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Polymorphic segregation in Arctic charr *Salvelinus alpinus* (L.) from Vatnshlídarvatn, a shallow Icelandic lake

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We studied the salmonid fish Arctic charr, *Salvelinus alpinus*, in a small and shallow landlocked lake in NW Iceland. The lake is productive but the only fish present is Arctic charr. Despite the apparent absence of discrete benthic and limnetic habitats for fish, two forms of Arctic charr are found in the lake. They show subtle differences in morphology related to swimming performance and manoeuvrability, but differences in life history such as growth, and age and size at sexual maturation are more pronounced. Both forms have benthic feeding habits with one form consuming greater number of species than the other. We suggest that the segregation of these forms is based on the evolution of a specialist from a local generalist and that this has been made possible by the absence of a common fish competitor in similar lakes, the threespined stickleback *Gasterosteous aculeatus*.

ADDITIONAL KEY WORDS:—morphology – competition — local adaptation – ecological specialization – polymorphism – speciation – ontogeny – phonotypic plasticity.

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INTRODUCTION

Resource polymorphism, the occurrence of discrete intraspecific forms displaying differential niche use, is found in various vertebrate species (Skúlason & Smith, 1995), and such diversification is thought to be important in inducing diverse morphologies within and among species of fish (Echelle & Kornfield, 1984). Intraspecific forms can arise through the utilization of different niches associated with variable habitats and diets (Malmquist *et al.*, 1992; Schluter & McPhail, 1992; Robinson *et al.*, 1993; Smith, 1993; Day, Pritchard & Schluter, 1994; Snorrason *et al.*, 1994). Divergence of sympatric forms can be facilitated by an absence of competition for these resources from other species (Schluter, 1988; Robinson & Wilson, 1994). Such resource polymorphism in fish is commonly associated with the presence of discrete benthic and pelagic habitats in lakes. Examples include whitefish (*Coregonus* and *Prosopium* spp.), threespine sticklebacks (*Gasterosteus aculeatus*), sunfishes (*Lepomis gibbosus* and *L. macrochirus*), and Arctic charr (*Salvelinus alpinus*) (Skúlason & Smith, 1995). The occurrence of sympatric forms of Arctic charr, like many other salmonids, is also known to be related to piscivory and/or cannibalism, and anadromy versus resident life history (Griffiths, 1994; Reist *et al.*, 1995; Skúlason & Smith, 1995). The salmonid fish, Arctic charr (*Salvelinus alpinus* L.), has a northern circumpolar distribution, and can be anadromous or residential (Nyman, Hammar & Gydemo, 1981; Snorrason *et al.*, 1994). It is frequently found as two or three coexisting forms differing mainly in size (Nordeng, 1983; Griffiths, 1994). Life history of Arctic charr is variable, both within and among localities (Hindar & Jonsson, 1993; Griffiths, 1994), and is characterized by high levels of phenotypic plasticity (Nordeng, 1983; Hindar & Jonsson, 1993).

Considering the numerous examples of coexisting forms, few studies have reported distinct morphological differentiation among sympatric forms of Arctic charr (Snorrason *et al.*, 1994). In Thingvallavatn, Iceland, differences in morphology have been observed among four sympatric forms of Arctic charr (Skúlason, Noakes & Snorrason, 1989; Snorrason *et al.*, 1994). In Loch Rannoch, Scotland, three forms co-occur (Adams *et al.*, 1998), and in Lake Hazen, Elsmere Island two sympatric forms are found (Reist *et al.*, 1995). Some of the morphological studies have failed to take into account allometric changes associated with increasing body size (Griffiths, 1994), and age. However, it is important to investigate ontogenetic trends in shape, for instance to see if adult forms are diverging from each other, or converging. Forms may also exhibit differential ontogenetic trajectories in shape early in life, and then maintain their differences through the remainder of the ontogeny, by parallel change in shape (Strauss & Fuiman, 1985).

Bimodal size distribution of Arctic charr has been identified in several Icelandic lakes (Skúlason *et al.*, 1992), including Lake Vatnshlídarvatn in NW Iceland (Tómasson, 1987). With the exception of Thingvallavatn, the ecology of such populations in Iceland is mostly unexplored (Snorrason *et al.*, 1994).

Vatnshlídarvatn is a landlocked lake in NW Iceland. It is in many ways different from other lakes where sympatric forms of Arctic charr have been investigated (Jonsson & Hindar, 1982; Hindar & Jonsson, 1982, 1993; Jonsson, 1983; Sparholt, 1985; Hindar, Ryman & Ståhl, 1986; Skúlason *et al.*, 1989; Svedäng, 1990; Snorrason *et al.*, 1994; Reist *et al.*, 1995). The lake is small (70 ha), shallow and physically simple, providing no discrete segregation into limnetic and benthic habitats for fish. As in many Arctic lakes the only fish present in Vatnshlídarvatn is Arctic charr. However, compared with Arctic lakes, Vatnshlídarvatn is in a warmer climate and has more abundant food resources. Thus, this relatively simple lake system provides an interesting setting for studying evolution of phenotypic segregation and possible speciation.

The primary objective of the study was to examine if there are two separate growth forms of Arctic charr in Vatnshlídarvatn, and if the charr in the lake represent two morphologically distinct forms, distinguished as the 'brown form' and the 'silver form'.

We then relate the morphological data with onotogenetic trends in shape and diet, and discuss functional and evolutionary implications of our results.

METHODS

Study site

Vatnshlídarvatn (65° N, 19° W) is a shallow 70 ha lake (mean depth 2–3 m, maximum depth 5–6 m, length 1.5 km, width 0.55 km). The bottom is mainly mud, with gravel close to shore and near the outlet of the lake. The submerged vegetation is characterized by patches of eelgrass (*Myriophyllum* sp.). The lake is in a basaltic area at an elevation of 280 m, and is a part of a runoff system, with shallow lakes and wetlands near the origin. The lake has one major inlet and one outlet and is additionally fed by short spring-fed creeks (Fig. 1). Water temperature follows seasonal air temperature (mean air temperature in January −5°C, and July 7°C) and can range from 0 to 15°C. The lake is usually ice-covered from October/November to April/May. Water conductivity is 161 μS/cm (at 25°C), and pH 8.50 (in August 1994). The lake was formed after the last Pleistocene glaciation, and has been landlocked by a waterfall for the last 6000–8000 years. Arctic charr is the only fish species present in the lake.

Sampling

Arctic charr ($n = 848$) were sampled in the lake during the night of 16 August 1994 with bottom gill nets (panel sizes 1.5 × 25 m and mesh sizes 10 mm–52 mm).

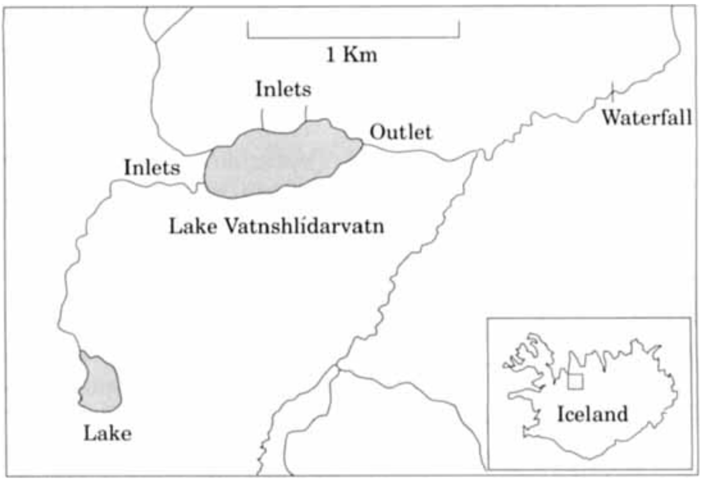

Figure 1. Study site, Lake Vatnshlídarvatn and its tributaries.

Sub-sample ($n=346$) for diet analysis and ($n=492$) for morphometric measurements was taken by randomly picking 10 fish at a time from each of the gillnets. The whole sample was used for determination of sexual maturity. Two more samples for diet analysis were taken by the same gill nets during the nights of 28 September 1994 ($n=213$), and 15 July 1995 ($n=130$). Fork-length on each fish was measured to the nearest 0.1 cm. Degree of sexual maturity was determined according to Dahl (1917). Age was determined from otolith surface analysis (Barber & MacFarlane, 1987).

Diet

The prey in each stomach was allocated to one of 10 food categories and the number of individuals in each category counted. The food categories were: *Lymnea* sp.; (2) *Pisidium* sp.; (3) *Eurycercus* sp.; (4) miscellaneous crustacea; (5) Orthocladiinae sp.; (6) Chironominae sp.; (7) Tanypodinae sp.; (8) miscellaneous insecta; (9) *Lepidurus arcticus*; (10) fish eggs. Percentage by number (% N) of each food taxon was determined as:

$$\%\, N = 100 N_i / N_j$$

where N_i is the total number of organisms of food category i, and N_j is the total number of organisms of all food categories. Overlap in diet (Levin's index LO) and diet breadth (Levin's index B) of the two forms are estimated following Ludwig & Reynolds (1988). Diet overlap (LO) of form 1 with form 2 is given by:

$$\mathrm{LO}_{1,2} = \frac{\Sigma_j^r[(p_{1j})(p_{2j})]}{\Sigma_j^r(p_{1j}^2)}$$

Where r is the number of food categories, p is percent of each food category in the diet, and subscripts *i*, *j* represent the *i*th and the *j*th food category. LO can range between 0 and 1, from no overlap to complete overlap. Diet breadth is measured as:

$$B_i = \frac{1}{\Sigma_j^r (p_{ij}^2)}$$

Where *r* is the number of food categories, *p* is percent of each food category in the diet, and subscripts *i*, *j* represent the *i*th form and the *j*th food category. The denominator is termed the breadth of the *i*th form.

B can range from 1, one food category present in the diet, to 10, when contribution of all food categories in the diet is equal. Tests for differences in the number of different food items in the stomachs of the charrs are performed by employing Mann–Whitney U tests.

Classification

Arctic charr were pre-classified by eye into either 'brown form' or 'silver form'. The following criteria were used:

(1) Brown form has stocky body, no silvery colour on sides, parr marks are sometimes present, there is melanization on operculum and usually on ventral sides of lower jaw, body colour is light brownish, and sexually mature individuals have dark bluish back.

(2) Silver form has fusiform body, no parr marks, dark greyish to dark bluish back, silvery sides; melanization on operculum is absent, but sometimes occurs on ventral sides of lower jaw on sexually mature fish.

Fish that did not meet these criteria (9% of the sample) were classified as 'unknown'.

Morphometric and meristic measurements

Morphometric characters (adapted from Reist *et al.*, 1995; Fig. 2) were measured to the nearest 0.1 mm with vernier calipers on the left side of the fish. Measurements made parallel to the longitudinal body axis are: (1) Preorbital length (POL) – the distance from the anteriormost part of the snout to the anterior margin of eye; (2) orbital length (OOL) – the distance from the anterior to the posterior margin of the eye; (3) head length (HL) – the distance from the anteriormost part of the snout to posterior bony margin of the operculum; (4) length of anal fin base (ANL) – the distance from the origin to the insertion of anal fin; (5) caudal penduncle length (CPL) – the distance from the insertion of the anal fin to the origin of the caudal fin rays on the hypural plate (corresponds to the end of the fleshy portion of the body); (6) caudal fin length (CFL) – the distance from the last unmodified vertebrae to the posteriormost tip of compressed caudal fin lobes; (7) Fork depth of caudal fin (FLT) – fork length minus standard length.

Measurements made parallel to the dorso-ventral body axis were: (8) Head depth

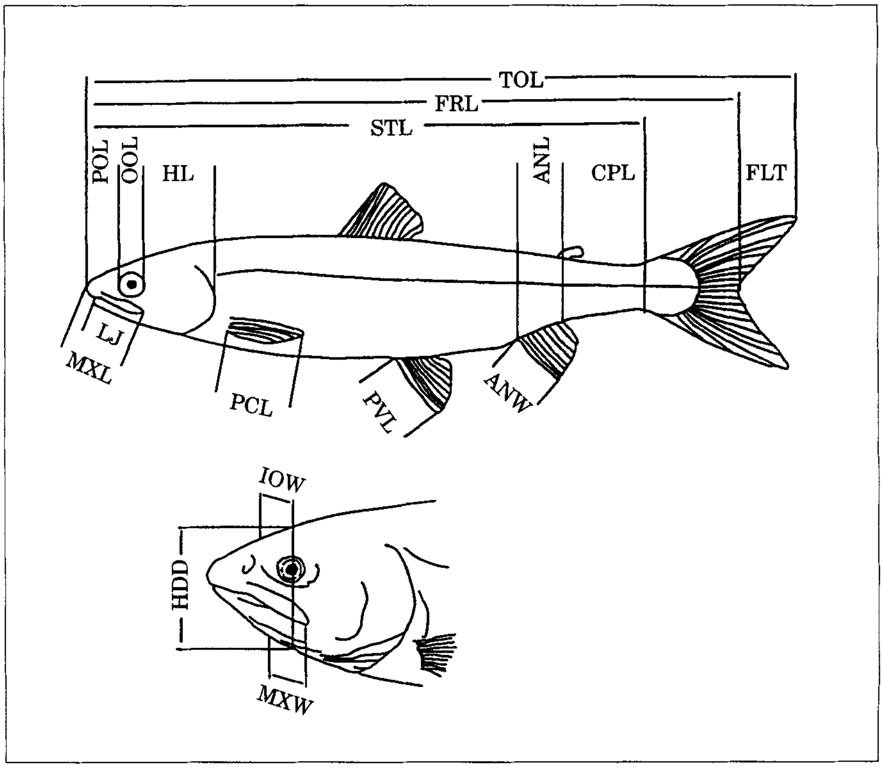

Figure 2. Illustration of morphological measurements taken on the left side of each specimen of Arctic charr from Vatnshlídarvatn, Iceland. See text for explanations.

(HDD) – the distance from the bottom of the jaw to the top of the head centred mid-pupil with mouth held closed; (9) Interorbital width (IOW) – the distance across the bony margins between the orbits; (10) caudal penduncle depth (CPD) – the depth of the caudal penduncle, anterior to the origin of the caudal fin rays on the hypural plate.

The remaining variables were measured following the axis of the body part: (11) Length of upper jaw (MXL) – tip of snout to end of maxilla; (12) length of lower jaw (LJ) – tip of lower jaw to end of maxilla, measured with closed mouth; (13) maxillary width (MXW) – widest distance across the maxilla; (14) pectoral fin length (PCL); (15) pelvic fin length (PVL); (16) length of anal fin (ANW). Fins were measured from the origin of the fin to the tip of the longest ray.

Standard length (STL) was defined as the distance from the anteriormost part of the snout to the end of the caudal penduncle, and total length (TOL) as the distance from the anteriormost part of the snout to the posteriormost tip of compressed caudal fin lobes. Both were measured to the nearest 1.00 mm.

Measurement precision was verified by blind repeated measurements on 30 specimens. The measurement error varied between 0.3–3.9% depending on the size of the morphometric character involved. Gill rakers were counted on the first left gill arch of the fish.

Statistical analysis of morphological data

Morphometric data were analysed using both univariate and multivariate statistical procedures. Prior to analysis, raw measurements (except standard length) were size-adjusted by computing the residuals from the regression of untransformed morphological variables on standard length (Reist, 1985). This method approaches size-free shape variables. Univariate testing consisted of comparison of mean values using analysis of variance (ANOVA).

The pattern of morphological variation was analysed using Principal Component Analysis (PCA), and Canonical Discriminant Analysis (CDA; Pimentel, 1979). Principal components were derived from the variance–covariance matrix, and the canonical correlations were computed using the total variability. PCA reduces and summarizes multivariate trends in shape variation to a set of statistically independent variables (PC axes). CDA derives several independent linear combinations of the original variables that have the highest possible multiple correlation with the groups which are being investigated. CDA provides a test of *a priori* designation to forms. In order to include 'unknowns' in the PCA results, the residual standardization involved three groups; brown form ($n=166$), silver form ($n=281$), and unknowns ($n=45$). In the residual standardization for CDA results, unknowns were excluded. Bivariate allometric coefficients were calculated with the covariance–ratio method, which is independent of assumptions on the ratio (denoted by λ) of the error variance of y to that of x (Kuhry & Marcus, 1977). Data on a third, so-called 'instrumental' variable is required for the estimation of the covariance ratio (here, head length, HL). T-tests for homogeneity of slopes were made according to Sokal & Rohlf (1981).

For the estimation of multivariate allometric coefficients, PCAs were computed on each of the two forms and sexes separately from the covariance matrixes on ln transformed data (Jolicoeur, 1963). The multivariate coefficients were determined according to Shea (1985), as ratios of the first component loading of the other variables relative to that of standard length. Standard length was included in the analysis, in order to make the multivariate and bivariate allometric coefficients comparable.

RESULTS

Growth and sexual maturation

There are two growth forms of Arctic charr in Vatnshlídarvatn, the smaller brown form and the larger silver form (Fig. 3). They are of similar size at one and two years after which they diverge in growth. The silver form, with the theoretical asymptotic sizes 33.4 cm ($k=0.179$) for males and 31.6 cm ($k=0.180$) for females (Jónsson, 1996), grows relatively fast until eight years of age, after which growth slows. The brown form, with the asymptotic size of 18.0 cm ($k=0.369$) for males, and 20.1 cm ($k=0.364$) for females (Jónsson, 1996), ceases growth at an earlier age.

The brown form mostly reaches sexual maturity at two years of age, while the silver form matures at an older age, females earlier than males (Fig. 4).

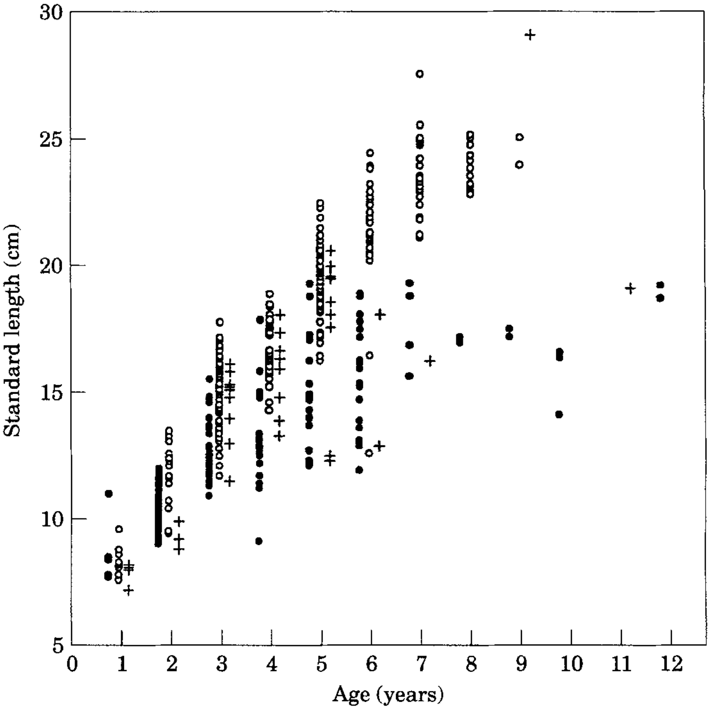

Figure 3. Length–age relationships of Arctic charr from Vatnshlídarvatn, Iceland. Brown form (●), silver form (○), and unknown (+).

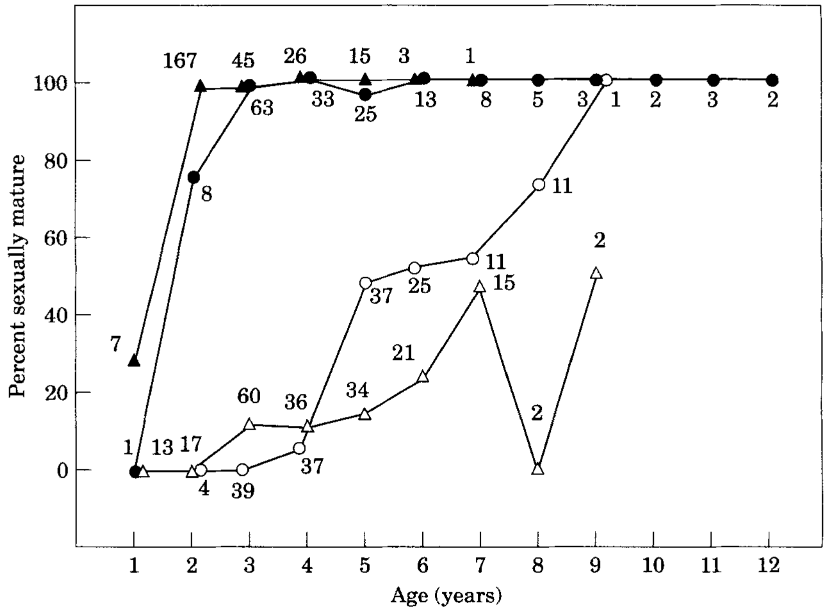

Figure 4. Percentage of sexually mature male (triangles) and female (circles) Arctic charr from Vatnshlídarvatn, Iceland. Brown form (●, ▲); silver form (○, △). Male sample size is given above symbols and female sample size below symbols.

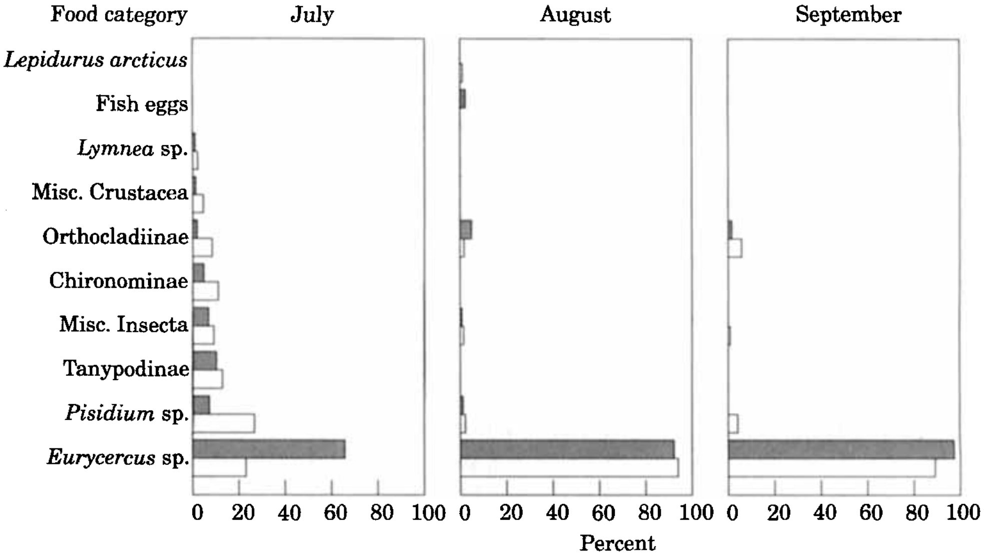

Figure 5. Percent contribution of each food category in the diet of Arctic charr in Vatnshlídarvatn (number of food items). Samples from 16 August, 28 September 1994 and 12 July 1995. Brown form (▨); Silver form (☐).

Diet

Eurycercus sp. constitutes 70% of all food items eaten by the brown form in July and the percentage increases throughout the summer—94% in August and 98% in September (Fig. 5). In Icelandic lakes *Eurycercus* sp. appears in July and is at its peak abundance in August/September (Adalsteinsson, 1979). The second most important food item of the brown form in July consists of Tanypodinae larvae and pupae, constituting 14% of the food items (Fig. 5). *Pisidium* sp. 24% and *Eurycercus* sp. 37% are the most important food items of the silver form in July. Other important food items of this form in July include Chironominae and Tanypodinae larvae and pupae, 12% and 10% respectively. Although the silver form feeds mostly on *Eurycercus* sp. in August and September (Fig. 5), it does significantly less so than the brown form (Table 1). At all sampling dates the silver form eats significantly more *Pisidium* sp. than the brown form (Table 1). Cannibalism is observed in one individual of silver form. *Lepidurus arcticus*, which is the largest food item available besides Arctic charr, is only infrequently found in the diet of either form. There are no apparent size trends in the diet of the charrs that could explain the differences between forms (Table 1).

Levin's index indicates that the diet of the two forms overlaps greatly at all sampling dates (Table 2). The dietary breadth of the silver form is, however, greater than that of the brown form, except in August when both forms feed almost exclusively on *Eurycercus* sp. This difference between the forms is independent of size, and appears to develop early in life (Table 2). The number of different food items consumed is significantly greater for the silver than the brown form at all sampling dates (Mann–Whitney U tests; $P<0.05$), and these differences are also

TABLE 1. Percent contribution of *Pisidium* sp. and *Eurycercus* sp. in the stomachs of the brown and silver form Arctic charr in Vatnshlídarvatn, Iceland, with Mann–Whitney U tests for differences between forms in different size classes. The size classes are 10.1–15.0 cm (size class 1), 15.1–20.0 cm (size class 2), and fishes of all sizes combined (size class T). Sampling dates are July, August and September. Sample sizes are given in brackets

		Pisidium sp.				*Eurycercus* sp.	
Time	Size class	Brown form	Silver form	*P* value	Brown form	Silver form	*P* value
	1	0.36 (14)	23.10 (5)	0.153	70.49	20.73	0.135
July	2	7.32 (27)	26.88 (37)	0.037	65.44	22.98	0.001
	T	4.94 (41)	24.50 (89)	0.004	67.16	37.41	0.002
	1	0.00 (58)	0.12 (33)	0.185	92.85	91.79	0.062
Aug.	2	0.65 (39)	1.77 (126)	0.046	91.90	93.55	0.170
	T	0.26 (97)	1.32 (249)	<0.001	92.47	93.75	0.001
	1	0.00 (35)	4.05 (27)	0.019	98.23	91.21	0.023
Sept.	2	0.23 (20)	3.73 (111)	0.101	97.22	89.18	0.005
	T	0.08 (55)	3.32 (158)	0.003	97.86	90.09	<0.001

TABLE 2. Levin's index for diet overlap and dietary breadth of the brown and silver Arctic charr forms in Vatnshlídarvatn at three sampling dates; July, August and September. The numbers 1 and 2 represent fish in the size ranges 10.1–15.0 and 15.1–20.0 cm fork length respectively. T stands for fish of all sizes

		Diet overlap			Dietary breadth		
Form	Size	July	Aug.	Sept.	July	Aug.	Sept.
Brown	1	0.32	0.99	0.93	1.85	1.16	1.04
	2	0.44	1.00	0.92	2.21	1.18	1.06
	T	0.60	1.00	0.92	2.11	1.17	1.04
Silver	1	1.00	1.00	1.00	5.76	1.18	1.20
	2	1.00	0.98	1.00	5.68	1.14	1.25
	T	1.00	0.99	1.00	4.31	1.14	1.23

significant for charr in the size ranges 10.1–15.0 cm, and 15.1–20.0 cm separately in July and August (Mann–Whitney U tests; $P<0.05$; sample sizes are given in Table 1).

Univariate results

Univariate comparisons between the two forms were made for each sex separately as well as for the sexes combined. Adjusted means for males and females of the brown form were higher than means of the corresponding sex of the silver form, for all body measurements except two: caudal penduncle length (CPL) and caudal fin length (CFL). There were significant differences ($P<0.003$, Bonferroni adjustment) between the sexes of the brown and silver form for most adjusted character means

(Table 3). The greatest differences observed among both sexes were in caudal penduncle length (CPL), the paired fins (PCL and PVL) and anal fin width (ANW) (Table 3). There were significant differences between many adjusted character means of the two forms for five year old (5 +) males and females alone, although CPL and ANW of the males appeared to be linked with the development of sexual maturity at this age. Differences between adjusted means of the sexes combined were highly significant for all characters except fork depth of caudal fin (FLT) (Table 3).

PCA results

The residual standardization was efficient in removing size differences between forms, while significant correlations were not indicated between any of the principal components and standard length (P>0.05). Further, there was no significant correlation between any of the principal components and stage of sexual maturity (P>0.05). Principal component one (PC1) accounted for 40% of the variation and had a negative loading for caudal peduncle length and positive loading for all other characters (Table 4). Differences in mean scores of individuals between forms were highly significant (pooled variances t-test of PC1: $t = 10.823$, df = 445, P<0.001). Principal component two (PC2) accounted for 9.4% of the variation and had high positive loading for caudal fin length and caudal peduncle length; and negative loading for orbital length and anal fin width (Table 4). Between group differences in mean individual scores were highly significant (pooled variances t-test of PC2: $t = -8.523$, df = 445, P<0.001). Examination of the bivariate plots of PC1 and PC2 scores revealed grouping with respect to *a priori* designation of forms (Fig. 6). Although considerable overlap was evident, brown form charr tended to score positively on PC1 and negatively on PC2. Silver form charr tended to score negatively on PC1 and positively on PC2. Unknown individuals overlapped with both forms (Fig. 6).

Males of both forms appeared to score higher than females on both PC1 and PC2 (Fig. 6). Mean scores for males in various age classes were also better separated on PC1 than mean scores for females, but scores for females were more widely distributed on PC2 (Fig. 7A,B). Significant age trends in scores on PC1 and PC2 were indicated from linear regression (P<0.001). However, the brown and silver form charr were relatively well separated on means plots for age classes on the first two components. The oldest silver form and the youngest brown form charr were the age classes of both sexes that tended to overlap (Fig. 7A,B).

CDA results

Canonical discriminant analysis indicated that the two forms were significantly different in morphology (Wilks's $\lambda = 0.634$, $F_{15,431} = 16.6$, P<0.001). Pooled within canonical coefficients clearly showed discrimination contrast in caudal peduncle length versus pectoral fin length (Table 4). *A posteriori* classification accuracy was good; 86% and 76% of the brown and silver form charr were correctly classified respectively. Both forms showed trends of higher scores with increasing age. The 'misclassified' fish, 43 females and 45 males, were mostly young brown form and the oldest silver form fish (Fig. 8), which had overlapping shape scores in PCA (Fig. 7A,B).

TABLE 3. Difference between least-square means (LSMean) among all male and female brown and silver forms, estimated from the common within group regression lines of the variable against standard length. ANOVA tests for differences between adjusted means of brown versus silver form, among all males, five year old (5+) males, all females, five year old (5+) females, and between forms of the sexes combined

	LSMean	Males				LSMean	Females				Males and females	
	Brown–Silver	All		5+		Brown–Silver	All		5+		All	
Trait[a]		$F_{1,242}$	P	$F_{1,77}$	P		$F_{1,200}$	P	$F_{1,116}$	P	$F_{1,359}$	P
POL	0.041	18.41	<0.001	16.94	<0.001	0.029	8.50	0.004	3.23	0.074	9.93	<0.001
OOL	0.028	11.98	<0.001	0.00	0.992	0.031	12.05	<0.001	1.41	0.237	11.59	<0.001
HL	0.030	41.63	<0.001	10.54	0.002	0.012	7.09	0.008	1.34	0.249	14.47	<0.001
MXL	0.057	59.32	<0.001	18.20	<0.001	0.026	15.28	<0.001	7.77	0.006	21.44	<0.001
LJ	0.060	56.16	<0.001	12.39	<0.001	0.023	12.29	<0.001	5.49	0.020	16.19	<0.001
HDD	0.048	33.04	<0.001	5.90	0.017	0.036	32.20	<0.001	7.84	0.006	29.16	<0.001
MXW	0.066	17.94	<0.001	4.15	0.045	−0.008	0.55	0.460	1.80	0.183	6.70	0.001
IOW	0.050	48.48	<0.001	14.44	<0.001	0.046	38.77	<0.001	7.33	0.008	33.72	<0.001
PCL	0.082	111.87	<0.001	20.06	<0.001	0.053	47.72	<0.001	8.80	0.004	56.33	<0.001
PVL	0.087	90.66	<0.001	16.94	<0.001	0.049	32.77	<0.001	8.78	0.004	42.70	<0.001
ANL	0.067	55.59	<0.001	10.70	0.002	0.035	15.09	<0.001	6.92	0.010	24.40	<0.001
ANW	0.107	65.72	<0.001	2.39	0.126	0.056	27.63	<0.001	5.16	0.025	29.17	<0.001
CPL	−0.132	77.67	<0.001	3.41	0.069	−0.147	84.09	<0.001	16.21	<0.001	70.99	<0.001
CPD	0.042	30.96	<0.001	4.48	0.038	0.012	1.81	0.180	1.17	0.282	11.44	<0.001
CFL	−0.003	0.13	0.722	0.42	0.517	−0.043	18.90	<0.001	20.99	<0.001	9.15	<0.001
FLT	0.020	1.56	0.212	0.03	0.874	0.043	4.11	0.044	1.66	0.200	5.59	0.004

[a] For key to abbreviations, see caption to Fig. 2.

TABLE 4. Character loadings of the first two principal components (PC1 & 2), total canonical structure (TCS) and within standardized canonical coefficients (SCC) from canonical discriminant analysis. Data on 16 mensural characters (PCA: $n=492$; CDA: $n=446$) in Arctic charr from Vatnshlídarvatn, Iceland, size adjusted by regression technique, computation of residuals from the regression of untransformed morphological variables on standard length

Trait[a]	PC1	PC2	TCS	SCC
POL	0.699	0.272	0.326	0.004
OOL	0.242	−0.474	0.327	0.031
HL	0.768	0.181	0.399	0.030
MXL	0.865	0.133	0.473	0.003
LJ	0.833	0.155	0.410	−0.166
HDD	0.730	−0.079	0.530	0.051
MXW	0.401	0.027	0.236	0.019
IOW	0.777	−0.021	0.590	0.185
PCL	0.812	−0.017	0.735	0.537
PVL	0.831	−0.011	0.641	0.013
ANL	0.680	0.008	0.542	0.222
ANW	0.410	−0.453	0.542	0.000
CPL	−0.409	-.566	−0.790	−0.540
CPD	0.416	−0.269	0.280	−0.009
CFL	0.084	0.694	−0.327	−0.287
FLT	0.437	0.210	0.208	−0.023
Eigenvalue	6.395	1.504		0.577

[a] For key to abbreviations, see caption to Fig. 2.

Gill rakers

The silver and brown form charr differed significantly in gill raker numbers with the mean numbers of 22.2 and 23.1 respectively ($F_{2,488} = 13.3$, $P<0.001$). No significant correlations were observed between gill rakers, sex or size of either form.

Allometric slopes

Ontogenetic patterns of morphological differentiation between forms were investigated through the calculation of bivariate and multivariate allometric coefficients (Table 5). Tests were performed for statistical differences in the bivariate allometries. Differences between forms were not significant at the 0.05 level. Allometric slopes calculated from the covariance ratios were similar to the multivariate allometric slopes produced from the first PCA, as the ratio of characters with standard length (Table 5).

DISCUSSION

Growth and sexual maturation

The presence of two growth forms of Arctic charr in Vatnshlídarvatn is clear and cannot be explained by sexual dimorphism in size (Fig. 3). Furthermore, two

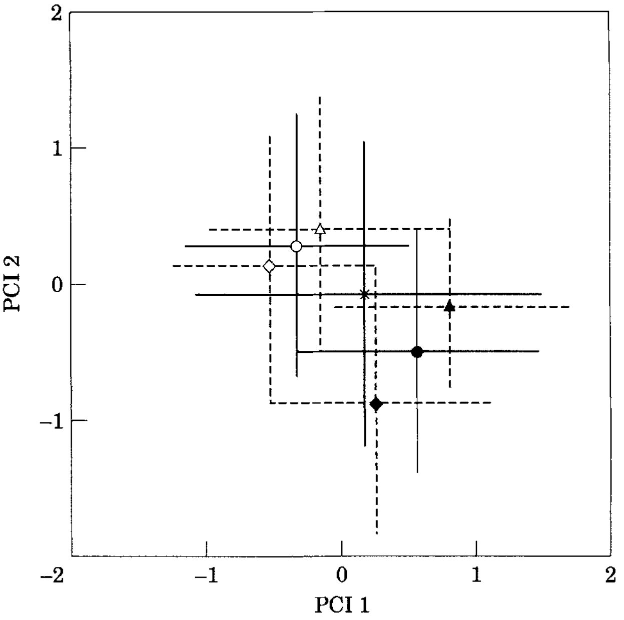

Figure 6. Plot of mean scores with standard deviations (1 SD) from between group PCAs, based on a variance–covariance matrix. Multivariate analysis of 16 mensural characters, size adjusted by regression technique, computation of residuals from the regression of untransformed morphological variables on standard length (STL). Groups are brown form (●, ◆, ▲), silver form (○, ◇, △) and unknown (×). Arctic charr from Vatnshlídarvatn, Iceland. Mean scores for sexes also shown separately on the plot: triangles, males, boxes, females.

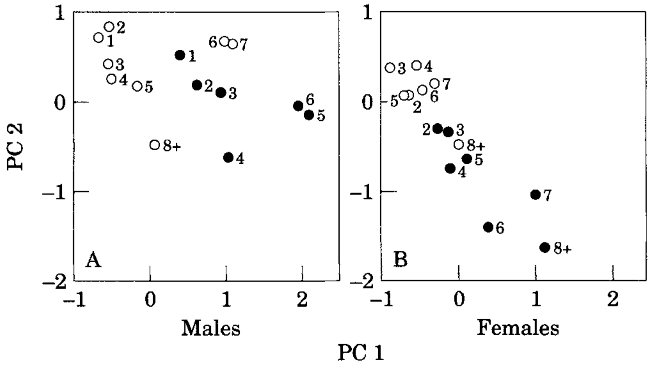

Figure 7. Plot of mean scores from between group PCAs, based on a variance–covariance matrix for (A) males and (B) females. Multivariate analysis of 16 mensural characters, size adjusted by regression technique, computation of residuals from the regression of untransformed morphological variables on standard length (STL). Means for age groups of male and female Arctic charr from Vatnshlídarvatn, Iceland. Brown form (●), silver form (○). Numerals indicate age of fish from 1 to 7 years; 8+ denotes fish eight years and older combined.

alternative maturation strategies are present among the Arctic charr; the brown form becomes sexually mature at a young age and small size, while the silver form reaches maturity at an older age and larger size (Figs 3 and 4).

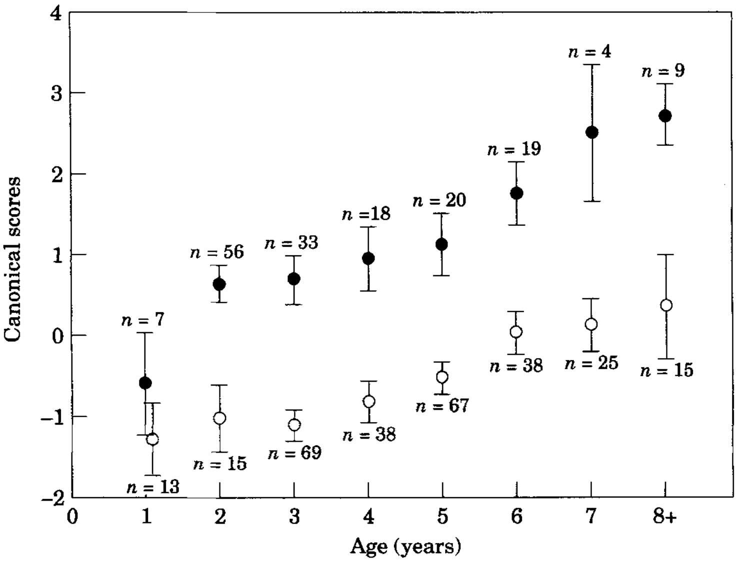

Figure 8. Plot of means and 95% confidence intervals of scores from canonical discriminant analysis of brown and silver form Arctic charr from Vatnshlidarvatn, Iceland. Multivariate analysis of 16 mensural characters, size adjusted by regression technique, computation of residuals from the regression of untransformed morphological variables on standard length (STL). Brown form (●), silver form (○).

Table 5. Bivariate and multivariate allometric coefficients of 16 mensural characters in Arctic charr from Vatnshlídarvatn, Iceland. Bivariate slopes calculated as covariance ratio, HL, head length, as third variable (PCL, pectoral fin length used as third variable for HL). Multivariate slopes calculated as first component loadings (PC1) of log-transformed data from within group PCAs (sex and form separately), based on a variance–covariance matrix, divided by the loading for STL, standard length

	Bivariate slopes				Multivariate slopes			
Trait[a]	BM	SM	BF	SF	BM	SM	BF	SF
POL	1.18	1.11	1.19	1.14	1.19	1.11	1.21	1.14
OOL	0.61	0.64	0.66	0.59	0.61	0.64	0.66	0.59
HL	0.98	0.96	0.92	0.97	0.97	0.96	0.92	0.97
MXL	1.19	1.09	1.12	1.09	1.19	1.09	1.12	1.09
LJ	1.20	1.13	1.13	1.11	1.20	1.14	1.13	1.11
HDD	1.04	0.98	1.03	1.02	1.04	0.99	1.03	1.02
MXW	1.00	0.95	0.89	0.90	1.05	0.96	0.90	0.91
IOW	1.10	1.05	1.05	1.09	1.09	1.05	1.05	1.09
PCL	1.07	1.02	1.01	1.02	1.07	1.03	1.02	1.03
PVL	1.10	1.01	1.03	1.00	1.11	1.01	1.04	1.01
ANL	1.10	1.00	1.08	1.02	1.11	1.01	1.10	1.03
ANW	1.15	1.13	1.07	1.07	1.15	1.14	1.09	1.10
CPL	0.99	0.98	0.84	0.93	1.01	0.97	0.89	0.95
CPD	1.02	1.01	0.91	1.05	1.01	1.01	0.91	1.05
CFL	0.95	0.95	0.73	0.92	0.95	0.96	0.75	0.93
FLT	0.91	0.78	1.05	1.05	0.95	0.91	1.16	1.12

[a] For key to abbreviations, see caption to Fig. 2.

BM = brown males; SM = silver males; BF = brown females; SF-silver females.

Diet

Arctic charr in Vatnshlídarvatn are benthic feeders with little zooplankton in the diet. This is evident from diet analysis (Fig. 5), and is supported by inspection of parasites in the diet (Jónsson, 1996). Both forms converge on feeding on the benthic crustacean, *Eurycercus* sp. when it is superabundant (August sample), and segregation is only important when that food resource is scarce (July sample), and competition between forms presumably high (Liem & Kaufman, 1984). The forms have similar diets, but the brown form forages almost exclusively on *Eurycercus* sp., while the silver form includes various other prey in its diet, most importantly the mollusc *Pisidium* sp. (Fig. 5, Tables 1 and 2). Analysing diet in terms of volume rather than frequency would amplify the differences in diet between charr forms, as *Pisidium* sp. are relatively large food items compared to *Eurycercus* sp. The forms appear to maintain their segregation by different feeding strategies, where the more variable diet of the silver compared to the brown form might relate to greater behavioural plasticity of the former. The presence of one abundant food resource – *Eurycercus* sp. – and lack of interspecific competition may provide the opportunity for the evolution of one feeding specialist, the brown form. The various other food items available may then be utilized by a second form, the silver form, that has more generalized feeding habits. Coexistence is then made possible by adaptive switching behaviour of the generalist, which in turn decreases temporal variation in habitat availability experienced by the specialist (Wilson & Yoshimura, 1994).

Day *et al.* (1994) found that variable diet of a limnetic threespined stickleback form was related to relatively high morphological plasticity, compared to a sympatric benthic form with more diet specialization. Griffiths (1994) reviewed the literature on bimodal size distribution among Arctic charr populations. His data indicate that the existence of larger forms is based on more variable food selection than exhibited by the coexisting smaller form. This is in agreement with our results, where it is also evident that differences in diet cannot be explained by size difference between the forms. Further, these different feeding strategies appear to be developed early in life (Tables 1 and 2), indicating that differences in early behaviour may be important in enhancing segregation.

Ontogeny of morphological segregation

The study supports the hypothesis that Arctic charr in Vatnshlídarvatn constitute two different forms. All the morphometric methods employed indicate similar trends in morphological segregation (Tables 3 and 4). The silver form has a elongated and fusiform body, while the brown form has a stocky body and relatively long paired fins. This dimorphism is not dependent on fish size, sex, age or state of maturity. The segregation between forms is independently reinstated by the brown form having significantly more gill rakers than the silver form. Age trends in morphometric data (Figs 7 and 8), and similarities in ontogenetic slopes between forms (Table 5), indicate that evolutionary changes in the timing of early ontogenetic events, heterochrony, are responsible for the morphological differentiation between the Arctic charr forms. Heterochronic change could be an evolutionary response to enhance the scope of resource utilization experienced by the charr, hence increasing the biomass of fish in the lake. The ontogenetic changes in shape might further decrease resource competition between individuals and age classes that can differ both in size and shape (Robinson & Wilson, 1994). The results are in agreement with Strauss (1990) that larval ontogenetic characters should be emphasized along with static adult traits, when studying evolutionary segregation in fish. The importance of such early differentiation has been underlined for Arctic charr forms from Thingvallavatn (Skúlason *et al.*, 1989). The age effects in this study highlight the importance of considering age in morphological studies in the future.

Functional significance of morphological divergence

The divergences in head morphology among Arctic charr forms in Thingvallavatn (Snorrason *et al.*, 1994) and Loch Rannoch (Gardner *et al.*, 1988) are among the best documented cases of morphological segregation in sympatric forms of salmonids. The forms in the present study show morphological divergence more related to swimming performance and manœuvrability than direct trophic features. The stocky body, relatively long paired fins and short caudal penduncle of the brown form (Table 3) are all characters allowing for greater manœuvrability, important for selective feeding (Stoner & Livingstone, 1984; Toline & Baker, 1993). Slimmer bodies and longer caudal regions should enhance swimming and speed performance in the silver form (Taylor & Foote, 1991), compared to the brown form. Similar pattern of morphological segregation has been observed between sympatric Arctic charr forms in Lake Hazen, Ellesmere Island (Reist *et al.*, 1995), between sockeye salmon and kokanee *Oncorhynchus nerka* W. (Taylor & Foote, 1991), and between allopatric anadromous and resident Arctic charr in Norway (Damsgård, 1991). Thus this mode of morphological diversification might be more pervasive throughout the Salmonidae than previously noted.

Explanations for polymorphism

The shape of the silver form bears resemblance to that of anadromous salmonids. During smolting, fish become silvery and develop elongated and fusiform bodies (Birt & Green, 1986; Damsgård, 1991). Historically, landlocked Arctic charr can exhibit basic smolting characteristics (Klemetsen & Grotnes, 1980; Schmitz, 1992), although less so than ancestral anadromous charr (Staurnes *et al.*, 1992). The silver form in Vatnshlídarvatn could be displaying remnants of smolt transformation, while the brown form is not. Smoltification is known to trigger often adaptive migratory shifts between habitats (Schmitz, 1992), while in other instances it can be seen as an energetically intensive process no longer relevant in the life history of non-anadromous fish (Birt & Green, 1986), and thus could be selected against (Foote, Wood & Withler, 1989). Juveniles of the silver form migrate from adjacent creeks into the lake at one (the outlet) and two years of age (the inlets), where they return later to spawn, while the brown form mostly moves short distances between habitats in the lake itself (Jónsson, 1996). A similar phenomenon has been observed in Thingvallavatn, Iceland, where the juveniles of the two benthic forms continue to occupy the littoral nursery habitat, while the limnetic forms leave the benthic habitat, probably early in life, and then return later to spawn (Skúlason, Snorrason & Jónsson, 1999; Sandlund *et al.*, 1987). The Arctic charr forms in Vatnshlídarvatn as well as Thingvallavatn might thus be displaying alternative adaptive strategies. According to this, the brown form and the benthic forms from Thingvallavatn have been undergoing rapid evolutionary departure from anadromy coupled with residency, early sexual maturation, stockier body (for Thingvallavatn see Snorrason *et al.*, 1994), and sacrifice of cruising ability for greater manœuvrability (the brown form), while the silver form and the limnetic forms in Thingvallavatn have conserved the ancestral anadromous characteristics, inducing the development of fusiform body and migratory habitat shifts. Such differences in rates of specialization could also be at least partly due to the brown form and the benthic forms in Thingvallavatn having shorter generation time than the silver form and the limnetic forms in Thingvallavatn.

This is the first report of morphological segregation of a salmonid species in a small and shallow landlocked lake which is not related to cannibalism. Further, diet analysis indicates that both Artic charr forms in Vatnshlídarvatn are mainly feeding on benthic invertebrates, showing segregation when food is limiting and interspecific competition presumably high (Fig. 5; Tables 1 and 2). Polymorphism in northern freshwater fish has most often been observed in lakes with discrete benthic and pelagic habitats resulting in ecological segregation of forms into benthivory and planktivory (Skúlason & Smith, 1995). Piscivory (including cannibalism), and anadromy versus residency are also commonly encountered (Griffiths, 1994; Reist *et al.*, 1995; Smith & Skúlason, 1996). None of this holds for the polymorphism observed in Vatnshlídarvatn. The Arctic charr forms in Vatnshlídarvatn exhibit resource polymorphism in the absence of ecological conditions generally thought to be necessary for its maintainance. Despite the apparent absence of discrete benthic and limnetic habitats, two forms are found in the lake. These forms show some spatial and temporal segregation in spawning (Jónsson, 1996). Gíslason (1998) in a molecular genetic study confirms that the forms are to some extent reproductively isolated (Nei's genetic distance = 0.053). Further, Gíslason (1998) studying sympatric Arctic charr forms in five Icelandic lakes, including Vatnshlídarvatn, demonstrates repeated intralacustrine origin and divergence of sympatric Arctic charr in these lakes. The forms in Vatnshlídarvatn show subtle differences in morphology related to swimming performance and manœuvrability, but differences in life history are more pronounced. Both forms have benthic feeding habits with the silver form consuming a greater variety of species than the brown form. This is independent of size differences between forms.

We suggest that the segregation of these forms is based on the evolution of a specialist (brown form) from a local generalist (silver form) which resembles the anadromous ancestor that invaded the lake, and that this has been made possible by the absence of a common fish competitor in similar Icelandic lakes, the threespined stickleback *Gasterosteous aculeatus*. We suggest that the specialization of the brown form has been accompanied by evolutionary loss of phenotypic plasticity.

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REFERENCES

Adalsteinsson H. 1979. Zooplankton and its relation to available food in Lake Mývatn. *Oikos* **32:** 162–194.

Adams CA, Fraser D, Huntingford FA, Greer RB, Askiew CM, Walker AF. 1998. Trophic polymorphism amongst Arctic charr from Loch Rannoch, Scotland. *Journal of Fish Biology* **52:** 1259–1271.

Barber WA, McFarlane GA. 1987. Evaluation of three techniques to age Arctic char from Alaskan and Canadian waters. *Transactions of the American Fisheries Society* **116:** 874–881.

Birt TB, Green JM. 1986. Par–smolt transformation in female and sexually mature male anadromous and nonanadromous Atlantic salmon, *Salmo salar. Canadian Journal of Fisheries and Aquatic Sciences* **43:** 680–686.

Dahl K. 1917. Studier and Forsök over örret og örretvand. Kristiania: Centraltrykkeriet (Studies on trout and trout-lakes). [In Norwegian].

Damsgård B. 1991. Smolting characters in anadromous and resident Arctic charr, *Salvelinus alpinus* (L.). *Journal of Fish Biology* **39:** 765–774.

Day T, Pritchard J, Schluter D. 1994. A comparison of two sticklebacks. *Evolution* **48:** 1723–1734.

Echelle AA, Kornfield I, eds. 1984. *Evolution of Fish Species Flocks.* Orono: University of Maine Press.

Foote CJ, Wood CC, Withler RE. 1989. Biochemical genetic comparison of sockeye and kokanee, the anadromous and non-anadromous forms of *Oncorhynchus nerka. Canadian Journal of Fisheries and Aquatic Sciences* **46:** 149–158.

Gíslason D. 1990. Genetic and morphological variation in polymorphic arctic charr, *Salvelinus alpinus*, from Icelandic lakes. Unpublished Masters thesis University of Guelph.

Griffiths D. 1994. The size structure of lacustrine Arctic charr (Pisces: Salmonidae) populations. *Biological Journal of the Linnean Society* **51:** 337–357.

Hindar K, Jonsson B. 1982. Habitat and food segregation of dwarf and normal Arctic charr (*Salvelinus alpinus*) from Vangsvatnet lake, Western Norway. *Canadian Journal of Fisheries and Aquatic Sciences* **39:** 1030–1045.

Hindar K, Jonsson B. 1993. Ecological polymorphism in Arctic charr. *Biological Journal of the Linnean Society* **48:** 63–74.

Hindar K, Ryman N, Ståhl G. 1986. Generic differentiation among local populations and morphotypes of Arctic charr, *Salvelinus alpinus. Biological Journal of the Linnean Society* **27:** 269–285.

Johnson L. 1983. Homeostatic characteristics of single species fish stocks in arctic lakes. *Canadian Journal of Fisheries and Aquatic Sciences* **40:** 987–1024.

Jolicoeur P. 1963. The multivariate generalization of the allometry equation. *Biometrics* **19:** 497–499.

Jonsson B, Hindar K. 1982. Reproductive strategy of dwarf and normal Arctic charr (*Salvelinus alpinus*) from Vangsvatnet lake Western Norway. *Canadian Journal of Fisheries and Aquatic Sciences* **39:** 1404–1413.

Jónsson B. 1996. Polymorphic segregation in Arctic charr *Salvelinus alpinus* (L.) from lake Vatnshlíd-arvatn, Northern Iceland. Unpublished Masters thesis, Oregon State University.

Klemetsen A, Grotnes PE. 1980. Coexistence and immigration of two sympatric Arctic charr. In: Balon EK, ed. *Charrs, salmonid fishes of the genus Salvelinus.* The Hague: Dr. W. Junk, 757–219.

Kuhry B, Marcus LF. 1977. Bivariate linear models in biometry. *Systemic Zoology* **26:** 201–209.

Liem KF, Kaufman LS. 1984. Intraspecific macroevolution: functional biology of the polymorphic cichlid species *Cichlasoma minckleyi.* In: Echelle AA, Kornfield I, eds. *Evolution of fish species flocks.* Orono: University of Maine Press, 203–215.

Ludwig JA, Reynolds JF. 1988. *Statistical ecology. A primer on methods and computing.* New York: Wiley.

Malmquist HJ, Snorrason SS, Skúlason S, Jonsson B, Sandlund OT, Jónasson PM. 1992. Diet differentiation in polymorphic Arctic charr in Thingvallavatn Iceland. *Journal of Animal Ecology* **61:** 21–34.

Nordeng H. 1983. Solution to the 'char problem' based on Arctic char (*Salvelinus alpinus*) in Norway. *Canadian Journal of Fisheries and Aquatic Sciences* **40:** 1372–1387.

Nyman L, Hamar J, Gydemo R. 1981. The systematics and biology of landlocked populations of Arctic char from Northern Europe. *Institute of Freshwater Research Drottningholm, Report* **59:** 128–41.

Pimentel RA. 1979. *Morphometrics.* Iowa: Kendal/Hunt Publishing Company.

Reist JD. 1985. An empirical evaluation of several univariate methods that adjust for size variation in morphometric data. *Canadian Journal of Zoology* **63:** 1429–1439.

Reist JD, Gyselman E, Babaluk JA, Johnson JD, Wissink R. 1995. Evidence for two morphotypes of Arctic char (*Salvelinus alpinus* (L.)) from Lake Hazen, Ellesmere Island, Northwest Territories, Canada. *Nordic Journal of Freshwater Research* **71:** 396–410.

Robinson BW, Wilson DS, Margosian AS, Lotito PT. 1993. Ecological and morphological differentiation of pumpkinseed sunfish in lakes without bluegill sunfish. *Evolutionary Ecology* **7:** 451–464.

Robinson BW, Wilson DS. 1994. Character release and displacement in fishes, a neglected literature. *American Naturalist* **144:** 596–627.

Sandlund OT, Jónsson B, Malmquist HJ, Gydemo R, Lindem T, Skúlason S, Snorrason SS, Jonasson PM. 1987. Habitat use of Arctic charr *Salvelinus alpinus* in Thingvallavatn, Iceland. *Environmental Biology of Fishes* **20:** 263–274.

Schluter D. 1988. Character displacement and the adaptive divergence of finches on islands and continents. *The American Naturalist* **131:** 799–824.

Schluter D, McPhail JD. 1992. Ecological character displacement and speciation in sticklebacks. *The American Naturalist* **140:** 85–108.

Schmitz M. 1992. Annual variations in rheotactic behavior and seawater adaptability in landlocked Arctic char (*Salvelinus alpinus*). *Canadian Journal of Fisheries and Aquatic Science* **49:** 448–452.

Shea BT. 1985. Bivariate and multivariate growth allometry: statistical and biological considerations. *Journal of Zoology London* (A) **206:** 367–390.

Skúlason S, Antonsson T, Gudbergsson G, Malmquist HJ, Snorrason SS. 1992. Variability in Icelandic Arctic charr. *Icelandic Agricultural Science* **6:** 143–153.

Skúlason S, Noakes DLG, Snorrason SS. 1989. Ontogeny of trophic morphology in four sympatric morphs of Arctic charr *Salvelinus alpinus* in Thingvallavatn, Iceland. *Biological Journal of the Linnean Society* **38:** 281–301.

Skúlason S, Smith TB. 1995. Resource polymorphism in vertebrates. *Tree* **10:** 347–388.

Skúlason S, Snorrason SS, Jónsson B. 1999. Sympatric morphs, populations and speciation in freshwater fish with emphasis on Arctic charr. In: Magurran AE, May R, eds. *Evolution of Biological Diversity.* Oxford: Oxford University Press.

Smith TB. 1993. Disruptive selection and the genetic basis of bill size polymorphism in the African finch *Pyrenestes*. *Nature* **363:** 618–620.

Smith TB, Skúlason S. 1996. Evolutionary significance of resource polymorphisms in fishes, amphibians, and birds. *Annual Review of Ecology and Systematics* **27:** 111–133.

Snorrason SS, Skúlason S, Jónsson B, Malmquist HJ, Jónasson PM, Sandlund OT, Lindem T. 1994. Trophic specialization in Arctic charr *Salvelinus alpinus* (Pisces; Salmonidae): morphological divergence and ontogenetic niche shifts. *Biological Journal of the Linnean Society* **52:** 1–18.

Sokal RR, Rohlf FJ. 1981. *Biometry.* New York: W.H. Freeman and Co.

Sparholt H. 1985. The population, survival, growth, reproduction and food of Arctic charr, *Salvelinus alpinus* (L.), in four unexploited lakes in Greenland. *Journal of Fish Biology* **26:** 313–330.

Staurnes M, Sigholt T, Lyssfjord G, Gulseth OA. 1992. Difference in the seawater tolerance of anadromous and landlocked populations of Arctic char (*Salvelinus alpinus*). *Canadian Journal of Fisheries and Aquatic Sciences* **49:** 443–447.

Stoner AW, Lvingstone RJ. 1984. Ontogenetic patterns in diet and feeding morphology in sympatric sparid fishes from seagrass meadows. *Copeia* **1984** (1): 174–187.

Strauss RE, Fuiman LA. 1985. Quantitative comparisons of body form and allometry in larval and adult Pacific sculpins (Teleostei: Cottidae). *Canadian Journal of Zoology* **63:** 1582–1589.

Strauss RE. 1990. Heterochronic variation in the developmental timing of cranial ossifications in poeciliid fishes (Cyprinodontiformes). *Evolution* **44:** 1558–1567.

Svedäng H. 1990. Genetic basis of life-history variation of dwarf and normal Arctic charr, *Salvelinus alpinus* (L.), in Stora Rösjön, central Sweden. *Journal of Fish Biology* **36:** 917–932.

Taylor EB, Foote CJ. 1991. Critical swimming velocities of juvenile sockeye salmon and kokanee, the anadromous and non-anadromous forms of *Oncorhynchus nerka* (Walbaum). *Journal of Fish Biology* **38:** 407–419.

Toline CA, Baker AJ. 1993. Foraging tactic as a potential selection pressure influencing geographic differences in body shape among populations of dace (*Phoxinus eos*). *Canadian Journal of Zoology* **71:** 2178–2184.

Tómasson T. 1987 *unpublished.* The connection between growth and size at sexual maturity in Icelandic Arctic charr (*Salvelinus alpinus*). A paper prepared for the International conference on alternative life history styles of fishes and other organisms. Grahamstown, South Africa.

Wilson DS, Yoshimura J. 1994. On the coexistence of specialists and generalists. *The American Naturalist* **144:** 692–707.