexico: direct evidence of conspecificity among distinct trophic morphs. - Evolution 36: 658 - 664.

Lagler, K.F., J.E. Bardach, R.R. Miller and D.R.M. Passino 1977. Ichthyology (2nd edition). - J. Wiley and Sons, New York.

Langeland, A. and H. Reinertsen 1982. Interactions between phytoplankton and zooplankton in a fertilized lake. - Holarct. Ecol. 5: 253 - 272.

Larsson, P., J.E. Brittain, L. Lien, A. Lillehammer and K. Tangen 1978. The lake ecosystem of Øvre Heimdalsvatn. - Holarct. Ecol. 1: 304 - 320.

Lavin, P.A. and J.D. McPhail 1987. Morphological divergence and the organization of trophic characters among lacustrine populations of the threespine stickleback (*Gasterosteus aculeatus*). - Can. J. Fish. Aquat. Sci. 44: 1820 - 1829.

Layzer, J.B. and M.D. Clady 1987. Phenotypic variation of young-of-year bluegills (*Lepomis macrochirus*) among microhabitats. - Copeia 1987 (3): 702 - 707.

Lindsey, C.C. 1981. Stocks are chameleons: plasticity in gill rakers of coregonid fishes. - Can. J. Fish. Aquat. Sci. 38: 1497 - 1506.

MacArthur, R.H. 1972. Geographical ecology. Patterns in the distribution of species. - Harper and Row, New York.

MacArthur, R.H. and E.O. Wilson 1967. The theory of island biogeography. - Princeton Univ. Press, Princeton, New Jersey.

McKaye, K.R., T. Kocher, P. Reinthal, R. Harrison and I. Kornfield 1984. Genetic evidence for allopatric and sympatric differentiation among color morphs of Lake Malawi cichlid fish. - Evolution 38: 215 - 219.

Meyer, A. 1987. Phenotypic plasticity and heterochrony in *Cichlasoma managuense* (Pisces, Cichlidae) and their implication for speciation in cichlid fish. - Evolution 41: 1357 - 1369.

Meyer, A., T.D. Kocher, P. Basasibwaki and A.C. Wilson 1990. Monophyletic origin of Lake Victoria cichlid fishes suggested by mitochondrial DNA sequences. - Nature 347: 550 - 553.

Milinski, M. 1986. Constraints placed by predators on feeding behavior. - pp. 236-252 in: T.J. Pitcher (ed.) The behaviour of teleost fishes. Croom Helm, London and Sydney.

Mittelbach, G.G. 1984. Predation and resource partitioning in two sunfishes (Centrarchidae). - Ecology 65: 499-515.

Nikolsky, G.V. 1963. The ecology of fishes. - Academic Press, London.

Nilsson, N.-A. 1967. Interactive segregation between fish species. - pp. 295-313 in: S.D. Gerking (ed.) Biological basis of freshwater fish production. Blackwell Scientific Publications, Oxford.

Nilsson, N.-A. 1978. The role of size biased predation in competition and interactive segregation in fish. - pp. 303-325 in: S.D. Gerking (ed.) Ecology of freshwater fish production. Blackwell Scientific Publications, Oxford.

Nordeng, H. 1983. Solution to the "char problem" based on Arctic char (*Salvelinus alpinus*) in Norway. - Can. J. Fish. Aquat. Sci. 40: 1372 - 1387.

Nyman, L. 1972. A new approach to the taxonomy of the "*Salvelinus alpinus* species complex". - Rep. Inst. Freshwat. Res. Drottningholm 52: 103 - 131.

Nyman, L., J. Hammar and R. Gydemo 1981. The systematics and biology of landlocked populations of Arctic char from northern Europe. - Rep. Inst. Freshwat. Res. Drottningholm 59: 128 - 141.

O'Brien, W.J. 1987. Planktivory by freshwater fish: thrust and parry in the pelagia. - pp. 3 - 16 in: W.C. Kerfoot and A. Sih (eds.) Predation. Direct and indirect impacts on aquatic communities. Univ. Press of New England, Hanover and London.

Osenberg, C.W., E.E. Werner, G.G. Mittelbach and D.J. Hall 1988. Growth patterns in bluegill (*Lepomis macrochirus*) and pumpkinseed (*L. gibbosus*) sunfish: environmental variation and the importance of ontogenetic niche shifts. - Can. J. Fish. Aquat. Sci. 45: 17 - 26.

Persson, L. 1990. Predicting ontogenetic niche shifts in the field: what can be gained by foraging theory? - pp. 303 - 321 in: R.N. Hughes (ed.) Behavioural mechanisms of food selection. NATO ASI Series Vol. G20, Springer-Verlag, Berlin.

Pimm, S.L. 1979. Sympatric speciation: a simulation model. - Biol. J. Linn. Soc. 11: 131 - 139.

Polis, G.A. 1984. Age structure component of niche width and intraspecific resource partitioning: can age groups function as ecological species? - Am. Nat. 123: 541 - 564.

Power, M.E. 1984. Depth distribution of armored catfish: predator-induced resource avoidance? - Ecology 65: 523-528.

Pyke, G.H., H.R. Pulliam and E.L. Charnov 1977. Optimal foraging: a selective review of theory and tests. - Q. Rev. Biol. 52: 137 - 154.

Reisinger, E. 1953. Zum Saiblingsproblem. - Carinthia II 143: 74 - 102.

Roberts, T.R. 1974. Dental polymorphism and systematics in *Saccodon*, a neotropical genus of freshwater fishes (Parodontidae, Characoidei). - J. Zool., Lond. 173: 303 - 321.

Rosenzweig, M.L. 1978. Competitive speciation. - Biol. J. Linn. Soc. 10: 275 - 289.

Ryman, N., F.W. Allendorf and G. Ståhl 1979. Reproductive isolation with little genetic change in sympatric populations of brown trout (*Salmo trutta*). - Genetics 92: 247 - 262.

Sage, R.D. and R.K. Selander 1975. Trophic radiation through polymorphism in cichlid fishes. - Proc. Nat. Acad. Sci. USA 72: 4669 - 4673.

Sandlund, O.T. and T.F. Næsje 1986. Sikbestanden i Femund. Undersøkelser 1982 - 1984. - DN-Fiskeforskningen. Rapport 2: 1 - 51.

Schlosser, I.J. 1987. The role of predation in age- and size-related habitat use by stream fishes. - Ecology 68: 651 - 659.

Schoener, T.W. 1974. Resource partitioning in ecological communities. - Science 185: 27 - 39.

Scott, W.B. and E.J. Crossman 1973. Freshwater fishes of Canada. - Bull. Fish. Res. Board Can. 184: 1 - 966.

Selander, R.K. 1966. Sexual dimorphism and differential niche utilization in birds. - The Condor 68: 113 - 151.

Shugart, H.H. and B.G. Blaylock 1973. The niche variation hypothesis: and experimantal study with *Drosophila* populations. - Am. Nat. 107: 575 - 579.

Smith, G.R. and T.N. Todd 1984. Evolution of species flocks of fishes in north temperate lakes. - pp. 45 - 68 in: A.A. Echelle and I. Kornfield (eds.) Evolution of fish species flocks. University of Maine at Orono Press, Orono, Maine.

Ståhl, G. and K. Hindar 1988. Genetisk struktur hos norsk laks: status og perspektiver. - DN-Fiskeforskningen. Rapport nr. 1: 1 - 57.

Steiner, W.W.M. 1980. On niche width and genetic variation, parametrical problems, and gene pool differentiation in *Drosophila*. - Am. Nat. 115: 596 - 599.

Stephens, D.W. and J.R. Krebs 1986. Foraging theory. - Princeton Univ. Press, Princeton, New Jersey.

Stuart, T.A. 1953. Spawning migration, reproduction and young stages of loch trout (*Salmo trutta* L.). - Sci. Invest. Freshw. Salm. Fish. Res. Scott. Home Dep. 5: 1 - 39.

Stuart, T.A. 1957. The migration and homing behaviour of brown trout (*Salmo trutta* L.). - Sci. Invest. Freshw. Salm. Fish. Res. Scott. Home Dep. 8: 1 - 27.

Svärdson, G. 1976. Interspecific population dominance in fish communities of Scandinavian lakes. - Rep. Inst. Freshwat. Res. Drottningholm 55: 144-171.

Svärdson, G. 1979. Speciation of Scandinavian *Coregonus*. - Rep. Inst. Freshwat. Res. Drottningholm 57: 3 - 95.

Svärdson, G. 1988. Pleistocene age of the spring-spawning cisco, *Coregonus trybomi*. - Nordic J. Freshw. Res. 64: 101 - 112.

Turner, B.J. and D.J. Grosse 1980. Trophic differentiation in *Ilyodon*, a genus of stream dwelling goodeid fishes: speciation versus ecological polymorphism. - Evolution 34: 259 - 270.

van Valen, L. 1965. Morphological variation and width of ecological niche. - Am. Nat. 99: 377 - 390.

Vrijenhoek, R.C., G. Marteinsdottir and R. Schenk 1987. Genotypic and phenotypic aspects of niche diversification in fishes. - pp. 245 - 250 in: W. Matthews and D. Heins (ed.) Community and evolutionary ecology of North American stream fishes. Univ. of Oklahoma Press.

Vuorinen, J., A. Champigneulle, K. Dabrowski, R. Eckmann and R. Rösch 1986. Electrophoretic variation in Central European coregonid populations. - Arch. Hydrobiol. Beih. 22: 291 - 298.

Vuorinen, J., K.-J.M. Himberg and P. Lankinen 1981. Genetic differentiation in *Coregonus albula* (L.) (Salmonidae) populations in Finland. - Hereditas 101: 85 - 96.

Weatherley, A.H. 1976. Factors affecting maximization of fish growth. - J. Fish. Res. Board Can. 33: 1046 - 1048.

Werner, E.E. 1986. Species interactions in freshwater fish communities. - pp. 344 - 358 in: J. Diamond and T.J. Case (eds.) Community ecology. Harper and Row Publishers, New York.

Werner, E.E. and J.F. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. - Ann. Rev. Ecol. Syst. 15: 393-425.

Werner, E.E., J.F. Gilliam, D.J. Hall and G.G. Mittelbach. 1983a. An experimental test of the effects of predation risk on habitat use in fish. - Ecology 64: 1540-1548.

Werner, E.E. and D.J. Hall 1976. Niche shifts in sunfishes: experimental evidence and significance. - Science 191: 404 - 406.

Werner, E.E. and D.J. Hall. 1988. Ontogenetic habitat shifts in bluegill: the foraging rate-predation risk trade-off. - Ecology 69: 1352-1366.

Werner, E.E., D.J. Hall, D.R Laughlin, D.J. Wagner, L.A. Wilsmann and F.C. Funk 1977. Habitat partitioning in a freshwater fish community. - J. Fish. Res. Board Can. 34: 360 - 370.

Werner, E.E., G.G. Mittelbach and D.J. Hall. 1981. Foraging profitability and the role of experience in habitat use by the bluegill sunfish. - Ecology 62: 116-125.

Werner, E.E., G.G. Mittelbach, D.J. Hall and J.F. Gilliam 1983b. Experimental tests of optimal habitat use in fish: the role of relative habitat profitability. - Ecology 64: 1525 - 1539.

Wilson, D.S. 1975. The adequacy of body size as a niche difference. - Am. Nat. 109: 769 - 784.

Wilson, D.S. and M. Turelli 1986. Stable underdominance and evolutionary invasion of empty niches. - Am. Nat. 127: 835 - 850.

Paper I

The Vertical Distribution of Fish Species in Lake Mjøsa, Norway, as Shown by Gill-net Catches and Echo Sounder

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ABSTRACT

The vertical distribution of fish species in the deep Lake Mjøsa was observed by means of benthic and pelagic gill nets and echo sounder.

The water column was utilized by a significant number of fish of several species down to a depth of 80—100 m, both in the pelagic zone and along the bottom. The dominant species in the benthic catches were smelt, whitefish, roach, perch, ruffe and burbot. Roach was a littoral species. Perch was caught down to nearly 50 m depth, whereas both smelt, whitefish, ruffe and burbot were utilizing most of the bottom profile down to 80 m or more for parts of, or the whole year. The pelagic zone was dominated by vendace, whitefish and smelt. Vendace was caught within 25 m from the surface. Whitefish were common down to approx. 40 m, and smelt down to 80 m in late summer and autumn.

The distribution pattern is discussed in relation to food supply, predation and competition.

I. INTRODUCTION

Information on the horizontal and vertical distribution of fish species is of prime importance in discussions of habitat selection, and possible inter- and intraspecific competition for food and space. Until recently, there has been little systematic information on the vertical distribution of multispecies fish communities in deep Scandinavian lakes (*e.g.* NILSSON 1979). Most of the published information on fish distribution is from relatively shallow lakes (*e.g.* NORTHCOTE and RUNDBERG 1970, HAMRIN 1973, ELORANTA and ELORANTA 1978).

Mjøsa is a deep fjord lake (Fig. 1), which gives an excellent opportunity to study the utilization of the deep water column by a fish community of 20 species (Table 1).

II. STUDY AREA

Mjøsa (Fig. 1) is Norway's largest lake, with a surface area of approx. 365 km^2, and a maximum depth of 449 m. Since 1912 it has been regulated for hydroelectric power production. The maximum regulation amplitude is 3.6 m, leaving much of the littoral zone dry in late winter. The lake is usually ice covered from the end of January to the beginning of May. In summer the thermocline is established at a depth of 10—20 m, usually by the end of June or in July (HOLTAN *et al.* 1980a). Because of the thermal stratification, and the summer floods, the epilimnic water is theoretically renewed twice during the summer period (HOLTAN *et al.* 1979).

The main inlet is the River Gudbrandsdalslågen, draining large mountaineous areas. The outlet is in the south, the River Vorma.

In the twentieth century, especially after 1950, Lake Mjøsa has been subject to an accellerating cultural eutrophication caused by domestic sewage, agricultural runoff, and industrial wastes (HOLTAN 1981). This development culminated in 1976, with a mass bloom of the blue green algae *Oscillatoria rubescens*, making the water unsuitable for drinking and industrial use. Since 1976, measures taken by the authorities have resulted in a pronounced improvement of the water quality. In 1979—80 the primary production was back to the satisfactory level of the early 1950's (HOLTAN *et al.* 1980a). The eutrophication did never, not even in 1976, reach a level of reducing the oxygen content of the deep waters.

The Furnes Fiord is an arm of the lake in direct connection with the deep central basin, whereas

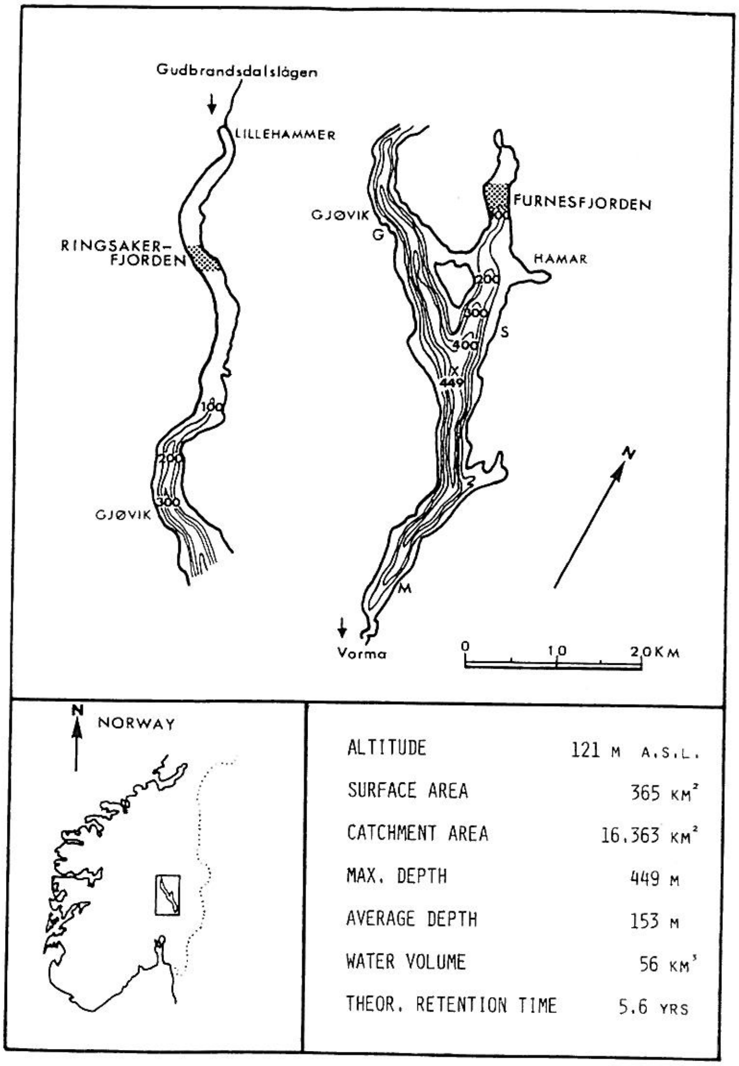

Fig. 1. Lake Mjøsa. The test fishing areas are shaded. G, S, and M are localities for benthic net fishing in deeper water.

ALTITUDE	121 M A.S.L.
SURFACE AREA	365 KM²
CATCHMENT AREA	16.363 KM²
MAX. DEPTH	449 M
AVERAGE DEPTH	153 M
WATER VOLUME	56 KM³
THEOR. RETENTION TIME	5.6 YRS

The Ringsaker Fiord is isolated by a relatively shallow area (Fig. 1).

The zooplankton community in Lake Mjøsa has an August—September maximum dominated by *Daphnia galeata* (Holtan *et al.* 1980b). The main zooplankton biomass is found in the upper 30 m of the water column. There is also a relatively large population (approx. 150 ind. m^{-2}) of *Mysis relicta* (Kjellberg and Sandlund 1983). The *M. relicta* population lives pelagically, and in the ice-free season occupies the water layers between approx. 25 and 110 m.

The zoobenthos in Lake Mjøsa is dominated by insect larvae (mostly Chironomidae), molluscs, oligochaetes and amphipods. The highest zoobenthos biomass and diversity is found in shallow water, from the lower regulation limit to approx. 25 m. The chironomids, molluscs, and oligochaetes are the dominant benthic fauna in this zone. The amphipods *Pallasea quadrispinosa* and *Gammaracanthus loricatus* are most important in deeper waters, but *P. quadrispinosa* is also found in the littoral zone in summer (Holtan *et al.* 1980b, Næsje *et al.* 1981).

Table 1. *Total catch by gill net sampling in Lake Mjøsa (localities Furnesfjorden and Ringsakerfjorden, Fig. 1), October 1978—November 1979.* N=number of fish, W=weight of catch (kg), C.P.U.E.=catch per unit effort (number of fish per 100 m² net area per 24 hrs), p.n.=pelagic nets, b.n.=benthic nets. + indicates that the species is rare in gill net catches, — indicates that the species was only caught with other methods.

Species	Total Catches				C.P.U.E.	
	N	%	W	%	p.n.	b.n.
Lamprey *Lampetra fluviatilis* (L.)	—	—	—	—	—	—
Brown trout *Salmo trutta* L.	98	0.7	90	7.0	0.1	+
Vendace *Coregonus albula* (L.)	1194	8.8	84	6.6	0.9	0.1
Whitefish *Coregonus lavaretus* (L.)	1173	8.7	280	21.9	0.4	1.4
Smelt *Osmerus eperlanus* (L.)	5427	40.2	54	4.2	2.4	5.1
Grayling *Thymallus thymallus* (L.)	72	0.5	13	1.0	—	0.1
Pike *Esox lucius* L.	21	0.2	69	5.4	+	+
Roach *Rutilus rutilus* (L.)	1688	12.5	184	14.4	+	3.4
Ide *Leuciscus idus* (L.)	93	0.7	63	4.9	+	0.1
Dace *Leuciscus leuciscus* (L.)	1	+	+	+	+	—
Bream *Abramis brama* (L.)	15	0.1	25	2.0	—	+
Bleak *Alburnus alburnus* (L.)	78	0.6	3	0.2	+	0.2
Minnow *Phoxinus phoxinus* (L.)	—	—	—	—	—	—
Crucian carp *Carassius carassius* (L.)	—	—	—	—	—	—
Perch *Perca fluviatilis* L.	1047	7.7	103	8.1	+	2.1
Ruffe *Gymnocephalus cernua* (L.)	2131	15.8	25	2.0	+	4.3
Burbot *Lota lota* (L.)	439	3.2	284	22.2	—	0.9
Miller's thumb *Cottus poecilopus* HECKEL	38	0.3	+	+	—	0.1
Deepwater sculpin *Myoxocephalus quadricornis* (L.)	2	+	+	+	—	+
Stickleback *Pungitius pungitius* (L.)	—	—	—	—	—	—

III. METHODS

The two major localities for gill-net sampling were chosen to cover different levels of eutrophication in Lake Mjøsa (Fig. 1). The investigations by the Norwegian Institute of Water Research (NIVA) indicate clearly that the Furnes Fiord is the most eutrophic, and the Ringsaker Fiord the most oligotrophic part of the lake (HOLTAN *et al.* 1980a). This is mainly due to the influence of the main inlet, River Gudbrandsdalslågen, in the Ringsaker Fiord. For practical reasons, the moderate depth (80—100 m) of these two arms of the lake make them suitable for sampling with pelagic gill nets. Echo soundings over the deeper parts of the lake clearly showed that the density of fish in the pelagic zone was very low deeper than 80—90 m (LINDEM 1977, 1978). The sampling sites in the Furnes and Ringsaker Fiords are therefore assumed to show the main pattern in the vertical distribution of the pelagic fish species in the lake.

To collect more information on the distribution of benthic fish species in the deeper parts of Lake Mjøsa, benthic nets were used at three additional localities (S, G, and M in Fig. 1).

The sampling was done by gill nets of twelve different mesh sizes (8—50 mm knot to knot). The benthic nets (2 m deep) were mounted in gangs of twelve nets with a fixed succession of mesh sizes (15, 35, 18, 45, 8, 29, 22.5, 50, 10, 39, 12.5, and 26 mm). The nets were set from the shoreline to the deepest part of the sampling station. The exact depth of the nets on the bottom profile was registered by an echosounder (Simrad EL). The nets were fished for 24 hrs, and the sequence of mesh sizes reversed to get the best cover of mesh sizes in each depth zone. The benthic nets were set on two localities in each sampling area, to cover variations in bottom profile and substrate.

The pelagic nets (6 m deep) were mounted in three gangs of four mesh sizes each, and all twelve mesh sizes were set for 24 hrs within each of five different depth zones (0—10, 15—25, 30—40, 50—60, 70—80 m in the Furnes Fiord and 0—10, 15—25, 30—40, 45—55, 60—70 m in the Ringsaker Fiord. The position of the pelagic nets were controlled by echo sounding. The catches were sorted in species and counted. Catch per unit effort (cpue) was calculated as number of fish per

100 m^2 net area per 24 hrs. This is used as cpue throughout this paper. The methods are described in further detail by SANDLUND *et al.* (1980a).

The test fishing in the Furnes Fiord was performed in October and November 1978, February 1979 (through the ice) and monthly from May through November 1979. In the Ringsaker Fiord, fishing was performed in March 1979 (through the ice) and monthly from May through November 1979.

In localites S, G, and M fishing with benthic nets were performed in September/October 1979. To investigate the distribution of fish in the deeper part of the pelagial zone, fish was registered with an echo sounder system designed for calculating fish density and size distribution (LINDEM 1981a, LINDEM and SANDLUND 1984). During the project period, fishing was also performed with beach seine, pelagic pair trawl, traps etc., and some observations from this sampling will be referred to in this paper.

The selectivity of gill nets is well known (*e.g.* HAMLEY 1975), both in respect to fish species and fish size. By using a wide spectrum of mesh sizes and performing the fishing in exactly the same way in all sampling periods, the errors caused by the selectivity of the gear will be minimized. The results can therefore be used to study qualitative and quantitative changes in distribution (cf. *e.g.* FILIPSSON 1972, NILSSON and NORTHCOTE 1981, HINDAR and JONSSON 1982). As the nets were fished during 24 hrs, the diurnal migrations of pelagic fish in Lake Mjøsa, which have been demonstrated by hydroacoustic methods (LINDEM 1978), were not detected in the net catches.

IV. RESULTS

Species composition of the gill net catches

Sixteen fish species were recorded in the gill-net catches from Lake Mjøsa (Table 1). Approx. 40 % of the total number was smelt. Ruffe and roach constituted approx. 16 and 12 %, and vendace, whitefish and perch 7—8 % each. Burbot were also common in the gill net catches (3 %), whereas nine other species each contributed less than 1 % of the total number of fish caught. Based on the weight of the catches, whitefish and burbot were dominating. Roach, vendace, trout and pike were also important in the total catch.

Table 2. *Relative fish density (number of fish per 1000 m^3) in the central part of Lake Mjøsa between 50 and 120 m depth, calculated from echograms of the Simrad EY-M echosounder.*

Depth (m)	May	June	Sept	Oct	Nov
50— 60	4.53	2.19	3.26	1.81	1.40
60— 70	3.07	0.53	2.49	2.21	0.76
70— 80	0.66	0.39	2.49	2.19	1.08
80— 90	0.08	0.02	1.54	1.20	1.81
90—100	—	—	0.51	0.24	0.71
100—110	—	—	0.13	0.01	0.02
110—120	—	—	0.01	—	0.01

The overall catch per unit effort indicates that only four species were common in the pelagic zone (Table 1). These were smelt, vendace, whitefish and predatory trout. Seven additional species were caught in the pelagic nets on rare occasions. In the benthic net catches, the five species smelt, ruffe, roach, perch, and whitefish were most frequent. There is only one form of whitefish in Mjøsa, with approx. 31 gillrakers (AASS 1972a, NÆSJE 1984).

The spatial distribution of the main species in Lake Mjøsa

Echo soundings in Lake Mjøsa, in the period 1977 through 1981, show that the density of fish is very low in the pelagic zone deeper than 80—100 m (Table 2). Fish schooling greatly influence density estimates by echo sounding (LINDEM and SANDLUND 1984). During the echo soundings in Mjøsa, fish schools were never detected deeper than approx. 40 m. Echograms from waters deeper than 120 m in Mjøsa show very low fish density (less than 0.01 fish per 1000 m^3). The density of fish deeper than 70 m increases in autumn (September—November). A typical echo recording from September is shown in Fig. 2.

Smelt were very prominent in the pelagic and benthic gill-net catches in the Furnes and Ringsaker Fiords (Table 1). The size of the catches varied throughout the year, but in the benthic catches, smelt was common in all months (Fig. 3). The benthic catches of smelt in the Furnes Fiord indicated that this species mainly utilizes the

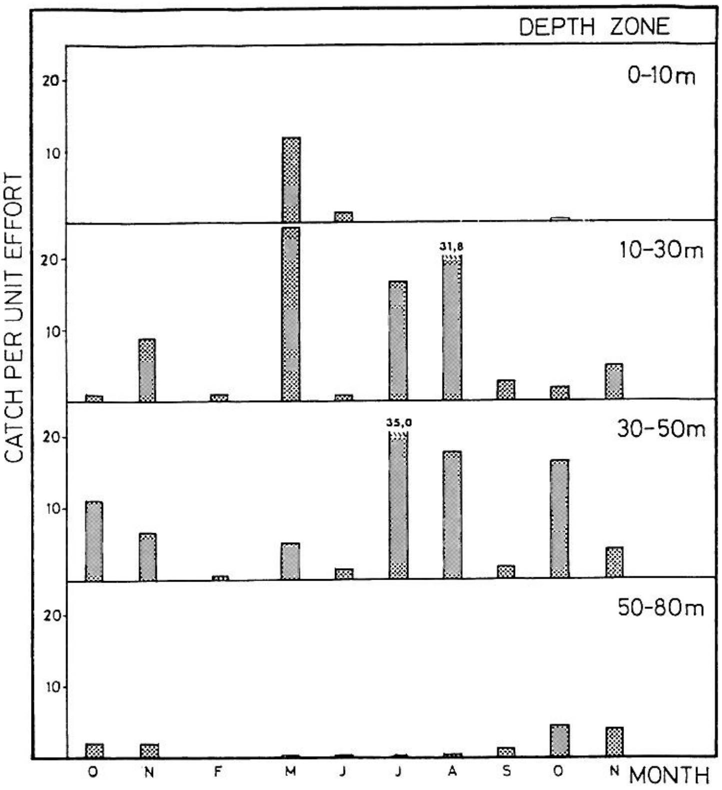

Fig. 5. Catch per unit effort of smelt in benthic nets in four depth zones in Furnesfjorden, 1978—79.

to be the only place in Mjøsa to catch benthic whitefish in deep waters. Whitefish catches in pelagic nets during winter and early summer were small. The catches of pelagic whitefish reached maximum from August to November, similar to smelt (Fig 8). This coincides with the maximum in zooplankton biomass (Fig. 3, and SANDLUND *et al.* 1980 a). The pelagic net catches in the Furnes Fiord indicates that pelagic whitefish keep mainly to the upper 40 m of the water masses (Fig. 8). This differs from smelt, which were caught in appreciable numbers down to 80 m.

Vendace is the only species in Lake Mjøsa that was almost completely pelagic. Only on a very few occasions vendace were caught in the benthic habitat during our investigations (Table 1). In late summer and autumn, during the spawning migration towards the main inlet, River Gudbrandslågen, local fishermen catch vendace with floating beach seine. This commercial fishery yield some 50—150 tons (average 136 tons, AASS 1978) of vendace every year. The main catches of vendace were made in the upper 25 m of the pelagial zone, and only very rarely deeper than 40 m (Fig. 9). In both fishing areas, the catches were low during winter and spring. In the Furnes Fiord, the catches increased from July onwards, and reached a maximum in August—September. In the Ringsaker Fiord, the catches remained low throughout July, and maximum was reached in September—October.

Brown trout and, to a lesser degree, pike are living as pelagic predators in Lake Mjøsa, preying mainly on smelt, and some vendace and whitefish (HUITFELDT-KAAS 1917, SANDLUND *et al.* unpubl. data). Being large predators, however, these species are present in low numbers, and catches are small (Table 1).

Gill-net catches indicate that roach, perch, ruffe and burbot were the most numerous of the benthic fish species in Lake Mjøsa. Roach is a littoral species, rarely caught deeper than 10 m (Fig. 10). Perch were commonly caught down to 30 m, whereas ruffe were common at all depths down to

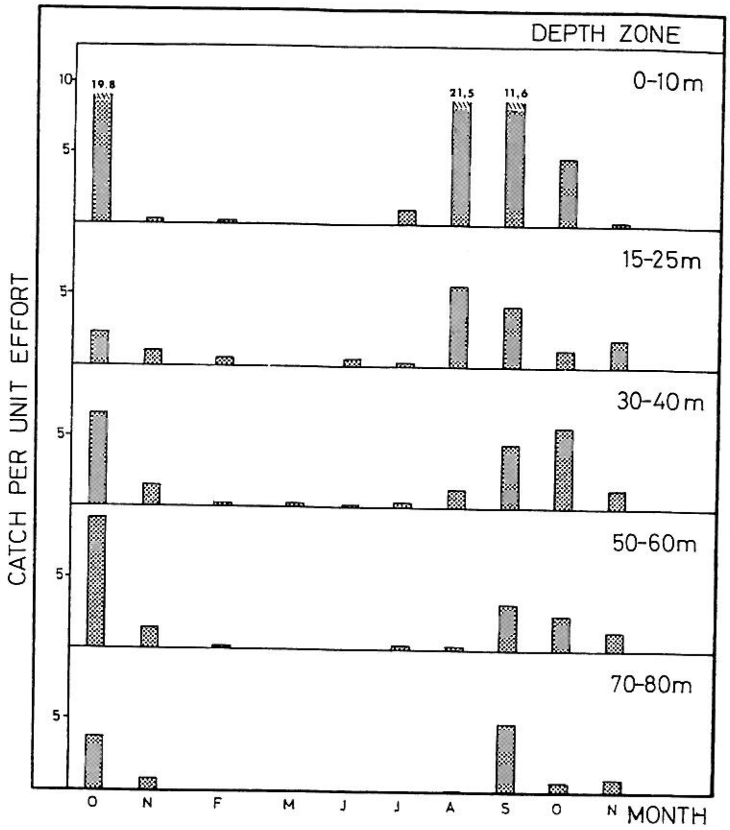

Fig. 6. Catch per unit effort of smelt in pelagic nets in five depth zones in Furnesfjorden, 1978—79.

80 m, exept in summer when most of the population appeared to be living shallower than 30 m (Fig. 10). This might be connected with spawning, which takes place in June. The burbot spawns in winter and early spring, and they were caught above 10 m only at this period (Sandlund *et al.* 1985). During winter they were not caught in the 50—80 m zone, but at all other seasons, they were common in the bottom net catches from 10 to 80 m (Fig. 10). Neither ruffe nor burbot were caught deeper than 80 m (Fig. 4).

Perch and ruffe have been caught very occasionally in pelagic nets and trawl, whereas burbot appear to live strictly within one metre from the substratum.

Several other species, *e.g.* bream, bleak and ide, were of less importance in our gill-net catches (Table 1), but appear to be quite common in shallow, protected bays of the lake. This is shown both in trap and beach seine catches.

V. DISCUSSION

The spatial distribution of fish species is most often related to food supply, suitable spawning localities, and inter- and intraspecific competition, including predation (Nilsson 1967, Keast 1977, Pyke *et al.* 1977, Werner and Mittelbach 1981).

The fish distribution in Lake Mjøsa appears to be in accordance with earlier investigations in lakes where the large, so called "glacial relict" crustaceans are present (Johnson 1975, Nilsson 1979). In Lake Mjøsa, *Mysis relicta* create a hypolimnetic food supply with a vertical distribution from 25 to 110 m (Kjellberg and Sandlund 1983), and *Pallasea quadrispinosa* a benthic food supply down to more than 100 m depth (Mathisen 1953). *Gammaracanthus loricatus* seems to have an intermediate habitat between these two species, being semibenthic down to depths of more than 200 m (Næsje *et al.* unpubl. data). *G. loricatus* is more

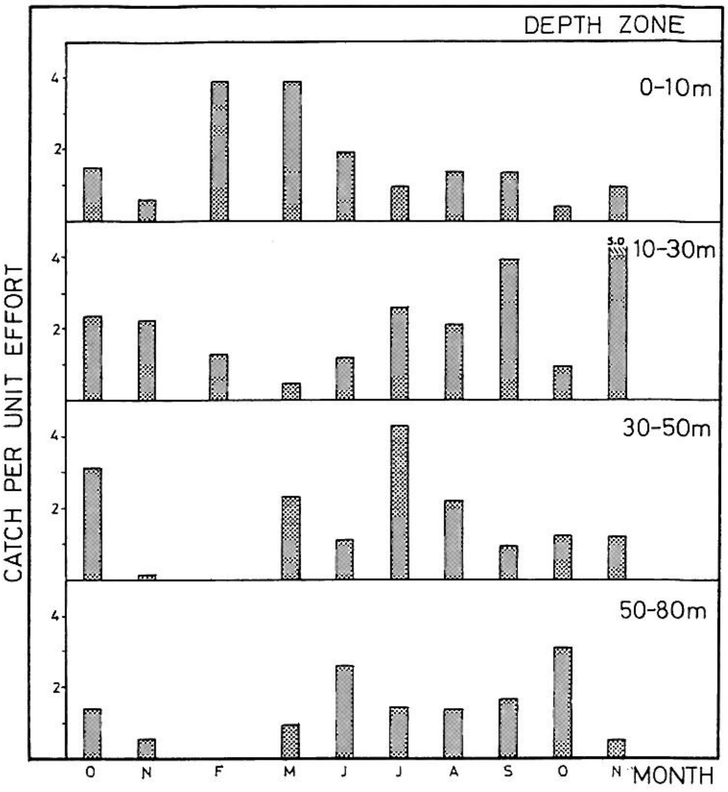

Fig. 7. Catch per unit effort of whitefish in benthic nets in four depth zones in Furnesfjorden, 1978—79.

mobile and swim faster than *P. quadrispinosa*, and is therefore less likely to be eaten by fish (Næsje *et al.* 1981).

In Lake Mjøsa, benthic fish density is relatively high down to approx. 80 m depth. In Lake Vänern, where the potential food resources of glacial relicts are similar to that of Lake Mjøsa, several fish species utilize the water column down to at least 85 m, which was the maximum depth in the sampling areas of Nilsson (1979). Similar results are reported from Great Bear Lake, where benthic *M. relicta* was found down to approx. 200 m (Johnson 1975). The *Mysis*-eating deepwater sculpin and its predator, lake trout (*Salvelinus namaycush*), were also caught down to this depth, but catches were very low deeper than 80—100 m. In Lake Mjøsa a low number of deepwater sculpin was caught down to at least 150 m, but no predators were caught deeper than approx. 80 m. The catches of smelt and whitefish deeper than 100 m at locality G demonstrate the importance of food supply in determining the distribution of fish. At this locality industrial effluents containing organic fibers have created a sediment with high organic content down to at least 300 m. This supports an exceptionally high density of oligochaetes (Holtan *et al.* 1979), which can be utilized as food by whitefish and smelt.

In oligotrophic lakes where the "glacial relicts" are missing, fish are rarely found in any significant densities deeper than 40—60 m (Sandlund 1979, Lindem 1981a, b, Skurdal and Qvenild 1982, Hindar and Jonsson 1982). In eutrophic lakes oxygen depletion may reduce the possibilities for fish to live in deep waters (Andreasson and Stake 1970, Brabrand *et al.* 1981). The presence of the "glacial relicts" *M. relicta* and *P. quadrispinosa* thus appears to enable the fish to utilize a larger part of the water volume in oligotrophic lakes.

In Lake Mjøsa the upper 30 m of the water volume support the largest fish biomass and the most diverse fish fauna. This is the usual pattern in lakes, and is due to the more abundant food supply of zooplankton, zoobenthos, phytobenthos,

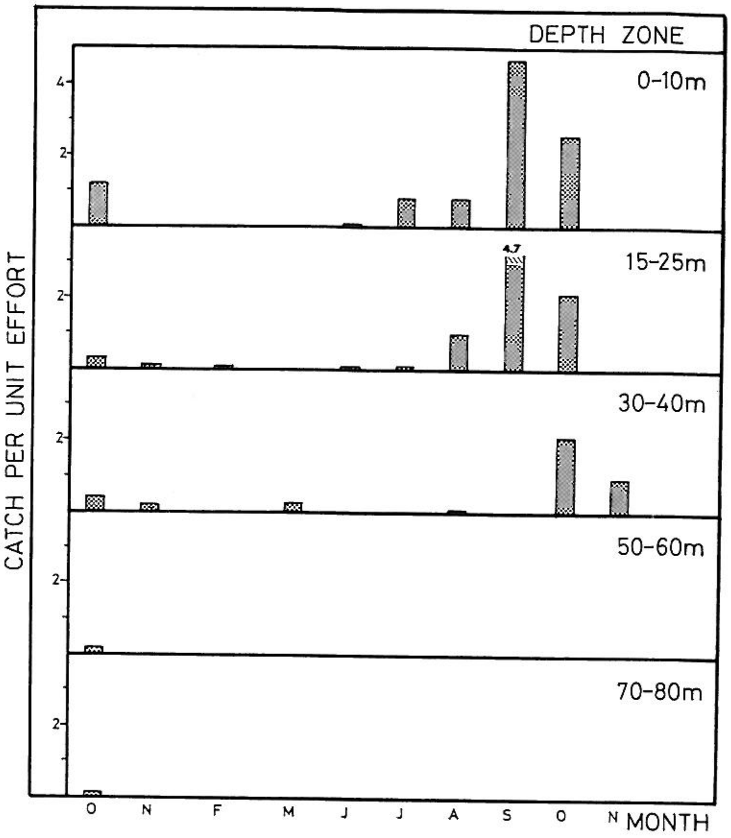

Fig. 8. Catch per unit effort of whitefish in pelagic nets in five depth zones in Furnesfjorden, 1978—79.

and prey fish (Johnson 1975, Nilsson 1979, Holtan *et al.* 1980 a). The regulation zone appears not to alter this picture, although within the 3.6 m that are left dry in winter, zoobenthos production will be low.

The benthic species

In Lake Mjøsa, roach were dominating in the littoral zone, eating both phyto- and zoobenthos. This is commonly observed in oligo- and mesotrophic lakes (Hartmann and Löffler 1978). When the lake becomes more eutrophic, other cyprinids, especially bream, become more abundant in the littoral zone (Tuunainen 1971, Hakkari and Granberg 1977, Hartmann and Löffler 1978). The mouth apparatus of bream is specially adapted to catching food organisms buried in the soft sediment found in eutrophic littoral zones (Nikolsky 1969, p. 286).

The two most important fish species feeding almost exclusively on zoobenthos are ruffe, and small to medium sized perch. Larger perch also eat fish, mainly smelt. In Lake Mjøsa, perch is restricted to the 0—50 m depth zone, whereas ruffe utilize the bottom profile down to at least 80 m. Ruffe are commonly found in deeper waters than perch (Hamrin 1973, Hansen 1978, Nilsson 1979), but due to its small size, ruffe are often missing from gill-net catches done with mesh sizes from approx. 20 mm upwards (*e.g.* Northcote and Rundberg 1970). The different distribution of these two species might be due to differences in their ability to catch various food organisms (Nikolsky 1969, p. 286).

The typical distribution of the two benthic predators pike and burbot is that the pike is littoral and the burbot lives in deeper waters (Svärdson 1976). In Lake Mjøsa, large pike also move out into the pelagic zone, preying on smelt and vendace in near-surface waters. The pike is

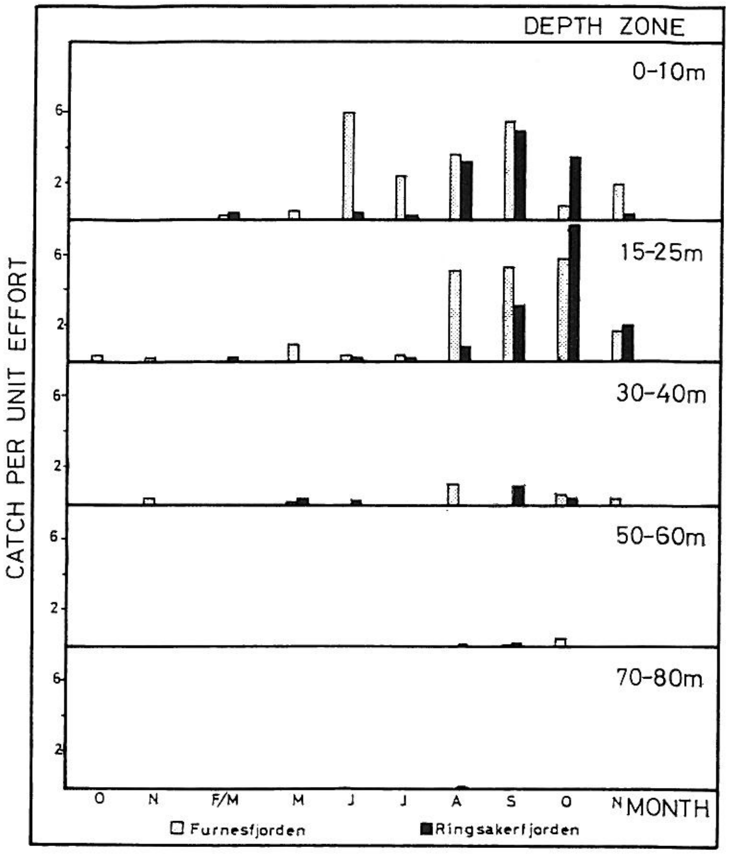

Fig. 9. Catch per unit effort of vendace in pelagic nets in five depth zones in Furnesfjorden (October 1978—November 1979) and Ringsakerfjorden (March—November 1979).

very much depending on sight to catch its prey (Nikolsky 1969, p. 264), and must therefore keep close to the surface. The burbot is less dependent on sight, and in Lake Mjøsa it feeds almost exclusively on *P. quadrispinosa* and smelt (Huitfeldt-Kaas 1917, Sandlund *et al.* 1985). Its distribution mainly follows that of its prey on the bottom, *i.e.* down to approx. 80 m.

The pelagic species

Vendace is considered the most specialized zooplanktivore in the Scandinavian freshwater fish fauna (Svärdson 1976). It is commonly found in the upper layers of the pelagic zone feeding on crustacean zooplankton (Vallin 1964, Hamrin 1979, Nilsson 1979). This is in accordance with the strictly pelagic way of life of the Lake Mjøsa vendace. In some warmer lakes vendace move down into the meta- or hypolimnion in summer when surface water temperature exceeds approx. 20°C (Northcote and Rundberg 1970, Hamrin 1979). In Lake Mjøsa, surface temperature rarely reach 20°C, and no such downward movement was detected in summer. In Lake Mälaren, Northcote and Rundberg (1970) observed that vendace in summer moved in close to the bottom at midday. In Lake Mjøsa almost no vendace were caught close to the bottom, probably due to the relatively high density of smelt and whitefish, increasing competition in this zone.

In addition to vendace, whitefish and smelt are important in the pelagic catches in late summer and autumn. This dominance of salmonids in the pelagic zone indicates the oligo-mesotrophic state of the lake. With increasing eutrophication other species, particularly roach, have been observed to migrate into the pelagic zone (*e.g.* Northcote and Rundberg 1970, Brenner 1973, Brabrand *et al.* 1981).

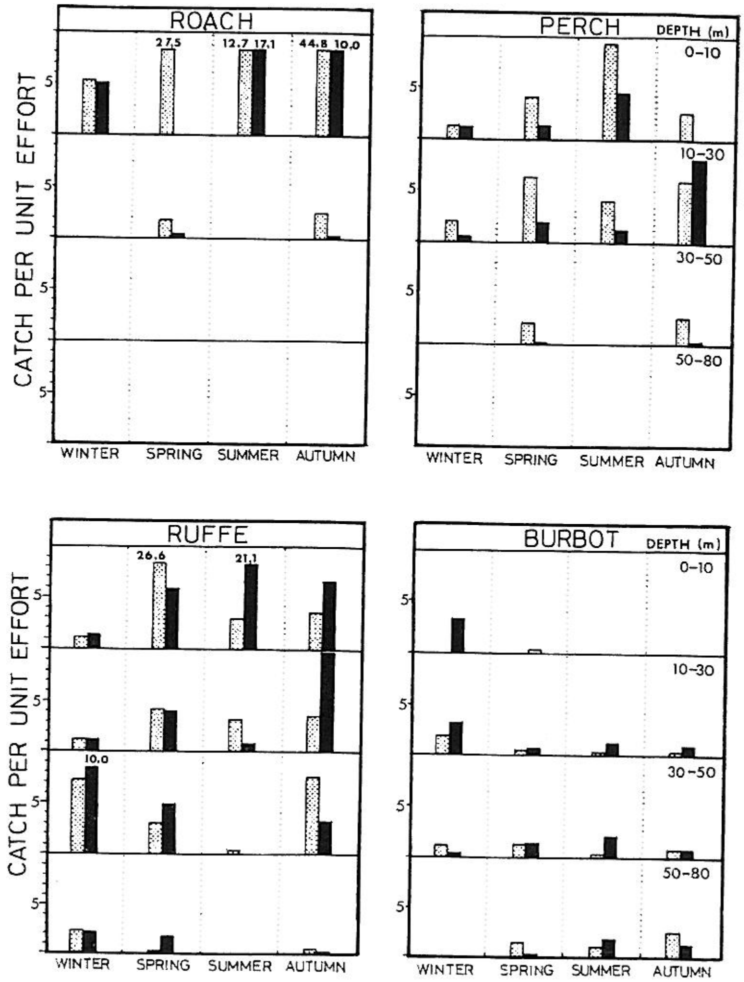

Fig. 10. Catch per unit effort in benthic nets of roach, perch, ruffe and burbot in four depth zones in Furnesfjorden (shaded) and Ringsakerfjorden (black) in 1979. The four seasons are represented by catches in February/March, May, July and October.

Species utilizing both the benthic and the pelagic habitat

Whitefish and smelt appear to be the most versatile species in Lake Mjøsa, utilizing almost all habitats where fish were found. Both species are commonly found to occupy both the benthic and the pelagic zone (SVÄRDSON 1976, NILSSON 1979, SKURDAL and QVENILD 1982). Whitefish is often found in two or more different "morphs" or semispecies, living sympatrically, but in different habitats (SVÄRDSON 1976, BERGSTRAND 1977). In Lake Mjøsa, however, only one morph of whitefish is found (AASS 1972a, NÆSJE 1984), and it is only the medium sized part of the population (approx. 30 cm body length) that migrates out into the pelagic zone in late summer. Analyses of stomach contents show that its main food source is crustacean zooplankton and some surface insects, and that there is no diurnal migration between benthic and pelagic habitat (NÆSJE 1984). The benthic part of the whitefish population had eaten a much greater proportion of zoobenthos, especially *P. quadrispinosa*, than the pelagic part. The same separation of stomach content was found between benthic and pelagic smelt (SANDLUND *et al.* 1980b). Pelagic smelt utilize crustacean zooplankton, *M. relicta* and smelt fry, while the benthic smelt also eats *P. quadrispinosa*. The reason for the habitat shift in parts of the whitefish and smelt populations in Lake Mjøsa might be as follows: In the benthic habitat, in addition to smelt and whitefish, at least four species (ruffe, perch, burbot and deepwater sculpin) prey on *P. quadrispinosa*. Both smelt and whitefish are generalists able to utilize both zoobenthos and zooplankton (Svärdson 1976). With a strong competition for food in the benthic habitat, it seems natural for these facultative planktivores to migrate out into the pelagic zone when this habitat offers abundant food, *i.e.* in late summer and autumn. The smelt, being a more effective predator (Svärdson 1976), can utilize the deeper part of the pelagic zone, preying on *M. relicta*, which is living below the thermocline (Kjellberg and Sandlund 1983). The reason that the zooplankton specialist, the vendace, does not exclude these two generalists in the pelagic zone might be that the vendace is subject to quite extensive fishing. Fishing mortality of adult vendace is estimated to 40 % (Aass 1972b). Fishing mortality of whitefish in Lake Mjøsa is very low (Aass 1978), and smelt are not fished at all.

As smelt is the main prey of all predators in the lake (Huitfeldt-Kaas 1917), natural mortality of this species is relatively high, approx. 55 % in adult fish (Sandlund *et al.* 1980b). In adult whitefish, however, natural mortality is apparently very low (Næsje 1984). The smelt and whitefish both take other prey in addition to zooplankton, and utilize a larger part of the pelagic zone. In addition, there might exist a more subtle habitat partitioning concerning space, time of feeding etc. than we are able to detect by 24 hrs gill-net fishing. Thus the habitat utilization indicates interactive segregation (*sensu* Nilsson 1967), with smelt and whitefish as the generalist species widening and contracting their niche according to food supply.

VI. ACKNOWLEDGMENTS

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VII. REFERENCES

Aass, P. 1972a. Årsmelding 1971. DVF, Den vitenskapelige avdeling. 16 p. (In Norwegian.)

— 1972b. Age determination and year-class fluctuations of cisco, *Coregonus albula* L., in the Mjøsa hydroelectric reservoir. Rep. Inst. Freshw. Res., Drottningholm 52: 5—22.

— 1978. The whitefish and cisco fisheries of Lake Mjøsa, Norway. Fauna, Oslo 31: 80—83. (In Norwegian with English summary.)

Andreasson, S. and E. Stake. 1970. Fish distribution in a deep polluted lake. Inform. Inst. Freshw. Res., Drottningholm (4). 13 p. (In Swedish with English summary.)

Bergstrand, E. 1977. The four whitefish species in Lake Parkijaure, River Lilla Lule Älv. Inform. Inst. Freshw. Res., Drottningholm (12). 33 p. (In Swedish with English summary.)

Brabrand, Å., B. Faafeng and J. P. Nilssen. 1981. Registrering av fisk i Gjersjøen ved hjelp av hydroakustisk utstyr. Rapp. Lab. Ferskv. Økol. Innlandsfiske 52: 36 p. (In Norwegian with English summary.)

Brenner, T. 1973. Die Auswirkung der Eutrophierung des Bodensees auf Nährung und Wachstum der Plötze (*Rutilus rutilus*). Der Fischwirt 23: 1—2. (In German.)

Eloranta, P. and A. Eloranta. 1978. Vertical distribution of fishes in one lake deep (Lake Kuusvesi, Central Finland). Verh. Internat. Verein. Limnol. 20: 2092—2097.

Filipsson, O. 1972. Sötvattenslaboratoriets provfiske och provtagningsmetoder. Inform. Inst. Freshw. Res., Drottningholm (16), 24 p. (In Swedish.)

Hakkari, L. and K. Granberg. 1977. The evaluation of eutrophication in Lake Päijänne, Central Finland. p. 185—193. *In* Biological monitoring of inland fisheries. Ed.: J. S. Alabaster. Applied Science Publishers Ltd, London.

Hamley, J. M. 1975. Review of gillnet selectivity. J. Fish. Res. Board Can. 32: 1943—1969.

Hamrin, S. 1973. Fiskepopulationens vertikala fördelning och relativa sammansättning i Södra och Norra Bolmen 1970—1972. Limn. Inst., Univ. Lund. (In Swedish.)

— 1979. Population dynamics, vertical distribution and food selection of ciscoe (*Coregonus albula* L.) in south Swedish lakes. Dissertation, Limn. Inst., Univ. Lund. 66 p. (In Swedish with English summary.)

Hansen, L. P. 1978. Relative abundance of some fish species in the northern part of Lake Øyeren. Fauna, Oslo 31: 178—183. (In Norwegian with English summary.)

Hartmann, J. and H. Löffler. 1978. Saisonale bodennahe Verteilung von Fischen im eutrophierten Bodensee. Arch. Hydrobiol. 83: 69—79. (In German.)

Hindar, K. and B. Jonsson. 1982. Habitat and food segregation of dwarf and normal Arctic charr (*Salvelinus alpinus*) from Vangsvatnet Lake, western Norway. Can. J. Fish. Aquat. Sci. 39: 1030—1045.

HOLTAN, H. 1981. Eutrophication of Lake Mjøsa and its recovery. Water Qual. Bull. 6: 99—103, 156.

— G. KJELLBERG, P. BRETTUM, T. TJOMSLAND and T. KROGH. 1979. Mjøsprosjektet. Hovedrapport for 1971—76. NIVA-rapport O-69091, 176 p. (In Norwegian.)

— G. KJELLBERG, P. BRETTUM and T. TJOMSLAND. 1980a. Gudbrandsdalslågen og Mjøsa. Resipientvurderinger i forbindelse med reguleringsinngrep i Jotunheimen. NIVA-rapport O-79079, 212 p. (In Norwegian.)

— G. KJELLBERG and P. BRETTUM. 1980b. Overvåking av Mjøsa. Fremdriftsrapport 10. Undersøkelser i 1979. NIVA-rapport O-78012 (II). 71 p. (In Norwegian.)

HUITFELDT-KAAS, H. 1917. Mjøsens fisker og fiskerier. Det Kgl. Norske Videnskabers Selsk. Skrifter 2. 257 p. (In Norwegian.)

JOHNSON, L. 1975. Distribution of fish species in Great Bear Lake, Northwest Territories, with reference to zooplankton, benthic invertebrates, and environmental factors. J. Fish. Res. Board Can. 11: 1989—2004.

KEAST, A. 1977. Mechanisms expanding niche width and minimizing intraspecific competition in two centrachid fishes. p. 333—395. *In* Evolutionary biology. Vol. 10. Eds.: M. K. Steere and B. Wallace. Plenum Press, New York.

KJELLBERG, G. and O. T. SANDLUND. 1983. Næringsrelasjoner i Mjøsas pelagiske økosystem. DVF-Mjøsundersøkelsen. Rapport 6. 61 p. (In Norwegian.)

LINDEM, T. 1977. Hydroakustiske undersøkelser på fisk i Mjøsa 28/11—1/12 1977. Fysisk Inst., Univ. Oslo. 7 p. (In Norwegian.)

— 1978. Registrering av fisk i Mjøsa ved hjelp av hydroakustisk utstyr. Fysisk Inst., Univ. Oslo. 19 p. (In Norwegian.)

— 1981a. The application of hydroacoustical methods in monitoring the spawning migration of whitefish *Coregonus lavaretus* in Lake Randsfjorden, Norway. p. 925—939. *In* Meeting on hydroacoustical methods for the estimation of marine fish populations. 25—29 June 1979. II: Contributed papers. Ed.: J. B. Suomala. The Carles Stark Draper Laboratory, Inc., Cambridge, Mass., USA.

— 1981b. Registrering av fisk i Tyrifjorden ved hjelp av hydroakustisk utstyr 1979. Tyrifjordundersøkelsen. Fagrapport 12. 24 p. (In Norwegian.)

— and O. T. SANDLUND. 1984. New methods in assessment of pelagic freshwater fish stocks — coordinated use of echo sounder, pelagic trawl and pelagic nets. Fauna, Oslo 37: 105—111. (In Norwegian with English summary.)

MATHISEN, O. A. 1953. Some investigations of the relict crustaceans in Norway, with special reference to *Pontoporeia affinis* LINDSTRÖM and *Pallasea quadrispinosa* G. O. SARS. Nytt Mag. Zool. 1: 49—86.

NIKOLSKY, G. V. 1969. The ecology of fishes. Academic Press, London. 352 p.

NILSSON, N.-A. 1967. Interactive segregation between fish species. p. 296—313. *In* The biological basis of freshwater fish production. Ed.: S. D. Gerking. Blackwell's, Oxford.

— 1979. Food and habitat of the fish community of the offshore region of Lake Vänern, Sweden. Rep. Inst. Freshw. Res., Drottningholm 58: 126—139.

— and T. G. NORTHCOTE. 1981. Rainbow trout (*Salmo gairdneri*) and cutthroat trout (*S. clarki*) interactions in coastal British Columbia lakes. Can. J. Fish. Aquat. Sci. 38: 1228—1246.

NORTHCOTE, T. G. and H. RUNDBERG. 1970. Spatial distribution of pelagic fishes in Lambarfjärden (Mälaren, Sweden) with particular reference to interaction between *Coregonus albula* and *Osmerus eperlanus*. Rep. Inst. Freshw. Res., Drottningholm 50: 133—167.

NÆSJE, T. F. 1984. Sikens livshistorie og habitatutnyttelse i Furnesfjorden og Ringsakerfjorden, Mjøsa. Unpubl. cand. real. Thesis, Univ. Oslo, 82 p. (In Norwegian.)

— O. T. SANDLUND, L. KLYVE and H. HAGEN. 1981. The amphipode *Gammaracanthus loricatus* var. *lacustris* in Lake Mjøsa. Fauna, Oslo 34: 44—45. (In Norwegian with English summary.)

PYKE, G. H., H. R. PULLIAM and E. L. CHARNOV. 1977. Optimal foraging: a selective review of theory and tests. Q. Rev. Biol. 52: 137—154.

SANDLUND, O. T. 1979. Sik og lågåsild i Osensjøen. Fiskeribiol. undersøkelser i Osenområdet, Rapport 6. 57 p. (In Norwegian.)

— H. HAGEN, L. KLYVE and T. F. NÆSJE. 1980a. Test fishing in Lake Mjøsa, 1978—79. DVF-Mjøsundersøkelsen. Rapp. 1. 48 p. (In Norwegian with English summary.)

— L. KLYVE, H. HAGEN and T. F. NÆSJE. 1980b. The smelt (*Osmerus eperlanus* (L.)) in Mjøsa. Age composition, growth and food selection. DVF-Mjøsundersøkelsen. Rapp. 2. 70 p. (In Norwegian with English summary.)

— L. KLYVE and T. F. NÆSJE. 1985. Growth habitat and food of burbot *Lota lota* in Lake Mjøsa. Fauna, Oslo 38: 37—43. (In Norwegian with English summary.)

SKURDAL, J. and T. QVENILD 1982. Prøvefiske i Tyrifjorden 1977—81. Tyrifjordundersøkelsen. Fagrapport 13. 52 p. (In Norwegian.)

SVÄRDSON, G. 1976. Interspecific population dominance in fish communities of Scandinavian lakes. Rep. Inst. Freshw. Res., Drottningholm 55: 144—171.

TUUNAINEN, P. 1971. Observations on the composition and abundance of fish fauna in Lake Päijänne, Central Finland. Preliminary report. Hydrobiol. Res. Inst. Jyväskylä, Rep. 15. 19 p.

VALLIN, S. 1969. The feeding habits of the vendace in the Lambar Bay of Lake Mälaren. Inform. Inst. Freshw. Res., Drottningholm (7). 57 p. (In Swedish.)

WERNER, E. E. and G. G. MITTELBACH. 1981. Optimal foraging: Field tests of diet choice and habitat switching. Am. Zool 21: 813—829.

Paper II

Environmental Biology of Fishes Vol. 15, No. 4, pp. 309–314, 1986

Habitat use and growth of age-0 whitefish, *Coregonus lavaretus*, and cisco, *C. albula*

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Keywords: Food-difference, Growth-difference, Habitat shift, Year-class variability, Zooplankton

Synopsis

Whitefish and cisco hatch in the River Gudbrandsdalslågen during May, and drift downstream into the Lake Mjøsa where the alevins start exogenous feeding in littoral backwaters in late May and early June. Age-0 whitefish dwell in littoral areas during summer and autumn, whereas age-0 ciscoes abandon the littoral zone and become pelagic from August onwards. Early food of cisco and whitefish are *Cyclops*, and *Bosmina*, whereas whitefish also eat early instars of Chironomidae. Later, age-0 ciscoes feed on zooplankton (cladocerans), although surface insects are also eaten. Whitefish feed on a wider range of food items including zooplankton, surface insects, chironomid larvae and pupae, cyprinid larvae, and benthic cladocerans. Cisco grew from 1.0 to ~11 cm, and whitefish from 1.6 to ~12 cm, during the first summer and autumn.

Introduction

The present paper gives data on habitat, food and growth during summer and autumn of age-0 whitefish, *Coregonus lavaretus*, and cisco, *C. albula*, in the northern part of Lake Mjøsa, Norway. There are few studies of habitat use and growth during the first growth season of these species in Europe (Lindström 1962, Hartmann 1983, Wilson 1984). The first food of young whitefish are slow-moving zooplankton not larger than 0.5–0.6 mm (John & Hasler 1956, Kokova 1979), but later during the first summer the diet appears to vary with the availability of potential food items (Lindström 1962, 1970).

Both whitefish and cisco produce widely fluctuating year-classes (Järvi 1942a, b, Aass 1972, Healey 1980). Several authors relate year-class variations to feeding and other environmental conditions during the first year (e.g. John & Hasler 1956, Aass 1972, Vladimirov 1975, Toneys & Coble 1979). As very little is known about the first year ecology of European coregonids, we studied habitat, food and growth of whitefish and cisco during the first summer and autumn. We discuss the data in relation to food availability, and give circumstantial evidence for a connection between year-class strength and zooplankton biomass.

Methods

Study area

Lake Mjøsa (61° 30′ N, 10° 25′ E, 122 m a.s.l., surface area 365 km^2) is a deep (max. depth 449 m)

All correspondence to B. Jonsson.

fjord lake. The main inlet, River Gudbrandsdalslågen empties into the part of the lake, Ringsakerfjorden (max. depth 80 m), where sampling was performed. Zooplankton in this part of Mjøsa during 1972–74 and 1978–81 were dominated by *Limnocalanus macrurus* during late autumn and winter, *Cyclops lacustris* during spring, and *Bosmina longispina, Daphnia galeata,* and *D. cristata* during summer and early autumn (Gösta Kjellberg, personal communication). During summer, the densities of the cladocerans in the Ringsakerfjord were high in 1973 and 1979 (Table 1). Lake Mjøsa contains 20 fish species, with cisco, smelt, *Osmerus eperlanus*, and whitefish numerically dominant in the pelagic zone. In shallow water along the shore, roach, *Rutilus rutilus*, perch, *Perca fluviatilis*, and ruffe, *Gymnocephalus cernuum*, are most numerous. The study area and fish community are further described by Holtan (1981) and Sandlund et al. (1985), respectively.

Sampling and material treatment

During June–October 1979 to 1981, we sampled 249 age-0 whitefish and 427 age-0 cisco. In the pelagic zone, we sampled 2–4 times each month with 2 pelagic trawls (Bagenal & Braum 1978) (0.7 mm and 5.0 mm bar mesh, 2 × 1.5 m and 12 × 6 m opening frames). The smallest trawl was an otter trawl, pulled by one boat. The larger trawl was a pair trawl pulled by two boats as described by Dahm (1980). Trawling depths and speeds were 0–40 m and 2–3 knots (Lindem & Sandlund 1984). Newly hatched embryos (May–June) were weekly sampled with dip net (0.7 mm bar mesh) and the small otter trawl. Larger young (late June–July) were sampled 2–4 times each month with shot gun and dip net. The schooling young were stunned by firing a shot gun load at the water surface over the school. The stunned young were caught with the dip net (0.7 mm bar mesh). Large young (August–October) were monthly sampled with pelagic and benthic gill nets (5 nets with 8–18.5 mm bar mesh, 2–3.5 mm in mesh increment), beach seine (7.8 mm bar mesh, 60 m × 4 m) and the large pair trawl. The pelagic and benthic gill nets were used at depths between 0–80 m (panel size of pelagic nets: 15 × 6 m, benthic nets: 15 × 2 m) (Hindar & Jonsson 1982, Sandlund et al. 1985). We measured total lengths (0.1 cm), and identified and counted the number of food items of each fish under a stereoscopic microscope. Wet weights of stomach contents were estimated from undigested food items (Hindar & Jonsson 1982).

Zooplankton were sampled with a 50 l Schindler sampler (Schindler 1969, Langeland & Rognerud 1974) at the depths: 0.5, 2, 5, 8, 12, 16, 20, 30, and 50 m. Number of crustacean zooplankton in the 0–50 m zone per m^2 surface area (Table 1) was calculated (Holtan et al. 1980, Kjellberg 1982).

Results

Whitefish and cisco hatch in the River Gudbrandsdalslågen during May (Aass 1972, Næsje 1984), and the eleutheroembryos drift directly into Lake Mjøsa where they aggregate in backwaters along the shore. There they start exogenous feeding. Both species occurred in the littoral zone until the

Table 1. Densities of zooplankton (number at depths 0–50 m per m^2 surface area) in Ringsakerfjorden, July 1972–74 and 1978–81 (Kjellberg 1982).

Year	*B. longispina*	*D. galeata*	*D. cristata*	*Cyclops*	Total
1972	1710	650	0	21820	24180
1973	447180	151820	17570	37510	654080
1974	13827	2838	1353	9360	27378
1978	157570	11400	19150	19460	207580
1979	229900	81440	29620	10460	341420
1980	41220	15380	10200	26120	92920
1981	7500	1000	960	9680	19140

end of July, often in mixed schools. From August onwards, cisco abandoned littoral areas. All later catches of age-0 cisco were in the pelagic zone at depths between 15–30 m. Age-0 whitefish stayed in littoral areas, and were never caught in the pelagic zone.

During June, zooplankton were important food items for both species (Table 2). In addition, whitefish fed on chironomid larvae and pupae, and surface insects. In July the importance of the latter food items increased for whitefish. *Bosmina* was the most important food for cisco. In August and September zooplankton were important food for whitefish, in addition to smaller amounts of chironomid larvae and pupae in August and surface insects in August and September. In September and October cisco fed almost exclusively on zooplankton. Zooplankton were overall more important food items for cisco than whitefish (Mann-Whitney *U*-test, $P<0.05$). Surface insects and chironomid larvae and pupae were less important for cisco than for whitefish ($P<0.05$).

Whitefish and cisco were 1.0 and 1.6 cm, respectively at the start of exogenous feeding (Fig. 1). Growth-rate of whitefish was almost rectilinear until late August or early September. Whitefish were ~12 cm in September. We believe that fish growth is negligible later in the autumn, as mean size of age-1 whitefish was ~12 cm in early June (Næsje 1984). Growth-rate of cisco was low during May, and increased rapidly in the beginning of June. Cisco were ~11 cm in the beginning of October corresponding to the mean-size of age-1 cisco in June (Sandlund et al. 1981a).

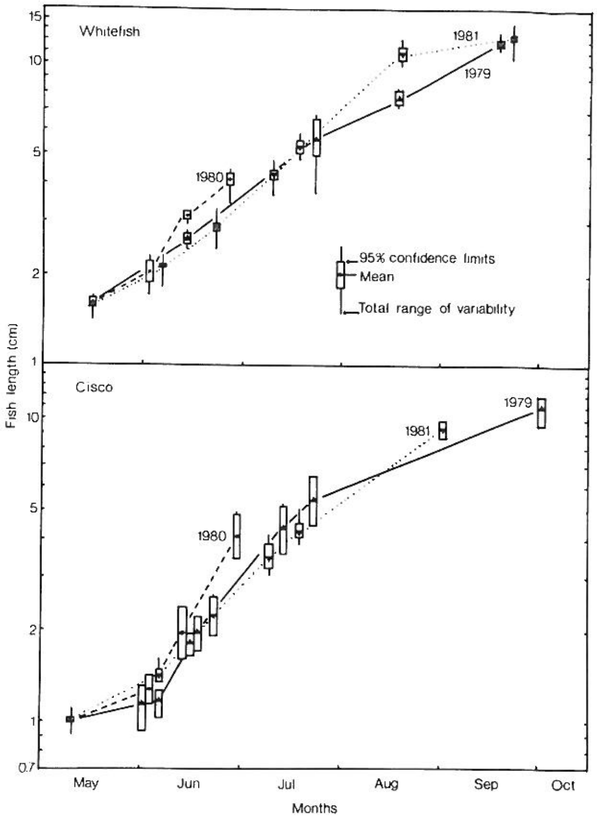

Fig. 1. Summer growth of age-0 whitefish and cisco in Lake Mjøsa 1979–81. The growth curves are based on total catch.

Discussion

Whitefish and cisco of age-0 start exogenous feeding in littoral areas of the lake. In calm weather, mixed schools were observed close to surface. Age-0 whitefish dwell in this habitat throughout the growth-season, whereas age-0 cisco abandon littoral areas from August onwards. Later, young cisco were difficult to catch. Our observations, however, indicate that they move into the pelagic zone, which also is the feeding habitat of older cisco (Svärdson 1976, Sandlund et al. 1981a). These results support Lindström (1970) who found that whitefish are littoral the first weeks after they start exogenous feeding. There are very little published data on summer and autumn habitat of European whitefish. Our results, however, parallel those of Hoagman (1973) on lake whitefish, *C. clupeaformis*, in Lake Michigan. He found that whitefish larvae occupied shallow inshore areas and bays to depths of not more than 3 m. There are very few studies on the feeding habitat of age-0 European cisco. However, Clady (1976) found that the closely related lake herring, *C. artedii*, lived near the surface in shallow bays during the first month after hatching. Later, they moved offshore, although they remained in near-surface water. Pelagic age-0 ciscoes in Lake Mjøsa were caught at depths between 15–30 m.

Several authors have found that nauplii and

Table 2. Food percentage by weight of whitefish and cisco age-0 in Lake Mjøsa. An '–' signifies that no fish was collected during a sampling period.

Date	Food items	Whitefish				Cisco			
		1979	1980	1981	Mean	1979	1980	1981	Mean
1–6	Number of fish	6	10	10		58	17	18	
June	Per cent empty stomachs	0	0	0		3.4	0	38.9	
	Cyclops spp.	20	88	0	36	85	89	23	66
	Bosmina spp.	0	2	100	34	0	0	77	26
	Daphnia spp.	0	0	0	0	6	0	0	2
	Calanoida	0	0	0	0	0	11	0	4
	Rotatoria	0	0	0	0	9	1	0	3
	Chironomidae	80	0	0	27	0	0	0	0
	Surface insects	0	10	0	3	0	0	0	0
13–30	Number of fish	26	24	10		32	16	4	
June	Per cent empty stomachs	0	16.7	0		0	6.3	25	
	Cyclops spp.	0	0	0	0	31	0	0	10
	Bosmina spp.	52	10	0	21	0	26	2	9
	Daphnia spp.	48	0	0	16	10	0	0	3
	Polyphemus pediculus	0	0	0	0	10	57	0	22
	Leptodora kindti	0	0	0	0	0	17	0	6
	Rotatoria	0	0	0	0	49	0	0	16
	Benthic Cladocera	0	0	23	8	0	0	0	0
	Chironomidae	0	19	53	24	0	0	0	0
	Surface insects	0	71	15	29	0	0	98	33
	Cyprinid larvae	0	0	9	3	0	0	0	0
July	Number of fish	15	–	20		23	15	20	
	Per cent empty stomachs	0	–	0		4.3	6.7	5	
	Bosmina spp.	34	–	7	21	70	94	65	76
	Leptodora kindti	0	–	8	4	0	0	0	0
	Rotatoria	0	–	3	2	0	0	1	0
	Chironomidae	4	–	61	33	7	2	0	3
	Surface insects	62	–	20	41	23	4	34	20
	Cyprinid larvae	0	–	1	1	0	0	0	0
Aug	Number of fish	6	–	9		–	–	–	
	Per cent empty stomachs	0	–	0		–	–	–	
	Bosmina spp.	3	–	59	31	–	–	–	–
	Polyphemus pediculus	27	–	0	14	–	–	–	–
	Leptodora kindti	62	–	0	31	–	–	–	–
	Benthic Cladocera	0	–	6	3	–	–	–	–
	Chironomidae	8	–	20	14	–	–	–	–
	Surface insects	0	–	15	8	–	–	–	–
Sept	Number of fish	6	–	–		–	–	3	
	Per cent empty stomachs	50	–	–		–	–	33.3	
	Bosmina spp.	4	–	–	4	–	–	43	43
	Daphnia spp.	64	–	–	64	–	–	49	49
	Leptodora kindti	16	–	–	16	–	–	0	0
	Alona spp.	0	–	–	0	–	–	5	5
	Surface insects	16	–	–	16	–	–	2	2
Oct	Number of fish	–	–	–		6	–	–	
	Per cent empty stomachs	–	–	–		0	–	–	
	Cyclops spp.	–	–	–	–	10	–	–	10
	Daphnia spp.	–	–	–	–	34	–	–	34
	Limnocalanus macrurus	–	–	–	–	56	–	–	56

small copepodids of cyclopoid copepods are the first food of whitefish larvae (John & Hasler 1956, Lindström 1962, Braum 1964, Kokova 1979), but feeding will vary with the availability of food organisms (Lindström 1970). Larvae of whitefish have a more diverse diet than cisco in that surface insects, chironomid larvae and pupae, cyprinid larvae, and benthic cladocerans are more frequently eaten in addition to zooplankton. These food differences parallel the dietary differences between older whitefish and cisco (Sandlund et al. 1981a, b). The whitefish is known as a generalist feeder. Zoobenthos, zooplankton, and surface insects are major food items and are the same food items eaten by age-0 whitefish in the present study. The cisco is known as the most specialized zooplankton eater among Scandinavian freshwater fishes (Svärdson 1976), and our results show that they feed mostly on zooplankton from the onset of exogenous feeding.

First year growth of whitefish and cisco in Lake Mjøsa is average to relatively good compared to other Scandinavian populations (Hamrin 1979, Svärdson 1979). Back calculation of growth from scales and otoliths indicates that Swedish whitefish and cisco grow 6–14 cm the first year.

Growth-rate of whitefish was almost rectilinear during the first summer. Growth-rate of cisco was low during the first weeks, but increased rapidly during late June, concurrently with increasing biomass of *Bosmina* (Holtan et al. 1980, Holtan 1981). We found no seasonal or annual differences in growth-rate which corresponded to differences in zooplankton density.

Differences in zooplankton density during summer may, however, influence year-class strength of cisco. Abundant cisco year-classes in 1973 and 1979 (Per Aass, personal communication), corresponded to years with high densities of cladocerans. This result supports the hypothesis that variations in year-class strength are caused by variations in food availability during the first summer, and strong year-classes appear when food is abundant and competition is lax (John & Hasler 1956, Aass 1972, Vladimirov 1975, Toneys & Coble 1979). Thus, our results suggest that zooplankton density influences the survival-rate of age-0 ciscoes. Those which survive, however, grow at approximately the same rate whether zooplankton are abundant or scarce.

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References cited

Aass, P. 1972. Age determination and year-class fluctuations of cisco, *Coregonus albula* L., in the Mjøsa hydroelectric reservoir, Norway. Rep. Inst. Freshw. Res. Drottningholm 52: 5–22.

Bagenal, T.B. & E. Braum. 1978. Eggs and early life history. pp. 165–201. *In*: T. Bagenal (ed.) Methods for Assessment of Fish Production in Fresh Waters, IBP Handbook no 3, 3rd ed., Blackwell Scientific Publications, Oxford.

Braum, E. 1964. Experimentelle Untersuchungen zur ersten Nahrungsaufnahme und Biologie an Jungfischen von Blaufelchen (*Coregonus wartmanni* Block), Weissfelchen (*C. fera* Jurine) und Hechten (*Esox lucius* L.). Arch. Hydrobiol. Suppl. 28: 183–244.

Clady, M.D. 1976. Distribution and abundance of larval ciscoes, *Coregonus artedii*, and burbot, *Lota lota*, in Oneida Lake. J. Great Lakes Res. 2: 234–247.

Dahm, E. 1980. Sampling with active gear. pp. 71–89. *In*: T. Backiel & R.L. Welcomme (ed.) Guidelines for Sampling Fish in Inland Waters, EIFAC Technical Paper 33.

Hamrin, S.F. 1979. Population dynamics, vertical distribution and food selection of ciscoe (*Coregonus albula* L.) in south Swedish lakes. Ph.D. Dissertation, University of Lund, Lund. 196 pp.

Hartmann, J. 1983. Two feeding strategies of young fishes. Arch. Hydrobiol. 96: 406–509.

Healey, M.C. 1980. Growth and recruitment in experimentally exploited lake whitefish (*Coregonus clupeaformis* Michill) populations. Can. J. Fish. Aquat. Sci. 37: 255–267.

Hindar, K. & B. Jonsson. 1982. Habitat and food segregation of dwarf and normal Arctic charr (*Salvelinus alpinus*) from Vangsvatnet lake, western Norway. Can. J. Fish. Aquat. Sci. 39: 1030–1045.

Hoagman, W.J. 1973. The hatching, distribution, abundance, growth, and food of the larval lake whitefish (*Coregonus clupeaformis* Michill) of Central Green Bay, Lake Michigan.

Rep. Inst. Freshw. Res. Drottningholm 53: 1–20.

Holtan, H. 1981. Eutrophication of Lake Mjøsa and its recovery. Water Quality Bulletin 6: 99–103, 156.

Holtan, H., G. Kjellberg & P. Brettum. 1980. Limnological investigations of Lake Mjøsa 1979. Progress report 10. Norwegian Institute of Water Research Report O-79079. 212 pp. (In Norwegian).

Järvi, T.H. 1942a. Die Bestände der kleinen Maränen (*Coregonus albula* L.) und ihre Schwankungen. 1. Pyhäjärvi (Südkarelien). Acta Zool. Fenn. 32: 1–89.

Järvi, T.H. 1942b. Die Bestände der kleinen Maränen (*Coregonus albula* L.) und ihre Schwankungen. 2. Ober- und Mittel-Keitele. Acta Zool. Fenn. 33: 1–145.

John, K.R. & A.D. Hasler. 1956. Observations on some factors affecting the hatching of eggs and the survival of young shallowwater cisco, *Leucichthys artedii* LeSeuer, in Lake Mendota, Wisconsin. Limnol. Oceanogr. 1: 176–194.

Kjellberg, G. 1982. Limnological investigations in Lake Mjøsa, 1976–1981. Norwegian Institute of Water Research Report O-8000203. 50 pp. (In Norwegian).

Kokova, V.Ye. 1979. Feeding of larvae of the whitefish, *Coregonus lavaretus ladoga*, the Baikal omul, *Coregonus autumnalis migratorius*, and the 'peled', *Coregonus peled*. J. Ichthyol. 18: 953–960.

Langeland, A.L. & S. Rognerud. 1974. Statistical analyses used in comparison of 3 methods of freshwater zooplankton sampling. Arch. Hydrobiol. 73: 403–410.

Lindem, T. & O.T. Sandlund. 1984. New methods in assessment of pelagic freshwater fish stocks – coordinated use of echo sounder, pelagic trawl and pelagic nets. Fauna (Oslo) 37: 105–111. (In Norwegian).

Lindström, T. 1962. Life history of whitefish young (*Coregonus*) in two lake reservoirs. Rep. Inst. Freshw. Res. Drottningholm 44: 113–144.

Lindström, T. 1970. Habitats of whitefish in some north Swedish lakes at different stages in life history. pp. 461–479. *In*: C.C. Lindsey & C.S. Woods (ed.) Biology of Coregonid Fishes, University of Manitoba Press, Winnipeg.

Næsje, T. 1984. Life history and habitat use of whitefish in the Furnesfjord and the Ringsakerfjord, Mjøsa Lake. M.Sc. Thesis, University of Oslo, Oslo. 82 pp. (In Norwegian).

Sandlund, O.T., T.F. Næsje, H. Hagen & L. Klyve. 1981a. Cisco in Mjøsa Lake. Age, growth and food. DVF-Mjøsundersøkelsen Report 3: 1–58. (In Norwegian).

Sandlund, O.T., T.F. Næsje, L. Klyve & H. Hagen 1981b. Whitefish in Mjøsa Lake. Age, growth and food. DVF-Mjøsundersøkelsen Report 5: 1–54. (In Norwegian).

Sandlund, O.T., T.F. Næsje, L. Klyve & T. Lindem. 1985. The vertical distribution of fish species in Lake Mjøsa, Norway, as shown by gillnet catches and echo sounder. Rep. Inst. Freshw. Res. Drottningholm 62 (in press).

Schindler, D.W. 1969. Two useful devices for vertical plankton and water sampling. J. Fish. Res. Board Can. 26: 1948–1955.

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.

Toneys, M.L. & D.W. Coble. 1979. Size-related, first winter mortality of freshwater fishes. Trans. Amer. Fish. Soc. 108: 415–419.

Vladimirov, V.I. 1975. Critical periods in the development of fishes. J. Ichthyol. 15: 851–868.

Wilson, J.P.F. 1984. The food of the pollan, *Coregonus autumnalis pollan* Thompson, in Lough Neagh, northern Ireland. J. Fish Biol. 24: 253–261.

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Paper III

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Ontogenetic changes in habitat use by whitefish, *Coregonus lavaretus*

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Key words: Habitat use, Diet, Growth, Zooplankton, Zoobenthos, *Pallasea quadrispinosa*

Synopsis

The whitefish, *Coregonus lavaretus*, in the lake Mjøsa exhibited two niche changes during their life cycle. Juveniles (< 25 cm body length) were confined to the shallow (0–30 m) epibenthic zone. Medium sized whitefish (25–35 cm body length) expanded their habitat use to include the deep (30–90 m) epibenthic zone as well as the pelagic zone. From a body length of 35 cm, habitat use was restricted to the deep epibenthic zone. Small fish in the shallow epibenthic zone ate small and medium-sized prey (zooplankton, insect larvae and surface insects). Medium-sized fish in this zone were in addition feeding on the larger amphipod, *Pallasea quadrispinosa*. In the pelagic zone, the diet of medium-sized whitefish was dominated by zooplankton, although some larger prey like surface insects and age-0 smelt, *Osmerus eperlanus*, were also eaten. In the deep epibenthic zone, the diet of both medium-sized and large (< 35 cm) whitefish consisted mainly of the large prey *P. quadrispinosa*.

Introduction

Ontogenetic niche shifts have been shown to occur during the life of many fish species (Werner & Gilliam 1984, Persson 1990). As the fish grow, its habitat choice and diet change. Optimal prey size is generally positively correlated with fish size (Wankowski & Thorpe 1979), and diet shifts are often accompanied by relatively abrupt increases in food particle size or abundance of available prey (Larkin et al. 1957, Martin 1970, Werner 1979). Shifts to larger or more abundant prey may occur within one habitat, but are often associated with habitat shifts (Werner et al. 1981).

The optimal diet model predicts that the fish will select the prey that gives the highest net rate of energetic return (Mittelbach 1981, Stephens & Krebs 1986), modified by the relative predation risk in the various habitats available (Mittelbach 1984, Werner & Hall 1988). The risk of predation is a major factor in habitat choice by small fish, but as fish size increases, predation risk decreases (Crowder & Cooper 1982, Werner et al. 1983). The optimal prey size, however, usually increases with increasing fish size.

Whitefish, *Coregonus lavaretus*, are omnivorous, and may feed on zooplankton, zoobenthos, surface insects and fish (Nilsson 1967, Svärdson 1976). As whitefish populations contain many size and age groups, we would expect this variability in diet to be associated with ontogenetic development. We would predict that the changes in diet and habitat use reflects the spatial variation in prey abundance and predation risk.

Whitefish in the deep, oligotrophic lake Mjøsa, Norway, are monomorphic, with a subterminal mouth and a mean gillraker number of 30 (Sandlund et al. 1987). Whitefish reach a body length of 12 cm during the first year and 20 cm during the second year. Asymptotic length was 31 cm. Fifty percent sexual maturity was attained at age 5, at a mean length of 29 cm. Thus, post-maturity growth was low. However, a large proportion of the fish was old; more than 10% of the adults were older than 20 years. The whitefish stock is exploited only as a by-catch when fishing for other species.

In Mjøsa, food availability differs seasonally. Maximum abundance of the zoobenthos groups (insect larvae, molluscs, and oligochaetes) is found in July (Holtan et al. 1980). The amphipods *Pallasea quadrispinosa* and *Gammaracanthus loricatus* are also important zoobenthos, but, as they cannot be sampled quantitatively with an Ekman grab, their actual abundance is not known (Næsje et al. 1981). Maximum abundance of zooplankton is found in August/September, when the zooplankton community is dominated by *Daphnia galeata* and *Bosmina longispina* (Holtan et al. 1980, Kjellberg & Sandlund 1983).

Of the 20 fish species present in the lake, 3 are potential predators on whitefish older than a few weeks: piscivorous brown trout, *Salmo trutta*, in the pelagic zone; pike, *Esox lucius*, in littoral waters; and burbot, *Lota lota,* in profundal areas (Huitfeldt-Kaas 1917, Sandlund et al. 1985a, b).

Based on this, one might expect that benefits and costs for the whitefish should vary between habitats, and depend on the size of the fish. We therefore wanted to investigate the possible changes in habitat use of whitefish with increasing body size.

Methods

Study area

Mjøsa (61°30′N, 10°25′E, 121 m a.s.l.) is an oligo-mesotrophic, dimictic fjord lake in south-eastern Norway. Surface area is 365 km^2, maximum depth is 449 m, and mean depth is 153 m (Holtan 1979).

Sampling

Whitefish were sampled in Mjøsa from February to November 1979, by use of epibenthic and pelagic gill nets (Sandlund et al. 1985b). The gill nets consisted of 12 panels (panel size, epibenthic: 25 × 2 m; pelagic: 25 × 6 m) with varying mesh sizes (8–52 mm bar mesh, mesh increments 2–7 mm). The pelagic nets were placed at the following depths: 0–10, 10–30, 30–50, and 50–90 m. The benthic nets were set from the shoreline down to 90 m. The exact depth of each net was recorded by an echo sounder (Simrad EL). The nets were fishing for 24 h, and catch per unit effort (CPUE) was calculated as number of fish per 100 m^2 net area for 24 hours fishing. A total of 806 whitefish between 17 and 46 cm in length were caught. Abundance of pelagic whitefish was estimated from data for fish density and relative size distribution collected with a Simrad EY-M echosounder (Lindem & Sandlund 1984).

Treatment of material

Fish were measured to the nearest 0.1 cm with the tail in a natural position and weighed to the nearest 1 g. Fish were aged by burning and breaking the otoliths (Christensen 1964).

Stomach contents were analyzed, and prey categories identified and counted, under a stereoscopic microscope. Wet weight of stomach contents were estimated from undigested food items. The degree of diet similarity between size groups was calculated according to Schoener's (1968) similarity index

$D = 1-1/2 \sum_{i=1}^{n} |p_i-q_i|)$, where p_i is weight proportion of food item i in population 1, q_i is weight proportion of food item i in population 2, and n the number of food categories. D varies between 0 and 1, representing no and complete food similarity, respectively.

Results

Habitat

Catch per unit effort (CPUE) of whitefish in the epibenthic zone varied between 0.9 and 2.6, with a minimum during winter (Næsje et al. 1991). In the

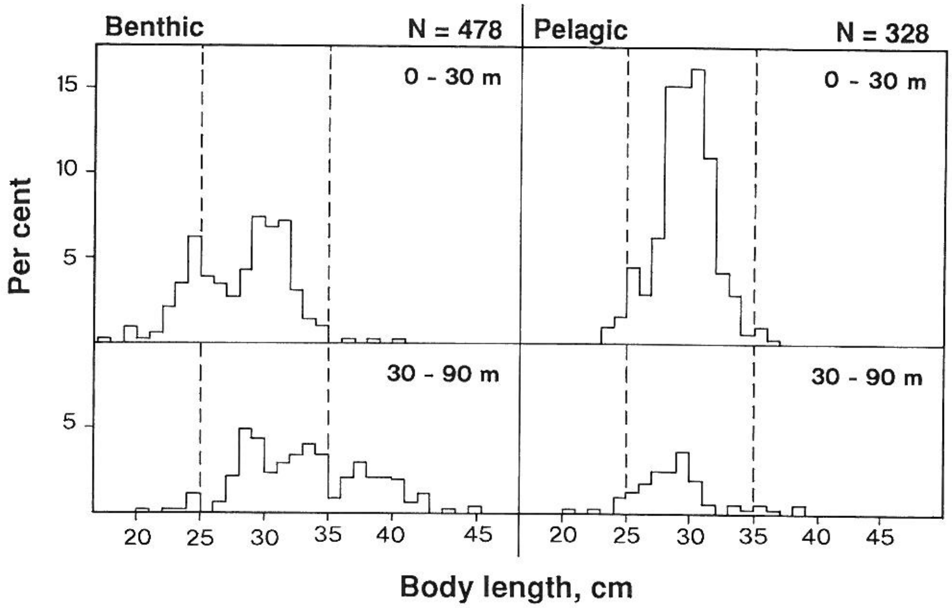

Fig. 1. Length distribution of whitefish caught in the epibenthic and pelagic habitat (depth zones 0–30 and 30–90 m) in Mjøsa, February–November 1979. N = number of fish in each habitat, all depths = 100%. Number of fish in the two depth zones were adjusted for catch effort.

pelagic zone whitefish catches were low from December through June (CPUE: 0.02–0.12), and high during August–October (CPUE: 0.40–2.09). A similar variation in the number of pelagic whitefish was also shown by hydroacoustic estimates, with the number of pelagic whitefish increasing from 24 fish ha^{-1} in May to a maximum of 182 fish ha^{-1} in September and decreasing to a minimum of 21 fish ha^{-1} in November (T. Lindem personal communication).

There was a partial habitat segregation between size groups of whitefish caught in gill nets (Fig. 1). Whitefish smaller than 25 cm in length were largely restricted to 0–30 m depth in the epibenthic zone. Fish between 25 and 35 cm in length were found from 0 to 90 m in the epibenthic zone and in the pelagic zone. In the pelagic zone, however, very few fish were caught deeper than 50 m. Fish larger than 35 cm in length were mainly found deeper than 30 m in the epibenthic zone. The difference in length distribution between depths in the epibenthic zone was highly significant ($X^2 = 209.4$, 2 d.f., $p < 0.005$). Furthermore, mean size of epibenthic whitefish increased significantly from the 0–30 m to the 30–90 m depth zone (t-test, $p < 0.05$). In the pelagic zone length distributions between depths were also significantly different, due to relatively more small and large fish in the 30–90 m zone ($X^2 = 10.4$, 2 d.f., $p < 0.01$).

The partial habitat segregation between size groups concurs with segregation between age groups (Fig. 2). The 15–25 cm size group, living in the shallow epibenthic zone, consisted of fish younger than 6 years, with a mean age of 2.3 years. The 25–35 cm size group, which was living in all three habitats, included fish of ages from 2 to more than 20 years. Within this size group there was a significant difference in age distribution between the pelagic and shallow epibenthic habitat ($X^2 = 20.9$, 3 d.f., $p < 0.005$), although mean ages in the two habitats were not significantly different (10.2 vs. 8.8 years, t-test, $p > 0.05$). There was a significantly larger proportion of old fish among 25–35 cm fish in the deep epibenthic habitat than in the shallow epibenthic habitat ($X^2 = 74.6$, 3 d.f., $p < 0.005$). This is also reflected in the significantly higher mean age in the deep epibenthic habitat than in the shallow epibenthic and pelagic habitats

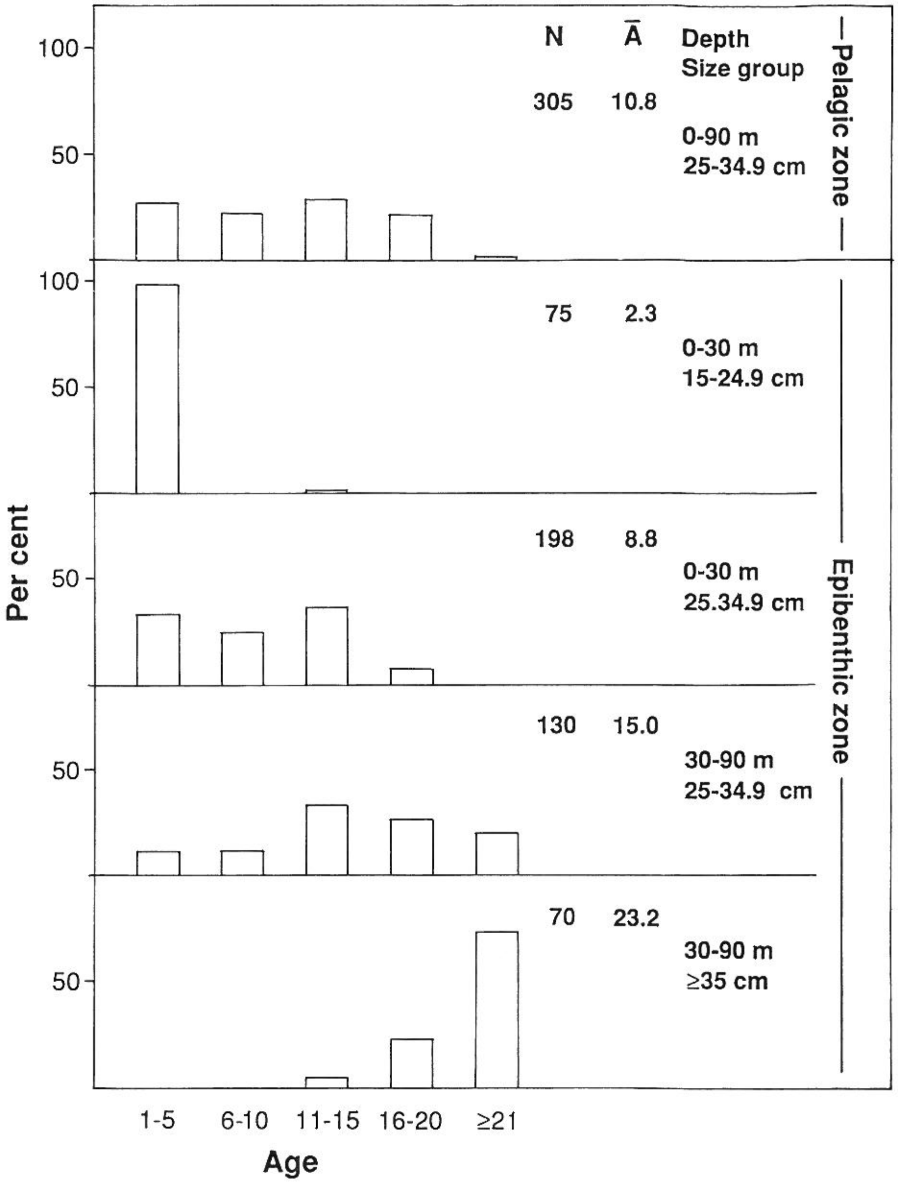

Fig. 2. Age distribution of the various size groups of whitefish caught in the pelagic zone (0–90 m) and in the shallow (0–30 m) and deep (30–90 m) epibenthic zone in Mjøsa, February–November 1979. N = number of fish. A = mean age (years) in sample.

(15.0 vs. 8.8 and 10.2 years, respectively, t-tests, $p < 0.05$). There was no significant difference in age distribution between 25–34.9 cm pelagic whitefish and the pooled material of this length group from the epibenthic habitat (0–90 m) ($X^2 = 3.66$, 3 d.f., $p > 0.05$). Mean age of fish larger than 35 cm, restricted to the deep epibenthic zone, was 23.2 years.

Diet

The prey taken by whitefish may be grouped according to their wet weight into three size classes (Table 1). Small prey (< 1 mg wet weight) are crustacean zooplankton, mainly within a pelagic habitat, although they may also be found close to the substratum. Medium sized prey (1–5.9 mg wet weight) are large cladoceran zooplankton, molluscs, insect larvae and pupae, and surface insects. Thus, this prey size is found in all habitats. Among large prey (≥ 6 mg wet weight), the benthic amphipod *P. quadrispinosa* was important whitefish food, whereas *Mysis relicta* and age-0 smelt, *Osmerus eperlanus*, were eaten occasionally.

In the epibenthic zone, there was a segregation in diet between whitefish caught in the 0–30 m depth zone and in deeper waters (Fig. 3). In the 0–30 m depth zone, all size groups had a varied diet, dominated by small and medium sized prey (cladocerans and chironomid larvae, cf. Table 1). Deeper than 30 m the diet of 25–35 cm fish and fish > 35 cm was nearly identical, as both groups depended heavily on *P. quadrispinosa*. The similarity in diet between the size groups in deep waters is indicated by the high diet overlap (Schoener's D = 0.913–0.997; Fig. 4) which was significantly higher (Wilcoxon's rank test, $p < 0.01$) than the corresponding indices of diet overlap between 15–25 cm and 25–35 cm fish in shallow waters (0.337–0.789).

Table 1. Wet weights of prey in subadult and adult whitefish stomachs, Lake Mjøsa 1979 (approximate means, over all months). Only prey groups constituting more than 1% wet weight of stomach contents at any time are included. Habitat (P = pelagic, SB = epibenthic 0–30 m, DB = epibenthic 30–90 m) indicates where this prey was important food.

Taxon	Average wet weight (mg)	Habitat
Weight group < 1 mg		
Bosmina longispina	0.04	P, SB
Daphnia galeata	0.12	P, SB
Cyclops lacustris	0.12	P, SB
Eudiaptomus gracilis	0.05	P, SB
Limnocalanus macrurus	0.24	P, SB
Weight group 1–5.9 mg		
Leptodora kindti	2.0	P, SB
Bythotrephes longimanus	2.0	P, SB
Chironomidae larvae	1.7	SB
Chironomidae pupae	1.7	SB
Trichoptera larvae	5.4	SB
Pisidium spp.	1.7	SB, DB
Gyraulus spp.	3.7	SB
Surface insects	3.0	P, SB
Weight group ≥ 6 mg		
Pallasea quadrispinosa	16.8	SB, DB
Mysis relicta	8.0	SB
Fish (age-0 smelt)	90.0	P

In the epibenthic habitat, the frequency of fish with large prey (≥ 6 mg wet weight) in the stomachs increased with increasing fish size (Wilcoxon-tests, $p < 0.01$; Fig. 5).

In the pelagic zone there was no significant difference in diet between fish caught in various depth zones, and they were therefore pooled. Pelagic whitefish had eaten essentially the same proportion of size groups of prey as the smaller fish in the shallow epibenthic habitat (Fig. 3). The frequency of pelagic 25–35 cm fish that had eaten large prey (≥ 6 mg wet weight) was significantly lower than among fish of the same size, and similar to the frequency among smaller fish (15–25 cm), in the epibenthic zone (Wilcoxon-tests, $p < 0.01$ and $p > 0.05$, respectively: Fig. 5).

Discussion

Our data demonstrate two changes in habitat use during the life span of whitefish in Mjøsa. When the fish reach a body length of approximately 25 cm, their habitat is expanded from the shallow (0–30 m) epibenthic zone to include all three main habitats; the shallow and the deep (30–90 m) epibenthic zone as well as the pelagic zone. At the same time, the diet is diversified to include zooplankton in the pelagic zone and *P. quadrispinosa* in the deep epibenthic zone.

The second ontogenetic change in habitat use occurs when the whitefish reach a body length of approximately 35 cm. From this size, their habitat is confined to the deep epibenthic zone, and the diet is chiefly restricted to *P. quadrispinosa*.

Ontogenetic habitat shifts in animals are the results of trade-offs between feeding (growth rate) and predation risks (mortality) (Stamps 1983, Power 1984, Gilliam & Fraser 1987, Werner & Hall 1988). In the absence of predation risk, as in large-sized fish, the shifts between habitats should be determined by prey available, and energy spent on search, capture and handling of prey (Werner & Hall 1974, Abrahams & Dill 1989).

The juvenile whitefish in Mjøsa stay in the littoral zone from the time of metamorphosis, and start feeding as larvae at a length of 16 mm (Næsje et al.

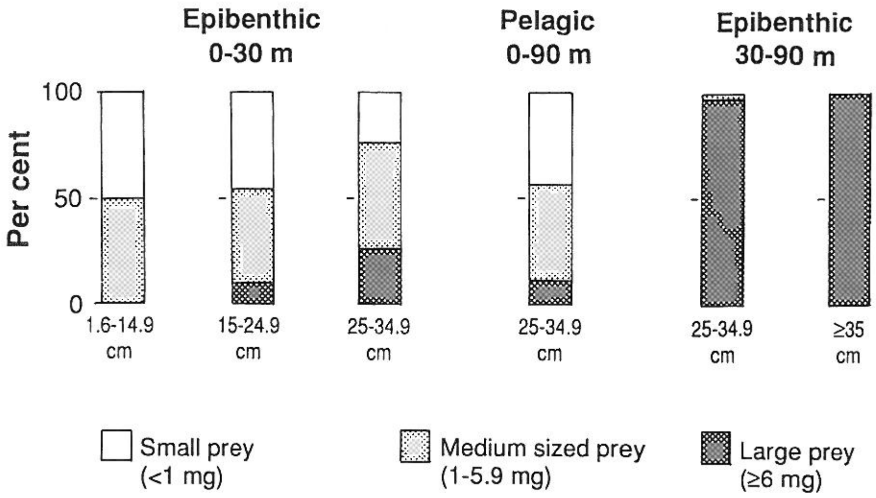

Fig. 3. Diet of whitefish in the epibenthic habitat (depth zones 0–30 m and 30–90 m) and in the pelagic habitat (0–90 m); mean over the sampling periods February–November 1979, in Mjøsa. Sample sizes: Epibenthic 0–30 m, < 15 cm: 59 fish; 15–24.9 cm: 39 fish; 25–34.9 cm: 138 fish. Pelagic 0–90 m: 247 fish. Epibenthic 30–90 m, 25–34.9 cm: 87 fish; > = 35 cm: 69 fish. Data for fish ≤ 14.9 cm from Næsje et al. (1986).

1986). This is the habitat which the most abundant zoobenthos (Holtan et al. 1980), but the availability of benthic prey may be low, due to interspecific competition, as most other fish species in the lake also live in the littoral zone (Sandlund et al. 1985b). A part of the stock of medium-sized whitefish exploit pelagic waters during late summer and autumn, and the offshore movement is significantly correlated with the abundance of zooplankton (Næsje et al. 1991). This accords with the prediction that parts of the stock should change habitat when the food situation improves offshore. However, we do not know whether the relative distribution of medium-sized whitefish is in proportion to the abundance of food resources in the various habitats (the ideal free distribution model; Fretwell & Lucas 1970). From a fish-size/prey-size consideration, we would expect zooplankton to be a more profitable prey for small whitefish (Wankowski & Thorpe 1979), but the smaller whitefish may stay

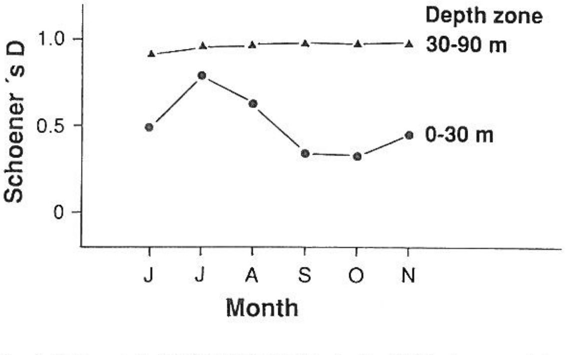

Fig. 4. Schoener's (1968) diet overlap index (D) between whitefish length groups in the epibenthic habitat in Mjøsa: 0–30 m depth zone: between 15–24.9 cm and 25–34.9 cm length groups, 30–90 m depth zone: 25–34.9 cm and > = 35 cm length groups. Sample sizes as in Fig. 3.

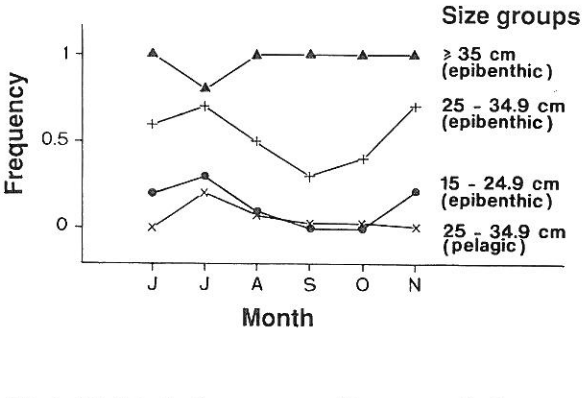

Fig. 5. Frequency of occurrence of large prey (≥ 6 mg wet weight, cf. Table 1) in the stomachs of the various size groups of whitefish in L. Mjøsa. Fish ≤ 14.9 cm had eaten no large prey (cf. Fig. 3).

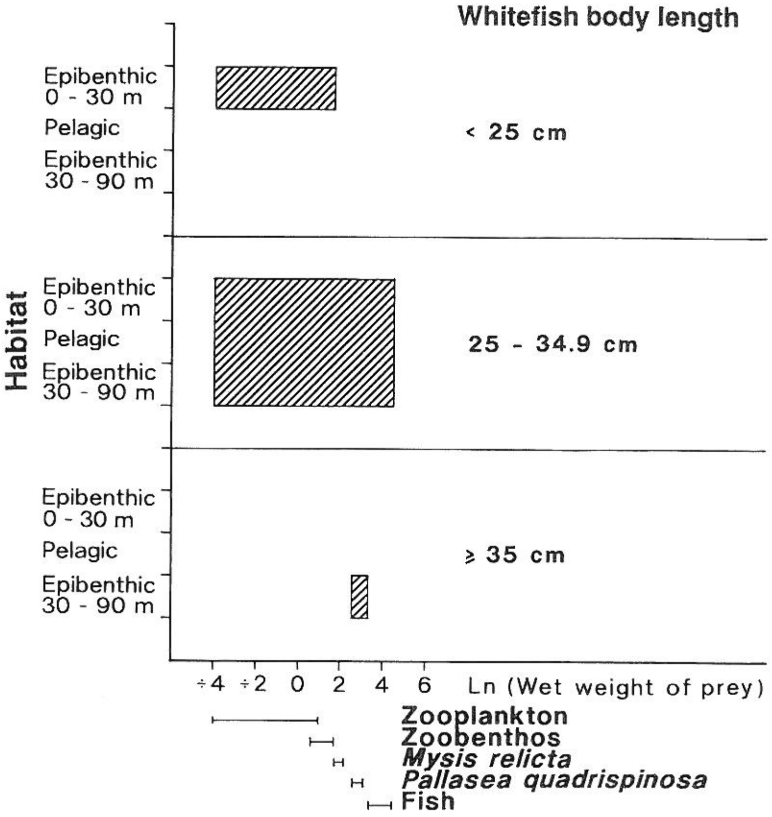

Fig. 6. Summary of ontogenetic niche shifts (in terms of prey size and habitat) in whitefish in L. Mjøsa. Sizes of prey in some prey groups of importance for whitefish is indicated below the horizontal axis. Three habitats are defined within the lake (vertical axis). Based on present data and Næsje et al. (1986).

close to the bottom because it is safer to dwell in a structured habitat than moving offshore (Crowder & Cooper 1982).

In the pelagic zone, brown trout and the occasional large pike are potential predators on whitefish. Brown trout in Mjøsa eats mainly smelt, which is usually less than 15 cm in length. Only 4% of the prey fishes in the stomachs of 75 predatory brown trout were larger than 15 cm (Taugbøl et al. 1989). Small pike (<60 cm) in Mjøsa tend to stay in shallow protected bays where there is some macrovegetation. Larger pike tend also to move in the exposed littoral areas, and are occasionally caught in the pelagic zone (Sandlund et al. 1985b). Little is known about the diet of pike in Mjøsa, but in the Norwegian lake Tyrifjorden, with a similar fish community, only large pike (>60 cm) to some extent ate adult whitefish (≈30 cm) (Vøllestad et al. 1986). The third potential predator in Mjøsa, burbot, live mainly in the deep epibenthic zone, and feeds on smelt (Sandlund et al. 1985a). The apparent concentration of prey sizes below 15 cm is probably due to this being the adult size of smelt, which seems to be the most easily available prey species. Even so, for whitefish predation risk will probably decrease quite quickly as they approach adult size.

The change in habitat use by whitefish at the size of 25 cm might be termed an expansion of the niche (Fig. 6). Whitefish between 25 and 35 cm utilize all main habitats, including the shallow benthic zone used by smaller fish and the deep benthic zone used by larger fish, and a wide spectrum of prey sizes. Individuals moving into the deeper benthic zone find larger prey (*P. quadrispinosa*). However, because the whitefish is a visual predator (Braum 1978), searching time may be longer in darkness. Feeding in the pelagic zone involves utilizing smaller prey, but at high zooplankton densities searching and handling time is short (Werner & Hall 1974).

The asymptotic length of the Mjøsa whitefish is 31 cm. Thus, relatively few fish ever reach the > 35 cm length group. We may hypothesize that the post-maturity growth necessary to become larger than 35 cm may depend on a diet shift from small and medium-sized prey to the large *P. quadrispinosa*, giving a larger energy surplus. In bluegills, *Lepomis macrochira*, Mittelbach (1983) demonstrated that the fish ceased growing if the availability of large prey was low.

Broadly speaking, the whitefish stock thus consists of three ecologically functional units: small littoral fish, medium-sized fish utilizing all habitats, and large profundal fish. These ecological units each include a high number of age groups. Medium-sized fish include more than 20 age groups, whereas large fish include from age 12 upwards. Age distribution in the two groups overlap to a large extent, indicating that the whitefish population is size-structured rather than age-structured (Ebenman & Persson 1988).

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References cited

Abrahams, M.V. & L.M. Dill. 1989. A determination of the energetic equivalence of the risk of predation. Ecology 70: 999–1007.

Braum, E. 1978. Ecological aspects of the survival of fish eggs, embryos and larvae. pp. 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.

Crowder, L.B. & W.E. Cooper. 1982. Habitat structural complexity and the interaction between bluegills and their prey. Ecology 63: 1802–1813.

Ebenman, B. & L. Persson (ed.). 1988. Size-structured populations. Ecology and evolution. Springer-Verlag, Berlin. 284 pp.

Fretwell, S.L. & H.L. Lucas, Jr. 1970. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. Acta Biotheoretica 19: 315–357.

Gilliam, J.F. & D.F. Fraser 1987. Habitat selection under predation hazard: test of a model with foraging minnows. Ecology 68: 1856–1862.

Holtan, H. 1979. The Lake Mjøsa story. Arch. Hydrobiol. Beih. Ergebn. Limnol. 13: 242–258.

Holtan, H., G. Kjellberg & P. Brettum. 1980. Monitoring of Lake Mjøsa. Progress report 10. Investigations in 1979. Norwegian Institute of Water Research Report 0-79079: 1–212. (In Norwegian.)

Huitfeldt-Kaas, H. 1917. The fish & fisheries of Lake Mjøsa. Det Kgl. Norske Videnskabers Selskap, Skrifter 2: 1–257. (In Norwegian.)

Kjellberg, G. & O.T. Sandlund. 1983. Trophic relationships in the pelagic zone of Lake Mjøsa. Direktoratet for vilt og ferskvannsfisk, Mjøsundersøkelsen, Report 6: 1–61. (In Norwegian.)

Larkin, P.A., J.G. Terpenning & R.R. Parker. 1957. Size as a determinant of growth rate in rainbow trout *Salmo gairdneri*. Trans. Amer. Fish. Soc. 86: 84–96.

Lindem, T. & O.T. Sandlund. 1984. New methods in assessment of pelagic freshwater fish stocks – coordinated use of echosounder, pelagic trawl and pelagic nets. Fauna (Oslo) 37: 105–111. (In Norwegian.)

Martin, N.W. 1970. Long-term effects of diet on the biology of the lake trout and the fishery in Lake Opeongo, Ontario. J. Fish. Res. Board Can. 27: 125–146.

Mittelbach, G.G. 1981. Foraging efficiency and body size: a study of optimal diet and habitat use by bluegill. Ecology 62: 1370–1386.

Mittelbach, G.G. 1983. Optimal foraging and growth in bluegills. Oecologia 59: 157–162.

Mittelbach, G.G. 1984. Predation and resource partitioning in two sunfishes (Centrarchidae). Ecology 65: 499–515.

Næsje, T.F., B. Jonsson, O.T. Sandlund & G. Kjellberg. 1991. Habitat switch and niche overlap in coregonids: effects of zooplankton abundance. Can. J. Fish. Aquat. Sci. (in press).

Næsje, T.F., O.T. Sandlund & B. Jonsson. 1986. Habitat use and growth of age-0 whitefish, *Coregonus lavaretus*, and cisco, *C. albula*. Env. Biol. Fish. 15: 309–314.

Næsje, T.F., O.T. Sandlund, L. Klyve & H. Hagen. 1981. The amphipode *Gammaracanthus loricatus* var. *lacustris* in Lake Mjøsa. Fauna (Oslo) 34: 44–45. (In Norwegian.)

Nilsson, N.-A. 1967. Interactive segregation between fish species. pp. 295–313. *In:* S.D. Gerking (ed.) Biological Basis of Freshwater Fish Production, Blackwell Scientific Publications, Oxford.

Persson, L. 1990. Predicting ontogenetic niche shifts in the field: what can be gained by foraging theory? pp. 303–321. *In:* R.N.

Hughes (ed.) Behavioural Mechanisms of Food Selection, Springer-Verlag, Berlin.

Power, M.E. 1984. Depth distribution of armored catfish: predator-induced resource avoidance? Ecology 65: 523–528.

Sandlund, O.T., L. Klyve & T.F. Næsje. 1985a. Growth, habitat and food of burbot *Lota lota* in Lake Mjøsa. Fauna (Oslo) 38: 37–43. (In Norwegian.)

Sandlund, O.T., T.F. Næsje, L. Klyve & T. Lindem. 1985b. The vertical distribution of fish species in Lake Mjøsa, Norway, as shown by gill-net catches and echo sounder. Rep. Inst. Freshwat. Res. Drottningholm 62: 136–149.

Sandlund, O.T., T.F. Næsje & G. Kjellberg. 1987. The size selection of *Bosmina longispina* and *Daphnia galeata* by co-occuring cisco (*Coregonus albula*), whitefish (*C. lavaretus*) and smelt (*Osmerus eperlanus*). Arch. Hydrobiol. 110: 357–363.

Schoener, T.W. 1968. The *Anolis* lizards of Bimini: resource partitioning in a complex fauna. Ecology 49: 704–726.

Stamps, J.A. 1983. The relationship between ontogenetic habitat shifts, competition and predator avoidance in a juvenile lizard (*Anolis aeneus*). Behav. Ecol. Sociobiol. 12: 19–33.

Stephens, D.W. & J.R. Krebs. 1986. Foraging theory. Princeton University Press, Princeton. 247 pp.

Svärdson, G. 1976. Interspecific population dominance in fish communities of Scandinavian lakes. Rep. Inst. Freshwat. Res. Drottningholm 55: 144–171.

Taugbøl, T., O. Hegge, T. Qvenild & J. Skurdal. 1989. The diet of brown trout in Lake Mjøsa. Fylkesmannen i Oppland, Miljøvernavdelingen. Report 15: 1–17. (In Norwegian.)

Vøllestad, L.A., J. Skurdal & T. Qvenild. 1986. Habitat use, growth, and feeding of pike (*Esox lucius* L.) in four Norwegian lakes. Arch. Hydrobiol. 108: 107–117.

Wankowski, J.W.J. & J.E. Thorpe. 1979. The role of food particle size in the growth of juvenile Atlantic salmon (*Salmo salar* L.). J. Fish Biol. 14: 351–370.

Werner, E.E. 1979. Niche partitioning by food size in fish communities. pp. 311–322. *In:* H. Clepper (ed.) Predator-Prey Systems in Fisheries Management, Sport Fishing Institute, Washington.

Werner, E.E. & J.F. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. Ann. Rev. Ecol. Syst. 15: 393–425.

Werner, E.E., J.F. Gilliam, D.J. Hall & G.G. Mittelbach. 1983. An experimental test of the effects of predation risk on habitat use in fish. Ecology 64: 1540–1548.

Werner, E.E. & D.J. Hall. 1974. Optimal foraging and the size selection of prey by the bluegill sunfish (*Lepomis macrochirus*). Ecology 55: 1042–1052.

Werner, E.E. & D.J. Hall. 1988. Ontogenetic habitat shifts in bluegill: the foraging rate-predation risk trade-off. Ecology 69: 1352–1366.

Werner, E.E., G.G. Mittelbach & D.J. Hall. 1981. Foraging profitability and the role of experience in habitat use by the bluegill sunfish. Ecology 62: 116–125.

Paper IV

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Habitat switch and niche overlap in coregonid fishes: effects of zooplankton abundance

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Patterns of habitat use by vendace *Coregonus albula* and whitefish *C. lavaretus* were investigated in a natural experiment in Lake Mjøsa, Norway. Vendace lived almost exclusively in the pelagic habitat and catch per unit effort in gill nets was significantly correlated with water temperature ($r^2=0.457$, $P<0.005$). Whitefish exploited both epibenthic and pelagic areas. During summer one part of the population lived in epibenthic areas whereas the rest of the population moved out into the pelagic zone. The pelagic part returned to the epibenthic habitat in the autumn. Cladocerans were important food items for both fish species in the pelagic zone. However, only vendace ate the large copepod *Limnocalanus macrurus*, whereas surface insects were more important prey for whitefish. This suggests that vendace is the most specialized zooplanktivore. The pelagic gill net catches of whitefish, and the pelagic habitat overlap (Schoener's (1968) D) between whitefish and vendace increased with increasing zooplankton densities at depths between 0 and 50 m ($r^2=0.609$ and $r^2=0.494$, respectively, $P<0.01$). Both during spring and autumn we observed a time-lag between the change in zooplankton abundance and habitat switches of whitefish, indicating an element of learning in choice of habitat. There was no significant correlation between diet overlap (Schoener's D) between pelagic whitefish and vendace and zooplankton densities

($P>0.05$). Our study indicates that for whitefish the habitat shifts between benthic and pelagic habitats are induced by the abundance of crustacean zooplankton in the pelagic zone, and that the pelagic habitat overlaps of whitefish and vendace are correlated with the abundance of zooplankton.

Introduction

Seasonal habitat switches of animals are supposed to result from changes in the environmental conditions, and habitat choices are considered to be trade-offs between profitabilities and risks in the environment (Krebs and Davis 1984; Stephens and Krebs 1986). Solitary animals will move from one food patch to another in order to maximize their energy gains (Charnov 1976; McNair 1982), and animals may evaluate profits and costs of different habitats (Dill 1987; Werner and Hall 1988). Behaviour of fish may be modified by the process of learning about the quality of food patches (Milinski 1984; Holbrook and Schmitt 1988; Werner and Hall 1988), by the risk of predation (Werner et al. 1983; Mittelbach 1984; Holbrook and Schmitt 1988), and by the presence of competitors (Krebs et al. 1972; Barnard et al. 1982; Pitcher et al. 1982; Sutherland 1983).

In northern temperate lakes, prey abundance fluctuates seasonally and is an important factor influencing temporal habitat switches of fish. In many lakes whitefish (_Coregonus lavaretus_), may exhibit seasonal habitat switches between benthic and pelagic habitats (Svärdson 1976). The closely related vendace, _C. albula_, is usually pelagic when co-occurring with whitefish (Svärdson 1976; Nilsson 1979). In such situations the two fish species segregate in food selection (Hamrin and Person 1985). Vendace is the most specialized zooplankton feeder, whereas whitefish is a more generalized feeder, exploiting both epibenthic and pelagic food resources (Svärdson 1976; Hamrin and Person 1986). Little is known, however, about the seasonal and spatial habitat use of these fishes in relation to pelagic food abundance.

Thus we studied habitat use of vendace and whitefish in the Norwegian lake Mjøsa, where we tested: (1) if habitat shifts of whitefish between epibenthic and pelagic habitats were correlated with the abundance of crustacean zooplankton; (2) if habitat overlaps between whitefish and vendace were correlated with the abundance of crustacean zooplankton; (3) if diet overlaps between whitefish and vendace were correlated with the abundance of crustacean zooplankton.

Study site and methods

Study area

Mjøsa (61°30′N, 10°25′E) is an 449 m deep, oligo-mesotrophic, dimictic fjord lake. The lake has a surface area of 365 km^2. The circulation periods last from late April until the end of June, and from October until ice cover usually in January/February (Holtan 1979). The thermocline is established at 12 - 20 m depth. In 1979, hypolimnetic temperatures varied between 3.5 and 8 °C. Epilimnic temperatures reached 10°C by the middle of June and a maximum of 14°C in July. Total pelagic primary production in 1979 was approximately 20 gC m^{-2}yr^{-1} (Kjellberg and Sandlund 1983).

A total of 20 crustacean zooplankton species occur in the pelagic zone in Mjøsa; 8 are copepods and 12 are cladocerans. The most common are the copepods *Limnocalanus macrurus* Sars, *Eudiaptomus gracilis* Sars, *Cyclops lacustris* Sars, and the cladocerans *Daphnia galeata* Sars, *D. cristata* Sars and *Bosmina longispina* Leydig.

Zoobenthos is dominated by chironomid larvae, oligochaetes, bivalves, and the amphipods *Pallasea quadrispinosa* Sars and *Gammaracanthus loricatus* Sabine (Holtan et al. 1980). *Mysis relicta* Lovén occurs in both epibenthic and pelagic habitats (Kjellberg and Sandlund 1983). Among zoobenthos eaten by epibenthic whitefish, chironomid larvae and pupae, and *P. quadrispinosa* are the most important.

Mjøsa supports 20 fish species, with vendace, whitefish and smelt *Osmerus eperlanus* (L.) being numerically dominant in the pelagic zone (Sandlund et al. 1985) (Table 1). In shallow water, roach Rutilus rutilus L., perch Perca fluviatilis L., and ruffe Acerina cernua (L.) are most numerous. The main predators are brown trout Salmo trutta L., burbot Lota lota L. and pike Esox lucius L.

Vendace and whitefish grow at about the same rate during the first two years of life, reaching 11 - 12 cm at age 1 and 18 - 20 cm at age 2. The growth rate of vendace levels off earlier than for whitefish; asymptotic lengths and Brody's coefficient of the von Bertalanffy's growth equations were respectively 22.7 cm and 1.03 for vendace and 31.0 cm and 0.52 for whitefish. The growth rate of males and females did not differ significantly ($P>0.05$).

Sampling

Zooplankton (February - December 1979), benthic insects and molluscs (May - November 1979), and fish (October 1978 - February 1980) were sampled at two localities in Mjøsa, Brøttum and Furnes. In both areas, maximum depth is around 90 m.

Zooplankton were sampled with a 25 l Schindler trap at the following depths: 0.5, 2, 5, 8, 10, 12, 16, 20, 30, and 50 m, and subsequently identified and counted in an inverted microscope.

Benthic invertebrates were sampled with an Ekman grab in the following depths: 2, 4, 6, 8, 12, 20, and 50 m. 5 parallel profiles were taken in both sampling areas.

Fish were sampled by using epibenthic and pelagic gill nets. The gill nets consisted of 12 panels (panel size, epibenthic: 25 x 2 m; pelagic: 25 x 6 m) with varying mesh sizes (8-52 mm bar mesh, mesh increments 2 - 7 mm). The pelagic nets were placed at the following depths: 0-10, 10-30, 30-50, and 50-80 m. The benthic nets were set from the shoreline down to the deepest part of the sampling area (90 m). The exact depth of each net was registered with an echo sounder (Simrad EL). Catch per unit effort (CPUE) was calculated as number of fish pr 100 m^2 net area for 24 hours fishing. A total of 1172 vendace and 1161 whitefish were caught. Very few whitefish and vendace were caught deeper than 50 m in the pelagic zone.

Treatment of material

Fish were measured to the nearest 0.1 cm (natural tip length) and aged by burning and breaking the otoliths (Christensen 1964).

Stomach contents were analyzed, and prey categories identified and counted under a stereoscopic microscope. Wet weight of stomach contents was estimated from undigested food items. The degree of diet overlap was calculated according to Schoener's (1968) similarity index $D=1-1/2\sum_{i=1}^{n}|p_i-q_i|)$, where p_i is weight proportion of food item i in population 1, q_i is weight proportion of food item i in population 2, and n the number of food categories. D varies between 0 and 1, representing no and complete food overlap, respectively. Degree of habitat overlap in the pelagic zone was calculated using Schoener's (1968) index, letting p_i and q_i represent percent of vendace and whitefish at the ith depth zone relative to the respective depth distributions of the species.

Zooplankton selection was estimated according to Ivlev's (1961) electivity index: $E = (a-b)/(a+b)$, where a is the frequency by number of the prey organism in the stomach and b is the frequency by number of the prey organism in the environment.

Results

Zooplankton

The zooplankton community was dominated by Limnocalanus macrurus (spring), and Eudiaptomus gracilis, Bosmina longispina, Daphnia galeata, Daphnia cristata (summer and early autumn) (Fig. 1). Densities of zooplankton were generally higher at Furnes than at Brøttum. At Furnes, maximum biomass of crustacean zooplankton occurred in August (6,400 mg m^{-2}), and at Brøttum in July (2,400 mg m^{-2}). At Furnes, maximum densities of adult D. galeata was recorded in August (7,780 ind. m^{-3}) and September (5,100 ind. m^{-3}). At Brøttum, densities of D. galeata were lower, with largest numbers of adults in July (1,040 ind. m^{-3}) and August (940 ind. m^{-3}). At Furnes, B. longispina occurred in maximum densities in July (1,320 ind. m^{-3}), August (2,880 ind. m^{-3}), and September (1,360 ind. m^{-3}). Densities of B. longispina at Brøttum were higher, with maximum numbers in July (3,220 ind. m^{-3}), August (2,240 ind. m^{-3}), and September (1,010 ind. m^{-3}).

Vendace and whitefish

Habitat

Gillnet catches of vendace were low in winter, spring and early summer (November - July) (Fig. 2A). In epibenthic habitat catch per unit effort (CPUE) of vendace remained low through the rest of the year, except for a slight increase in October at Brøttum, situated near the spawning grounds. CPUE in the pelagic habitat, however, were high in late summer and autumn (August - October) (Fig. 2A). In June - July, pelagic vendace were mainly caught at depths between 0-10 m, but from August through November they were also abundant at depths between 10 and 30 m.

Whitefish were caught in both benthic and pelagic habitats (Fig. 2B). In the epibenthic habitat mean CPUE of whitefish varied between 0.80 and 1.54. The pelagic catches of whitefish were very low during winter, spring and early summer, but increased during late summer and autumn. In both sampling areas, Brøttum and Furnes, a part of the whitefish population started to migrate into the pelagic habitat in July, whereas maximum pelagic catches were taken in September (Fig. 2B). In November most of the whitefish had returned to the epibenthic habitat. Pelagic densities of whitefish were highest at depths between 0 and 30 m.

Diet

In the pelagic zone, the diet of vendace and whitefish differed between the sampling areas (Fig. 3). At Furnes vendace fed largely on the zooplankton species B. longispina, D. galeata and L. macrurus. At Brøttum vendace fed on the same food items, but the relative proportions were different. D. galeata was less important, whereas L. macrurus was more important as a food source (Mann-Whitney Tests, P<0.05). In addition vendace at Brøttum also fed on Leptodora kindti (Focke) and fish (age-0 smelt).

Whitefish fed largely on zooplankton in the pelagic zone (Fig. 3). At Furnes the most important zooplankters eaten were L. kindti and D. galeata. In addition they fed on surface arthropods and fish (age-0 smelt). At Brøttum whitefish fed on the same food items, but in addition cyclopoid copepods were a more important food source. Whitefish caught in the pelagic zone appeared to stay in that zone for some time as the frequency of bottom animals in their stomachs was very low. A small fraction of the amphipod P. quadrispinosa, however, indicated some exchange of fish between epibenthic and pelagic areas.

Vendace and whitefish differed in their selection of L. macrurus (Fig. 4). This species was positively selected by vendace during spring and late summer and autumn, but never selected by whitefish. Both vendace and whitefish selected B. longispina and D. galeata during summer and autumn, respectively. The large cladocerans L. kindti and Bythotrephes longimanus Leydig were also positively selected for shorter periods during summer. All other zooplankters were negatively selected.

Correlations in habitat and diet

The pelagic catches (CPUE) of vendace were more highly correlated with epilimnic water temperature (0-16 m) than with abundance of pelagic food, expressed as total number of crustacean zooplankton in 0-50 m depth (Temperature: r^2=0.457, P=0.004; Zooplankton no.: r^2=0.337, P=0.018) (Fig. 5A). On the other hand, the pelagic catches (CPUE) of whitefish showed higher correlation with number of crustacean zooplankton than with the epilimnic water temperature (Temperature: r^2= 0.503, P=0.002 Zooplankton no.: r^2=0.609, P=0.0004) (Fig. 5B). Water temperature and total number of crustacean zooplankton, however, were intercorrelated (r^2=0.737, P=0.0001). The two regressions ($CPUE_{whitefish}$ on zooplankton abundace; $CPUE_{vendace}$ on epilimnic water temperature) were not improved by adding water temperature and zooplankton, respectively, as a second independent variable.

Figure 5B gives the regression of pelagic catch of whitefish over total number of crustacean zooplankton. Points above the regression line represents months where CPUEs were higher than expected from the number of zooplankton, and points below represents months when the catch is lower. It can be noted that the points are below the line in June and July when the abundance of zooplankton is increasing, and above the line in September and October after the abundance has passed its maximum and is decreasing. Ln-transformed curves fitted for cladocerans and copepods separately gave r^2 equal to 0.568 and 0.458 (P<0.01), respectively. The pelagic catch also increased with the biomass of crustacean zooplankton (0-50 m), but the fit was not as good as for total numbers (r^2=0.477, P<0.01).

Neither the pelagic nor the benthic catches of whitefish were significantly (P>0.05) correlated with the abundance or wet weight of insects and molluscs in the benthic habitat (Table 2).

In most sampling periods there was a high vertical habitat overlap between whitefish and crustacean zooplankton, and vendace and crustacean zooplankton in the pelagic habitat (Table 3). In periods with more than 15 fish caught, the Schoener's (1968) index D was lower than 0.5 for whitefish in August at Brøttum, and for vendace in May at Furnes and during the spawning run in October and November at Brøttum. Including all periods with more than 10 fish caught of each fish species, there was no significant difference in the habitat overlap of the two fish species, whitefish and vendace, and crustacean zooplankton (Mann-Whitney U-test $P>0.05$).

The vertical habitat overlap (Schoener's (1968) index) between whitefish and vendace in the pelagic zone at Furnes was high ($D>0.6$) during June - September, and low during the rest of the sampling period ($D<0.3$) (Table 4). The index at Brøttum was high during July-October and in May, and low in June, August and November. The habitat overlap increased with increasing number of crustacean zooplankton per m^3 at 0-50 m depth ($r^2=0.494$, $P<0.01$; Fig. 5C), and with the biomass of zooplankton at 0-50 m depth, although this fit was somewhat lower ($r^2=0.462$, $P<0.01$).

Diet overlap (Schoener's (1968) index) between vendace and whitefish at Furnes was highest in September and lowest in July (Table 5). At Brøttum the diet overlap was highest in August and lowest in October. There was no significant correlation ($P>0.05$) between diet overlap and habitat overlap or diet overlap and the abundance of different categories of zooplankton.

Discussion

The increase in pelagic gill net catches of whitefish from May until September demonstrates a movement of fish from epibenthic to pelagic areas. This is also indicated by density estimates based on echo soundings which showed a density increase parallel to the pelagic net catch (Sandlund et al. MS submitted). The pelagic whitefish probably remain in the offshore areas for a considerable period of time, as few pelagic fish have remains of zoobenthos in their stomachs. Vendace, on the other hand, stayed in the pelagic zone throughout the year, and zoobenthos was never registered in the stomach contents.

The habitat switch of whitefish, from an epibenthic to a pelagic way of life, was positively correlated with zooplankton abundance. Therefore, the habitat shift of whitefish between the two habitats, is probably due to increased abundance of crustacean zooplankton. Furthermore, habitat overlap between whitefish and vendace within the pelagic zone was also correlated with zooplankton abundance. The diet overlap between the two fish species, however, was not correlated with zooplankton abundance. Both habitat switch and habitat overlap were more highly correlated with the number than the biomass of zooplankton. These results indicate that the fish respond to the numbers rather than the biomass of zooplankton.

In assessing the profitability of alternative feeding habitats, a process of learning is probably involved (Werner et al. 1983; Milinski 1984; Ehlinger 1990). Werner and Hall (1988), citing Ehlinger (1986), maintain that when bluegills Lepomis macrochirus Rafinesque were fed prey from one habitat and switched to prey from another habitat, they suffered nearly a 50% decrease in capture rates on the original prey type, as the new prey type was added to the diet. According to Werner and Hall (1988), learning and search image type phenomena prevented maximum efficiency on both prey types simultaneously.

If learning is involved in the habitat switch of whitefish in Mjøsa, a delay in fish movement relative to the increase in zooplankton abundance should be anticipated. This is supported by our results showing that in the period with increasing abundance of zooplankton, CPUE of pelagic whitefish was lower than expected. On the other hand, the CPUE was above the expected value in the period with decreasing abundance of zooplankton. The fish may need some time to experience that food availability has changed, and accommodate to the new situation. In bluegill, Werner et al. (1981) indicate that the timelag between increase in food abundance and habitat change is about one week. Such a learning mechanism has been described in a simple model called the Relative Payoff Sum (RPS) (Harley 1981; Regelmann 1984). Switching into feeding on zooplankton in the pelagic zone pays off for the first number of whitefish trying this option when zooplankton densities are high. When zooplankton densities decrease in autumn, whitefish perform an opposite migration back to the, by then, more profitable epibenthic zone.

An alternative explanation to the delay in habitat switch may be that it is influenced by zoobenthos abundance. We did not find any significant correlation between CPUE of benthic whitefish and the abundance of benthic insects and molluscs. A more detailed analysis of all benthos groups might reveal some correlations between benthic food supply and CPUE of benthic whitefish. We do not, however, have sufficient quantitative zoobenthos data to discuss this possibility.

Ehlinger (1990) found that bluegill sunfish select foraging habitats as a function of the difference in return rate between habitats, spending more time in a habitat when its return rate is relatively higher. Our results indicate that whitin a species the return rate may differ between different size groups. In Lake

Mjøsa medium sized whitefish (25 - 35 cm) move into the pelagic zone during summer and autumn, whereas smaller and larger fish remain in epibenthic areas. This may be explained by foraging theory, as the smaller fish stay in more sheltered, epibenthic habitat where predation probably is lower than in the unstructured pelagic zone (Crowder and Cooper 1982; Stephens and Krebs 1986). The large, mobile, epibenthic amphipod Pallasea quadrispinosa (8 - 18 mm in length) is a suitable food item for large whitefish (Næsje 1984, Sandlund et al. MS.). Feeding on this prey may be more profitable than zooplankton for large fish. There seems to be very little predation on large whitefish in the lake.

In Mjøsa, habitat, but not diet overlap between pelagic whitefish and vendace increased with increasing abundance of zooplankton. This might be an indication of exploitative competition, similar to what has been found in sunfishes (Werner and Hall 1977, 1979; Werner et al. 1977, 1981). Exploitative competition between two species occurs when one species reduce available food supply to a level making the habitat unprofitable for the other species (Werner and Hall 1976, 1977). In Mjøsa the more efficient zooplanktivore vendace may render the pelagic zone an unprofitable feeding habitat for whitefish, except in periods of maximum zooplankton density. Segregation by habitat rather than by diet seems to be the common means of resource partitioning among animal species (Schoener 1974; Werner et al. 1977; Schmitt and Coyer 1983). Interference competition, on the other hand, is not easily envisaged in the pelagic zone, as it often involves some aggressive behaviour, e.g. territoriality

(Miller 1967; Schutz and Northcote 1972; Schoener 1983; Hindar et al. 1988).

Whitefish and vendace feed to some extent on the same zooplankton species, and select the same sizes within the species (Sandlund et al. 1987). However, their diet overlap (Schoener's D) is never above 0.65. This is due to the fact that pelagic whitefish also utilize two other pelagic food sources which are abundant during summer: surface insects and age-0 smelts. Vendace, on the other hand, eat the copepods *Limnocalanus macrurus* and *Eudiaptomus gracilis* which are not utilized by whitefish. Copepods are generally considered difficult to catch for non-specialist zooplanktivores (Szlauer 1965; Drenner et al. 1978; Wright and O'Brien 1984). The difference in trophic morphology (cf. Nikolsky 1963) of the two species reflects the specialist vs. the generalist: vendace has a superterminal mouth and dense gillrakers, whereas whitefish has a subterminal mouth and sparse gillrakers (mean number of gillrakers: 47 and 30, respectively; Sandlund et al. 1987). Whitefish, being the more generalized feeder, perform a habitat shift in relation to the zooplankton abundance, whereas vendace, the more specialized zooplankton feeder, occupy pelagic waters throughout the year.

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References

Barnard, C.J., D.B.A. Thompson, and H. Stephens. 1982. Time budgets, feeding efficiency and flock dynamics in mixed species flocks of lapwings, golden plovers and gulls. Behavior 80: 44-69.

Charnov, E.L. 1976. Optimal foraging theory: the marginal value theorem. Theor. Pop. Biol. 9: 129-136.

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.

Crowder, L.B., and W.E. Cooper. 1982. Habitat structural complexity and the interaction between bluegills and their prey. Ecology 63: 1802-1813.

Dill, L.M. 1987. Animal decision making and its ecological consequences: the future of aquatic ecology. Can. J. Zool. 65: 803-811.

Drenner, R.W., J.R. Strickler, and W.J. O'Brien. 1978. Capture probability: the role of zooplankton escape in the selective feeding of planktivorous fish. J. Fish. Res. Board Can. 35: 1370 - 1373.

Ehlinger, T.J. 1986. Learning, sampling and the role of individual variability in the foraging behavior of bluegill sunfish (Lepomis macrochirus). Dissertation, Michigan State University, East Lansing, Michigan, USA.

Ehlinger, T.J. 1990. Habitat choice and phenotype-limited feeding efficiency in bluegill: individual differences and trophic polymorphism. Ecology 71: 886 - 896.

Hamrin, S.F., and L. Persson. 1986. Asymmetrical competition between age classes as a factor causing population oscillations in an obligate planktivorous fish species. Oikos 47: 223-232.

Harley, C.B. 1981. Learning the evolutionary stable strategy. J. Theor. Biol. 89: 611-633.

Hindar, K., B. Jonsson, J.H. Andrew, and T.G. Northcote. 1988. Resource utilization of sympatric and experimentally allopatric cutthroat trout and Dolly Varden charr. Oecologia (Berlin) 74: 481-491.

Holbrook, S.J., and R.J. Schmitt. 1988. The combined effects of predation risk and food reward on patch selection. Ecology 69: 125-134.

Holtan, H. 1979. The Lake Mjøsa story. Arch. Hydrobiol. Beih. Ergebn. Limnol. 13: 242-258.

Holtan, H., G. Kjellberg, and P. Brettum. 1980. Overvåking av Mjøsa. Fremdriftsrapport nr. 10. Undersøkelser i 1979. Norwegian Institute of Water Research, Report 0-79079, 212 p. (In Norwegian).

Ivlev, V.S. 1961. Experimental ecology of the feeding of fishes. Yale University Press, New Haven, Connecticut, USA. 302 p.

Kjellberg, G., and O.T. Sandlund. 1983. Næringsrelasjoner i Mjøsas pelagiske økosystem. Direktoratet for vilt og ferskvannsfisk, Mjøsundersøkelsen, Report 6, 61 p. (In Norwegian).

Krebs, J.R., and N.B. Davis. 1984. Behavioral ecology: an evolutionary approach. Blackwell Sci. Publ., Oxford.

Krebs, J.R., M. MacRoberts, and J.M. Cullen. 1972. Flocking and feeding in the great tit Parus major: an experimental study. Ibis 114: 507-530.

McNair, J.N. 1982. Optimal giving-up times and the marginal value theorem. Amer. Nat. 119: 511-529.

Milinski, M. 1984. Competitive resource sharing: an experimental test of a learning rule for ESSs. Anim. Behav. 32: 233-242.

Miller, R.S. 1967. Pattern and process in competition. Advances Ecol. Res. 4: 1-74.

Mittelbach, G.G. 1984. Predation and resource partitioning in two sunfishes (Centrarchidae). Ecology 65: 499-515.

Nikolsky, G.V. 1963. The ecology of fishes. Acad. Press, New York, NY.

Næsje, T.F. 1984. Sikens livshistorie og habitatutnyttelse i Furnesfjorden og Ringsakerfjorden, Mjøsa. Unpublished cand. real. thesis, University of Oslo, 82 pp. (In Norwegian).

Nilsson, N.-A. 1979. Food and habitat of the fish community of the offshore region of Lake Vänern, Sweden. Rep. Inst. Freshw. Res. Drottningholm 58: 126-139.

Pitcher, T.J., A.E. Magurran, and I. Winfield. 1982. Fish in larger shoals find food faster. Behav. Ecol. Sociobiol. 10: 149-151.

Regelmann, K. 1984. Competitive resource sharing: a simulation model. Anim. Behav. 32: 226-232.

Sandlund, O.T., T.F. Næsje, L. Klyve, and T. Lindem. 1985. The vertical distribution of fish species in Lake Mjøsa, Norway, as shown by gill-net catches and echo sounder. Rep. Inst. Freshwat. Res. Drottningholm 62: 136-149.

Sandlund, O.T., T.F. Næsje, and G. Kjellberg. 1987. The size selection og *Bosmina longispina* and *Daphnia galeata* by co-occuring cisco (*Coregonus albula*), whitefish (*C. lavaretus*) and smelt (*Osmerus eperlanus*). Arch. Hydrobiol. 110: 357-363.

Sandlund, O.T., T.F. Næsje, and B. Jonsson. Ontogenetic niche shifts in whitefish (*Coregonus lavaretus*). Submitted for publication.

Schmitt, R.J., and J.A. Coyer. 1983. Variation in surfperch diets between allopatry and sympatry: circumstantial evidence for competition. Oecologia (Berlin) 58: 402-410.

Schoener, T.W. 1968. The *Anolis* lizards of Bimini: resource partitioning in a complex fauna. Ecology 49: 704-726.

1974. Resource partitioning in ecological communities. Science 185: 27-39.

1983. Field experiments on interspecific competition. Amer. Nat. 122: 240-285.

Schutz, D.C., and T.G. Northcote. 1972. An experimental study of feeding behaviour and interaction of coastal cutthroat trout (*Salmo clarki clarki*) and Dolly Varden (*Salvelinus malma*). J. Fish. Res. Board Can. 29: 555-565.

Stephens, D.W., and J.R. Krebs. 1986. Foraging theory. Princeton Univ. Press., Princeton, NJ.

Sutherland, W.S. 1983. Aggregation and the "ideal free distribution". J. Anim. Ecol. 52: 821-828.

Svärdson, G. 1976. Interspecific population dominance in fish communities of Scandinavian lakes. Rep. Inst. Freshwat. Res. Drottningholm 55: 144-171.

Szlauer, L. 1965. The refuge ability of plankton animals before models of plankton eating animals. Pol. Arch. Hydrobiol. 13: 89-95.

Werner, E.E., J.F. Gilliam, D.J. Hall, and G.G. Mittelbach. 1983. An experimental test of the effects of predation risk on habitat use in fish. Ecology 64: 1540-1548.

Werner, E.E., and D.J. Hall. 1976. Niche shifts in sunfishes: experimental evidence and significance. Science 191: 404-406.

Werner, E.E., and D.J. Hall. 1977. Competition and habitat shift in two sunfishes (Centrarchidae). Ecology 58: 869-876.

1979. Foraging efficiency and habitat switching in competing sunfishes. Ecology 60: 256-264.

1988. Ontogenetic habitat shifts in bluegill: the foraging rate-predation risk trade-off. Ecology 69: 1352-1366.

Werner, E.E., D.J. Hall, D.R. Laughlin, D.J. Wagner, L.A. Wilsmann, and F.C. Funk. 1977. Habitat partitioning in a freshwater fish community. J. Fish. Res. Board Can. 34: 360 -370.

Werner, E.E., G.G. Mittelbach, and D.J. Hall. 1981. Foraging profitability and the role of experience in habitat use by the bluegill sunfish. Ecology 62: 116-125.

Wright, D.I., and W.J. O'Brien. 1984. The development and field test of the planktivorous feeding of white crappie (Pomoxis annularis). Ecol. Monogr. 54: 65-98.

Table 1. Catch per unit effort (CPUE) of the most important fish species in Lake Mjøsa, 1978-80 (after Sandlund et al. 1985).

SPECIES	CPUE PELAGIC NETS	CPUE BENTHIC NETS
Brown trout *Salmo trutta*	0.1	<< 0.1
Vendace *Coregonus albula*	0.9	0.1
Whitefish *Coregonus lavaretus*	0.4	1.4
Smelt *Osmerus eperlanus*	2.4	5.1
Roach *Rutilus rutulus*	<< 0.1	3.4
Perch *Perca fluviatilis*	<< 0.1	2.1
Ruffe *Acerina cernua*	<< 0.1	4.3
Pike *Esox lucius*	<< 0.1	<< 0.1
Burbot Lota lota	0.0	0.9

Table 2. Abundance and weight of benthic insects and molluscs in the sampling areas Furnes and Brøttum in Mjøsa, 1979. N = no. of animals m^{-2}, Ww = wet weight (g) of animals m^{-2}.

MONTH	FURNES		BRØTTUM	
	N	Ww	N	Ww
May	796.2	0.731	1.589	2.510
July	943.7	3.161	696.2	0.933
August	484.7	0.865	486.0	0.629
October	543.5	0.667	589.2	1.656
November	733.2	1.451	492.1	0.942

Table 3. Vertical habitat overlap between whitefish and zooplankton, and vendace and zooplankton (Schoener's (1968) index D) in the pelagic zone of the sampling areas Furnes and Brøttum in Mjøsa, May - November, 1979. Number of fish in brackets.

	MAY	JUN	JUL	AUG	SEP	OCT	NOV
FURNES							
Whitefish	0.521	0.651	0.710	0.715	0.683	0.788	0.253
	(3)	(2)	(11)	(58)	(119)	(83)	(12)
Vendace	0.184	0.893	0.704	0.667	0.679	0.508	0.551
	(17)	(76)	(34)	(289)	(132)	(89)	(48)
BRØTTUM							
Whitefish	0.216	0.250	0.954	0.418	0.788	0.769	0.577
	(14)	(3)	(15)	(59)	(72)	(11)	(7)
Vendace	0.073	0.670	0.834	0.799	0.908	0.490	0.298
	(2)	(8)	(5)	(57)	(127)	(213)	(45)

Table 4. Vertical habitat overlap (Schoener's (1968) index D) between vendace and whitefish in the pelagic zone of the sampling areas Furnes and Brøttum in Mjøsa, February-November, 1979.

	FEB	MAY	JUN	JUL	AUG	SEP	OCT	NOV
Furnes	0.000	0.202	0.658	0.994	0.952	0.958	0.295	0.133
Brøttum	-	0.857	0.117	0.833	0.297	0.880	0.603	0.298

Table 5. Diet overlap (Schoener's (1968) index D) between vendace and whitefish in the pelagic zone of the sampling areas Furnes and Brøttum in Mjøsa, July - October, 1979.

	JUL	AUG	SEP	OCT
Furnes	0.076	0.236	0.551	0.289
Brøttum	0.056	0.648	0.516	0.008

Legend to figures

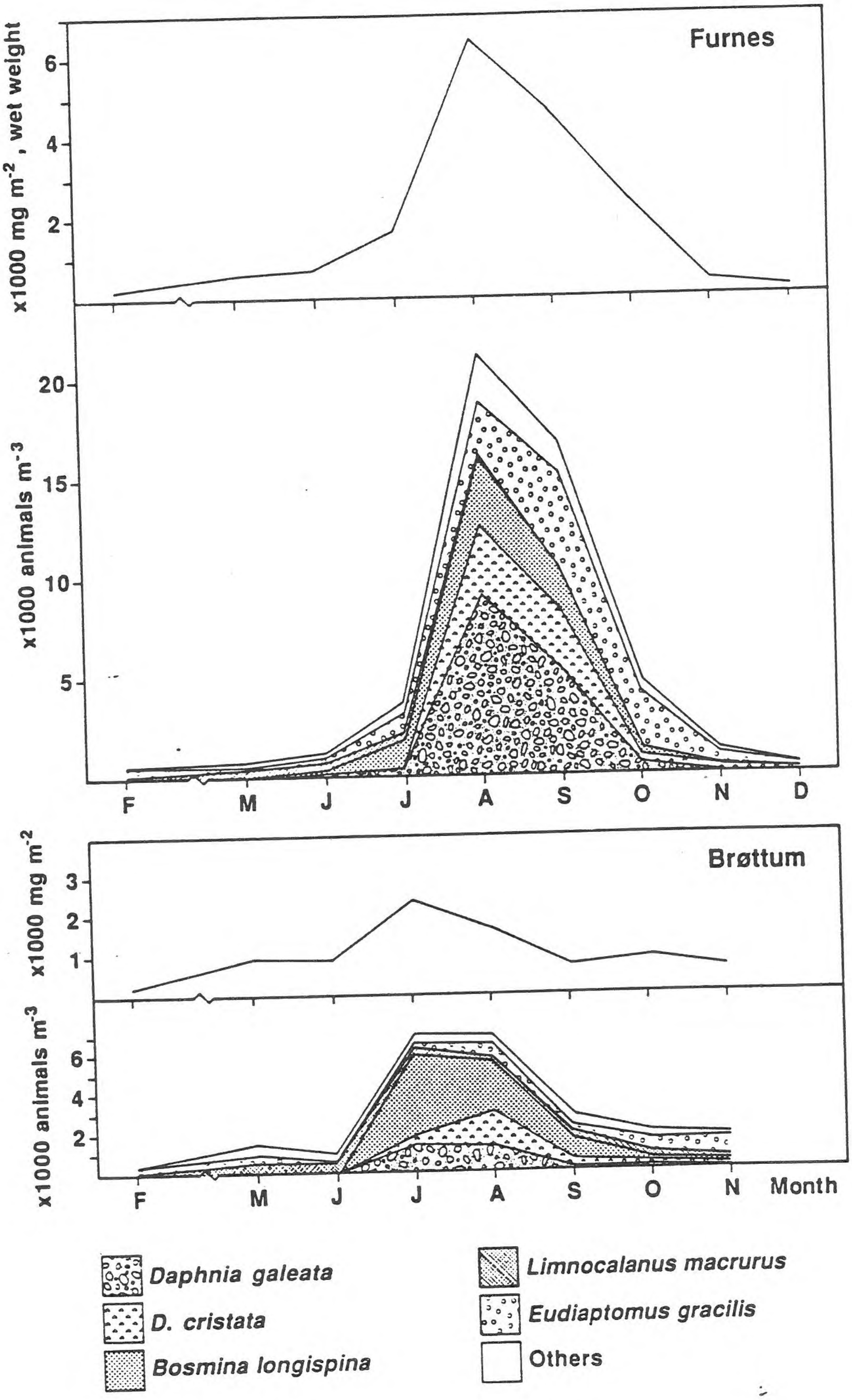
Fig. 1 Number of crustacean zooplankton per m^3 in the 0 - 50 m depth zone in the sampling areas Furnes and Brøttum in Mjøsa, February - December, 1979. Copepod nauplii and cladoceran embryos were omitted.

Fig. 2 Catch per unit effort (CPUE) of vendace (A) and whitefish (B) in pelagic and benthic gill nets, February - November 1979.

Fig. 3 Composition of stomach content (per cent wet weight) of pelagic vendace and whitefish in the sampling areas Furnes and Brøttum in Mjøsa, 1979.

Fig. 4 Ivlev's electivity index (E) for the selection of three crustacean zooplankton species by pelagic whitefish (squares) and vendace (circles) at Furnes, May-December 1979.

Fig. 5 A: Linear regression of ln ($\log_e$) catch per unit effort of vendace in pelagic gill nets (CPUE) on water temperature, 0-16 m depth. B: Linear regression of ln ($\log_e$) catch per unit effort of whitefish in pelagic gill nets (CPUE) on natural logaritm of number of crustacean zooplankton per m^3, 0 - 50 m depth (ln N, zooplankton). C: Linear regression of pelagic habitat overlap between vendace and whitefish (Schoener's (1968) D) on natural logaritm of number of crustacean zooplankton per m^3, 0 -50 m depth (ln N, zooplankton).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Eudiaptomus gracilis
Others

FiG. 1

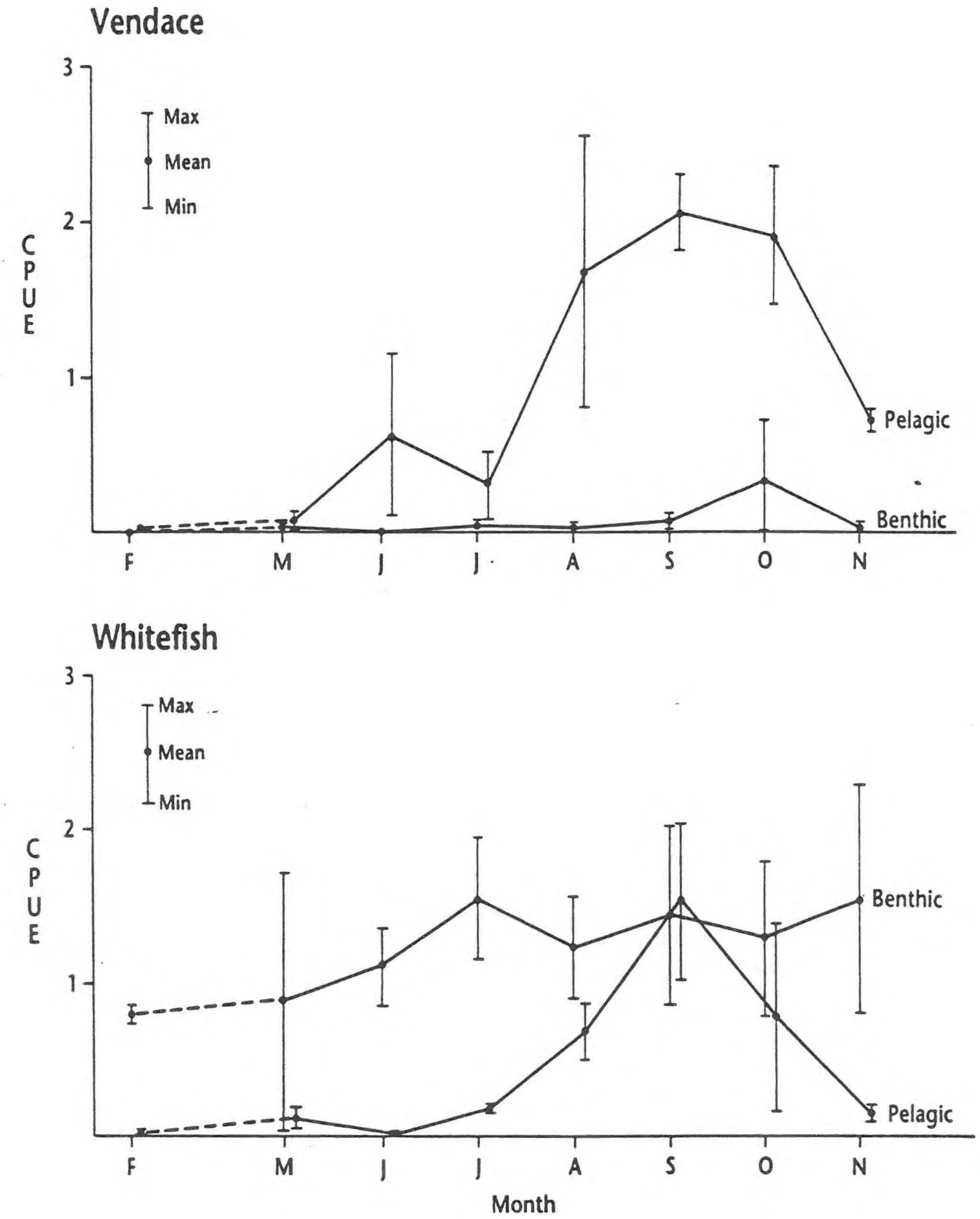
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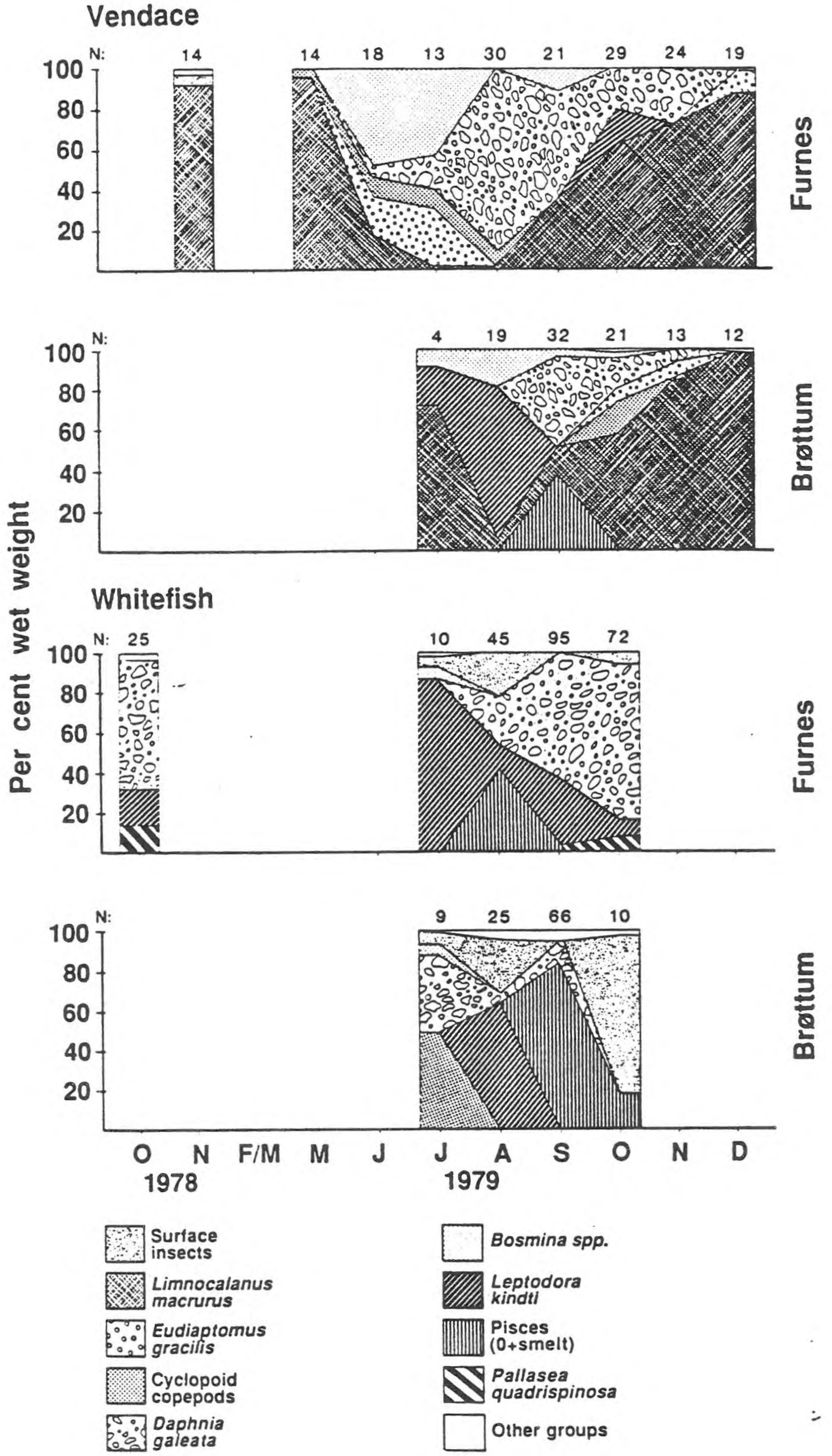
Fig. 2


Vendace
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Brøttum
Whitefish
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Furnes
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Brøttum
Per cent wet weight
100
80
60
40
20
O N F/M M J J A S O N D
1978
1979
Surface insects
Limnocalanus macrurus
Eudiaptomus gracilis
Cyclopoid copepods
Daphnia galeata
Bosmina spp.
Leptodora kindti
Pisces (0+smelt)
Pallasea quadrispinosa
Other groups

Fig. 3

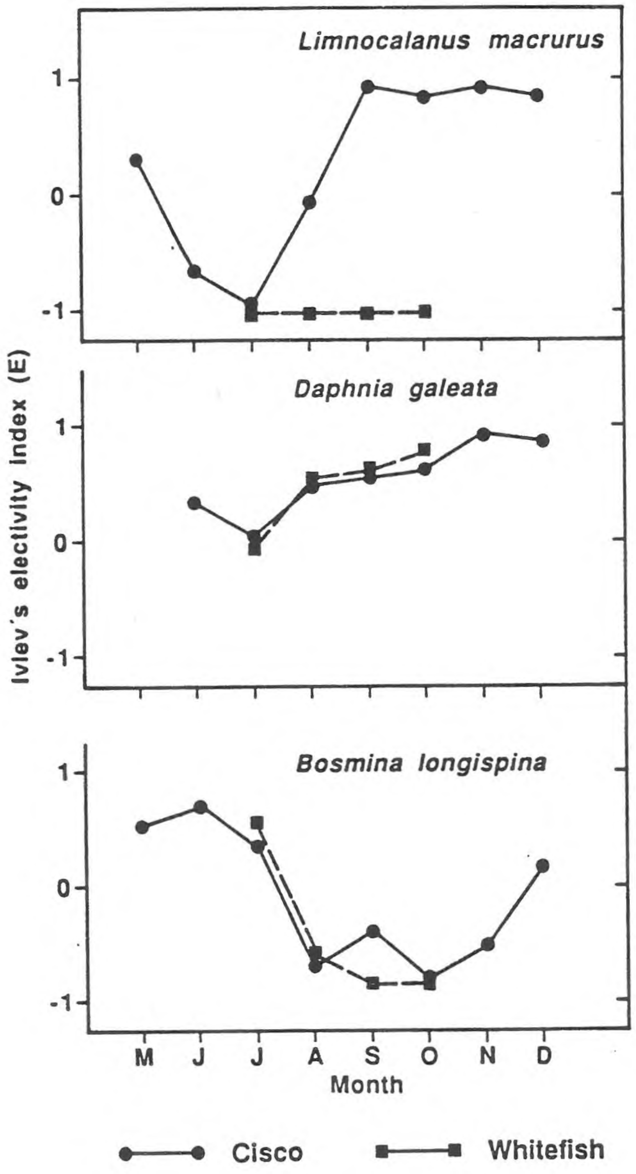
Limnocalanus macrurus
Daphnia galeata
Bosmina longispina
Ivlev's electivity index (E)
1
0
-1
M
J
J
A
S
O
N
D
Month
Cisco
Whitefish

Fig. 4

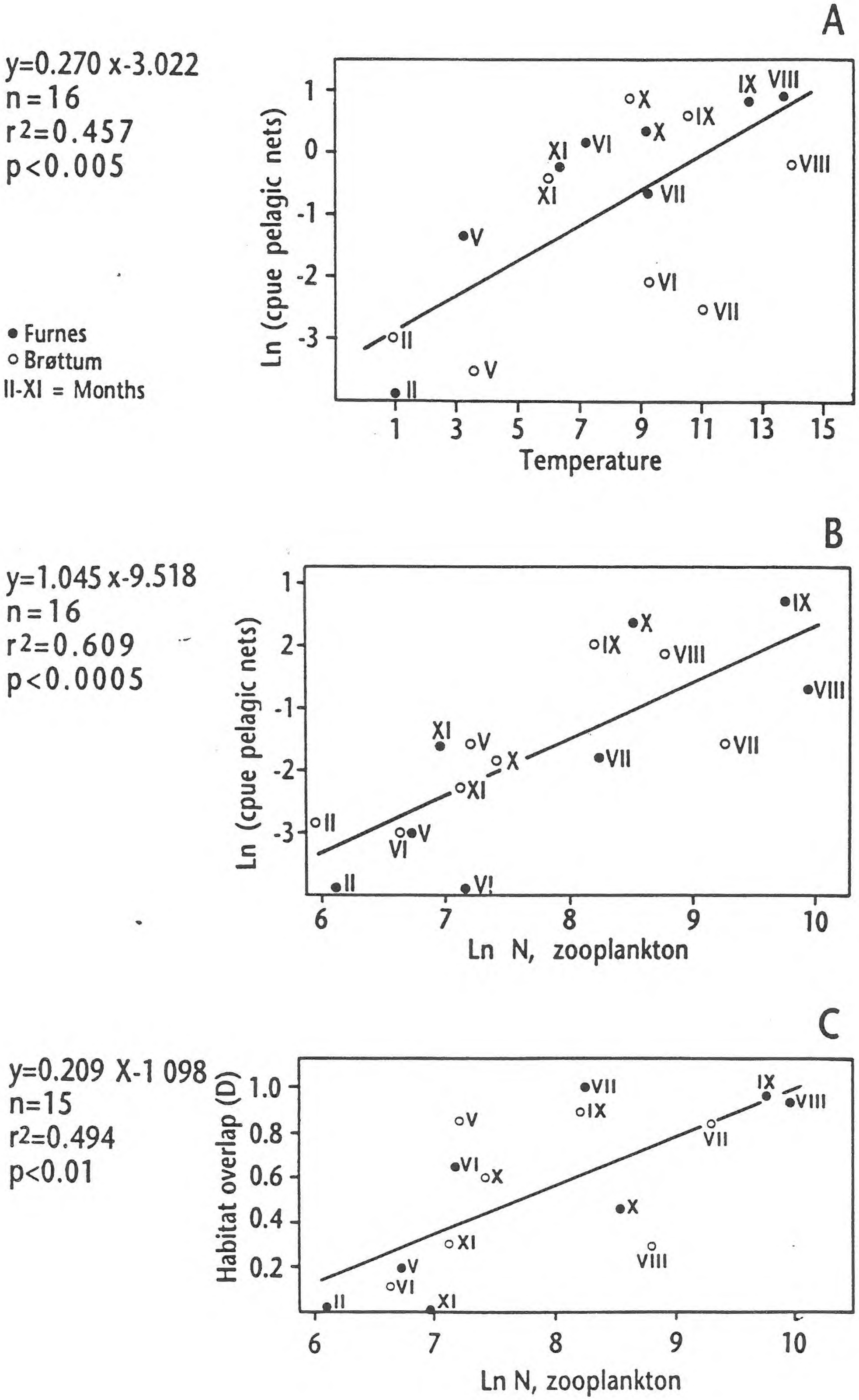A
y=0.270 x-3.022
n=16
r2=0.457
p<0.005
● Furnes
○ Brøttum
II-XI = Months
Ln (cpue pelagic nets)
1
0
-1
-2
-3
1
3
5
7
9
11
13
15
Temperature
II
V
VI
VII
VIII
IX
X
XI
B
y=1.045 x-9.518
n=16
r2=0.609
p<0.0005
Ln (cpue pelagic nets)
1
2
-1
-2
-3
6
7
8
9
10
Ln N, zooplankton
II
V
VI
VII
VIII
IX
X
XI
C
y=0.209 X-1 098
n=15
r2=0.494
p<0.01
Habitat overlap (D)
1.0
0.8
0.6
0.4
0.2
6
7
8
9
10
Ln N, zooplankton
II
V
VI
VII
VIII
IX
X
XI

Fig. 5

Paper V

Arch. Hydrobiol. | 110 | 3 | 357 – 363 | Stuttgart, September 1987

The size selection of *Bosmina longispina* and *Daphnia galeata* by co-occurring cisco (*Coregonus albula*), whitefish (*C. lavaretus*) and smelt (*Osmerus eperlanus*)

By ODD TERJE SANDLUND, TOR FREDRIK NAESJE and GÖSTA KJELLBERG

With 2 figures and 2 tables in the text

Abstract

There is no significant correlation between gillraker spacing and size selection of cladoceran zooplankton by whitefish, cisco and smelt. When co-occurring in the pelagic zone of Lake Mjøsa they showed positive size selection for both *Bosmina longispina* and *Daphnia galeata*. Whitefish had significantly larger gillraker spacing than cisco and smelt, but selected smaller individuals of *D. galeata*. *D. cristata* were abundant in the water, but it was not eaten by the fish. *D. cristata* was nearly of the same size as *D. galeata* and significantly larger than *B. longispina*. Both *Daphnia*-species were hyaline, whereas *B. longispina* was brown all over the carapax. The area of the eye spot of *D. cristata* was about one third of the eye spot of *D. galeata*. These results show that the feeding behaviour of the predator and the visual size of the prey are more important than gill raker spacing in the size selective feeding of planktivorous fish.

Introduction

The size distribution of zooplankton in lakes is influenced by the size-selective predation by planktivorous fish species (HRBACEK 1962, BROOKS & DODSON 1965, NILSSON & PEJLER 1973, LANGELAND 1978, KOHLER & NEY 1981). The short term objective of the predators will be to eat those prey categories which maximize energy intake relative to handling time (TOWNSEND & WINFIELD 1985). In the fish/cladoceran interaction handling time is fairly constant irrespective of prey species or size, given a sufficient fish size (WERNER & HALL 1974, TOWNSEND & WINFIELD 1985). We may therefore assume that the predator will have a net energy gain by selecting larger cladoceran prey. Fish strain the zooplankton away from the water taken into the buccal cavity by use of the gill rakers. One might therefore expect that the fish species with the smallest gill raker spacing are better at feeding on small zooplankton. However, the size selection by planktivorous fish also depend on the feeding behaviour of the fish (O'BRIEN 1979). Visual feeders like whitefish, smelt, and cisco (SEGHERS 1975, JANSSEN 1978, O'BRIEN 1979) seek their prey actively and select relatively large food items (O'BRIEN et al. 1976). In visual feeders, the apparent prey size may be more important than actual prey size (ZARET & KERFOOT 1975).

0003-9136/87/0110-0357 $ 1.75

Thus, we tested cladoceran zooplankton selection by three fish species, cisco (*Coregonus albula*), whitefish (*C. lavaretus*), and smelt (*Osmerus eperlanus*), feeding together in the pelagic zone of Lake Mjøsa, Norway.

Material and methods

Monthly from June through October 1979 20 adult whitefish (28—32 cm), smelt (12—15 cm) and cisco (21—25 cm) were randomly chosen from pelagic gillnet catches (mesh increment 8—52 mm) in Lake Mjøsa. All fish investigated were sampled from the same catches taken at depths between 0 and 30 cm. This is the depth zone with the highest density of fish in the Lake (Sandlund et al. 1985). Stomach contents were analyzed under a stereoscopic microscope, and the total length of undamaged *Daphnia galeata* and *Bosmina longispina* were measured by inverted microscope. Due to seasonal variations in the abundance of zooplankton, the number of undamaged *B. longispina* and *D. galeata* varied between 20 and 180. Mean number of each group was approx. 70 individuals. Zooplankton were sampled at the same time and location as the fish, using a 50 l Schindler trap at depths 0.5, 2, 5, 8, 12, 16, 20, 30 m (Holtan et al. 1980). Total body length and eye diameter of *Daphnia galeata, D. cristata* and *Bosmina longispina* were measured by inverted microscope. The number of zooplankton measurements is given in Table 2.

Distance between gillrakers were measured on the anterior left gill arch. Most of the straining of prey occur in the bend of the gill arches (Galbraith 1967). We therefore measured the space between the base of 15 gillrakers in the central part of the gillarch by use of a stereoscopic microscope (Table 1). The gillraker spacing does not give the exact "mesh size" of the gillraker sieve, but gives a relative measure of the filtering ability of the gillrakers (Seghers 1975, Wright et al. 1983).

Results

In June and October copepods were the most abundant zooplankton in the water masses (Fig. 1). In August and September the cladocerans *Daphnia galeata, D. cristata*, and *Bosmina longispina* were most abundant. During the period June—October, between 33 and 100 % of the cladoceran zooplankton was found in the upper 20 m of the water column.

In Lake Mjøsa cisco, whitefish and smelt feed largely on *Bosmina longispina* in June and July (Kjellberg & Sandlund 1983). This species represented up to approx. 14, 15, and 50 % wet weight of the stomach content of smelt,

Table 1. Mean number of gillrakers and distance between gillraker bases on the anterior left gill arch in whitefish, cisco and smelt from Lake Mjøsa. The differences between species are significant ($p < 0.01$).

	Smelt	Cisco	Whitefish
Mean no. of gillrakers	33.9	46.6	30.1
95 % confidence limits	0.4	1.0	0.1
Gillraker distance (μm)	308.0	436.5	680.0
95 % confidence limits	24.4	31.3	81.2

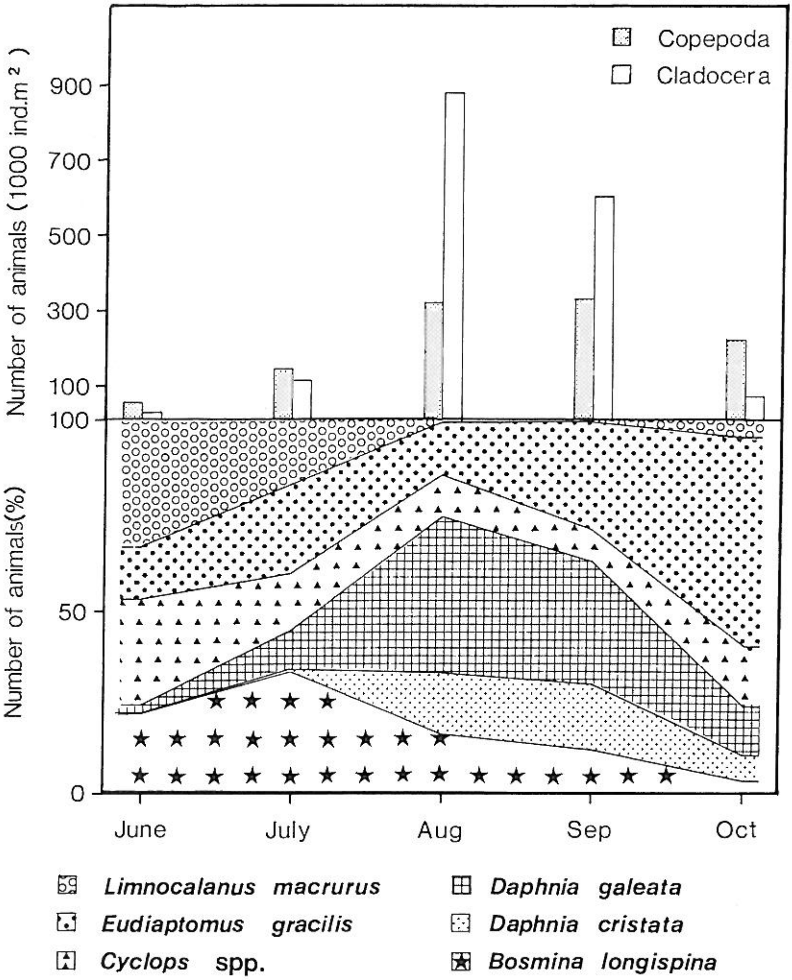

Fig. 1. Crustacean zooplankton abundance and composition in Lake Mjøsa, June—October 1979.

whitefish and cisco, respectively. In August, September, and October *Daphnia galeata* was the most important cladoceran in the stomachs, representing up to approx. 27, 68, and 93 % wet weight in smelt, whitefish and cisco, respectively (SANDLUND et al. 1980, 1981 a, b). In Lake Mjøsa the diet of cisco was dominated by *D. galeata, B. longispina* and *Limnocalanus macrurus*, the diet of whitefish by *D. galeata, B. longispina, Leptodora kindti*, and *Cyclops* spp., surface insects and smelt fry, and the diet of smelt by *D. galeata, B. longispina*, and *Mysis relicta. D. cristata* was not eaten by any of the three species (KJELLBERG & SANDLUND 1983).

Table 2. Body size and eye diameter (μm) of three most abundant cladoceran zooplankton in Lake Mjøsa. N = number of animals measured.

Species	Body length			Eye diameter		
	N	mean	95 % c.l.	N	mean	95 % c.l.
Daphnia galeata	484	965.2	18.6	20	105.2	6.2
D. cristata	50	925.7	39.6	50	61.6	2.7
Bosmina longispina	327	454.5	10.5	50	58.5	1.5

Average widths between the gillrakers differed significantly between the three fish species, it was smallest in smelt and largest in whitefish (t-tests, $p < 0.01$, Table 1).

Measurements of zooplankton from water samples showed that body length of *D. galeata* was more than twice that of *B. longispina*. *D. cristata* was only slightly smaller than *D. galeata* (Table 2). The size of the eye spot was approximately the same in *B. longispina* and *D. cristata*, whereas the area of the eye spot in *D. galeata* was nearly three times larger.

All three planktivorous species showed size-selective predation on *Bosmina longispina* and *Daphnia galeata* (Fig. 2). Throughout the sampling period the zooplankton in the fish stomachs were significantly larger than in the water masses (t-tests, $p < 0.05$).

In June and August smelt had eaten significantly larger *B. longispina* than cisco and whitefish ($p < 0.05$) (Fig. 2). In October whitefish had eaten significantly larger *B. longispina* than cisco and smelt.

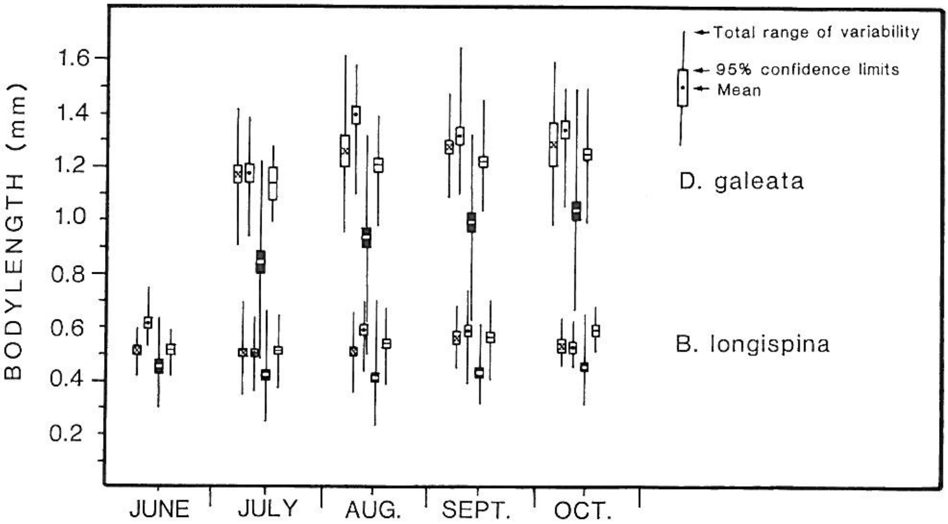

Fig. 2. Body size of *Daphnia galeata* and *Bosmina longispina* in water samples (dark) and in stomachs of cisco (x), smelt (.), and whitefish (-) from Lake Mjøsa, 1979.

Whitefish ate smaller individuals of *D. galeata* than cisco and smelt. Measurements of *D. galeata* from whitefish and smelt were significantly different in August, September, and October ($p < 0.05$), whereas the difference between whitefish and cisco were significant only in September ($p < 0.05$). There were no significant differences in the size of *D. galeata* eaten by smelt and cisco.

Discussion

As whitefish, cisco and smelt are visual predators, any differences between their zooplankton selection might be due to differences in their ability to detect prey, their feeding behaviour or feeding apparatus (O'Brien 1979). Mean gillraker spacing in smelt is approximately half of whitefish. In spite of this, whitefish eats significantly smaller individuals of *D. galeata* than smelt and cisco. Seghers (1975) found that whitefish eat *Daphnia* with smaller body size than the measured space between the gillrakers. He concluded that there must be a way to narrow the actual "mesh size" of the filtering apparatus. One way might be that the openings of the filtering apparatus is narrowed by diminishing the distance between the gill arches (Wankowski 1979). If the distance is small, the overlap between gill arches will make the actual openings of the filter sieve smaller than the gill raker spacing. The fish might be able to regulate the distance between the gill arches by regulating the water flow through the gill slits (Wright et al. 1983). By increasing the water velocity, either by increased pump action or increased swimming speed, the fish may widen the distance between the gill arches and thereby retain only the larger zooplankton in the buccal cavity.

The size difference between *B. longispina* (0.5—0.6 mm) and *D. galeata* (1.1—1.4 mm) eaten, probably reflects the difference in pigmentation between the two species. The visible size of *Daphnia* spp. is largely determined by the eye pigmentation, whereas *B. longispina* is brownishly coloured on the whole carapax (cf. Zaret 1972, 1978, Zaret & Kerfoot 1975). The important role of zooplankton pigmentation on fish predation is also demonstrated by the predation on *Daphnia cristata* in Lake Mjøsa. Although this species is rather large (0.8—1.0 mm) and abundant, it is eaten neither by whitefish, cisco nor smelt. This might be explained by the hyaline carapax and the small eyes of *D. cristata*, which are approximately one third of the size of the eyes of *D. galeata*.

We did not find any significant correlation between the size of zooplankton selected and the relative abundance of *Bosmina longispina* and *Daphnia galeata*. This contradicts the results of Ivlev (1961) and Werner & Hall (1974) who found that fish increase their prey selectivity at high prey densities. However, the reason for the strong positive selection of *B. longispina* and *D. galeata* could be that the zooplankton densities in Lake Mjøsa all through our investigations were at sufficiently high levels for strong zooplankton selectivity.

Our results clearly indicate that the visual size of the prey is of prime importance in selective feeding of cisco, whitefish and smelt. Concerning these species, it must also be concluded that the gillraker spacing of the predator is not the dominant factor in determining the size of cladoceran zooplankton eaten. This is in accordance with the findings of other investigators, e.g. SEGHERS (1975) and WRIGHT et al. (1983).

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We want to thank HELGE HAGEN, GERD JUSTÅS, LEIF KLYVE, and EINAR KULSVEHAGEN for helpful cooperation during field and laboratory work. BROR JONSSON, ARNFINN LANGELAND and PETUR M. JONASSON commented on drafts of this paper. We received economical support from the Directorate for Nature Management and the Norwegian Institute of Water Research.

References

BROOKS, J. L. & DODSON, S. I. (1965): Predation, body size and composition of zooplankton. — Science **150**: 28—35.

GALBRAITH, M. G. Jr. (1967): Size-selective predation on *Daphnia* by rainbow trout and yellow perch. — Trans. Amer. Fish. Soc. **96**: 1—10.

HOLTAN, H., KJELLBERG, G. & BRETTUM, P. (1980): Overvåking av Mjøsa. — Fremdriftsrapport nr. 10. Undersøkelser i 1979. — NIVA-Rapport 0-78012, 71 s.

HRBACEK, J. (1962): Species composition and amount of zooplankton in relation to the fish stock. — Rozpr. Cesk. Avad. Ved. **72**: 1—116.

IVLEV, V. S. (1961): Experimental ecology of the feeding of fishes. — Yale Univ. Press, New Haven.

JANSSEN, J. (1978): Feeding behaviour repertoire of the alewife, *Alosa pseudoharengus*, and the ciscoes, *Coregonus hoyi* and *C. artedii*. — J. Fish. Res. Board Can. **35**: 249—253.

KJELLBERG, G. & SANDLUND, O. T. (1983): Næringsrelasjoner i Mjøsas pelagiske økosystem. — DVF-Mjøsundersøkelsen. Rapport nr. 6, 61 s.

KOHLER, C. C. & NEY, J. J. (1981): Consequences of an alewife die-off to fish and zooplankton in a reservoir. — Trans. Amer. Fish. Soc. **110**: 360—369.

LANGELAND, A. (1978): Effect of fish (*Salvelinus alpinus*) predation on the zooplankton in ten Norwegian lakes. — Verh. Internat. Verein. Limnol. **20**: 2065—2069.

NILSSON, N.-A. & PEJLER, B. (1973): On the relation between fish fauna and zooplankton composition in north Swedish lakes. — Rep. Inst. Freshwat. Res. Drottningholm **53**: 51—77.

O'BRIEN, W. J. (1979): The predator-prey interaction of planktivorous fish and zooplankton. — Am. Scientist **67**: 572—581.

O'BRIEN, W. J., SLADE N. A. & VINYARD G. L. (1976): Apparent size as the determinant of prey selection by bluegill sunfish (*Lepomis macrochirus*). — Ecology **57**: 1304—1311.

SANDLUND, O. T., KLYVE, L., HAGEN, H. & NAESJE, T. F. (1980): Krøkla i Mjøsa. Alderssammensetning, vekst og ernæring. — DVF-Mjøsundersøkelsen. Rapport nr. **2**: 1—70.

SANDLUND, O. T., NAESJE, T. F., HAGEN, H. & KLYVE, L. (1981): Lagesilda i Mjøsa. Alderssammensetning, vekst og ernæring. — DVF-Mjøsundersøkelsen. Rapport nr. **3:** 1—58.

SANDLUND, O. T., NAESJE, T. F., KLYVE, L. & HAGEN, H. (1981): Siken i Mjøsa. Alderssammensetning, vekst og ernæring. — DVF-Mjøsundersøkelsen. Rapport nr. **5:** 1—54.

SANDLUND, O. T., NAESJE, T. F., KLYVE, L. & LINDEM, T. (1985): The vertical distribution of fish species in Lake Mjøsa, Norway, as shown by gill net catches and echo sounder. — Rep. Inst. Freshwat. Res. Drottningholm **62:** 136—149.

SEGHERS, B. H. (1975): Role of gillrakers in size-selective predation by lake whitefish, *Coregonus clupeaformis*, (MITCHILL). — Verh. Internat. Verein. Limnol. **19:** 2401—2405.

SVÄRDSON, G. (1976): Interspecific population dominance in fish communities of Scandinavian lakes. — Rep. Inst. Freshwat. Res. Drottningholm **55:** 144—171.

TOWNSEND, C. R. & WINFIELD, I. J. (1985): The application of optimal foraging theory to feeding behaviour in fish. — In: P. TYTLER & P. CALOW (eds.) Fish energetics: New perspectives, Croom Helm, London & Sydney, 349 pp.

WANKOWSKI, J. W. J. (1979): Morphological limitations, prey size selectivity, and growth response of juvenile atlantic salmon, *Salmo salar*. — J. Fish. Biol. **14:** 89—100.

WERNER, E. E. & HALL, D. J. (1974): Optimal foraging and the size selection of prey by the bluegill sunfish (*Lepomis macrochirus*). — Ecology **55:** 1042—1052.

WRIGHT, D. I., O'BRIEN, W. J. & LUECKE, C. (1983): A new estimate of zooplankton retention by gill rakers and its ecological significance. — Trans. Am Fish. Soc. **112:** 638—646.

ZARET, T. M. (1972): Predators, invisible prey and the nature of polymorphism in the Cladocera (class Crustacea). — Limnol. Oceanogr. **17:** 171—184.

— (1978): A predation model of zooplankton community structure. — Verh. Intern. Ver. Limnol. **20:** 2496—2500.

ZARET, M. & KERFOOT, W. C. (1975): Fish predation on *Bosmina longirostris*: Body size selection versus visibility selection. — Ecology **56:** 232—237.

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Paper VI

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Year-class fluctuations in vendace, *Coregonus albula* (Linnaeus): Who's got the upper hand in intraspecific competition?

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The vendace *Coregonus albula* (L.) populations in the lakes Mjøsa and Osensjøen exhibited fluctuating year-class strength. In Mjøsa, a strong year-class emerged every third year, except for the four year period between the strong year-classes 1969 and 1973. The difference between the strong and weak year-classes decreased from the 1960s, through the 1970s to the 1980s. The Mjøsa vendace matured sexually at age 2+, and more than ten sexually mature age-groups were present in the population. Growth ceased at maturation, and asymptotic length was 23·6 cm. In Osensjøen, one strong year-class (1969) dominated the population during the period 1976–1987. The Osensjøen vendace matured sexually at age 3, and more than 15 sexually mature age-groups were present in the population. Growth ceased at maturation, and asymptotic length was 28·4 cm. In both lakes, vendace fed on crustacean zooplankton in the epilimnion throughout summer and autumn. Our data indicate that regular year-class oscillations occur as a result of the juvenile survival being negatively correlated to the number of adults.

Key words: zooplanktivores; age structure; recruitment; fishing mortality; iteroparity.

I. INTRODUCTION

In size-structured populations inter-cohort competition is asymmetric, as the effects of large animals upon small are different from the effects of small animals upon large (Lawton & Hassell, 1981; Connell, 1983; Schoener, 1983). Inter-cohort competition is common among fishes (Mittelbach, 1981, 1983; Persson, 1985). Larger fish will have an advantage over smaller ones in terms of search and capture efficiency. Smaller fish will have an advantage over larger ones due to their smaller metabolic demands, and the ability to feed on small food particles not available to larger fish of the same species (Hamrin & Persson, 1986).

The commonly observed oscillations in stock size of many fish species are often believed to be governed by intraspecific mechanisms (Healey, 1980; Persson, 1985). If the balance between the foraging advantage of large individuals and the metabolic and sufficient-prey-size advantage of small individuals is strongly skewed in favour of one or the other, this may be one mechanism to explain these oscillations.

Based on inter-cohort competition, we have two alternative models explaining regular year-class fluctuations in fish populations.

THE JUVENILE DOMINANCE MODEL

Age-0 fish dominate over old fish, causing high adult mortality and low population fecundity due to a small spawning population and low quality of gonadal

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products (Cryer *et al.*, 1986; Hamrin & Persson, 1986; Wyatt, 1988). A strong year-class gives rise to a new strong year-class at its first spawning.

THE ADULT DOMINANCE MODEL

Older fish dominate over age-0 fish so that a large subadult and adult population causes high age-0 mortality (Aass, 1972; Amundsen, 1988).

From the juvenile dominance model we may deduce that the fish should be semelparous, and that the number of eggs spawned restricts recruitment to the population. Young and old fish depend on the same prey groups, and the old fish are at a disadvantage as the prey are too small to be utilized efficiently by adult fish. In years with abundant age-0 stocks, the older fish will grow less and experience higher mortality than in years with scarce age-0 stocks.

From the adult dominance model we may deduce that the adult fish deplete the food resources or in some other way suppress the activity of young fish (cf. Healey, 1980), so that a strong year-class emerges when the number of subadult and adult fish is substantially reduced. In this case the prey-sizes present are also available to adult fish, and size at growth cessation depends on abundance of prey relative to fish density. This model does not assume semelparity in the population, although regular oscillations will depend on large or simultaneous adult mortality. If the adult mortality is low, the regularity and amplitude in year-class oscillations will be reduced.

These two models of explanation can be evaluated by analysing the vendace *Coregonus albula* (L.) populations of the lakes Mjøsa and Osensjøen, Southeast Norway. In Mjøsa vendace, until the early 1970s, annual fishing mortality over all adult age-groups was estimated as *c.* 40% (Aass, 1967, 1978). In recent years, exploitation has declined in this lake. In Osensjøen, where vendace from Mjøsa were introduced in 1895, fishing for vendace is negligible.

II. MATERIALS AND METHODS

STUDY AREA

Lakes Mjøsa and Osensjøen are situated in southeastern Norway (Fig. 1), in the Glomma watercourse. Both are large, deep, oligotrophic lakes (Table I). In Mjøsa, water temperatures during the ice free season may reach 18° C in the epilimnion and 10° C in the hypolimnion during late summer (Kjellberg, 1986). Corresponding temperatures for Osensjøen are 16 and 7° C, respectively (Lien *et al.*, 1981).

Primary production in Mjøsa is 20 gC m^{-2} $year^{-1}$, which is approximately 2·5 times higher than in Osensjøen (Table I). This difference in productivity is also reflected in the crustacean zooplankton biomass (Table I). In both lakes the zooplankton biomass increases during summer and reaches its maximum in August–September (Fig. 2).

The fish fauna in Mjøsa includes 20 species (Sandlund *et al.*, 1985), of which whitefish, *Coregonus lavaretus* (L.), and smelt, *Osmerus eperlanus* (L.), co-occur with vendace in the pelagic zone (Sandlund *et al.*, 1987). Large brown trout, *Salmo trutta* L., (maximum size approximately 100 cm, 15 kg) and, occasionally, pike, *Esox lucius* L., are pelagic predators. Hydroacoustic estimates of the pelagic zooplanktivore fish stock (i.e. vendace, whitefish and smelt) in Mjøsa in autumn are 695 fish ha^{-1} (Lindem, 1978), corresponding to a biomass of approximately 26 kg ha^{-1} wet weight (Kjellberg & Sandlund, 1983). In 1979 the adult vendace population was estimated as $4 \cdot 10^6$ fish, corresponding to 9·3 kg ha^{-1} wet weight (Kjellberg & Sandlund, 1983).

In Osensjøen the fish fauna includes eight species (Sandlund, 1979), and vendace co-occur with whitefish in the pelagic zone. A few brown trout are also present in the pelagic zone,

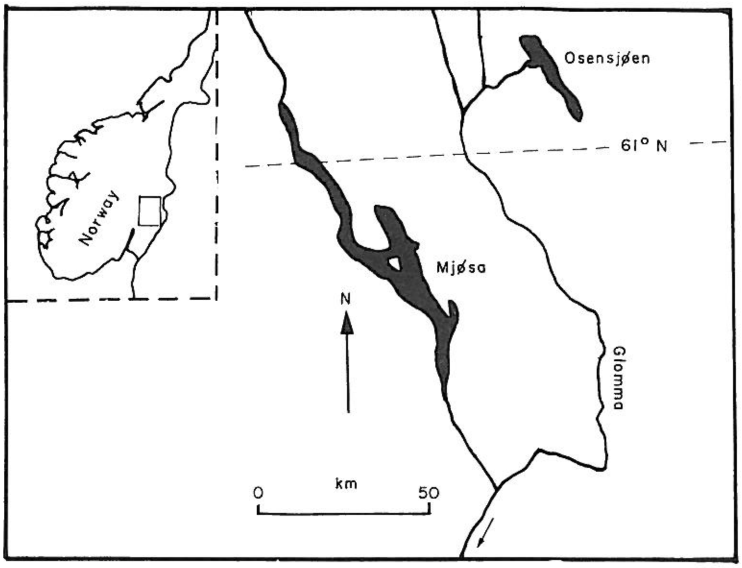

FIG. 1. Location of Lakes Mjøsa and Osensjøen.

TABLE I. Physical and chemical characteristics of Lakes Mjøsa and Osensjøen (Lien *et al.*, 1981; Kjellberg, 1986)

	Mjøsa	Osensjøen
Altitude (m a.s.l.)*	123	437
Surface area (km^2)*	362	45
Maximum depth (m)*	449	117
Mean depth (m)*	153	37
Regulation amplitude (m)	3·6	6·6
Secchi disc transparency (m)	2·5–8·0	3·4–6·4
Thermocline level (m)	12–20	8–15
pH	6·7–7·4	6·4–6·7
Conductivity (μS)	20–40	18–19
Total phosphorous ($\mu g\ P\ l^{-1}$)	8·6–9·0	3·2–5·0
Primary production ($g\ C\ yr^{-1}$)	20	8
Zooplankton biomass (g wet weight m^{-2})	30	9·8

*Measured at maximum regulated water level.

but they rarely reach a body length of 40 cm, and fish constitutes only a minor part of their diet (Sandlund & Næsje, 1983). The pelagic zooplanktivore fish stock in Osensjøen has been estimated as 64 fish ha^{-1}, corresponding to a biomass of approximately 4 kg ha^{-1} wet weight (Linløkken & Qvenild, 1986). Based on this, the ratios of pelagic fish biomass to crustacean zooplankton biomass in Mjøsa and Osensjøen were 0·09 and 0·04, respectively.

In Mjøsa, vendace spawn in the main inflowing river in the middle of October, and the newly-hatched larvae drift into the lake in April–May (Næsje *et al.*, 1986*a*). In Osensjøen spawning takes place at 5–20 m depth in the lake during the second half of October.

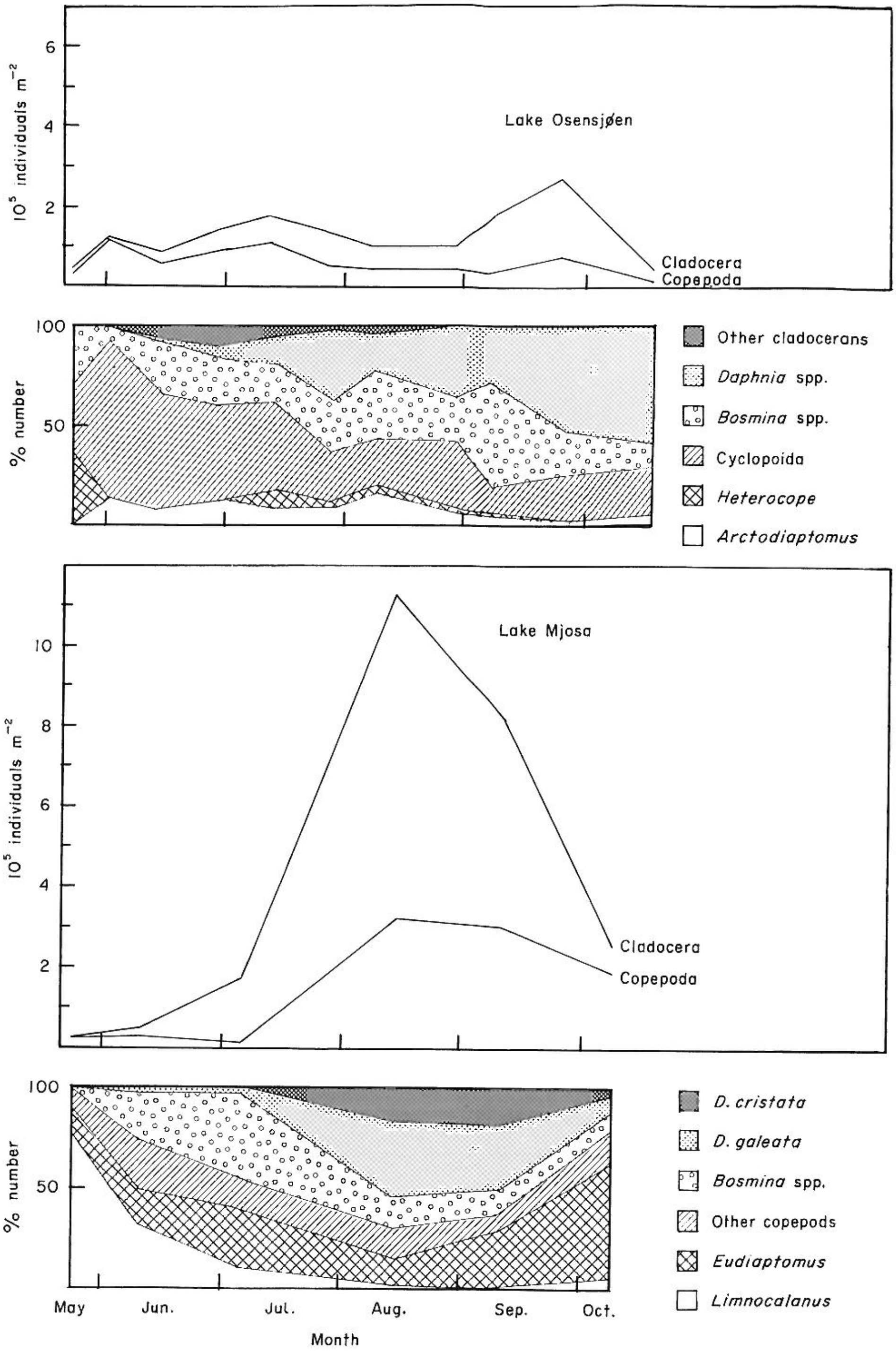

FIG. 2. Number of crustacean zooplankton per m^2 surface area (0–50 m depth), and per cent composition of zooplankton in Lake Mjøsa (year of sampling, 1979) and Lake Osensjøen (year of sampling, 1978). Copepod nauplii and cladoceran embryos have been omitted.

The vendace population in Mjøsa is subject to a commercial beach seine fishery, which exploits the sexually mature stock during its migration towards the spawning sites (Aass, 1972; Rugsveen, 1985). Therefore, fishing mortality is negligible in vendace until it is maturing sexually for the first time. In the period 1965–1975, the yield varied between 80 and 190 metric tonnes (mean ± S.D.: 136·4 ± 32·0 tonnes; 3·7 kg ha^{-1}) (Aass, 1978). Most fish were caught less than 10 km away from the mouth of the spawning river Gudbrandsdalslågen. Since then, fishing activity has decreased gradually, and by 1989 the 24 beach seine localities used in the 1960s had been reduced to seven localities. In 1987 total vendace yield was reduced to less than 1 kg ha^{-1} yr^{-1}, or 25–30% of the former catch (I. Løvseth, pers. commn.).

The exploitation of Osensjøen vendace is very small. According to interviews with local fishermen, annual catches amount to less than 500 kg (0·1 kg ha^{-1}).

SAMPLING

In Mjøsa, vendace were sampled with pelagic and epibenthic survey nets (bar mesh 8–52 mm) in 1978–1980, and with beach seine during their spawning migration in September 1978 and 1987. In Osensjøen, sampling was performed with survey nets in 1976–1978, and 1985, and with 25, 29, and 32 mm bar mesh nets on the spawning grounds in October 1976–1979, 1981–1985 and 1987. The survey net method is described in detail by Sandlund *et al.* (1985), and the beach seine by Rugsveen (1985).

TREATMENT OF MATERIAL

Altogether 1405 vendace from Mjøsa and 2563 vendace from Osensjøen were sampled. The following variables were studied: total length (0·1 cm), total wet weight (1 g), sex, degree of sexual maturity (Dahl, 1917), and otolith age by the burning and breaking method described by Christensen (1964). In coregonid populations with an almost complete growth cessation, ageing by scales seriously underestimates the age of the fish (Aass, 1972). For Mjøsa vendace, data on tagged and recaptured fish supported the conclusion that lateral reading of otoliths showed a correct age (Aass, 1972). Even lateral reading of otoliths may give too low ages in old fish, whereas the burning and breaking method appears to show the correct age, as shown in e.g. another coregonid, whitefish, *C. lavaretus* (L.), (Skurdal *et al.*, 1985), and in brook trout, *Salvelinus fontinalis* (Mitchill) (Reimers, 1979). Diet was studied by counting and measuring the various food items under a stereoscopic microscope, and the composition was calculated based on the weight of undigested food items.

Individual fecundity of females was estimated from gonads in fish just prior to spawning (maturity stage 5; Dahl, 1917).

III. RESULTS

YEAR-CLASS STRENGTH

Vendace in Mjøsa exhibited fluctuating year-class strength, but the pattern changed from 1969 to 1987. The data from 1969 (Fig. 3) demonstrate the regular fluctuations typical in the 1960s (Aass, 1972), with a strong year-class every third year. The data from 1978 and 1979, however, indicate that from 1969 to 1973 there were four years between the strong year-classes. During 1956 to 1970, the fluctuations were extreme, as very few fish emerged from intermediate year-classes (Aass, 1972). In 1978 and 1979, the difference in year-class abundance was less pronounced, although the dominant year-classes 1973 and 1976 constituted 50 and 10% of the catches, respectively. All intermediate year-classes were, however, represented in the catches. In 1987, the year-classes were even more equally distributed. The prevalent age-group 4 constituted 27%, and five year-classes constituted more than 10% of the catch. A similar age distribution was also indicated in a small sample from 1986.

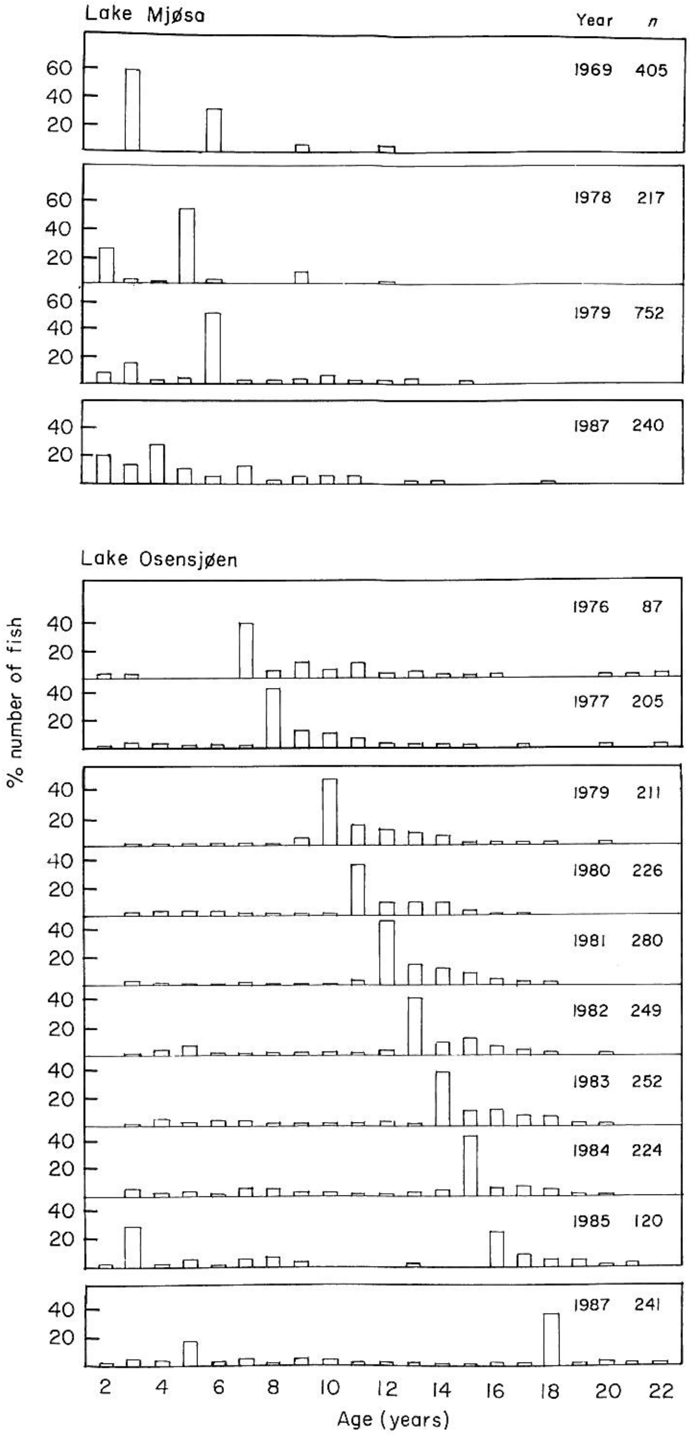

FIG. 3. Age distribution (per cent) in catches of sexually mature vendace from Lake Mjøsa, 1969 (redrawn from Aass (1972)), 1978–1979 and 1987; and Lake Osensjøen, 1976–1977, 1979–1985 and 1987. *n*, number of fish aged.

TABLE II. No. of fish (*n*) and per cent sexually mature fish (% M) in age-groups 1–4 and 1–5, in Mjøsa and Osensjøen, respectively. The fish were sampled prior to spawning (July–October)

Age group	Mjøsa				Osensjøen			
	Females		Males		Females		Males	
	n	% M	*n*	% M	*n*	% M	*n*	% M
1	46	2·2	47	0	0	0	5	0
2	28	71·4	32	96·9	25	36·0	22	40·9
3	73	100	52	96·2	46	45·7	33	60·6
4	2	100	2	100	28	89·3	22	100
5					12	100	14	100

The variability in year-class strength may be indicated by the coefficient of variation (CV) of the number of fish in one strong and subsequent two weak year-classes. Mean CV for the four sets of three year-classes in each of the years 1969, 1979, and 1987 (cf. Fig. 3) were 1·73, 1·44, and 0·92, respectively.

In Osensjøen the 1969 year-class was numerically dominant from 1976 through 1987 (Fig. 3), constituting between 24·5 and 47% of the catches. In 1985 and 1987 the proportion of young fish had increased compared to the earlier years, but no new year-class appeared to become as abundant as the 1969 cohort.

MATURITY AND GROWTH

Most vendace in Mjøsa attained sexual maturity at an age of 2+ (Table II), whereas the Osensjøen vendace matured significantly older and less synchronously ($Z^* = 13{\cdot}05$, 2 d.f., $P < 0{\cdot}005$; Siegel, 1956). Males matured significantly younger than females in Mjøsa ($Z^* = 11{\cdot}24$, 3 d.f., $P < 0{\cdot}005$), but not in Osensjøen ($Z^* = 7{\cdot}00$, 3 d.f., $P > 0{\cdot}05$). In both populations, sexual maturity and growth stagnation occurred simultaneously.

Both populations are iteroparous. In Mjøsa, there were three to four age-groups of juvenile fish and more than 10 age-groups of adult fish (Fig. 3). In Osensjøen, four to five age-groups were juveniles, and at least 15 age-groups were adults (Fig. 3). Mark–recapture experiments indicate that individual fish spawn every year (Aass, 1967).

In both lakes vendace ceased growing at early ages; in Mjøsa at age 3, and in Osensjøen at age 4 (Fig. 4). Vendace in Osensjøen grew larger than in Mjøsa (Fig. 4), and the size at each age differed for all ages higher than 1 (simultaneous *t*-tests, $P < 0{\cdot}005$). The growth cessation was less abrupt among vendace in Osensjøen than in Mjøsa, as indicated by the lower Brody's growth coefficient (K) (Fig. 4).

Back-calculated lengths of various year-classes demonstrated no systematic body length differences between strong and weak year-classes among Mjøsa vendace (Table III). After the first growth season body lengths of strong year-classes were not significantly different from subsequent weak year-classes (*t*-tests, $P > 0{\cdot}05$). Length at first maturity (age-2) was increasing over the year-classes 1969–1976, irrespective of year-class strength.

Individual fecundity ($F \pm$ S.D.) measured as number of eggs per female (mean length ± S.D.: $23{\cdot}7 \pm 0{\cdot}5$ cm, $n = 8$) in Mjøsa vendace was $7350{\cdot}4 \pm 1219{\cdot}5$. The

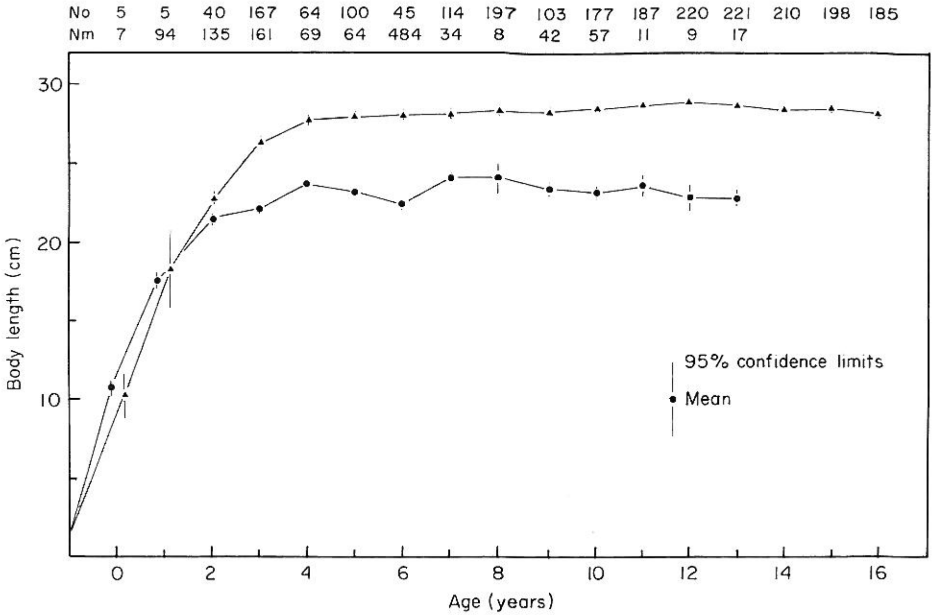

FIG. 4. Empirical growth curves of vendace from Lake Mjøsa (●) and Lake Osensjøen (▲). Number of fish: Nm and No, respectively. Asymptotic lengths (L_∞), and Brody's growth coefficients (K) of the von Bertalanffy growth equation: Mjøsa: $L_\infty = 236$ mm, $K = 0{\cdot}82$; Osensjøen: $L_\infty = 284$ mm, $K = 0{\cdot}60$.

TABLE III. Back-calculated lengths (cm) of vendace year-classes 1969–1978 after first (L0) and third (L2) growth season in Mjøsa

Year-class	*n*	L0	C.L.	L2	C.L.
1978	24	11·59	0·54	—	—
1977	32	12·24	0·44	—	—
1976	**24**	**13·14**	**1·03**	**20·80**	**0·33**
1975	2	11·45	—	20·50	—
1974	13	12·32	0·67	19·86	0·70
1973	**37**	**12·14**	**0·41**	**19·06**	**0·31**
1972	1	10·90	—	17·30	—
1971	—	—	—	—	—
1970	4	10·58	3·11	17·48	2·82
1969	**7**	**10·17**	**4·81**	**17·29**	**1·10**

Strong year-classes are given in bold type. *n* = Number of fish, C.L. = 95% confidence limits.

corresponding number in Osen vendace (mean length ± S.D.: 27·9 ± 0·8 cm, *n* = 26) was 11 890·2 ± 2893·3.

DIET AND FOOD PARTICLE SIZE

The feeding habitats of vendace in the two lakes were similar. Adult fish lived in the epilimnion throughout summer. In Mjøsa, age-0 vendace fed from emergence

TABLE IV. Mean size (L, mm) and maximum occurrence by number (max %) of dominating crustacean zooplankton in vendace stomachs from Lakes Mjøsa and Osensjøen, data from Sandlund (1979), Kjellberg & Sandlund (1983) and Sandlund *et al.* (1987)

Zooplankton species	Mjøsa		Osensjøen	
	L	Max %	L	Max %
Daphnia cristata	0·85	<5	1·11	20
D. galeata	1·25	88	—	—
D. galeata/longispina	—	—	2·13	21
Bosmina spp.	0·50	81	0·65	40
Holopedium gibberum	—	—	0·97	6
Heterocope appendiculata	—	—	2·08	17
Arctodiaptomus laticeps	—	—	1·48	74
Eudiaptomus gracilis	1·15	29	—	—
Cyclops scutifer	—	—	1·03	67
C. lacustris	1·12	29	—	—
Limnocalanus macrurus	1·78	90	—	—

in May until June–July in the littoral zone. Subsequently, they moved out into the pelagic zone eating the same crustacean zooplankton species as the adults (Næsje *et al.*, 1986*b*; Sandlund *et al.*, 1987). In Osensjøen, age-0 vendace were occasionally caught in 10 mm benthic nets, but not in pelagic nets, in autumn. In this lake, age-0 vendace have also been found in the stomach of littoral pike, indicating a littoral way of life.

Zooplankton was the dominating prey type from the time the vendace moved into the pelagic habitat (Sandlund, 1979; Kjellberg & Sandlund, 1983; Næsje *et al.*, 1986*b*). Although different species dominated the diet of vendace in the two lakes, the overall size variation of the main prey species was similar (Table IV). In Mjøsa the most important prey were *Bosmina longispina* Lilljeborg, *Daphnia galeata* Sars, and *Limnocalanus macrurus* Sars. In Osensjøen, *B. longispina, Arctodiaptomus laticeps* Sars and *Cyclops scutifer* Sars were the main prey.

IV. DISCUSSION

Our results indicate that the heavy exploitation of the Mjøsa vendace was instrumental in creating the regular oscillations in year-class abundance observed in the 1960s and 1970s. The difference between strong and weak year-classes has decreased concurrently with the reduced exploitation rate. The lack of regularity in year-class fluctuations in the unexploited Osensjøen vendace supports this conclusion. Thus, we maintain that in these vendace populations, older fish dominate over age-0 fish, and the adult dominance model is valid.

The juvenile dominance model is not valid because the fish are not semelparous, cohort fecundity is not limiting for year-class abundance, the fish may grow well on the available prey sizes, and age-0 and older fish live in separate habitats until July–August when zooplankton density is at its maximum. Before that, age-0 vendace live in the littoral zone. Consequently, the necessary conditions for the juvenile dominance model are not present.

The results may be generally valid, not only concerning the two lakes treated in the present paper. It has been assumed that vendace is a semelparous species (e.g. Svärdson, 1966). In many cases, this may be due to the inadequate methods used for age determination (Aass, 1972; Ricker, 1975). In most studies, scales have been used for age determination (e.g. Järvi, 1942*a,b*; Svärdson, 1966). As the growth of vendace ceases at sexual maturation, the scales stop growing. Therefore, ageing by the use of scales underestimates the age of adult vendace, as strongly indicated by Aass (1972) for the Mjøsa population when he compared length distributions with age distributions, according to otoliths and scales, respectively, in catches from six consecutive years. Reimers (1979) provided conclusive evidence for the correct ageing of brook trout up to 24 years from transverse sectioning of otoliths. When vendace have been aged by the use of otoliths, they have in many cases been found to be iteroparous (Aass, 1972; Hamrin, 1979; Vøllestad, 1983). The necessity of applying the proper ageing method to estimate correct age structure and degree of iteroparity have also been demonstrated in other fish populations with ceasing growth, e.g. whitefishes (*Coregonus* spp.) and charrs (*Salvelinus* spp.) (Power, 1978; Jonsson & Østli, 1979; Skurdal *et al.*, 1985).

The individual fecundity and the large number of year-classes present at each spawning in Mjøsa and Osensjøen vendace indicate that the number of spawned eggs is not limiting the recruitment to the populations. To maintain the population, a survival of two individuals from the repeated spawning of more than 7000 eggs would be adequate. In this situation, it does not appear reasonable to expect that the number of eggs spawned regulates the number surviving to maturity. The total number of vendace larvae drifting into Lake Mjøsa in the spring of 1986 and 1987 was estimated as $221 \cdot 10^6$ and $138 \cdot 10^6$ individuals, respectively (Hegge & Skurdal, 1987). This may be related to an estimated adult stock in 1979 of approximately $4 \cdot 10^6$ fish (Kjellberg & Sandlund, 1983).

According to the adult dominance model, the abundance of older fish limits recruitment because they deplete the common food resources. The importance of prey abundance for recruitment has been stressed for many other fish species. Prey abundance during the first days or weeks of external feeding appears to be particularly important (John & Hasler, 1956; Braum, 1978; Bogdanova, 1980; Frank & Leggett, 1982; Leggett, 1986).

The apparent competition for the same prey groups between age-0 and older fish, and the ontogenetic niche shift during the first summer may provide an explanation for an age-0 mortality which seems to be dependent mainly on the abundance of older conspecifics. After hatching in May, the larvae drift from the spawning river into the lake where they aggregate in the littoral zone and feed mainly on crustacean zooplankton (Næsje *et al.*, 1986*a,b*). Common predators in the littoral zone are perch, pike and ide, *Leuciscus idus* (L.) (Sandlund *et al.*, 1985). In May and early June, the littoral zone might be a profitable and sheltered habitat for coregonid larvae, as these predators are all spawning during this period. In addition, the density of similarly sized fish of other species is probably low until the offspring of the spring spawners reach this size. However, after the spring spawning period, predation pressure and interspecific competition might be expected to increase. Facing increased mortality in the littoral zone, the specialized pelagic zooplanktivore age-0 vendace may find the pelagic habitat more profitable, with only brown trout and the occasional pike as predators. The profitability of the pelagic habitat in early summer, however, depends both on the development of the crustacean zooplankton abundance, and on the abundance of older conspecifics already in this zone. Thus, we may postulate that there is a juvenile bottleneck (Neill, 1988; Persson & Greenberg, 1990) in the vendace stock, so that the survival of age-0 fish depends on the time of summer when the pelagic zone becomes a profitable alternative to the littoral zone.

Year-class strength variations in vendace have also been related to year to year variations in environmental conditions (e.g. Järvi, 1942*a*,*b*). This was excluded as a possible explanation for the regular fluctuations in Mjøsa vendace by Aass (1972). None of the available data on the environmental conditions in Osensjøen are able to explain the unusually strong 1969 year-class.

In conclusion we maintain that regular year-class oscillations occur in iteroparous size-structured populations. Prerequisites for this to occur are: (1) age-0, juveniles and adults depend on the same dietary resources; (2) age-0 survival depends on a bottleneck event, the severity of the bottleneck depends on the number of subadult and adult conspecifics; and (3) a selective high mortality occurs on the spawning stock, due to e.g. fisheries.

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References

Aass, P. (1967). *Fisheries Investigations in Mjøsa and Lågen 1966*. Vollebekk: Directorate of Wildlife and Freshwater Fish, Science Department (mimeo, in Norwegian).

Aass, P. (1972). Age determination and year-class fluctuations of cisco, *Coregonus albula* L., in the Mjøsa hydroelectric reservoir. *Report Institute of Freshwater Research, Drottningholm* **52,** 4–21.

Aass, P. (1978). The whitefish and cisco fisheries of Lake Mjøsa, Norway. *Fauna* **31,** 80–83. (In Norwegian, English summary.)

Amundsen, P. A. (1988). Effects of an intensive fishing programme on growth and parasite infection of stunted whitefish in Stuorajarvi, northern Norway. *Finnish Fisheries Research* **9,** 425–434.

Bogdanova, L. S. (1980). The development and feeding of the larvae of the lake Syamozero whitefish *Coregonus lavaretus pallasi* n. *exilis* under different temperature conditions and feeding regimes. *Journal of Ichthyology* **20,** 66–73.

Braum, E. (1978). Ecological aspects of the survival of fish eggs, embryos and larvae. In *Ecology of Freshwater Fish Production* (Gerking, S. D., ed.), pp. 102–131. Oxford: Blackwell Scientific Publications.

Connell, J. H. (1983). On the prevalence and relative importance of interspecific competition: evidence from field experiments. *American Naturalist* **122,** 661–696.

Christensen, J. M. (1964). Burning of otoliths, a technique for age determination of soles and other fish. *Journal du Conseil International pour l'Exploration de la Mer* **29,** 73–81.

Cryer, M., Peirson, G. & Townsend, C. R. (1986). Reciprocal interactions between roach, *Rutilus rutilus*, and zooplankton in a small lake: Prey dynamics and fish growth and recruitment. *Limnology and Oceanography* **31,** 1022–1038.

Dahl, K. (1917). *Trout and Trout Waters in Norway*. Centraltrykkeriet, Kristiania. (In Norwegian, English summary in *Salmon and Trout Magazine*, Nos 17 and 18, December 1918 and April 1919.)

Frank, K. T. & Leggett, W. C. (1982). Environmental regulation of growth rate, efficiency, and swimming performance in larval capelin (*Mallotus villosus*), and its application to the match–mismatch hypothesis. *Canadian Journal of Fisheries and Aquatic Sciences* **39,** 691–699.

Hamrin, S. (1979). *Population Dynamics, Vertical Distribution, and Diet in Vendace,* Coregonus albula *L., in South Swedish Lakes.* University of Lund: Institute of Limnology.

Hamrin, S. & Persson, L. (1986). Asymmetrical competition between age classes as a factor causing population oscillations in an obligate planktivorous fish species. *Oikos* **47,** 223–232.

Healey, M. C. (1980). Growth and recruitment in experimentally exploited lake whitefish (*Coregonus clupeaformis*) populations. *Canadian Journal of Fisheries and Aquatic Sciences* **37,** 255–267.

Hegge, O. & Skurdal, J. (1987). *Drift of Vendace and Whitefish alevins in Lågen.* Oppland County Environmental Department. Report No. 12/87. (In Norwegian.)

Järvi, T. H. (1942*a*). Die Bestände den kleinen Maräne (*Coregonus albula* L.) und ihre Schwankungen. 1. Pyhäjärvi (Südkarelien). *Acta Zoologica Fennica* **32,** 1–89.

Järvi, T. H. (1942*b*). Die Bestände den kleinen Maräne (*Coregonus albula* L.) und ihre Schwankungen. 2. Ober- und Mittel-Keitele. *Acta Zoologica Fennica* **33,** 1–145.

John, K. R. & Hasler, A. D. (1956). Observations on some factors affecting the hatching of eggs and survival of young shallow-water cisco, *Leucichthys artedii* LeSueur, in Lake Mendota, Wisconsin. *Limnology and Oceanography* **1,** 176–194.

Jonsson, B. & Østli, T. (1979). Demographic strategy in char compared with brown trout in Lake Løne, western Norway. *Report Institute of Freshwater Research, Drottningholm* **58,** 45–54.

Kjellberg, G. (1986). *Monitoring of Mjøsa. Summary, Trends and Comments 1976–85.* Norwegian Institute of Water Research. Report O-8000203 (241/86). (In Norwegian.)

Kjellberg, G. & Sandlund, O. T. (1983). Trophic relationships in the pelagic zone of Mjøsa. *Directorate of Wildlife and Freshwater Fish, The Mjøsa Project.* Report no. 6. (In Norwegian.)

Lawton, J. H. & Hassell, M. P. (1981). Asymmetrical competition in insects. *Nature, London* **289,** 793–795.

Leggett, W. C. (1986). The dependence of fish larvae survival on food and predator densities. In *The Role of Freshwater Outflow on Coastal Marine Ecosystems. NATO ASI Series* Vol G7 (Skreslet, S. ed.), pp. 117–127. Berlin: Springer-Verlag.

Lien, L., Bakketun, Å., Bendiksen, E., Halvorsen, R., Kjellberg, G., Lindstrøm, E.-A., Mjelde, M., Sandlund, O. T., Tjomsland, T. & Aanes, K. J. (1981). *Effects of the Hydropower Developments in Osensjøen and Søre Osa.* Norwegian Institute of Water Research. Report O-77084. (In Norwegian.)

Lindem, T. (1978). *Hydroacoustic Recordings of Fish in Mjøsa.* Report, Institute of Physics, University of Oslo. (In Norwegian.)

Linløkken, A. & Qvenild, T. (1986). *Hydroacoustic Recordings of Fish in Storsjøen (Rendalen), Osensjøen and Engeren, summer and fall 1985.* Hedmark County Environmental Department. Report No. 6. (In Norwegian.)

Mittelbach, G. G. (1981). Foraging efficiency and body size: a study of optimal diet and habitat use by bluegill. *Ecology* **62,** 1370–1386.

Mittelbach, G. G. (1983). Optimal foraging and growth in bluegills. *Oecologia (Berlin)* **59,** 157–162.

Næsje, T. F., Jonsson, B. & Sandlund, O. T. (1986*a*). Drift of cisco and whitefish larvae in a Norwegian river. *Transactions of the American Fisheries Society* **115,** 89–93.

Næsje, T. F., Sandlund, O. T. & Jonsson, B. (1986*b*). Habitat use and growth of age-0 whitefish, *Coregonus lavaretus*, and cisco, *C. albula. Environmental Biology of Fishes* **15,** 309–314.

Neill, W. E. (1988). Complex interactions in oligotrophic lake food webs: Responses to nutrient enrichment. In *Complex Interactions in Lake Communities. Workshop,* *Notre Dame, Indiana, U.S.A.* (Carpenter, S. R., ed.), pp. 31–44. New York: Springer-Verlag.

Persson, L. (1985). Asymmetrical competition: are larger animals competitively superior? *American Naturalist* **126,** 261–266.

Persson, L. & Greenberg, L. A. (1990). Juvenile competitive bottlenecks: The perch (*Perca fluviatilis*)—roach (*Rutilus rutilus*) interaction. *Ecology* **71,** 44–56.

Power, G. (1978). Fish population structure in Arctic lakes. *Journal of the Fisheries Research Board of Canada* **35,** 53–59.

Reimers, N. (1979). A history of a stunted brook trout population in an alpine lake: a life span of 24 years. *California Fish and Game* **65,** 196–215.

Ricker, W. E. (1975). Computation and interpretation of biological statistics of fish populations. *Bulletin of the Fisheries Research Board of Canada* **191,** 1–382.

Rugsveen, M. (1985). *The Vendace Fishery in Fåberg.* Norwegian Museum of Forestry, Hunting and Fishing, Elverum. Special publication no. 7. (In Norwegian, English summary.)

Sandlund, O. T. (1979). *Whitefish and Vendace in Osensjøen.* Fisheries Investigations in the Osen Area. Report no. 6. (In Norwegian.)

Sandlund, O. T. & Næsje, T. F. (1983). *Brown Trout in Osensjøen.* Fisheries Investigations in the Osen Area. Report no. 11. (In Norwegian.)

Sandlund, O. T., Næsje, T. F. & Kjellberg, G. (1987). The size selection of *Bosmina longispina* and *Daphnia galeata* by co-occurring cisco (*Coregonus albula*), whitefish (*C. lavaretus*) and smelt (*Osmerus eperlanus*). *Archiv für Hydrobiologie* **110,** 357–363.

Sandlund, O. T., Næsje, T. F., Klyve, L. & Lindem, T. (1985). The vertical distribution of fish species in Lake Mjøsa, Norway, as shown by gill net catches and echo sounder. *Report Institute of Freshwater Research, Drottningholm* **62,** 136–149.

Schoener, T. W. (1983). Field experiments on interspecific competition. *American Naturalist* **122,** 240–285.

Siegel, S. (1956). *Nonparametric Statistics for the Behavioral Sciences.* New York: McGraw-Hill.

Skurdal, J., Vøllestad, L. A. & Qvenild, T. (1985). Comparison of scales and otoliths for age determination of whitefish *Coregonus lavaretus. Fisheries Research* **3,** 237–243.

Svärdson, G. (1966). Growth and distribution of vendace. *Information. Institute of Freshwater Research, Drottningholm (4).* (In Swedish.)

Vøllestad, A. (1983). *The Fish Stocks in Bjørkelangen, Øgderen and Rødenessjøen.* Haldensvassdraget River Authority, Fisheries Investigations. Report no. 2. (In Norwegian.)

Wyatt, R. J. (1988). The cause of extreme year class variation in a population of roach, *Rutilus rutilus* L., from a eutrophic lake in southern England. *Journal of Fish Biology* **32,** 409–421.

Paper VII

Ecology of two vendace, *Coregonus albula*, populations separated in 1895

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Key words: Growth, Life history, Fecundity, Spawning ecology, Habitat, Diet.

Synopsis

The vendace stock 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, and spawning biology. The ages at maturity are 2+ and 3 - 4+, and asymptotic lengths are 234 mm and 289 mm in Mjøsa and Osensjøen, respectively. The Mjøsa stock spawns in an inlet river whereas the Osensjøen stock spawns at approximately 10 m depth in the lake. Peak spawning occur 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, Reznick and Bryga 1987). Within one or a few generations the new environment may result in adaptive changes in a number of population characteristics compared to the donor population. The short term changes are due to adaptations to a new and different environment. Among important environmental factors are food quality and abundance (Alm 1959), and presence or absence of competing fish species (Lindsey 1981). When a species is introduced into a locality with a lower number of competing species, the ecological niche of the new population is expected to be wider than the donor population (van Valen 1965).

Long term changes may involve changes in genotype (Vuorinen et al. 1990). 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 adapt 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, 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 (Svärdson 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 Svärdson (1979) and Lindsey (1981)). Relative to whitefish, ciscoes have rarely been transplanted into new lakes (Svärdson 1966, Viljanen 1986), and morphological and ecological changes following introduction has not been documented (Lindsey 1981). Vendace is considered to vary little in ecological and morphological characters among natural populations (Svärdson 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 Mjøsa population were transferred to 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 Osensjøen are descendants from the introduction in 1895.

Based on this, I wanted to investigate the possible differences in morphology, life history, habitat and diet of the vendace populations in Mjøsa and Osensjøen. The genetic divergence has been investigated by Vuorinen et al. (1990). 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

Mjøsa and Osensjøen are situated in the southeastern part of Norway (Fig. 1). Physical and chemical characteristics of the two lakes are given i Table 1, showing some potentially important differences. Due the difference in altitudes, the air temperature is lower in the area of Osensjøen than Mjøsa. Annual pelagic primary productivity is higher in Mjøsa than in Osensjøen. The epilimnic zone is smaller in Osensjøen, and due to the high humic content, Secchi disc transparency is also lower than in 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 Mjøsa are *Daphnia galeata*, *D. cristata*, *Bosmina longispina*, *Limnocalanus macrurus*, *Eudiaptomus gracilis* and *Cyclops lacustris* (Kjellberg 1986). In 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 Mjøsa is higher than in Osensjøen (Table 1).

Twenty species of fish occur in Mjøsa (Sandlund et al. 1985b). Of these whitefish, *Coregonus lavaretus*, and smelt, *Osmerus eperlanus*, are co-occurring with vendace in the pelagic zone. Brown trout, *Salmo trutta*, is a pelagic predator. In 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 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, due to water falls, no migration by lacustrine fishes like vendace have ever been possible between them.

In 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 Osensjøen, fishing for vendace is negligible, and the yield is less than 0.1 kg ha^{-1} yr^{-1}.

Sampling

In Mjøsa sampling was performed with pelagic and benthic gill nets of mesh size 8 - 52 mm during 1978-1980 (Sandlund et al. 1985b). In 1987, vendace was caught with a beach seine (mesh size 20 mm). In Osensjøen, sampling was performed with pelagic and benthic gill nets of mesh size 10 - 52 mm during 1976-1978 and 1985, and with benthic gill nets (mesh size 26 - 32 mm) on the spawning sites of vendace in 1977 - 1979, 1981 - 1985, and 1987. Altogether 1248 and 2623 vendace were analyzed from Mjøsa and Osensjøen, respectively.

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).

Van Bertallanfy growth parameters were calculated as described by Dickie (1978). Length/weight relationship was calculated by linear regression of $\log_e$-transformed (ln-) 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):

$$GSI = Wg/(Wt - Wg),$$

where Wg is the weight of gonads, and Wt is total body weight.

Results

Growth pattern and sexual maturation

The growth rates of juvenile vendace in Mjøsa and Osensjøen were similar (Fig. 3), and there were no significant difference in body lengths after the first and second growth season (t-tests, $p>0.05$). However, growth stagnation appeared one year later in the Osensjøen (at age 4 - 5) than in the Mjøsa stock (at age 3 - 4), resulting in asymptotic lengths: $L_\infty = 28.4$ cm, and $L_\infty = 23.6$ cm, respectively (Fig. 3, Table 2). As indicated by the higher Brody's growth coefficient (Table 2), growth stagnation was more abrupt in Mjøsa vendace.

In both sexes, the age at sexual maturity differed significantly between lakes ($Z^* = 37.65$, 2 d.f., $p<0.005$; and Z^*

= 23.54, 4 d.f., p<0.005; for males and females, respectively; Siegel 1956). In Mjøsa, nearly all males and 75% of the females were mature at age 2+ (Fig. 4). In 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.

The mean individual female fecundity was significantly higher (t=5.938, 27 d.f., p<0.001) in Osen than in Mjøsa vendace (Table 2). The gonadosomatic index was also significantly higher in Osen vendace (t=23.77, 27 d.f., p<0.001), but the mean number of eggs per gram mean body weight was lower in this stock than in Mjøsa vendace, indicating larger eggs in the Osen vendace.

Both populations were iteroparous (Sandlund et al. 1990). In Mjøsa more than 10 age groups, and in 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 Osensjøen vendace (t-tests, p<0.05), but the ratios between the various mensural head characters and body lengths were similar in the two stocks. 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 Osensjøen than in Mjøsa (t = 2.194, p<0.05). The relative variance (as measured by the coefficient of variation) was larger in the Osensjøen stock in all characters except upper jaw length (Table 3). There was also a difference in body colouration, as the Osensjøen population frequently exhibited red pectoral and pelvic fins. This was never observed in Mjøsa. The weight/length equations of the two populations show that the Osensjøen vendace has a lower weight/length ratio than the Mjøsa vendace (Table 4).

Habitat and diet

Spawning occured during late October in both lakes. However, the spawning habitat differed greatly between the populations. The Mjøsa population spawn in the main inlet river, whereas the Osensjøen population spawn in the lake at 10 - 20 m depth. In Mjøsa, the incubation period from peak spawning until hatching corresponds to approximately 165 degree-days (Næsje et al. 1986a). In Osensjøen, the actual date of hatching is not known, but it presumably occurs some time before or around ice-break. 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 April and May is approximately 3 °C. Thus, hatching approximately one month before ice-break would correspond to 575 degree-days from peak spawning.

In 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 Osensjøen a few age-0 fish were caught in benthic nets and none in pelagic nets, which may indicate a littoral habitat also in this lake. Catches of age-0 vendace in Osensjøen were, however, small.

In both lakes subadult and adult vendace utilized the upper 20 m of the pelagic zone. Gill net 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 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 Osensjøen were: *D. cristata* (1.11), *D. galeata/longispina* (2.13), *B. longispina* (0.65), *Arctodiaptomus laticeps* (1.48), *C. scutifer* (1.03), and *Heterocope appendiculata* (2.08) (Sandlund et al. 1987, 1990).

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. The prediction that the niche width in terms of habitat use and diet should increase in a fish community with fewer competitors, however, was not supported by the present study.

As a consequence of spawning in the lake where winter temperatures are higher than in the river, the population in Osensjøen experiences a higher energy supply (as measured by degree-days) during egg incubation than the river spawning population in Mjøsa. At the spawning site in 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. As the coregonid larvae are visual feeders, and probably need exogeneous food within a month after hatching (Braum 1978), it appears reasonable that hatching must occur close to ice-break. 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 Osen stocks. Investigations on the hatching of the river spawning Mjøsa population indicate that hatching is triggered by mechanical disturbances of the eggs caused by the start of the river spring spate (Næsje et al. 1986a, Næsje and Jonsson 1988), and the larvae drift into the lake soon after ice-break. 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 (Svärdson 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 Osensjøen than in the Mjøsa vendace. 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 an experiment with cutthroat trout (*Salmo clarki*) and Dolly Varden charr (*Salvelinus malma*), Jonsson et al. (1984) showed that high values of Brody's growth coefficient (K) and low values of t_0 decreased the optimal age at maturity. In Mjøsa and Osensjøen vendace, the values of K are equal, but the lower value of t_0 and the lower age at maturity in Mjøsa accord with the model of Jonsson et al. (1984). 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 Mjøsa is 6.5 times higher than that in Osensjøen, whereas the corresponding zooplankton biomass in Mjøsa is only 3.1 times higher. This gives ratios of fish biomass relative to crustacean zooplankton biomass at approximately 0.09 in Mjøsa and 0.04 in Osensjøen, indicating higher food availability for individual fish in Osensjøen.

The observed differences between the populations in mensural characters of the head were apparently due to differences in body length. Number of scales along the lateral line did not differ between populations, and although the mean gillraker count in Osensjøen vendace was somewhat lower than in 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.

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References cited

Aass, P. 1978. The whitefish and cisco fisheries in Lake Mjøsa, Norway. Fauna 31: 80 - 83. (In Norwegian, English summary).

Alm, G. 1959. Connection between maturity, size and age in fishes. Rep. Inst. Freswat. Res. Drottningholm 40: 5 - 145.

Bagenal, T.B. and F.W. Tesch 1978. Age and growth. pp. 101 - 130. In: T.B. Bagenal (ed.) Methods for assessment of fish production in fresh waters. Blackwell Scientific Publications, Oxford.

Braum, E. 1978. Ecological aspects of the survival of fish eggs, embryos and larvae. pp. 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 pp. (In Norwegian).

Dickie, L.M. 1978. Mathematical models of growth. pp. 130 - 136. In: T.B. Bagenal (ed.) Methods for assessment of fish production in fresh waters. Blackwell Scientific Publications, Oxford.

Huitfeldt-Kaas, H. 1923. Einwanderung und Verbreitung der Süsswasserfische in Norwegen mit einem Anhang über den Krebs. Arch. Hydrobiol. 14: 223 - 314.

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 0-8000203 (241/86), 80 pp. (In Norwegian).

Lien, L., Bakketun, Å., Bendiksen, E., Halvorsen, R., Kjellberg, G., Lindstrøm, E.-A., Mjelde, M., Sandlund, O.T., Tjomsland, T. and Aanes, K.J. 1981. Impact of hydroelectrical power developments in Osensjøen and Søre Osa. - Norwegian Institute of Water Research. Report 0-77084, 112 pp. (In Norwegian).

Lindem, T. 1978. Recordings of pelagic fish in Mjøsa by use of hydroacoustics. Institute of Physics, Univ. of Oslo. Mimeographed report, 19 pp. (In Norwegian).

Lindroth, A. 1957. A study of the whitefish (*Coregonus*) of the Sundsvall bay district. Rep. Inst. Freshwat. 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 Qvenild, T. 1986. Hydroacoustic recordings in Storsjøen (Rendalen), Osensjøen and Engeren, summer and autumn 1985. Hedmark County, Dept. of the Environment, Hamar. Report no. 6, 15 pp. (In Norwegian).

Løvik, J.E. and Kjellberg, G. 1982. The Glåma watercourse in Hedmark. Report on zooplankton 1978 - 80. Norwegian Institute of Water Research. Report No. 0-78045-III, 58 pp. (In Norwegian).

Luczynski, M. 1985. Survival of *Coregonus albula* (L.) (Teleostei) 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 barbatulus*. 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. Am. Fish. Soc. 155: 89 - 93.

Næsje, T.F., Sandlund, O.T. and Jonsson, B. 1986b. Habitat use and growth of age-0 whitefish, *Coregonus lavaretus*, and cisco, *C. albula*. Environ. Biol. Fish. 15: 309 - 314.

Nikolskii, G.V. 1969. Fish population dynamics. Oliver and Boyd, Edinburgh. 323 pp.

Nysæther, J.K. 1977. The fisheries in Osensjøen. pp. 249 - 267. In: T. Fossum (ed.) Yearbook, The Norwegian Museum of Forestry, Hunting and Fishing. No. 8, 1976 - 1977. Elverum, Norway (In Norwegian, 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. pp. 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 pp. (in Norwegian).

Sandlund, O.T., B. Jonsson, T.F. Næsje and P. Aass 1990. Year-class fluctuations in vendace (*Coregonus albula*): Who's got the upper hand in intraspecific competition? MS submitted for publication.

Sandlund, O.T., Klyve, L. and Næsje, T.F. 1985a. Growth, habitat and food of burbot *Lota lota* in Lake Mjøsa. Fauna 38: 37 - 43. (In Norwegian, English summary).

Sandlund, O.T. and Næsje, T.F. 1983. The brown trout in Osensjøen. Investigations in fish biology in the Osen area. Report no. 11, 23 pp. (in Norwegian).

Sandlund, O.T., Næsje, T.F., Klyve, L. and Lindem T. 1985b. The vertical distribution of fish species in Lake Mjøsa, Norway, as shown by gill net catches and echo sounder. Rep. Inst. Freshwat. Res. Drottningholm 62: 136 - 149.

Sandlund, O.T., Næsje, T.F. and Kjellberg, G. 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 pp.

Smith, S. 1957. Early development and hatching. pp. 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. Freshwat. Res. Drottningholm (4), 24 pp. (In Swedish).

Svärdson, G. 1976. Interspecific population dominance in fish communities of Scandinavian lakes. Rep. Inst. Freshwat. Res. Drottningholm 55: 144 - 171.

Svärdson, G. 1979. Speciation of Scandinavian *Coregonus*. Rep. Inst. Freshwat. Res. Drottningholm 57: 3 - 95.

Taugbøl, T., Hegge, O., Qvenild, T. and Skurdal, J. 1989. The diet of brown trout in Mjøsa. Oppland County. Dept. of the Environment, Lillehammer. Report no. 15, 17 pp. (In Norwegian).

van Valen, L. 1965. Morphological variation and width of ecological niche. Am. Nat. 99: 377 - 390.

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 1990. Genetic changes in a vendace (*Coregonus albula*) population 92 years after introduction. MS submitted for publication.

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).

	Mjøsa	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)	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^{-2})	26	4

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

	Mjøsa	Osensjøen
Von Bertallanfy parameters:		
L_∞ (mm)	236	284
K (Brody's growth coeffecient)	0.82	0.60
t_0	0.45	1.24
Spawning locality	inlet river	lake
Spawning time	15-30 Oct.	15-30 Oct.
Mean ind. fecundity (no of eggs) ±95% c.l.	7350.4 ± 845.1	11890.2 ±1317.0
GSI ± 95% c.l.	0.25 ±0.02	0.29 ±0.02
Mean body weight (W)	121.9 ±6.7	225.4 ±7.5
No of eggs per g body weight	60.3	52.8

Table 3 Mean length (mm), length of various head characters (mm), number of scales along the sideline, and gillraker number of 50 sexually mature vendace from Mjøsa and Osensjøen. SD = standard deviation, C.V. = coefficient of variation (SD/mean), Ratio = ratio of head character on (body length - head length).

	Mjøsa				Osensjøen			
	Mean	SD	C.V.	Ratio	Mean	SD	C.V.	Ratio
Body length	239.9	7.6	0.032		280.8	11.7	0.041	
Head length	44.9	2.2	0.043	0.230	52.9	3.1	0.059	0.232
Eye diameter	9.8	0.6	0.064	0.050	11.3	1.1	0.095	0.049
Snout length	10.8	0.7	0.067	0.055	13.2	1.1	0.081	0.058
Upper jaw	15.1	1.0	0.064	0.077	18.2	1.1	0.061	0.080
Lower jaw	16.0	1.0	0.065	0.082	18.7	1.8	0.098	0.082
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 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.
Mjøsa	$lnW = -12.52 + 3.22 lnL$	0.99	101	82 - 245
Osensjøen	$lnW = -10.45 + 2.77 lnL$	0.98	101	65 - 324

Captions to figures

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

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 (numbers of fish: Nm and No, respectively). Vertical lines indicate 95% confidence limits.

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

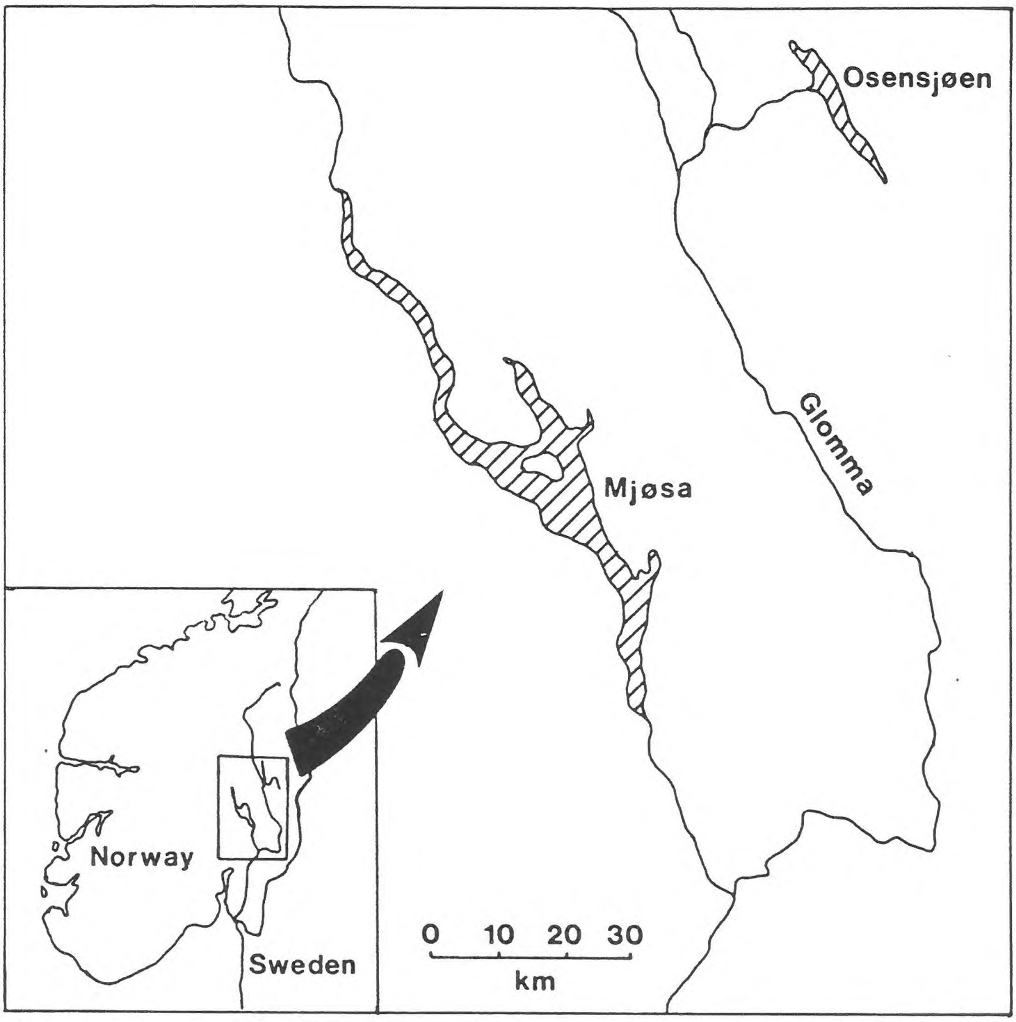

Fig 1

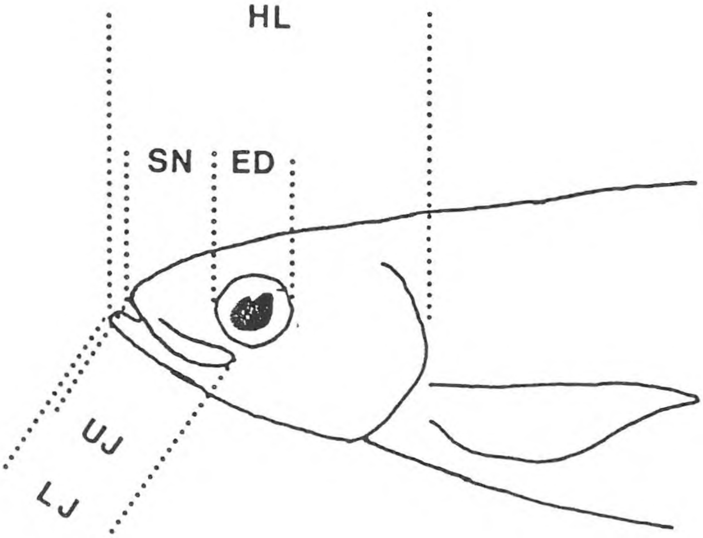

Fig. 2

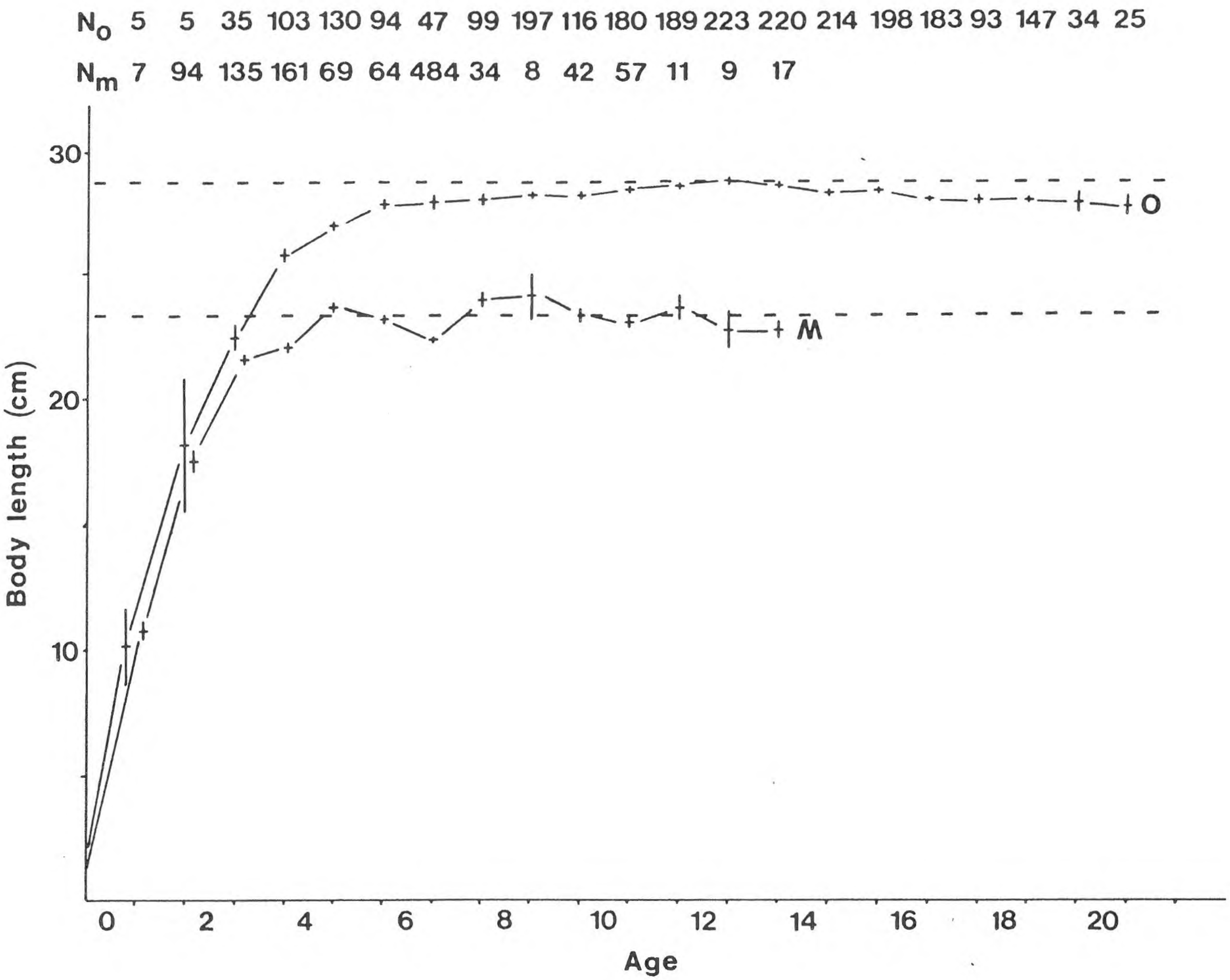
N₀ 5 5 35 103 130 94 47 99 197 116 180 189 223 220 214 198 183 93 147 34 25
Nm 7 94 135 161 69 64 484 34 8 42 57 11 9 17
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Fig.3

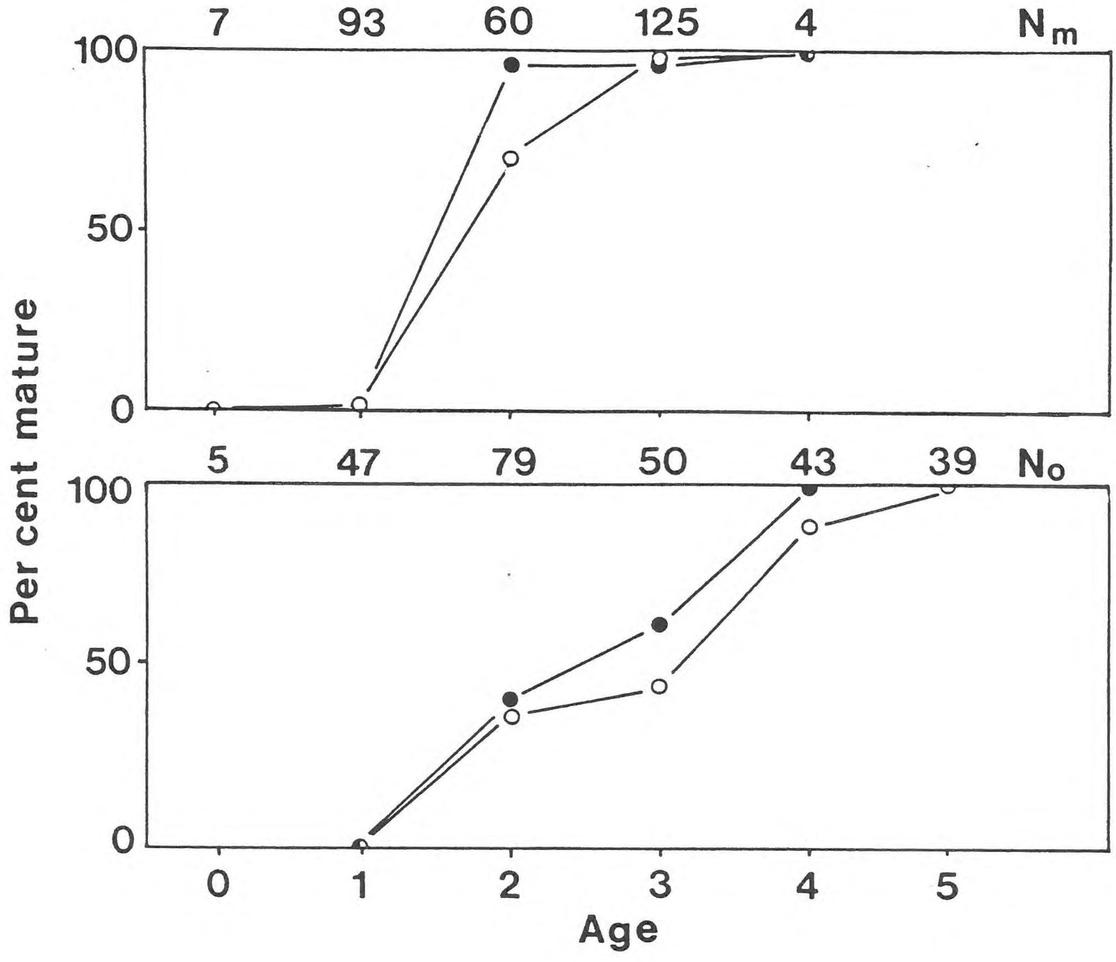
7
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Fig. 4

Paper VIII

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Impact of a Pelagic Gill-Net Fishery on the Polymorphic Whitefish (*Coregonus lavaretus* L. s.l.) Population in Lake Femund, Norway

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ABSTRACT

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There are 3 morphs of whitefish in Lake Femund. These are characterized by different mean numbers of gill-rakers, mean adult fish length and age at maturity. During summer and autumn, D-whitefish live both in demersal and pelagic habitat. R- and S-whitefish live mainly in the demersal habitat, as do juvenile fish of all morphs. Prior to 1981, the total whitefish yield was approximately 0.7 kg ha^{-1}. A commercial pelagic gill-net fishery with bar mesh sizes 35 to 39 mm started in 1981, and by 1982 total yield had increased to about 1.6 kg ha^{-1}. Commercial catches were dominated by D-whitefish. Catch per unit effort (CPUE, no. of fish) of this morph decreased from 10.8 in 1982 to 3.6 in 1984, and stayed around 4 in 1985 and 1986. CPUE of R- and S-whitefish showed no obvious downward trend, but varied between 0.7-2.1, and 0.1-0.3 fish per net night, respectively. The commercial nets were clearly selective, catching more of the larger fish ($TL > 35$ cm), and fish with the higher condition coefficient in the pelagic stock. As a consequence, the main changes in the pelagic whitefish stock over the sampling period 1982-1986 were reduction in fish size (length and weight), and reduction in the size-at-age of adult pelagic D-whitefish.

INTRODUCTION

In lakes with polymorphic whitefish populations (*Coregonus lavaretus*-complex, Ferguson et al., 1978), the different morphs are usually distinguished by habitat choice, diet, spawning time and spawning locality in addition to gill-raker count and other morphological characters (review in Svärdson, 1979). The intermorph differences in habitat and diet might indicate interactive segregation between the morphs (Lindström and Nilsson, 1962; Lindsey, 1981).

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This means that niche overlap, e.g. in terms of habitat and diet, is low when resources are scarce, and increases with increasing resource abundance. When exploitation is sufficiently strong to reduce stock density, increased niche overlap should be expected owing to increased relative food availability.

A gill-net fishery will increase mortality among the most active fish in the population. A commercial gill-net fishery is usually aimed at catching adult fish. As whitefish commonly exhibits stagnating growth at sexual maturation, a fishery based on a few mesh sizes will still catch several age groups fairly efficiently. Within each year class, the fastest growing individuals and those with the highest weight/length ratio will reach a size vulnerable to the gill-nets at the youngest age (Hamley, 1975; Handford et al., 1977). Based on this we expect the immediate effect of a selective fishery to be a lower average size-at-age.

In Lake Femund there are 3 whitefish morphs, distinguished by mean number of gill-rakers and adult body size (Svärdson, 1979; Sandlund and Næsje, 1986). Before 1981, the exploitation of whitefish in Lake Femund was relatively low, and performed with demersal gill-nets and beach seine just prior to, or during spawning (Sandlund, 1986). In 1981 a commercial fishery with pelagic gill-nets was initiated, resulting in more than a doubling of total whitefish yield (Sandlund and Næsje, 1986). This fishery is performed during August and early September, i.e. more than a month prior to spawning, and thus exploiting a mixed stock. This gave an excellent opportunity to study the effects of the size-selective fishery on the polymorphic whitefish stock.

The aim of the present paper is to document the effects of the increased and selective exploitation on the polymorphic whitefish stock.

MATERIALS AND METHODS

Study area

Lake Femund (Fig. 1) is an oligotrophic lake, with a zooplankton community reflecting heavy fish predation (Løvik and Kjellberg, 1982).

Of the 8 fish species in the lake: whitefish, arctic charr (*Salvelinus alpinus*), brown trout (*Salmo trutta*), pike (*Esox lucius*), perch (*Perca fluviatilis*), grayling (*Thymallus thymallus*), burbot (*Lota lota*) and minnow (*Phoxinus phoxinus*), the first 4 are subject to exploitation (Sandlund and Næsje, 1986). Prior to 1981 the yearly yield of whitefish was approximately 15 tons. The pilot season of the commercial pelagic gill-net fishery, 1981, yielded 11.6 tons. Additional whitefish catches during this year resulted in a total yield of approximately 22 tons. From 1982 the commercial fishery was performed in the period 1 August–15 September. The pelagic gill-nets used in the commercial fishery from 1982 onwards were approximately 85% 39-mm and 15% 35-mm bar mesh (Sandlund and Næsje, 1986).

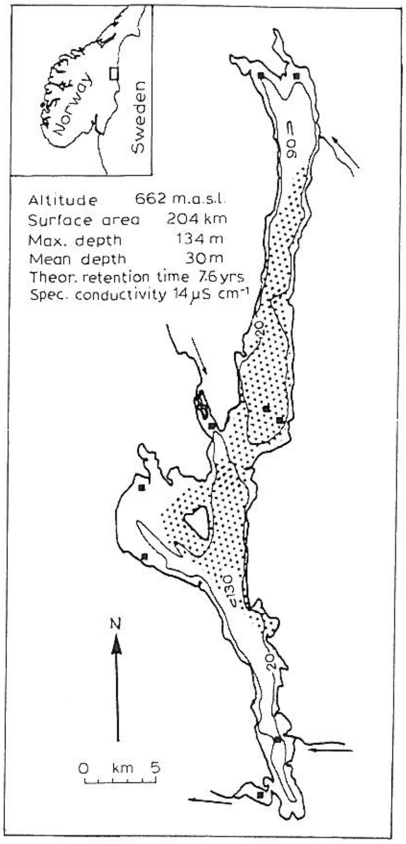

Fig. 1. Lake Femund with the 20-m depth contour indicated. Black squares indicate survey net localities. The dotted area was utilized by the commercial fishery.

Lake Femund has never been subject to introductions of whitefish from other stocks.

Test fishing

Fish were sampled with pelagic survey gill-nets in June–July 1982, and August–September 1982, 1983 and 1984, and demersal survey gill-nets in August–September 1983 and 1984, at the locations shown in Fig. 1. Both pelagic and demersal net series consisted of 12 different mesh sizes (8–52 mm bar). The pelagic nets were 6-m deep and 25-m long, while the demersal nets were 2-m deep and 25-m long. In 1982 pelagic fishing was performed in the depth zones 0–6, 10–16, 15–21 and 30–36 m, but as no fish was caught deeper than 20 m, pelagic fishing was later restricted to the 0–21 depth zone. Echo surveys also showed that the fish density was very low at deeper than approximately 20 m (Lindem and Sandlund, 1986). Demersal fishing was performed between 0 and 80 m. During the period 1982–1985, 2072 whitefish were caught in the surveys (Table 1).

TABLE 1

Number of whitefish sampled in Lake Femund, 1982-1986

	1982		1983	1984	1985	1986	Total
	J[a]	A	A	A	A	A	
Pelagic survey nets	146	229	399	100	68	–	942
Benthic survey nets	–	–	490	397	243	–	1130
Commercial catches	–	463	450	452	200	230	1795
Total	146	692	1339	949	511	230	3867

[a] J = June/July, A = August/September.

TABLE 2

Characteristics of whitefish morphs in Lake Femund. Van Bertallanfy parameters were calculated according to Dickie (1978)

Character	D-whitefish	R-whitefish	S-whitefish
Modal gill-raker count	28	35	43
Range	23-33	34-40	41-50
Size of sexually mature fish			
Mean (cm)	31.5	36.0	37.9
Range (cm)	25-46	28-47	29-59
No.[a]	1821	682	116
Age at sexual maturity[b] (years)			
Females	9	8	5
Males	8	7	3
L_{∞} (cm)	32.2	38.3	40.5
k (Brody's growth coefficient)	0.39	0.26	0.26
t_0	2.10	0.42	−0.77
Dominating year classes[c] (in 1983-1984 survey net catches)	1972 1973 1983	1972 1973 1974 1976	1972 1978 1979 1980
Male/female ratio	0.94	0.76	1.09
No.[a]	2684	909	171
Main spawning locality	> 20 m In the lake	Inlet rivers	< 20 m In the lake
Spawning time	November	Late October	Late October

[a] No. = no. of samples.

[b] Age at sexual maturity is given as the age when more than 50% of the fish are mature.

[c] Dominating year classes are year classes that constituted more than 10% each of the total survey net catches in 1983 and 1984 (Sandlund and Næsje1986, unpublished data).

Commercial catches

Throughout the commercial fishing seasons, weekly samples were taken from the commercial gill-net catches. Care was taken to get samples from the whole area of fishing (Fig. 1). During the period 1982–1986, 1795 whitefish were sampled from the commercial fisheries (Table 1).

Treatment of material

The fish were measured to the nearest 1 mm (total length, TL) and weighed to the nearest 1 g. The sex and the degree of sexual maturity were determined (Dahl, 1917). The anterior left gill-arch was removed for counting of gill-rakers. Ageing of the fish was done by burning and breaking the otoliths (Christensen, 1964). Annual survival rate (S) was calculated from catch per unit effort (CPUE) data for the individual year classes in the commercial catches for 1982–1986, based on 5000–6000 net nights year^{-1} (Ricker, 1975). CPUE was calculated as kg or number of fish per gill-net (25×6 m) per night. This was only done for commercial catches, as effort (number of net nights) during test fishing was not considered sufficiently large to give reliable estimates.

Based on the number of gill-rakers, the whitefish were classified into 3 different morphs. The classification criteria (Table 2) were based on the trimodal distribution of gill-raker counts from 3774 fish (cf. Sandlund and Næsje, 1986). The number of gill-rakers is considered a stable morphological character in Scandinavian whitefish, and the final number of gill-rakers can be detected in fish from approximately 12 cm TL (Svärdson, 1979). The names adopted for the morphs, Deepwater (D-) whitefish, River (R-) whitefish and Shallow water (S-) whitefish, refer to their main spawning localities.

RESULTS

Habitat use

In autumn, juvenile whitefish (TL < 20 cm) of all 3 morphs, and adult R- and S-whitefish, live mainly in the demersal habitat (Fig. 2). Approximately 90% of the juvenile fish between 12 and 20 cm TL had less than 34 gill-rakers, and were consequently classified as D-whitefish. Adult D-whitefish live both in pelagic and demersal habitats. Both R- and S-whitefish are occasionally caught in the pelagic habitat (Fig. 2). The proportions of R- and S-whitefish were significantly higher in the demersal than in the pelagic survey net catches ($\chi^2 = 124.3$, 2 d.f., $P < 0.005$). The proportion of D-, R- and S-whitefish among adult fish in the pelagic survey net catches from 1982 to 1985 were 93.2, 5.7

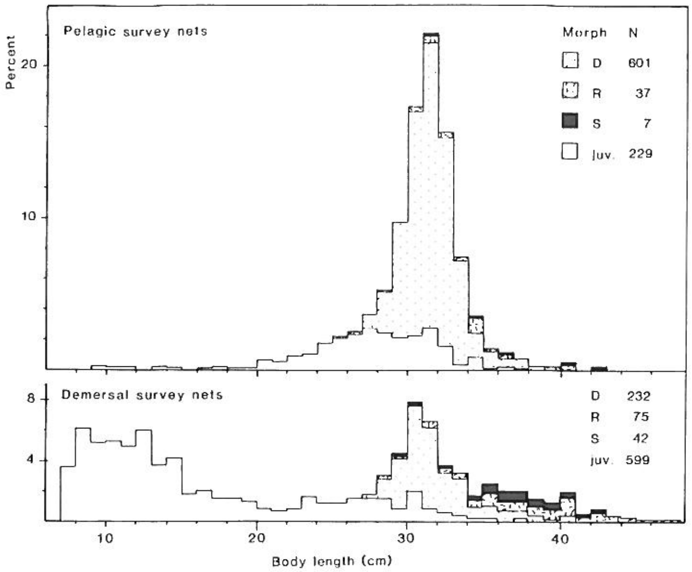

Fig. 2. Length distribution of adult D-, R-, and S-whitefish and juveniles in pelagic and demersal survey nets in 1982–1985. N = number of fish.

and 1.1%, respectively. Corresponding figures for the demersal survey net catches were 66.5, 21.5 and 12.0%.

The age composition of whitefish in the demersal survey net catches during 1983–1985 showed high proportions of juvenile fish. Age group 1 (body size approximately 7–11 cm) constituted between 10 and 31% of the total demersal catches in these years. However, more than 15 age groups were represented in the demersal survey net catches in all years.

Exploitation of the pelagic whitefish population

The age structure of D-whitefish in commercial pelagic gill-net catches showed variable year-class strength (Fig. 3). The year classes 1971, 1972 and 1973 were all relatively strong, but in all years (1982–1986) more than 15 year classes were represented in the commercial catches. In 1982 the year classes 1971–1973 (age group 9–11) constituted 71.3% of the commercial catches. The proportion made up by these 3 year classes declined over the years, and in 1986 they constituted 39.5%.

The commercial pelagic gill-net catches varied between 12.8 and 22.2 tons during 1982–1986 (Fig. 4A). The catches of D-, R- and S-whitefish varied between 8.3–16.5, 3.9–7.2 and 0.3–1.3 tons, respectively. An additional estimated 10 tons were annually caught through other fisheries, mainly at the spawning

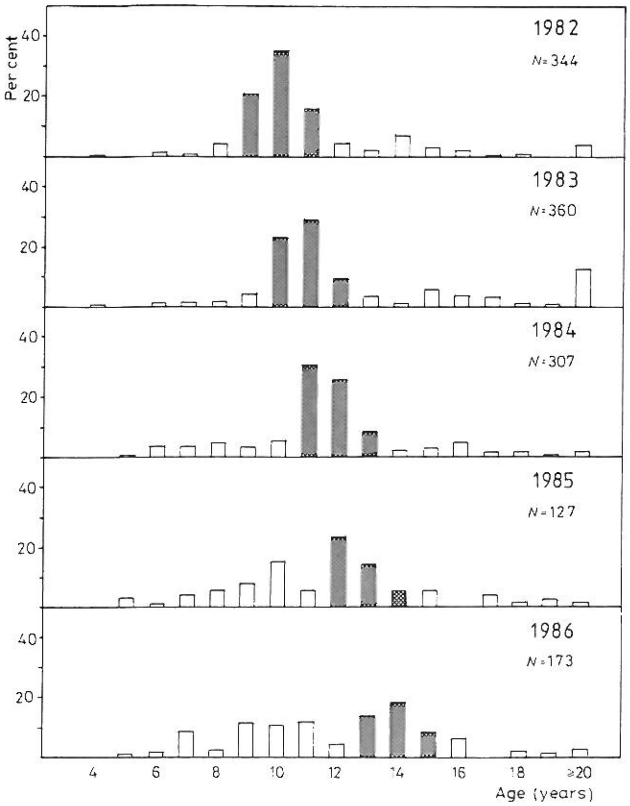

Fig. 3. Age distribution of D-whitefish in the commercial pelagic gill-net catches, 1982–1986. Year classes 1971–1973 are shaded.

grounds of R- and S-whitefish. Thus, the total yield of whitefish varied between approximately 22 and 32 tons, corresponding to 1.1 and 1.6 kg ha^{-1}.

The CPUE of D-whitefish in the commercial fishery decreased from 3.39 kg in 1982 to approximately 1 kg in 1984–1986 (Fig. 4B). For R- and S-whitefish there was no such obvious downward trend over the 5 years of sampling. CPUE of R-whitefish reached a maximum of 0.88 kg in 1985 and a minimum of 0.31 kg in 1986. Corresponding figures for S-whitefish were 0.13 kg in 1984 and 1985 and 0.04 kg in 1986.

CPUE calculated as number of fish varied in a similar fashion (Table 3). CPUE of D-whitefish decreased from nearly 11 in 1982 to approximately 4 in 1984–1986, whereas CPUE of R-whitefish varied between 2.0 and 0.7 fish, and S-whitefish varied between 0.3 and 0.1 fish. As a consequence of the decreasing D-whitefish catches, the proportion of this morph in the commercial catches decreased significantly from 1982 to 1985 (Table 3; 1982 vs. 1985; $\chi^2 = 28.0$, 2 d.f., $P < 0.005$). From 1985 to 1986 the proportion of D-whitefish in commer-

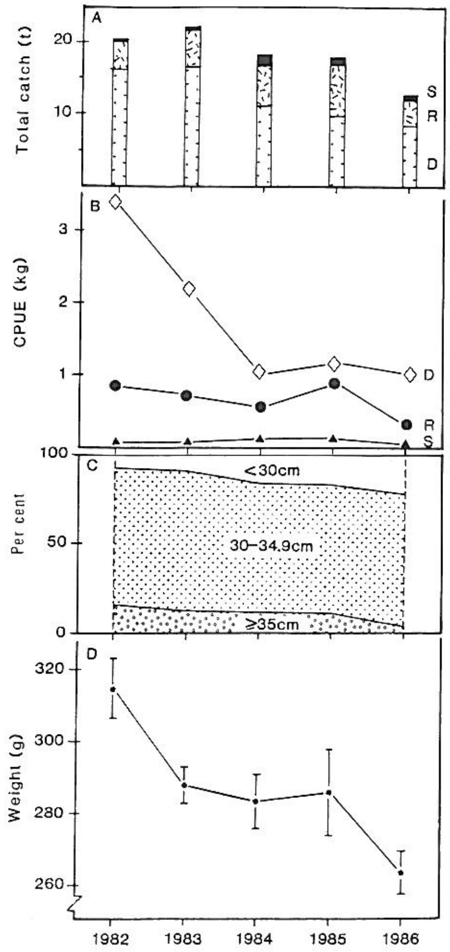

Fig. 4. (A) Total catch in commercial fisheries 1982-1986.
(B) Catch per unit effort in kg per net night for D-whitefish (◇), R-whitefish (●) and S-whitefish (▲). (C) Length distribution (all morphs) in commercial catches, 1982-1986. (D) Mean weight (all morphs) in commercial catches, 1982-1986.

cial catches increased significantly (1985 vs. 1986: $\chi^2=6.63$, 2 d.f., $P<0.05$). This was, however, mainly owing to the decreased CPUE of R- and S-whitefish as CPUE of D-whitefish did not increase from 1985 to 1986.

The proportion of D-whitefish in the pelagic survey net catches was also significantly lower in 1984–1985 than in 1982–1983 (Table 3; 1982–1983 pooled vs. 1984–1985 pooled; $\chi^2=20.8$, 2 d.f., $P<0.005$).

Both in pelagic survey net and commercial catches most fish caught were 30–33 cm. The proportion of fish smaller than 30 cm in the commercial catches increased from 1982 to 1986 (Fig. 4C), while the proportion of fish larger than

TABLE 3

Per cent whitefish morphs, CPUE (number of fish), and per cent mature fish in commercial catches, 1982–1986, and per cent morphs and mature fish in pelagic survey net catches, 1982–1985

	1982	1983	1984	1985	1986
Commercial catches					
D-whitefish					
No.	346	365	310	128	173
%	83.1	81.1	70.1	63.8	75.2
CPUE	10.8	7.7	3.6	4.2	3.9
R-whitefish					
No.	65	80	109	64	51
%	15.7	17.8	24.7	32.2	22.2
CPUE	2.0	1.7	1.3	2.1	0.7
S-whitefish					
No.	5	5	23	8	6
%	1.2	1.1	5.3	4.0	2.6
CPUE	0.1	0.1	0.3	0.3	0.1
Total No.	416	450	442	200	230
Per cent mature	87.5	70.7	60.9	67.0	82.2
Pelagic survey net catches					
D-whitefish					
No.	352	376	83	57	
%	93.9	94.0	83.0	83.3	
R-whitefish					
No.	20	18	17	9	
%	5.2	4.6	17.0	13.6	
S-whitefish					
No.	3	6	0	2	
%	0.6	1.4	0.0	3.3	
Total No.	375	400	100	68	
Per cent mature	77.6	80.3	51.0	48.5	

34.9 cm decreased during the same period. This change in size distribution was significant ($\chi^2=49.9$, 8 d.f., $P<0.005$). Also in the pelagic survey net catches there was a decrease in large fish and an increase in small fish during the period 1982–1985 ($\chi^2=227.6$, 6 d.f., $P<0.005$). A corresponding significant decrease in mean weight of whitefish (all morphs pooled) caught in the commercial fishery was registered (1982 vs. 1986: $t=4.05$, 645 d.f., $P<0.001$) (Fig. 4D).

Mean lengths of age groups 9–16 of D-whitefish in the commercial catches showed a decreasing trend during 1982–1986, whereas age groups 7 and 8 (sub-adult fish) remained constant in length (Fig. 5). The decrease was significant

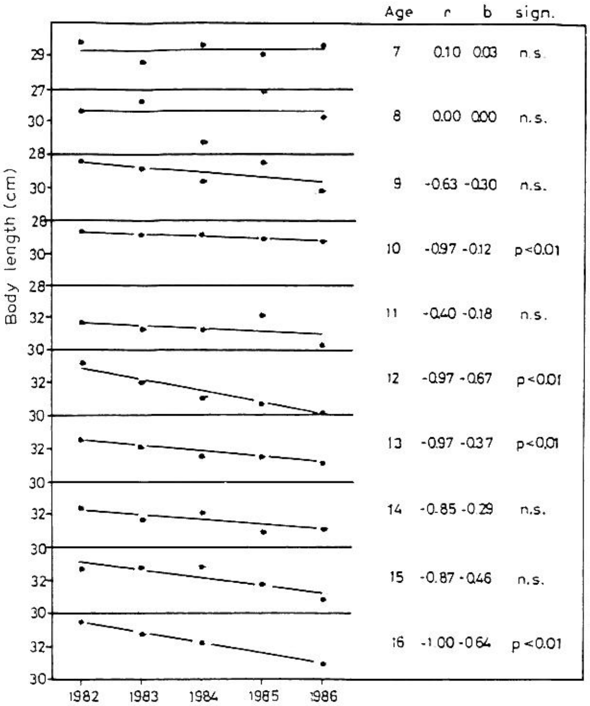

Fig. 5. Mean body length of age groups 7-16 of D-whitefish in commercial catches, 1982-1986. *r* is the correlation coefficient and *b* is the regression coefficient in the linear regression model $L = bY + a$, where L is mean body length (cm) and Y is fishing season; n.s.; $P > 0.05$.

in age groups 10, 12, 13 and 16. In pelagic survey net catches the numbers of D-whitefish in each age group were too small to allow similar comparisons between years.

The commercial nets caught fish with a higher condition coefficient (Fulton's *K*, Bagenal and Tesch, 1978) than did the pelagic survey nets. In catches from both net types, females always had a higher condition coefficient than males (survey nets: female $K = 0.86$–0.95, male $K = 0.85$–0.93, commercial nets: female $K = 0.95$–0.97, male $K = 0.93$–0.97). As a consequence, the commercial fishery caught a significantly higher proportion of females than the pelagic survey nets. Male/female ratio was 0.82 and 1.05, respectively ($\chi^2 = 7.1$, 1 d.f., $P < 0.01$).

Annual survival rate (S) for the year classes of D-whitefish dominating in the commercial catches (1971–1973) was 0.624 in 1982–1983, decreased to 0.477 in 1983–1984, and increased to 0.806 in 1984–1985 and 0.956 in 1985–1986. Mean survival rate for the younger year classes represented (1975–1978) was 2.139, and for the older year classes (1966–1969) 0.584.

DISCUSSION

During summer and autumn different size groups and morphs of whitefish lived in different habitats. Juveniles of all three whitefish morphs were mainly restricted to the demersal habitat. Among adults, D-whitefish utilized both pelagic and demersal habitat, whereas R- and S-whitefish mainly lived in the demersal habitat. This habitat segregation greatly influences the exploitation of the various components of the whitefish stock. The commercial fishery with pelagic gill-nets of mesh sizes 35 and 39 mm catches mainly adult D-whitefish. Demersal gill-nets of the same mesh sizes will catch a larger proportion of R- and S-whitefish.

Over the 5 years of sampling, there was a reduced proportion of fish larger than 35-cm TL, a reduced mean weight of fish, and a reduced length-at-age of adult D-whitefish in the pelagic catches. As the mesh sizes used did not change over this period, the decreases observed in fish size in the catches probably reflect a real change in the size distribution of the pelagic whitefish stock. The change is probably caused by the size-selective effect of the commercial pelagic nets. Assuming that the catches of the pelagic survey nets give a less biased picture of the pelagic fish stock than the commercial catches, the higher condition coefficients and the surplus of females in the commercial catches indicate the selectivity of the commercial nets. These results accord with the findings of Handford et al. (1977) on lake whitefish in Lesser Slave Lake, Canada. The decreasing length-at-age contrasts with the observations of Healey (1980) and Henderson et al. (1983), who found increased growth rate of lake whitefish when stock density was reduced. However, in these two cases the exploitation of the lake whitefish stocks was less selective than that of the commercial fishery in Lake Femund. The adult D-whitefish in Lake Femund have a very low growth rate after sexual maturation (Sandlund and Næsje, 1986). Any positive effects on growth rate owing to increased food availability as stocks are reduced may therefore be offset by the size-selective mortality owing to the commercial fishery.

Healey (1980) also found that the increased growth rate led to reduced age at maturity, and Jensen (1981, 1985) suggested that increased juvenile survival and reduced age at maturity were the two most powerful means of compensating increased adult mortality in lake whitefish. In Lake Femund we found neither an increased juvenile growth rate nor a reduction in age at sexual maturity. This may, however, be owing to the relatively short period of sampling, covering less than one generation of D-whitefish.

Most investigations on coregonids show that juvenile fish are strongly underrepresented in survey net catches (Ricker, 1975; Johnson, 1976; Healey, 1980). Thus, the relatively high proportion of small juvenile fish in the demersal survey net catches in Lake Femund might indicate an unusually good recruitment to the whitefish population. Based on the present data, however, we are not able to state whether this is owing to the increased adult mortality.

According to the interactive segregation theory (Lindström and Nilsson, 1962) niche overlap between morphs is to be expected when relative resource abundance increases as stock density is reduced. As the commercial pelagic gill-net fishery was selective for D-whitefish, increased niche overlap was expected between this morph and R- and S-whitefish. Thus, we would expect an increase in pelagic CPUE of R- and S-whitefish in response to the substantial decrease in CPUE of pelagic D-whitefish. This was, however, not the case, and our observations rather indicate an overall reduction in the pelagic whitefish stock.

The decrease in the commercial fishery might be caused by the fluctuating year-class strength of the D-whitefish. In 1982 the adult D-whitefish stock was dominated by a few relatively old year classes. As these year classes are depleted, CPUE will be decreasing. This might be viewed as the removal of the surplus of an accumulated stock, in which case a new and lower equilibrium yield will be reached. However, the high frequency of juvenile fish in the benthic survey net catches indicate that the commercial CPUE will increase as these year classes reach adult size. Strongly fluctuating yields have been observed in most commercial whitefish fisheries (e.g. Bell et al., 1977; Henderson et al., 1983; Lehtonen, 1981).

A certain immigration of adult D-whitefish into the areas of the commercial fishery from areas without commercial fishing is indicated by the continued presence of older year classes in the pelagic catches, as well as the apparent increase in yearly survival rate S in the 1971–1973 year classes of D-whitefish over the study period. Inter-year S for these year classes was 0.674, 0.477, 0.806 and 0.956, respectively. Through the immigration of fish into exploited areas, the unfished areas may help to sustain a steady yield from the commercial fishery (Cucin and Regier, 1965).

In conclusion, as D-whitefish utilizes the pelagic habitat more than R- and S-whitefish, it is also most affected by the commercial pelagic gill-net fishery. The commercial nets were clearly size selective, reducing mean weight and the proportion of fish larger than 35-cm TL in the pelagic stock. Within D-whitefish, this size selectivity resulted in a reduced length-at-age of adult fish. The expected increase in habitat overlap between morphs was not observed.

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REFERENCES

Bagenal, T.B. and Tesch, F.W., 1978. Age and growth. In: T.B. Bagenal (Editor), Methods for Assessment of Fish Production in Fresh Waters. IBP Handbook No. 3, Blackwell Scientific Publishers, Oxford, pp. 101-130.

Bell, G., Handford, P. and Dietz, C., 1977. Dynamics of an exploited population of lake whitefish (*Coregonus clupeaformis*). J. Fish. Res. Bd. Can., 34: 942-953.

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.

Cucin, D. and Regier, H.A., 1965. Dynamics and exploitation of lake whitefish in Southern Georgian Bay. J. Fish. Res. Bd. Can., 23: 221-274.

Dahl, K., 1917. Studier og forsøk over ørret og ørretvand. Centraltrykkeriet, Kristiania, 107 pp. (in Norwegian).

Dickie, L.M., 1978. Mathematical models of growth. In: T.B. Bagenal (Editor), Methods for Assessment of Fish Production in Fresh Waters, IBP Handbook No. 3, Blackwell Scientific Publishers, Oxford, pp. 130-136.

Ferguson, A., Himberg, K.-J. M. and Svärdson, G., 1978. Systematics of the Irish pollan (*Coregonus pollan* Thompson): an electrophoretic comparison with other Holarctic/Coregoninae. J. Fish Biol., 12: 221-233.

Hamley, J.M., 1975. Review of gill-net selectivity. J. Fish. Res. Bd. Can., 32: 1943-1969.

Handford, P., Bell, G. and Reimchen, T., 1977. A gillnet fishery considered as an experiment in artificial selection. J. Fish. Res. Bd. Can., 34: 954-961.

Healey, M.C., 1980. Growth and recruitment in experimentally exploited lake whitefish (*Coregonus clupeaformis*) populations. Can. J. Fish. Aquat. Sci., 37: 255-267.

Henderson, B.A., Collins, J.J. and Reckahn, J.A., 1983. Dynamics of lake whitefish (*Coregonus clupeaformis*) in Lake Huron. Can. J. Fish. Aquat. Sci., 40: 1556-1567.

Jensen, A.L., 1981. Population regulation in lake whitefish, *Coregonus clupeaformis* (Mitchill). J. Fish Biol., 19: 557-573.

Jensen, A.L., 1985. Relations among net reproductive rate and life history parameters for lake whitefish (*Coregonus clupeaformis*). Can. J. Fish. Aquat. Sci., 42: 164-168.

Johnson, L., 1976. Ecology of Arctic populations of lake trout, *Salvelinus namaycush*, lake whitefish, *Coregonus clupeaformis*, Arctic charr, *Salvelinus alpinus*, and associated species in unexploited lakes of the Canadian Northwest Territories, J. Fish. Res. Bd. Can., 33: 2459-2488.

Lehtonen, H., 1981. Biology and stock assessments of coregonids by the Baltic coast of Finland. Finn. Fish. Res., 3: 31-83.

Lindem, T. and Sandlund, O.T., 1986. Ekkoloddregistreringer i Femund 1982-84. Report from the Fish Research Division, Dir. of Nature Management, No. 3, pp. 1-14 (in Norwegian).

Lindsey, C.C., 1981. Stocks are chameleons: plasticity in gill rakers of coregonid fishes. Can. J. Fish. Aquat. Sci., 38: 1497-1506.

Lindström, T. and Nilsson, N.-A., 1962. On the competition between whitefish species. In: E.D. LeCren and M.W. Holdgate (Editors), The Exploitation of Natural Animal Populations. Blackwell Scientific Publishers, Oxford, pp. 326-340.

Løvik, J.E. and Kjellberg, G., 1982. Glåma i Hedmark. Delrapport om dyreplankton. Undersøkelser i tidsrommet 1978-80. Norwegian Institute of Water Research, Report No. 0-78045-III, pp. 1-58 (in Norwegian).

Ricker, W.E., 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Bd. Can., 191: 1-382.

Sandlund, O.T., 1986. The annual catch of whitefish (*Coregonus lavaretus*) in the River Tufsinga, Eastern Norway. Nor. Skogbruksmuseum, Årbok no. 11, pp. 284-296 (in Norwegian with English summary).

Sandlund, O.T. and Næsje, T.F., 1986. Sikbestanden i Femund. Undersøkelser 1982-84. Report from the Fish Research Division, Dir. of Nature Management, No. 2, pp. 1-51, (in Norwegian).

Svärdson, G., 1979. Speciation of Scandinavian *Coregonus*. Rep. Inst. Freshwater Res. Drottningholm, 57: 3-95.

Paper IX

OIKOS 64: 305–351. Copenhagen 1992

The arctic charr Salvelinus alpinus in Thingvallavatn

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Sandlund, O. T., Gunnarsson, K., Jónasson, P. M., Jonsson, B., Lindem, T., Magnússon, K. P., Malmquist, H. J., Sigurjónsdóttir, H., Skúlason, S. and Snorrason, S. S. 1992. The arctic charr *Salvelinus alpinus* in Thingvallavatn. – Oikos 64: 305–351.

The coexistence of four morphs of arctic charr in Thingvallavatn, Iceland, was demonstrated by investigations of morphology, habitat use, diet, endoparasitic fauna, life history, time and place of spawning, early ontogeny, and population genetics. Head morphology in embryos, juveniles and adults revealed the presence of two charr morphotypes, each including two morphs: (1) a benthic morphotype including large benthivorous (LB-) and small benthivorous (SB-) charr, featuring overshot mouth and relatively large pectoral fins, and (2) a pelagic morphotype including planktivorous (PL-) and piscivorous (PI-) charr, featuring terminal mouth and relatively small pectoral fins. SB-charr mature sexually (50%) at 2 (males) and 4 yr (females); asymptotic length is 133 mm. LB-charr mature sexually at 8 yr; asymptotic length is 553 mm. PL-charr mature sexually at 4 (males) and 5 yr (females); asymptotic length is 205 mm. PI-charr mature sexually at 6 yr; asymptotic length is 302 mm. SB- and LB-charr both live in the littoral zone, but they segregate in microhabitat: LB-charr live epibenthically, whereas SB-charr live mainly in the interstitial spaces of the stony substrate. Their diet, however, is similar (Schoener's D = 0.34 – 0.89). Both feed mainly on the snail *Lymnaea peregra*. PI-charr live mainly epibenthically, feeding on sticklebacks and juvenile charr. PL-charr is the most numerous morph in the lake. It lives both in the pelagic and in the epibenthic zone, feeding on crustacean zooplankton and chironomid pupae. The young of the year of all morphs live in the littoral zone where they feed on chironomid larvae. All morphs spawn in the littoral zone, LB-charr spawn in July–August, PL- and PI-charr spawn in September–November, whereas SB-charr spawn during August to November. Genetically, the morphs are very similar; Nei's genetic distances were between 0.00004 to 0.00126. The only significant difference found was between SB-charr and the other three morphs combined. The four morphs are conspecifics, although they may be reproductively segregated to some extent.

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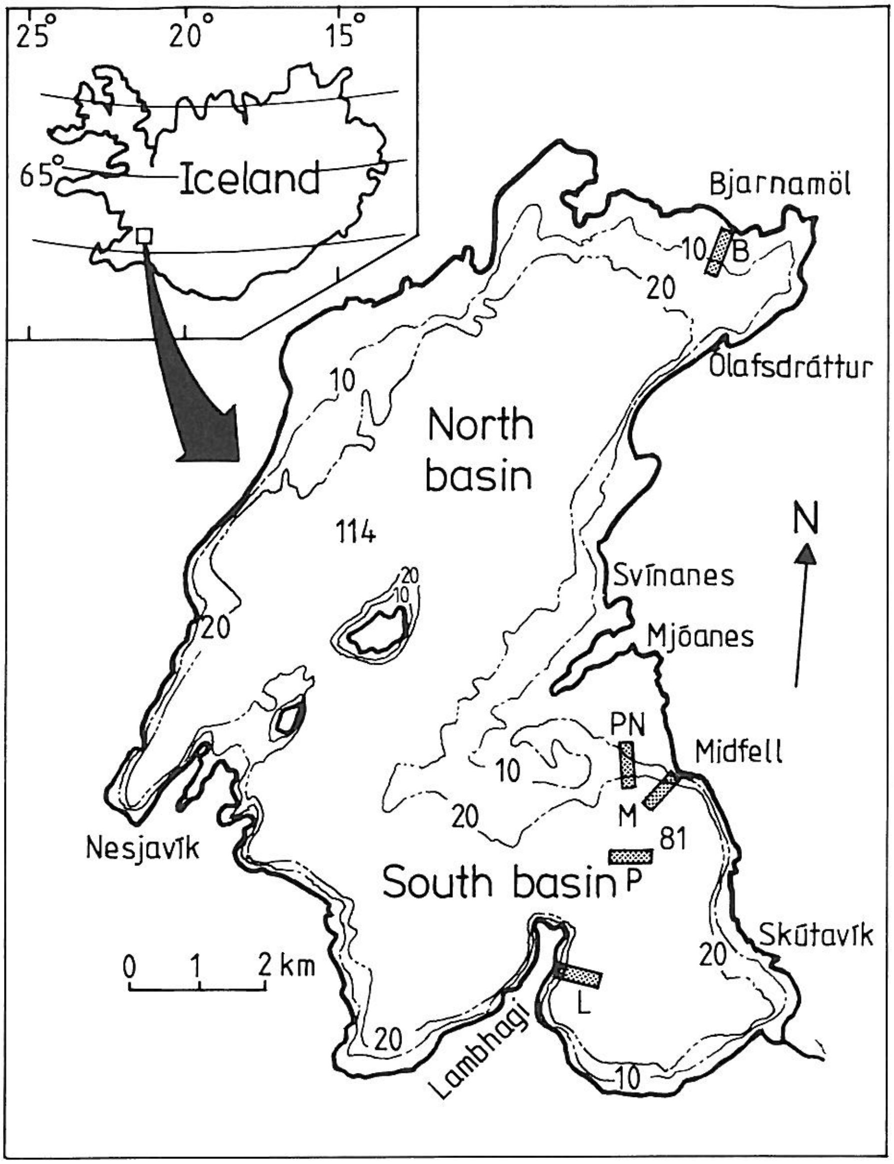

Fig. 1. Thingvallavatn with the 10 and 20 m depth contours and the deepest points in the northern (114 m) and the southern (81 m) basin indicated. M (Midfell), L (Lambhagi) and B (Bjarnamöl) are benthic gill net localities. P (deep pelagic) and PN (pelagic over *Nitella*) are pelagic gill net localities.

Introduction

Arctic charr *Salvelinus alpinus* (L.) is an important fish species in many subarctic and northern temperate freshwater systems. Throughout its area of distribution, this species shows extensive phenotypic variation, both among and within localities. Arctic charr may occur in 1–4 distinct morphs in the same lake (Nikolskii 1969a, Behnke 1972, 1980, 1984). The differences among sympatric morphs may include coloration, meristic characters, growth rate, size and age at sexual maturity, time and place of spawning, food and habitat choice, and parasites (Balon 1980a, Johnson and Burns 1984). The sympatric morphs may be reproductively isolated (Frost 1965).

The phenotypic variability of arctic charr has given

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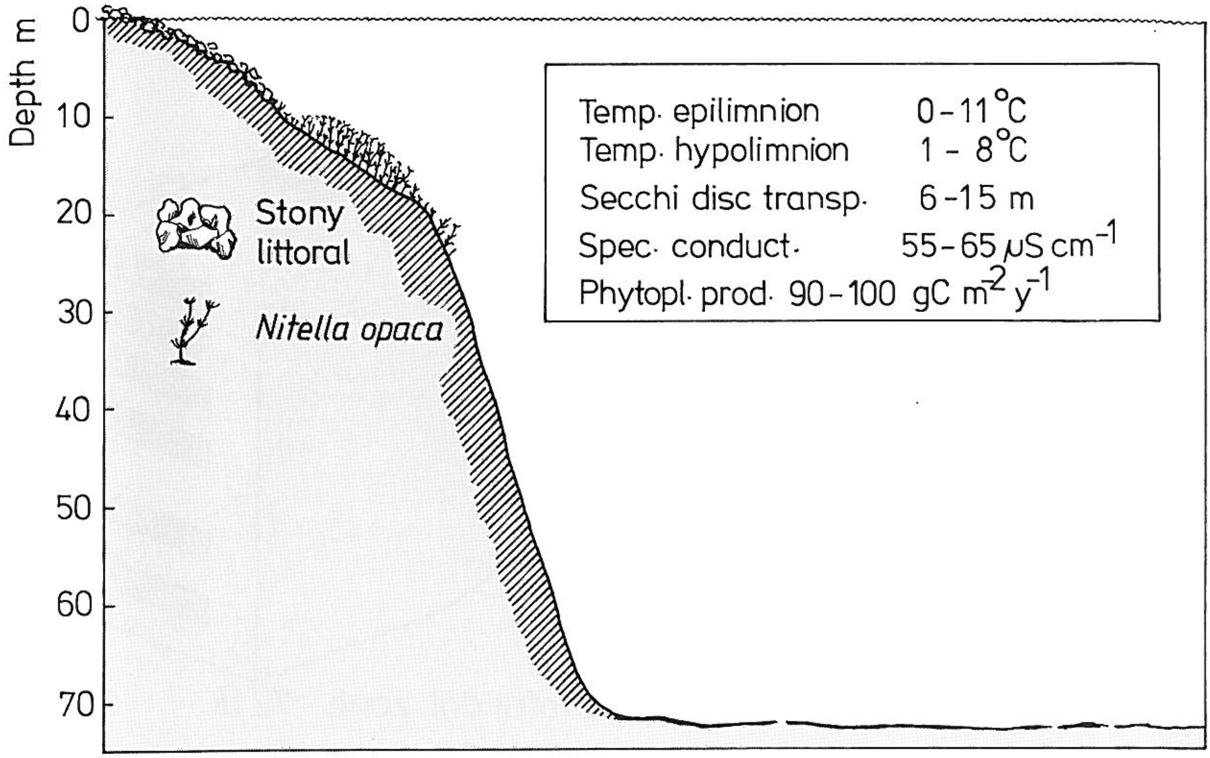


Fig. 2. Schematic outline of the main habitats for fish in Thingvallavatn, and some major physical and chemical characteristics of the water masses.

rise to a debate about the origin of the variation and hence the systematic status of the morphs. Some authors have claimed that arctic charr constitute a species-complex consisting of sibling species that evolved allopatrically during the Pleistocene glaciations (Svärdson 1961, Nilsson and Filipsson 1971). According to this view sympatric charr morphs would stem from multiple immigrations of two or more of these sibling species. The morphs now reside as genetically distinct entities or in various stages of genetic retrogression (Henricson and Nyman 1976, Klemetsen and Grotnes 1980, Nyman et al. 1981).

An opposing view holds that the arctic charr morphs belong to one polymorphic species (Reisinger 1953, Savvaitova 1961, 1980, Frost 1965, Skreslet 1973, Balon 1980b, Jonsson and Hindar 1982). Recent rearing experiments and genetical studies support this view. Nordeng (1983) studied three morphs of arctic charr in the Salangen river system in North Norway, and found that intra-morph fertilizations gave rise to all three morphs. Based on material from a number of arctic charr lakes in Norway, Hindar et al. (1986) found that genetic distances were greater between stocks of the same morph from different lakes than between different morphs from the same lake. They concluded that sympatric morphs of arctic charr should generally be regarded as locally differentiated populations and not different species.

In lakes where fish encounter heterogeneous environments and vacant resources they may diverge in terms of habitat use and diet, and consequently in trophic morphology and growth. This may explain the propensity of arctic charr and many other fish species to develop morphs through trophic differentiation, or ecological polymorphism, within breeding populations (Skreslet 1973, Sage and Selander 1975, Campbell 1979, Turner and Grosse 1980, Hindar and Jonsson 1982, Kornfield et al. 1982, Grudzien and Turner 1984, Sparholt 1985). Some salmonids have also been shown to evolve genetically divergent local populations (Kirkpatrick and Selander 1979, Ryman et al. 1979, Ferguson and Mason 1981, Ryman 1981, Ferguson 1986, Hindar et al. 1986), a phenomenon enhanced by their well-documented reproductive homing behaviour (Stuart 1953, 1957, Frost 1965, Behnke 1972). From the perspective of evolutionary genetics, the discontinuous trophic variation may well be the type of niche specific polymorphism that e.g. Maynard Smith (1966), and Turner and Grosse (1980) have regarded as a fundamental requisite for sympatric speciation.

In Iceland, the arctic charr is one of only three lake resident freshwater fish species, and in Thingvallavatn it is the dominating species, the others being the brown

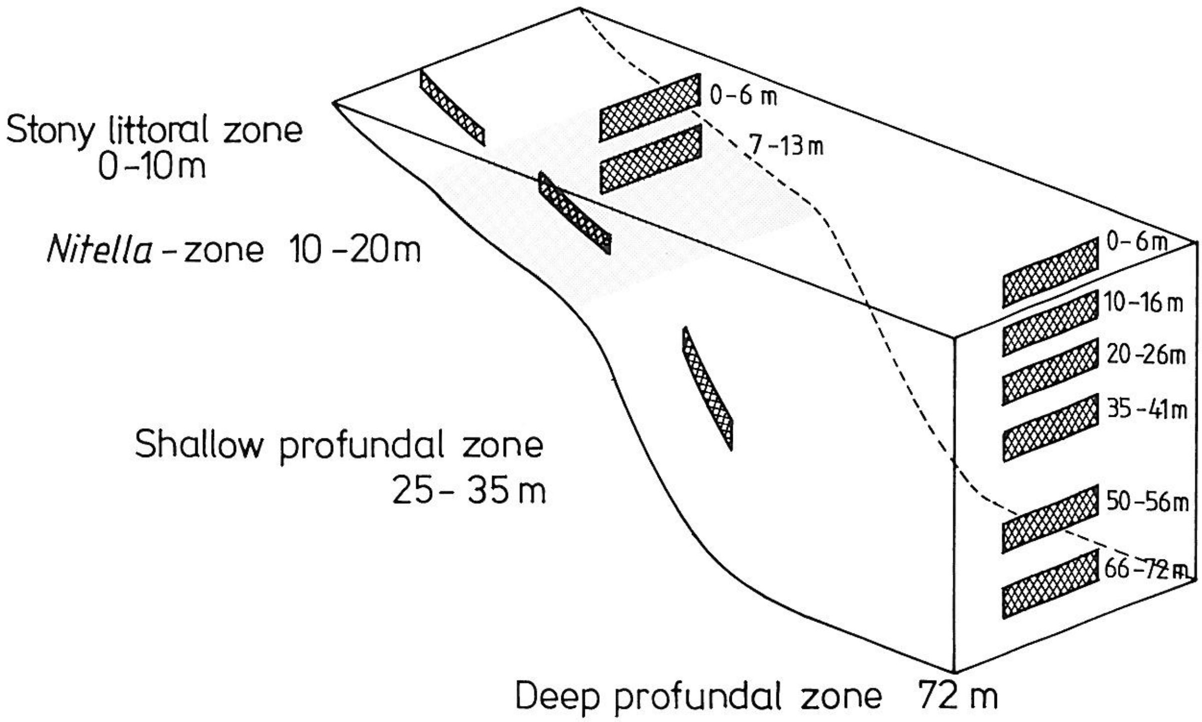


Fig. 3. Schematic outline of the gill net sampling procedures.

trout *Salmo trutta* L. and the threespine stickleback *Gasterosteus aculeatus* L. The occurrence of several phenotypes of arctic charr in Thingvallavatn was recognized early by local people and reported by Sæmundsson (1904, 1926) and Frídriksson (1939). More recent investigations suggested the presence of four ecologically and morphologically different variants (Snorrason 1982, Skúlason 1983, Malmquist et al. 1985). Two morphs are benthivorous (large, LB, and small, SB), with overshot mouth and blunt snouts. The two other morphs are planktivorous (PL) and piscivorous (PI), respectively, with terminal mouths and pointed snouts.

To establish the distinctiveness of the morphs we tested the null hypotheses that there is one uniform phenotype of arctic charr in Thingvallavatn. The prediction from this hypothesis would be that the external morphology, life history and ecological characters of arctic charr in the lake should have continuous distributions. This we tested by investigating morphology, life history traits, habitat, diet, parasites, and genetic variation of the arctic charr present.

This paper is based on reports by Skúlason (1986), Magnússon and Ferguson (1987), Sandlund et al. (1987, 1988), Malmquist (1988), Jonsson et al. (1988), Frandsen et al. (1989), Snorrason et al. (1989), Skúlason et al. (1989a,b), Sigurjónsdóttir and Gunnarson (1989), as well as unpublished data.

Study area

Thingvallavatn (83 km^2) is Iceland's largest lake (Fig. 1), with maximum depth 114 m and mean depth 34 m. The lake is situated in the neovolcanic zone, which is an exposed part of the Mid-Atlantic Ocean Ridge system (Jónasson and Lindegaard 1987). The lake basin was formed at the end of the last glaciation, approximately 10,000 years ago. Since then, its size and morphometry have at intervals undergone considerable changes due to tectonic events like eruptions and subsidence, as the continental shields are sliding apart (Sæmundsson 1965, 1992). Due to the permeability of the neovolcanic rockbeds, up to 90% of the water inflow is subterraneous. The inflow is steady throughout the year and relatively rich in dissolved solids. The water level fluctuates approximately 0.5 m throughout the year. Annual fluctuations were even smaller before the construction of the outlet dam in 1959.

The physical habitat of Thingvallavatn consists of a sizeable pelagic zone, and a benthic zone subdivided into three different substrates (Fig. 2). In shallow waters, 0–10 m, wave action creates a hard bottom with a stony substrate. On the north, east and partly on the west shores, this substrate consists of lava, often with scattered lava stones, and is spatially very complex, with porous lava stones, innumerable crevices, and extended interstitial spaces, providing a highly diverse habitat for zoobenthos and benthivorous fish (Snorrason 1982, Lindegaard et al. 1992). In some areas. e.g. Lambhagi (Fig. 1), the stony substrate consists of smaller, rounder, and more weathered stones, and interstitial rooms are less diverse. The stony substrate is absent only in the most protected bays, where stones are covered by silt. In smaller areas the bottom consists of black basaltic sand or gravel. A dense vegetation of *Nitella opaca* Ag. is found at depths between 10 and 25 m in most areas (Kairesalo et al. 1987). Individual plants may reach a height of 1 m. The littoral zone thus reaches down to a depth of approximately 25 m and covers an area of approximately 30 km^2, including the stony littoral and *Nitella*-zones. In the profundal zone, at depths greater than 25 m, the bottom is soft with a firm diatomic gyttja substrate (Lindegaard 1980).

In summer, surface temperatures in the lake rarely exceed 11°C. At that time temperatures below 25 m are around 6°C (Fig. 2). No classically defined thermocline is developed (Lindegaard 1980), although a thermal stratification does exist (Lastein 1983). The lake can be classified as oligo- to mesotrophic, and phytoplankton production is fairly high (Fig. 2).

The zooplankton of the lake is dominated by *Daphnia longispina* (Müll.), *Cyclops abyssorum medianus* (Lindberg), and *Leptodiaptomus minutus* (Lilljeborg). The zoobenthos is dominated by chironomids, tubificids and the snail *Lymnaea peregra* (Müll.). with a maximum density of chironomids and molluscs in the stony littoral zone, 0–10 m (Antonsson 1992, Lindegaard 1980, Snorrason 1982, Lindegaard et al. 1992).

The fish fauna of Thingavallavatn is greatly dominated by arctic charr, which are found in all habitats. The threespine stickleback is common in sheltered bays, and abundant in the *Nitella*-zone, whereas brown trout are very rare, mostly due to the lack of spawning facilities after the regulation of the lake outlet.

Material and methods

Electrofishing

Age-0 charr were sampled with an electric fishing apparatus in the surf zone at 0–0.5 m depth. In September 1983, sampling was carried out at two localities. Skútavík and Mjóanes (Fig. 1). In June – August 1984, three littoral localities, Midfell, Lambhagi and Ólafsdráttur were sampled. In 1985 the two localities Midfell and Ólafsdráttur were sampled at least monthly from May through September, and in November. A total of 833 age-0 charr were examined.

Densities of age-0 charr in the surf zone were estimated through repeated samplings (cf. Seber and LeCren 1967) in 11 and 13 areas around the lake in August 1984 and June 1985, respectively.

Gill netting

A total of 5808 arctic charr was caught with pelagic and benthic gill nets in August 1983, May/June 1984 (later called May 1984) and August/September 1984 (later called August 1984). During this sampling five brown trout and two threespine sticklebacks were caught. The benthic nets consisted of 12 panels 1.8 × 6 m, with mesh sizes 10, 12.5, 15, 18.5, 22, 25 mm in spun nylon, and 29, 33, 38, 43, 50, 60 mm in monofilament nylon. The pelagic nets consisted of the same mesh sizes and materials in 6 × 6 m panels. These nets caught arctic charr between 7 and 47 cm in length.

Pelagic nets were used at two locations (Fig. 1), over 72 m depth between Lambhagi and Midfell, and over 13 m depth above the *Nitella*-zone at Midfell. At the deep pelagic station fishing was carried out at six different depth zones between surface and bottom (Fig. 3). The pelagic net close to surface (0–6 m) was sectioned horizontally at 2 m, to distinguish the catch in the topmost surface water (epipelagic habitat, 0–2 m) from that in deeper water The 66–72 m pelagic net stood on the bottom. This net was sectioned horizontally to separate the catch closest to the bottom (epibenthic habitat 70–72 m). Over the *Nitella*-zone fishing was performed at two depths: close to the surface (0–6 m) and on the bottom (7–13 m). These nets were also horizontally sectioned to separate catches in the surface layer (0–2 m) and epibenthic (11–13 m) habitats.

Benthic nets were used at three locations (Fig 1), Midfell, Lambhagi and Bjarnamöl. At all locations, fishing was performed on the shallow stony substrate (0–10 m). On the *Nitella*-substrate (10–20 m), fishing was carried out at Lambhagi and Midfell and on the muddy substrate deeper than 30 m at Lambhagi (Fig. 3).

Arctic charr for genetic and parasitological analysis were caught with 10–60 mm benthic gill nets during July – November 1983.

Pelagic trawling

In September 1983 trawling was performed with a pelagic pair trawl with cod end mesh size 5 mm (Lindem and Sandlund 1984) over the deep area between Lambhagi and Midfell. This sampling caught planktivorous charr between 3.8 cm and 24.0 cm fork length.

Echosounding

Echosounding was carried out with a Simrad EY-M portable echosounder in August 1983, and June and September 1984. The echosounding was done on 12–17 transects covering the lake basin at a depth over 10 m. The echo signals were recorded on tape and later computer analyzed. The analyses give minimum estimates

Table 1. Regression of ovarian weight (OW, g) on individual fecundity (F) of four arctic charr morphs from Thingvallavatn. All coefficients (R^2) of determination are significant ($P < 0.05$) (from Skúlason 1983).

Morph	Regression	Fecundity range	R^2	N
SB-charr	$\log_e OW = 0.01045F + 0.0665$	13– 385	0.70	46
LB-charr	$\log_e OW = 0.00087F + 2.9640$	135–2974	0.77	21
PL-charr	$\log_e OW = 0.00373F + 1.7468$	90– 297	0.55	26
PI-charr	$\log_e OW = 0.00094F + 3.0872$	293–2076	0.89	12

for pelagic fish density, and by an indirect statistical method the echostrength distribution is transformed to a target strength (TS) distribution (Lindem 1983). The size distribution of pelagic fish is found by relating TS-distribution to the size distribution of fish caught in pelagic gill nets and trawl (Lindem and Sandlund 1984, Rudstam et al. 1987).

Mark-recapture experiments

A total of 560 charr were tagged with floy tags during 1983. The fish were caught, tagged and released at Ólafsdráttur, Skútavík and Nesjavík (Fig. 1). Recaptures were made by local fishermen, and during our own gill net sampling.

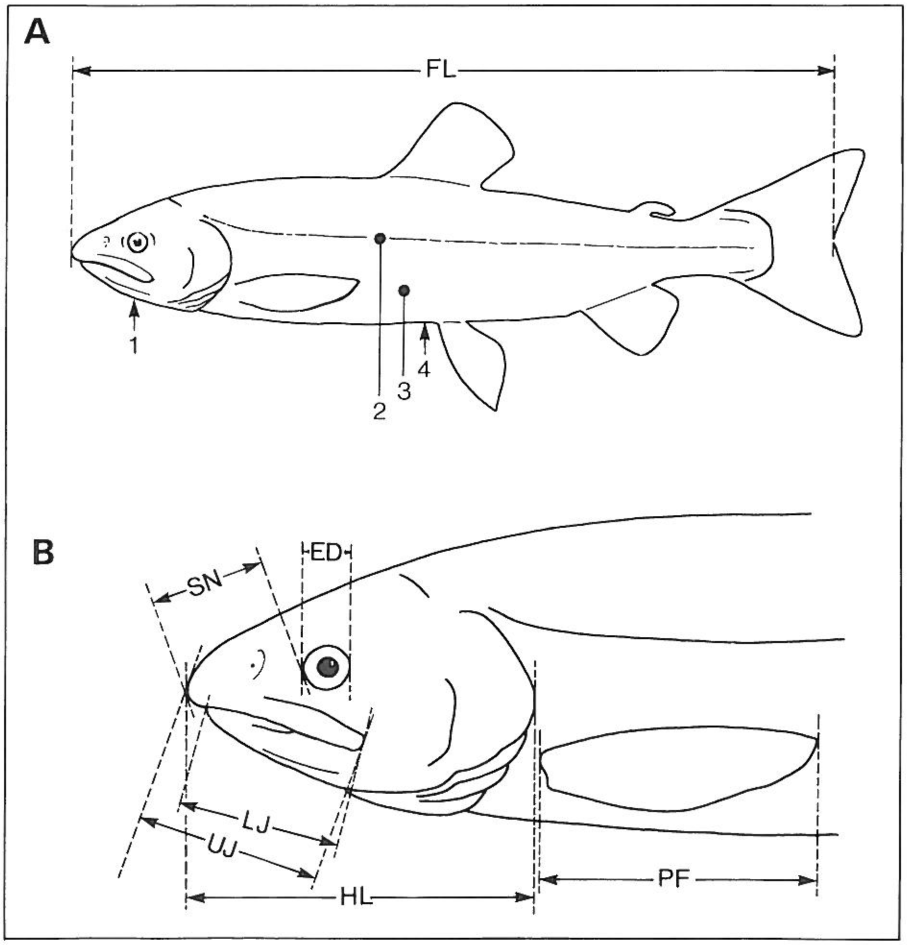


Fig. 4. External colour pattern and mensural characters determined.
A.
FL = fork length,
1 = presence or absence of melanization on ventral side of lower jaw,
2 = presence or absence of parr marks,
3 = colour of belly edge (white, beige, orange),
4 = colour of belly (white, beige, orange).
B.
HL = head length,
PF = length of pectoral fin,
LJ = length of lower jaw, measured with mouth held close,
UJ = length of upper jaw,
ED = eye diameter,
SN = snout length, measured from the anterior edge of the eye socket to the tip of the snout.

Treatment of material

Site and depth were recorded for each fish sampled, and specimens were classified into one of four morphs according to mouth position and coloration. Of the 5808 charr caught during test fishing with gill nets. A total of 103 fish (1.8%) were impossible to classify to morph.

Fork length was measured (mm), weighed (g), sexed and degree of sexual maturity recorded. Weight-length relationships were estimated from wet weights (W, g) and fork lengths (L, mm) by the general regression model: $\log_e W = b \log_e L + a$.

Ages of the charr were estimated by use of sacculus otoliths. The otoliths were both read whole, as described by Jonsson (1976), and transversely after being burnt and divided as described by Christensen (1964). Annual adult survival rate was estimated by use of the Chapman-Robson method (Youngs and Robson 1978). Age groups giving significant fit ($P > 0.05$) to the model were used.

Individual fecundity (F) was defined as number of mature eggs per adult female just prior to spawning. Regressions of fecundity on fork length were calculated with both untransformed and $\log_e$-transformed data sets, and the data set giving the better fit was used. Age specific population fecundity was estimated as a function of the number of fish in each age group, and their mean fecundity:

$$PF_i = N_i F_i \, 100 \sum_{x=a}^{x} N_x F_x,$$

where N_i = number of mature females at age i, F_i = mean age specific fecundity, a = age of youngest mature female, n = age of oldest mature female.

Gonadosomatic indices (GSI) of females were estimated as ovarian wet weight (OW, g) on somatic wet weight (SW, g): $GSI = 100\,(OW/SW)$. Ovarian weights were estimated on basis of their fecundity. This was based on data from Skúlason (1983) (Table 1).

Relative annual investment into reproduction (RAI) of females at age i was estimated as ovarian weight (OW_i) on ovarian weight plus annual increase in somatic weight (ISW_i): $RAI_i = OW_i/OW_i + ISW_i$ (Mills and Eloranta 1985).

Stomach contents were dissected out and stored frozen until analyzed. Prey groups were identified under a stereoscopic microscope, the stomach content was sorted to taxonomic groups, and the organisms counted. Ash free dry weight (AFDW) of the various groups was determined (Malmquist 1988), and the diet is presented here as per cent AFDW. Diet overlaps of morphs occurring in the same habitat were calculated by Schoener's (1968) index:

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

where p_i and q_i are weight proportions of prey group i in stomachs of morphs p and q, respectively. n is number of prey groups. D varies from 0 (no diet overlap) to 1 (complete diet overlap).

Dietary breadth (B) of each morph was estimated according to Levins (1968):

$$B = \left(\sum_{i=1}^{6} p_i^2 \right)^{-1}$$

where p_i is the weight proportion of prey group i. B may vary between 1 (narrow food niche) and 6 (wide food niche), as we defined the following six prey groups: 1) *Lymnaea peregra*, 2) insect larvae, 3) insect pupae, 4) crustacean zooplankton, 5) surface insects, and 6) fish (threespine stickleback and arctic charr).

The following organs were examined for parasites: digestive tract, liver, kidney, urinary ducts, gonads, swimbladder, and eye. External parasites were excluded due to the methods of catching, when nets were out for 10 hours. Thirty-one fish were examined fresh whereas 100 fish were frozen and examined later. The analyses were performed according to methods described by Bylund et al. (1980) and Frandsen et al. (1989). The terms prevalence, intensity and mean intensity applied here follow the definitions given by Margolis et al. (1982).

From the arctic charr caught during test fishing in 1983, 1461 adult fish (230 SB-charr, 100 LB-charr, 1031 L-charr, 100 PI-charr) were scored for external body colours and flesh colour. Morphological characters were measured on 411 adults (123 SB-charr, 58 LB-charr, 158 PL-charr, 72 PI-charr) (Fig. 4).

Measurements were performed with a dial caliper to the nearest 0.1 mm. Gillrakers were counted on the anterior left gill arch from 387 adults. Adult fish were defined as SB-charr older than 2 yr, PL-charr older than 3 yr and PI- and LB-charr older than 5 yr. The reasons for not including younger fish in the morphological analysis were that young fish grew faster than adults and exhibited different allometric relationships.

The morphological data were analysed using software from SAS Statistical Institute (Freund and Littel 1981, Ray 1982a). To facilitate comparisons of shape between morphs, mensural variables were adjusted or transformed, thereby removing the effects of fish body size. Two methods were used to achieve this: Principal Components Analysis, PCA, deriving sheared components of shape, as described by Humphries et al. (1981) and Canonical Discriminant Analysis, CDA (Pimentel 1979), with size adjusted characters (Thorpe 1976, Reist 1985). The data on external coloration, flesh colour and gill raker number were analysed using the FREQ procedure in SAS, testing for association (Ray 1982b).

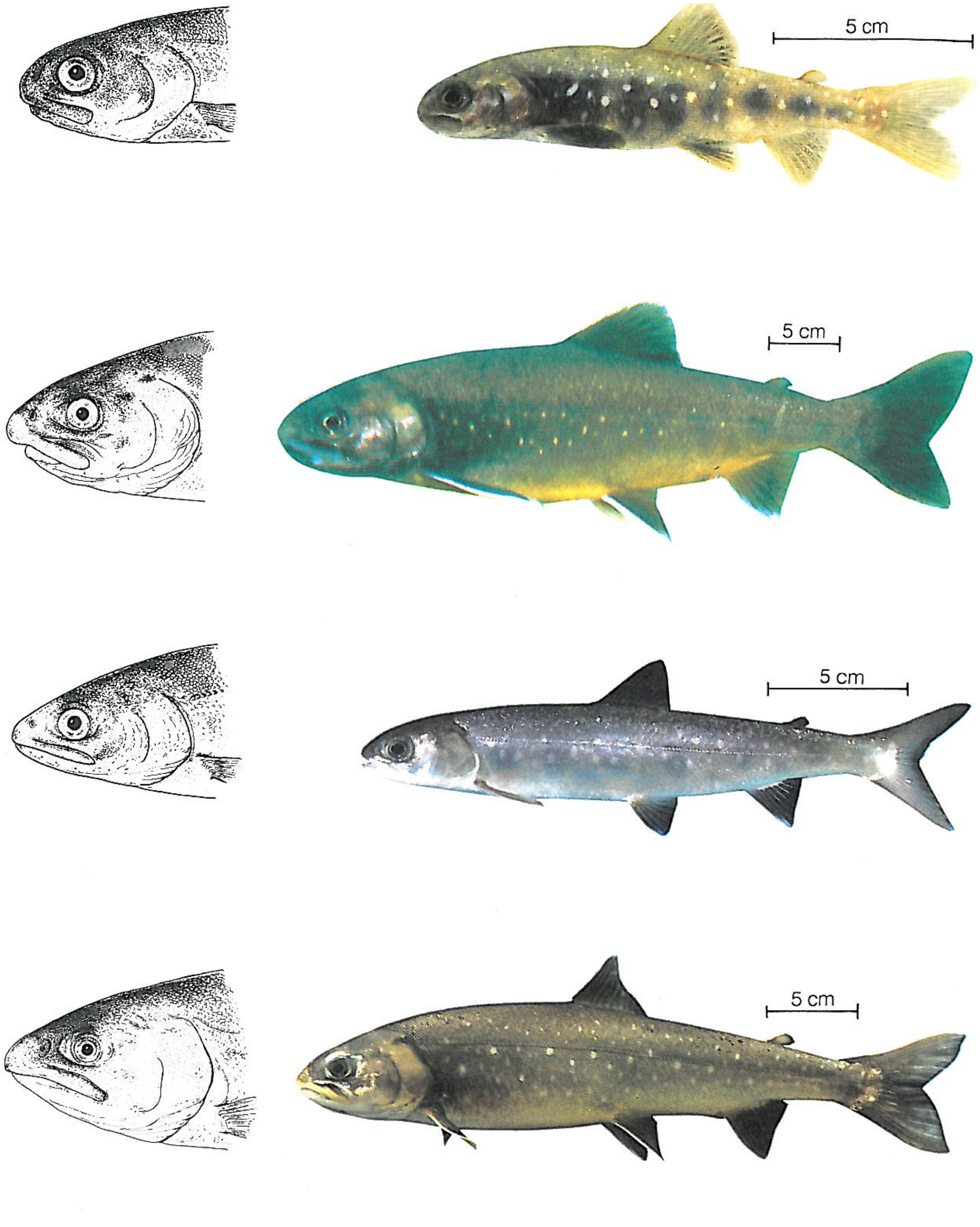
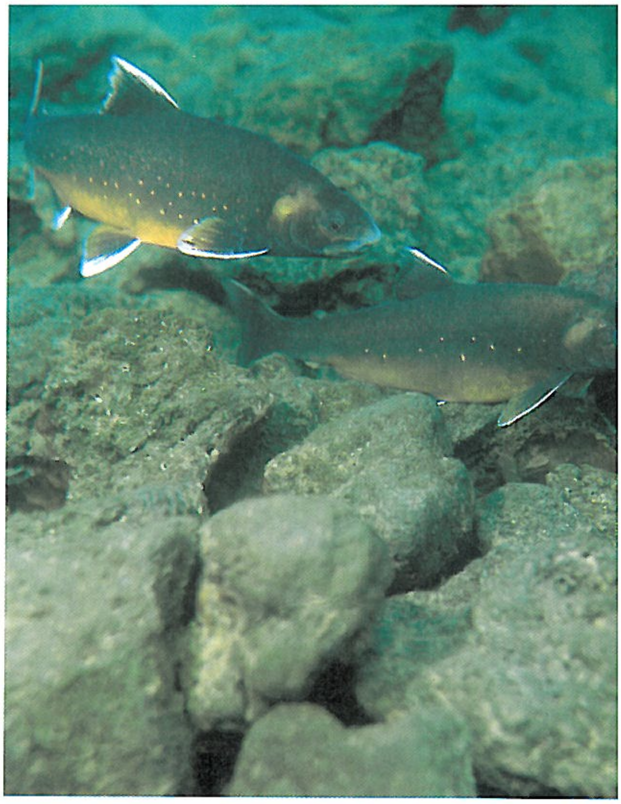
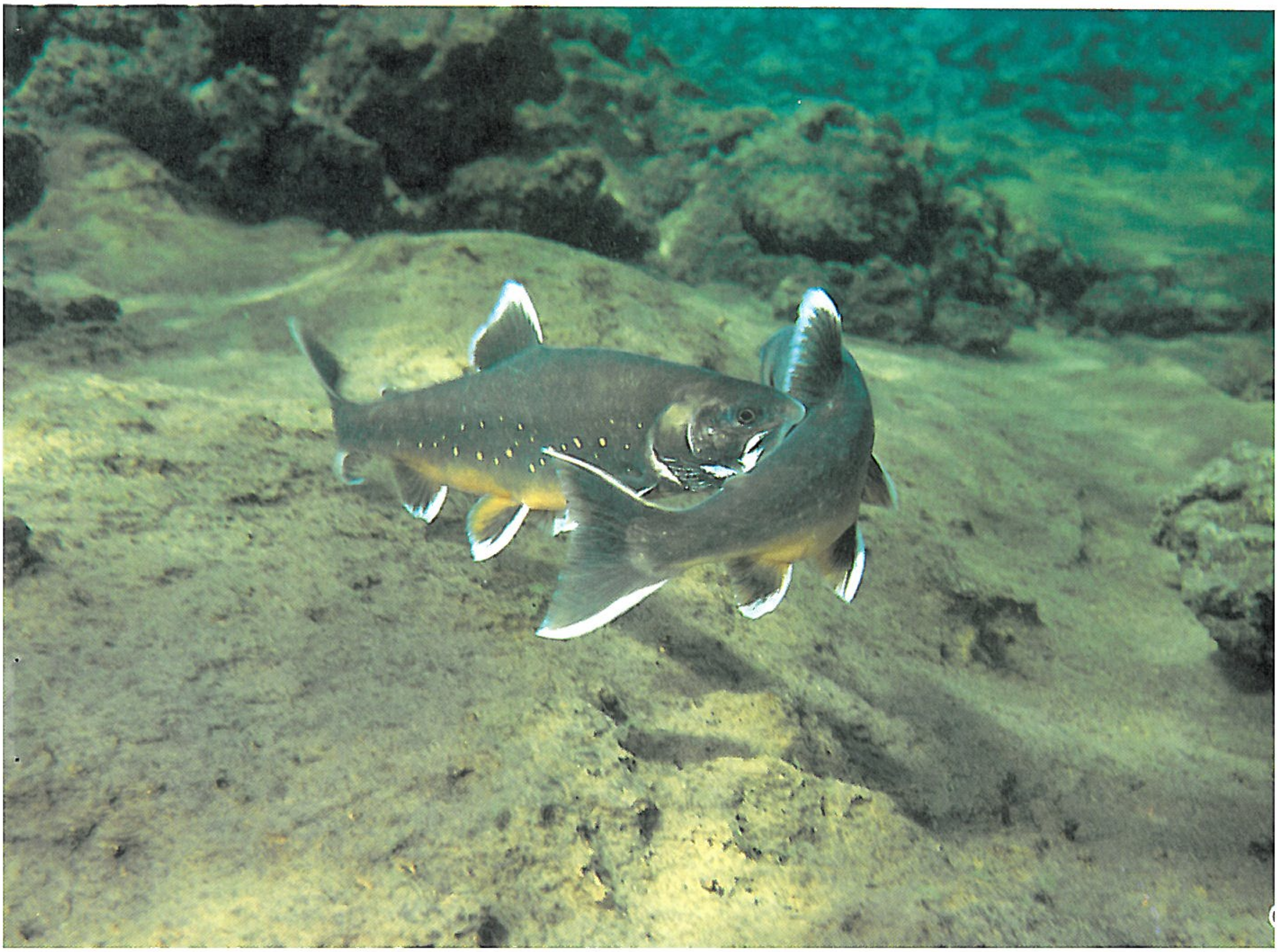
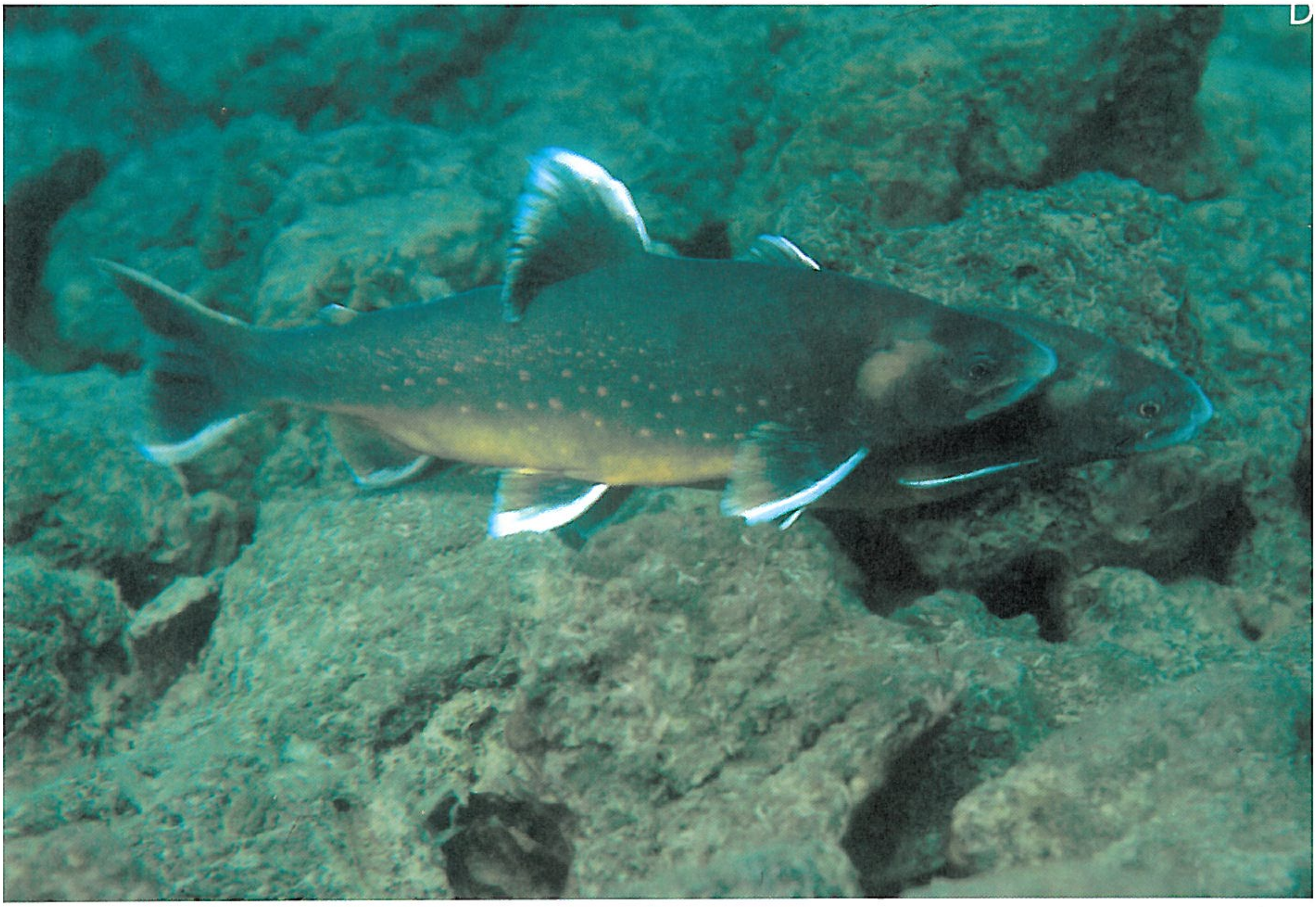


Fig. 5. The four arctic charr morphs, with drawings of lateral view of their heads. From top: Small benthivorous (SB-) charr, Large benthivorous (LB-) charr, Planktivorous (PL-) charr, Piscivorous (PI-) charr. Body lengths ofthe individuals shown were: SB-charr 11.3 cm; LB-charr 34.0 cm; PL-charr 12.5 cm; PI-charr 31.5 cm. (Karl Gunnarsson and A. Gardarson phot.)


A



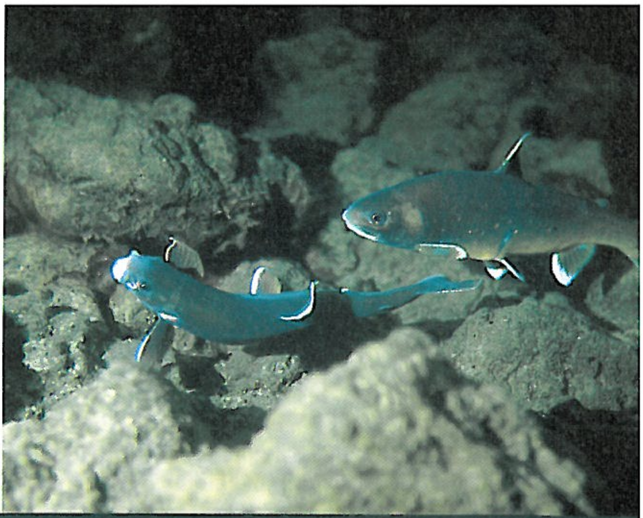


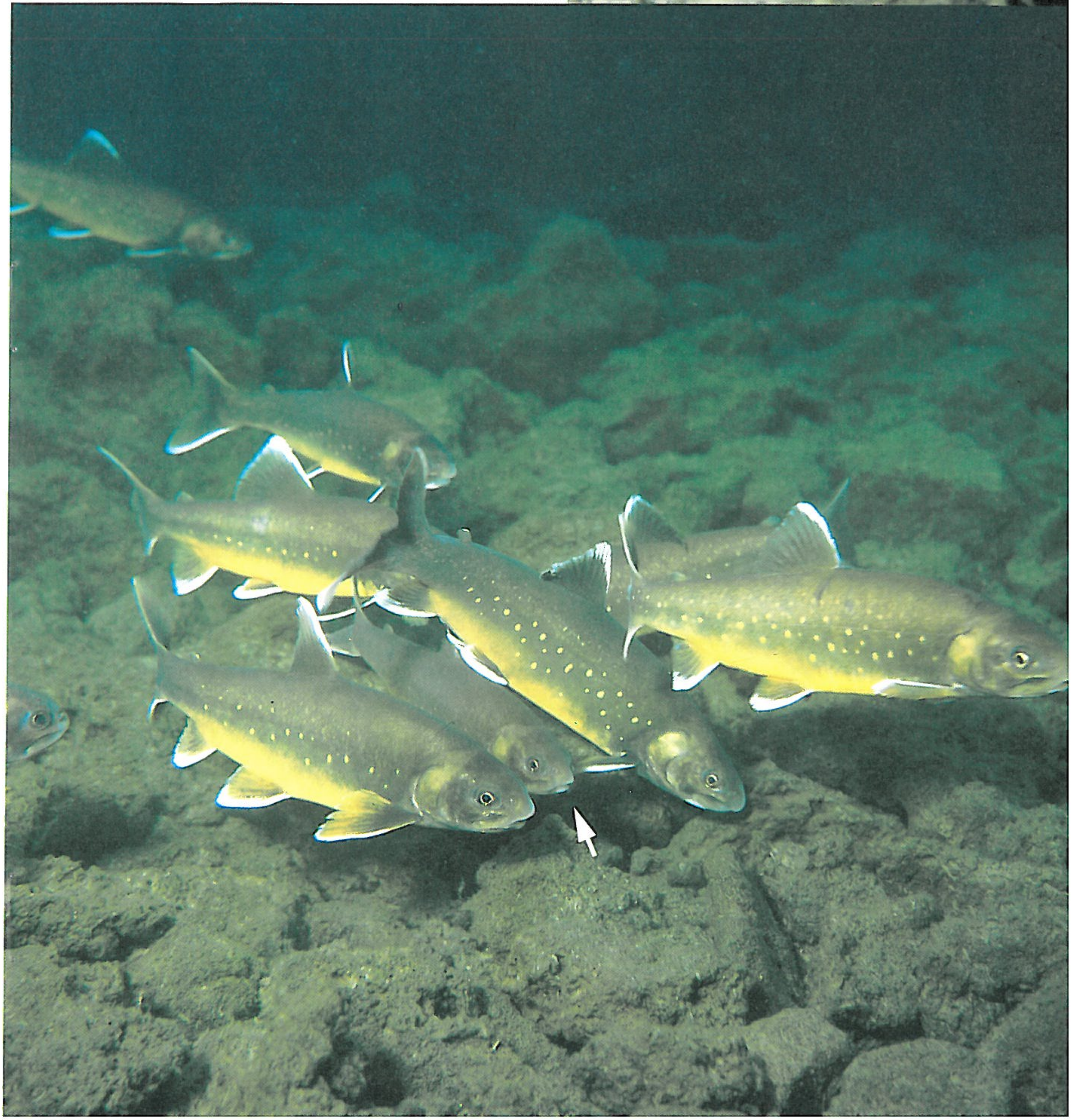


D

E

Fig. 27. Behaviour of LB-charr on the spawning site. A. A female cleaning the site. B. The male is situated above and posterior to the female, guarding her against potential sneakers. C. One male attacking another. D. Courtship behaviour. The male glides alongside the female, its body shivering. E. Orgasm (release of gametes). F. The female is sweeping the eggs down into the substrate after oviposition. G. At times of high density, many males will compete for access to the female (indicated by an arrow). (Karl Gunnarsson phot.)





Spawning time and place

Information on spawning periods and spawning places was compiled from Skúlason (1983), from our present sampling, from samples of commercial catches of PL-charr (Snorrason et al. 1991) and from interviews with local fishermen. Frequencies of potential spawners (maturity stages 5–6) in catches indicate spawning periods.

Spawning behaviour

Spawning behaviour was observed in LB-charr spawning at Ólafsdráttur (Fig. 1). The mating fish were photographed and filmed, and parameters such as number of courting males per female, size differences between and within sexes and the succession of behaviour during mating and spawning were recorded. Number of fish on the spawning ground was estimated by counting along zig-zag transects covering the spawning ground.

Early ontogeny

Experimental progeny groups were obtained from artificial matings within each morph (Skúlason 1986). In the laboratory, fertilized ova were incubated in Reykjavík tap water, mean temperature 4.7°C (range 4.4–5.1°C). Egg diameter was measured with a caliper. Embryo growth was recorded until the onset of exogeneous feeding, to test the relationship between yolk volume and free embryo size, and how this correlated with size differences among the morphs. After exogeneous feeding started, the fish were fed freeze dried brine shrimp (*Artemia* sp.) and later commercial salmonid rearing food (EWOS ST40 No. 1). Mortality was negligible throughout the laboratory experiment.

Eight mensural head characters in addition to fish standard length were measured on the laboratory reared progeny groups at age 153 d, 183 d and 225 d after fertilization. The data were analysed using canonical discriminant analysis (CDA) (Ray 1982a), to obtain information on the relationship between the a priori classified progeny groups (Pimentel 1979). To compare shapes, the measurements were adjusted for fish size (Thorpe 1976, Reist 1985).

To examine early development among morphs in the field, fertilized eggs were placed in Whitlock-Vibert boxes placed inside a closed box full of gravel at two different spawning localities, Ólafsdráttur (OD) and Svínanes (SV) (Fig. 1). At OD, cold spring water influences water temperatures in the substrate (Fig. 26). Two places (OD-A and OD-B) with slightly different temperature regimes were used at this location. At SV, there is no spring water influence.

Morphology

Results

Colour patterns and seasonal colour changes

SB-charr always feature benthic camouflage coloration (Fig. 5). The back is very dark and the sides are set with parr marks and irregular golden or yellow specks. The belly is yellow or beige with a golden tinge. The ventral side of body and head is often melanized to various degrees. The external colours do not change much during spawning (August–November).

Outside the spawning season (July–August) mature LB-charr exhibit typical benthic camouflage coloration (Fig. 5). The back is very dark, and the sides are a shade lighter, with a silvery tinge. The adults lack parr marks but the sides are frequently set with small round light specks. The belly is white or yellowish.

Outside the spawning period (September–November), PI-charr feature a brown back, the sides are somewhat lighter, often silvery, frequently with small round light specks, and the belly is white or pale yellow (Fig. 5). During spawning, both LB- and PI-charr become darker on the sides and develop brilliant white stripes on the anterior edge of the fins. The belly becomes bright yellow or orange (Fig. 27).

PL-charr exhibit pelagic camouflage colours (Fig. 5). The back is dark with a green tinge, the sides are silvery, often with small round lighter specks, and the belly is white. During spawning (September–October), which takes place in the littoral zone, the males develop benthic camouflage, as they become darker and some even develop faint parr marks. The females retain their pelagic colours also during spawning. This difference may be due to the fact that males stay at the spawning grounds for a relatively long period, whereas the females only stay to release their eggs.

Analysis of size and shape

The morphs showed significant differences in all 7 log-transformed mensural characters (univariate ANOVA, $F's_{3,407} = 253 - 472$, $P < 0.001$), reflecting a distinct difference in body size among mature fish of the morphs (Fig. 19).

In the principal component analyses of $\log_{10}$-transformed mensural characters, we found that the first component (PC1) accounted for 97.1% of total variation (Table 2). There was a clear size effect and isometry among characters as all character loadings of PC1 were positive and uniform. Eye diameter was the only character that departed from multiple isometry (0.22 vs expected value for isometric character loading: 0.38). The eyes became relatively smaller as the fish grew larger (see also Table 4).

The second principal component, PC2, indicated variation in the ratio eye diameter on snout length (Table 2). Although variation among morphs was highly

Table 2. Variable loadings of the first three principal components (1–3), sheared component 3 (H_3), total canonical structure (CS1) and within standardized canonical coefficients (SC1) of seven (for CS1 and SC1: six) $\log_{10}$-transformed mensural characters of 411 adult arctic charr from Thingvallavatn.

Character	Principal component:			H_3*	CS1	SC1
	1	2	3			
Fork length (FL)	0.42	0.44	−0.02	−0.03		
Upper jaw length (UJ)	0.41	−0.13	−0.22	−0.23	0.32	0.88
Lower jaw length (LJ)	0.42	−0.00	−0.66	−0.67	−0.42	−1.54
Pectoral fin length (PF)	0.36	0.19	0.67	0.66	0.76	0.59
Head length (HL)	0.37	0.12	0.03	0.01	0.63	0.49
Eye diameter (ED)	0.22	0.36	0.08	0.08	0.27	−0.02
Snout length (SN)	0.41	−0.78	0.24	0.22	0.46	0.13
Variances	0.1598	0.0015	0.0012			
Per cent variation	97.13	0.92	0.72			

* shear coefficients $a_3 = 0.030$, $b_{1,3} = 1.00$, $b_{2,3} = 0.026$.

significant (ANOVA of PC2: $F_{3,407} = 50.25$, $P < 0.0001$), the group definition was poor as variation within SB-charr overlapped to a large extent with the other morphs.

The lower jaw length and pectoral fin length accounted for most of the variation in the third principal component, PC3 (0.72% of total variation). Among-group variation was highly significant (ANOVA of PC3: $F_{3,407} = 112.56$, $P < 0.0001$), and the means were all significantly different; LB-charr > SB-charr > PL-charr > PI-charr (Duncan's multiple range test) (Table 3). The grouping of morphs in the plane of the first and third principal component was clear (Fig. 6). The third principal component was therefore used in order to generate a size-free shape discriminator, H_3 (Table 2) (Humphries et al. 1981). The shape discriminator, H_3, indicated distinct differences between the benthivorous morphs on one hand and the planktivorous and piscivorous morphs on the other (Fig. 6).

We found that the morphs differed in allometric relationships of some mensural characters versus fork length (Table 4). Therefore we had to use within group coefficients for allometric size adjustments before canonical discriminant analysis. Hence, the removal of size effects in the transformed measurements was incomplete ($R^2 = 0.181$, $F_{6,404} = 14.9$, $P < 0.001$). All adjusted characters were significantly different among morphs (Table 5). There were also significant differences between all morph pairs (Table 6). The difference was smallest between PL- and PI-charr, and between LB- and SB-charr. In the canonical discriminant analysis the first axis covered 91.5% of the variation in discriminant space, and therefore interpretations were restricted to information contained in this axis. There was high correlation between canonical variables and original variables for all mensural characters (Table 2), the highest being lower jaw length, pectoral fin length, snout length and head length. We found discrimination contrasts in lower jaw length versus pectoral fin length, snout length and head length (Table 2). Among group variation in the first canonical variable was significant ($F_{3,407} = 471.8$, $P < 0.0001$).

Plotted against each other the shape discriminators H_3 and CAN1 showed two main clusters; one for LB- and SB-charr, and one for PI- and PL-charr (Fig. 7). There was a high positive correlation between these discriminators ($R^2 = 0.721$, $F_{7,403} = 149.2$, $P < 0.0001$).

Analysis of discontinuous variables

Presence of parr marks clearly discriminated SB-charr from the other morphs (Table 7). The six (2.6%) SB-charr found without parr marks were all relatively old and large individuals. The ten (1.0%) PL-charr found with parr marks were mostly young and relatively small individuals. The four (4.0%) LB-charr found with parr marks were all small.

SB-charr also differed from the other morphs by having melanin (black colour) on the ventral side (Table 7). The beige colour of the belly in SB-charr may be a mixture of the yellow-orange pigment and the melanin. PL-charr was very homogeneous in external coloration, whereas the large morphs were more variable. Flesh colour differed significantly between the morphs (Table 7). The small morphs (SB- and PL-charr) had mainly white flesh whereas the large morphs (PI- and LB-charr) had mostly orange flesh.

The four morphs differed in mean number of gill rakers (± standard error): SB-charr 24.3 ± 0.16, LB-charr 25.9 ± 0.21, PL-charr 27.4 ± 0.10 and PI-charr 26.8 ± 0.19. The distribution of gill raker number did not differ significantly between PL- and PI-charr, but there was a significant difference between all other pairs of morphs (G-tests, $P < 0.05$).

Table 3. Mean scores of principal component (PC) 1–3, sheared component 3 (H_3) and the first canonical axis (CAN1) of seven $\log_{10}$-transformed mensural characters for four morphs of arctic charr from Thingvallavatn. Based on measurements from 411 adult arctic charr.

Morph	PC1	PC2	PC3	H_3	CAN1
SB-charr	−0.45	−0.017	0.011	0.024	2.35
LB-charr	0.37	0.009	0.047	0.035	1.46
PI-charr	0.47	−0.026	−0.027	−0.041	−1.39
PL-charr	−0.00	0.022	−0.013	−0.013	−1.73

Discussion

These morphological analyses demonstrate that the classification of arctic charr morphs in Thingvallavatn based on mouth position and external coloration has a sound quantitative basis.

The shape analyses clearly identify two morphotypes of arctic charr in Thingvallavatn: a "pelagic" morphotype, with terminal mouth (i.e. long lower jaw) and small pectoral fins, including the two morphs PL- and PI-charr, and a benthic morphotype, including SB- and LB-charr, featuring subterminal mouth (i.e. short lower jaw) and large pectoral fins. The pelagic morphotype is within the range of morphological variation shown by arctic charr in general (Cavender 1980, Behnke 1980). The benthic morphotype, however, shows trophic morphology that has not been described for arctic charr from other places (Behnke 1980).

The dichotomy in mouth position and pectoral fin size appears to be a clear case of trophic adaptation (Schutz and Northcote 1972, Lavin and McPhail 1986), as it corresponds well with habitat and diet divergence between the two morphotypes (see Habitat use and Food, below). Subterminal mouth and large pectoral fins are typical of benthic feeders. Terminal or undershot mouth is more common in plankton feeders and predators that snap food particles (Nikolsky 1963, Keast and Webb 1966). The differences in gill raker number also fit with the diet of the morphs. The planktivore PL-charr has the highest, and the benthivores, LB- and SB-charr, the lowest gill raker number.

Within both morphotypes the most marked difference between morphs was that of adult body size (Fig. 18). There were also significant shape differences between morphs within the morphotypes. The differences were smallest between PL- and PI-charr, as these two morphs differ significantly in mensural characters, but not in gill raker number. SB- and LB-charr differed both in mensural characters and in gill raker number. SB-charr are also quite different from the other morphs in coloration, commonly featuring parr marks, beige belly and melanized lower jaw.

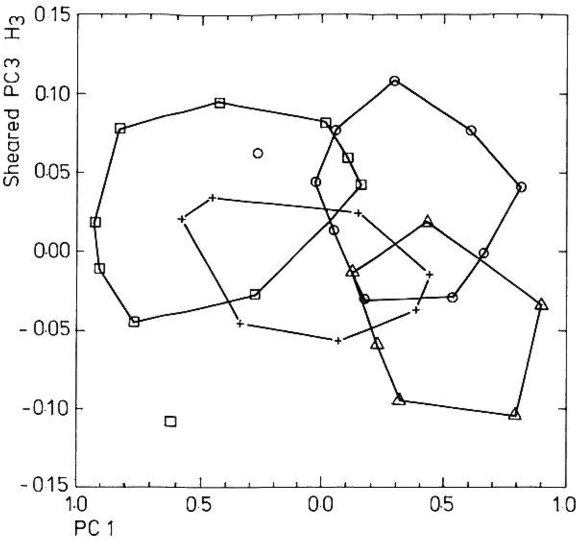


Fig. 6. Outlines of score clusters for the sheared principal component 3 (H_3) on principal component 1 (PC1) of $\log_{10}$-transformed mensural characters in 411 arctic charr from Thingvallavatn. □ = SB-charr, ○ = LB-charr, + = PL-charr, △ = PI-charr. Cluster outlines inclide peripheral individuals, except individuals deviating more than 0.2 PC1 units from the respective main clusters.

Habitat use

Results

Habitat of young of the year

Young of the year charr were living in the surf zone (0–0.5 m depth) from May through November (Fig. 8). In May and early June, length distribution of age-0 fish in this zone was unimodal and variation small (coefficient of variation, $CV < 0.08$). From late June a few larger age-0 fish appeared in the catches, and variation in length increased significantly ($P < 0.05$, test of equality of two variances). Later during summer and autumn, variation remained high ($CV > 0.10$).

Mean densities of age-0 charr in the surf zone were

Table 4. Slopes of regression $\log_{10}(Y)$ on $\log_{10}(FL)$ (FL: fork length) for individual measurements of each mensural character (Y) for each morph, and F-tests of homogeneity of slopes among morphs (P gives the significance level). Based on measurements from 411 adult arctic charr from Thingvallavatn.

Mensural character	SB-charr	LB-charr	PI-charr	PL-charr	F	P
Upper jaw	0.943	1.006	1.032	1.079	2.69	0.046
Lower jaw	0.865	0.980	1.064	1.112	9.19	< 0.001
Pectoral fin	0.941	0.942	0.886	0.953	0.32	0.811
Head length	0.930	0.860	0.929	0.914	0.84	0.472
Eye diameter	0.644	0.467	0.338	0.636	11.69	< 0.001
Snout length	0.979	0.892	1.044	1.142	2.93	0.033

Table 5. Means of size adjusted mensural characters ($\bar{X}$) of 411 adult arctic charr from Thingvallavatn. P-values denote significance of F-tests between morphs (univariate ANOVA).

Character	$\bar{X}$	$\bar{X}_{SB}$	$\bar{X}_{LB}$	$\bar{X}_{PI}$	$\bar{X}_{PL}$	$F_{3,407}$	P
Upper jaw	19.08	19.79	18.79	19.78	18.32	35.97	0.001
Lower jaw	17.13	16.61	16.27	18.41	17.28	43.53	0.001
Pectoral fin	30.75	33.05	32.33	29.54	28.93	113.34	0.001
Head length	42.41	44.78	42.87	42.67	40.19	83.19	0.001
Eye diameter	8.90	9.21	8.65	9.01	8.70	23.61	0.001
Snout length	9.19	9.77	9.33	9.49	8.56	46.22	0.001

(± 95% confidence limits) 1.83 ± 1.07 m^{-2} in August 1984 (11 sampling areas, range: 0.1–6.1 m^{-2}) and 4.70 ± 3.13 m^{-2} in June 1985 (13 sampling areas, range: 0–16.6 m^{-2}). Of the total of 441 fish caught during sampling for density estimates, seven (1.6%) were threespine stickleback.

Pelagic trawlings in August 1983 caught young of the year PL-charr at 15–20 m depth between Midfell and Lambhagi. Mean length of these fish was 42.25 ± 3.62 mm. Thus they were similar in size to the larger among age-0 charr from the surf zone at that time of the year.

Vertical distribution of morphs in pelagic and epibenthic habitats

Vertical distribution of the four Arctic charr morphs in pelagic and epibenthic habitats in May and August is demonstrated by the gill net catches made in August 1983 (Fig. 9), May 1984 (Fig. 10) and August 1984 (Fig. 11). PL-charr dominated in all habitats and depths. In the total catches during August 1983, May 1984, and August 1984 PL-charr made up 95.6, 99.6 and 99.0% of the pelagic catches and 55.4, 58.3 and 67.4% of the epibenthic catches, respectively. Only in the shallow littoral zone (< 10 m depth) and the *Nitella*-zone (10–20 m) were other morphs of any prominence. LB-charr was important in both these epibenthic habitats, whereas SB-charr was restricted to the shallow littoral zone. PI-charr was found in low numbers in the epibenthic habitat, and also occasionally in the pelagic zone.

In August, gill net catches were significantly higher at night than during day in all habitats except for those deeper than 35 m in the pelagic zone (Wilcoxon's signed rank test, $P < 0.01$) (Figs 9 and 11). The day and night catches in May were not significantly different ($P > 0.05$) (Fig. 10). Catches were generally lower in May than in August. Epibenthic catches were low above 10 m in May.

SB-charr showed low activity during the day. In four out of six sampling series in the shallow littoral zone (0–10 m) there were no catches of SB-charr at all during the day. Visual observations and electrofishing in the littoral zone suggested that SB-charr hide between stones during the day. To test this, small meshed nets (10 mm) were laid out horizontally covering sections of the stony bottom at depths between 0.2–1.0 m. These

Table 6. Mahalanobis distances (MD) between four morphs of arctic charr, based on six size adjusted (by fork length) mensural characters. F-statistics for comparisons between groups and probabilities (P) of higher F under null-hypothesis of equal centroids.

Morph	SB-charr	PL-charr	PI-charr
PL-charr (MD)	4.12		
F	247.7		
P	< 0.001		
PI-charr (MD)	3.83	1.35	
F	64.3	6.8	
P	< 0.001	< 0.001	
LB-charr (MD)	1.38	3.25	3.28
F	5.8	27.1	45.9
P	< 0.001	< 0.001	< 0.001

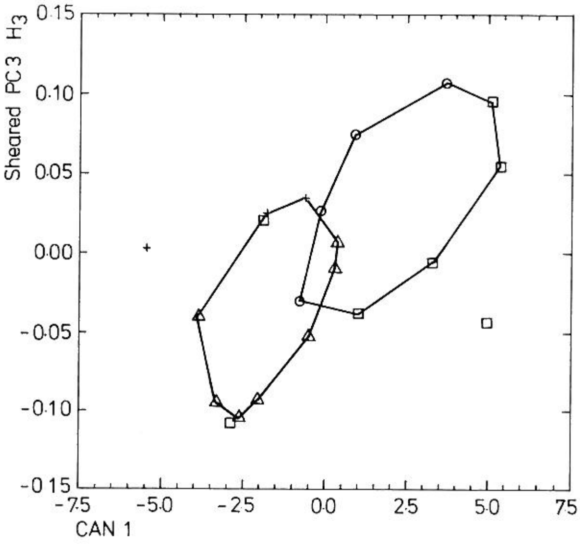


Fig. 7. Outlines of score clusters for sheared component 3 (H_3) and the first canonical variable (CAN1) from canonical discriminant analysis on size adjusted mensural characters in 411 arctic charr from Thingvallavatn. □ = SB-charr, ○ = LB-charr, + = PL-charr, △ = PI-charr. Cluster outlines include peripheral individuals, except individuals deviating more than 1.0 CAN1 units from the respective main clusters.

Table 7. Number of fish in colour categories, and χ^2-tests of independence of score distribution and morph classification.

Character	Scores	SB-charr	PL-charr	PI-charr	LB-charr	Tests of association
Parrmarks	+	224	10	0	4	$\chi^2 = 1317$
	–	6	1021	100	96	$P < 0.001$
Belly edge	beige	54	0	0	0	$\chi^2 = 789$
	yellow	167	1007	52	45	$P < 0.001$
	orange	9	24	48	55	
Belly	white	49	1030	89	55	$\chi^2 = 1442$
	beige	168	0	0	0	$P < 0.001$
	orange	13	1	11	45	
Melanized lower jaw	+	204	6	10	19	$\chi^2 = 1071$
	–	26	1025	90	81	$P < 0.001$
Flesh	white	227	697	17	16	$\chi^2 = 327$
	orange	3	334	83	84	$P < 0.001$
Number of fish		230	1031	100	100	

nets only caught SB-charr during night, always from below. The other morphs showed smaller diel activity variation. Average CPUE day/CPUE night for the shallow littoral and *Nitella*-zones over all sampling periods were 0.61, 0.58, 0.14 and 0.56 for PL-, PI-, SB- and LB-charr, respectively.

In August pelagic PL-charr were most abundant close to the surface, and the abundance decreased gradually with depth. Near the bottom, however, the abundance increased again (Figs 9 and 11). In May, on the other hand, PL-charr was most abundant at a depth of 20–26 m (Fig. 10). PL-charr caught over the *Nitella*-zone in August were also most abundant near the surface and the bottom. PL-charr was relatively abundant along the bottom at all depths investigated.

Hydroacoustic recordings were made on six occasions during 1983–1985. In the pelagic zone, target strength (TS) distributions on all occasions show an increasing proportion of small fish with depth small fish: TS < -46 dB, corresponding to fork length < 14 cm), indicating that small PL-charr live in deeper pelagic waters (Fig. 12). This was supported by the size distribution of PL-charr in the pelagic gill net catches. In August 1983 and May 1984, there were significantly more small PL-charr in the catches from deeper waters (August 1983: $\chi^2 = 41.6$, 3 d.f., $P < 0.001$, May 1984: $\chi^2 = 33.0$, 2 d.f., $P < 0.001$). Mean lengths of PL-charr caught at 0–26 m and 35–72 m were in August 1983 17.6 and 15.8 cm, respectively, and in May 1984 18.0 and 16.6 cm, respectively.

Horisontal distribution of the charr

In general there were higher catches in the benthic nets at Midfell and Bjarnamöl than at Lambhagi (Figs 9, 10, 11). There were differences in age composition in both PL-, LB- and SB-charr between the three benthic localities (χ^2-tests, all $P < 0.025$). Among LB-charr there were more young fish at Midfell than at Lambhagi and Bjarnamöl (Table 8). The SB-charr were younger at Lambhagi than at Midfell and Bjarnamöl. In benthic PL-charr the fish at Bjarnamöl and Lambhagi were more evenly distributed between age groups than at Midfell, where age group 5 made up 54.1%. The catches of PI-charr were too small to permit such comparisons.

Fish migrations in the lake

The mark-recapture experiments showed that per cent recapture varied considerably between morphs, being highest among PI-charr (13.2%) and lowest among PL-charr (1.4%) (Table 9). Recaptures of the two large morphs, PI- and LB-charr were made around most of the lake, indicating extensive migrations (Fig. 13). Recaptures of the two small morphs were too few to allow any conclusions.

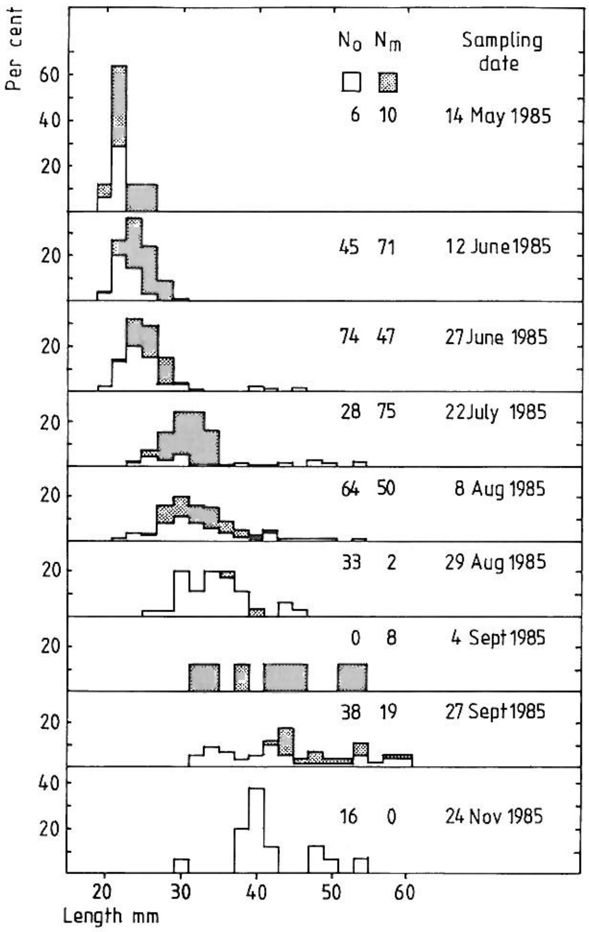


Fig. 8. Length frequency distribution of littoral age-0 charr, caught at Ólafsdráttur (number: No), and Midfell (number: Nm), May 14 – November 24, 1985.

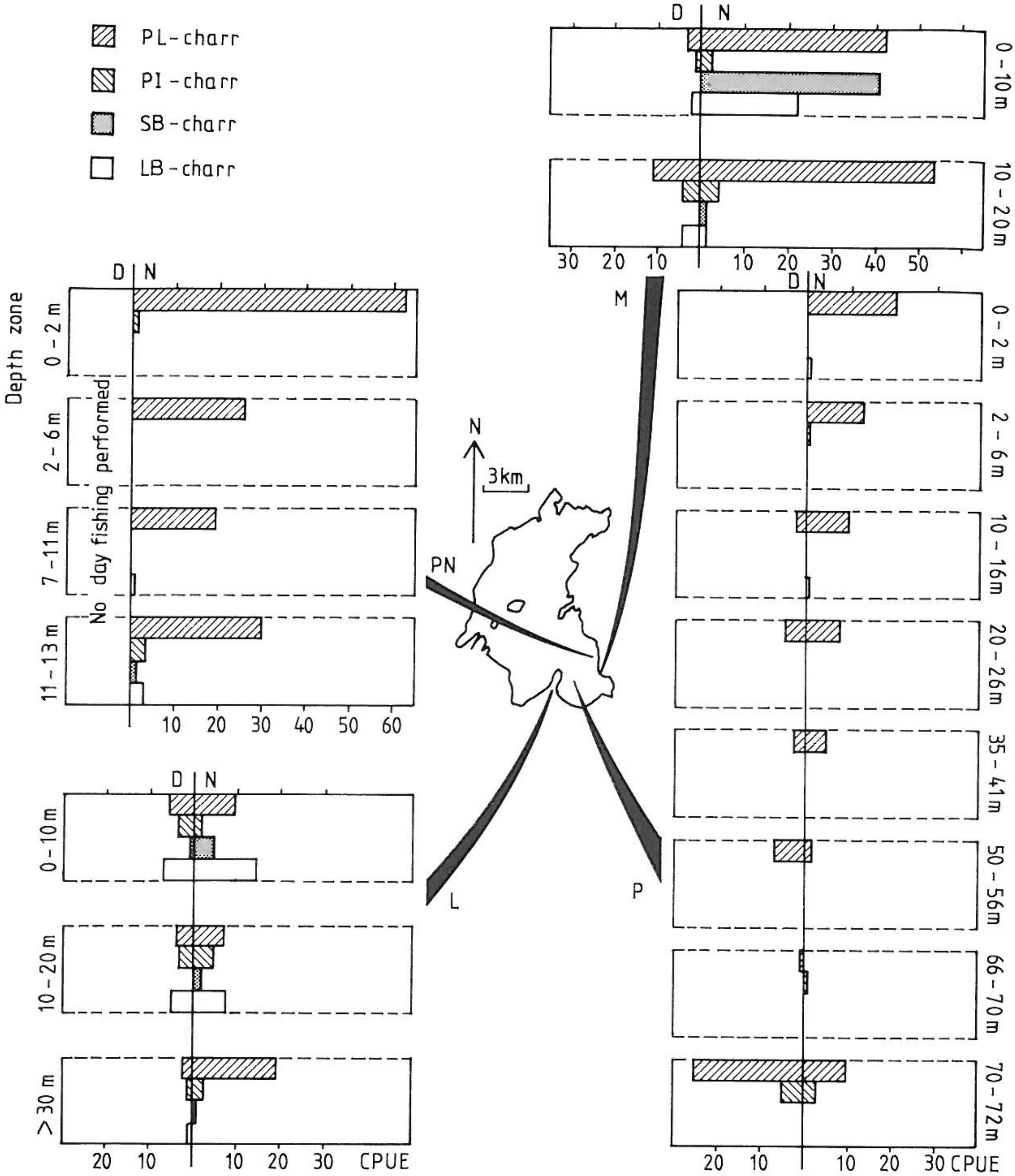


Fig. 9. Vertical distribution of arctic charr morphs in day (D) and night (N) gill net catches in Thingvallavatn, August 1983. Benthic localities: Midfell (M), Lambhagi (L). Pelagic localities: Deep pelagic, 72 m (P), Pelagic over *Nitella*, 13 m (PN).

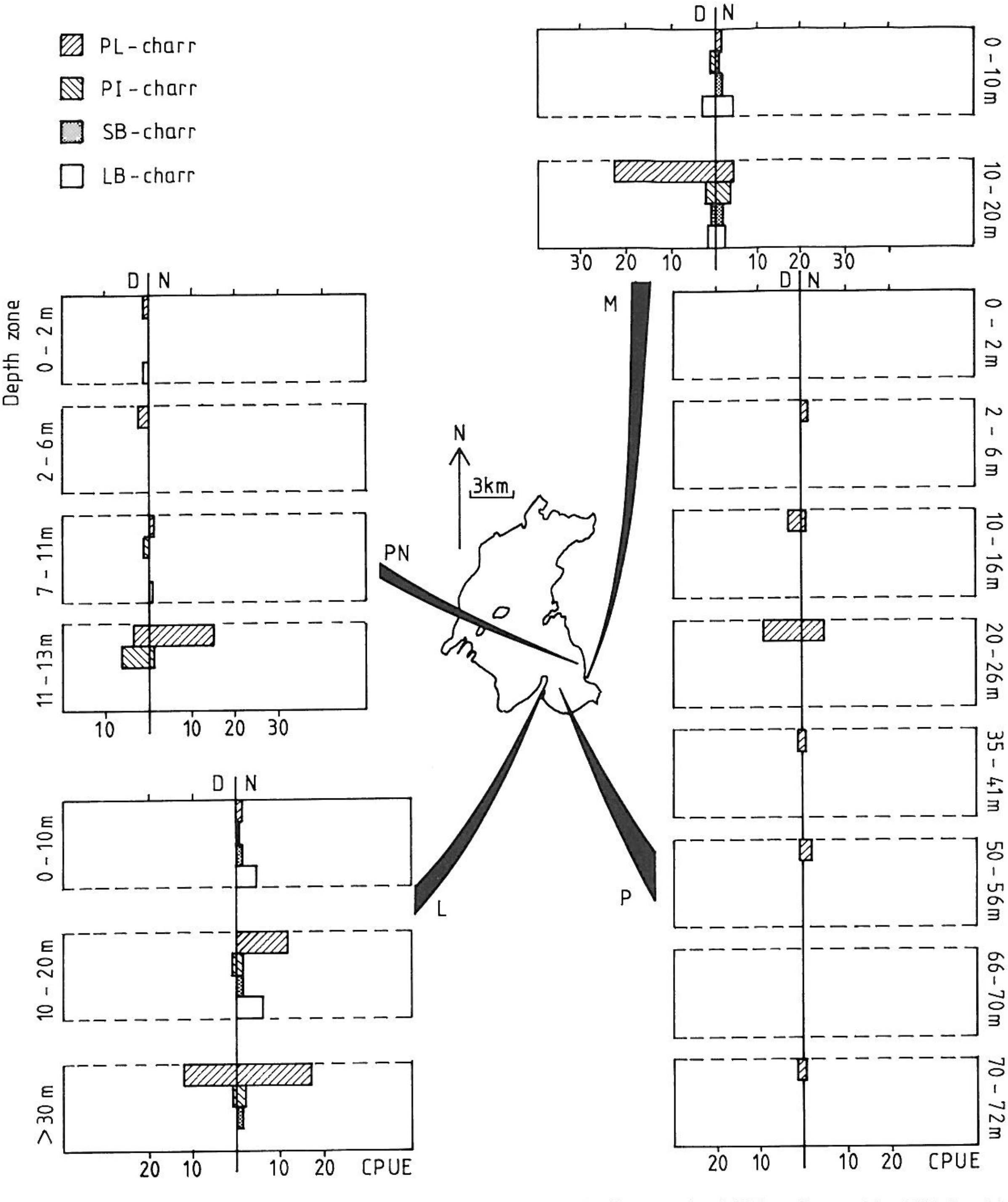


Fig. 10. Vertical distribution of arctic charr morphs in day (D) and night (N) gill net catches in Thingvallavatn, May 1984. Benthic localities Midfell (M), Lambhagi (L). Pelagic localities: Deep pelagic, 72 m (P), Pelagic over *Nitella*, 13 m (PN).

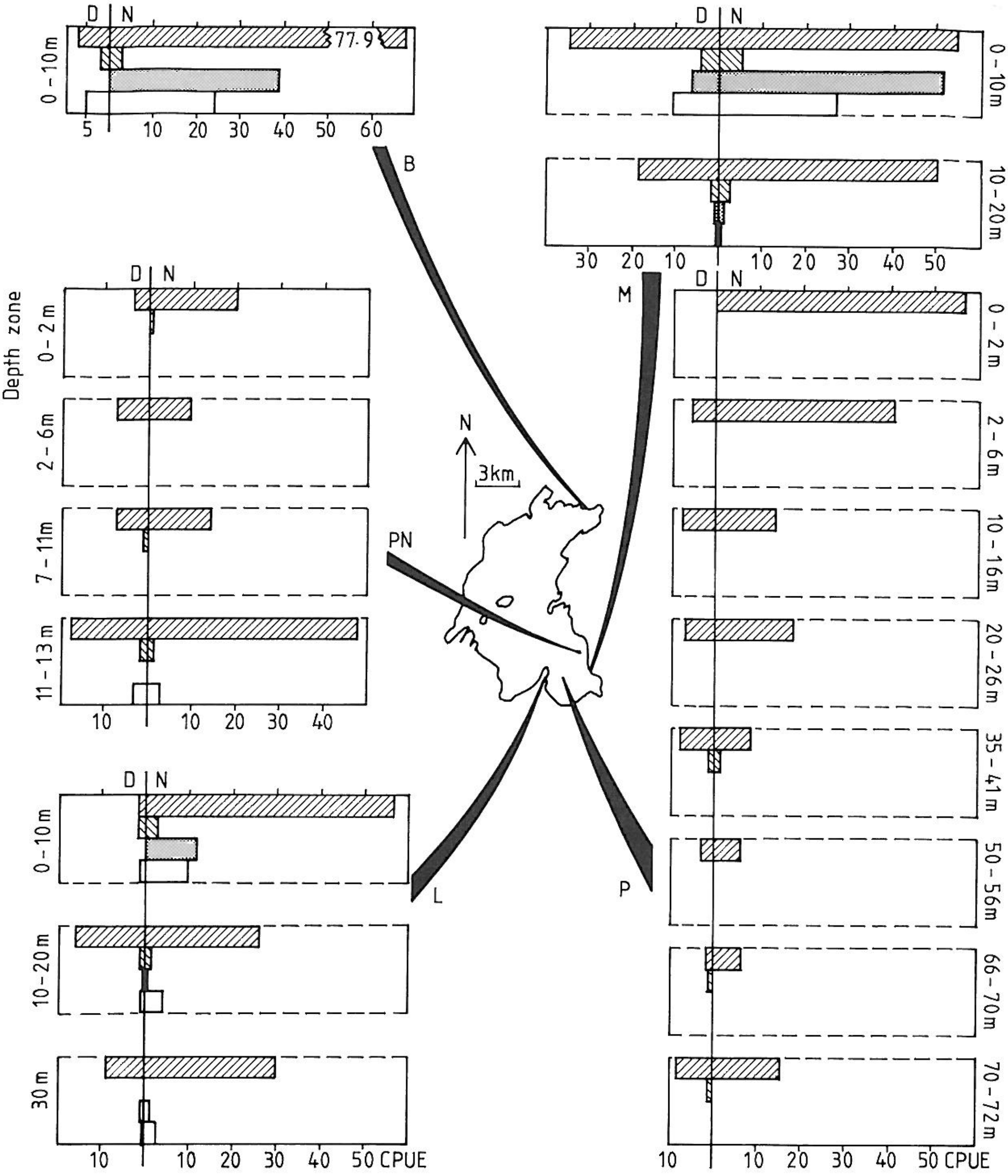


Fig. 11. Vertical distribution of arctic charr morphs in day (D) and night (N) gill net catches in Thingvallavatn, August 1984. Benthic localities: Bjarnamöl (B), Midfell (M), Lambhagi (L). Pelagic localities: Deep pelagic, 72 m (P), Pelagic over *Nitella*, 13 m (PN).

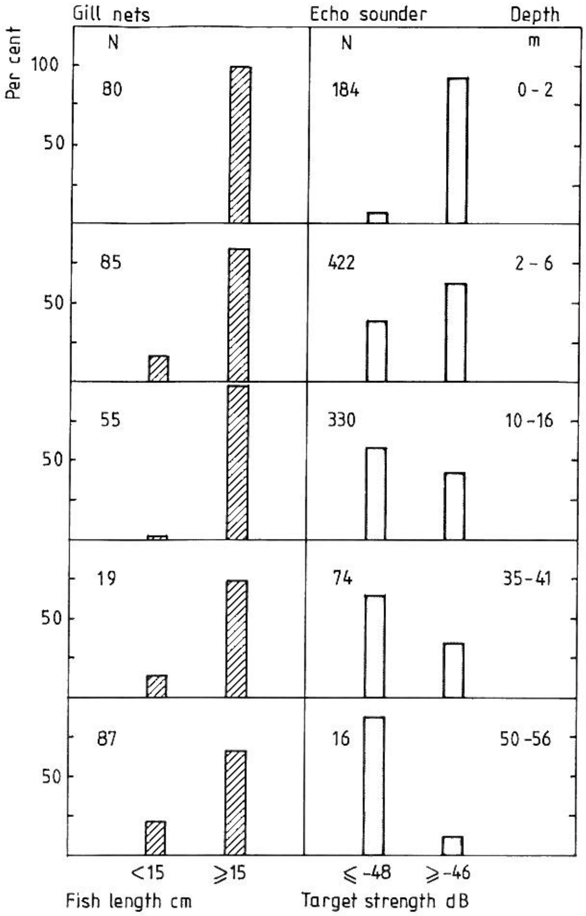


Fig. 12. Length frequency distribition and target strength (TS; dB) distribution of arctic charr at the deep pelagic station, August 1983.

Discussion

The densities of arctic charr below 60 mm in length in the surf zone of Thingvallavatn were high (1.83–4.70 fish m^{-2}). Similar investigations on salmonids in shallow rivers with comparable substrates have shown numbers between 0.02 and 0.53 fish m^{-2} (Heggberget 1984, Saltveit and Styrvold 1984, Jonsson and Gravem 1985).

The surf zone is an important habitat for age-0 charr, but less so for older fish. As the surf zone is scoured and covered by ice during winter, incubating charr eggs cannot survive in this area. Consequently, newly emerged charr must migrate into the surf zone during spring. Some of them seemed to move out from the surf zone to pelagic waters or to deeper epibenthic waters during summer. From visual observations during electrofishing, it appeared that some age-0 charr in the surf zone stay in small schools above the substrate, and some hide between the stones. Older SB-charr occurred frequently in the surf zone. However our observations indicated that this morph stayed in the interstitial space between the lava stones during daylight hours. Older PL-charr were numerous in the stony littoral zone in late summer, but not in early summer. In neither case did the surf zone appear to be an important habitat for these fish. However, all fish have to abandon the surf zone before the ice cover develops, which usually occurs in January.

Age-0 charr caught in the pelagic zone were of the PL-morph. These young of the year were caught at 15 m depth. In the pelagic gill nets, age-1 and -2 PL-charr were found mainly at this depth and deeper (Snorrason et al. 1991). This was also supported by the echo sounder results, showing a higher percentage of fish less than 14 cm in deep pelagic waters. The older PL-charr occurred at all depths in the lake, but in August densities were highest close to the surface, where zooplankton biomass also was highest (Antonsson 1977, 1991). Thus, young charr which abandon the surf zone seem to avoid the uppermost pelagic waters, although food is most abundant here.

The pelagic way of life observed for some of the age-0 charr in Thingvallavatn differs from what has been found in earlier studies. Generally, little is known about habitat selection among the young of the year, but the few studies that exist indicate a benthic way of life

Table 8. Age distribution (%) of PL-, SB- and LB-charr on three benthic sampling stations Bjarnamöl (B), Lambhagi (L) and Midfell (M). N = number of fish.

Morph	Locality	Age group									N
		1	2	3	4	5	6	7	8	< 9	
PL	B	0	0	0.3	26.3	37.0	25.0	9.8	0.6	0.9	316
	L	0	1.2	2.8	26.9	34.1	17.3	10.8	3.2	3.6	249
	M	0	0.2	1.3	22.0	54.1	13.3	6.0	2.5	0.6	481
SB	B	0	1.4	12.0	16.2	25.4	23.9	12.0	4.2	4.9	142
	L	0	16.9	40.2	27.4	10.6	2.1	3.0	0	0	61
	M	0	2.4	17.0	17.0	26.3	19.4	9.3	6.5	2.0	247
LB	B	1.8	16.2	27.9	8.1	6.3	6.3	8.1	4.5	20.7	111
	L	4.2	22.2	9.7	15.3	6.9	8.3	15.3	9.7	8.3	72
	M	21.0	26.9	19.3	5.9	8.4	8.4	5.0	0.8	4.1	119

Table 9. Number (N) of charr tagged and released at Ólafsdráttur, Skútavík and Nesjavík, July – September 1983, and per cent recaptures.

Morph	PL	PI	SB	LB	Total
Ólafsdráttur (N)	57	44	43	282	426
% recaptures	1.8	9.8	2.3	6.0	5.4
Skútatavík (N)	8	31	13	32	84
% recaptures	0	22.6	7.7	15.6	15.5
Nesjavík (N)	5	39	–	6	50
% recaptures	0	10.	–	16.7	10.0
Total	70	114	56	320	560
% recaptures	1.4	13.2	3.6	7.2	7.3

(Frost 1965, Kircheis 1976, Johnson 1980, Hindar and Jonsson 1982). The reason for this may be that the pelagic zone in Thingvallavatn offers a more stable feeding habitat than in systems studied earlier. In addition no other fish species is present in the pelagic zone in Thingvallavatn.

Among older fish, the spatial distribution of morphs corresponded well with expectations according to their morphology and diets.

SB- and LB-charr lived close to bottom. Both were largely restricted to the littoral zone (0–20 m), and occurred in highest number over the shallow stony substrate (0–10 m). PL-charr usually dominated in all habitats reflecting the large population and high activity levels of this morph. PI-charr were found in highest numbers in benthic and epibenthic habitats. A few PI-charr preying on PL-charr were also caught in the pelagic zone. The presence of the visual predator appears to influence the distribution of small PL-charr in this zone, as they were mostly caught in deep waters where the lack of light provides some protection against predation.

Mark-recapture experiments showed quite extensive migrations among the large morphs. PI-charr were obviously utilizing the whole lake basin, whereas LB-charr kept to the littoral zone, and migrations must therefore be performed along the shores. The presence of young LB-charr at Midfell quite some distance from known spawning areas, either indicates extensive migrations in this morph or suggests the existence of unknown spawning grounds.

The differences in age structure of morphs caught at the three different benthic localities may indicate local differences in substrate as well as prey types and availability. E.g. the low frequency of old SB-charr in Lambhagi may indicate the relative lack of large interstitial rooms suitable for shelter for large SB-charr in the weathered stony substrate on this locality. The proximity of spawning grounds and the level of fishing mortality may also influence the age structures. The high frequency of LB-charr older than 8 yr at Bjarnamöl may be because fishing is prohibited in this area, as it is situated inside the Thingvellir national park.

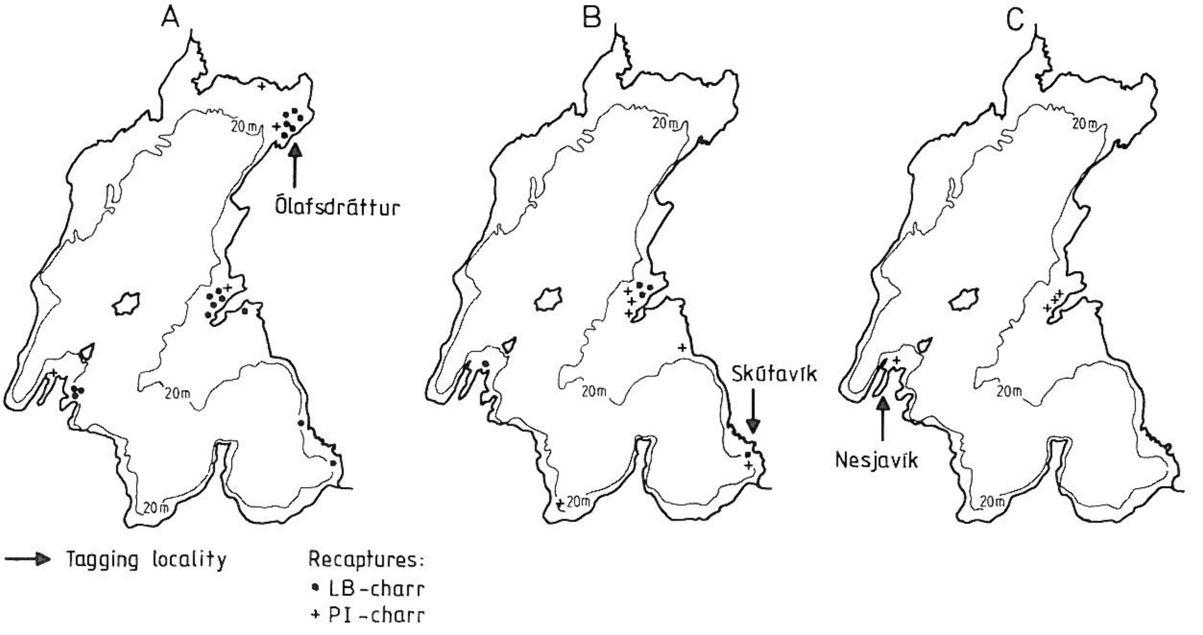


Fig. 13. Recaptures of PI- and LB-charr, tagged and released at Ólafsdráttur (A), Skútavík (B) and Nesjavík (C). 1983.

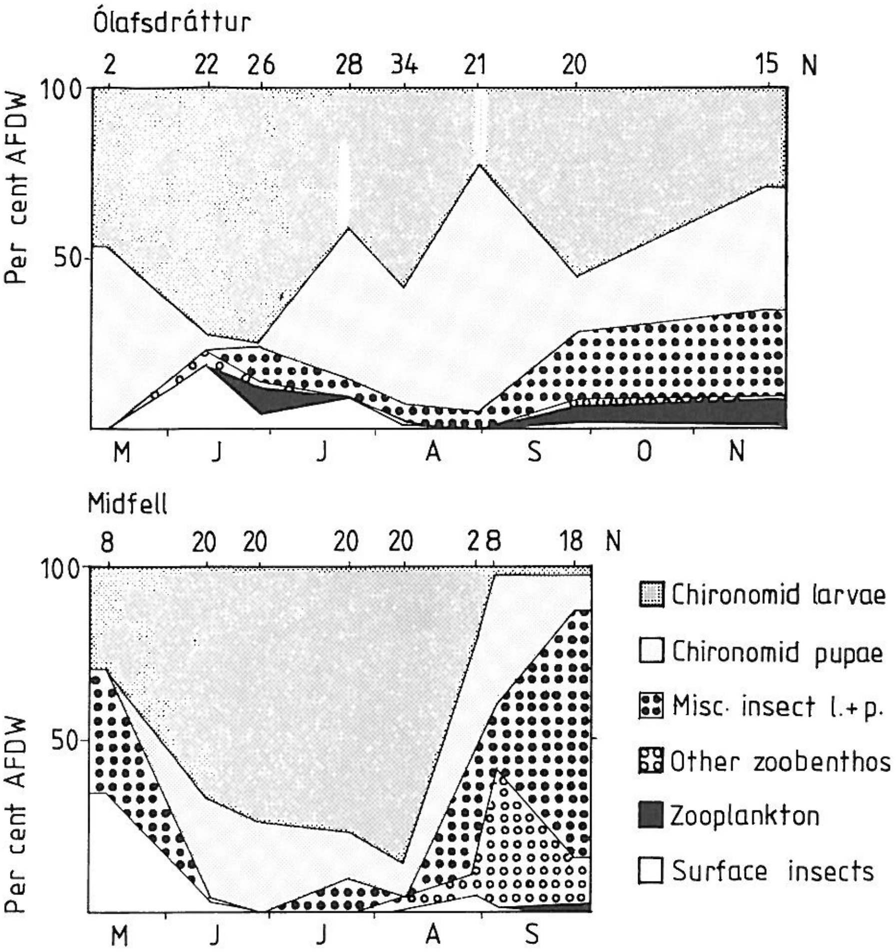


Fig. 14. Composition (per cent ash free dry weight, AFDW) of stomach contents of littoral age-0 charr, 1985. N = number of analyzed stomachs with contents.

Table 10. Number of stomachs analyzed (N total), per cent empty stomachs, and frequency of occurrence of the various groups of prey in littoral age-0 charr from Midfell and Ólafsdráttur, 1985.

Sampling date	May 14	June 12	June 27	July 2	Aug. 8	Aug. 29	Sept. 4	Sept. 27	Nov. 24
Midfell									
N total	10	20	20	20	20	2	8	19	–
% empty	20.0	0	0	0	0	0	0	5.3	–
Chir. l. + p.	75.0	100	100	100	100	50.0	100	50.0	–
Insect l. + p.	12.5	0	0	5.0	0	50.0	12.5	72.2	–
Other zoobenthos	12.5	5.0	5.0	5.0	35.0	50.0	100	66.7	–
Zooplankton	0	0	5.0	0	5.0	0	0	11.1	–
Surface insects	25.0	5.0	0	0	5.0	50.0	12.5	5.5	–
Ólafsdráttur									
N total	8	23	27	28	34	27	–	20	16
% empty	75.0	4.3	3.7	0	0	22.2	–	0	6.3
Chir. l. + p.	100	87.0	100	100	100	100	–	90.0	73.3
Insect l. + p.	0	0	18.5	17.9	14.7	47.6	–	35.0	53.3
Other zoobenthos	50.0	4.5	7.4	10.7	17.6	23.8	–	45.0	40.0
Zooplankton	0	13.5	3.7	3.4	26.5	4.5	–	55.0	46.7
Surface insects	0	9.0	0	17.9	2.9	0	–	5.0	6.7

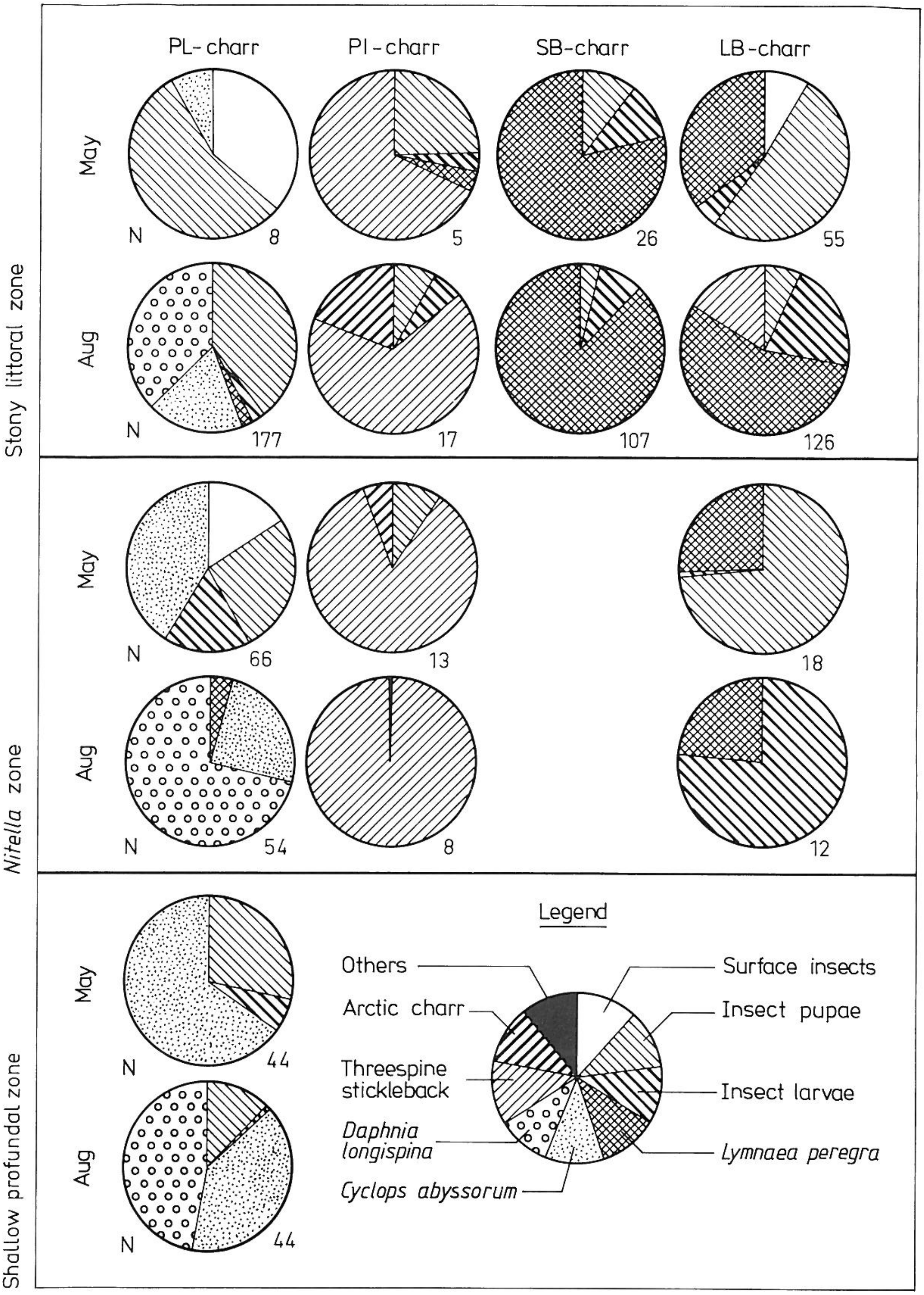


Fig. 15. Stomach contents (per cent ash free dry weight) of four morphs of arctic charr caught in epibenthic gill nets in the stony littoral zone, in the *Nitella*-zone and in the shallow profundal zone in June and August 1984. The material from the localities Bjarnamöl, Midfell and Lambhagi was pooled. N = number of fish analysed.

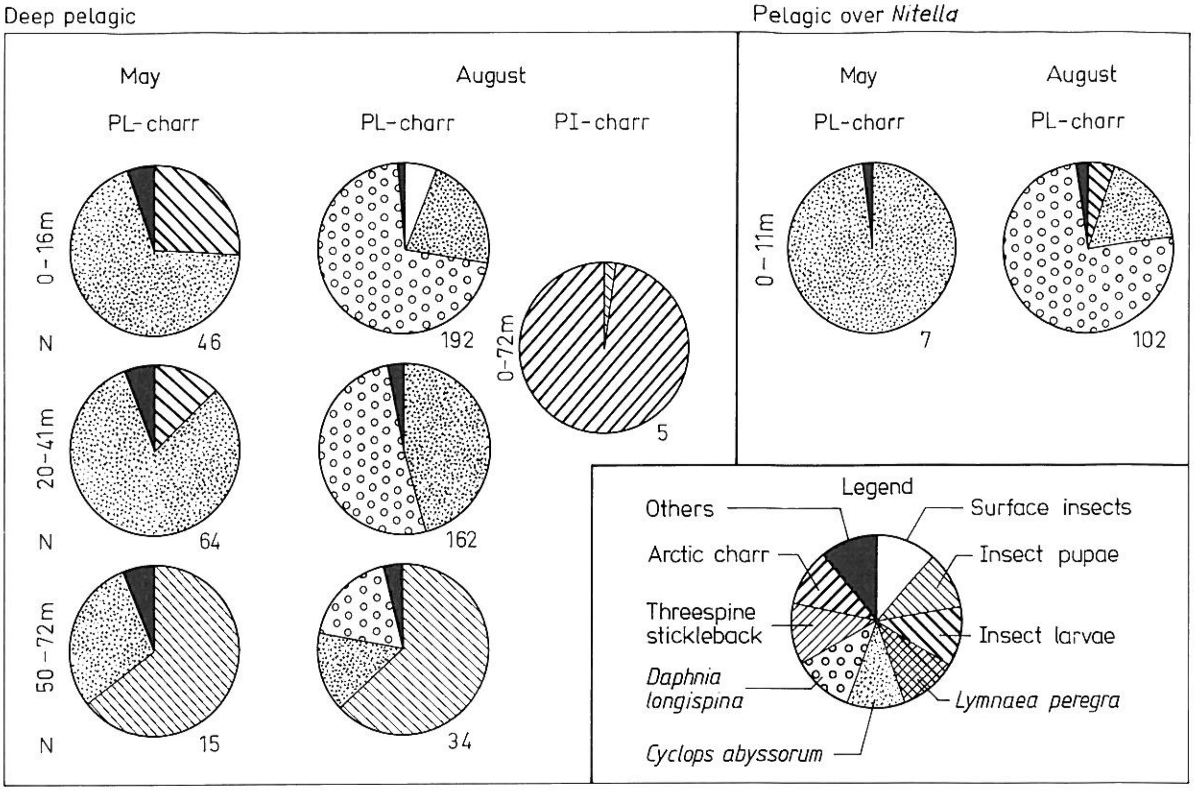


Fig. 16. Stomach contents (per cent ash free dry weight) of two morphs of arctic charr caught in pelagic gill nets over *Nitella* at Midfell and at the deep pelagic station, June and August 1984. N = number of fish analysed.

Food

Results

The diet of young of the year charr

There was no significant difference in diet of small and large age-0 charr living together (cf. Fig. 8) (Mann-Whitney U-test, $P > 0.05$). The results were therefore pooled (Fig. 14). The stomach contents of age-0 charr in the surf zone was dominated by chiromid larvae and pupae (Table 10). Only in May and late August and September were other groups of zoobenthos of any importance. Zooplankton (*Cyclops abyssorum* and *Daphnia longispina*) was of minor importance as food for young surf zone charr. Mean weight of stomach contents relative to fish weight reached a maximum in June, July and early August, indicating high feeding activity during this period. The number of empty stomachs was low except on 14 May and 29 August (Table 10). On both occasions, fish with empty stomachs were significantly smaller than those with filled stomachs (t-tests, $P < 0.05$).

The chironomids present in the stomachs were almost all large orthocladiine larvae (instar 3 and 4). The main species were *Euorthocladius frigidus* (Zett.), *Eukiefferiella minor* (Edw.), *Orthocladius oblidens* (Walker), *Diamesa* spp. and *Rheocricotopus effusus* (Walker). *Diamesa* spp. was significantly more prominent as fish food at Ólafsdráttur than at Midfell (Mann-Whitney U-test, $P < 0.01$).

There were some differences in charr diet between Ólafsdráttur and Midfell, especially in May and in late August and September (Fig. 14). The differences in spring may be due to small sample sizes. In late August and September, chironomids were significantly more important fish food at Ólafsdráttur than at Midfell ($z^* = 128.05$, 2 d.f., $P < 0.005$; Siegel 1956). However, at both localities other insects (plecopteran nymphs, house building caddis larvae, and larvae and pupae of *Atalanta stagnalis* (Haliday)) and the snail *Lymnaea peregra* increased their importance as fish food in the autumn. A similar dominance of chironomids was also found in the diet of littoral age-0 charr caught in 1983 and 1984.

In September 1983 pelagic age-0 charr had all eaten *Cyclops abyssorum*, in addition to a few chironomid pupae and ostracods. *Cyclops* was only found in 3.2% of the stomachs of age-0 charr in the surf zone during late August and September 1985.

Stomach contents of age-0 charr from the surf zone at various localities during 1983 and 1984 revealed a similar dominance of chironomid larvae and pupae as shown for 1985.

Table 11. Dietary niche breadth indices (Levins 1968) of four arctic charr morphs in the various habitats of Thingvallavatn.

	May 1984	August 1984
Stony littoral zone		
PL-charr	2.17	2.25
PI-charr	1.93	1.47
SB-charr	1.49	1.20
LB-charr	2.36	2.46
Nitella-zone		
PL-charr	3.06	1.12
PI-charr	1.21	1.00
LB-charr	1.87	1.57
Profundal zone		
PL-charr	2.68	2.22
Pelagic zone		
PL-charr	1.76	2.36

The diet of subadult and adult charr

The diet varied among morphs. By weight, PL-charr fed chiefly on zooplankton in all habitats, except for close to bottom (50–72 m) at the deep pelagic station in May and August, and in the littoral zone in May (Figs 15 and 16). A shift from *Cyclops* in May to *Daphnia* in August was observed in all habitats where zooplankton was important food for PL-charr. PL-charr caught close to bottom at the deep pelagic station had eaten mainly insect larvae (mostly instar 4 of *Chironomus islandicus* Kieffer) both in May and August. The diet of PL-charr in the shallow littoral zone in May was dominated by insect pupae (mainly Orthocladiinae) and surface insects. The diet of epibenthic PL-charr living in the *Nitella*-zone in May was more diverse, including, in addition to *Cyclops*, chironomid larvae and pupae, plecopteran nymphs, trichopteran pupae, as well as surface insects.

PI-charr fed chiefly on fish. In the epibenthic habitat the prey species was threespine stickleback (Fig. 15), whereas in the pelagic habitat arctic charr were taken (Fig. 16). Fish was found in the stomachs of PI-charr from a length of 22 cm. Only occasionally, insect pupae and arctic charr were found in the diet of PI-charr in the epibenthic habitat.

SB- and LB-charr co-occurred in the stony littoral zone and to some extent ate the same main prey types, i.e. *Lymnaea* and some groups of insect larvae and pupae (Fig. 15). Both morphs ate chironomid larvae, mainly instar 4 of the large species *Pseudodiamesa nivosa* and *Chironomus islandicus*. In May, nymphs of the plecopteran *Capnia vidua* were also found in the stomachs of both benthivorous morphs. However, their diets also differed in many aspects. In May, insect pupae constituted a larger part of the diet of LB-charr than SB-charr (d = 95.12, $P < 0.001$). In August, caddis larvae (mainly *Apatania zonella*) constituted a larger part of the diet of LB-charr (d = 44.61, $P < 0.001$). LB-charr had also occasionally eaten sticklebacks. *Lymnaea* constituted a larger part of the diet of SB-charr than of LB-charr both in May and August (binomial tests, $P < 0.001$).

The length of *Lymnaea* (L_{Ly}, mm) eaten by SB-charr (L_{SB}) and LB-charr (L_{LB}) increased with increasing fish size in both species (L_{SB} and L_{LB} are $\log_{10}$ fish length in mm):

$$L_{Ly} = 0.63 + 0.02\ L_{SB},\ N = 74,\ R^2 = 0.15,\ P < 0.001$$
$$L_{Ly} = 1.13 + 0.01\ L_{LB},\ N = 102,\ R^2 = 0.55,\ P < 0.001.$$

Regression slopes were not significantly different (F-test, $F_{1,172} = 3.54$, $P > 0.05$). However, mean sizes of snails eaten by SB- and LB-charr of the same body size (75–185 mm and 80–185 mm, respectively) were significantly different (t-test, t = 2.36, 112 d.f., $P < 0.05$). Mean size (± SD) of *Lymnaea* in SB-charr and small LB-charr was 3.36 ± 1.78 mm and 2.61 ± 1.37 mm, respectively. Large LB-charr (FL = 190 – 470 mm), however, ate larger snails (5.08 ± 0.91) than SB-charr (t = 6.80, 132 d.f., $P < 0.001$).

In the stony littoral zone at Midfell in May both PL- and LB-charr had consumed chironomid pupae. However, LB-charr ate more large *Pseudodiamesa nivosa* and less small *Orthocladius* spp. than PL-charr (binomial tests, d = 7.46 and d = 313.66, respectively, $P < 0.001$).

Levins' (1968) dietary breadth index (B) was usually lower than 2.5 for all morphs (Table 11). Only for PL-charr in the *Nitella*- and profundal zone in May did B exceed this value. In the stony littoral zone, where all morphs co-occur, dietary breadth was lowest for SB-charr and highest for LB-charr, both in May and August.

The diet overlap between morphs co-occurring in the same habitats as measured by Schoener's (1968) index (D), were generally lower than 0.3, except between LB- and SB-charr (Table 12).

Table 12. Schoener's indices (Schoener 1968) for diet overlap between arctic charr morphs co-occurring in the same habitats in Thingvallavatn.

	May 1984			August 1984		
	PL-charr	PI-charr	SB-charr	PL-charr	PI-charr	SB-charr
Stony littoral zone						
PI-charr	0.260			0.090		
SB-charr	0.070	0.065		0.055	0.085	
LB-charr	0.225	0.165	0.475	0.135	0.275	0.660
Nitella-zone						
PI-charr	0.095			0.000		
LB-charr	0.205	0.095		0.050	0.000	

Table 13. Per cent distribution of number of helminth species found in the four arctic charr morphs in Thingvallavatn. Number of helminth species are significantly different among charr morphs (G-test, 15 d.f., $P < 0.001$).

Number of helminth species	0	1	2	3	4	5
SB-charr	12	54	19	15		
LB-charr		13	42	32	11	
PL-charr		3	8	43	29	17
PI-charr		3	19	22	28	28

Discussion

The food of littoral age-0 charr was dominated by chironomid larvae and pupae from May until late August. In autumn larger zoobenthos increased in importance.

This is somewhat different from findings in Swedish Jämtland lakes and Vangsvatn, Western Norway, where benthic crustaceans seem to be the most important food for arctic charr in the early alevin phase (Lindström 1955, Hindar and Jonsson 1982). In these lakes, however, age-0 charr live in the sublittoral or profundal zones where available prey groups may differ from those in the surf zone of Thingvallavatn. The zoobenthos of the surf zone in Thingvallavatn is totally dominated by chironomids (Lindegaard 1980, Lindegaard et al. 1991) and this prey may therefore be the most easily available food. In Mývatn, chironomid larvae dominated the diet of littoral age-0 charr from April through November, although benthic crustaceans also were significant (Ranta-Aho 1983).

Twenty mm charr caught in May/June had already resorbed their yolk sacs, and probably had just begun external feeding (Skúlason 1986). Arctic charr start external feeding at approximately 20 mm (Nielsen 1961, Balon 1980b, Hindar and Jonsson 1982, Ranta-Aho 1983). Thus, there is good evidence that the initial food of arctic charr in Thingvallavatn is chironomid larvae and pupae and some adult chironomids. There was no evidence during our sampling that food choice differs between the size groups of age-0 charr present in the surf zone.

The diet of older charr varied among morphs; PL-charr fed largely on zooplankton, PI-charr was a fish eater, and SB- and LB-charr fed mainly on the gastropod *Lymnaea peregra* and other zoobenthos. This dif-

Table 14. Prevalence, geometric mean (GM) intensity, geometric mean (GM) relative density and range of parasites in four arctic charr morphs from Thingvallavatn. N = number of fish examined. Differences in prevalence were tested by G-tests, intensities and densities by Mann-Whitney tests.

N:	SB-charr 26	LB-charr 38	PL-charr 35	PI-charr 32	Morph comparison	P
Trematoda						
Crepidostomum farionis (Müller)						
Prevalence	19	55	16	47	SB + PL vs LB + PI	< 0.001
GM intensity	1.2	8.7	1.8	6.0	SB + PL vs LB + PI	< 0.01
GM relative density	0.2	0.5	0.4	0.3	SB vs PI	< 0.05
Range	1–3	1–407	1–5	2–90		
Diplostomum sp.						
Prevalence	85	100	100	100		
GM intensity	133.3	131.9	42.4	100.8	PL vs PI	< 0.01
GM relative density	36.9	14.6	8.1	6.6	SB vs LB, LB vs PL	< 0.01
Range	4–900	22–850	6–165	11–720		
Cestoda						
Diphyllobothrium spp.						
Prevalence	8	16	89	78	SB + LB vs PL + PI	< 0.001
GM intensity	5.6	6.2	9.8	21.8	PL vs PI	< 0.001
GM relative density	0.5	0.2	2.1	1.8	SB vs PI	< 0.001
Range	1–31	1–31	1–76	2–295		
Eubothrium salvelini (Schrank)						
Prevalence	–	29	17	44	PL vs PI	< 0.001
GM intensity	–	2.6	2.0	3.2		
GM relative density	–	0.1	0.0	0.2	PL vs PI	< 0.05
Range	–	1–30	1–31	1–46		
Proteocephalus longicollis Zeder						
Prevalence	23	24	86	53	PL vs PI	< 0.001
GM intensity	2.3	4.4	10.9	12.2	PL vs PI	< 0.001
GM relative density	0.3	0.2	2.9	0.6	SB vs PI	< 0.001
Range	1–12	1–20	1–255	1–196		
Nematoda						
Philonema oncorhynchi Kuitunen-Ekbaum						
Prevalence	4	24	43	38	SB + LB vs PL + PI	< 0.001

ferentiation corresponds well with morphology, coloration, and habitat use of the morphs (see above), and the spatial distribution of their prey types (Lindegaard 1992, Antonsson 1992).

In addition to zooplankton, PL-charr fed on chironomid pupae, and in early summer also on surface insects. The zooplankton species eaten were *Cyclops abyssorum* and *Daphnia longispina,* and their dominance in the stomachs reflected their relative dominance in the water column (Antonsson 1977, 1991). When both species were present, however, *D. longispina* was clearly selected over *C. abyssorum* (Malmquist 1988).

PI-charr had eaten sticklebacks in the epibenthic habitat and small PL-charr in the pelagic habitat. This reflects the availability of prey in the two habitats. In the pelagic habitat PL-charr is the only small fish present. In the epibenthic habitat, sticklebacks are abundant in the *Nitella*-zone, whereas charr of a similar size (<6 cm) mainly are restricted to the surf zone. The large sized predators may not easily move into these very shallow waters.

The apparent niche overlap of SB- and LB-charr is somewhat reduced by the fact that the two morphs ate snails of different sizes. Large LB-charr ate larger snails than the smaller SB-charr. Among fish with similar body size, however, SB-charr ate larger snails than LB-charr.

There also appears to be some dietary convergence by LB- and PL-charr on chironomid pupae in May, when this prey is abundant (Lindegaard 1992). However the two morphs utilized different chironomids, with LB-charr taking the larger species.

Thus, the morphs are well segregated in diet even when they co-occur in the same habitat. The low values of diet overlap and niche breadth indices indicate that segregation is strong both in May and August. The segregation in diet between the charr morphs in Thingvallavatn appears more complete than what has been observed in most dimorphic arctic charr populations, where segregation breaks down during parts of the year (e.g. Hindar and Jonsson 1982, Sparholt 1985). The strong diet segregation in the Thingvallavatn population is probably due to mainly two factors: 1) the well developed differentiation in trophic morphology between the two morphotypes (PL- and PI-charr vs SB- and LB-charr), and 2) the large difference in body size between morphs within the morphotypes (PL- vs PI-charr and SB- vs LB-charr). In some dimorphic arctic charr populations it appears that diet segregation is stronger between size groups within one morph than between morphs (Klemetsen and Grotnes 1980).

Parasites

Results

The number of parasite species per infected fish varied significantly among morphs increasing from SB- through LB- and PL- to PI-charr (Table 13).

In total, seven parasite species were identified (Table 14). Positive identification of the cestodes *Diphyllobothrium ditremum* and *D. dendriticum* is very difficult for frozen samples, and they were therefore pooled. Differences in site preference and size of the pleurocercoids (Halvorsen 1970, Henricson 1977) indicated, however, that *D. ditremum* and *D. dendriticum* occurred approximately in the ratio 5 : 1.

The intestinal fluke *Crepidostomum farionis* occurred more often and in higher intensity in the two larger morphs LB- and PI-charr than in the smaller SB- and PL-charr. Mean relative density of this species followed the same pattern among morphs. In LB-charr, intensity of *C. farionis* increased significantly with length (Kendall's coefficient of rank correlation $\varrho = 0.418$, $P < 0.01$).

The prevalence of the eye fluke *Diplostomum* sp. was very high, and all the fish, except three SB-charr, were infected (Table 14). The mean intensity of *Diplostomum* sp. was high and not significantly different among SB-, LB- and PI-charr, whereas PL-charr had a significantly lower number of metacercariae. The relative density of *Diplostomum* sp. was significantly lower in PL- and PI-charr than in the benthivorous morphs, and also significantly lower in LB- than in SB-charr. The intensity of the eye fluke increased significantly with age ($\varrho = 0.514$, $P < 0.01$) and length ($\varrho = 0.423$, $P < 0.01$) in SB-charr.

The infection patterns of the cestodes *Diphyllobothrium* spp. and *Protocephalus longicollis* differed significantly among morphs (Table 14). PL- and PI-charr had high prevalences, high mean intensities, and high relative densities, whereas SB- and LB-charr were lightly infected. PL-charr had higher relative density of *P. longicollis* than PI-charr, whereas relative density of *Diphyllobothrium* spp. was similar in the two morphs. In PI-charr, high infection rates of *Diphyllobothrium* spp. were frequently accompanied by internal hemorrhaging and intense adhesion of organs. For both PL- and PI-charr the mean intensity of *Diphyllobothrium* spp. increased with length ($\varrho = 0.321$ and $\varrho = 0.315$, respectively, $P < 0.05$), but not with age.

The prevalence of the cestode *Eubothrium salvelini* was low compared with the other cestodes, and this species was not found in SB-charr (Table 14).

The nematode *Philonema oncorhynchi* occurred more often in PL- and PI-charr than in the benthic morphs (Table 14).

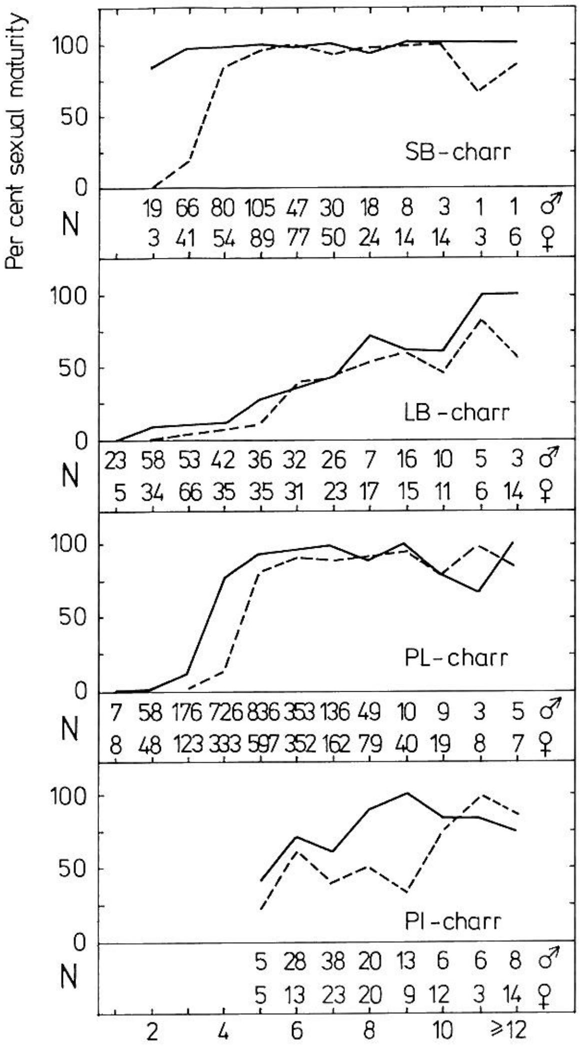


Fig. 17. Percentage sexually mature males (———) and females (– – –) of the four morphs of arctic charr in Thingvallavatn. The fish were caught in August/September 1983 and 1984. N = sample size, males (♂) and females (♀).

Discussion

The charr morphs show clear differences in composition and infection patterns of their helminth species: SB- and LB-charr carry relatively few parasite species and are primarily infected by the trematodes *Diplostomum* sp. and *Crepidostomum farionis*. PL- and PI-charr carry relatively many parasite species, and are mainly infected by the cestodes *Protocephalus longicollis* and *Diphyllobothrium* spp., and the nematode *Philonema oncorhynchi*.

This difference is in accordance with the differences in diet and habitat between morphs, and can be explained by different host-specific pathways in the transmission of the parasite species.

All the four cestode species and the nematode found in the charr morphs have copepods, mainly *Cyclops* spp. as the first intermediate host before entering the fish (Vik 1963, 1964, Lien and Borgstrøm 1973, Smith 1973, Henricson 1978). The threespine stickleback is a potential host for *D. ditremum* (Bérubé and Curtis 1986) and probably also for *Eubothrium salvelini* (Vik 1963). The charr may be infected either by eating copepods or sticklebacks carrying the parasite (Vik 1963, 1964, Halvorsen and Wisler 1973, Curtis 1984). Thus, PL-charr is infected when feeding on *Cyclops*, whereas PI-charr is infected when eating threespine stickleback, which is also eating *Cyclops* (Sandlund et al. 1992). On the other hand, the benthic morphs very rarely feed on zooplankton or fish, and consequently they are only lightly infected by these parasites.

The first intermediate host of *Diplostomum* sp. is the snail *Lymnaea peregra*, which constitutes a major food item for the benthic charr morphs. *Diplostomum* may also be transmitted through the skin of fish living close to the intermediate host (Shigin 1986). The higher relative density of *Diplostomum* in SB-charr than in LB-charr may be due to the fact that SB-charr live in the interstitial rooms of the stony substrate, swimming very close to the surfaces where *Lymnaea* is living. In contrast, LB-charr live epibenthically.

PL- and PI-charr live in pelagic waters or epibenthically at some distance from the substrate and very rarely feed on *Lymnaea*. Thus they are more lightly infected by *Diplostomum*.

Protocephalus longicollis is not transmitted through a second intermediate host like sticklebacks, and consequently relative density of this species was much higher in the zooplanktivorous PL-charr than in the piscivorous PI-charr.

The life cycle of *Crepidostomum farionis* in Thingvallavatn is uncertain, as none of its known second intermediate hosts (amphipods and mayfly nymphs, Thomas 1958) occur in the lake.

Life history

Results

Age and sex

Age at sexual maturity differed between morphs (Fig. 17). SB-charr (2 to 17 yr of age) and PL-charr (1 to 14 yr of age), both matured within a few age groups. Among SB-charr, more than 50% of the males in age group 2 were mature, and 50% of the females in age group 4 were mature. The difference in maturity age between sexes was significant ($z^* = 105.34$, 4 d.f., $P < 0.0001$). Among PL-charr more than 50% of the males in age group 4, and females in age group 5, were mature. This difference between sexes was also highly significant ($z^* = 508.26$, 5 d.f., $P < 0.0001$). LB- (2 to 18 yr of age) and PI-charr (5 to 18 yr of age) matured over wider

Table 15. Adult annual rate of survival (S) ± 95% confidence limits, χ^2-test for goodness of fit to the Chapman-Robson model, and sample sizes of the various arctic charr morphs from Thingvallavatn based on catch data from August-September 1983 and 1984. None of the χ^2-values are significant. This indicates agreement between sample observations and the model used.

Morph	Year	S	χ^2	Age (yr)	Sample size
SB-charr	1983	0.63 ± 0.04	0.078	5–13	209
	1984	0.51 ± 0.04	2.887	6–11	164
	Pooled	0.57 ± 0.03	3.225	5–13	488
LB-charr	1983	0.65 ± 0.05	0.037	6–14	112
	1984	0.59 ± 0.07	0.004	6–14	72
	Pooled	0.63 ± 0.05	0.011	7–15	145
PL-charr	1983	0.47 ± 0.05	1.890	6–14	501
	1984	0.41 ± 0.01	0.074	5–13	1789
	Pooled	0.43 ± 0.02	0.572	6–14	2179
PI-charr	1983	0.63 ± 0.06	0.063	7–15	89
	1984	0.62 ± 0.07	0.221	7–14	78
	Pooled	0.63 ± 0.05	0.030	7–15	169

ranges of years. Among LB-charr, 50% maturity of both sexes was attained at age-8, and among PI-charr at age-6. Age at maturity differed between sexes for PI-charr ($z^* = 24.69$, 5 d.f., $P < 0.001$), but not for LB-charr ($z^* = 8.52$, 4 d.f., $0.1 > P > 0.05$). Some non-breeding fish, males in particular, may be previous spawners which omit gonadal development in some years. Maturity ages did not differ between 1983 and 1984 ($P > 0.05$), and the data were therefore pooled.

The estimated annual adult survival rate (Table 15) was lowest for PL-charr (0.41–0.47), but higher for the other morphs (0.51–0.65). The data indicated some inter-year difference in age structure among SB-, LB- and PL-charr (t-tests, $P < 0.05$).

Sex ratios were investigated during spring (May – June). August – September samples were omitted in this respect because the various morphs spawn between July and November. During spawning sex ratios in gill net catches may be influenced by differences in activity between the sexes (Alm 1959, Jonsson and Hindar 1982). Females predominated among SB-charr (M/F = 0.36, binomial test: $N = 49$, $Z = 3.14$, $P < 0.01$) at all ages. Among LB-charr, males were dominant in most age groups. The M/F ratio of the total sample, however, was not significantly different from unity (M/F = 1.38, $N = 100$, $P < 0.15$). Among PL-charr the sex ratio approached equality for age groups 2–4 (M/F = 1.29, $N = 176$, $P < 0.15$). In older fish, females were most abundant (M/F = 0.54, $N = 291$, $P < 0.001$). Among PI-charr, females were more numerous in most age groups, but the overall sex ratio was not significantly different from unity (M/F = 0.57, $N = 47$, $P < 0.10$).

Size and growth

The morphs varied in size distribution. The mean size of mature individuals increased from SB-charr through PL- and LB-charr to PI-charr (Table 16). The length interval covered by adult LB-charr was larger than any other adult morph. Growth rates estimated by von Bertalanffy's model (Allen 1966), based on empirical fork lengths, differed significantly between morphs.

The SB-charr were the slowest growing, and growth rates were successively higher in LB-, PL- and PI-charr. The growth rates levelled off at ca. 13, 20 and 30 cm in SB-, PL- and PI-charr, respectively. PI-charr feeding on PL-charr are sometimes caught in the lake, and such individuals may become larger than 60 cm in length (Malmquist et al. 1985). In the present sample, however, there were no PI-charr larger than 48 cm (Table 16). LB-charr continued to increase in length (L_{LB}, mm) with increasing age (A, years) at an almost rectilinear rate:

$$L_{LB} = 26.3\ (\pm\ 0.5)\ A + 51.3\ (\pm\ 2.8)$$
$$N = 644,\ R^2 = 0.80,\ P < 0.0001.$$

Fish which were classified as intermediate between SB-charr and LB-charr had L ± standard deviation equal to 200 ± 47 mm ($N = 48$). Those which on habitus were classified as intermediate between PL- and PI-charr had L equal to 229 ± 9 mm ($N = 15$).

Back calculation of growth by using otoliths (Table 17) corresponded well with empirical growth rates (Fig. 18). The growth curves of PL- and PI-charr were almost

Table 16. Empirical lengths (mm) and the parameter estimates (± 95% confidence limits) of L_∞ and k of the exponential growth model: $L_A = L_\infty(1 - e^{-kA})$, where A is age (yr) of arctic charr from Thingvallavatn based on pooled data from August–September 1983–1984.

Morph	Adult fork lengths				L_∞	k	Sample size
	Males		Females				
	Mean	Range	Mean	Range			
SB-charr	96	73–260	109	75–310	132.9 ± 6.7	0.333 ± 0.045	746
LB-charr	240	135–460	274	90–470	553.5 ± 74.2	0.086 ± 0.016	644
PL-charr	175	130–230	188	140–260	205.1 ± 1.6	0.417 ± 0.011	4224
PI-charr	268	180–480	295	200–440	302.4 ± 15.1	0.328 ± 0.064	224

Table 17. Regression of fork length (L, mm) on otolith radius (r_1, mm; cf. Jonsson and Stenseth 1977) of arctic charr morphs from Thingvallavatn. All coefficients of determination (R^2) are highly significant ($P < 0.001$).

Morph	Regression	Length	R^2	N
SB-charr	$\log_e L = 7.27 - 2.29 \log_e r + 0.37 (\log_e r)^2$	73–310	0.76	232
LB-charr	$\log_e L = 4.60 - 1.25 \log_e r + 0.28 (\log_e r)^2$	70–470	0.93	681
PL-charr	$\log_e L = 33.28 + 15.24 \log_e r - 1.51 (\log_e r)^2$	85–260	0.76	4467
PI-charr*	$\log_e L = -6.86 + 3.75 \log_e r - 0.26 (\log_e r)^2$	85–480	0.80	3406

N = sample size. * PL-charr was used for fish younger than 6 years.

parallel between 1 and 3 yrs of age, but PL-charr ceased to grow in length considerably younger than PI-charr. The back-calculated mean lengths of SB- and LB-charr were significantly different at all ages (t-tests, $P < 0.001$). There was no significant difference in growth rate between sexes, or sexually mature and immature fish within morphs.

Weight-length relationships differed significantly among morphs both in June and August (tests of homogeneity of regression coefficients, June: $F_{3,670} = 64.68$, $P < 0.0001$, August: $F_{3,3760} = 8.685$, $P < 0.05$) (Table 18). Significantly different weight-length relationships were found between the sexes within PL- and SB-charr, and spring and autumn samples within PL- and PI-charr. Among SB- and PL-charr, intramorph regression coefficients decreased with age within age groups 2–9 yr, wheras in LB- and PI-charr they did not (Fig. 19). A significant heterogeneity in regression coefficients among age groups ($F_{8,2721} = 7.49$, $P < 0.001$) was only found for PL-charr.

Fecundity and reproductive effort

Individual fecundity of females increased significantly with fork length (L, mm) for all morphs (Table 19). In the case of PL-charr, the predictive value of the individual regressions using length as the independent variable, was low. Adding age as a second independent variable increased the coefficient of determination, but it was still low ($R^2 = 0.22$) due to individual variability and a limited size range. Length specific fecundity of SB-charr also decreased significantly with age ($P < 0.0001$), whereas this was not the case for LB- and PI-charr ($P > 0.05$). Sample sizes for the two latter morphs were, however, small.

Age specific population fecundity demonstrated that among PL-charr a few age groups were important contributors to the fecundity of the morph, whereas within SB-, LB- and PI-charr, several age groups were of importance (Fig. 20). Some of the variation in relative contribution between age groups in LB- and PI-charr may be due to small sample sizes.

Gonadosomatic indices (GSI) of females decreased with age for all morphs, but were generally higher for PL- and PI-charr than for PL- and SB-charr (Fig. 21). Relative annual investments into reproduction (RAI) of females were less than 0.5 for LB- and SB-charr younger than 7 yr, and 0.7 and higher for PL-, PI- and SB-charr 7 yr and older (Fig. 22).

Discussion

The variation in adult size of charr morphs in Thingvallavatn embraces a large part of the total variation observed in lake resident stocks throughout the Holarctic distribution area of the species (Schmidt-Nielsen 1939, Nilsson 1955, Frost 1965, Nilsson and Filipsson 1971, Adalsteinsson 1979, Jonsson and Østli 1979, Johnson 1980, Jonsson and Hindar 1982, Gydemo 1984, Hindar et al. 1986). SB-charr are of the same size as the smallest adults observed, and their size at maturity may be close to the lower limit for gonadal development of the species. One of the females, 7.5 cm in length, had only 12 eggs. Myers et al. (1986) reported a threshold length of approximately 7 cm for the onset of sexual

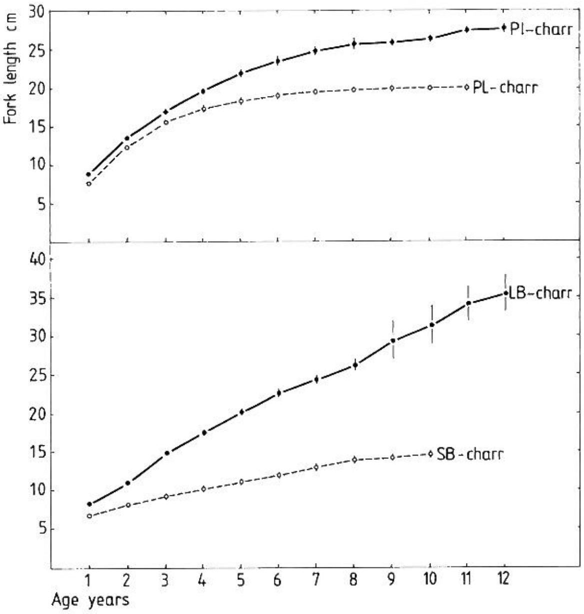


Fig. 18. Back-calculated fork lengths with 95% confidence limits of the estimates for four arctic charr morphs from Thingvallavatn, caught in August/September 1983 and 1984.

Table 18. Total weight (W, g)/fork length (L, mm) relationships of four arctic charr morphs from Thingvallavatn, 1984, fitted to the regression model: $\log_e W = a \log_e L - b$, where a and b are constants. N = sample size, R^2 = coefficient of determination, F-values for test of homogeneity between regression coefficiens (a) between sexes and times of the year.

Morph	Month	Sex	Regression		R^2	F		N
			a	b		sex	month	
SB-charr	August	Male	3.06	11.58	0.90	5.91*		244
		Female	2.83	10.51	0.92			217
		Pooled	2.94	11.03	0.91		1.08 NS	462
	May	Pooled	3.06	11.78	0.95			50
LB-charr	August	Male	3.10	11.82	1.00	0.04 NS		162
		Female	3.10	11.84	0.99			133
		Pooled	3.11	11.87	1.00		1.40 NS	313
	May	Pooled	3.14	12.16	0.99			102
PL-charr	August	Male	3.04	11.59	0.96	15.86***		1733
		Female	3.11	11.97	0.97			1049
		Pooled	3.08	11.82	0.97		1552.69***	2801
	May	Pooled	2.40	8.43	0.81			479
PI-charr	August	Male	3.20	12.44	0.97	1.27 NS		67
		Female	3.07	11.78	0.93			35
		Pooled	3.11	11.95	0.95		4.87*	102
	May	Pooled	3.22	12.66	0.94			47

NS = $P > 0.05$, * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

maturity in male Atlantic salmon (*Salmo salar* L.) which is the size of the smallest adult SB-charr observed in Thingvallavatn.

Maturity ages of 4–5 yr as in PL-charr, seem common among arctic charr elsewhere (Johnson 1980). The maturity age of SB-charr is low, whereas those of LB- and PI-charr are high, but not uncommon for subarctic populations (Klemetsen and Grotnes 1980, Nilsen and Klemetsen 1984), and even greater ages at maturity have been reported from populations in northern Canada (Johnson 1980) and in Bear Island (Klemetsen et al. 1985). The present data on maturity age and growth pattern are complemented by earlier findings (Skúlason 1983).

Optimization theory predicts that growth stagnation at an early age selects for young age at sexual maturity, whereas growth stagnation at an older age selects for late sexual maturity (Schaffer and Elson 1975, Jonsson et al. 1984, Stearns and Crandall 1984). The variation in age at sexual maturity of the arctic charr morphs in Thingvallavatn agrees well with the qualitative expectations based on optimization theory. SB- and PL-charr, which both have early growth stagnation, mature sexually at an early age. LB- and PI-charr have higher growth rates at older age, and mature late. In addition to this, the optimal maturity age may differ between

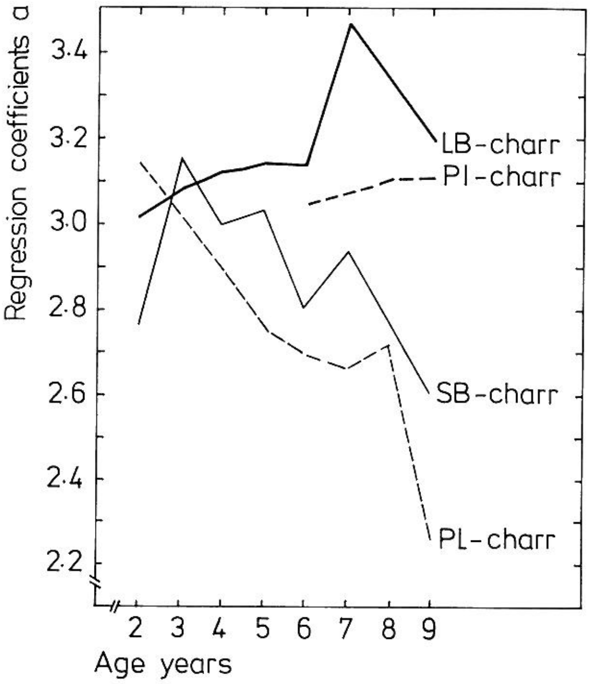


Fig. 19. Regression coefficients (a) of the weight (W, g)/length (L, mm) relationship: $\log_e W = a \log_e L$, for each age group within four arctic charr morphs from Thingvallavatn, August/September 1983 and 1984.

Table 19. Regression of individual fecundity (F) on fork length (L, mm) for four arctic charr morphs, and on fork length and age (A, yr) of two morphs from Thingvallavatn. All regressions are significant (F-tests, $P < 0.0001$). N = sample size. R^2 = coefficient of determination.

Morph	Regression	Fecundity range	R^2	N
LB-charr	$\log_e F = 2.719 \log_e L - 8.97$	149–1914	0.95	7
PI-charr	$\log_e F = 2.841 \log_e L - 9.70$	278–1795	0.68	26
SB-charr	$F = 1.28 L - 74.74$	12– 221	0.69	175
	$F = 1.38 L - 4.75 A - 57.91$	12– 221	0.71	172
PL-charr	$F = 1.47 L - 57.53$	96– 431	0.11	404
	$F = 2.08 L - 18.6 A - 66.11$	96– 431	0.22	397
Pooled	$\log_e F = 2.284 \log_e L - 6.63$	12–1914	0.89	612

LB- and SB-charr because of different physical constraints of their habitats. The stone matrix of the bottom is probably a better habitat for small individuals, as they may manoeuvre freely among the stones. Foraging efficiency in the epibenthic zone may, on the other hand, be positively correlated with size. Medium-sized fish may do relatively badly in both habitats. Selection may therefore favour maturity at young age among the most slow growing benthic charr, and maturity at old age for fast growers. The individual growth rate decreases when sexual maturity is attained because gonadal development and reproductive activity reduces somatic growth (Calow 1979, 1985, Reznick and Endler 1982, Roff 1983), and early maturing fish become small, while late maturing ones may grow large. Thus, the individual growth rate appears to influence the onset of sexual maturation, and is itself reduced by the allocation of energy into gonadal development.

The relative amount of energy allocated to gonadal production increases with age in all morphs. Increased investment into reproduction relative to somatic growth may be a general trend among adult iteroparous fish species until they grow older (Nikolsky 1963). One reason may be that the chance for surviving another year decreases with age. On the other hand, young fish may show restraint in their gonadal production, thus decreasing post spawning mortality and increasing future growth and fecundity.

Individual fecundity varied among morphs; it was lowest in SB-charr and highest among LB- and PI-charr. The main reason is that fecundity increases with size. The benthivorous fish invested less in gonadal relative to somatic growth compared with the planktivorous and piscivorous morphs. Furthermore, the length specific fecundity decreased with age in SB- and PL-charr, even though the relative amount of energy allocated to gonadal development increased with age. Reduction in length specific fecundity with increasing age has also been found in other populations of arctic charr (Jonsson and Hindar 1982) as well as in other salmonids such as brown trout (Jonsson 1985). Variations in number of eggs developed each year is partly influenced by the variable food consumption of the fish (Simpson 1951, Nikolskii 1969b). This is supported by the fact that the weight/length ratio is reduced with age in SB- and PL-charr.

Sex ratios of SB-, PI- and adult PL-charr showed an

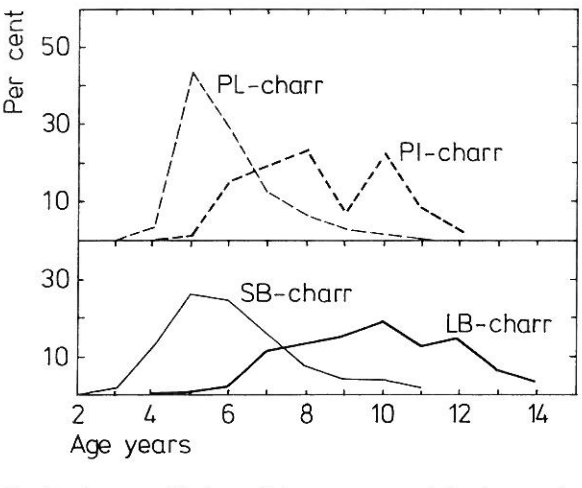


Fig. 20. Age specific fecundities, per cent, of the four arctic charr morphs from Thingvallavatn, August/September 1983 and 1984.

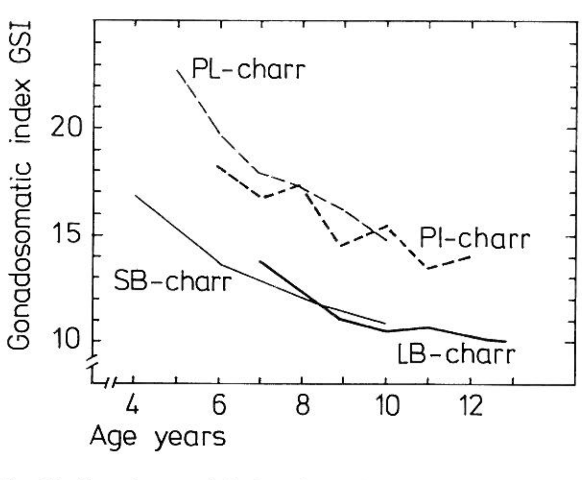


Fig. 21. Gonadosomatic index (GSI) within age groups of four arctic charr morphs from Thingvallavatn, August/September 1983 and 1984.

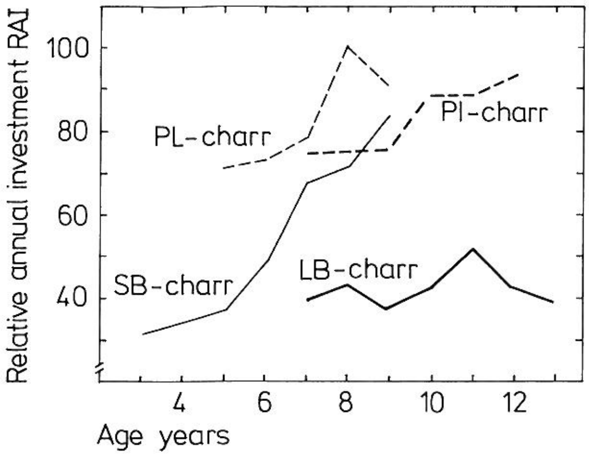


Fig. 22. Annual investments in gonadal relative to somatic growth of age groups of four arctic charr morphs from Thingvallavatn, August/September 1983 and 1984.

excess of females, whereas males were more abundant in most age groups of LB-charr. The excess of females in the three former morphs may result from earlier maturation of males than of females. Natural mortality of fish which are sexually mature is higher than that of immature individuals of the same age (Svärdson 1951, Calow 1979, Jonsson et al. 1984). Among LB-charr the sexes attained maturity at the same age.

Fishing mortality has an impact on the life history variables of PL-, PI- and LB-charr. Most SB-charr die from natural causes, as most of them are small and of little interest for human exploitation. PL-charr, on the other hand, are heavily exploited by gill net fishing during spawning, from late September till late October; up to 30–40% of the adult population are caught annually. PI-charr and LB-charr are caught in considerable numbers during May – August by local fishermen. The fishing removes predominantly old and large individuals of each morph, thus influencing size and age distributions as well as variables based on these.

Spawning and early ontogeny

Results

Spawning time and localities

The occurrence of sexually mature fish in maturity stages 5 and 6 in gill net catches made throughout the season indicates the approximate annual timing of spawning for the four arctic charr morphs (Fig. 23). The exact timing of spawning is based on direct observation or collection of spawning fish.

SB-charr spawned over a relatively long period (Fig. 23). The early SB-charr spawners were probably confined to sites with upwelling cold ground water. This was observed in the northern basin, where SB-charr were spawning from early September until November.

LB-charr were rarely found in stage 5–6 in the southern lake basin (Fig. 23). Catches in the northern basin indicated a main spawning period in July and August, although a few ripe males were also caught in September. Observations on spawning sites indicate a spawning period from late July to early August (cf. Fig. 26).

PL-charr in stage 5–6 were caught from late August to late October in the southern part of the lake (Fig. 23). Although fewer samples were taken in the northern basin, the material from this part of the lake also indicated the main spawning period to be September – October. The commercial fishery for PL-charr catches spawning fish, and is mainly taking place from 15 September to 20 October, with the vast majority of females in stage 6 present during the first week of October. The exact spawning period of PL-charr thus appears to be quite short.

PI-charr were found in a state ready to spawn approximately over the same period as PL-charr (Fig. 23). However, the catches indicate that spawning in this morph may take place well into November.

Ripe males of all morphs were found to stay longer on the spawning grounds than ripe females. LB-charr spawned both at day and night, and they were easy to observe. PL-charr spawned during the night, whereas little is known about the diel pattern in spawning activity in PI- and SB-charr.

The spawning localities of the four charr morphs in Thingvallavatn are shown in Fig 24. PL-charr appear to be spawning over large areas of stony substrate in the littoral zone around most of the lake. This is based on the commercial fishing for this morph during spawning.

Less is known about spawning localities of PI-charr, but ripe (stage 6) male-female pairs of PI-charr have been caught at a few localities, strongly indicating the position of spawning grounds. Other observations suggest that PI-charr spawn more or less in the same areas as PL-charr.

Spawning LB-charr were observed in two areas, both with inflowing cold groundwater. This clearly influences the water temperature in the spawning redds. In the groundwater well areas interstitial water temperature in the substrate remains stable at approximately 3–4°C throughout the year. At the same water depth in areas without groundwater influx, interstitial water temperatures in the substrate may go down from 10°C in August to 2°C in December – April, and increase to 7°C in June (Fig. 25).

Spawning SB-charr was caught in the shallow littoral zone (0–10 m) in all areas where fishing was performed. In August, ripe SB-males were caught among spawning LB-charr.

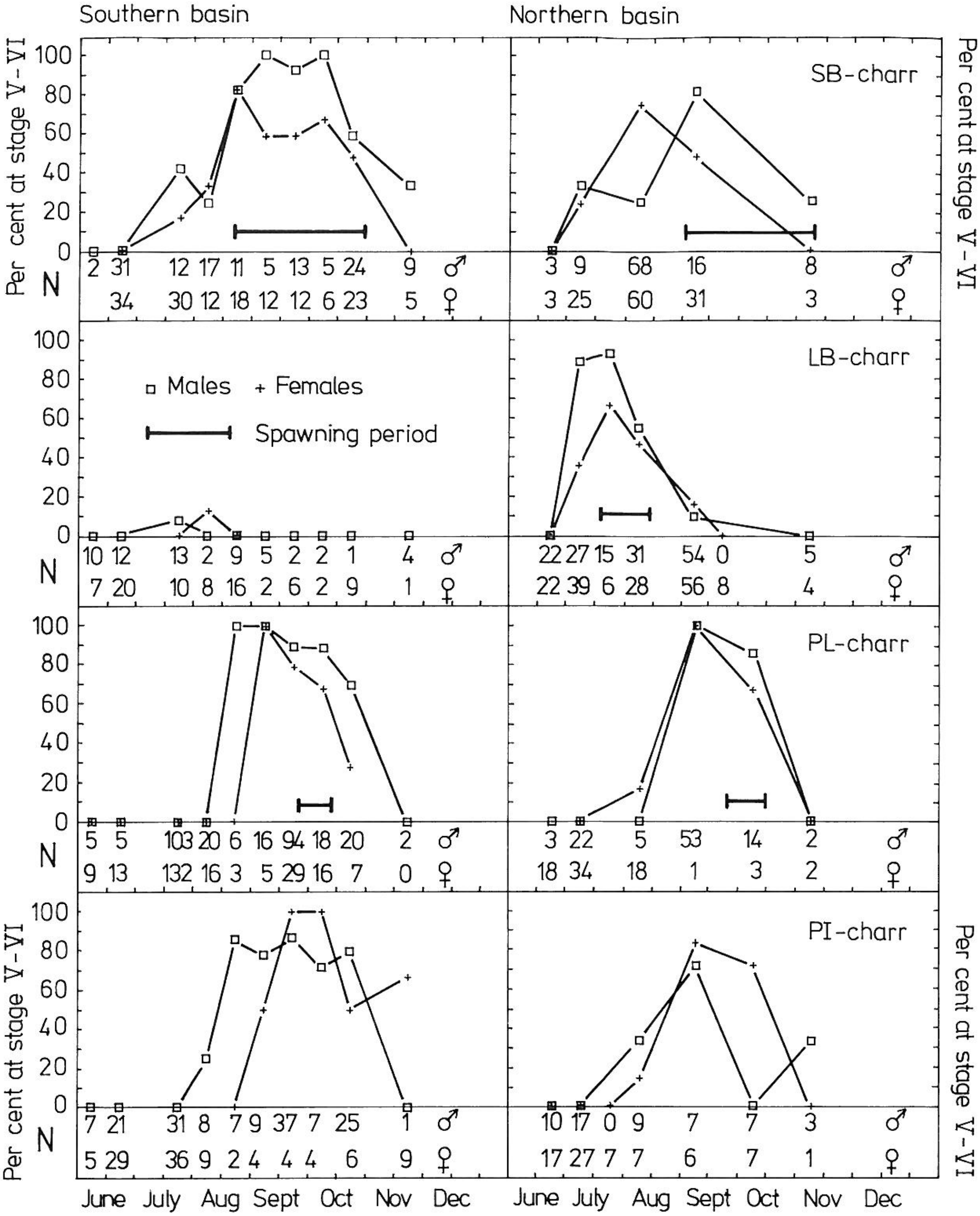


Fig. 23. Frequency of potential spawners (maturity stage 5 and 6) of the four charr morphs in gill net catches from northern and southern basin of Thingvallavatn. When exact data are available, solid bars indicate main spawning period. The figure is based on gill net catches from several localities in the littoral zone in 1981–1982 (Skúlason 1983, Malmquist et al. 1985). N = sample size males (♂) and females (♀).

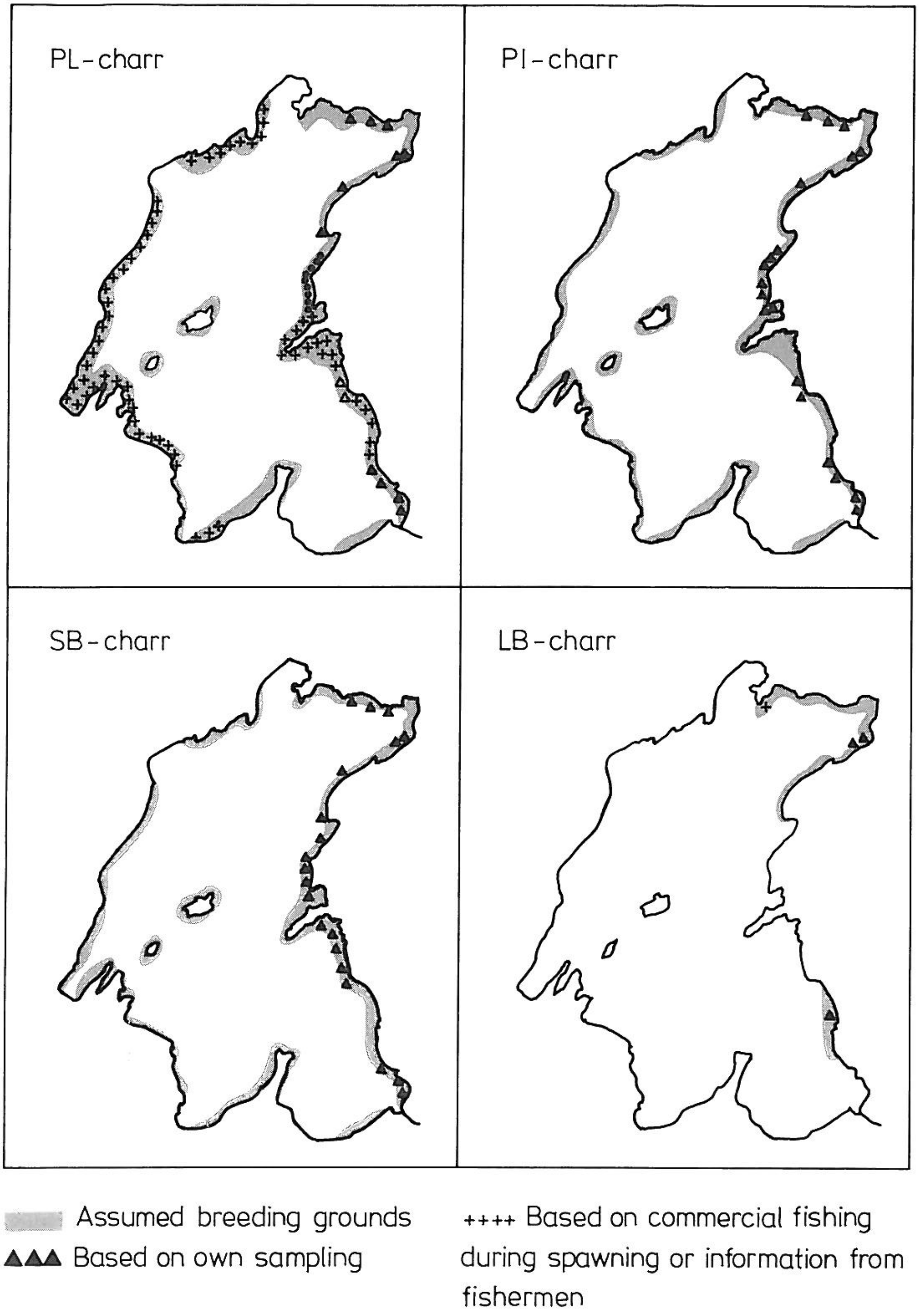


Fig. 24. Recorded spawning localities of the four arctic charr morphs in Thingvallavatn. The map is based on our own observations and observations from local fishermen.

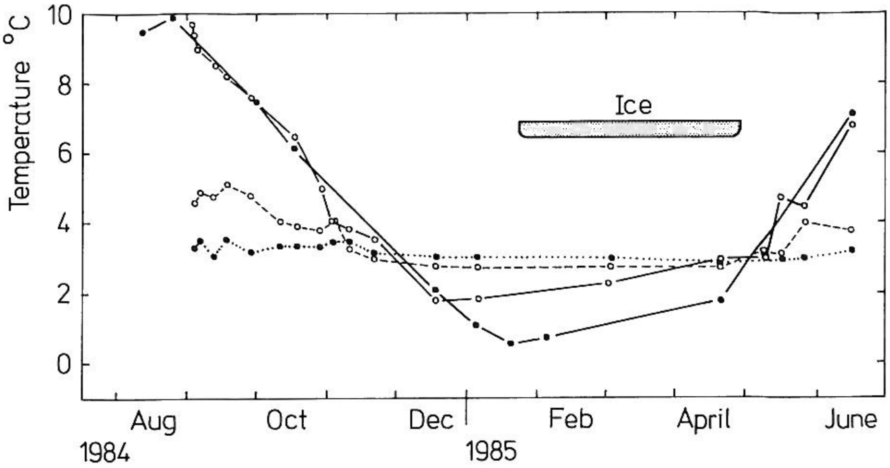


Fig. 25. Water temperatures in the lake water (solid line, filled circles) and in the substrate at two sites at Ólafsdráttur (OD-A and OD-B; broken line) and Svínanes (SV; solid line, open circles).

Spawning behaviour

The spawning site at Ólafsdráttur covers an area approximately 40 m wide and 170 m along the shore. Spawning occurred at depths of 0.2–5 m. In 1986 spawning activity peaked during the first week of August (Fig. 26). Males greatly outnumbered females, as mean male/female ratio was 4.4 (range 2.4–7.2) Tagging of LB-charr in the spawning areas showed that breeding LB-charr were rather stationary, and that males stayed longer than females. This probably explains the skewed sex-ratio on the breeding grounds.

Females selected spawning sites, and cleaned the substrate. Most of the time they stayed close to the nest spot, circled it, and accepted courtships from males (Fig. 27). Usually a female was surrounded by a group of males, but one (the guarding male) defended her against potential intruders, i.e. satellites. The satellites employed a sneaking technique both to court the female and to join in with a spawning pair. Release of gametes was a relatively rare event. Most males present were medium sized, but the probability of being in a guarding position increased with fish size (Table 20). The satellite males usually fled when attacked, but sometimes they tried to take the position of the guarding male. The intruder's rate of sucess was, however, low, because the guarding male usually won these conflicts ($\chi^2 = 48.6$, $P < 0.001$). The female sometimes attacked males approaching her, especially when the intruding male was small. Small males were chased away significantly more often than medium sized males ($\chi^2 = 6.4$, $P < 0.011$). Large males were never chased away by the female.

It is envisaged that the males behaved according to a pure conditional strategy which is dependent on size so that relatively large males employ a guarding tactic, whereas smaller males sneak. Although the success of the different tactics in terms of number of fertilized ova was not measured, the fact that guarding males spent more time courting the females than did sneaking males may indicate that the guarding tactic is more successful (Sigurjónsdóttir and Gunnarsson 1989).

SB-charr males were on rare occasions seen sneaking close to the LB-females but they were chased away by the LB-female and her guarding male. Both SB- and PL-charr were observed eating eggs on the spawning ground, and LB-charr were often seen eating their own eggs.

Early ontogeny

There were significant differences between morphs in both pre- and post-activated egg diameter (Table 21). Corresponding differences were also found in newly hatched embryos (103 d after fertilization) as well as in older free embryos. Under equal conditions all progeny groups appeared to develop at a similar rate, and started exogeneous feeding 145–160 d after fertilization. Close to the start of exogeneous feeding (143 d, Table 21), progeny of all morphs were about 20 mm in length, but SB-charr progeny were the smallest and PI- and

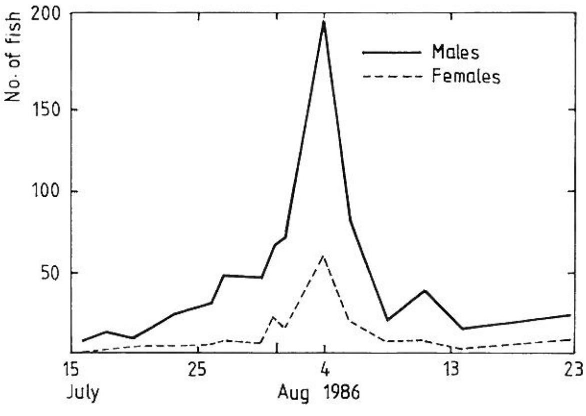


Fig. 26. Fluctuations in number of LB-charr spawners on the spawning ground at Ólafsdráttur, July – August 1986.

Table 20. Number of paired and single males within size groups small ($<=25$ cm), medium (26–35 cm) and large (>35 cm) counted along the transect. The proportion of paired fish were significantly larger among large males ($\chi^2 = 67.57$, 2 d.f., $P < 0.001$).

	Small	Medium	Large
Paired	4	34	27
Single	78	446	48

LB-charr progeny were the largest. In addition to yolk volume paternity may influence embryo growth. In progeny groups where eggs from PI-, PL- and LB-charr were fertilized with sperm from SB-charr males, resulting embryos tended to be smaller than embryos from groups where eggs from the same females were fertilized with sperm from the corresponding morph.

In the field experiment, the free embryos of LB-charr were approximately 20 mm already in January and 24 mm in April (Table 22). As the alevins were mostly unable to feed in the incubation boxes, this indicates their length at first exogeneous feeding. The free embryos of autumn spawning PI- and PL-charr were about 20 mm in April, and in June reached a length of 22 and 25 mm, respectively (Table 22). These fish had no yolk left, but had not started exogeneous feeding. Length distributions of electrofished charr alevins from the surf zone at Ólafsdráttur in June are bimodal (cf. Fig. 8), similar to what is indicated in Table 22.

The head morphology of the progeny strongly indicates two groups. SB- and LB-charr progeny resemble each other, as do PI- and PL-charr progeny (Fig. 28). However, differences were also significant between SB- and LB-charr, and between PL- and PI-charr already at an age of 153 d after fertilization (Table 23). The differences increased with age up to 225 d. At 153 d, characters like head length and eye diameter contributed much to the variation, indicating that embryonic characters were still prominent. At age 183 d, and even more at age 225 d, lower jaw length and snout length contributed relatively more to the variation. These are characters prominent in separating morphs among juvenile and adult fish (see Morphology). A short lower jaw and a round snout are embryonic characters that are retained in juvenile and adult LB- and SB-charr. PL- and PI-charr adults have a head morphology more diverted from the embryonic phenotype. This indicates that developmental heterochrony is the ontogenetic mechanism behind the variation between morphotypes. It should be noted that SB-charr progeny tended to form a distinct group (Fig. 28, Table 23). In general these fish tended to have relatively larger heads and head features than the other progeny groups. This suggests further genetic differences between morphs.

Discussion

Arctic charr are usually autumn spawners (Johnson 1980). In Thingvallavatn LB- and some SB-charr spawn unusually early, in July – September. This early spawning occurs in areas with cold water springs, where water temperatures in the spawning redds stay around 3–4°C even in summer. PL- and PI-charr and some SB-charr spawn in areas not influenced by cold water springs, and their main spawning time is the usual for arctic charr; in October.

In Windermere, England the arctic charr includes one autumn and one spring spawning stock (Frost 1965). The former stock spawns in shallow waters (2–4 m), the latter in deeper waters (15–18 m). In Attersee, Austria, arctic charr in spawning condition have been caught in all months of the year (Brenner 1980). This may be attributed to the reduced effects of seasonality in the deep habitat (40–60 m) of arctic charr in this lake. An interesting parallel to the situation in Thingvallavatn is found in the landlocked kokanee salmon *Oncorhynchus nerka* (Walbaum) of Lake Kronotskiy in Kamchatka, where two morphs of this species differ in spawning season due to the presence of cold water springs and variable feeding habits (Kurenkov 1977).

LB- and SB-charr feed extensively on the snail *Lymnaea peregra*, which is abundant throughout the year,

Table 21. Egg diameters (mm ± 95% confidence limits) of pre- and post-activated ova, and total lengths of free embryos of the four arctic charr morphs in Thingvallavatn, during laboratory incubation, and rearing 103–143 days after activation (Skúlason 1986). N = number of eggs or embryos. Postactivated egg sizes and embryo lengths were measured on material preserved in 10% formalin.

Morph	N	PL-charr	N	PI-charr	N	SB-charr	N	LB-charr
Egg diameter:								
Pre-activated	54	4.74 ± 0.07	43	5.11 ± 0.08	32	4.58 ± 0.09	43	4.95 ± 0.06
Post-activated	25	4.84 ± 0.09	26	5.11 ± 0.01	26	4.82 ± 0.12	45	5.16 ± 0.05
Free embryo length:								
103 d	17	16.3 ± 0.3	25	16.8 ± 0.3	14	15.4 ± 0.3	11	17.6 ± 0.4
113 d	23	17.3 ± 0.3	25	18.1 ± 0.4	11	16.3 ± 0.4	16	18.4 ± 0.5
123 d	19	18.4 ± 0.3	27	19.6 ± 0.9	13	16.8 ± 0.5	18	19.5 ± 0.5
133 d	18	19.3 ± 0.4	24	20.3 ± 0.5	13	18.5 ± 0.4	13	21.0 ± 0.4
143 d	15	20.5 ± 0.5	25	21.1 ± 0.4	12	19.2 ± 0.6	13	21.1 ± 0.4

Table 22. Total lengths (mm ± 95% confidence limits) of free embryos from ova of three arctic charr morphs incubated in incubation boxes at Svínanes (SV) and Ólafsdráttur (OD), January–June 1985 (Skúlason 1986). N = number of fish measured. The material had been preserved in 10% formalin for more than 6 months before being measured.

Morph	Locality	N	Jan 6	N	Apr 19	N	Jun 16
PL	SV		–	9	20.5 ± 1.1	19	23.1 ± 0.4
	OD		–	2	20.2 –	28	22.2 ± 0.3
PI	SV		–	27	17.4 ± 0.5	19	24.2 ± 0.3
	OD		–	13	20.8 ± 0.5	9	25.6 ± 0.6
LB	OD	15	19.3 ± 0.6	7	24.0 ± 0.7		–

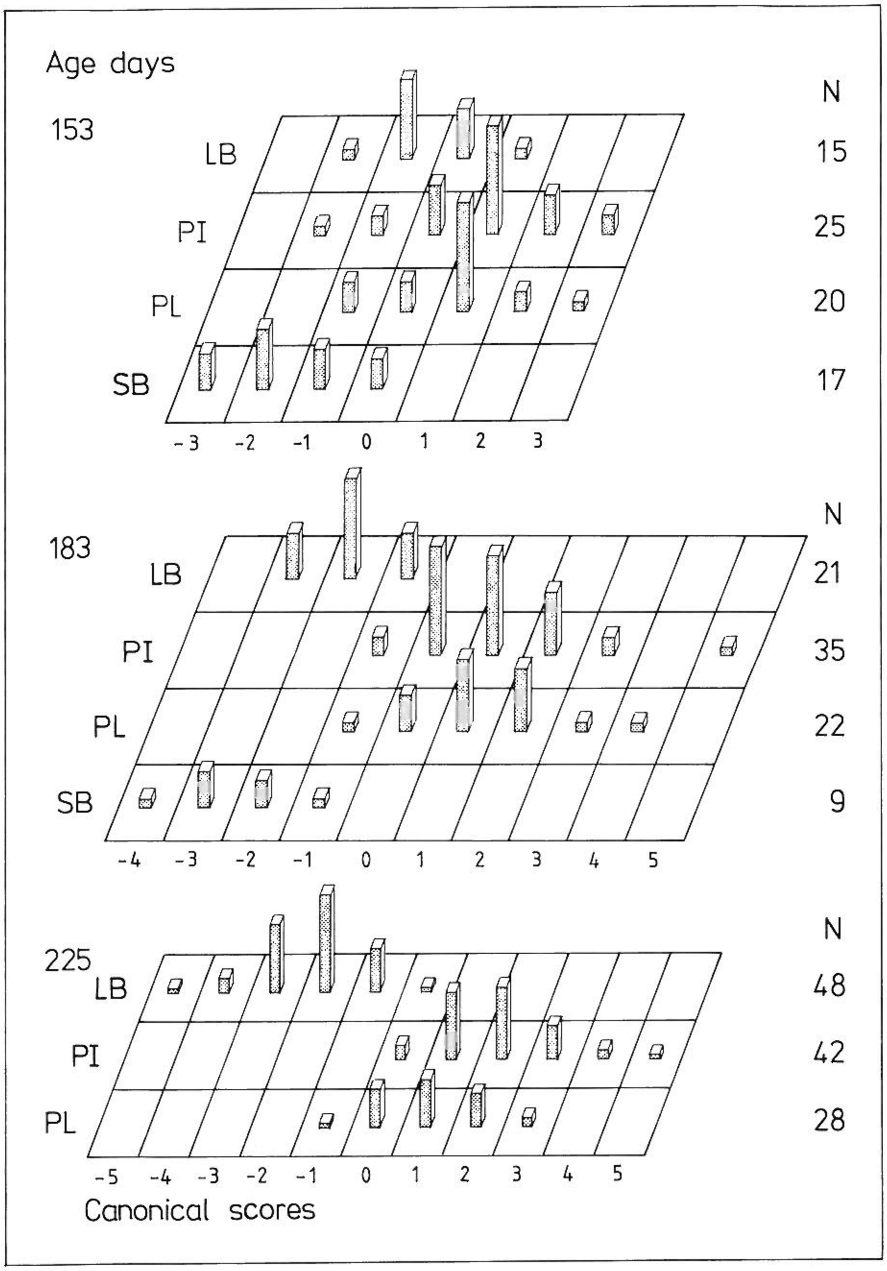


Fig. 28. Absolute frequency of scores on first canonical axis, derived from canonical discriminant analysis, for four progeny groups (of LB-, PI-, PL-, and SB-charr) at ages 153 and 183 d after activation, and for three progeny groups (of LB-, PI-, and PL-charr) at age 225 d after activation.
N = Number of fish.

Table 23. Mahanalobis' distances between progeny groups of PL-, PI-, SB- and LB-charr within age groups 153 d, 183 d and 225 d (no SB-charr) after activation. Significance (P <) of F-values are given in brackets (Skúlason 1986).

Age (d)		PL-charr	PI-charr	SB-charr
153	PI	1.59 (0.003)		
	SB	2.60 (0.0001)	2.70 (0.0001)	
	LB	2.42 (0.002)	2.08 (0.03)	2.20 (0.004)
183	PI	1.42 (0.0003)		
	SB	4.50 (0.0001)	3.99 (0.0001)	
	LB	3.34 (0.0001)	3.26 (0.0001)	2.65 (0.0001)
225	PI	2.32 (0.0001)		
	LB	3.73 (0.0001)	4.29 (0.0001)	

including spring and early summer. This enables the benthic charr morphs to develop their gonadal tissue at this time of the year. The main food of PL-charr, zooplankton, is on the other hand not abundant until July.

The variable spawning season has obvious consequences for early life history of the progeny. LB-charr progeny start exogeneous feeding in January–February, i.e. 2–3 months earlier than progeny of the autumn spawners. The progeny of September-spawning SB-charr may start exogeneous feeding in between these two periods. This is indicated by the great variation in lengths of age-0 fish in the surf zone at Ólafsdráttur in June. Further sampling at this locality in 1987 indicated a trimodal length distribution of age-0 charr (Skúlason et al. 1989b). The constant water temperature of the groundwater springs in Ólafsdráttur is relatively warm in winter, providing suitable conditions for feeding and growth of age-0 charr. By starting to feed early, the progeny of summer spawners may avoid competition with progeny of autumn spawners, thus reducing mortality risks (Elliott 1984a, b, 1986).

The differences in spawning times indicate that LB-charr at Ólafsdráttur may be reproductively isolated from PL- and PI-charr. The behaviour of LB-females on the spawning redds also indicates isolation from SB-charr. They behave aggressively towards SB-males as well as small LB-males trying to come close. This may partly be a defence against egg predation (Campbell 1979) but it also reduces the chance of SB-males mating with LB-females. Such size selective mating may be of particular importance when a mixture of morphs is in spawning condition. Thus, although SB-charr partly overlap in spawning time with the other morphs, behavioural isolating mechanisms may be present. The fact that SB-charr differ significantly from the other morphs in polymorphic allozyme frequencies (see below) also indicates reproductive isolation.

Egg size and embryonic growth was clearly connected with parent body size among morphs; SB-charr being smallest and PI- and LB-charr being largest. Survival and growth rate of age-0 salmonids are strongly dependent on body size (Bagenal 1969, Elliott 1984a, Taylor and McPhail 1985), so this variation probably influences morph segregation.

The morphology of progeny groups of the four morphs strongly indicates two morphotypes: one benthivorous (including SB- and LB-charr) with an undershot mouth, and one morphotype featuring terminal mouth including PL- and PI-charr. The significant differences in morphology at this early stage indicate genetic differences between the morphotypes. The significant differences between SB- and LB-charr progeny furthermore indicate that SB-charr may be genetically distinct.

Population genetics

Results

Protein products of 36 enzyme loci in 39 to 40 fish of each of the four morphs were analysed according to the electrophoretic methods described by Utter et al. (1974) and Allendorf et al. (1983). Locus designations are according to Andersson et al. (1983).

Variation was detected at five loci (Table 24). The remaining 31 loci were considered fixed for the same allele in all four morphs. Only *Est2* and *Mdh4,5* showed enough variation to permit statistical analysis of variation among morphs. There was no significant deviation from Hardy-Weinberg proportions at *Est2* neither

Table 24. Allozyme variation at five polymorphic loci in four morphs of arctic charr from Thingvallavatn, Iceland.

Locus	Alleles	Morph			
		SB-charr	LB-charr	PI-charr	PL-charr
Est2	100	0.913	0.863	0.795	0.795
	90	0.087	0.137	0.205	0.205
Gpi3	100	0.963	1.000	1.000	1.000
	92	0.037	–	–	–
Ldh4	100	0.963	0.963	0.987	1.000
	65	0.037	0.037	0.013	–
Mdh4,5*	100	0.419	0.325	0.250	0.281
	130	0.581	0.675	0.750	0.719
Pgm2	100	0.975	0.987	1.000	1.000
	114	0.025	0.013	–	–
H		0.032	0.029	0.028	0.026
P		0.139	0.111	0.083	0.056

H: average expected heterozygosity.
P: proportion of loci polymorphic.
* considered a single duplicated locus in all analyses.

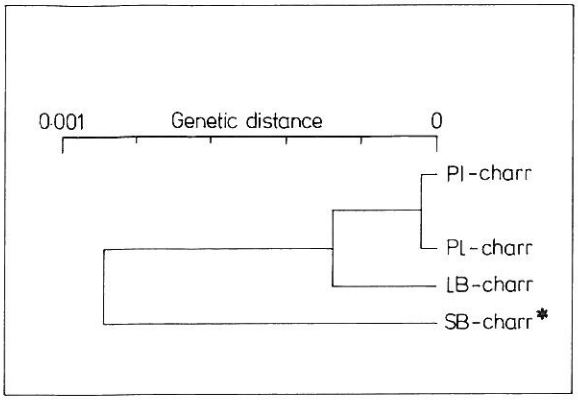


Fig. 29. Dendrogram for the genetic relationship among four sympatric morphs of arctic charr in Thingvallavatn, constructed from Nei's D based upon 36 enzyme loci. * indicates that branch is significant based on frequencies of *Est2* and *Mdh4,5* phenotypes, $P < 0.05$.

within morphs nor in the combined sample of all four morphs ($N = 158$) (χ^2 goodness of fit, 1 d.f., $P > 0.05$). At the *Mdh4,5* locus, five phenotypes were observed: the homozygotes *(100)* and *(130)* and three heterozygotes. All have been described by Andersson et al. (1983), and are considered products of a duplicated locus. Due to difficulties in distinguishing between the three heterozygous phenotypes, they were combined into a single heterozygous class in the chi-square analysis. Frequencies of phenotypes at the *Mdh4,5* locus were also in Hardy-Weinberg proportions within all morphs, but for the combined sample of all four morphs there was a significant deviation from the expected frequencies (χ^2 goodness of fit, 1 d.f., $P < 0.05$). There was a deficit of heterozygotes and an excess of the *(130)* homozygote. The biological meaning of this result is, however, unclear, due to the difficulties in correct scoring of the three different heterozygotes.

Nei's genetic distance (D) (Nei 1972) was calculated for each pair of morphs (36 loci). A high degree of similarity was observed, with D ranging from 0.00004–0.00126. A dendrogram was constructed with the unweighted pair group method of arithmetic averages (UPGMA: Sneath and Sokal 1973) (Fig. 29). Chi-square analysis showed that SB-charr differed significantly from the other three morphs. There was a significant difference in the numbers of *(100)* and *(90)* alleles at *Est2* between SB-charr and the other three morphs combined (contingency $\chi^2 = 4.02$, 1 d.f., $P < 0.05$).

Using *Mdh4,5* we compared the frequencies of individuals in the two homozygous classes *(100* and *130)* and the combined heterozygous classes *(100/130)* and found no significant difference between SB-charr and the other three morphs ($P > 0.05$). However, summing up the χ^2-values and the degrees of freedom from the two analyses gave significant differentiation between SB-charr and the other three morphs combined.

Discussion

The four sympatric morphs of arctic charr in Thingvallavatn are genetically very similar. Genetic distance

Table 25. Summary of morphological and ecological characteristics of the four arctic charr morphs of Thingvallavatn. TL = total length, L_∞ = asymptotic length, S = annual survival rate ± 95% confidence limits, F = individual fecundity range (no. of eggs).

Morph	Morphology	Life history traits	Spawning period	Habitat	Main food
Small benthivorous (SB-charr)	Overshot mouth, Adult TL: 7–31 cm, Parr marks along the flanks, dark coloration 25.2 gill rakers	L_∞ = 13.3 cm, Age at maturity: female = 4, male = 2, S = 0.57 ± 0.03 F = 12 – 221,	July – November	Littoral	*Lymnaea peregra*
Large benthivorous (LB-charr)	Overshot mouth, Adult TL: 9–55 cm, No parr marks, dark coloration 25.9 gill rakers	L_∞ = 55.4 cm, Age at maturity: female = male = 8, S = 0.63 ± 0.05 F = 149 – 1914	July – August	Littoral	*Lymnaea peregra*
Planktivorous (PL-charr)	Terminal mouth, Adult TL: 13–26 cm, No parr marks, silvery coloration 27.4 gill rakers	L_∞ = 20.5 cm, Age at maturity: female = 5, male = 4, S = 0.43 ± 0.02 F = 96 – 431	September – October	Whole lake	Crustacean zooplankton, chironomid pupae
Piscivorous (PI-charr)	Terminal mouth, Adult TL: 23–65 cm, No parr marks, light to silvery coloration 27.1 gill rakers	L_∞ = 30.2 cm, Age at maturity: female = male = 6, S = 0.63 ± 0.05 F = 278 – 1795	September – October (?)	Whole lake	Threespine stickleback, small charr

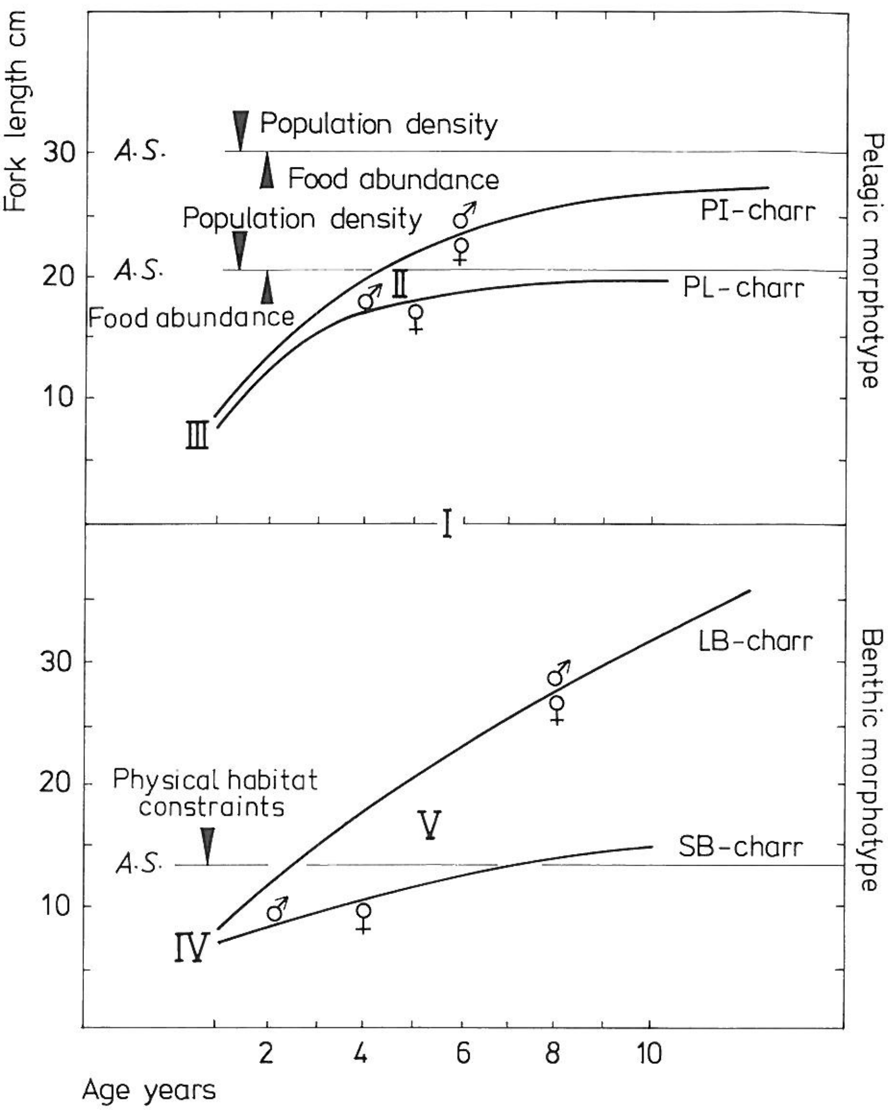


Fig. 30. Schematic summary of the proposed interrelations between and factors creating the four morphs of arctic charr in Thingvallavatn. Roman figures indicate decisive points in the separation of morphotypes and morphs: Reproductive isolation between the two morphotypes (I) is indicated by differences in embryonal, juvenile and adult morphology. The reproductive barrier may be behavioural, and to some extent temporal and spatial. PL- and PI-charr are two trophically specialized morphs that may develop from the same parents. The adult size difference (II) between the two pelagic morphs is mainly determined by food particle size (crustacean zooplankton vs fish). The proportion of PI-offspring is probably larger from PI- than PL-parents due to diffences in egg size (III). SB- and LB-charr are two trophically specialized morphs that may be reproductively isolated. Reproductive isolation (IV) is indicated by gill raker number, genetic distance and spawning time. Difference in adult size (V) is due to physical habitat constraints favouring small body size in SB-charr. Male (♂) and female (♀) symbols indicate age at 50% sexual maturity within morphs. Triangular arrows indicate factors influencing asymptotic sizes (A.S.) of morphs.

values (D < 0.001) and the absence of fixed alternate alleles among morphs indicate that SB-, LB-, PL- and PI-charr are conspecific, and should not be considered different evolutionary lineages. Therefore, these data do not support Gydemo's (1984) proposal that Thingvallavatn contains at least two sibling species of arctic charr.

General discussion

Our null hypothesis was that there is one uniform phenotype of arctic charr in Thingvallavatn. The prediction from this hypothesis was that the external morphology, life history, and ecological characters of arctic charr in the lake should have continuous distributions.

Our analyses show that this hypothesis must be rejected. The four morphs of arctic charr in Thingvallavatn differ in a number of biological variables, summarized in Table 25. Significant differences were found in e.g. embryonal, juvenile and adult morphology, ontogeny, life history variables, habitat distribution, diet, endoparasites, spawning time and place, and allele frequencies in polymorphic loci. The variation among morphs was discontinuous.

Analysis of shape clearly reveal two morphotypes (Fig. 30): 1) a benthic morphotype, including SB- and LB-charr, with subterminal mouth and relatively large pectoral fins, and 2) a pelagic morphotype, including PL- and PI-charr with terminal mouth and relatively small pectoral fins. The benthic morphs have significantly fewer gill rakers than the pelagic morphs. The two morphotypes also differ significantly in the morphology of newly hatched progeny. This dichotomy in morphology correlates clearly with the distinct divergence in food and habitat preferences, with resulting patterns of growth, relative gonadal investments, and parasite infection. SB- and LB-charr live in the littoral zone, and feed to a large extent on *Lymnaea peregra*. The pelagic morphs are found in all habitats, with PL-charr feeding on zooplanton and chironomid pupae and PI-charr feeding on fish. Thus it appears that the distinct diferences in morphology represent trophic adaptation to different habitats and food (Keast and Webb 1966, Schutz and Northcote 1972, Moyle and Cech 1982, Lavin and McPhail 1986).

The pronounced phenotypic and ecological differences and the fact that we have found no signs of interbreeding between the morphotypes, suggest reproductive isolation between them. The insignificant genetic distance between the morphs, however, indicates that the segregation must have taken place in recent times, probably within the lake basin itself, and it may not be complete (cf. Turner and Grosse 1980, Hindar et al. 1986).

The two morphs within each morphotype differ in life history characteristics, such as growth rate, age and size at sexual maturity and asymptotic length (Fig 30). Within the pelagic morphotype, back-calculated growth shows that PL- and PI-charr grow at a similar rate during the first years of life. PL-charr mature early and growth stagnates at a size of approximately 20 cm. Asymptotic length, however, may vary with year class strength and food abundance (Snorrason et al. 1992). PI-charr start fish feeding at a length of approximately 22 cm, and they mature 1–3 yr later than PL-charr. PI-charr reach an asymptotic length of 30.2 cm. Both PL- and PI-charr appear to develop from one morphologically homogeneous group of juvenile fish. Furthermore, these two morphs have practically identical allele frequencies and do not differ significantly in number of gill rakers. These observations suggest that PL- and PI-charr stem from the same population. Although both PL- and PI-charr may develop to PI-charr, a larger proportion of PI-progeny than PL-progeny may reach the size necessary for fish eating, becoming PI-charr (cf. Nordeng 1983). Eggs and embryos of PI-charr were larger than those of PL-charr. Egg size is a parental component that may have some influence on the ontogenetic path taken by the offspring (Fig. 30). Such initial differences in progeny may be enlarged in juveniles if relative size within year classes is positively correlated with their performance in competition for food or predator avoidance (cf. Allendorf et al. 1983, Elliott 1984b, Taylor and McPhail 1985). Thus, PI-charr, being larger when they commence external feeding, retain their size advantage throughout their life span.

The process leading to the ontogenetic divergence may be envisaged as follows: Part of the juvenile PL/PI-charr population tend to stay close to the bottom, both in the *Nitella*-zone and deeper. In the *Nitella*-zone they encounter high densities of threespine stickleback of all sizes up to approximately 6 cm (Sandlund et al. 1992). We suggest that such encounters can induce a shift to predation on stickleback in the largest PL/PI-juveniles, resulting in increased growth rate and delayed maturation. The majority of juveniles, however, continue as planktivores and mature early at a small size. PI-charr that turn to piscivory may also find abundant prey in PL-charr up to more than 20 cm in length. This might be the dietary base for the occasional PI-charr with weights up to more than 5 kg caught by the local fishermen.

According to this scenario, the differencies in adult size between PL- and PI-charr are determined by their food. Each prey type, i.e. zooplankton vs fish, yields optimal returns at a given predator size, explaining the growth stagnation at different body sizes (Werner and Gilliam 1984, Werner 1986). Bimodality in size due to shifts in diet and habitat has been documented in salmonids (Skreslet 1973, Campbell 1979, Hindar and Jonsson 1982, Sparholt 1985, Jonsson 1985, Riget et al. 1986) as well as other groups of fish (Timmons et al. 1980, Keast and Eadie 1985).

Spawning periods overlap in PL- and PI-charr. Arctic charr probably mate assortatively, as similar looking fish tend to spawn together (Jonsson and Hindar 1982, Sigurjónsdóttir and Gunnarson 1989). Whether PL- and PI-charr actually spawn together is not known. This may, however, be immaterial, since genetic mixing may occur in every generation through polymorphic progeny, as demonstrated by Nordeng (1983).

Based on this, PL- and PI-charr are two trophically specialized morphs, but both morphs may develop from each of the two parental types.

The relationship between the two benthic morphs appears to be of a different nature. SB-charr grow slowly and mature early, reaching an asymptotic length of merely 13.3 cm, whereas LB-charr have a higher growth rate and grow almost rectilinearly throughout all age groups represented in our material (Fig. 30). On average, they mature late and reach an asymptotic length of 55.4 cm.

SB- and LB-charr resemble each other closely in head morphology, they have a similar diet, and both live in the littoral zone. This seem to counter theories on niche utilization and overlap (McArthur and Levins 1967, May 1973). However, the complex structure of the lava bottom creates two physically different habitats, which may enable the coexistence of the two morphs. In addition to the open epibenthic habitat, the lava bottom has myriads of clefts, crevices and large interstitial spaces between and under lava stones, constituting a habitat rich in benthic invertebrates, giving ideal shelter to fish below a certain size. Our data indicate that SB-charr, as well as some age-0 and age-1 individuals of the other morphs, for the most part stay in this interstitial habitat. To efficiently utilize the interstitial habitat for feeding as well as for shelter during daylight hours the fish must stay small. This constraint has profound effects on the life history of SB-charr. They stay small by maturing at an early age, and by markedly increasing relative investment into gonadal tissue as they approach a critical age (size), i.e when size becomes costly in terms of decreased manoeuvrability in the interstitial habitat (Fig. 30). The costs of being small; particularly low individual fecundity and restricted foraging area, are met by higher juvenile survival as both sexes mature young.

Adult LB-charr must, due to their large body size, forage above the stone matrix. The mark-recapture experiments indicate that their foraging area includes the whole littoral zone of the lake, and that they are able to migrate at will, e.g. between patches of high food density. The rectilinear growth in LB-charr throughout the age groups represented (Fig. 30), indicates that most LB-charr do not live long enough to reach the asymptotic size presumably imposed by their foraging strategy (cf. Werner and Gilliam 1984, Werner 1986). Thus, the differences in life history between SB- and LB-charr are maintained through a size dependent asymmetry in habitat use.

In spite of similarities in head morphology and diet, the benthic morphs differ significantly in external coloration and gill raker number. They also have significantly different allele frequencies in polymorphic loci. Yet SB-charr overlap in spawning time with all other morphs, including to some extent also LB-charr. Observations on the spawning grounds of LB-charr revealed the presence of both PL- and SB-charr eating eggs of LB-charr. The aggressiveness of spawning LB-females towards SB-males trying to sneak close, as well as towards smaller LB-males courting them, suggests behavioural isolating mechanisms between SB- and LB-charr. However, considering the high densities of SB-charr in the stony littoral zone, successful sneak matings by SB-males with females of other morphs cannot be ruled out altogether.

Based on this, SB- and LB-charr are two trophically specialized morphs that may be reproductively isolated through differences in spawning time and assortative mating behaviours.

Several mechanisms for intralacustrine population divergence have been presented in the literature (review in Echelle and Kornfield 1984). The reasons we have chosen to stress the hypotheses based on sympatric diversification into unoccupied niches are twofold: 1) the habitat diversity, productivity, stability and lack of interspecific competition in the lake should facilitate such processes, and 2) the differentiation in trophic characters and life histories seen in the charrs of Thingvallavatn fit well to predictions emerging from such hypotheses (e.g. Hypothesis 5 in Smith and Todd 1984). During the process of divergence of the morphs, intraspecific competition may have been an important agent, favouring the individuals best adapted to the distinct habitat and food niches available. At present, the inter-morph competition may appear largely to be avoided through habitat and diet segregation. What we observe may be an example of a "ghost of competition past" (Connell 1980). However, inter-morph competition may still be an important factor in maintaining the morphs as distinct morphological and ecological entities.

Genetic difficulties are inherent in the processes of sympatric population divergence (Mayr 1976, Vrijenhoek et al. 1987), though some authors claim that these can be overcome (e.g Maynard Smith 1966, Tauber and Tauber 1977, Wilson and Turelli 1986). Strong spawning site fidelity and adaptations to local incubation and nursery environments may have played a key role in the development of the trophic specializations observed in Thingvallavatn today.

In summary, our conclusion is that the two morphs of the pelagic morphotype belong to one breeding population different from SB- and LB-charr, and that SB- and LB-charr also belong to different breeding populations. As stressed above, Thingvallavatn is, through its stability, habitat diversity and productivity, a lake system where it is easy to envisage processes leading to polymorphism, either through ontogenetic divergence or by intralacustrine population divergence. Over the whole area of arctic charr distribution the occurrence of sympatric charr morphs seems in accordance with our observations. The number of sympatric morphs in any one lake appears to be related to the number of vacant niches available to the species (Savaittova 1961, Johnson 1980, Hindar et al. 1986). The pattern of distribution renders improbable an explanation based on allopatric speciation and successive immigration.

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References

Adalsteinsson, H. 1979. Size and food of arctic char *Salvelinus alpinus* and stickleback *Gasterosteus aculeatus* in Lake Mývatn. – Oikos 32: 228–231.

Allen, K. R. 1966. A method of fitting growth curves of the van Bertalanffy type to observed data. – J. Fish. Res. Bd Can. 23: 163–179.

Allendorf, F. W., Knudsen, K. L. and Leary, R. F. 1983. Adaptive significance of differences in the tissue specific expression of a phosphoglucomutase gene in rainbow trout. – Proc. Nat. Acad. Sci. 80: 1397–1400.

Alm, G. 1959. Connection between maturity, size and age in fishes. – Rep. Inst. Freshwat. Res. Drottningholm 40: 5–145.

Anderson, L., Ryman, N. and Ståhl, G. 1983. Protein loci in the Arctic charr, *Salvelinus alpinus* L.: electrophoretic expression and genetic variability patterns. – J. Fish Biol. 23. 75–94.

Antonsson, Ú. 1977. Zooplankton in Lake Thingvallavatn 1972–1975. – Postgraduate Thesis. Univ. of Iceland, Reykjavik (In Icelandic).

– 1992. The structure and function of the zooplankton community in Thingvallavatn. – Oikos 64: 188–221.

Bagenal, T. B. 1969. Relationship between egg size and fry survival in brown trout (*Salmo trutta* L.). – J. Fish Biol. 1: 349–353.

Balon, E. K. (ed.) 1980a. Charrs: Salmonid fishes of the genus *Salvelinus*. – Junk, The Hague.

– 1980b. Early ontogeny of the European landlocked arctic charr – atricial form, *Salvelinus (Salvelinus) alpinus alpinus*. – In: Balon, E. K. (ed.), Charrs. Salmonid fishes of the genus *Salvelinus*. Junk, The Hague, pp. 607–630.

Behnke, R. J. 1972. The systematics of salmonid fishes in recently glaciated lakes. – J. Fish. Res. Bd Can. 29: 639–671.

– 1980. A systematic review of the genus *Salvelinus*. In: Balon, E. K. (ed.), Charrs. Salmonid fishes of the genus *Salvelinus*. Junk, The Hague, pp. 441–480.

– 1984. Organizing the diversity of the Arctic charr complex. – In: Johnson, L. and Burns, B. (eds), Biology of the Arctic charr. Proc. Int. Symp. Arctic Charr, Winnipeg, Manitoba, May 1981. Univ. of Manitoba Press, Winnipeg, pp. 3–21.

Bérubé, M. and Curtis, M. A. 1986. Transmission of *Diphyllobothrium ditremum* to arctic char *(Salvelinus alpinus)* in two subarctic Quebec lakes. – Can. J. Fish. Aquat. Sci. 43: 1626–1634.

Brenner, T. 1980. The Arcic charr *Salvelinus alpinus salvelinus* in the prealpine Attersee, Austria. – In: Balon, E. K. (ed.), Charrs. Salmonid fishes of the genus *Salvelinus*. Junk, The Hague, pp. 765–772.

Bylund, G., Fagerholm, H.-P., Calenus, G., Wikgren, B.-J. and Wiström, M. 1980. Parasites of fish in Finland. II. Methods for studying parasite fauna in fish. – Acta Acad. Åboensis 40: 1–23.

Calow, P. 1979. The cost of reproduction – a physiological approach. – Biol. Rev. 54: 23–40.

– 1985. Adaptive aspects of energy allocation. – In: Tytler, P. and Calow, P. (eds), Fish energetics: New perspectives. Johns Hopkins Univ. Press, Baltimore, MD, pp.13–31.

Campbell, R. N. 1979. Ferox trout, *Salmo trutta* L., and charr, *Salvelinus alpinus* (L.), in Scottish lochs. – J. Fish Biol. 14: 1–29.

Cavender, T. M. 1980. Systematics of *Salvelinus* from the North Pacific Basin. – In: Balon, E. K. (ed.), Charrs. Salmonid fishes of the genus *Salvelinus*. Junk, The Hague, pp. 441–481.

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.

Connell, J. H. 1980. Diversity and the coevolution of competitors, or the ghost of competition past. – Oikos 35: 131–138.

Curtis, M. A. 1984. *Diphyllobothrium* spp. and the arctic charr: parasite acquisition and its effect on a lake-resident population. – In: Johnson, L. and Burns, B. (eds), Biology of the arctic charr, Proc. Int. symp. arctic charr, Winnipeg, Manitoba, May 1981. Univ. of Manitoba Press, Winnipeg, pp. 395–411.

Echelle, A. A. and Kornfield, I. (eds) 1984. Evolution of fish species flocks. – Univ. of Maine at Orono Press. Orono, ME.

Elliott, J. M. 1984a. Numerical changes and population regulation in young migratory trout *Salmo trutta* in a Dartmoor stream 1966–83. – J. Anim. Ecol 53: 327–350.

– 1984b. Growth, size, biomass and production of young migratory trout, *Salmo trutta*, in a Lake District stream. – J. Anim. Ecol. 53: 939–994.

– 1986. Spatial distribution and behavioural movements of migratory trout *Salmo trutta* in a Lake District stream. – J. Anim. Ecol. 55: 907–922.

Ferguson, A. 1986. Lough Melvin. A unique fish community. – Occ. Pap. Irish Science Technology No. 1.

– and Mason, F. M. 1981. Allozyme evidence for reproductively isolated sympatric populations of brown trout *Salmo trutta* L. in Lough Melvin, Ireland – J. Fish Biol. 18: 629–642.

Frandsen F., Malmquist H. J. and Snorrason, S. S. 1989. Ecological parasitology of polymorphic arctic charr, *Salvelinus alpinus*, in Lake Thingvallavatn, Iceland. – J. Fish Biol. 34: 281–297.

Freund, R. J. and Littel, R. C. 1981. SAS for linear models. A guide to the ANOVA and GLM procedures – SAS Statistial Institute Inc., Cary, NC.

Fridriksson, Á. 1939. About the murta in Thingvallavatn with respect to other salmonids in the lake. – Náttúrufrædingurinn 9: 1–30 (In Icelandic).

Frost, W. E. 1965. Breeding habits of Windermere char, *Salvelinus willoghbii* (Gunther), and their bearing on speciation in these fish. – Proc. R. Soc. Edinb. B. 163: 232–284.

Grudzien, T. A. and Turner, B. J. 1984. Direct evidence that the *Ilyodon* morphs are a single biological species. – Evolution 38: 402–407.

Gydemo, R. 1984. Preliminary survey results of the distribution of the Arctic charr complex in Iceland. – In: Johnson, L. and Burns, B. (eds), Biology of the arctic charr, Proc. Int. symp. arctic charr, Winnipeg, Manitoba, May 1981. Univ. of Manitoba Press, Winnipeg, pp. 91–107.

Halvorsen, O. 1970. Studies on the helminth fauna of Norway. XV. On the taxonomy and biology of plerocercoids of *Diphyllobothrium* Cobbold, 1858 (Cestoda: Pseudophyllidea) from North-Western Europe. – Nytt Mag. Zool. 21: 201–210.

– and Wissler, K. 1973. Studies on the helminth fauna of Norway. XXVIII. An experimental study of the ability of *Diphyllobothrium latum* (L.), *D. dendriticum* (Nitzsch) and *D. ditremum* (Creplin) (Cestoda: Pseudophyllidea) to infect paratenic hosts. – Norw. J. Zool. 21: 201–210.

Heggberget, T. 1984. Habitat selection and segregation of parr of Arctic char *(Salvelinus alpinus)*, brown trout *(Salmo trutta)* and Atlantic salmon (*S. salar* L.) in two streams in North Norway. – In: Johnson, L. and Burns, B. (eds), Biology of the arctic charr, Proc. Int. symp. arctic charr, Winnipeg Manitoba, May 1981. Univ. of Manitoba Press, Winnipeg, pp. 217–231.

Henricson, J. 1977. The abundance and distribution of *Diphyllobothrium dendriticum* (Nitzsch) and *D. ditremum* (Creplin) in the char *Salvelinus alpinus* (L.) in Sweden. – J. Fish Biol. 11: 231–248.

– 1978. The dynamics of infection of *Diphyllobothrium dendriticum* (Nitzsch) and *D. ditremum* (Creplin) in the char *Salvelinus alpinus* (L.) in Sweden. – J. Fish Biol. 13: 51–71.

– and Nyman, L. 1976. The ecological and genetical segregation of two sympatric species of dwarfed char (*Salvelinus* *alpinus* (L.) species complex). – Rep. Inst. Freshwat. Res. Drottningholm 52: 15–37.

Hindar, K. and Jonsson, B. 1982. Habitat and food segregation of dwarf and normal Arctic charr *(Salvelinus alpinus)* from Vangsvatnet Lake, Western Norway. – Can. J. Fish. Aquat. Sci. 39: 1030–1040.

– Ryman, N. and Ståhl, G. 1986. Genetic differentiation among local populations of Arctic charr, *Salvelinus alpinus*. – Biol. J. Linn. Soc. 27: 269–285.

Humphries, J. M., Bookstein, F. L., Cherloff, B., Smith, G. R., Elder, R. L. and Poss, S. G. 1981. Multivariate discrimination by shape in relation to size. – Syst. Zool. 30: 291–308.

Johnson, L. 1980. The arctic charr, *Salvelinus alpinus*. – In: Balon, E. K. (ed.), Charrs. Salmonid fishes of the genus *Salvelinus*. Junk, The Hague, pp. 15–98.

– and Burns, B. (eds) 1984. Biology of the arctic charr, Proc. Int. symp. arctic charr, Winnipeg, Manitoba, May 1981. – Univ. of Manitoba Press, Winnipeg.

Jónasson, P. M. and Lindegaard, C. 1987. Ecosystem studies of North Atlantic Ridge lakes. – Verh. Internat. Verein. Limnol. 23: 394–402.

Jonsson, B. 1976. Comparison of scales and otoliths for age determination in brown trout *Salmo trutta* L. – Norw. J. Zool. 24: 295–301.

– 1985. Life history pattern of freshwater resident and sea-run migrant brown trout in Norway. – Trans. Am. Fish. Soc. 114: 182–194.

– and Gravem, F. R. 1985. Use of space and food by resident and migrant brown trout, *Salmo trutta*. – Env. Biol. Fish 14: 281–293.

– and Hindar, K. 1982. Reproductive strategy of dwarf and normal Arctic charr *(Salvelinus alpinus)* from Vangsvatnet Lake, Western Norway. – Can. J. Fish. Aquat. Sci. 39: 1404–1413.

– , Hindar, K. and Northcote, T. G. 1984. Optimal age at sexual maturity in sympatric and experimentally allopatric cutthroat trout and Dolly Varden charr. – Oecologia (Berl.) 61: 319–325.

– and Østli, T. 1979. Demographic strategy in char compared with brown trout in Lake Løne, Western Norway. – Rep. Inst. Freshwat. Res. Drottningholm 58: 45–54.

– and Stenseth, N. C. 1977. A method for estimating fish length from otolith size. – Rep. Inst. Freshwat. Res. Drottningholm 56: 81–86.

– , Skúlason, S., Snorrason, S. S., Sandlund, O. T., Malmquist, H. J., Jónasson, P. M., Gydemo, R. and Lindem, T. 1988. Life history variation of polymorphic arctic charr in Thingvallavatn, Iceland. – Can. J. Fish. Aquat. Sci. 45: 1537–1547.

Kairesalo, T., Gunnarson, K., Jónsson, G. St. and Jónasson, P. M. 1987. The occurrence and photosynthetic activity of epiphytes on the tips of *Nitella opaca* Ag. (Charophyceae). – Aquat. Bot. 28: 333–340.

Keast, A. and Eadie, J. 1985. Growth depensation in year-0 largemouth bass: the influence of diet. – Trans. Am. Fish. Soc. 114: 204–213.

– and Webb, D. 1966. Mouth and body form relative to feeding ecology in the fish fauna of a small Lake Opinicon, Ontario. – J. Fish. Res. Bd Can. 23: 1845–1874.

Kircheis, F. W. 1976. Reproductive biology and early life history of the Sunapee trout of Floods Pond, Maine. – Trans. Am. Fish. Soc. 105: 615–619.

Kirkpatrick, M. and Selander, R. K. 1979. Genetics of speciation in lake whitefishes in the Allegash basin. – Evolution 33: 478–485.

Klemetsen, A. and Grotnes, P. 1980. Coexistence and migration in two sympatric arctic charr – In: Balon, E. K. (ed.), Charrs. Salmonid fishes of the genus *Salvelinus*. Junk, The Hague, pp. 757–763.

– , Grotnes, P. E., Holthe, H. and Kristoffersen, K. 1985. Bear Island charr. – Rep. Inst. Freshwat. Res. Drottningholm 62: 98–119.

Kornfield, I., Smith, D. C., Gagnon, P. S. and Taylor, J. N. 1982. The cichlid fish of Cuatro Cienegas, Mexico: Direct evidence of conspecificity among distinct trophic morphs. – Evolution 36: 658–664.

Kurenkov, S. I. 1977. Two reproductively isolated groups of kokanee salmon, *Oncorhynchus nerka kennerlyi*, from lake Kronotskyi – J. Ichthyol. 17: 526–534.

Lastein, E. 1983. Decomposition and sedimentation processes in oligotrophic, subarctic Lake Thingvalla, Iceland. – Oikos 40: 103–112.

Lavin, P. A. and McPhail, J. D. 1986. Adaptive divergence of trophic phenotype among freshwater populations of the threespine stickleback *(Gasterosteus aculeatus)*. – Can. J. Fish. Aquat. Sci. 43: 2455–2463.

Levins, R. 1968. Evolution in changing environments. – Princeton Univ. Press, Princeton, NJ.

Lien, L. and Borgstrøm, R. 1973. Studies of the helminth fauna of Norway. XXXI. Distribution and seasonal occurrence of *Protocephalus* sp. Wienland, 1858 (Cestoda: Protocephala) in brown trout. *Salmo trutta* L., from southern Norway. – Norw. J. Zool. 21: 293–297.

Lindegaard, C. 1980. Bathymetric distribution of Chironomidae (Diptera) in the oligotrophic Lake Thingvallavatn, Iceland. – In: Murray, A. (ed.), Chironomidae. Ecology, systematics, cytology and physiology. Pergamon Press, Oxford, pp. 225–232.

– 1992. Zoobenthos ecology of Thingvallavatn: vertical distribution, abundance, population dynamics and production. – Oikos 64: 257–304.

Lindem, T. 1983. Successes with conventional in situ determination of fish target strength. – In: Nakken, O. and Vennema, C. (eds), Symposium on fisheries acoustics. Selected papers of the ICES/FAO symposium on fisheries acoustics, Bergen, Norway, 21–24 June 1982. FAO Fish. Rep. (300), pp. 104–111.

– and Sandlund, O. T. 1984. New methods in assessment of pelagic freshwater fish stocks – coordinated use of echosounder, pelagic trawl and pelagic nets. – Fauna (Oslo) 37: 105–111 (In Norwegian with English summary).

Lindström, T. 1955. On the relation fish size – food size. – Rep. Inst. Freshwat. Res. Drottningholm 36: 133–147.

Magnússon, K. P. and Ferguson, M. M. 1987. Genetic analysis of four sympatric morphs of Arctic charr, *Salvelinus alpinus*, from Thingvallavatn, Iceland. – Environ. Biol. Fish. 20: 67–73.

Malmquist, H. J. 1988. Diet differentiation in polymorphic Arctic charr (*Salvelinus alpinus* (L.)) in Thingvallavatn, Iceland: diel and seasonal foraging activity. – Cand. scient. thesis, Univ. of Copenhagen, Copenhagen.

– , Snorrason, S. S. and Skúlason, S. 1985. The biology of artic charr (*Salvelinus alpinus* L.) in Lake Thingvallavatn, Iceland. I. Feeding ecology. – Náttúrufræðingurinn 55: 195–217 (In Icelandic).

Margolis, L., Esch, G. H., Holmes, J. C., Kuris, A. and Schad, G. A. 1982. The use of ecological terms in parasitology (Report of an ad hoc committee of the Am. Soc. Parasitol). – J. Parasitol. 68: 131–133.

May, R. M. 1973. Stability and complexity in model ecosystems. – Princeton Univ. Press, Princeton, NJ.

Maynard Smith, J. 1966. Sympatric speciation. – Am. Nat. 100: 637–650.

Mayr, E. 1976. Evolution and the diversity of life. – Harvard Univ. Press, Cambridge, MA.

McArthur, R. H. and Levins, R. 1967. The limiting similarity, convergence, and divergence of coexisting species. – Am. Nat. 101: 377–385.

Mills, C. A. and Eloranta, A. 1985. Reproductive strategies in the stone loach *Neomacheilus barbatulus*. – Oikos 44: 341–349.

Moyle, P. B. and Cech, J. J., jr. 1982. Fishes. An introduction to ichthyology. – Prentice-Hall, NJ.

Myers, R. A., Hutchings, J. A. and Gibson, R. J. 1986. Variation in male parr maturation within and among populations of Atlantic salmon, *Salmo salar*. – Can. Fish. Aquat. Sci. 43: 1242–1248.

Nei, M. 1972. Genetic distance between populations. – Am. Nat. 106: 283–291.

Nielsen, J. 1961. Age and growth of the freshwater stage of anadromous char *Salvelinus alpinus*. – Medd. Grønland Vol. 159 (8): 49–75.

Nikolskii, G. V. 1969a. Fish population dynamics. – Oliver & Boyd, Edinburgh.

– 1969b. Parallel intraspecific variation in fishes. – Probl. Ichthyol. 9: 4–8.

Nikolsky, G. V. 1963. The ecology of fishes. – Academic Press, London.

Nilsen, P. and Klemetsen, A. 1984. Anadromous, resident and landlocked Arctic charr on the coast of Finnmark, N. Norway. – In: Johnson, L. and Burns, B. (eds), Biology of the arctic charr, Proc. Int. symp. arctic charr, Winnipeg, Manitoba, May 1981. Univ. of Manitoba Press, Winnipeg, pp. 79–89.

Nilsson, N.-A. 1955. Studies on the feeding habits of trout and char in North Swedish lakes. – Rep. Inst. Freshwat. Res. Drottningholm 36: 163–255.

– and Filipsson, O. 1971. Characteristics of two discrete populations of Arctic char (*Salvelinus alpinus* L.) in a North Swedish lake. – Rep. Inst. Freshwat. Res. Drottningholm 51: 90–108.

Nordeng, H. 1983. Solution to the "char problem" based on Arctic char (*Salvelinus alpinus*) in Norway. – Can. J. Fish. Aquat. Sci. 40: 1372–1387.

Nyman, L., Hammar, J. and Gydemo, R. 1981. The systematics and biology of landlocked populations of arctic char from northern Europe. – Rep. Inst. Freshwat. Res. Drottningholm 59: 128–141.

Pimentel, R. A. 1979. Morphometrics. – Kendall/Hunt, IA.

Ranta-Aho, K. 1983. Rödingens (*Salvelinus alpinus* L.) yngelbiologi och ekologi i sjön Mývatn. – B. Sc. Thesis, Univ. of Iceland (In Swedish).

Ray, A. A. 1982a. SAS user's guide: Basics. – SAS Institute Inc., Cary, NC.

– 1982b. SAS user's guide: Statistics. – SAS Institute Inc., Cary, NC.

Reisinger, E. 1953. Zum Saiblingsproblem – Carinthia II 143: 74–102.

Reist, D. R. 1985. An empirical evaluation of several univariate methods to adjust for size variation in morphometric data. – Can. J. Zool. 63: 1813–1818.

Reznick, D. and Endler, J. A. 1982. The impact of predation on life history evolution in Trinidadian guppies *(Poecilia reticulata)*. – Evolution 36: 160–177.

Riget, E. F., Nygaard, K. H. and Christensen, B. 1986. Population structure, ecological segregation and reproduction in a population of Arctic charr (*Salvelinus alpinus*) from Lake Tasersuaq, Greenland. – Can. J. Fish. Aq. Sci. 43: 985–992.

Roff, D. A. 1983. An allocation model of growth and reproduction in fish. – Can. J. Fish. Aquat. Sci. 40: 1395–1404.

Rudstam, L. G., Clay, C. S. and Magnuson, J. J. 1987. Density and size estimates of cisco *(Coregonus artedii)* using analysis of echo peak PDF from single transducer sonar. – Can. J. Fish. Aquat. Sci. 44: 811–821.

Ryman, N. 1981. Conservation of genetic resources: experiences from the brown trout *(Salmo trutta)*. – In: Ryman, N. (ed.), Fish gene pools. Preservation of genetic resources in relation to wild fish stocks. Ecol. Bull. (Stockholm) 34: 61–74.

– , Allendorf, F. W. and Ståhl, G. 1979. Reproductive isolation with little genetic divergence in sympatric populations of brown trout *(Salmo trutta)*. – Genetics 92: 247–262.

Sæmundsson, B. 1904. Fiskirannsóknir 1902. I. Thingvallavatn. – Andvari 1904: 80–102 (In Icelandic).

– 1926. Íslensk dýr I. Fiskarnir. – Reykjavik, pp. 363–371 (In Icelandic).

Sæmundsson, K. 1965. Geological history of Lake Thingvallavatn. – Náttúrufræðingurinn 35: 103–144 (In Icelandic).

– 1992. Geology of the Thingvallavatn area. – Oikos 64: 40–68.

Sage, R. D. and Selander, R. K. 1975. Trophic radiation through polymorphism in cichlid fishes. – Proc. Nat. Acad. Sci. USA 72: 4669–4673.

Saltveit, S. J. and Styrvold, J.-O. 1984. Density of juvenile Atlantic salmon (*Salmo salar* L.) and brown trout (*S. trutta* L.) in two Norwegian regulated rivers. – In: Lillehammer, A. and Saltveit, S. J. (eds), Regulated rivers. Universitetsforlaget, Oslo, pp. 309–319.

Sandlund, O. T., Jonsson, B., Malmquist, H. J., Gydemo, R., Lindem, T., Skúlason, S., Snorrason, S. S. and Jónasson, P. M. 1987. Habitat use of arctic charr *Salvelinus alpinus* in Thingvallavatn, Iceland. – Environ. Biol. Fish. 20: 263–274.

– , Malmquist, H. J., Jonsson, B., Skúlason, S., Snorrason, S. S., Jónasson, P. M., Gydemo, R. and Lindem, T. 1988. Density, length distribution, and diet of age-0 arctic charr *Salvelinus alpinus* in the surf zone of Thingvallavatn, Iceland. – Environ. Biol. Fish. 23: 183–195.

– , Jónasson, P. M., Jonsson, B., Lindem, T., Malmquist, H. J., Skúlason, S. and Snorrason, S. S. 1992. Threespine stickleback *Gasterosteus aculeatus* in Thingvallavatn: habitat and food in a lake dominated by arctic charr *Salvelinus alpinus*. – Oikos 64: 365–370.

Savaittova, K. A. 1961. Intraspecific biological forms of *Salvelinus alpinus* (L.) in Kamchatka. – Vopr. Ikthiol. 1: 695–706 (Transl. from Russian by Fish. Res. Bd Can. Trans. Ser. No. 795. 1966).

– 1980. Taxonomy and biogeography of charrs in the Palearctic. – In: Balon, E. K. (ed.), Charrs. Salmonid fishes of the genus *Salvelinus*. Junk, The Hague, pp. 281–294.

Schaffer, W. M. and Elson, P. F. 1975. The adaptive significance of variations in life history among local populations of Atlantic salmon in North America – Ecology 56: 291–303.

Schmidt-Nielsen, K. 1939. Comparative studies on the food competition between trout and char. – K. Norske Vidensk. Selsk. Skr. 4: 1–45.

Schoener, T. W. 1968. The *Anolis* lizards of Bimini: resource partitioning in a complex fauna. – Ecology 49: 704–726.

Schutz, D. C. and Northcote, T. G. 1972. An experimental study on feeding behavior and interaction of coastal cutthroat trout *(Salmo clarki clarki)* and Dolly Varden *(Salvelinus malma)*. – J. Fish. Res. Bd Can. 29: 555–565.

Seber, G. A. F. and LeCren, E. D. 1967. Estimating population parameters from catches large relative to the population. – J. Anim. Ecol. 36: 631–643.

Shigin, A. A. 1986. Trematoda fauna of the USSR. Genus *Diplostomum*. Metacercariae – Nauka, Moscow (In Russian).

Siegel, S. 1956. Nonparametric statistics for the behavioral sciences. – McGraw-Hill, New York.

Sigurjónsdóttir, H. and Gunnarson, K. 1989. Alternative mating tactics of artic charr, *Salvelinus alpinus*, in Thingvallavatn, Iceland. – Environ. Biol. Fish. 26: 159–176.

Simpson, A. C. 1951. The fecundities of the plaice. – Fishery Invest. Lond. Ser. 2, 17: 1–27.

Skreslet, S. 1973. Group segregation in landlocked Artic char, *Salvelinus alpinus* (L.), in relation to the char problem. – Astarte 6: 55–58.

Skúlason, S. 1983. Útlit, vöxtur og æxlunarlíffræði mismunandi gerda bleikjunnar, *Salvelinus alpinus* (L.), í Thingvallavatni. – 4th year dissertation at the Univ. of Iceland, Reykjavík (In Icelandic).

– 1986. Embryo size and early head shape in four sympatric morphs of arctic charr *(Salvelinus alpinus)* in Thingvallavatn Iceland. – M. Sc. thesis. Univ. of Guelph, Guelph.

– , Noakes, D. L. G. and Snorrason, S. S. 1989a. Ontogeny of trophic morphology in four sympatric morphs of arctic charr *Salvelinus alpinus* in Thingvallavatn, Iceland. – Biol. J. Linn. Soc. 38: 281–301.

– , Snorrasson, S. S., Noakes, D. L. G., Ferguson, M. M. and Malmquist, H. J. 1989b. Segregation in spawning and early life history among polymorphic Arctic charr, *Salvelinus alpinus*, in Thingvallavatn, Iceland. – J. Fish. Biol. (Supp. A) 35: 225–232.

Smith, G. R. and Todd, T. N. 1984. Evolution of species flocks of fishes in north-temperate lakes. – In: Echelle, A. A. and Kornfield, I. (eds), Evolution of fish species flocks. Univ. of Maine at Orono Press, Orono, ME, pp. 47–68.

Smith, H. D. 1973. Observations on the cestode *Eubothrium salvelini* in juvenile sockeye salmon *(Oncorhynchus nerka)* at Babine Lake. British Columbia. – J. Fish. Res. Bd Can. 30: 947–964.

Sneath, P. H. A. and Sokal, R. R. 1973. Numerical taxonomy. – Freeman, San Francisco.

Snorrason, S. S 1982. The littoral ecosystem and the ecology of *Lymnaea peregra* in Lake Thingvallavatn. Iceland. – Ph. D. thesis, Univ. of Liverpool.

– , Skúlason, S., Sandlund, O. T., Malmquist, H. J., Jonsson, B. and Jónasson, P. M. 1989. Shape polymorphism, in arctic charr, *Salvelinus alpinus*, in Thingvallavatn, Iceland. – Physiol. Ecol. Japan, Spec. Vol. 1.

– , Jónasson, P. M., Jonsson, B., Lindem, T., Malmquist, H. J. and Sandlund, O. T. 1992. Population dynamics of the planktivorous arctic charr *Salvelinus alpinus* ("murta") in Thingvallavatn. – Oikos 64: 352–364.

Sparholt, H. 1985. The population survival, growth, reproduction and food of arctic charr, *Savelinus alpinus* (L.), in four unexploited lakes in Greenland. – J. Fish Biol. 26: 318–330.

Stearns, S. C. and Crandall, R. E. 1984. Plasticity for age and size at sexual maturity: a life history response to unavoidable stress. – In: Potts, G. W. and Wootton, R. J. (eds), Fish reproduction: strategies and tactics. Academic Press, London, pp. 13–33.

Stuart, T. A. 1953. Spawning migration, reproduction and young stages of loch trout (*Salmo trutta* L.). – Sci. Invest. Freshw. Salm. Fish. Res. Scott. Home Dep. 5: 1–39.

– 1957. The migration and homing behaviour of brown trout (*Salmo trutta* L.) – Sci. Invest. Freshw. Salm. Fish. Res. Scott. Home Dep. 18: 1–27.

Svärdson, G. 1951. The coregonid problem. III. Whitefish from the Baltic successfully introduced into freshwater in the north of Sweden. – Rep. Inst. Freshwat. Res. Drottningholm 30: 151–162.

– 1961. The charr. – Fiske 1961: 25–37 (In Swedish).

Tauber C. A. and Tauber, M. J. 1977. Sympatric speciation based on allelic changes at three loci: evidence from natural populations in two habitats. – Science 197: 1298–1299.

Taylor, E. B. and McPhail, J. D. 1985. Burst swimming and size-related predation of newly emerged coho salmon *Oncorhynchus kisutch*. – Trans. Am. Fish. Soc. 114: 546–551.

Thomas, J. D. 1958. Studies on *Crepidostomum meteocus* (Braun) and *C. farionis* (Müller), parasite in *Salmo trutta* L. and *S. salar* L. in Britain. – Parasitology 48: 336–352.

Thorpe, R. S. 1976. Biometric analysis of geographic variation and racial affinities. – Biol. Rev. 51: 407–452.

Timmons, T. J., Shelton, W. L. and Davies, W. D. 1980. Differential growth in largemouth bass in Weast Point Reservoir, Alabama-Georgia. – Trans. Am. Fish. Soc. 109: 176–186.

Turner, B. J. and Grosse, D. J. 1980. Trophic differentiation in *Ilyodon*, a genus of stream dwelling godeid fishes: speciation versus ecological polymorphism. – Evolution 34: 259–270.

Utter, F. M., Hodgins, H. O. and Allendorf, F. W. 1974. Biochemical genetic studies of fishes: potentials and limitations. – In: Malins, D. C. and Sargent, J. R. (eds), Biochemial and biophysical perspectives in marine biology. Vol. 1., Academic Press, New York, pp. 213–238.

Vik, P. 1963. Studies of the helminth fauna of Norway. IV. Occurrence and distribution of *Eubothrium crassum* (Bloch, 1779) and *E. salvelini* (Schrank, 1790), (Cestoda) in Norway. – Nytt Mag. Zool. 11: 47–73.

– 1964. Notes on the life history of *Philomena aqubernaculum* Simon et Simon, 1963 (Nematoda). – Can. J. Zool. 42: 511–512.

Vrijenhoek, R. C., Marteinsdottir, G. and Schenck, R. 1987. Genotypic and phenotypic aspects of niche diversification in fishes. – In: Matthews, W. and Heins, D. (eds), Community and evolutionary ecology of North American stream fishes. Univ. of Oklahoma Press, Norman, OK, pp. 245–250..

Werner, E. E. 1986. Species interaction in freshwater fish communities. – In: Diamond, J. and Case, T. J. (eds), Community ecology. Harper and Row, New York, pp. 344–357.

– and Gilliam, J. F. 1984. The ontogenetic niche and species interactions in size-structured populations. – Ann. Rev. Ecol. Syst 15: 393–425.

Wilson, D. S. and Turelli, M. 1986. Stable underdominance and evolutionary invasion of empty niches. – Am. Nat. 127: 835–850.

Youngs, W. D. and Robson, D. S. 1978. Estimation of population number and mortality rates. – In: Bagenal, T. (ed.), Methods for assessment of fish production in fresh waters. IBP Handbook no. 3, 3rd edition, Blackwell, Oxford, pp. 137–164.