Life history variation of polymorphic Arctic charr in Thingvallavatn, Iceland

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Contribution from the Thingvallavatn Project

Jonsson, B., S. Skúlason, S.S. Snorrason, O.T. Sandlund, H.J. Malmquist, P.M. Jónasson, R. Gydemo, and T. Lindem. 1987. Life history variation of polymorphic Arctic charr in Thingvallavatn, Iceland. Can. J. Fish. Aquat. Sci. 44:000-000.

The Arctic charr (Salvelinus alpinus (L.)) in Thingvallavatn features four morphs: small benthivor~~ou~~es (SB-), large benthivor~~ou~~es (LB-), planktivor~~ou~~es (PL-) and piscivor~~ou~~es (PI-) charr. SB-charr have ~~overshot~~ subterminal mouth, adult fork length 7-31 cm, dark coloration and parr marks along the flanks. LB-charr have ~~overshot~~ subterminal mouth, adult fork length 9-55 cm, dark coloration but no parr marks. PL-charr have terminal mouth, adult fork length 13-26 cm, and silvery coloration with no parr marks. PI-charr have terminal mouth, adult fork length 23-65 cm, and light to silvery coloration with no parr marks. SB- and LB-charr live mainly in the littoral zone, SB-charr stay largely in crevices and under lava stones in the bottom substrat~~um~~e, whereas LB-charr stay upon the bottom substrat~~um~~e. Both feed mainly on the snail Lymnaea peregra. PL-charr and PI-charr exploit the whole lake, PL-charr feed mainly on crustacean zooplankton and chironomid pupae whereas PI-charr feed mainly on threespined sticklebacks (Gasterosteus aculeatus). SB- and LB-charr spawn during August-November and July-August, respectively, PL- and PI-charr spawn in September-October. The morphs attain sexual maturity at different ages; most SB-charr matured as 2-4 years of age, PL-charr as 3-5 years, PI-charr as 5-10 years, and LB-charr as 3-11 years. Among the first three morphs, males matured at significantly earlier than females, whereas both male and female LB-charr mature at the same age. Estimated annual, adult survival rates were lowest among PL-charr

(0.41 - 0.47), and highest among SB-charr, LB-charr and PI-charr (0.51 - 0.65). Sex ratios were in favour of females among adult SB-, PL-, and PI-charr, whereas males were in excess in most age-groups of LB-charr. Among SB- and PL-charr, the sex ratios were significantly different from unity. Estimated individual growth-rates increased gradually from SB-charr through LB-, and PL- to PI-charr. Growth of SB-, PL-, and PI-charr stagnated at mean fork lengths of 13, 20, and 30 cm, respectively. LB-charr continued to grow almost rectilinearly with age until at least 18 years of age, approximately 45 cm in length. Weight-length regressions differed among morphs, within PL-charr and PI-charr between spring and autumn, and within SB-charr and PL-charr among age-groups. Individual fecundity increased with length, but among PL-charr and SB-charr it decreased significantly with age in fish of the same lengths. Within PL-charr, mainly age-groups 5 and 6 contributed to the population fecundity, in the other morphs, more age-groups contributed. The gonadosomatic index and the annual allocation of energy into gonads relative to soma, was higher for PL-charr and PI-charr than for SB-charr and LB-charr. The results are discussed in relation to demographic theory and possible evolution of the morphotypes.

Introduction

Salmonid populations often feature more than one phenotypic variant within a locality (Nikolskii 1969a), and in Arctic charr (Salvelinus alpinus (L.)) up to four variants are known to occur sympatrically (Behnke 1972, 1980). Different morphs may be distinguished by a number of traits, such as food choice and habitat use, individual growth-rate, size and age at sexual maturity, time and place of spawning, body proportions, coloration, and parasites (Balon 1980a; Johnson and Burns 1984).

The taxonomic status of phenotypically different Arctic charr variants has been a topic under discussion over several years. Some authors have claimed that they are sibling species which have evolved allopatrically during the Pleistocene glaciations, and that in postglacial times, via multiple invasions, variants have immigrated into some lakes, where they now reside as different species (Svärdson 1961; Nilsson and Filipsson 1971; Klemetsen and Grotnes 1980; Nyman et al. 1981). Others have claimed that the morphs are conspecifics of one polymorphic species (Reisinger 1953; Savvaitova 1961, 1983; Frost 1965; Skreslet 1973; Balon 1980b; Jonsson and Hindar 1982; Nordeng 1983). Arctic charr may, like many other fish species, develop morphs through trophic differentiation (or ecological polymorphism) within breeding populations (Skreslet 1973; Sage and Selander 1975; Campbell re. Salmo trutta 1979; Turner and Grosse 1980; Hindar and Jonsson 1982; Kornfield et al. 1982; Grudzien and Turner 1984). This may stand from that in many lakes, fish may evolve several genetically divergent local populations (Kirkpatric and Selander 1979; Ryman et al. 1979; Ferguson and Mason 1981; Ryman 1981; Hindar et al. 1986), which at least in salmonids is based on a well documented reproductive homing behavour (Stuart 1953, 1957; Frost 1965; Behnke 1972; Stabell 1984). Based on a survey of Arctic charr in Norway, Hindar et al. (1986) documented that genetic distances were greater between stocks of the same morph in different lakes, than between morphs within the same lake. Thus, they maintained that morphs or other groupings of Arctic charr should be regarded as locally differentiated populations, and not different species, a view which is expanded upon in this paper.

The present study was carried out in Thingvallavatn (the suffix "vatn" means lake in Icelandic), the only known lake where the Arctic charr exhibits four phenotypically and ecologically different variants (Sæmundsson 1904; Snorrason 1982; Skúlason 1983; Malmquist et al. 1985) (Table 1). Based on differences in body size, diet and habitat utilization (Malmquist et al. 1985, in prep.; Sandlund et al. 1987; S.S Snorrason et al. in prep.), the morphs are called small benthivorous (SB-charr), large benthivorous (LB-charr), planktivorous (PL-charr) and piscivorous charr (PI-charr). The abbreviated terminology is applied throughout the rest of this paper (Table 1). We investigated vital life history variables of the morphs such as age and size at sexual maturity, individual growth-rates, sex ratios, weight-length relationships and individual and population fecundity. On this basis we speculate on the evolution of the morphs of Arctic charr in Thingvallavatn.

Methods

Study area

Thingvallavatn (64°6'N, 21°8'W) the largest lake in Iceland (Fig. 1), is situated in a fault valley in a n area of tectonic and geothermal activity, 101 m above sea level. Its area is 84 km^2, mean depth 34.1 m, and maximum depth 114 m (Rist 1975). The lake is situated in a fault valley, in an area of tectonic and geothermal activity. Apart from a large lava flow from the northeast, approximately 9,000 years ago, sporadic tectonic activity and minor local volcanic eruptions have disturbed parts of the lake basin, especially the northern basin. The southern basin has most probably remained unaltered since the glacial retreat about 11,500 years ago (Fig. 1). The major disturbances have occurred at intervals of several thousand years (Sæmundsson 1965).

Fig. 1

Approximately 90% of the inflow to the lake occurs as subterraneous affluence, due to porous lava rocks in the catchment area. Therefore the water level, water temperature, and water chemistry are stable within and among years (Rist and Olafsson 1986). The lake was dammed in 1959, and the water level fluctuates less than 50 cm during the year. Maximum summer temperatures at the surface are between 10-11°C in July/August, and at levels deeper than 25 m temperatures may vary between 1-9°C, with maximum in August/September (Snorrason 1982). Specific conductivity (κ_{20}) is approximately 65 μS cm^{-1} (Ólafsson 1980), and Secchi-disc transparency is 6-15 m in summer. The ecosystem of Thingvallavatn thus appears to be very stable for the subarctic region (Snorrason 1982; Jónasson and Lindegaard 1987).

μ and κ
Greek
letters

Thingvallavatn has a large pelagic zone and a benthic zone consisting of 3 main strata: a littoral zone consisting of lava and hard bottom often with loose boulders and rocks at 0-10 m depth, a littoral soft bottom covered by dense stands of *Nitella opaca* (Ag.) at 10-20 m depth, and a profundal soft bottom of diatomic gyttja (Lindegaard 1980; Lastein 1983) at depths below 20 m. The zoobenthos is dominated by chironomid larvae, tubificids and molluscs. Maximum densities of chironomids and molluscs are found in the stony littoral zone (0-10 m) (Lindegaard 1980; Snorrason 1982). The zooplankton is dominated by *Daphnia longispina* (Müll.), *Cyclops abyssorum medianus* (Lindberg), and *Leptodiaptomus minutus* (Liljeborg) (Antonsson 1977). The lake supports a dense population of Arctic charr as well as threespined sticklebacks, *Gasterosteus aculeatus* L., and a few brown trout, *Salmo trutta* L. Local farmers annually fish between 7 and 70 metric tons of PL-charr on the spawning grounds, which amounts to approximately 30% of the biomass of adult PL-charr (T. Lindem et al. in prep.). The larger morphs are also fished to some degree (Kristjánsson and Adalsteinsson 1984). Among SB-charr, only the very oldest and largest are fished as a by-product of the PL-charr fisheries.

Data collection and analysis

Arctic charr were collected (*N*=6332) from Thingvallavatn during three periods: August 1983, May/June 1984, and August/December 1984. Fish were caught with benthic and pelagic nets (Fig. 1). The benthic nets were 1.8 m and the pelagic nets 6 m in vertical dimension. The nets were gangs of panels with 12 mesh sizes: 10, 12.5, 15, 18.5, 22, 25, 29, 33, 38, 43, 50, and 60 mm. Benthic nets were used during at least two 24-hour periods in each sampling on the following substrata and depth zones: (1) stony bottom 0-10 m, (2) *Nitella* bottom 10-20 m, and (3) soft bottom 20-35 m. Pelagic nets were set at a wide range of depths in the south basin: 0-6, 6-12, 20-26, 35-41, 50-56, and 66-72 m, for at least two 24-hour periods at each depth zone and sampling series. In the *Nitella* zone at Midfell, pelagic nets were set for one 24-hour period in each sampling series, at depth zones 0-6 and 7-13 m (Fig. 1). Pelagic nets were lowered along ropes anchored on the bottom, and kept at the correct depths by a combined use of weights and floats. More details about sampling are given in Sandlund et al. (1987). The nets used caught fish from 7 to 48 cm in length.

Table 1

Arctic charr were classified into morphs on the basis of body length, jaw length, head shape, and colour patterns (see S.S. Snorrason et al. in prep. for details). Furthermore, fork length (L, mm), weight (W, g), sex, and degree of sexual maturity (Dahl 1917) were recorded for each fish (Table 1). Morph characterization of small fish was sometimes uncertain, as SB-charr may resemble small LB-charr, and PL-charr are difficult to distinguish from small PI-charr. Ages were determined from otoliths (Nordeng 1961; Christensen 1964). Individual fecundities were recorded as number of eggs of females in maturity stages 4-5. Age-specific population fecundities (PF_i) were estimated as: $PF_i = N_i F_i 100 / \sum_{x=a}^{n} N_x F_x$, where N_i is number of mature females in the i-th age-group of a morph, F_i is is the corresponding age-specific fecundity estimated from mean length, a is the age of the youngest sexually mature female and *n* is the age of the oldest mature female. Relative fecundity of various age-groups within each morph was estimated by multiplying mean individual fecundity of the age-group, with the number mature females from the age-group, to total numbers of mature females of the morph. Regressions of ovary weight (*OW*, g) on fecundity are based on data of Skúlason (1983) (Table 2). Gonadosomatic indexes (GSI) of females were estimated as ovarian weight on somatic weight (*SW*, g): $GSI = OW\ 100/SW$, where: $SW = W - OW$. Relative annual investment in reproduction (RAI_i) 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). The estimation is based on mean wet weights and percentages of mature and immature females in the various age-groups. Annual survival-rates and instantaneous mortality-rates were estimated using the Chapman-Robson method (Youngs and Robson 1978). Empirical growth-rates were calculated using von Bertalanffy's function:

$L_A = L_\infty(1-e^{-kA})$, where L_A is fork length at age A, L_∞ is asymptotic length, and k is a constant (Allen 1966). Von Bertalanffy's equation is not used in its more general form where the exponent kA is replaced by $k(A-A_0)$, because very few charr smaller than 7 cm were sampled. However, A_0 is generally small and has little effect (Roff 1984). Back calculation of growth was performed using otoliths measuring r_1, defined by Jonsson and Stenseth (1977), as the independent variable (Table 3). Weight-length relationships were estimated from wet weights (W, g) and fork lengths (L, mm) in the regression model: $\log_e W = b \log_e L + a$, where a and b are constants.

Table 2

Table 3

Tests for significant differences between sexes in age at sexual maturity, were based upon the normal approximation to the binomial distribution (Siegel 1956), with percentage by numbers as the data input. A two-sample test is expressed by:

$t_i = \sqrt{n_i m_i / n_i + m_i} \cdot (p_i - q_i) / \sqrt{r_i (1 - r_i)}$, and

$z^* = \sum_{i=a}^{b} t_i^2$

$p_i = x_i / n_i$, $q_i = y_i / m_i$, $r_i = x_i + y_i / n_i + m_i$

where x_i and y_i are the numbers of mature males and females at age i, n_i and m_i are the numbers of all males and females at age i, t_i is t-distributed with $(n_i + m_i - 2)$ degrees of freedom, and z^* is X^2-distributed with $(b+1-a)$ degrees of freedom.

X
Greek letter

Results

Age and sex

Fig. 2

Age at sexual maturity differed between morphs (Fig. 2). SB- (2 to 17 years of age) and PL-charr (1 to 14 years of age), both matured homogeneously. 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 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 years of age) and PI-charr (5 to 18 years of age), matured over a wider range 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 during some years. Maturity ages did not differ between 1983 and 1984 ($P>0.05$), and they were therefore pooled.

Table 4

Annual survival rate of adults was lowest for PL-charr (0.41-0.47) (Table 4). For SB-, LB- and PI-charr it was 0.51-0.65. Adult age-groups giving significant ($P<0.05$) fit to the Chapman-Robson model were used. The data indicated some inter year differences in age- structure among SB-charr, LB-charr 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 (Table 1). During spawning sex-ratios in gill-net catches may be influenced by differences in activity between 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 most frequent 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 distribution 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 predominated in most age-groups, but the overall M/F-ratio was not significantly different from unity (M/F=0.57, N=47, 0.1>P>0.05).

Age ?

Size and growth

Table 5

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 5). The length interval covered by adult LB-charr was larger than that of any other adult morphs.

Empirical growth-rates differed significantly between morphs (Table 5). The SB-morph was 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 (cannibals), are sometimes caught in the lake. Such individuals may become larger than 60 cm in length (Malmquist et al. 1985). In the present samples, however, there are no PI-charr larger than 48 cm (Table 5). LB-charr continued to increase in length ($\underline{L}_{LB}$, mm) with increasing age ($\underline{A}$, years) at an almost rectilinear rate:

$$\underline{L}_{LB} = 26.3(\pm 0.5)\underline{A} + 51.3(\pm 2.8) \qquad (3)$$

$\underline{N}=644$, $\underline{R}^2=0.80$, $\underline{P}<0.0001$

Fish which were classified as intermediate between SB- and LB-charr, had $\underline{L}_\infty$ ± standard deviation equal to 200±47 mm ($\underline{N}=48$). Those which on the basis of habit~~us~~at were classified as intermediate between PL- and PI-charr, had L_∞ equal to 229±9 mm ($\underline{N}=15$).

Fig. 3

Back calculation of growth using otoliths corresponded well with empirical growth rates (Fig. 3). The growth-curves of PL- and PI-charr were almost parallel between 1 and 3 years of age, but PL-charr ceased growing in length at a considerably earlier age than PI-charr. The back-calculated mean lengths of SB- and LB-charr were significantly different at all ages ($\underline{t}$-tests, $\underline{P}<0.001$). There was no significant difference in growth-rate between sexes, or sexually immature and mature fish within morphs.

Table 6

Weight-length relationships differed significantly among the morphs in both spring and autumn (test of homogeneity of regression coefficients, June: $\underline{F}_{3,\,670}=64.68$, $\underline{P}<0.0001$, August: $\underline{F}_{3,3760}=8.685$, $\underline{P}<0.05$). Significantly different weight-length relationships were found between the sexes within SB- and PL-charr, and spring and autumn samples within PL- and PI-charr (Table 6). Among SB- and PL-charr, intra morph regression coefficients decreased with age within age-groups 2-9 years, whereas in LB- and PI-charr it did not (Fig. 4). A significant heterogeneity in regression coefficients among age-groups ($F_{3,2721}=7.49$, $\underline{P}<0.001$) was found only for PL-charr.

Fig. 4

Fecundity and reproductive effort

Table 7

Individual fecundity of females (F) increased significantly with fork length (L, mm) for all morphs (Table 7). Calculations were performed with both untransformed and $\log_e$ - transformed data sets, and the data set giving the better fit was used. In the case of PL-charr, the predictory 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 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-morphs ($P>0.05$). Sample sizes of the two latter were however small.

Fig. 5

Age specific population fecundity of each morph gives relative contribution of each morph to the total female fecundity (Fig. 5). It is a function of the number of mature females of various age-groups and their mean fecundities estimated from mean lengths (Table 7). Among PL-charr a few age-groups were of importance, whereas among SB-, LB- and PI-charr, several age-groups were important contributors to the fecundity of the morph. Some of the variation in relative contribution between age-groups of LB- and PI-charr may be due to small sample sizes.

Fig. 6

Gonadosomatic indexes (*GSI*) of females decreased with age for all morphs, but were generally higher for PL- and PI-charr than for SB- and LB-charr (Fig. 6).

Fig. 7

Relative annual investments (*RAI*) in gonad and somatic growth by females, were estimated from mean gonad weights and annual increases of the somatic tissue (Fig. 7). *RAI* was less than 0.5

for LB-, and SB-charr younger than 7 years, and 0.7 and higher for PL-, PI-, and SB-charr 7 years and older.

Discussion

Life-history variation of morphs

Fish growth and ultimate maximum size are highly variable plastic, and largely dependent on the quality and quantity of food eaten (Alm 1939, 1959; Brett 1979). Differences in growth patterns among the Thingvallavatn morphs may result from different schemes of foraging and diet. PL-charr feeding on zooplankton and surface insects stop growing at a length of approximately 20 cm, whereas PI-charr feeding on threespined sticklebacks cease to grow at 30 cm. Growth stagnation may occur because the energetic gains from food consumption equals approach the energy expenditure of used for searching, capturing, handling and assimilating the food items, and maintenance of sustaining normal body functions and reproduction (Werner and Mittelbach 1981). ? Both morphology and growth-curves indicate that PI-charr develop from the fastest growing individuals that where classified as PL-charr, and they switch to fish-feeding at a fork length of approximately 23 cm (H.J. Malmquist et al. in prep.). Some PI-charr become cannibals and may grow to more longer than 60 cm.

The zoobenthos feeders are also divided into two adult size groups. Most SB-charr stop growing at 13 cm, whereas LB-charr grow almost rectilinearly throughout their life span, and may achieve a length of more than 50 cm. Both morphs live in the littoral zone, and the snail Lymnaea peregra is their main food (Malmquist et al. 1985). Thus, their growth differences cannot be explained on basis of diet. However, there are microhabitat differences between the two morphs, which may be partly responsible for the observed growth differences. During daylight hours, SB-charr stay in small crevices and under lava stones on the bottom. At dusk, however, they emerge and may feed together with LB-charr which live epibenthic day and night. The stone matrix of the bottom substratum is a good predatory refuge for small charr. However, that SB-charr consume relatively less food than LB-charr which appear to be the more successful forager in the littoral zone (Malmquist et al. 1985). The size of LB-charr enables them to extend their foraging area as well as decreasing the risk of predation. Thus, differences in growth-rates between SB- and LB-charr may at least partly, be explained by the way they exploit littoral areas.

The smaller sizes of SB- and PL-charr than of LB- and PI-charr may also partly be influenced by the small egg sizes of the former two morphs (Skúlason 1986). At first external feeding, SB- and PL-charr are smaller than the two other morphs. Elloitt (1984) showed that alevin weight was one of the chief factors affecting subsequent growth of brown trout, and this may hold true for Arctic charr as well.

The variation in the adult sizes of the 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 (Johnson 1980). 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 female, 7.5 cm in length, had only 13 eggs. In parallel to this, Myers et al. (1986) reported a threshold length of approximately 7 cm for the onset of sexual maturity in male Atlantic salmon (Salmo salar L.) which is the size of the smallest adult SB-charr observed in Thingvallavatn.

The other charr morphs, exibiting adult lengths of ca. 15-60 cm, are in the size range of most other studied Arctic charr (e.g. 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; Klemetsen et al. 1985; Hindar et al. 1986). Maturity ages of 4-5 years, as in PL-charr, seem common. The maturity age of SB-charr is low, whereas that of LB- and PI-charr is 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 lakes in northern Canada (Johnson 1980). The present data on maturity, age and growth are complemented by earlier findings (Skúlason 1983).

Optimization theory (Schaffer 1974) predicts that growth stagnation at an early age selects for young age at sexual maturity, whereas growth-stagnation in old 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 of Thingvallavatn agrees well with this qualitative expectations based on the optimization theory. SB- and PL-charr in both of which there is early growth stagnation, sexual maturity is attained at early age. LB- and PI-charr which have high growth-rates also at old age, mature late. In addition to this, the two benthic habitats exploited by SB- and LB-charr may select for different maturity ages. The rocky substrate stone matrix of the shallow littoral is probably the better habitat for small individuals, whereas the epibenthic littoral zone may best for large fish. Medium sized fish may do relatively poorly bad in both habitats. Selection may therefore favour young age at maturity among the most slow-growing charr, and old age at maturity 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; Reznick 1985), and early maturing fish are become small while late maturing ones may grow large. Thus, the individual growth-rate appears to influence the onset of maturity, as well as being slowed by the onset of maturity itself.

The relative amount of energy allocated to gonadal production increases with age, the same trend being observed in all morphs. This has been found among stone loach (oe Neomacheilus barbatulus sp. ~~(L.)~~) from Finland and England (Mills and Eloranta 1985). Increased investment in reproduction relative to somatic growth, may be a general trend among iteroparous fish species until they reach senility (Nikolsky 1963). One reason may be that the chance of surviving another year decreases with age. Young fish may restrain~~t~~ their gonadal production, thus decreasing post-spawning mortality, and increasing future growth and fecundity.

Individual fecundity varied among morphs: it is lowest in SB- and highest among LB- and PI-charr. The main reason is that fecundity increases with size. In addition, benthivorous fish invested less in gonadal production 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 like brown trout (Jonsson 1985). The number of eggs developed each year is partly limited by the food consumption (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 a female excess, whereas males were more abundant among LB-charr in most age-groups. The excess of females in the three former morphs may result from the 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 impact s on the life history variables of PL-, PI-, and LB-charr, but not of SB-charr. Most SB-charr die from natural causes, as most of them are small and therefore of little interest for human exploitation. PL-charr, on the other hand, are heavily exploited by gill net fishing during spawning, from late September until early October, amounting to approximately 30% of the adult population annually. PI- and LB-charr are caught in considerable numbers during May-August by local fishermen. The fishing removes predominantly old and large individuals of the different morphs, thus influencing size and age distributions as well as variables based on these.

Evolution of life history variation among morphs

The Arctic charr in Thingvallavtn is polymorphic. Genetically, the four morphs are very closely related (Magnússon and Ferguson

1987); the values of Nei's genetical distance (D) range from 0.00004 to 0.00126. LB-, PL- and PI-charr are very similar, SB-charr is the most different from the others. These results, which are based on electrophoresis of 36 enzyme loci of which five are polymorphic, show that the morphs are conspecifics and do not represent different evolutionary lineages. – needs elaboration ✓

Arctic charr seem prone to splitting into ecologically specialized sympatric groups throughout its range (Hindar et al. 1986). This may be related to: (1) phenotypic flexibility, (2) strong homing tendency where the spawners return to the spawning place of their parents (Frost 1965), (3) assortative mating with preference for phenotypically similar mates (Jonsson and Hindar 1982), + vacant niches and (4) early immigration after the Pleistocene glaciation (Svärdson 1976). As the ice retreated, they moved into barren lakes where they were able to radiate into different empty niches. Even today fish communities of Arctic charr lakes are often very simple, and sympatric morphs live in lakes scattered throughout the area of the species (Johnson 1980; Hindar and Jonsson 1982). The occurrence of four sympatric morphs, as in Thingvallavatn is, however, extreme.

The morphs in Thingvallavatn have probably developed within the lake, and the morphs are locally adapted to different niches. This is a large lake with a simple fish community, which offers relatively stable food niches making trophic specialization possible. Furthermore, phenotypically similar fish tend to mate with each other (K. Gunnarsson and H. Sigurjónsdóttir in prep.), and the morphs overlap only partly in spawning time. – place of spawning ? ✓ There are however, possibilities for cross breeding between the morphs, e.g. between SB-charr and the others, and between PL- and PI-charr, although sneak mating (sensu Gross 1985) may be very rare. We have no observations of natural crossbreeding between any of the morphs.

Morphologically (Snorrason et al. in prep), the morphs may be grouped into two main groups: (1) SB- and LB-charr, and (2) PL- and PI-charr. Soon after the onset of external feeding, progeny of SB- and LB-charr differ significantly from those of PL- and PI-charr in terms of head morphology (Skúlason 1986), whereas young immatures within each of the two groups cannot be distinguished morphologically. Ecologically, however, the morphs differ conspicuously. SB- and LB-charr grow at a very differt rate from their first year onwards, their sex ratios show opposite trends, their gonadosomatic indexes are approximately the same, but their relative annual investment into gonadal versus somatic tissues differ. Relative gonadal investment is higher among SB- than LB-charr. Although feeding for the most part on the same prey types, they exploit different habitats during the day, and they overlap only partly in spawning time. Among the two other morphs, the growth curves suggest that PI-charr are fast-growing PL-charr, which at the age of 3-6 years reach a size which enables them to switch from planktivory and begin fish-feeding, and grow large. Their sex ratios show the same general trend, with a surplus of females, their gonadosomatic indexes and relative annual investment into gonadal versus somatic tissues are approximately the same. PL- and PI-charr share habitat, but feed on different prey. They spawn at the same places and time of the year.

if so then 3 not 4 populations

In Arctic charr, it has experimentally been shown that progeny from the same parent may split into different morphs (Nordeng

1983). These results are supported by field studies which have demonstrated that e.g. fast-growing, late-maturing piscivorous individuals may develop from either planktivorous or benthivorous fish (Skreslet 1973, Campbell 1979, Klemetsen et al. 1985). Corresponding polymorphism also occur among other salmonids like brown trout and sockeye salmon (Oncorhynchus nerka Walb.) (Jonsson 1985, and references therein). However, less is known about the genetic mechanism behind such changes in morphology and life styles. For instance, some fish may either be genetically predestined to become piscivorous, or this may be a random phenomenon occurring among fish which happen to grow large enough to become fish-feeding. In the former case, the change in life style may be connected to the presence of certain regulatory genes as explained by Allendorf et al. (1983). In the latter case the mechanism may be connected to switch genes (Mayr 1970), or hormonal threshold levels associated with growth-rate or amount of surplus energy of the fish at a certain time of the year (Jonsson 1985; Thorpe 1986). Experimental evidence (Balon 1980b; Allendorf et al. 1983; Nordeng 1983) lend support to both theories, and more work is needed to reveal this.

In summary, the extreme variation in life history found between individuals of Arctic charr in Thingvallavatn, may partly be due to a direct environmental influence mediated mainly by differences in growth rate. In addition, individuals of the various morphs may have evolved by radiating into relatively stable niches of the large lake with a simple fish fauna, because of trophic specialization.

Acknowledgments

We thank Kristinn P. Magnússon and Thorleifur Eiriksson for helpful cooperation during field work, Jóhann Jónsson and his family at Mjóanes for placing their boat house and property at our disposal for field station, land owners at Thingvallavatn for positive interest and support, Nina Jonsson for ageing the fish and giving secretarial help, Jan Ruud Hansen for doing the computer work, Geoffrey Fryer, Torbjörn Järvi, Kjetil Hindar and John Thorpe has have critically read drafts of the paper, and Amy Lightfoot for improving the English. Furthermore, we are indebted to the National Power Plant Company (Landsvirkjun), particularly the staff at the Írafoss power plant, for housing and feeding us during periods with intensive field work. The Fisheries Research Group of the Thingvallavatn Project was supported by the Thingvalla Commission of the Icelandic Parliament, the National Power Plant Company, Danish Natural Science Research Council, Icelandic Natural Science Research Council, University of Iceland, Icelandic Foundation for Local Development (Byggdasjódur), Nordic Council for Ecology, Nordic Cultural Foundation, and NATO Science Foundation, all of which we gratefully acknowledge.

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Table 1. Morphological and ecological characteristics of the four Arctic charr morphotypes in Lake Thingvallavatn. Data from Malmquist et al. (1985), Sandlund et al. (1987) and Snorrason et al. (in prep.).

Morphotype	Abbreviation	Phenotypic characterization	Spawning period	Habitat	Main food
Small benthivorous	SB - charr	Overshot mouth, adult fish length 7 - 31 cm, parr marks along the flanks, dark coloration	August - November	Littoral	*Lymnaea peregra* chironomid larvae
Large benthivorous	LB - charr	Overshot mouth, adult fish length 9 - 55 cm, no parr marks, dark coloration	July - August	Littoral	*Lymnaea peregra*
Planktivorous	PL - charr	Terminal mouth, adult fish length 13 - 26 cm, no parr marks, silvery coloration	Sept. - October	Whole lake	Crustacean zooplankton Chironomid pupae
Piscivorous	PI - charr	Terminal mouth, adult fish length 23 - 65 cm, no parr marks, light to silvery coloration	Sept. - October	Whole lake	Three-spined sticklebacks (*Gasterosteus aculeatus*)

Table 2. Ovarian weight (*OW*, *g*) on individual fecundity (*F*) of Arctic charr morphs from Thingvallavatn. All coefficients of determination (R^2) are significant ($P<0.05$). (Data from Skúlason 1983)

Morph	Regression	Fecundity range	R^2	*N*
SB-charr	$\log_e OW_{sb} = 0.01045F + 0.0665$	13- 385	0.70	46
LB-charr	$\log_e OW_{lb} = 0.00087F + 2.9640$	135-2974	0.77	21
PL-charr	$\log_e OW_{pl} = 0.00373F + 1.7468$	90- 297	0.55	26
PI-charr	$\log_e OW_{pi} = 0.00094F + 3.0872$	293-2076	0.89	12

Table 3. Fork length (L, mm) on otolith radius (r, mm^{-2}) of morphs of Arctic charr from Thingvallavatn. All coefficients of determination (R^2) are highly significant ($P<0.001$)

Morph	Regression	Length	R^2	N
SB-charr	$\log_e L = 7.27-2.29\log_e r+0.37(\log_e r)^2$	73-310	0.76	232
LB-charr	$\log_e L = 4.60-1.25\log_e r+0.28(\log_e r)^2$	70-470	0.93	681
PL-charr	$\log_e L = -33.28+15.24\log_e r-1.51(\log_e r)^2$	85-260	0.76	4467
PI-charr[1]	$\log_e L = -6.86+3.75\log_e r-0.26(\log_e r)^2$	85-480	0.80	3406

[1] For fish younger than 6 years, PL-charr are used

Table 4. Adult annual rate of survival (S) + 95% confidence limits, X^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. All X^2-values are not significant ($P>0.05$) and indicate agreement between sample observations and the model used.

Morph	Year	S	X^2	Age (Years)	Sample size
SB-charr	1983	0.63±0.04	0.078	5-13	209
	1984	0.51±0.04	2.887	6-11	164
	Pooled	0.57±0.03	3.255	5-13	488
LB-charr	1983	0.65±0.05	0.037	6-14	112
	1984	0.59±0.07	0.004	6-14	72
	Pooled	0.63±0.05	0.911	7-15	145
PL-charr	1983	0.47±0.03	1.890	6-14	501
	1984	0.41±0.01	0.074	5-13	1789
	Pooled	0.43±0.02	0.572	6-14	2179
PI-charr	1983	0.63±0.06	0.063	7-15	89
	1984	0.62±0.07	0.221	7-14	78
	Pooled	0.63±0.05	0.030	7-15	169

Table 5. Empirical sizes (mm) and the parameters (± 95% confidence limits) L_∞ (mm) and k of the exponential growth model $L_A = L_\infty(1-e^{-kA})$, where A is age (years) of Arctic charr from Thingvallavatn, based on pooled data from August-September 1983-1984.

Morph	Adult fork lengths				L_∞	k	Sample sizes
	Males		Females				
	Mean	Range	Mean	Range			
SB-charr	96,	73-260	109,	75-310	132.9± 6.7	0.333±0.045	746
LB-charr	240,	135-460	274,	90-470	553.5±74.2	0.086±0.016	644
PL-charr	175,	130-230	188,	140-260	205.1± 1.6	0.417±0.011	4224
PI-charr	268,	180-480	295,	200-440	302.4±15.1	0.328±0.064	224

Table 6. Total weight (W, g) - fork length (L, mm) relationships of small benthivorous (SB), large benthivorous (LB), planktivorous (PL) and piscivorous (PI) Arctic charr from Thingvallavatn caught 1984, fitted to the regression model: $\log_e W = a \log_e L - b$, where a and b are constants. N= sample size, R^2= coefficient of determination, F-values for test of homogeneity between regression coefficients (a) between sexes and times of the year. n.s.=$P>0.05$, *=$P<0.05$, **=$P<0.01$, ***=$P<0.001$.

Morph	Month	Sex	Regression a	Regression b	R^2	F Sex	F Month	N
SB-charr	August	Male	3.06	11.58	0.90	5.91*		244
		Female	2.83	10.51	0.92			217
		Pooled	2.94	11.03	0.91		1.08n.s.	462
	June	Pooled	3.06	11.78	0.95			50
LB-charr	August	Male	3.10	11.82	1.00	0.04n.s.		162
		Female	3.10	11.84	0.99			133
		Pooled	3.11	11.87	1.00		1.40n.s.	313
	June	Pooled	3.14	12.16	0.99			102
PL-charr	August	Male	3.04	11.59	0.96	15.86***		1733
		Female	3.11	11.97	0.97			1049
		Pooled	3.08	11.82	0.97		1552.69***	2801
	June	Pooled	2.40	8.43	0.81			479
PI-charr	August	Male	3.20	12.44	0.97	1.27n.s.		67
		Female	3.07	11.78	0.93			35
		Pooled	3.11	11.95	0.95		4.87*	102
	June	Pooled	3.22	12.66	0.94			47

Table 7. Individual fecundity on length (L, mm) of large benthivorous (LB) and piscivorous charr (PI), and on length and age (A, years) of small benthivorous (SB) and planktivorous (PL) Arctic charr 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	$\log F=2.719\log_e L - 8.97$	149 - 1914	0.95	7
PI-charr	$\log F=2.841\log_e L - 9.70$	278 - 1795	0.68	26
SB-charr	$F=1.28L - 74.74$	12 - 221	0.69	175
	$F=1.38L - 4.75A - 57.91$	12 - 221	0.71	172
PL-charr	$F=1.47L - 57.53$	96 - 431	0.11	404
	$F=2.08L - 18.6A - 66.11$	96 - 431	0.22	397
Pooled	$\log F=2.284\log L - 6.63$	12 - 1914	0.89	612

Legend to figures

Fig. 1. Thingvallavatn with 20 m depth contour. Locations of benthic (B) and pelagic (P) gill net fishing are indicated.

Fig. 2. Percentage of sexually mature males (——) and females (----) of the four morphs of Arctic charr in Thingvallavatn. The fish were caught in August/September 1983 and 1984. Female sample size is always given below the corresponding male figure.

Fig. 3. Back-calculated fork lengths with 95% confidence limits of the estimates for small benthivorous (SB), large benthivorous (LB), planktivorous (PL) and piscivorous (PI) Arctic charr from Thingvallavatn, caught August-September 1983 and 1984.

Fig. 4. Regression coefficients (a) of the weight (*W*, g) - fork length (L, mm) relationship: $\log_e W = a \log_e L + b$, for each age-group within small benthivorous (SB), large benthivorous (LB), planktivorous (PL) and piscivorous (PI) Arctic charr caught in Thingvallavatn, August-September 1983 and 1984.

Fig. 5. Age specific population fecundities (%) of small benthivorous (SB), large benthivorous (LB), planktivorous (PL) and piscivorous (PI) Arctic charr caught in Thingvallavatn, August-September 1983 and 1984.

Fig. 6. Gonadosomatic index (GSI) within age-groups of small benthivorous (SB), large benthivorous (LB), planktivorous (PL), and Piscivorous (PI) Arctic charr caught in Thingvallavatn,

August-September 1983 and 1984.

Fig. 7. Annual investments in gonadal relative to somatic growth of age-groups of small benthivorous (SB), large benthivorous (LB), planktivorous (PL), and piscivorous (PI) Arctic charr caught in Thingvallavatn, August-September 1983 and 1984.

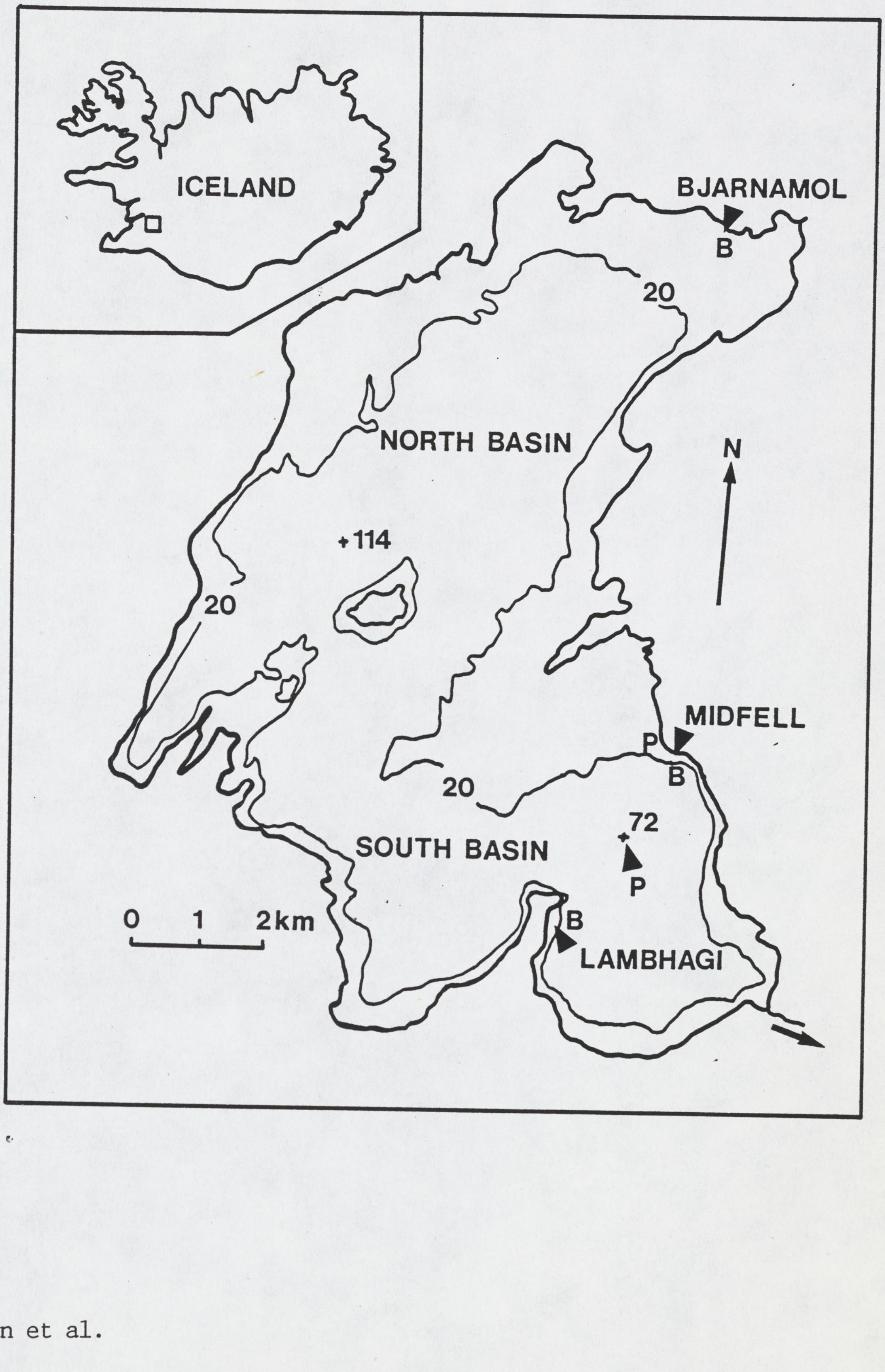

Fig. 1. Jonsson et al.

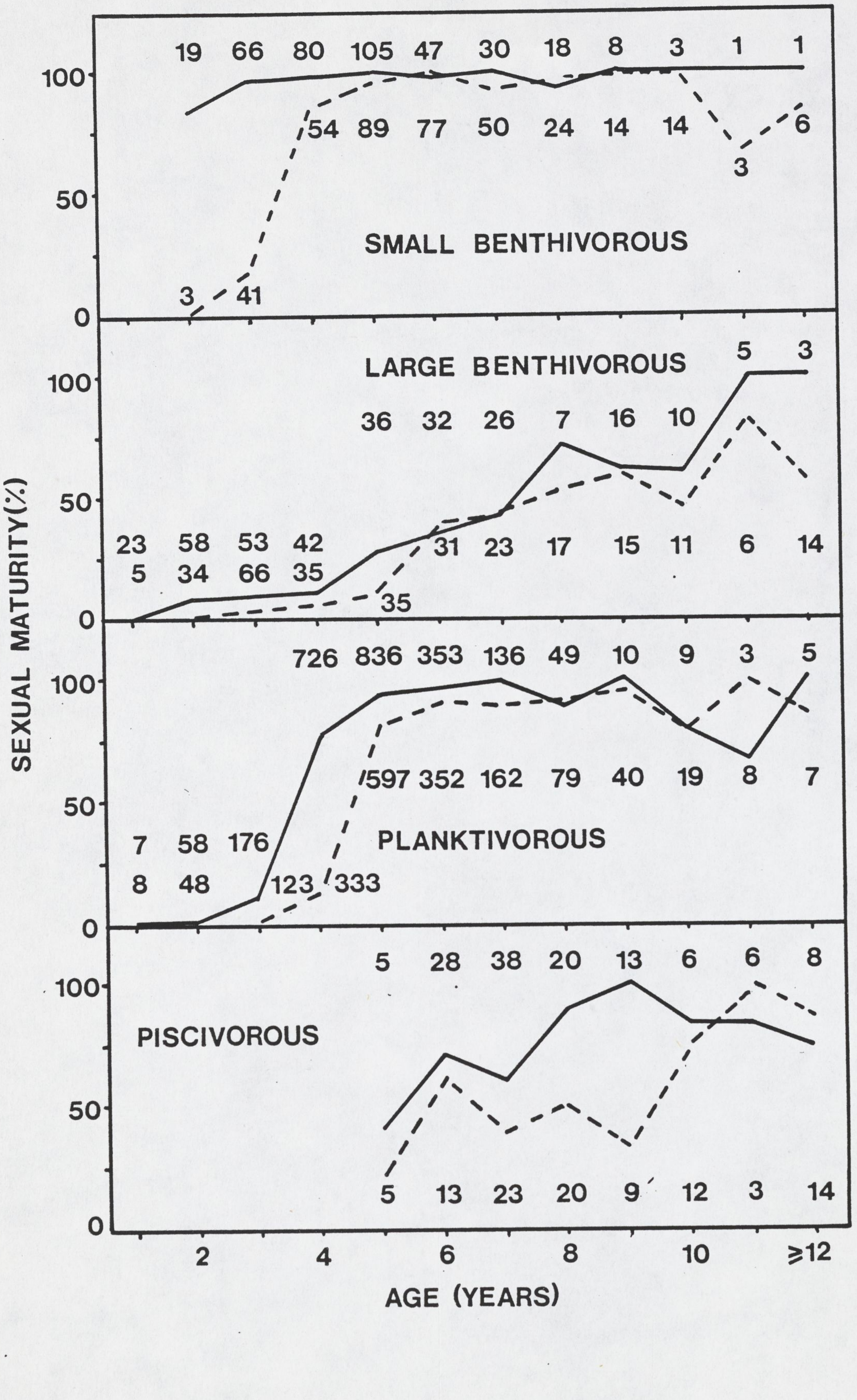

Fig. 2. Jonsson et al.

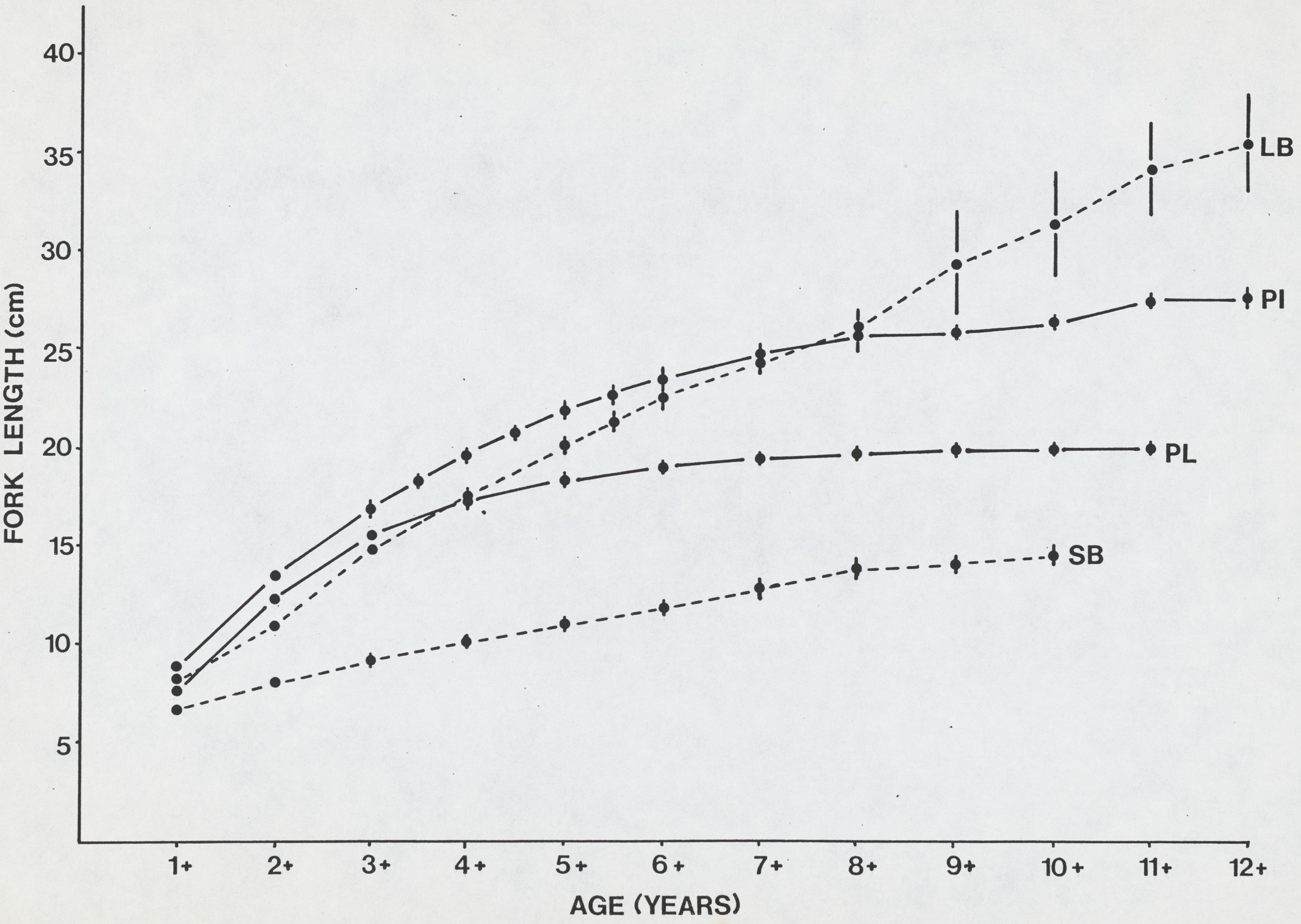

Fig. 3 Jonsson et al.

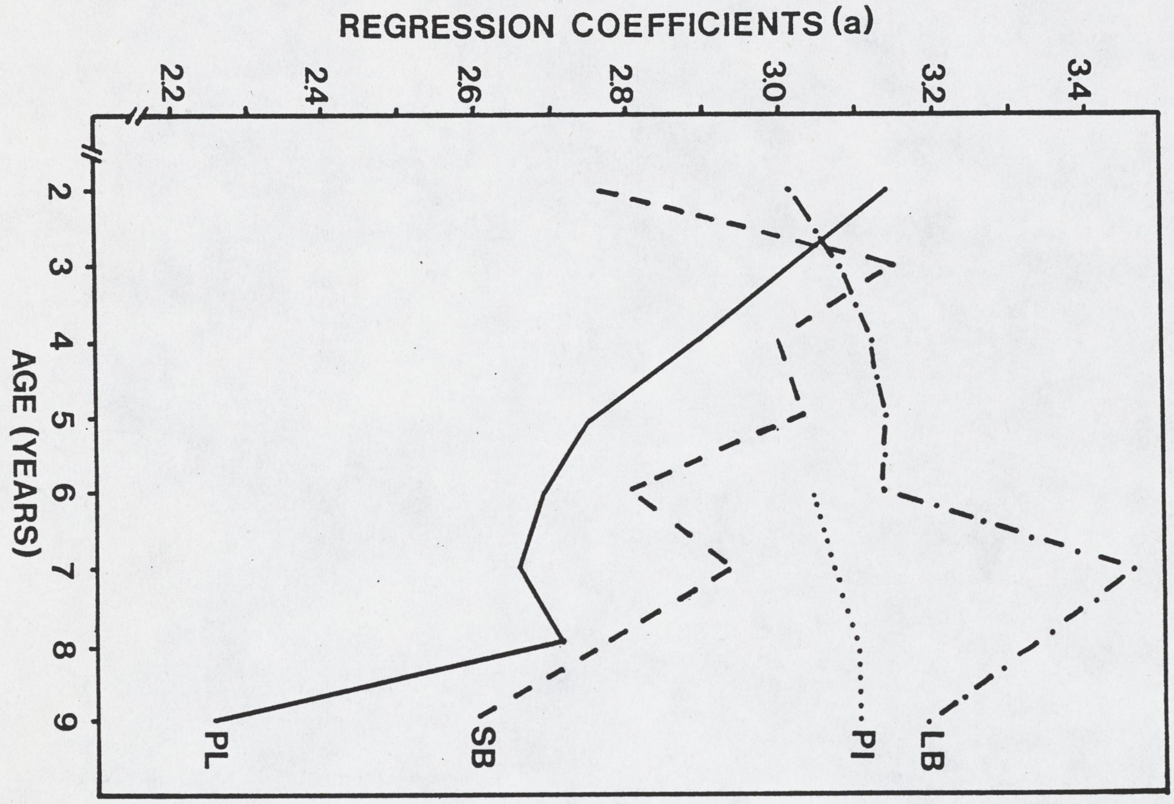

Fig. 4. Jonsson et al.

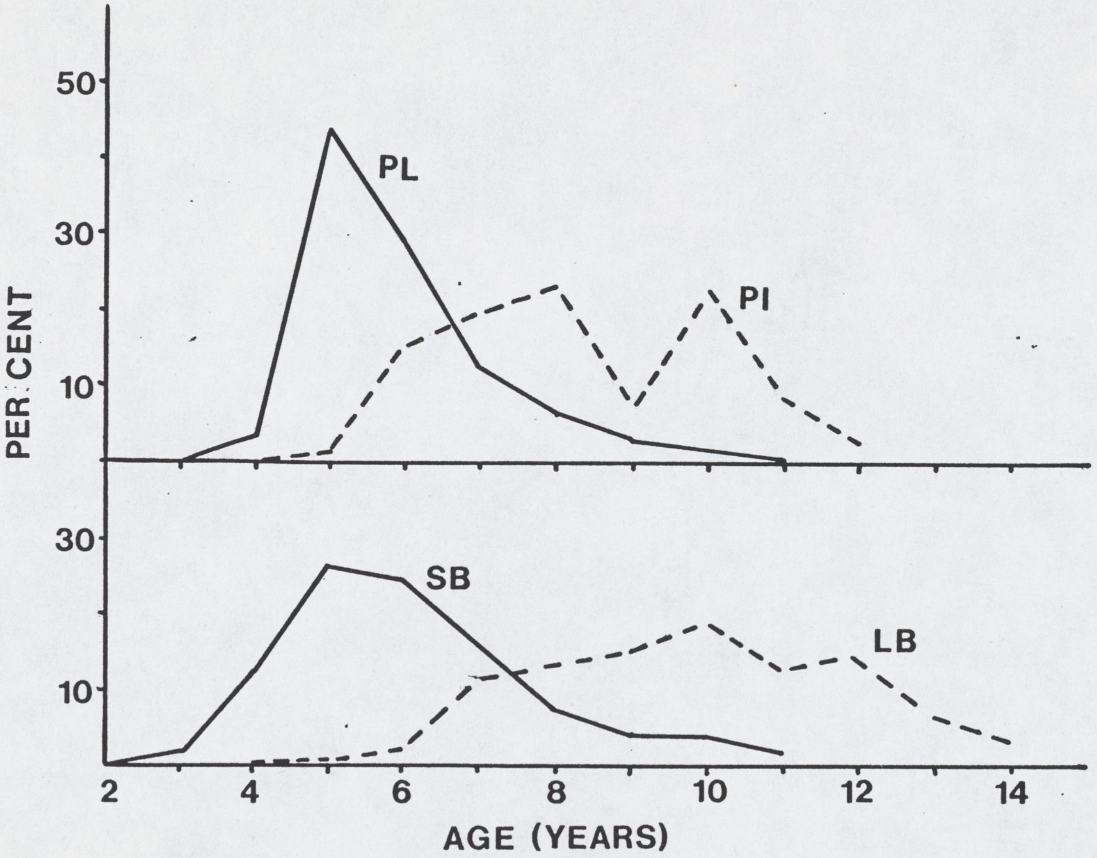

Fig. 5. Jonsson et al.

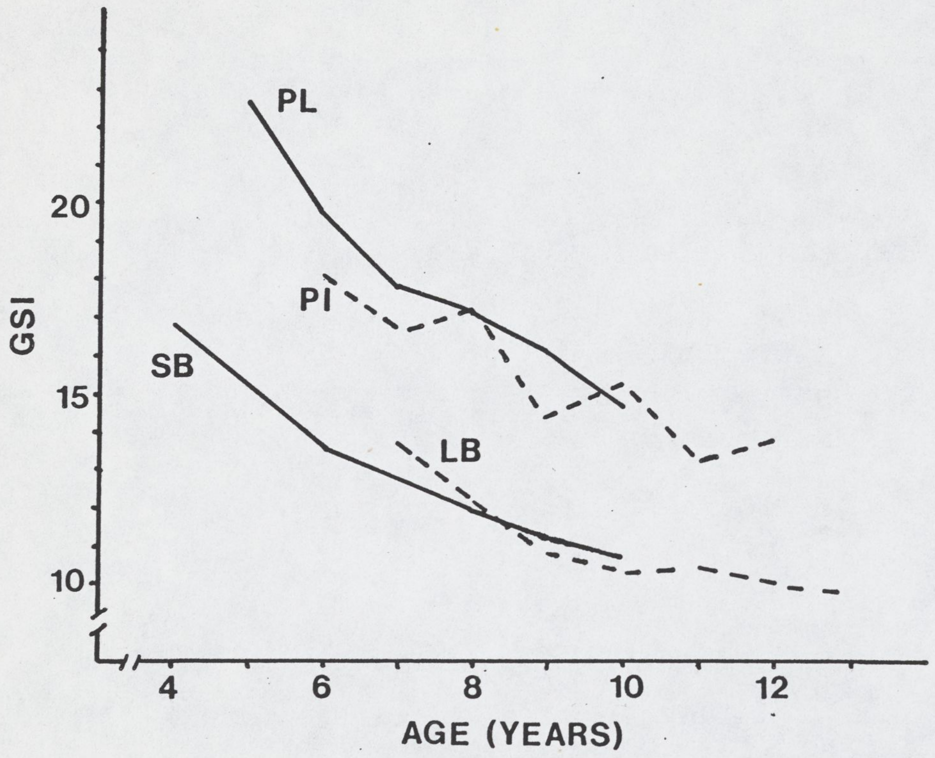

Fig. 6. Jonsson et al

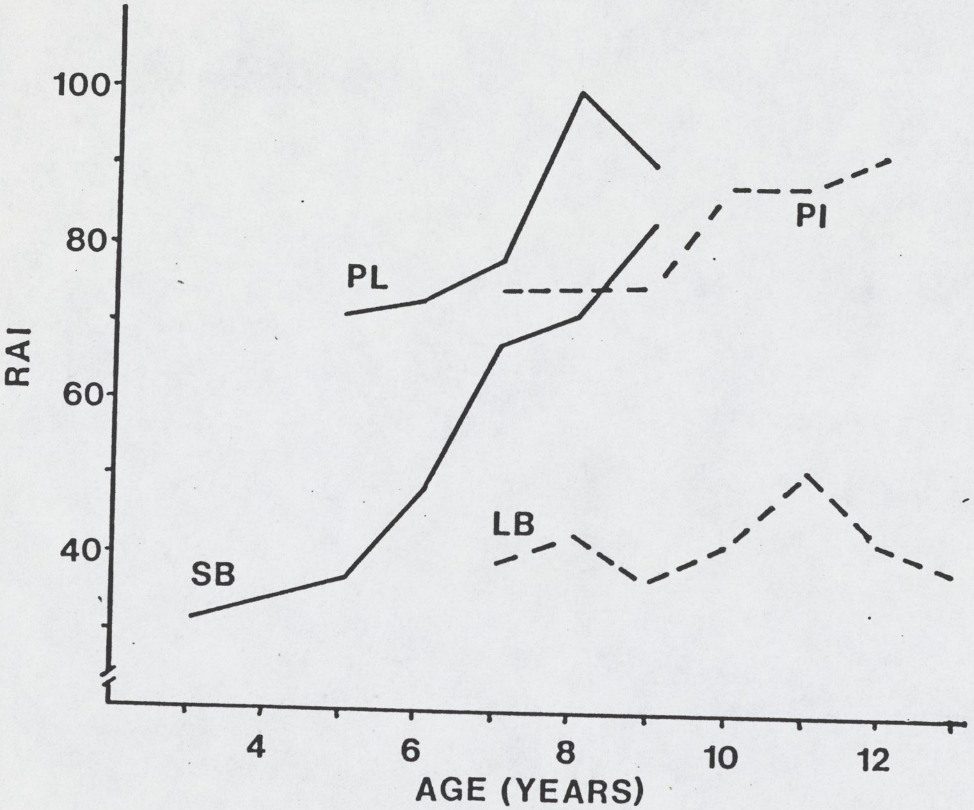

Fig. 7 Jonsson et al.

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Magnusson & Ferguson
results of 36 enzyme loci
show morphs are conspecific
and do not represent different
evolutionary lineages.

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Canada

Pl - PL ?
dit.
ope sel mat

Pl - .5-10
PL - 3-5

Mayr - Svardson.
Nyman.

~~Nymans~~
Gydems

"F"
.9 - 1.0 - dwarf
.4 - .7 - normal
.0 - .2 dwarf

how tall specimen.
Pl
or
PL ?

Gydems (84)
- Gydems
all 3 sp.

eel and
3-spine stickleback
only non-salmonid
native fish

Fridriksson.
' larger ' Bleikja '
' murta '
' svart murta '

Thingvallavatn
all .76

- dwarf (benthic) } .21

large .89
med. .74
raw .80
.25 in volcanic
cleft

fig
3c

"it is clear that all of the species
from Scandinavia as defined by Nyman et al (1981),
are present in Iceland also".

"... the landlocked charrs were
already separated into species
when immigrations occurred".

illustr
photo
svart murt

Savvaitova
Campbell Scotland
- Ferguson Ireland
& why not count native cases

Behnke (80)
- murta 29.7 -
bleikja - 26.7 -

morpho - polymorphism
in single site