



## Relationships between lake ecology and morphological characters in Icelandic Arctic charr, *Salvelinus alpinus*

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The common occurrence of parallel phenotypic patterns suggests that a strong relationship exists between ecological dynamics and micro-evolution. Comparative studies from a large number of populations under varying sets of ecological drivers could contribute to a better understanding of this relationship. We used data on morphology of arctic charr (*Salvelinus alpinus*) and ecological factors from 35 Icelandic lakes to test the hypothesis that morphological patterns among monomorphic charr populations from different lakes are related to interlake variation in ecological characteristics. There is extensive phenotypic diversity among populations of Icelandic charr, and populations are easily distinguished based on overall body morphology. The results obtained in the present study showed that the morphological diversity of charr was related to large-scale diversity in lake ecology. Variation in charr morphology was related to water origin (e.g. spring fed versus run-off), bedrock age, and fish community structure. The present study shows how various ecological factors can shape the biological diversity that we observe. © 2011 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2011, 103, 761–771.

**ADDITIONAL KEYWORDS:** adaptation – biodiversity – ESIL project – fish diversity – limnology – micro-evolution – morphometrics – natural selection – phenotypic plasticity.

### INTRODUCTION

Biological diversity is commonly equated with species diversity, which is a misconception because diversity does occur at multiple levels, including intraspecific diversity. Intraspecific phenotypic diversity is the product of genes and the environment and the interaction of these factors. Intraspecific biological diversity is influenced by evolutionary history among populations and species, which results in differences in phenotypes, even though they are found in similar environments (Langerhans & DeWitt, 2004). However, species or population may show morphological adaptations as a reaction to differences in the environment through phenotypic plasticity or through local adaptation by natural selection. Both processes

would result in parallel patterns in phenotypes under similar environmental conditions (Nagel *et al.*, 1998; Schluter, 2000; Schluter *et al.*, 2004).

An important factor of adaptive radiation and parallel evolution is the relationship between particular phenotype and specific niche, often referred to as phenotype–environment correlation (Schluter, 2000). Most commonly, this has been observed where feeding structure and behaviour is correlated with a specific diet niche (Wimberger, 1994; Schluter, 2000; Price, 2008). For example, this can be clearly seen in the divergence of beak morphology of Darwin's ground finches (*Geospiza* spp.), where beak morphology and feeding behaviour can be related to feeding on specific seeds (Grant, 1999). An example of this is the evolution of sympatric benthic/limnetic morphs seen in the adaptive radiation of Northern freshwater of fishes (Skúlason, Snorrason & Jónsson, 1999; Robinson & Schluter, 2000; Schluter, 2000).

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Parallel evolution and phenotype–environment correlations have been exclusively studied in sympatric populations. However, do ecological factors, through local adaptation, shape phenotypic diversity of monomorphic populations in a similar way as that observed among sympatric populations? Reimchen & Nosil (2006) compared 40 populations of freshwater threespine stickleback (*Gasterosteus aculeatus*) from British Columbia, Canada, and found that morphology of sticklebacks could be related to their habitats. Sticklebacks in smaller lakes or ponds had less defence structure and more ‘benthic’ trophic morphology than stickleback in larger lakes. Comparing populations and their habitats can provide valuable information on the ecological drivers of repeated evolutionary trajectories. However, this can be difficult to examine in complex ecosystems. Thus, studies on relatively simple ecosystems, such as areas that have recently become available or isolated islands, can prove valuable in this respect.

Northern freshwater systems are relatively young and have only been accessible to fishes since the end of the last glaciation, approximately 10 000 years ago (Skúlason *et al.*, 1999; Snorrason & Skúlason, 2004). These systems are generally species poor and colonizing fish species have been presented with a diversity of vacant niches. Thus, they have evolved great intraspecific diversity, where phenotypically similar morphs or species are often found to occupy similar niches in different lakes (Skúlason *et al.*, 1992; Snorrason & Skúlason, 2004). This has been observed in many unrelated fish species, including salmonids (*Salmo*, *Oncorhynchus* and *Salvelinus* spp.), sunfish (*Lepomis* spp.), smelt (*Osmerus* spp.), whitefish (*Prospium*, *Coregonus* spp.), and threespine stickleback (Wimberger, 1994; Skúlason *et al.*, 1999; Robinson & Schluter, 2000) Arctic charr (*Salvelinus alpinus*) offer great opportunities for comparative studies on ecological divergence. The species is widespread in lakes and rivers and occupies a range of different habitats (Klemetsen, 2010). Arctic charr have long been recognized for their extensive phenotypic variation and lakes that host sympatric morphs, frequently limnetic (planktonic and fish eating) versus benthic feeders, are relatively common throughout their range of distribution (Skúlason *et al.*, 1992, 1999; Snorrason & Skúlason, 2004; Klemetsen, 2010). Such morphs have been most extensively studied in Loch Rannoch, Scotland (Adams *et al.*, 1998), Fjellfröstvatn, Norway (Knudsen *et al.*, 2006), and Thingvallavatn, Iceland (Skúlason *et al.*, 1989a; Skúlason, Noakes & Snorrason, 1989b). In Thingvallavatn, four morphs of charr have been observed, and sympatric morphs have been documented in numerous other Icelandic lakes (Skúlason *et al.*, 1992). Phenotypic diversity among allopatric charr populations

is also extensive in Iceland (Skúlason *et al.*, 1992). A striking aspect of this diversity is the common occurrence of small benthic charr, associated with lava and groundwater spring habitats (Sigursteinsdóttir & Kristjánsson, 2005; Kristjánsson, 2008, Klemetsen, 2010). Genetic studies suggest that Icelandic Arctic charr populations, both sympatric and allopatric, have evolved independently, and that genetic mixing of populations after colonization has been limited (Gíslason *et al.*, 1999; Wilson *et al.*, 2004; Kapralova *et al.*, 2011). This offers important opportunity to study the effects of local ecology on evolutionary patterns and processes.

It has been suggested that the great diversity of Icelandic Arctic charr can be related to the diversity of freshwater habitats in Iceland (Malmquist *et al.*, 1992; Skúlason *et al.*, 1999; Snorrason & Skúlason, 2004), which can be linked to geological, hydrological, and geochemical features of the island (Garðarsson, 1979; Malmquist *et al.*, 2000; Karst-Riddoch, Malmquist & Smol, 2009). Long-term ‘plate-forming’ tectonic activity has created an age gradient in the bedrock of Iceland. The youngest rocks are within the active neo-volcanic zone, sometimes being only a few months old, whereas the oldest rocks (10–16 million years old) are furthest to the west and east (Pétursson & Jónsson, 2004) (Fig. 1). Older bedrock areas have been shaped by glaciers, are relatively impermeable to water, and are dominated by direct run-off water bodies, characterized by a variable water regime and temperature and low concentrations of nutrients (Garðarsson, 1979; Malmquist *et al.*, 2000; Karst-Riddoch *et al.*, 2009). The neo-volcanic zone is, however, characterized by post-glacial lava fields. This bedrock is porous, which makes it rich in groundwater and springs are common. Spring-fed water bodies are characterized by a relatively stable water regime and temperature and also are rich in nutrients (Cantonati, Gerecke & Bertuzzi, 2006; Karst-Riddoch *et al.*, 2009). Furthermore, lava provides a complex three-dimensional substrate, creating unique benthic habitats for fishes. Thus, invertebrates and fish have extensive hiding places and are often found in high densities (Sandlund *et al.*, 1992; Snorrason *et al.*, 1994; Malmquist *et al.*, 2000; Kristjánsson, 2008).

Despite the geographic diversity of Icelandic freshwater systems, their biological communities are relatively simple. The short time since glaciation, together with geographic isolation, may explain why only six freshwater fish species are found on the island (Sæmundsson, 1926; Albert, Jónsson & Bernatchez, 2006). Arctic charr was one of the first fish species to colonize water bodies in Iceland, which took place rapidly after the ice retreated (Wilson *et al.*, 2004; Kapralova *et al.*, 2011). In many drainage systems, charr must have colonized before isostatic



**Figure 1.** Lakes sampled in a study on the relationship between ecological characters and the morphology of monomorphic Arctic charr populations. The greyscale image shows the age of the bedrock; light grey, furthest to east and west upper Tertiary (> 3.3 Myr); mid-grey, upper Pliocene and lower Pleistocene (0.8–3.3 Myr); dark grey, upper Pleistocene (0.01–0.8 Myr); and darkest (nearest to the center), postglacial (0–0.01 Myr).

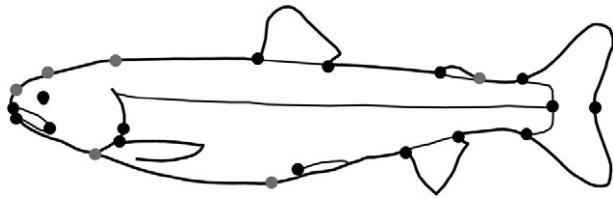
rebound and the formation of waterfalls closed off inland habitats from fish passage. The apparent colonization histories have resulted in a variable species composition in Icelandic lakes, which could have profound effect on lake ecology.

In general, ecological drivers of parallel evolution among animal species are not well documented. These factors are not easily approached by experimental studies and comparative studies require data from a large number of populations. Icelandic Arctic charr populations are ideal for such a study because numerous populations are easily accessible and data on ecological factors in their respective habitats have already been collected by The Ecological Survey of Icelandic Lakes (ESIL Project) (Malmquist *et al.*, 2000; Karst-Riddoch *et al.*, 2009). This project has created a comprehensive database that includes the chemical and physiological characteristics of lakes, invertebrate species numbers, and densities in pelagic and benthic habitats, as well as biological

information on fish populations. The ESIL database provides considerable analytical power for assessing the relationship between phenotypic diversity of Arctic charr and the ecological and physical factors of their habitat. In the present study, we test the hypothesis that morphological patterns among monomorphic Arctic charr populations from different lakes in Iceland are related to interlake variation in ecological characteristics.

## MATERIAL AND METHODS

The lakes in the present study were all included in the ESIL Project. Detailed information on the sampling in the ESIL Project is given by Jónsdóttir *et al.* (1998), Malmquist *et al.* (2000) and Karst-Riddoch *et al.* (2009). For the present study, it was necessary to identify lakes that had monomorphic charr populations. This was carried out by examining published records of charr in Iceland, by talking to fisheries



**Figure 2.** Landmarks digitized on the left side of Arctic charr in the present study. Five landmarks were sliding landmarks, shown in grey.

specialists, and by examination of the age and length relationships in relation to sexual maturation, photographs of fish, and differences in diet among fish in those lakes that did not have records of morphs. In the present study, we used only lakes where there were clear indications of only one morph. Out of the 59 lakes surveyed by the ESIL project, we used 35 lakes for the analysis (Fig. 1) because other lakes either had too small sample size or appeared to have more than one morph (18 lakes). For each lake, either all the Arctic charr, or a random sample from the catch to obtain a minimum of 30 fish, were used for further study. Each fish was photographed in the field (on the left side), using a film camera (a few different models were used), under natural light conditions. Fork length (to the nearest 0.1 cm) and wet weight (to the nearest 0.5 g) were measured for all fish and stomach contents were preserved for diet analysis. Otoliths were removed for age determination, and fish were dissected to determine sex and gonad maturation status. Stomach contents were stored in 5% buffered formalin for subsequent identification and analysis.

Photographs of fish were scanned in high resolution (Epson Perfection V700 Photo; Bergvík). Using the TPSDIG software (developed by F. James Rohlf; <http://life.bio.sunysb.edu/morph>), 22 landmarks were marked on each digital image. Six of these landmarks were sliding landmarks, and the remainder were fixed landmarks (Fig. 2). The sliding landmarks comprise landmarks that are allowed to slide to the left or right along a curve to minimize the shape change between the procrustes average of all the specimens and each specimen. Before analyzing morphology, caudal up and down bending of specimens was corrected for using the 'unbend' module in TPSUTIL software. The software creates a line between landmarks on the snout, at the end of caudal peduncle, and in the fork of the caudal fin. When the fish are bent, this line is curved. The procedure recalculates the position of landmarks on each fish so that the line is straightened. Relative warp analysis in TPS-RELW was used to analyze differences in morphology, at the same time as controlling for geometric body size. This analysis scales the landmarks from each fish to a centroid configuration (mean shape), position, and

rotation. The software then defines principal warps from the centroid configuration, which are axes along which shape variation can occur. Partial warps and two uniform components are then calculated and include a score for each fish (weight matrix) that describes the realized amount of bending and stretching necessary for the configuration of an individual to fit the centroid configuration. The weight matrix was used in further analyses. TPSREGR and TPSSPLINE were used to visualize morphological changes.

Data on ecological characters in each lake were obtained from the ESIL project (Malmquist *et al.*, 2000; Karst-Riddoch *et al.*, 2009). Lakes were classified into four groups (water origin, bedrock, salmonid community, stickleback presence) based on noncontinuous variables. The first group was based on the origin of the water, where 1 indicates spring fed, 2 indicates direct run off, 3 indicates a mixture of 1 and 2, and 4 indicates coastal. The second group was based on the age of predominant bedrock in the lake catchments, where 1 indicates historic [ $< 0.0011$  Myr], 2 indicates postglacial (0.0011–0.01 Myr), 3 indicates upper Pleistocene (0.01–0.8 Myr), 4 indicates upper Pliocene and lower Pleistocene (0.8–3.3 Myr), and 5 indicates Upper Tertiary ( $> 3.3$  Myr). The third group was based on the diversity of salmonids in each lake where category 1 indicates lakes with only Arctic charr, 2 indicates lakes with Arctic charr and brown trout, and 3 indicates lakes with Arctic charr, brown trout and Atlantic salmon. The fourth group was lakes with or without sticklebacks. Information of continuous variables expressing physical characters of each lake were also used (Table 1).

Discriminant function analysis (DFA) on the weight matrix was used to determine whether fish could be sorted based on the lake of their origin. We also used DFA to determine whether fish from different lake groups could be separated. Multivariate analysis of variance (MANOVA) on the weight matrix was used to determine whether there were morphological differences among Arctic charr coming from different lake groups (see above). The average morphology within each population was calculated from the weight matrix and the distribution of populations was examined using nonmetric scaling (NMS) (Kruskal, 1964), applying Sørensen distance measure and random starting configuration, in the software PCORD 5 (McCune & Mefford, 2006). The numbers of axis were not pre-assigned but allocated by the software based on calculated stress and instability. The software ran the analysis 50 times using the dataset and 50 times with random data from the dataset. Environmental variables were correlated to the NMS ordination axes using Pearson correlation and overlaid on the ordination plots.

**Table 1.** Averages of physical factors in 35 Icelandic lakes housing a single morph of Arctic charr

Population	Precipitation (mm)	Mean annual temperature (°C)	Altitude (m)	Surface area (km <sup>2</sup> )	Mean depth (m)	Maximum depth (m)	Volume (m <sup>3</sup> )	Catch per unit effort	Water temperature (°C)	Conductivity (µs cm <sup>-1</sup> )
Apavatn	1117.3	3.6	59	13.6	1.5	2.5	20.0	0.03	11.2	83
Amarvatn	483.2	1.8	540	3.9	1.0	3.0	3.9	0.02	7.6	64
Ánavatn	527.6	0.7	521	4.9	6.0	24.0	29.0	0.02	11.2	62
Ásbjarnarvatn	727.4	-1.1	770	0.5	0.7	2.0	0.3	0.14	8.7	79
Eiðavatn	617.9	3.0	32	1.2	4.0	10.0	5.0	0.03	13.8	64
Ellihöavatn	798.8	4.3	73	1.8	1.0	2.7	2.0	0.05	10.9	91
Eyrarvatn	889.6	3.2	75	0.8	3.4	12.5	2.8	0.07	12.2	56
Frostastaðavatn	727.4	-1.1	570	2.6	4.5	11.0	11.5	0.01	10.6	70
Geitabergsvatn	889.6	3.2	79	0.9	9.4	21.0	8.2	0.02	11.5	51
Gíslholtsvatn	889.6	3.2	65	1.4	6.6	24.0	9.0	0.07	11.6	64
Glammsstaðavatn	617.9	3.0	77	0.5	5.0	17.5	2.3	0.07	10.7	25
Heiðarvatn	744.9	3.0	585	7.6	8.8	24.0	67.0	0.03	12.4	56
Hítarvatn	1372.6	4.1	147	3.3	2.9	5.0	9.6	0.01	11.5	507
Hlíðarvatn	784.5	2.6	1	0.3	2.0	3.0	1.0	0.002	8.5	40
Hraunhafnarvatn	732.53	2.0	0	2.9	1.7	2.5	9.0	0.04	9.2	112
Kötluvatn	732.53	2.0	0	1.6	3.7	5.0	4.0	0.02	8.4	495
Langavatn	727.4	-1.1	158	0.4	7.2	19.0	2.8	0.01	7.0	109
Langisjór	727.4	-1.1	663	25.7	18.5	73.5	475.5	0.003	8.8	49
Mjóavatn	469.4	2.4	448	2.9	0.8	1.1	2.1	0.02	8.7	87
Nýpslón	653.0	2.9	1	5.5	7.0	12.0	38.5	0.002	12.7	381
Oddastaðarvatn	744.9	3.0	65	3.0	5.4	18.0	16.0	0.03	14.2	71
Ónefnt vatn	784.5	2.6	438	0.3	2.0	3.0	1.0	0.003	8.5	40
Sænautavatn	527.6	0.7	524	2.3	7.8	23.0	18.0	0.02	9.8	86
Selvatn	483.2	2.5	150	0.7	4.0	8.0	5.6	0.03	9.4	85
Sigurðarstaðarvatn	732.5	2.0	0	2.0	1.3	3.0	2.0	0.01	8.0	313
Skríðuvatn	617.9	3.0	155	1.0	3.0	10.0	3.0	0.05	9.5	37
Urriðavatn	617.9	3.0	38	1.0	4.4	10.5	4.5	0.005	14.6	98
Úlfsvatn	483.2	1.8	434	3.8	1.0	2.0	3.8	0.05	12.6	79
Vatnsholtsvatn	704.7	3.5	10	0.4	1.0	4.0	0.3	0.03	15.2	109
Vesturhóp	441.7	2.5	19	10.3	7.1	28.0	73.0	0.03	11.4	143
V-Friðmundarvatn	469.4	2.4	441	6.0	1.2	2.3	7.0	0.03	9.0	136
Vífilsstaðavatn	798.8	4.3	38	0.3	0.5	1.7	0.1	0.05	13.4	129
Ytra Deildarvatn	732.5	2.0	38	0.6	1.5	2.5	1.0	0.03	10.6	92
Þurriðarvatn	653.1	2.9	416	1.2	3.5	11.0	4.2	0.01	11.1	54
Ölvesvatn	474.8	2.5	169	2.7	2.5	3.5	8.1	0.05	9.2	96

**Table 2.** The proportion of Arctic charr from monomorphic populations in Iceland correctly classified using a discriminant function analysis

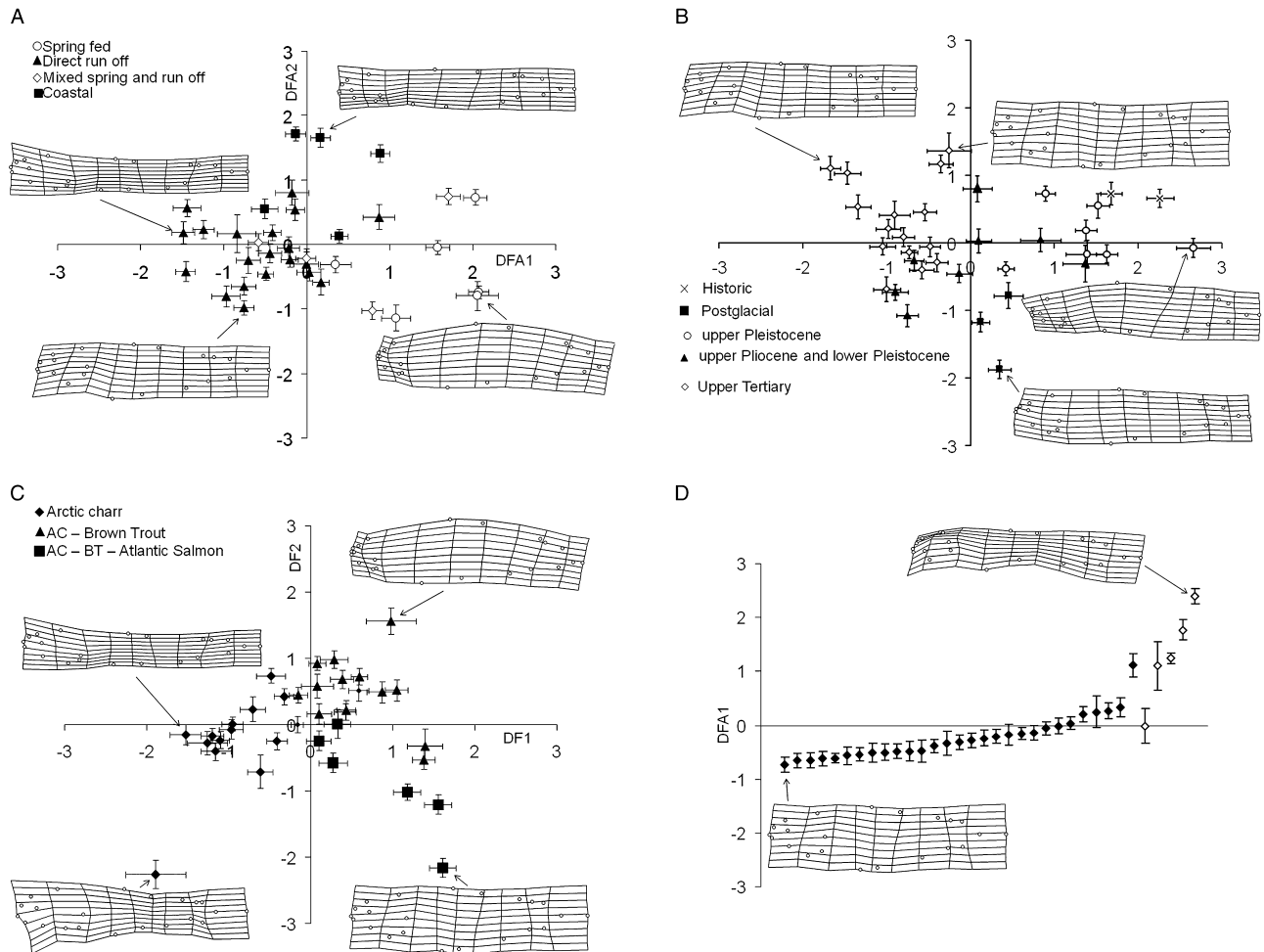
Lake	% Correctly classified	Water origin	Bedrock type	Salmonid diversity	Stickleback
Apavatn	80.6	3	3	2	1
Arnarvatn	65.2	2	4	2	1
Ánavatn	73.5	2	4	1	1
Ásbjarnarvatn	100.0	1	3	1	0
Eiðavatn	80.0	2	5	2	1
Ellíðavatn	68.6	1	1	3	1
Eyrarvatn	97.1	2	5	3	1
Frostastaðavatn	91.4	1	2	1	1
Geitabergsvatn	78.4	2	5	2	1
Gíslholtsvatn	82.8	2	3	2	1
Glammsstaðavatn	82.4	2	5	3	1
Heiðarvatn	77.5	2	5	1	0
Hítarvatn	86.0	3	5	2	1
Hlíðarvatn	54.9	4	2	1	1
Hraunhafnarvatn	91.9	4	3	2	1
Kötluvatn	81.6	4	3	1	1
Langavatn	81.5	1	1	2	1
Langisjór	88.2	1	3	2	0
Mjóavatn	94.1	2	4	1	1
Nýpslón	76.7	4	5	2	1
Oddastaðarvatn	63.2	3	5	2	1
Ónefnt vatn	92.9	2	5	1	0
Sænautavatn	81.1	2	4	1	1
Selvatn	67.6	3	5	2	1
Sigurðarstaðarvatn	80.0	4	3	1	1
Skriðuvatn	76.9	2	5	2	0
Urriðavatn	82.1	2	5	1	1
Úlfsvatn	58.3	2	4	2	1
Vatnsholtsvatn	73.5	2	5	3	1
Vesturhóp	73.0	2	5	3	1
V-Friðmundarvatn	88.9	2	4	1	1
Vífilsstaðavatn	86.4	1	3	2	1
Ytra Deildarvatn	60.0	2	2	3	1
Þuriðarvatn	83.8	2	5	1	1
Ölvesvatn	87.5	2	4	2	1

Classification of lakes according to; the; water origin (1 = spring fed, 2 = direct run-off, 3 = mixed 1 and 2, and 4 = coastal); bedrock type (1 = historic (< 0.0011 Myr); 2 = postglacial (0.0011–0.01 Myr); 3 = upper Pleistocene (0.01–0.8 Myr); 4 = upper Pliocene and lower Pleistocene (0.8–3.3 Myr); 5 = Upper Tertiary (> 3.3 Myr); diversity of salmonids: (1) only Arctic charr, (2) Arctic charr and brown trout, (3) Arctic charr, brown trout, and Atlantic salmon; presence and absence of sticklebacks.

## RESULTS

Landmarks were digitized on 1220 pictures of Arctic charr from 35 populations (Fig. 1, Table 1). The DFA was significant (Wilks lambda  $\leq$  0.0001,  $\chi^2_{1365} = 9945$ ,  $P < 0.001$ ) and correctly classified 79% of the fish to their population (Table 2). Correctly classified fish ranged from 100% in Ásbjarnarvatn to 55% in Hlíðarvatn.

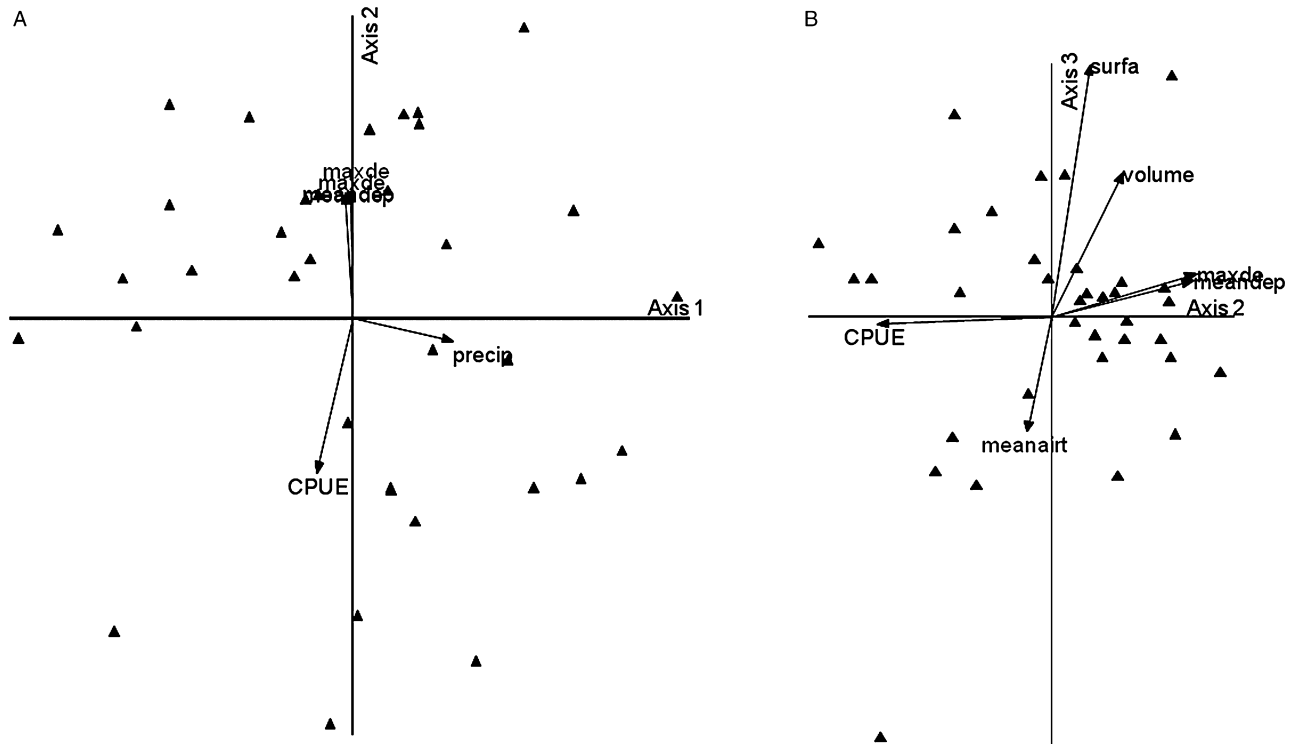
The MANOVA found significant differences ( $P < 0.001$ ) among all of the lake groups (water origin,  $F_{120,3513} = 8.0$ ,  $P < 0.001$ ; bedrock type,  $F_{160,4658} = 10.0$ ,  $P < 0.001$ ; salmonid diversity,  $F_{80,2342} = 11.6$ ,  $P < 0.001$ ; stickleback presence,  $F_{40,1171} = 10.2$ ,  $P < 0.001$ ) (Fig. 3). The DFA were as well always significant ( $P < 0.05$ ). The DFA classified 63% of the fish correctly based on origin of water (Fig. 3A). The first DFA axis separated fish from spring fed lakes and direct run off lakes.



**Figure 3.** Distribution of discriminant scores from an discriminant function analysis of Arctic charr from 35 monomorphic Arctic charr populations in Iceland. The symbols denote population average and the bars denote 1 standard error. A, the discriminant analysis separated fish from lakes with different water origin: spring fed (open circles), direct run-off (filled triangles), mixture of spring and run-off (open diamonds), and coastal (filled squares). B, fish from lakes in bedrock of different age, the age were 1 (x) = historic (< 0.0011 Myr); 2 (filled squares) = postglacial (0.0011–0.01 Myr); 3 (open circle) = upper Pleistocene (0.01–0.8 Myr); 4 (filled triangle) = upper Pliocene and lower Pleistocene (0.8–3.3 Myr); and 5 (open diamond) = Upper Tertiary (> 3.3 Myr). C, the symbols denote population average and the bars denote one standard error. The discriminant analysis separated fish from lakes having different salmonid species compositions: 1 (diamonds) = only Arctic charr; 2 (triangles) = Arctic charr and brown trout; and 3 (squares) = Arctic charr, brown trout, and Atlantic salmon. D, the discriminant analysis separated fish from lakes with sticklebacks (open triangles) and those without sticklebacks (filled triangles). Deformation grids show the morphology of an average fish in a given lake compared to the average fish from all the lakes, shown at  $\times 3$  magnification.

In general, fish from spring feed lakes were deeper bodied and had somewhat smaller heads. Axis 2 separated fish from coastal lakes from the other lakes. In coastal lakes, fish were in general thinner bodied, with more straight pointing mouth. The DFA correctly classified 58% of the fish based on bedrock (Fig. 3B). DFA axis 1 roughly separated the fish based on age of the bedrock with fish from lakes in historic bedrock having the highest scores. Axis 2 separated fish from lakes in postglacial bedrock from fish in lakes in upper Tertiary bedrock. The most pronounced body

shape differences seen here were in relation to head shape and mouth orientation, where fish from the younger lakes had somewhat smaller heads and thinner bodies. The DFA correctly classified 67% of the fish correctly based on salmonid diversity (Fig. 3C). Axis 1 separated fish from lakes where Arctic charr was the only salmonid present (low scores) from lakes that also had other salmonids. Arctic charr in lakes where there were other salmonids had deeper bodies, short and thick caudal peduncle, and somewhat smaller heads compared



**Figure 4.** Results of an NMS analysis on the average morphology of Arctic charr from 35 lakes in Iceland. The analysis resulted in three axes (A, axis 1 and 2; B, axis 2 and 3).

to individuals in lakes where Arctic charr occur alone. Axis 2 roughly separated lakes where all three species of salmonids were present from lakes where there were either only Arctic charr or Arctic charr and brown trout. Arctic charr in lakes where there were salmon present had longer caudal fin. The DFA correctly classified 82% of the fish based on the presence or absence of sticklebacks (Fig. 3D). Arctic charr in lakes where there were no sticklebacks had narrower bodies, and smaller heads with more subterminal mouth shape than those coming from lakes with sticklebacks.

The NMS on the average morphology of Arctic charr from 35 lakes gave a three-dimensional solution (stress = 11.9, instability = 0.00001; 108 iterations). Correlations between continuous physical environmental variables and morphological axes were low, in the range 0.0–0.38 (Fig. 4, Table 3).

## DISCUSSION

The analyses in the present study consolidate the notion of extensive phenotypic diversity among populations of Icelandic Arctic charr (Skúlason *et al.*, 1992). Charr populations are easily distinguished based on overall body morphology. This is consistent with variation seen in populations of small benthic

**Table 3.** Correlations of physical environmental factors with axis 1, 2, and 3 from ordination analysis examining morphological differences among Arctic charr from different lake groups

Variables	Axis 1	Axis 2	Axis 3
Precipitation	0.31	−0.15	−0.03
Mean air temperature	0.02	−0.14	−0.34
Altitude	−0.16	0.02	0.00
Surface area	0.07	0.18	0.51
Mean depth	−0.08	0.35	0.19
Maximum depth	−0.06	0.35	0.21
Volume	0.02	0.25	0.38
Catch per unit effort	−0.19	−0.38	−0.08
Water temperature	−0.27	0.13	−0.07
Conductivity	0.17	0.14	0.01

charr in Iceland (Kristjánsson, 2008) and in Scottish Arctic charr populations (Adams *et al.*, 2007), as well as in populations in other countries (Klemetsen, 2010). This morphological diversity is likely to be related to the genetic differentiation seen among different populations (Wilson *et al.*, 2004; Adams *et al.*, 2007; Kapralova *et al.*, 2011). Our hypothesis that morphological diversity of Arctic charr could be related to the ecology of their respective lake is



supported. Diverse morphology of Arctic charr from different lakes was associated with water origin, age of the surrounding bedrock, and the respective fish communities. Strongest relationships were found with structure of fish communities. However, when we related continuous ecological characters with morphology, the results were much less clear, probably because these variables show considerable variation among lakes within the same lake group.

In general, the relationship between the fish morphology and lake ecology suggests that ecological characters contribute to morphological evolution. The relatively strong relationship between charr morphology and structure of fish communities in lakes suggests that competition and/or predation may play an important role in shaping the observed morphological diversity, as has been observed in many fish populations (Schluter, 2000; Eklöv & Svanbäck, 2006), including charr (Knudsen, Amundsen & Klemetsen, 2010). Morphological differences were seen in head shape and traits related to locomotion, such as the shape of the caudal peduncle, as well as size and position of fins. In lakes where Arctic charr was the only fish species, individuals had relatively shallower bodies and smaller heads than in other lakes, which indicates relatively poorer somatic condition. This could result from larger population size of charr in such lakes and thus high intraspecific competition (Klemetsen *et al.*, 2002). In lakes where charr occur with brown trout, competition with brown trout may cause habitat shift in charr, resulting in the observed phenotypic diversity. Studies have shown that brown trout may displace Arctic charr of similar size from more rewarding areas in shallow waters in the littoral zone to deeper waters (Hegge *et al.*, 1989; Langeland *et al.*, 1991; Jansen *et al.*, 2002). Similarly, charr might compete with threespine stickleback for resources, which might result in the observed morphological differences. An alternative explanation is that in lakes with other salmonids species deeper-bodied charr may show plastic response to predation, most likely by brown trout (Brönmark & Miner, 1992; Brönmark & Pettersson, 1994).

There were clear morphological differences among charr from lakes on different aged bedrock and lakes that differed in water origin. These two ecological groups are obviously not independent (Garðarsson, 1979; Sigurðsson, 1993). Older bedrock is less permeable to water and direct run-off systems are more common there than in areas of younger bedrock where spring-fed systems are prominent. Lakes situated in areas of younger bedrock appear to generate a more 'benthic' morphotype. These charr have deeper bodies, a shorter and thicker caudal peduncle, and shorter heads, which are morphological differences that can be related to more benthic foraging (Malm-

quist, 1992; Malmquist *et al.*, 1992; Skúlason *et al.*, 1999). These lakes are often characterized by extensive benthic lava habitats, offering high densities of benthic invertebrate prey (Malmquist *et al.*, 2000), and are ideal environments for juvenile charr with ample spaces for hiding and avoiding predation (Snorrason & Skúlason, 2004)

It is likely that a considerable part of the observed morphological diversity has been caused by independent evolutionary processes in each lake (Gíslason *et al.*, 1999; Wilson *et al.*, 2004; Kapralova *et al.*, 2011), where factors such as founder effect and genetic drift might be involved (Langerhans & DeWitt, 2004). However, we observed direct relationships between charr morphology and the ecological characteristics of respective lakes. We propose two mechanisms to explain these patterns. The first is a result of adaptive divergence where similar ecological factors promote similar evolutionary responses in different populations. The other mechanism reflects a process where morphological patterns are shaped by repeated plastic responses in similar phenotypic characters. It is well established that fish can respond in a plastic way to diet (Day, Pritchard & Schluter, 1994) and, in some cases, substantial morphological differences between morphs or even species are almost entirely the result of diet-induced plasticity (Wimberger, 1992, 1994). The diverse diet of the Arctic charr populations in the present study is currently being analyzed in detail (Woods P. J. pers.observ) allowing for a future study of the relationship between morphology and dietary-induced plasticity. Plastic responses to predation are also well known. For example, fish exposed to waterborne cues from predators develop deeper bodies. This has been well established in crucian carp (*Carassius carassius*) preyed on by pike (*Esox lucius*) (Brönmark & Miner, 1992; Brönmark & Pettersson, 1994). Arctic charr is known to be very plastic (Skúlason *et al.*, 1999; Snorrason & Skúlason, 2004), and studies have also demonstrated that populations differ in the level of plastic responses (Skúlason *et al.*, 1989a, b; Adams & Huntingford, 2002, 2004; Klemetsen *et al.*, 2002; Snorrason & Skúlason, 2004; Kristjánsson, 2008; Parsons, 2008; Parsons, Skúlason & Ferguson, 2010). Thus, the level of plasticity in small benthic Arctic charr has been found to be related to ecological factors in springs (Kristjánsson, 2008). Therefore, the two potential mechanisms (i.e. selection and plasticity) contributing to parallel morphological patterns in Arctic charr are not mutually exclusive and are likely additive.

Understanding the origin and maintenance of biological diversity is a key question in biology. In recent years, scientists have increasingly realized that there is a strong relationship between ecological dynamics and micro-evolutionary processes. Evolutionary changes in populations can affect the

ecosystems they live in, and ecological changes can similarly affect the evolutionary processes of populations (Fussmann, Loreau & Abrams, 2007). Studies of the relationship between ecological factors and evolutionary changes, comparing traits in related populations, provide a powerful way of examining parallel evolution and its mechanisms. However, the strength of this approach is directly related to the number of populations compared. Therefore, studies of this kind are relatively few, especially when comparing large vertebrates such as fish. In the present study, we have used the availability of detailed ecological and morphological information from the Icelandic ESIL database to uncover relationships between morphological diversity of Arctic charr in Icelandic lakes and their ecology. The findings of study show that parallel evolution and natural selection may be important for the origin of intraspecific biological diversity. These findings set the stage for continuing studies that address more detailed questions on the nature of this diversity and its origin.

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