

The arctic charr *Salvelinus alpinus* in Thingvallavatn

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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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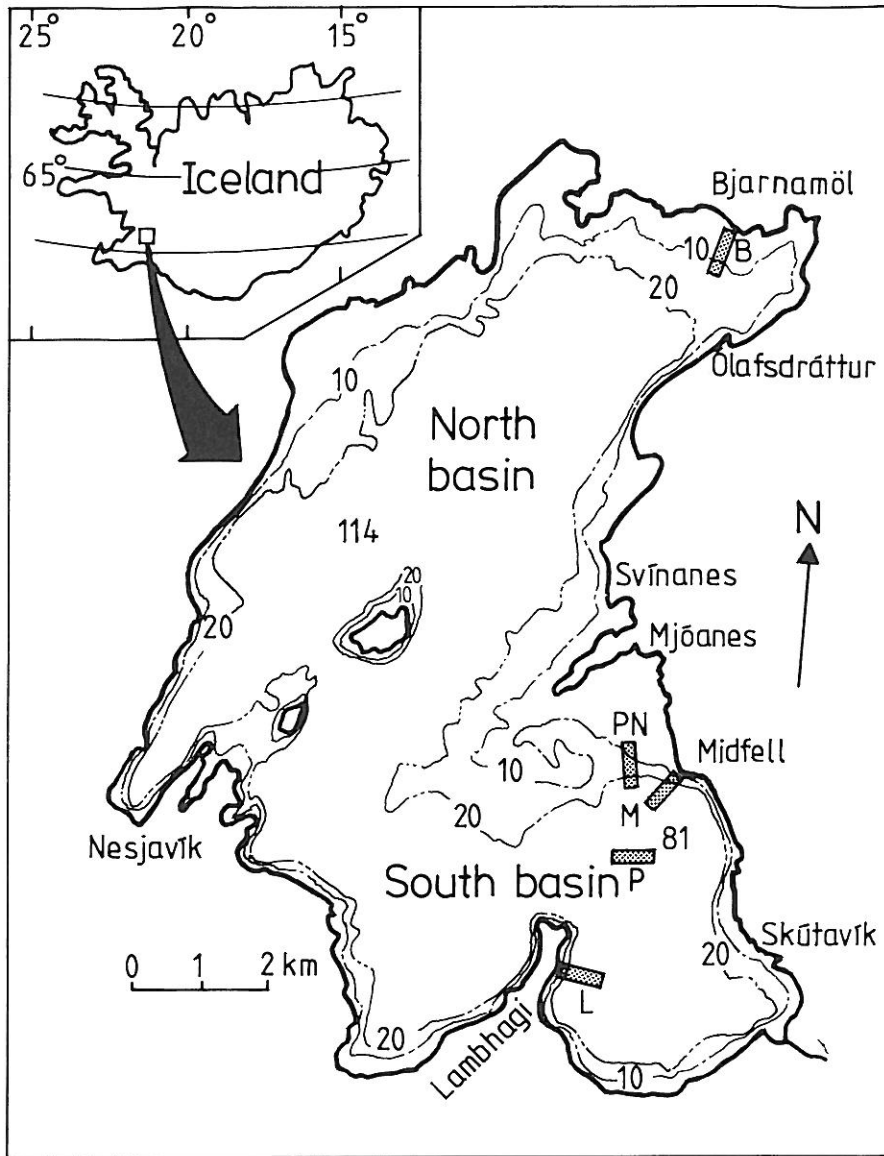


Fig. 1. Thingvallavatn with the 10 and 20 m depth contours and the deepest points in the northern (114 m) and the southern (81 m) basin indicated. M (Midfell), L (Lambhagi) and B (Bjarnamöl) are benthic gill net localities. P (deep pelagic) and PN (pelagic over *Nitella*) are pelagic gill net localities.

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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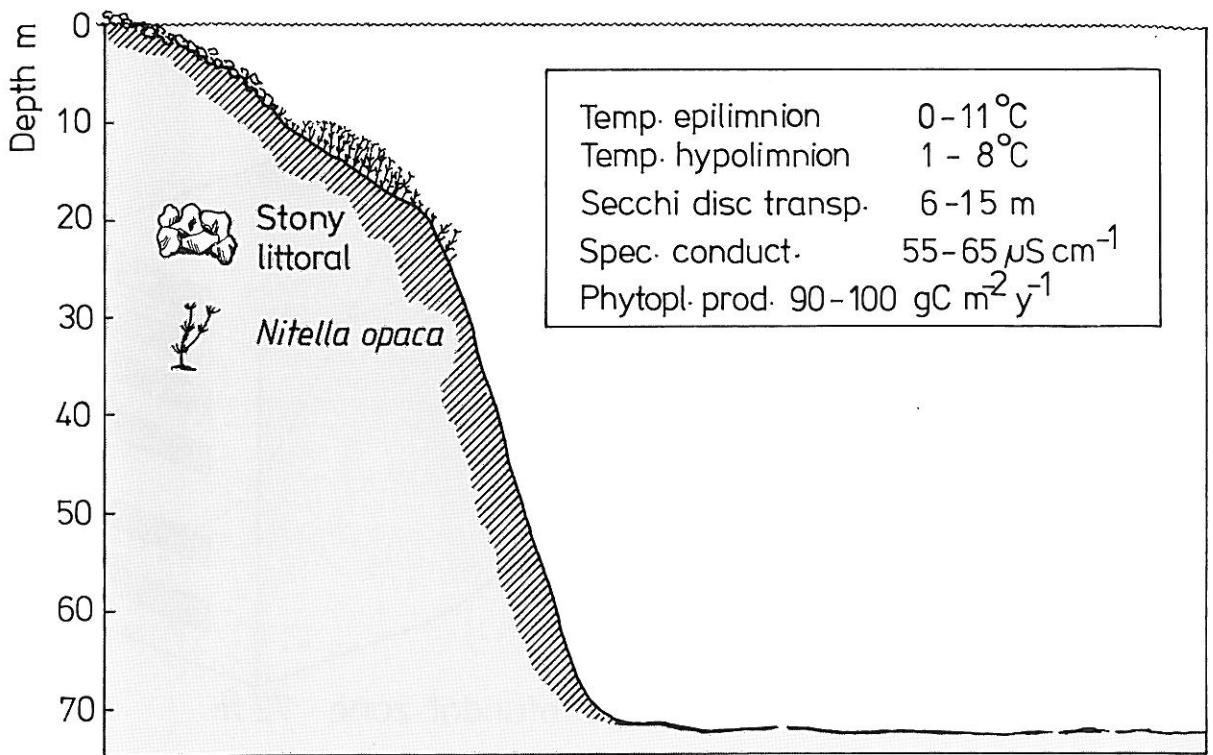


Fig. 2. Schematic outline of the main habitats for fish in Thingvallavatn, and some major physical and chemical characteristics of the water masses.

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 re-

garded 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

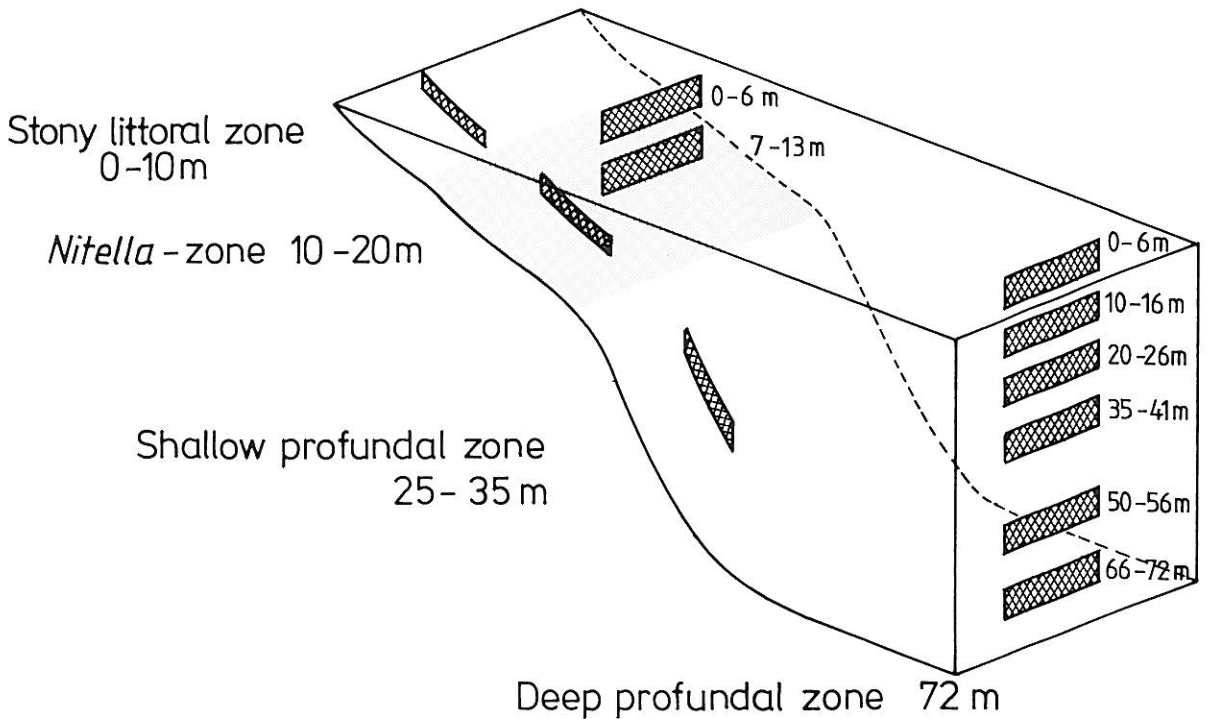


Fig. 3. Schematic outline of the gill net sampling procedures.

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 Fríðriksson (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 overshoot 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 km²) 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 subterranean. 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, Lin-

degaard 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 km², 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 *Leptodiptomus 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.

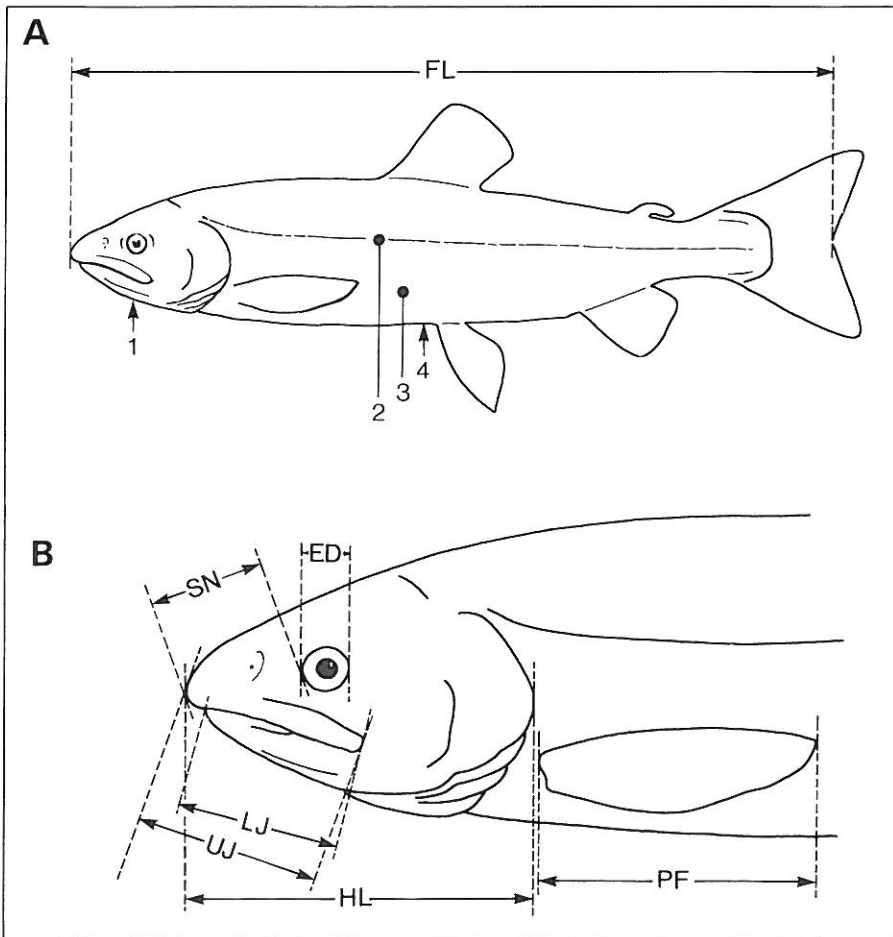


Fig. 4. External colour pattern and mensural characters determined.
 A.
 FL = fork length.
 1 = presence or absence of melanization on ventral side of lower jaw.
 2 = presence or absence of parr marks.
 3 = colour of belly edge (white, beige, orange).
 4 = colour of belly (white, beige, orange).
 B.
 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:

$$PF_i = N_i F_i \quad 100 \sum_{x=a}^n N_x F_x,$$

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 Littell 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).

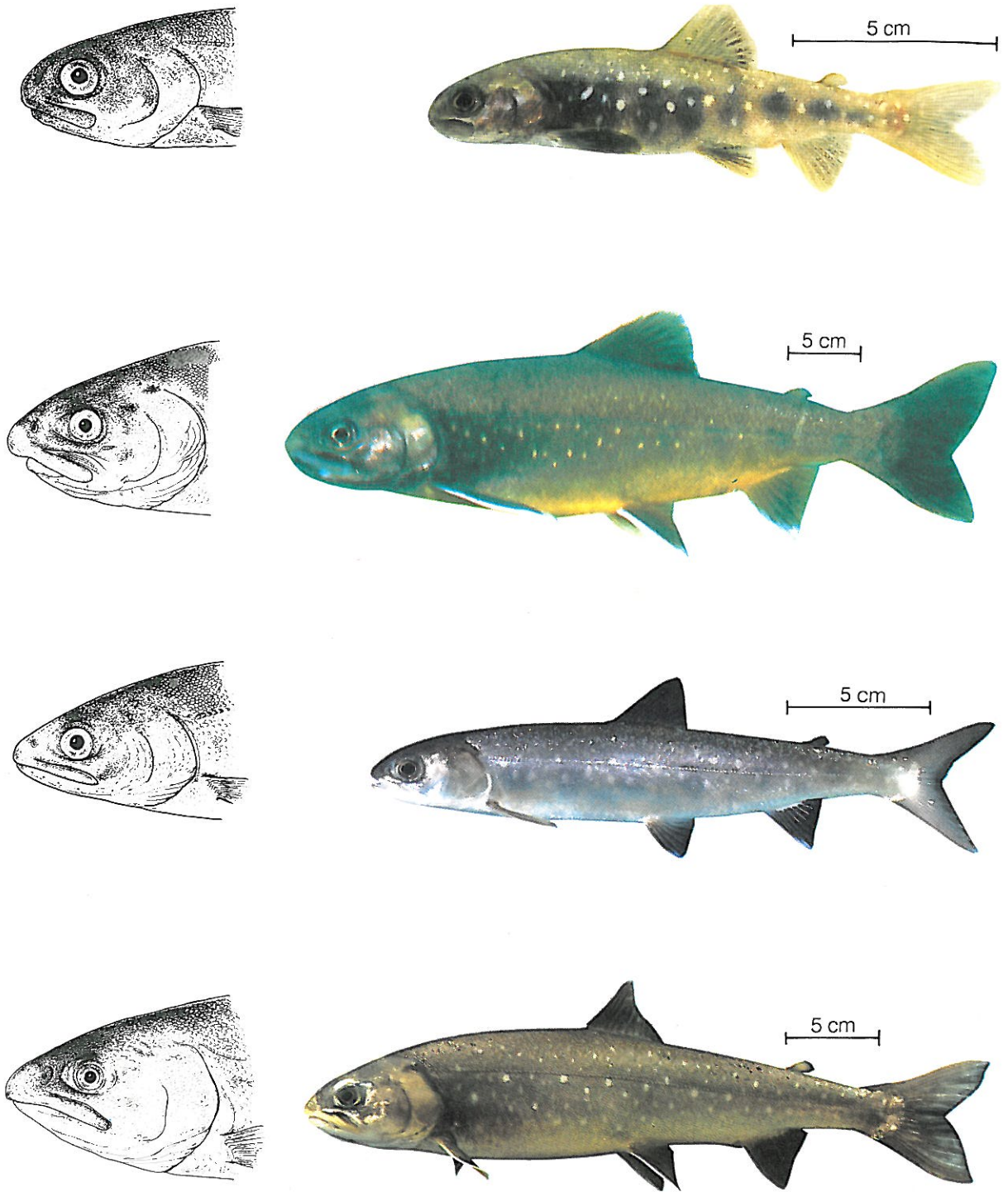


Fig. 5. The four arctic charr morphs, with drawings of lateral view of their heads. From top: Small benthivorous (SB-) charr, Large benthivorous (LB-) charr, Planktivorous (PL-) charr, Piscivorous (PI-) charr. Body lengths of the individuals shown were: SB-charr 11.3 cm; LB-charr 34.0 cm; PL-charr 12.5 cm; PI-charr 31.5 cm. (Karl Gunnarsson and A. Gardarson phot.)

A

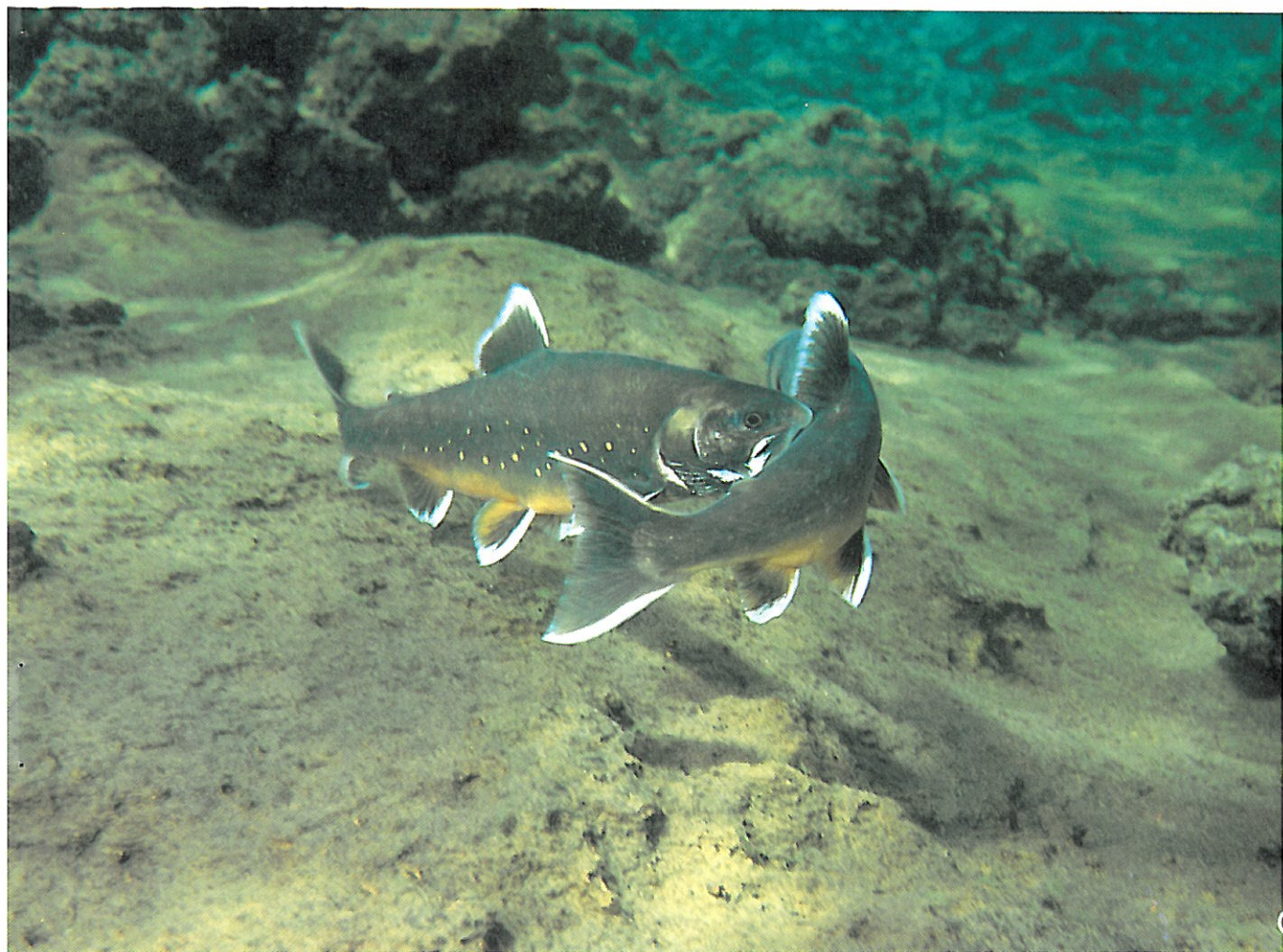
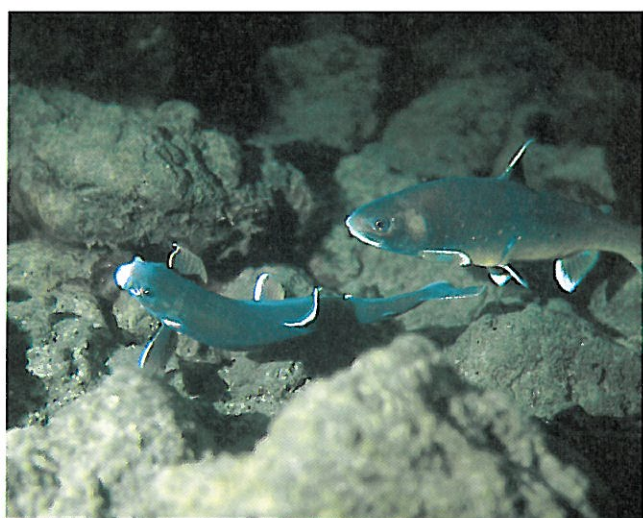




Fig. 27. Behaviour of LB-charr on the spawning site. A. A female cleaning the site. B. The male is situated above and posterior to the female, guarding her against potential sneakers. C. One male attacking another. D. Courtship behaviour. The male glides alongside the female, its body shivering. E. Orgasm (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 exogenous feeding, to test the relationship between yolk volume and free embryo size, and how this correlated with size differences among the morphs. After exogenous 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, $F_{5,407} = 253 - 472$, $P < 0.001$), 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
Variations	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 (\pm 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.

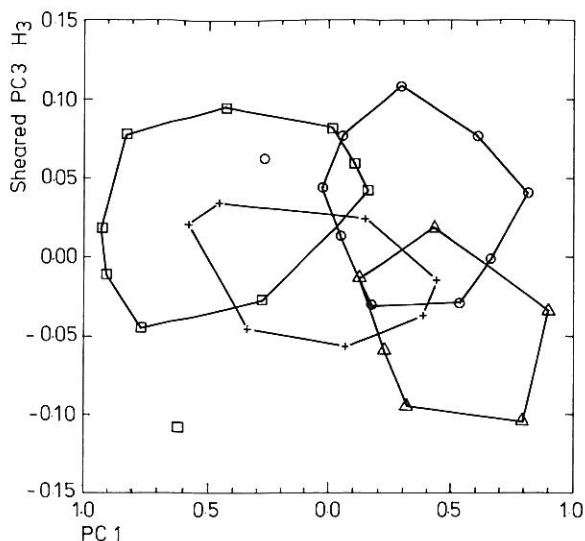


Fig. 6. Outlines of score clusters for the sheared principal component 3 (H_3) on principal component 1 (PC1) of \log_{10} -transformed mensural characters in 411 arctic charr from Thingvallavatn. \square = SB-charr, \circ = LB-charr, $+$ = PL-charr, \triangle = PI-charr. Cluster outlines include peripheral 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

(\pm 95% confidence limits) $1.83 \pm 1.07 \text{ m}^{-2}$ in August 1984 (11 sampling areas, range: 0.1–6.1 m^{-2}) and $4.70 \pm 3.13 \text{ m}^{-2}$ 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

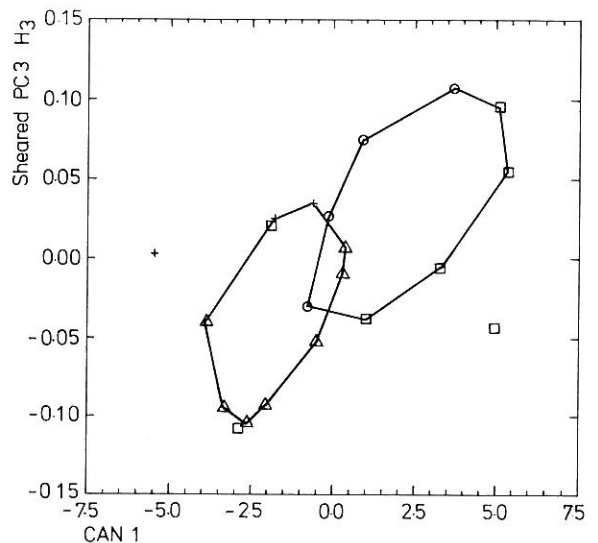


Fig. 7. Outlines of score clusters for sheared component 3 (H_3) and the first canonical variable (CAN1) from canonical discriminant analysis on size adjusted mensural characters in 411 arctic charr from Thingvallavatn. \square = SB-charr, \circ = LB-charr, + = PL-charr, \triangle = PI-charr. Cluster 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	$\chi^2 = 1317$ $P < 0.001$
	-	6	1021	100	96	
Belly edge	beige	54	0	0	0	$\chi^2 = 789$ $P < 0.001$
	yellow	167	1007	52	45	
	orange	9	24	48	55	
Belly	white	49	1030	89	55	$\chi^2 = 1442$ $P < 0.001$
	beige	168	0	0	0	
	orange	13	1	11	45	
Melanized lower jaw	+	204	6	10	19	$\chi^2 = 1071$ $P < 0.001$
	-	26	1025	90	81	
Flesh	white	227	697	17	16	$\chi^2 = 327$ $P < 0.001$
	orange	3	334	83	84	
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.

Horizontal 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 local-

ities (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.

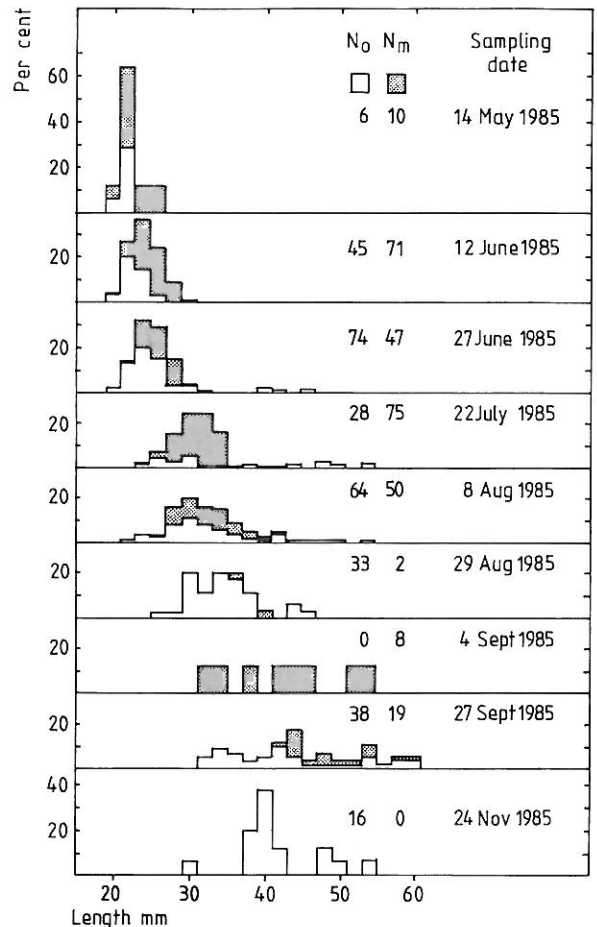


Fig. 8. Length frequency distribution of littoral age-0 charr, caught at Ólafsdraúttur (number: No), and Midfell (number: Nm), May 14 – November 24, 1985.

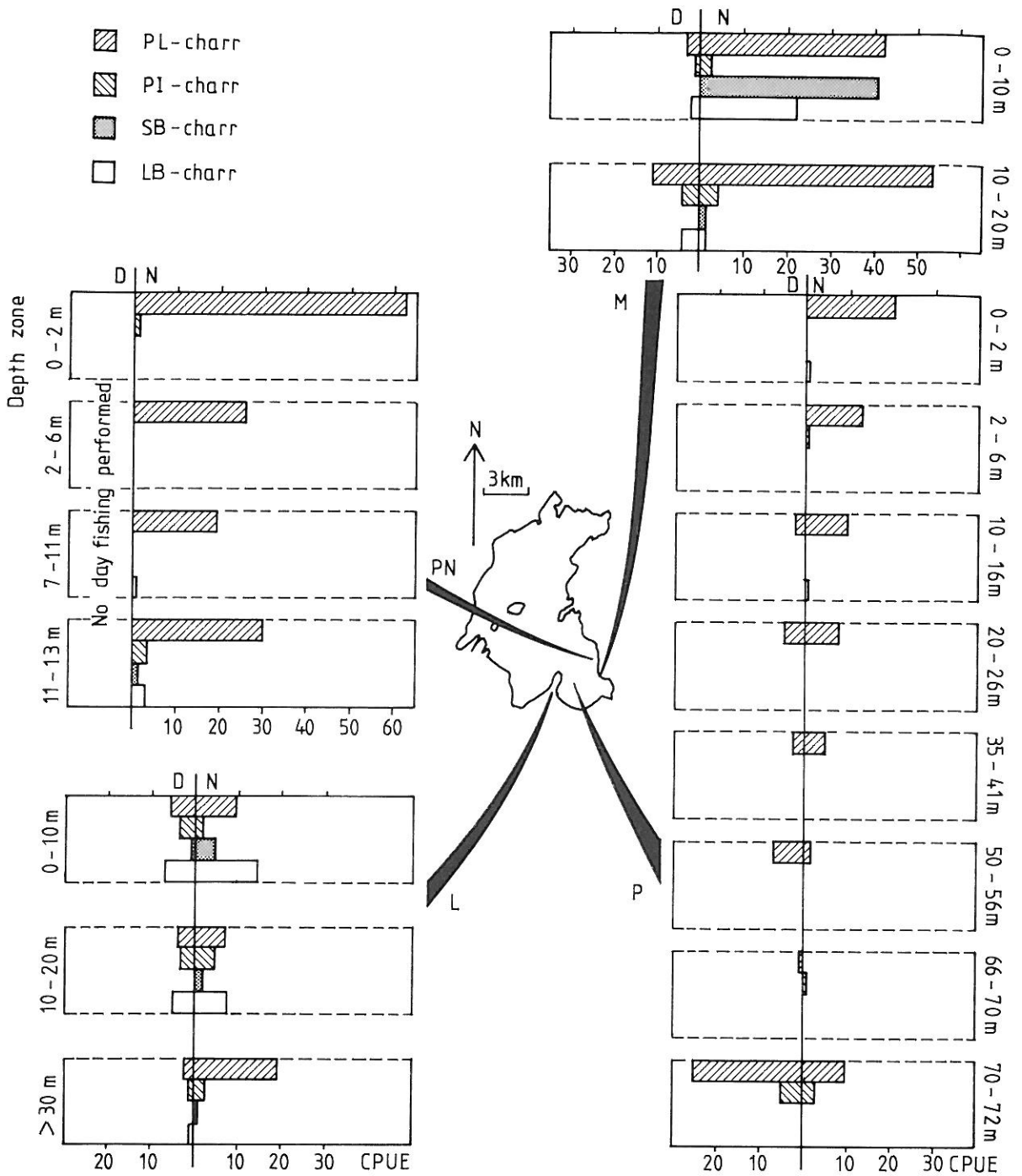


Fig. 9. Vertical distribution of arctic charr morphs in day (D) and night (N) gill net catches in Thingvallavatn, August 1983. Benthic localities: Midfell (M), Lambhagi (L). Pelagic localities: Deep pelagic, 72 m (P), Pelagic over *Nitella*, 13 m (PN).

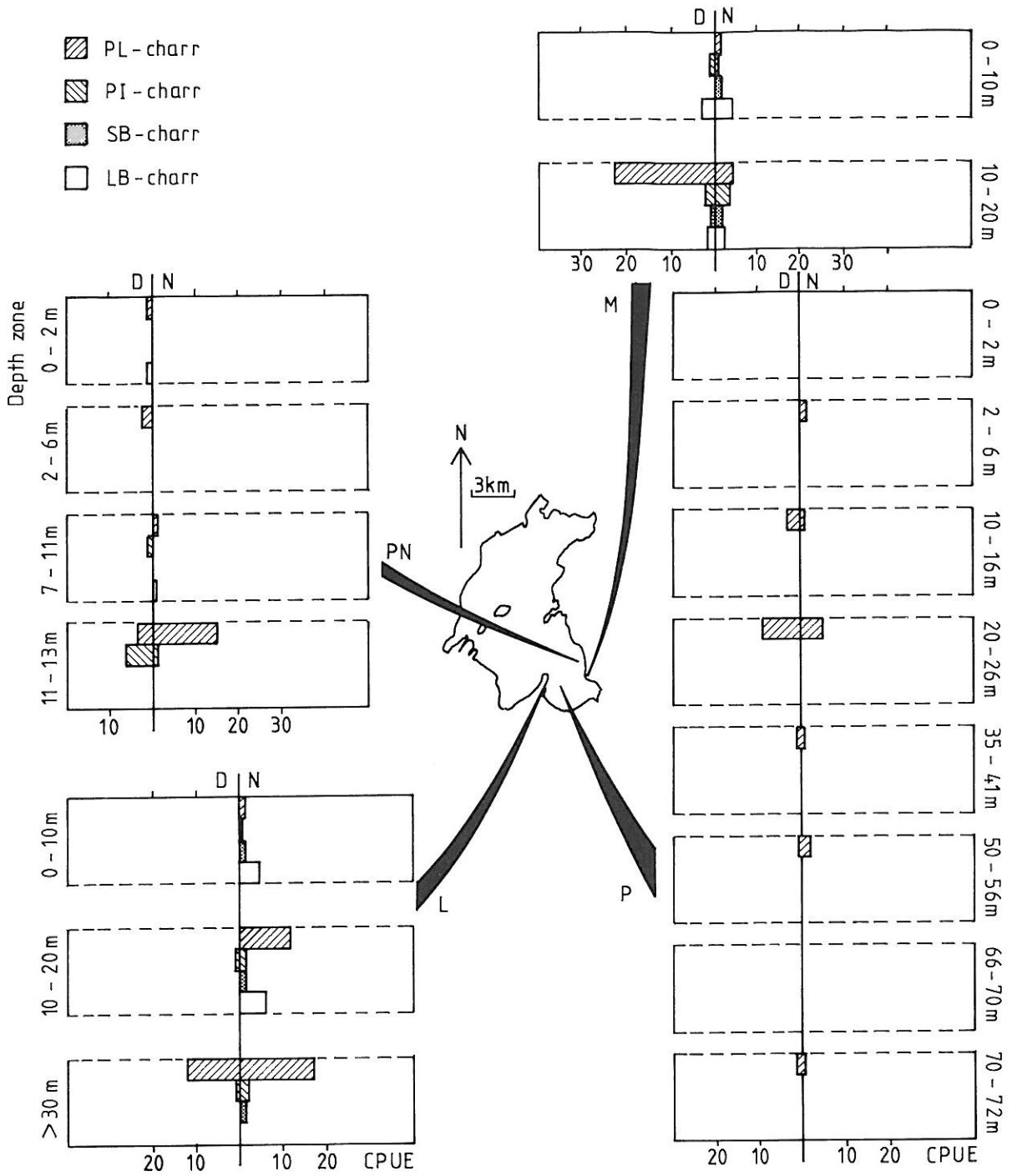


Fig. 10. Vertical distribution of arctic charr morphs in day (D) and night (N) gill net catches in Thingvallavatn, May 1984. Benthic localities Midfell (M), Lambhagi (L). Pelagic localities: Deep pelagic, 72 m (P), Pelagic over *Nitella*, 13 m (PN).

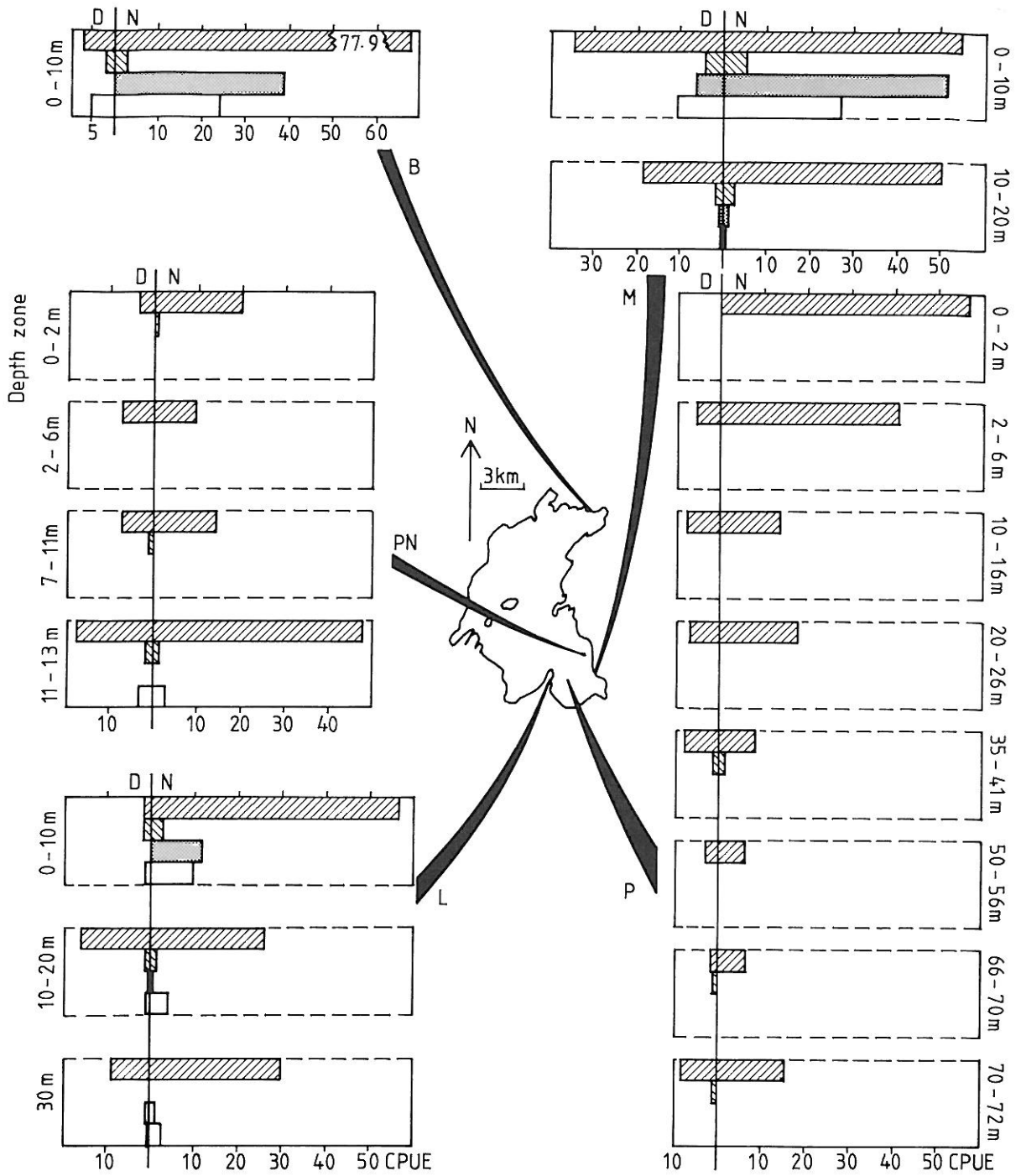


Fig. 11. Vertical distribution of arctic charr morphs in day (D) and night (N) gill net catches in Thingvallavatn, August 1984. Benthic localities: Bjarnamöl (B), Midfell (M), Lambhagi (L). Pelagic localities: Deep pelagic, 72 m (P), Pelagic over *Nitella*, 13 m (PN).

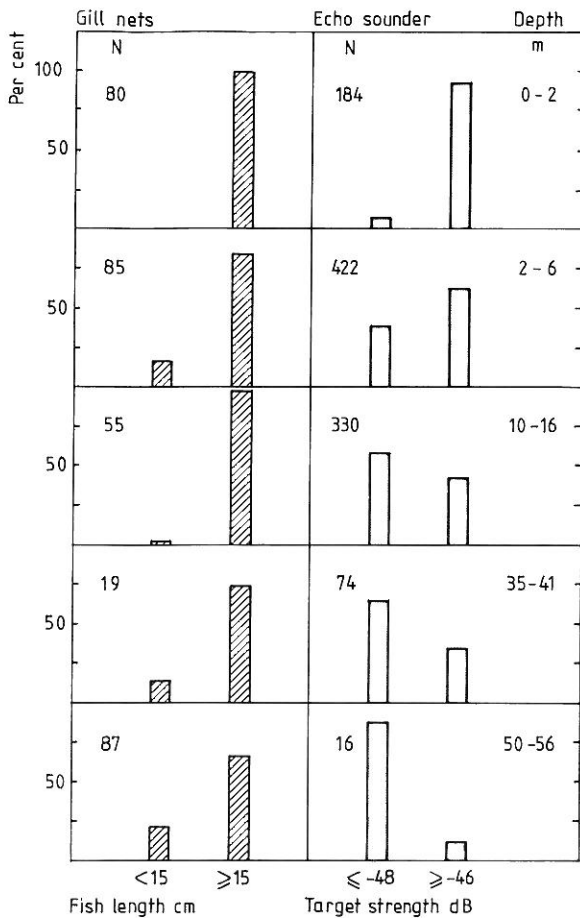


Fig. 12. Length frequency distribution and target strength (TS; dB) distribution of arctic charr at the deep pelagic station, August 1983.

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	Local-ity	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
Skútavík (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.

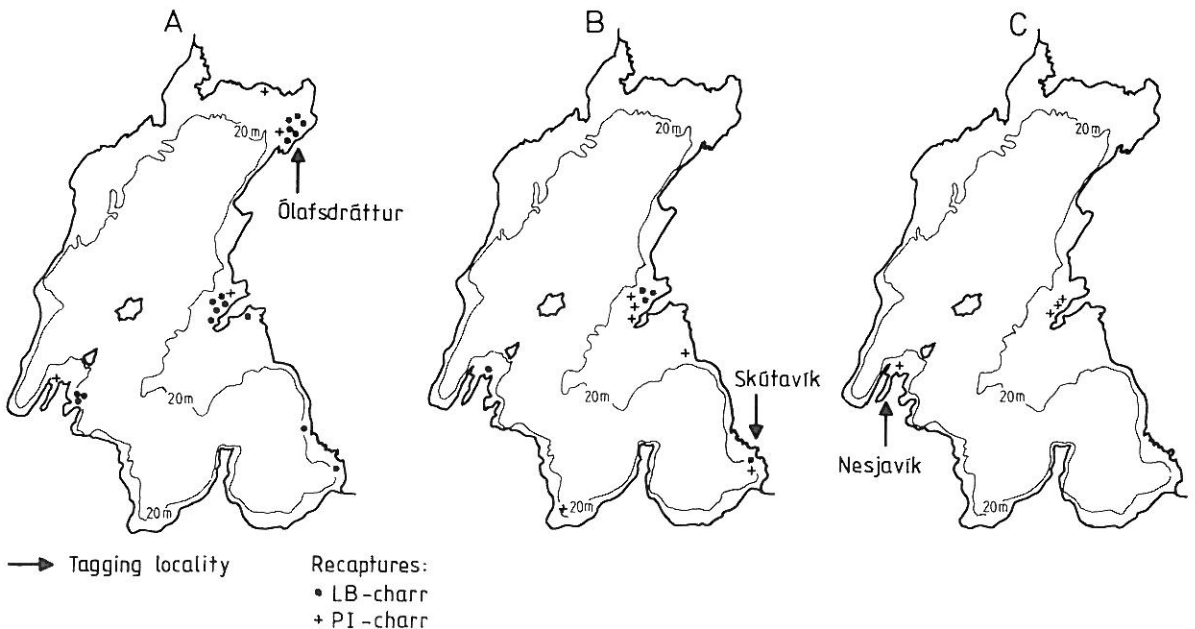


Fig. 13. Recaptures of PI- and LB-charr, tagged and released at Ólafsdráttur (A), Skútavík (B) and Nesjavík (C), 1983.

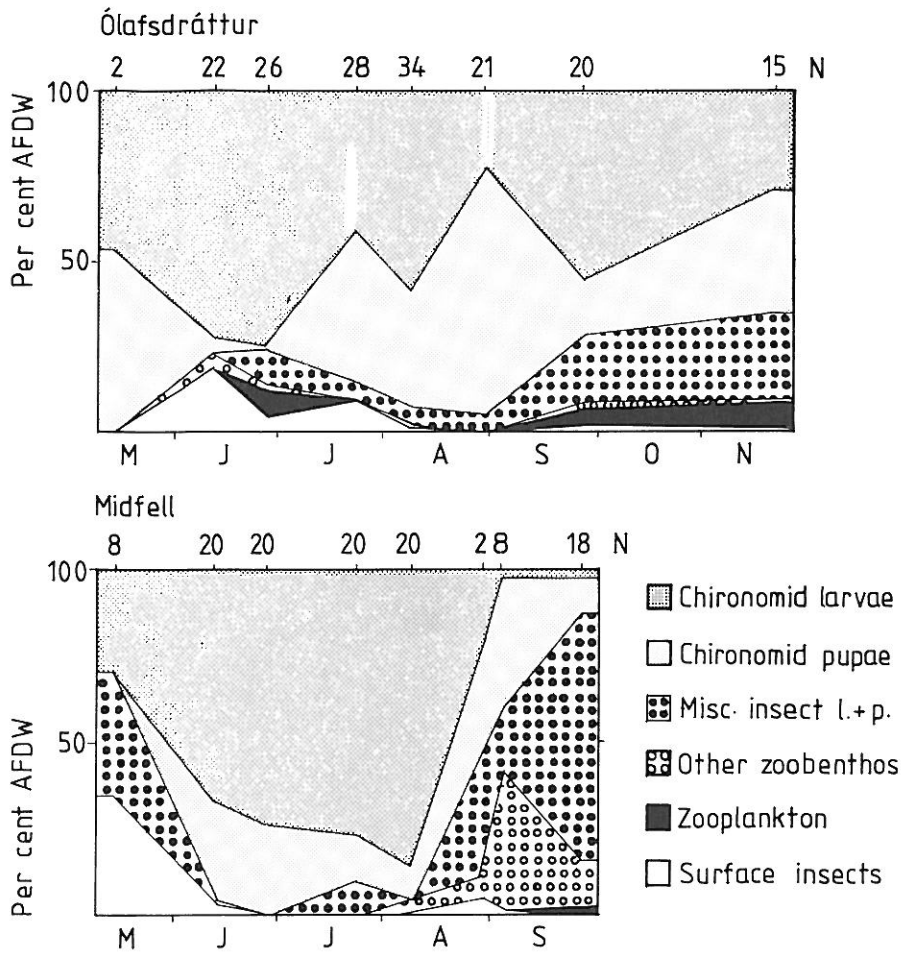


Fig. 14. Composition (per cent ash free dry weight, AFDW) of stomach contents of littoral age-0 charr, 1985. N = number of analyzed stomachs with contents.

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

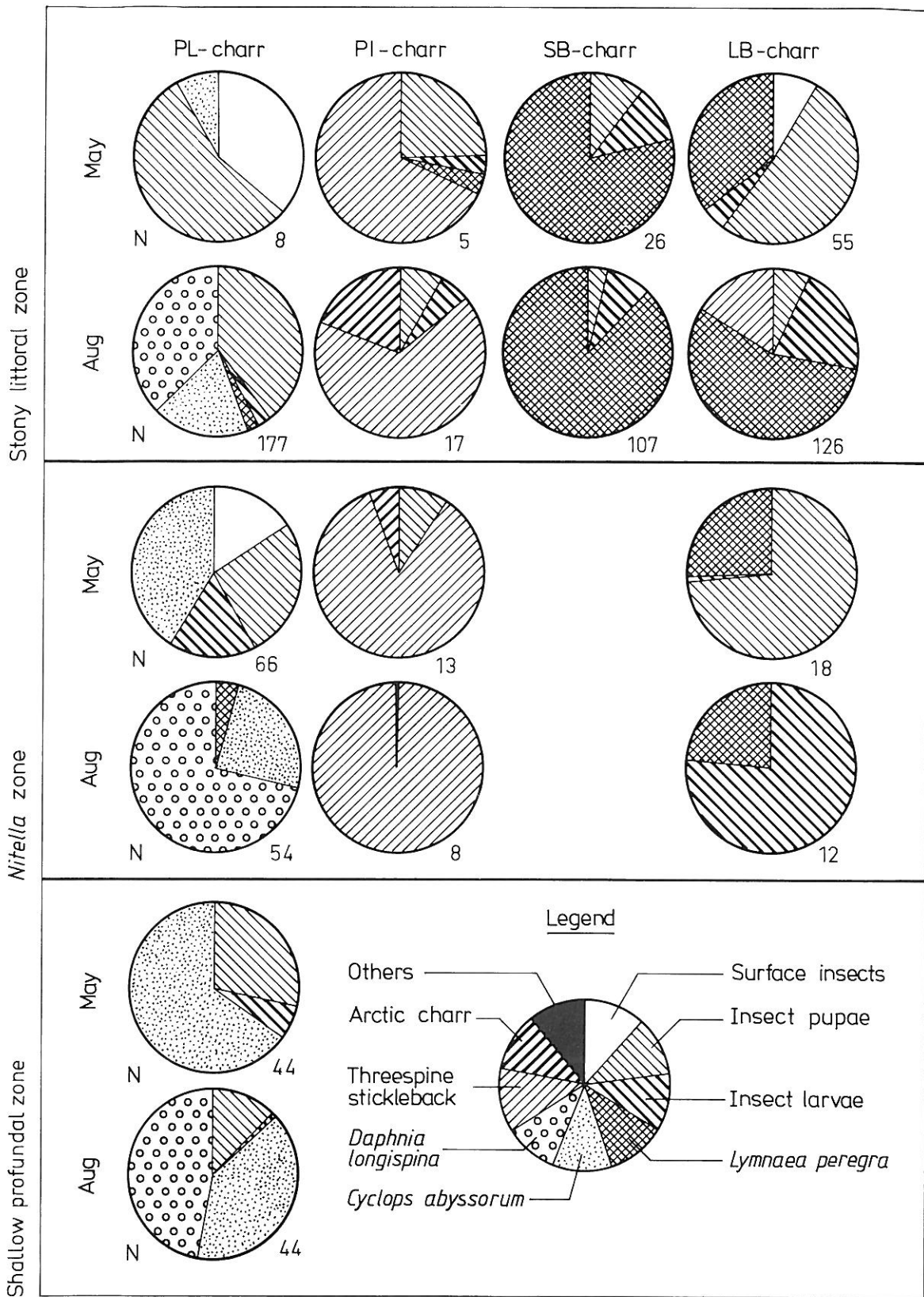


Fig. 15. Stomach contents (per cent ash free dry weight) of four morphs of arctic charr caught in epibenthic gill nets in the stony littoral zone, in the *Nitella*-zone and in the shallow profundal zone in June and August 1984. The material from the localities Bjarnamöl, Midfell and Lambhagi was pooled. N = number of fish analysed.

Deep pelagic

Pelagic over *Nitella*

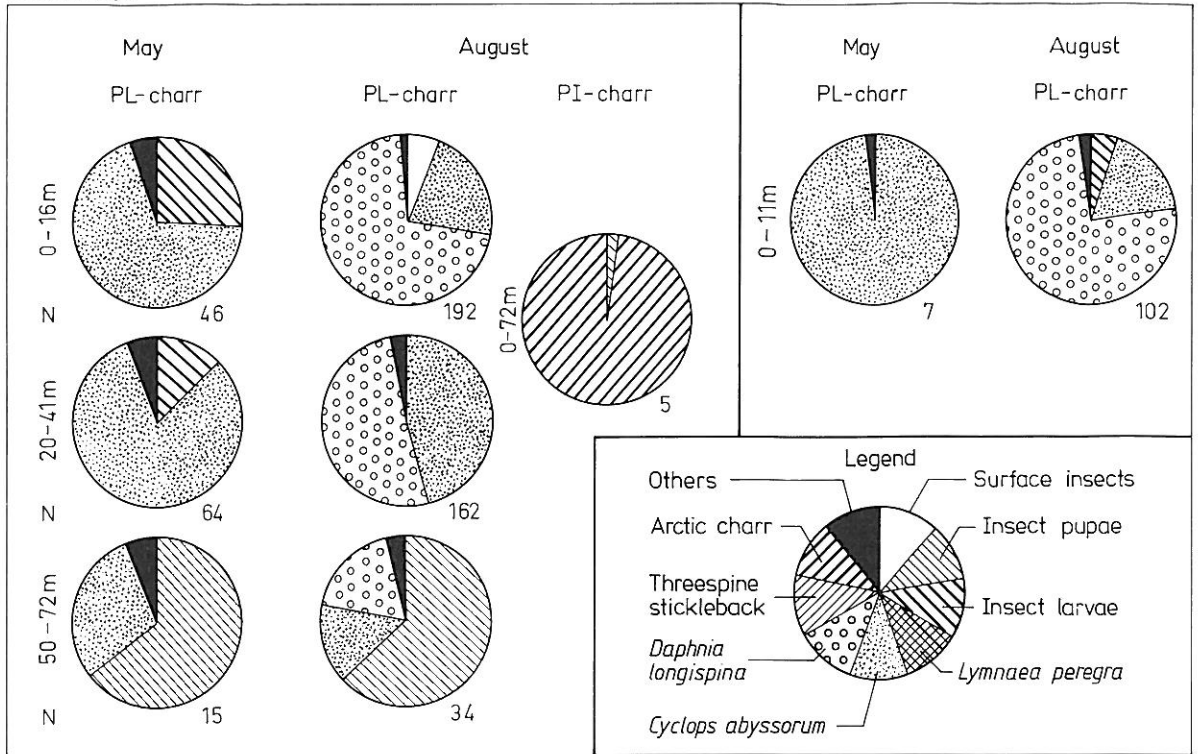


Fig. 16. Stomach contents (per cent ash free dry weight) of two morphs of arctic charr caught in pelagic gill nets over *Nitella* at Midfell and at the deep pelagic station, June and August 1984. N = number of fish analysed.

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 chironomid 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 orthocladine larvae (instar 3 and 4). The main species were *Euorthocladus frigidus* (Zett.), *Eukiefferiella minor* (Edw.), *Orthocladus 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		
PI-charr	2.17	2.25
PI-charr	1.93	1.47
SB-charr	1.49	1.20
LB-charr	2.36	2.46
<i>Nitella</i> -zone		
PI-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 Orthoclaadiinae) 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 *Cupnia 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 (\pm 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
<i>Nitella</i> -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 (Lindegård 1980, Lindegård 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							
<i>Crepidostomum farionis</i> (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		
<i>Diplostomum</i> 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							
<i>Diphyllbothrium</i> 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		
<i>Eubothrium salvelini</i> (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		
<i>Proteocephalus longicollis</i> 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							
<i>Philonema oncorhynchi</i> 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, Henriksen 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 $\rho = 0.418$, $P < 0.01$).

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 ($\rho = 0.514$, $P < 0.01$) and length ($\rho = 0.423$, $P < 0.01$) 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 ($\rho = 0.321$ and $\rho = 0.315$, 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).

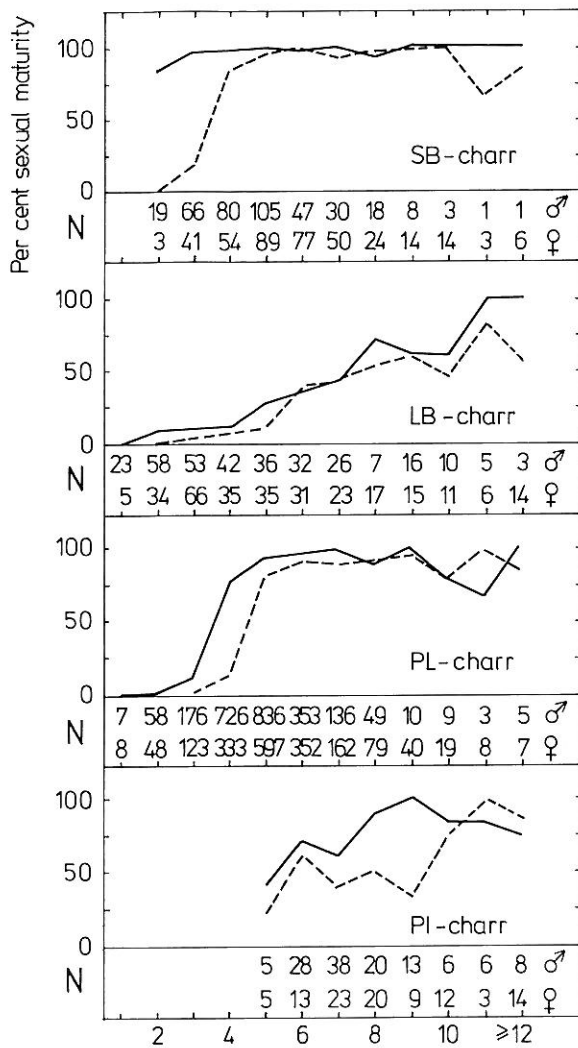


Fig. 17. Percentage sexually mature males (—) and females (---) of the four morphs of arctic charr in Thingvallavatn. The fish were caught in August/September 1983 and 1984. N = sample size, males (♂) and females (♀).

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 Borgström 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) \pm 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 \pm 0.04	0.078	5-13	209
	1984	0.51 \pm 0.04	2.887	6-11	164
	Pooled	0.57 \pm 0.03	3.225	5-13	488
LB-charr	1983	0.65 \pm 0.05	0.037	6-14	112
	1984	0.59 \pm 0.07	0.004	6-14	72
	Pooled	0.63 \pm 0.05	0.011	7-15	145
PL-charr	1983	0.47 \pm 0.05	1.890	6-14	501
	1984	0.41 \pm 0.01	0.074	5-13	1789
	Pooled	0.43 \pm 0.02	0.572	6-14	2179
PI-charr	1983	0.63 \pm 0.06	0.063	7-15	89
	1984	0.62 \pm 0.07	0.221	7-14	78
	Pooled	0.63 \pm 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 $L \pm$ 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 (\pm 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 \pm 6.7	0.333 \pm 0.045	746
LB-charr	240	135-460	274	90-470	553.5 \pm 74.2	0.086 \pm 0.016	644
PL-charr	175	130-230	188	140-260	205.1 \pm 1.6	0.417 \pm 0.011	4224
PI-charr	268	180-480	295	200-440	302.4 \pm 15.1	0.328 \pm 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	$\log_c L = 7.27 - 2.29 \log_c r + 0.37 (\log_c r)^2$	73–310	0.76	232
LB-charr	$\log_c L = 4.60 - 1.25 \log_c r + 0.28 (\log_c r)^2$	70–470	0.93	681
PL-charr	$\log_c L = 33.28 + 15.24 \log_c r - 1.51 (\log_c r)^2$	85–260	0.76	4467
PI-charr*	$\log_c L = -6.86 + 3.75 \log_c r - 0.26 (\log_c r)^2$	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, whereas 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

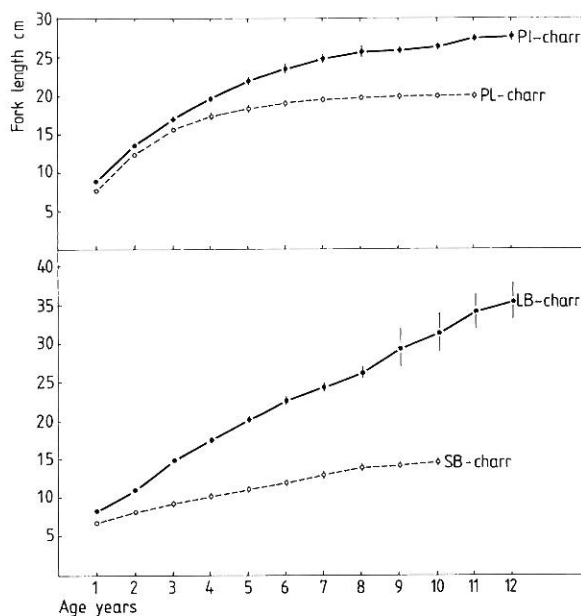


Fig. 18. Back-calculated fork lengths with 95% confidence limits of the estimates for four arctic charr morphs from Thingvallavatn, caught in August/September 1983 and 1984.

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, R² = coefficient of determination, F-values for test of homogeneity between regression coefficients (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			462
	May	Pooled	3.06	11.78	0.95		1.08 NS	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			313
	May	Pooled	3.14	12.16	0.99		1.40 NS	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			2801
	May	Pooled	2.40	8.43	0.81		1552.69***	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			102
	May	Pooled	3.22	12.66	0.94		4.87*	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

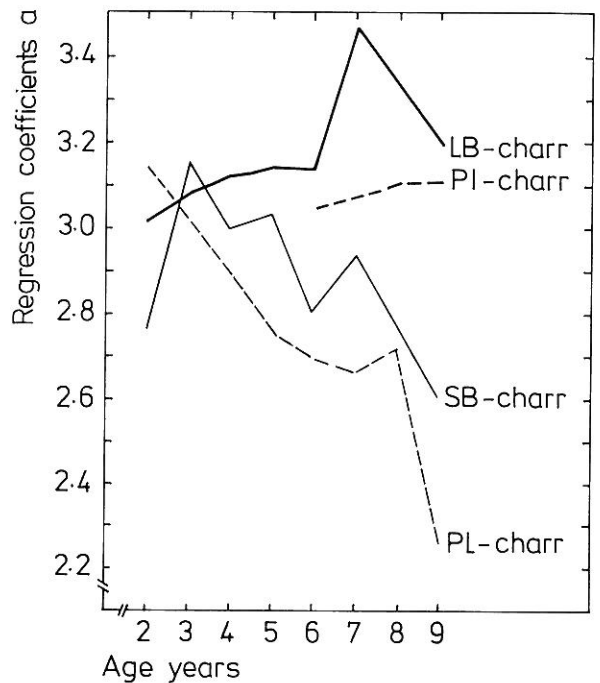


Fig. 19. Regression coefficients (a) of the weight (W, g)/length (L, mm) relationship: $\log_e W = a \log_e L$, for each age group within four arctic charr morphs from Thingvallavatn, August/September 1983 and 1984.

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 rea-

son 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

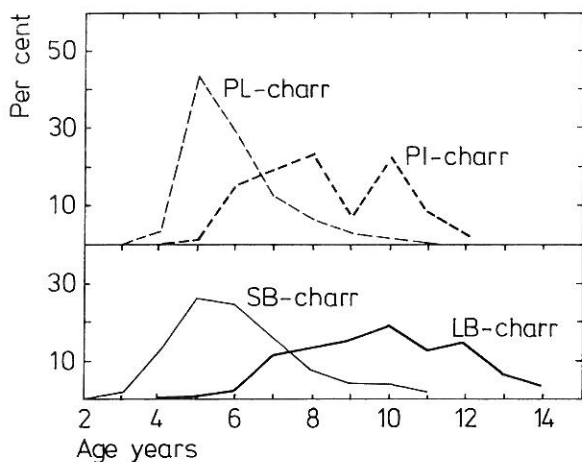


Fig. 20. Age specific fecundities, per cent, of the four arctic charr morphs from Thingvallavatn, August/September 1983 and 1984.

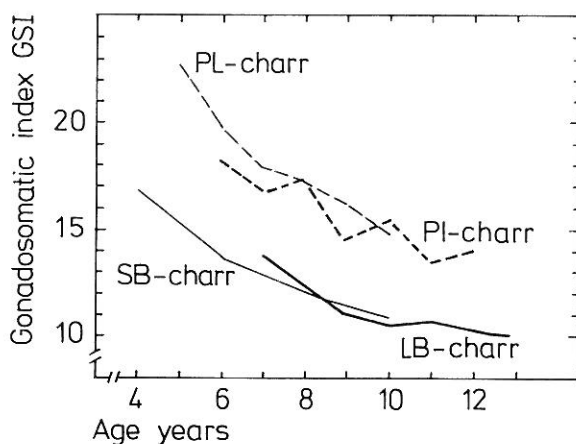


Fig. 21. Gonadosomatic index (GSI) within age groups of four arctic charr morphs from Thingvallavatn, August/September 1983 and 1984.

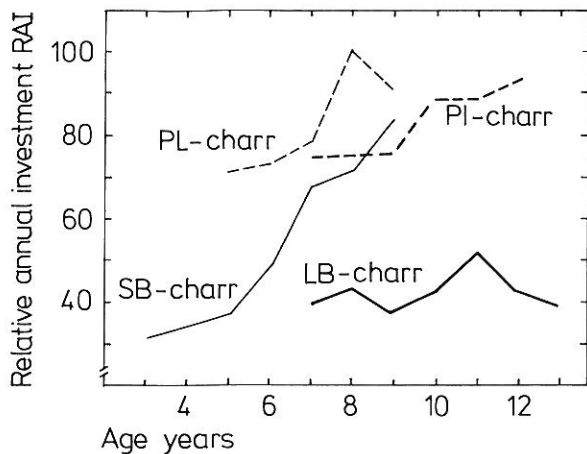


Fig. 22. Annual investments in gonadal relative to somatic growth of age groups of four arctic charr morphs from Thingvallavatn, August/September 1983 and 1984.

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.

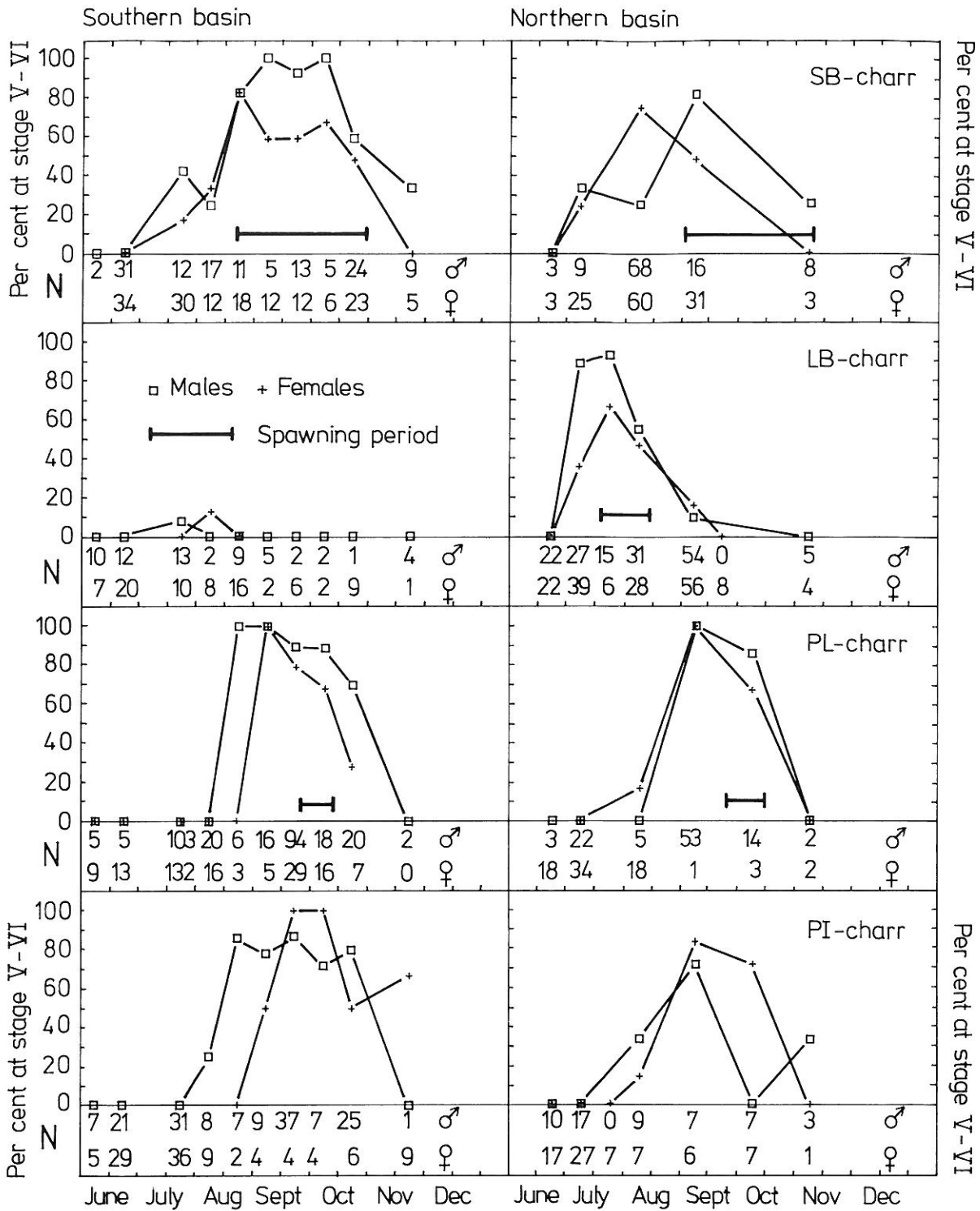
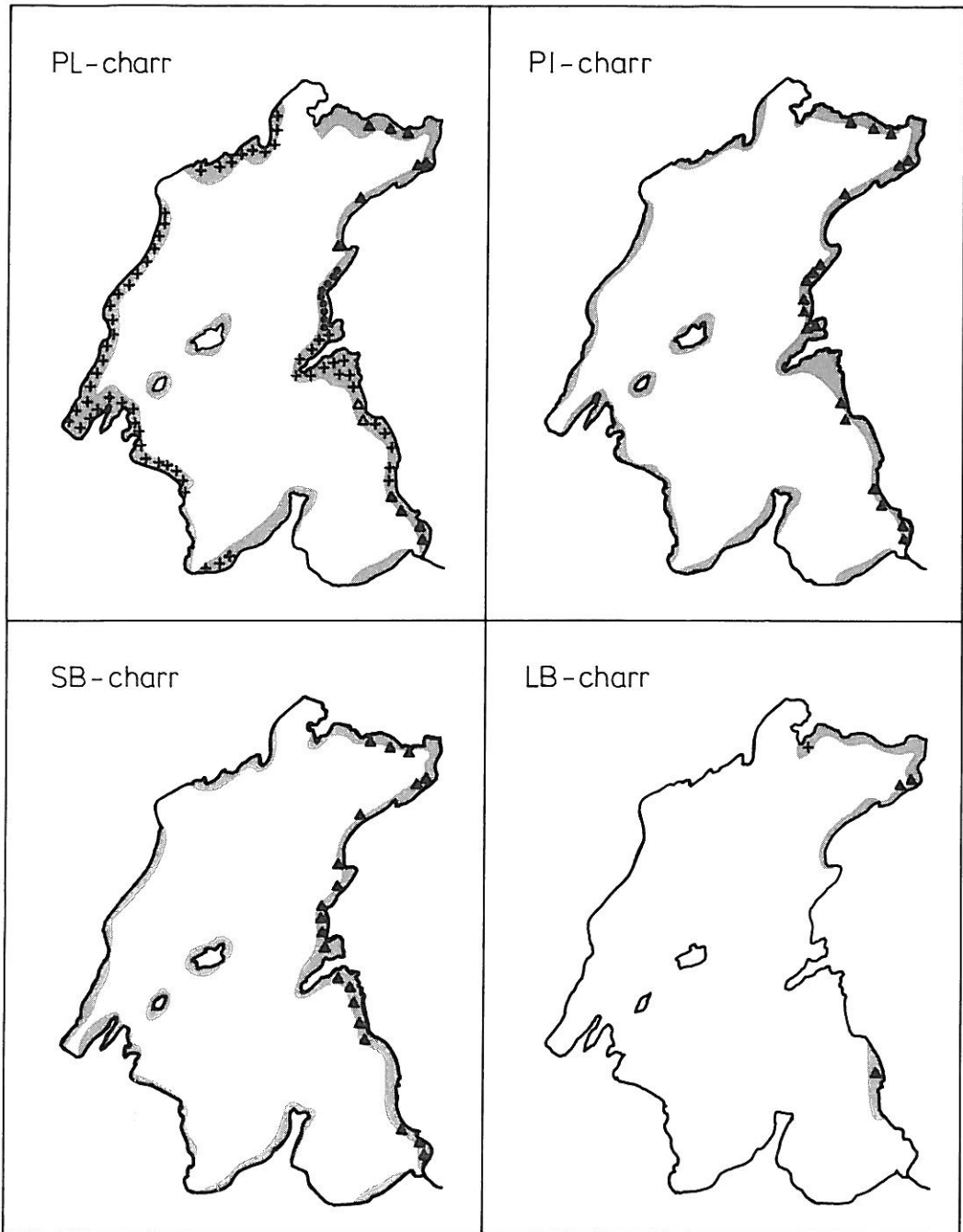




Fig. 23. Frequency of potential spawners (maturity stage 5 and 6) of the four charr morphs in gill net catches from northern and southern basin of Thingvallavatn. When exact data are available, solid bars indicate main spawning period. The figure is based on gill net catches from several localities in the littoral zone in 1981–1982 (Skúlason 1983, Malmquist et al. 1985). N = sample size males (♂) and females (♀).



 Assumed breeding grounds
 Based on own sampling

++++ Based on commercial fishing during spawning or information from fishermen

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.

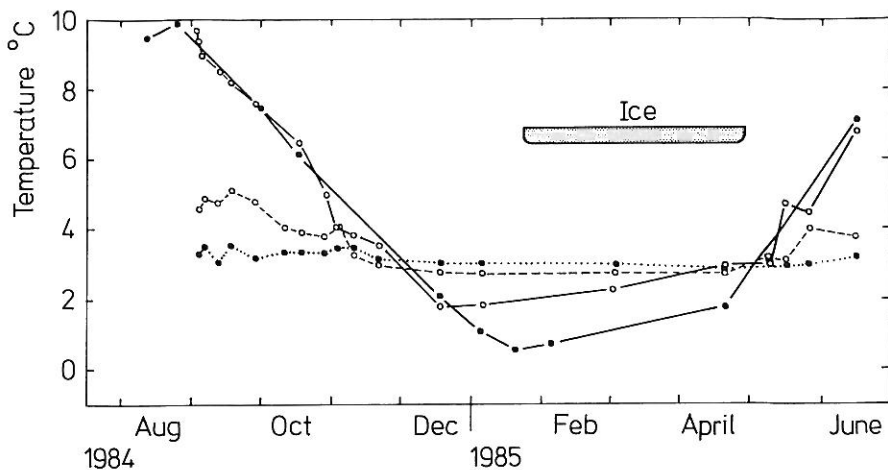


Fig. 25. Water temperatures in the lake water (solid line, filled circles) and in the substrate at two sites at Ólafsdráttur (OD-A and OD-B; broken line) and Svinanes (SV; solid line, open circles).

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 success 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 exogenous feeding 145–160 d after fertilization. Close to the start of exogenous 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

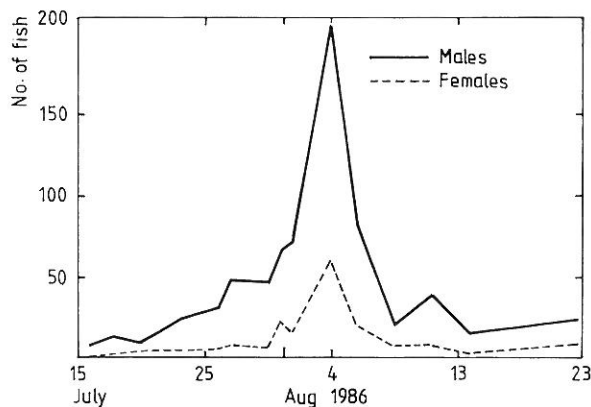


Fig. 26. Fluctuations in number of LB-charr spawners on the spawning ground at Ólafsdráttur, July–August 1986.

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 exogenous 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 exogenous feeding. Length distributions of electrofished charr alevins from the surf zone at Ólafsdraúttur 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 charac-

ters 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 \pm 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	PI-charr	N	PI-charr	N	SB-charr	N	LB-charr
Egg diameter:								
Pre-activated	54	4.74 \pm 0.07	43	5.11 \pm 0.08	32	4.58 \pm 0.09	43	4.95 \pm 0.06
Post-activated	25	4.84 \pm 0.09	26	5.11 \pm 0.01	26	4.82 \pm 0.12	45	5.16 \pm 0.05
Free embryo length:								
103 d	17	16.3 \pm 0.3	25	16.8 \pm 0.3	14	15.4 \pm 0.3	11	17.6 \pm 0.4
113 d	23	17.3 \pm 0.3	25	18.1 \pm 0.4	11	16.3 \pm 0.4	16	18.4 \pm 0.5
123 d	19	18.4 \pm 0.3	27	19.6 \pm 0.9	13	16.8 \pm 0.5	18	19.5 \pm 0.5
133 d	18	19.3 \pm 0.4	24	20.3 \pm 0.5	13	18.5 \pm 0.4	13	21.0 \pm 0.4
143 d	15	20.5 \pm 0.5	25	21.1 \pm 0.4	12	19.2 \pm 0.6	13	21.1 \pm 0.4

Table 22. Total lengths (mm \pm 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 \pm 1.1	19	23.1 \pm 0.4
	OD		–	2	20.2 –	28	22.2 \pm 0.3
PI	SV		–	27	17.4 \pm 0.5	19	24.2 \pm 0.3
	OD		–	13	20.8 \pm 0.5	9	25.6 \pm 0.6
LB	OD	15	19.3 \pm 0.6	7	24.0 \pm 0.7		–

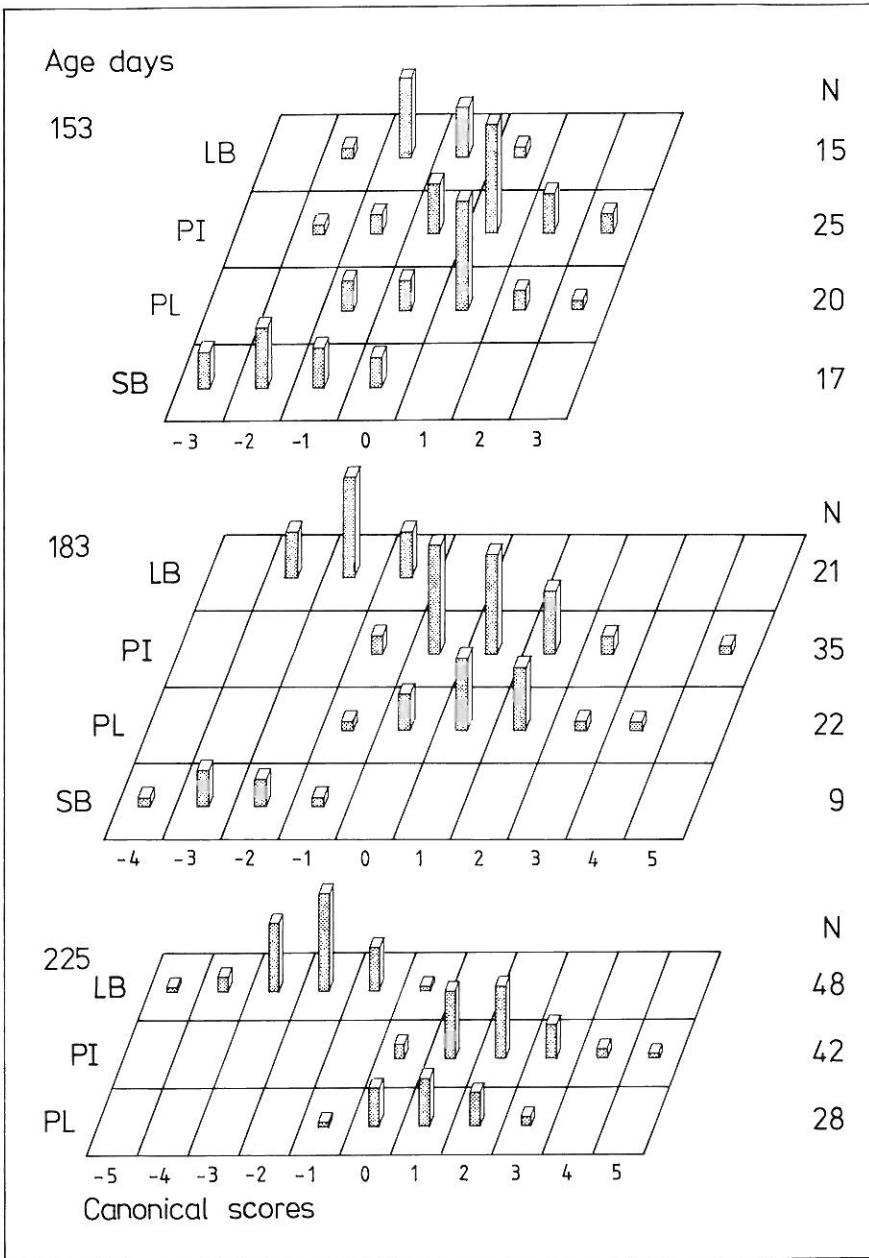


Fig. 28. Absolute frequency of scores on first canonical axis, derived from canonical discriminant analysis, for four progeny groups (of LB-, PI-, PL-, and SB-charr) at ages 153 and 183 d after activation, and for three progeny groups (of LB-, PI-, and PL-charr) at age 225 d after activation. N = Number of fish.

Table 23. Mahalanobis' 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 exogenous 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 exogenous 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 under-shot 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.

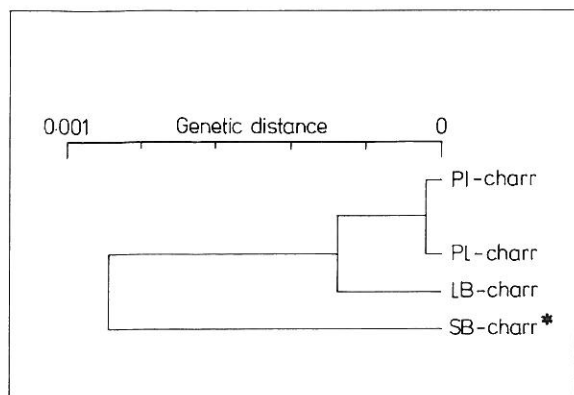


Fig. 29. Dendrogram for the genetic relationship among four sympatric morphs of arctic charr in Thingvallavatn, constructed from Nei's D based upon 36 enzyme loci. * indicates that branch is significant based on frequencies of *Est2* and *Mdh4,5* phenotypes, $P < 0.05$.

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.

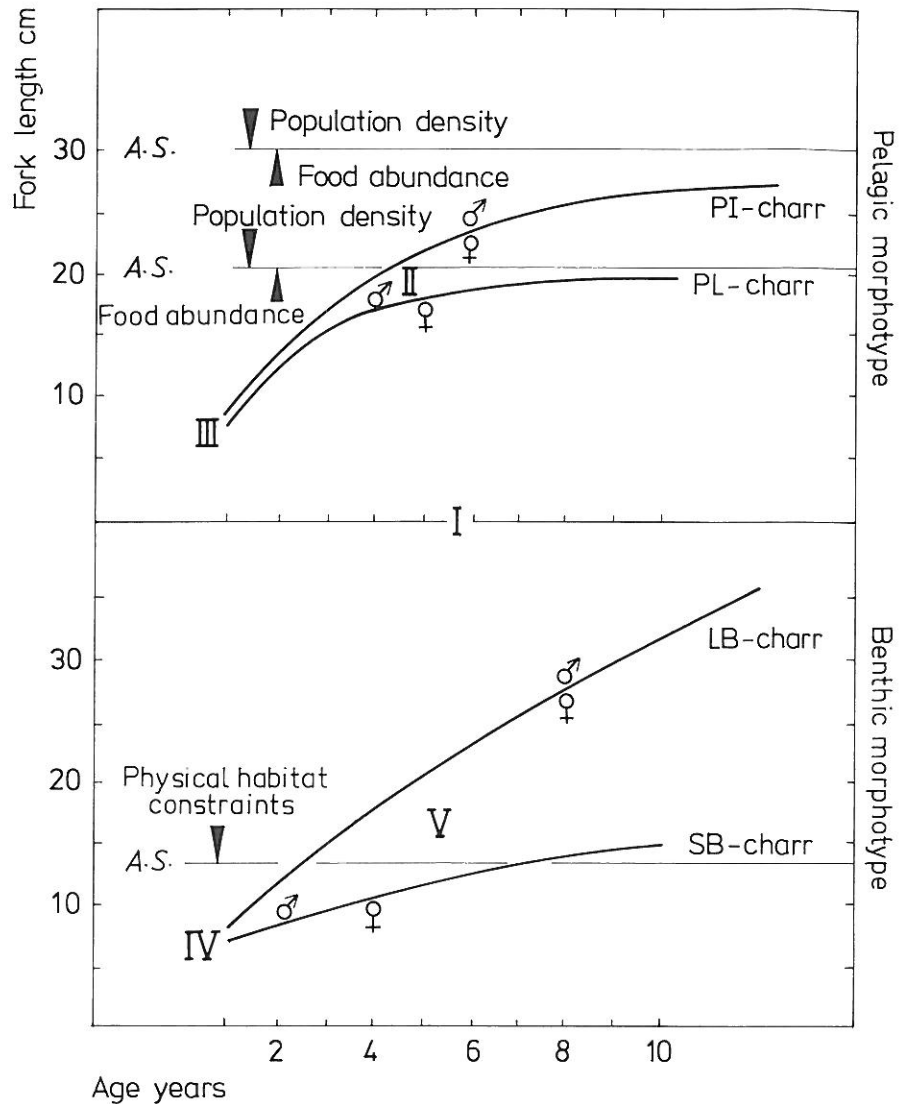
Discussion

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, \bar{S} = annual survival rate \pm 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	$L_\infty = 13.3$ cm. Age at maturity: female = 4, male = 2. $\bar{S} = 0.57 \pm 0.03$ F = 12 – 221.	July–November	Littoral	<i>Lymnaea peregra</i>
Large benthivorous (LB-charr)	Overshot mouth. Adult TL: 9–55 cm. No parr marks, dark coloration 25.9 gill rakers	$L_\infty = 55.4$ cm. Age at maturity: female = male = 8. $\bar{S} = 0.63 \pm 0.05$ F = 149 – 1914	July–August	Littoral	<i>Lymnaea peregra</i>
Planktivorous (PL-charr)	Terminal mouth, Adult TL: 13–26 cm. No parr marks, silvery coloration 27.4 gill rakers	$L_\infty = 20.5$ cm. Age at maturity: female = 5, male = 4. $\bar{S} = 0.43 \pm 0.02$ 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	$L_\infty = 30.2$ cm. Age at maturity: female = male = 6. $\bar{S} = 0.63 \pm 0.05$ 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 differences 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 (σ) and female (φ) 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 zooplankton and chironomid pupae and PI-charr feeding on fish. Thus it appears that the distinct differences 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 differences 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 hy-

potheses (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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