

Morphometric and genetic analyses of two sympatric morphs of Arctic char (*Salvelinus alpinus*) in the Canadian High Arctic

J.H. Arbour, D.C. Hardie, and J.A. Hutchings

Abstract: Multivariate morphometric analyses were used to examine variation in head, body, and fin shape between two sympatric morphotypes of Arctic char (*Salvelinus alpinus* (L., 1758)) from Lake Hazen, Ellesmere Island, Nunavut, Canada. Population structure of the Lake Hazen Arctic char was examined using five microsatellite loci. The “small” morph was found to have a larger (primarily deeper) head, larger and more elongate fins, and a deeper lateral profile than the “large” morph. The morphs also differed in allometric growth patterns. The large and small morphs do not appear to represent genetically distinct populations. The head morphology of the Lake Hazen small and large morphs exhibited similarities to benthic and pelagic morphs (respectively) from other lakes. We hypothesize that the large morph may be adapted to high-efficiency swimming and that the small morph may be adapted to low-efficiency, high-acceleration swimming. Such functional trade-offs are not uncommon among fish specializing in dispersed or mobile prey (fish and plankton) and benthic prey, respectively. The lack of apparent genetic differentiation between the morphs may suggest that the morphological differences result, to some extent, from phenotypic plasticity. Based on these results and previous analyses, it seems reasonable to conclude that Lake Hazen Arctic char represent a resource polymorphism.

Résumé : Des analyses morphométriques multidimensionnelles nous ont servi à étudier la variation de la forme de la tête, du corps et des nageoires chez deux morphotypes sympatriques de l'omble chevalier (*Salvelinus alpinus* (L., 1758)) du lac Hazen, île d'Ellesmere, Nunavut, Canada. Nous avons déterminé la structure de population des ombles chevaliers du lac Hazen par l'examen de cinq locus microsatellites. Le morphotype « petit » possède une tête plus grosse (surtout plus haute), des nageoires plus grandes et plus allongées et un profil latéral plus élevé que le morphotype « grand ». Les morphotypes diffèrent aussi par leurs patrons de croissance allométrique. Les morphotypes petit et grand ne semblent pas représenter des populations génétiquement distinctes. La morphologie de la tête des morphotypes petit et grand du lac Hazen rappelle les morphotypes (respectivement) benthique et pélagique décrits dans d'autres lacs. Nous émettons l'hypothèse selon laquelle le grand morphotype peut être adapté à la nage de grande efficacité et le petit morphotype l'est à la nage de faible efficacité, mais d'accélération rapide. De tels compromis fonctionnels ne sont pas rares chez les poissons qui se spécialisent respectivement pour les proies dispersées ou mobiles (poissons et plancton) et pour les proies benthiques. L'absence apparente de différenciation génétique entre les morphotypes peut laisser croire que les différences morphologiques proviennent, dans une certaine mesure, de la plasticité phénotypique. D'après nos résultats et des analyses antérieures, il semble raisonnable de conclure que les ombles chevaliers du lac Hazen présentent un polymorphisme basé sur les ressources.

[Traduit par la Rédaction]

Introduction

Resource polymorphisms occur when more than one discrete phenotype exists within a given population and different phenotypes exhibit differential resource utilization (Wimberger 1994; Skúlason and Smith 1995). Polymorphisms that result in differential habitat use, life histories, or significant visual cues (e.g., coloration and body shape) can promote assortative mating and contribute to reproductive isolation (Greenwood 1974; Wimberger 1994). Re-

source polymorphisms may convey a selective advantage by reducing intraspecific competition through niche specialization (Skúlason and Smith 1995; Swanson et al. 2003). Thus, such polymorphisms are thought to be more common in ecosystems with low interspecific competition and where novel resources are available (Gíslason et al. 1999).

Arctic char (*Salvelinus alpinus* (L., 1758)) is a highly polymorphic salmonid that has colonized postglacial lakes and rivers inhabited by few other species of fish (Smith and Skúlason 1996; Skúlason et al. 1999; Alekseyev et al. 2002).

Received 27 July 2010. Accepted 8 November 2010. Published on the NRC Research Press Web site at cjz.nrc.ca on 16 December 2010.

J.H. Arbour,^{1,2} D.C. Hardie,³ and J.A. Hutchings. Department of Biology, Dalhousie University, Halifax, NS B3H 4J1, Canada.

¹Corresponding author (e-mail: jessica.arbour@utoronto.ca).

²Present address: Department of Ecology and Evolutionary Biology, University of Toronto, Royal Ontario Museum, 100 Queen's Park, Toronto, ON M5S 2C6, Canada.

³Present address: Fisheries and Oceans Canada, Bedford Institute of Oceanography, P.O. Box 1006, Dartmouth, NS B2Y 4A2, Canada.

One of the most remarkable examples of resource polymorphisms in Arctic char is that of the four morphotypes (henceforth morphs) identified from Thingvallavatn, Iceland, which differ in terms of morphology, habitat use, trophic ecology, and life history (Sandlund et al. 1992). Differences in body shape and head morphology have been linked to differing trophic ecology in sympatric morphs of Arctic char, as well as other polymorphic fish populations, e.g., sticklebacks (genus *Gasterosteus* L., 1758) (Skúlason et al. 1989; Schluter 1993; Adams et al. 2006). Genetic analyses of Thingvallavatn Arctic char (as well as polymorphic Arctic char from other Icelandic lakes) have indicated that the lake was colonized once by Arctic char and that morphs subsequently diverged, rather than being colonized by benthic and pelagic morphs independently (Volpe and Ferguson 1996; Gíslason et al. 1999). The study of divergence among sympatric morphs of Arctic char provides an opportunity to examine the influence of functional morphology, heritable variation, and phenotypic plasticity during early stages of reproductive isolation and speciation (Smith and Skúlason 1996).

Two sympatric morphs of Arctic char have been previously identified from Lake Hazen, Ellesmere Island, Nunavut (Hunter 1960; Reist et al. 1995). The “small morph” has been described as having a dark olive or brown coloration, long pelvic fins, and a terete body form, while the “large morph” has been described as having a light coloration, small pelvic fins, and a rounded body form, as well as a higher growth rate (Fig. 1 is printed in black and white but appears in color on the Web) (Reist et al. 1995). Although it was initially hypothesized that the morphological differences were the result of differences in migratory behaviour, anadromy (seaward migration) has not been documented during the 30+-year life span of Lake Hazen Arctic char (Babaluk et al. 1997; Halden et al. 2000).

It has been suggested that differences between the two morphs represent an adaptive response to differential resource utilization, and that Lake Hazen Arctic char demonstrate a resource polymorphism. Guiguer et al. (2002) confirmed that the large morph feeds at a higher trophic level than the small morph. Several authors have observed that the large morph preys almost exclusively on other fish in the lake (i.e., other char <25 cm), whereas the small morph preys predominantly on benthic invertebrates (Babaluk et al. 1997; Guiguer et al. 2002). It has also been determined that the observed bimodality in sizes between the morphs is not a result of predation pressure on the small morph (Guiguer et al. 2002).

Lake Hazen Arctic char provide a unique opportunity to study the divergence of sympatric morphs. The geological and geographical history of the Lake Hazen plateau has permitted a relatively recent time period during which Arctic char could have colonized the lake (see site description in Materials and methods). Studies examining trophic ecology in Lake Hazen Arctic char have confirmed ecological differences between the two morphs but have been unable to directly identify these as the underlying cause of the observed morphological differences. It is possible, for example, that the differences in diet composition and trophic ecology are a by-product of other selective pressures (e.g., sexual selection) on morphology. Furthermore, without an examination

Fig. 1. Small morph (top, 39.5 cm fork length (FL)) and large morph (bottom, 59.5 cm FL) of Arctic char (*Salvelinus alpinus*) collected from Lake Hazen, Ellesmere Island, during August 2005. Note that the figure is printed in black and white but appears in color on the Web.



of the genetic relationships of the Lake Hazen Arctic char, the role of factors such as phenotypic plasticity and genotypic composition in determining morphological differences cannot be fully resolved.

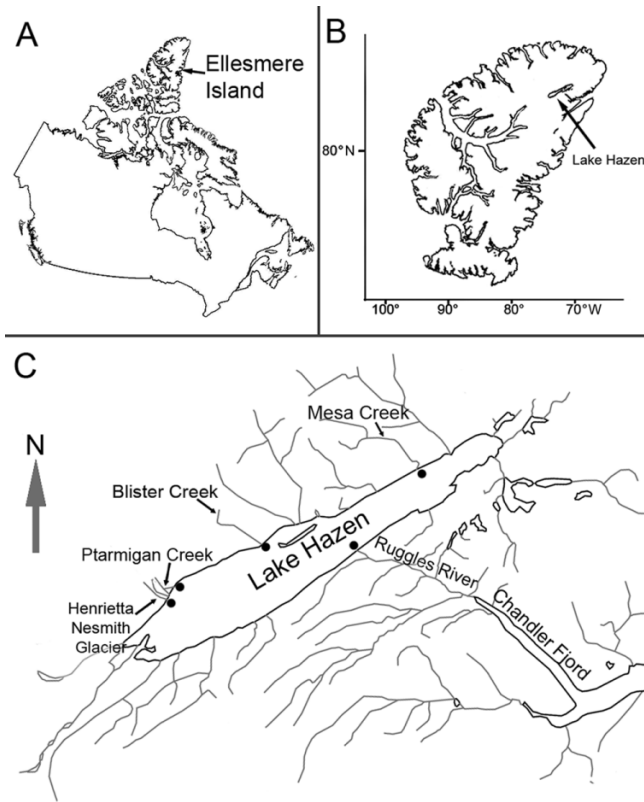
The objective of the present study is to quantify morphological and genetic differences between the two morphs of Lake Hazen Arctic char. Previous studies on Lake Hazen Arctic char have included only univariate morphological measures (Reist et al. 1995; Guiguer et al. 2002). This means that important spatial components of morphological variation have not been examined in morphs of Lake Hazen Arctic char (Rohlf 2002). Geometric morphometric analysis considers variation in the spatial configuration of homologous landmarks and thus represents a more powerful morphometric analysis than has been employed previously. This study also represents the first genetic analysis of morphs of Lake Hazen Arctic char.

Materials and methods

Study area and sampling procedure

Lake Hazen (81°50'N, 70°25'W), situated within the Quttinirpaaq National Park, Ellesmere Island, Nunavut, is the largest lake in the Canadian High Arctic, with an estimated area of 542 km² and a maximum depth of 280 m (Fig. 2) (McLaren 1964). The Lake Hazen plateau was entirely ice-covered during the last glacial maximum, with the glacial retreat reaching the plateau by 8000 years before present (BP) (Smith 1999). It is believed that the main breakup of glaciers across the Lake Hazen basin occurred between 5300 and 5000 years BP, with summer ice cover retreating by 4200–3300 years BP (Smith 1999; Smith 2002). Today the lake receives turbid glacial meltwater and is not infrequently ice-free for a period of several weeks annually (McLaren 1964). The lake is oligotrophic and lacks macrophytes. Both the zooplanktonic and benthic communities exhibit low diversity (Oliver 1963; McLaren 1964). Arctic char is the only species of fish found in the lake.

Fig. 2. Sampling locations from Lake Hazen in the Canadian High Arctic. (A, B) Location of Lake Hazen on Ellesmere Island in the Canadian High Arctic. (C) Five major regions from which Arctic Char (*Salvelinus alpinus*) were sampled during August 2005. Maps were produced using ArcView (version 3.2).



Nonlethal sampling of Arctic char was carried out at six sites across Lake Hazen (Table 1; Fig. 2). One hundred and thirty-nine Arctic char were collected by angling from 8–15 August 2005 (Table 1). All specimens were cared for in accordance with the Guidelines on the Care and Use of Wildlife (Austin-Smith et al. 2003) and all procedures were approved by the animal care review committee at Dalhousie University. Upon collection, Arctic char were visually assessed as a large morph or small morph according to criteria (body and fin color) identified in previous descriptions of Lake Hazen Arctic char (Babaluk et al. 2001; Guiguer et al. 2002). Large morphs were silver (dorsally) and white (ventrally) in body color, with pale (often reddish; J.H. Arbour, personal observation) ventral and anal fins with bright white marks along the leading edges. Small morphs possessed olive–green to brown flanks and an orange to rosy underbelly, as well as darkly colored ventral and anal fins with dull (greyish) white markings along the leading edges. Small specimens under 22.5 cm fork length (FL) were excluded from further analyses because of consistent difficulties in identifying landmarks from photographs. The FLs of the specimens of Arctic char were measured and digital photographs were taken of the right side of the specimen (full profile and a close up of the head, pelvic fins, and anal fin). A tissue sample (adipose fin clip) was obtained and preserved in 95% ethanol.

Table 1. Number of large morph (L), small morph (S), and juvenile (J) Arctic char (*Salvelinus alpinus*) collected at each of the Lake Hazen sampling sites during August 2005.

Location	L	S	J
Blister Creek East	4	3	0
Blister Creek West	29	17	0
Henrietta Nesmith Glacier	32	26	3
Mesa Creek	8	1	0
Ptarmigan Creek	5	0	0
Ruggles River	0	0	11

Morphometric analysis

Head morphology

Conventional linear morphometrics were used to examine variation in head morphology between large and small morphs, as variable jaw position precluded the use of geometric morphometrics (see body shape analysis below). Nine characters of head morphology were measured from the digital photographs using the image analysis software ImageJ (Figs. 3A, 3B). These measures have been found to relate to trophic polymorphisms in some populations of Arctic char and have been used widely in previous studies of head morphology of Arctic char (Skúlason et al. 1989; Adams et al. 1998; Adams et al. 2003). Each character was corrected to account for the effects of body size across all the sampled specimens, using an allometric size correction (Thorpe 1975; Reist 1985). Adjusted head characters did not show a relationship with body size, indicating that the correction effectively removed confounding size effects. The calculation of the corrected measures proceeded as follows: $\log \hat{Y} = \log Y - \beta(\log X - \log X_m)$, where Y is the unadjusted head character, \hat{Y} is the corrected head character, X is the fork length (individual), X_m is the mean fork length, and β is the slope of the regression of $\log Y$ vs. $\log X$.

A principle components (PCs) analysis was carried out on the corrected head morphology characters. The Kaiser method (eigenvalues > 1) was used to determine the number of critical PCs from the analysis. Individual PC scores were contrasted between the morphs using ANOVAs. In this and all following analyses, values are presented as mean \pm SD.

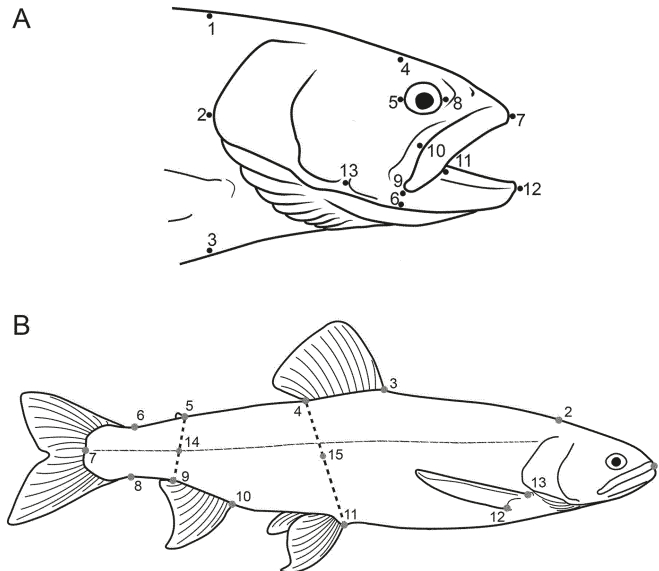
Body shape

The coordinates of 13 homologous landmarks and 2 reference points were digitized from the photograph of each specimen, using TPSdig2 (Fig. 3B; supplementary Table S1⁴). These landmarks were predominantly type 1 or 2 landmarks as defined by Bookstein (1991) and represented significant skeletal or structural features. Ventral or dorsal bending of the specimens initially represented a large proportion of the variance in shape. This was corrected by obtaining the perpendicular deviations of the landmarks from a quadratic curve fit using landmarks 1, 14, 15, and 7, and plotting these deviations onto a straight line (“unbending” procedure in TPSutil). Following this correction, landmarks 14 and 15 were excluded from further analysis.

A generalized least-squares Procrustes superimposition was performed on the coordinates of the straightened homol-

⁴Supplementary Tables S1 and S2 and Figs. S1–S3 are available on the Journal Web site (<http://cjz.nrc.ca>).

Fig. 3. (A) Landmarks used in the measure of head morphology characters of Lake Hazen Arctic char (*Salvelinus alpinus*): head depth at operculum (HDO, 1–3), head depth at eye (HDE, 4–6), head length (HL, 2–7), posteye distance (PED, 2–5), eye diameter (ED, 5–8), upper jaw length (UJL, 7–9), maxilla width (MW, 10–11), lower jaw length (LJL, 12–13), and snout length (SL, 4–7). (B) Landmarks used in a geometric morphometric analysis of body shape among Lake Hazen Arctic Char. Landmarks 14 and 15 are not homologous and are used only in straightening of specimens.



ogous landmarks using TPSrelw (Bookstein 1997; Rohlf and Slice 1990; Rohlf 2003). Relative warps (RW) were determined using the uniform and nonuniform components of shape changes from the consensus (mean) configuration to the landmark configuration of each specimen. RWs that explained at least 10% of the total variation were included in our analyses. Deviations from the consensus configuration along each RW axis were visualized using thin-plate splines (Bookstein 1991; Zelditch et al. 2000) (Figs. 5A, 5C). The mean RW scores for each morph were compared using a one-way ANOVA (or ANCOVAs if RWs varied significantly with body size, with log FL as a covariate).

Fin shape

The lengths of the anal and pelvic fins were determined from the closeup digital photographs and were allometrically corrected as previously described. Anal and pelvic fin shape was analyzed using the insertion points and tips of the fins as homologous landmarks. The outline of the fins was sampled repeatedly (20–30 times) between each of the landmarks, using the TPSdig2 outline drawing tool and the resulting lines were resampled by length so that curve landmarks were equally spaced between homologous landmarks, to make the landmarks comparable between specimens and to reduce small-scale variation (e.g., small rips or other temporary damage) not relevant to fin shape. The resulting outlines were converted to landmark coordinates, using TPSutil (Figs. 4A, 4B). A RW analysis (as described previously) was conducted on anal and pelvic fin shape. Fin position could not be accounted for using algorithms similar to those used to “unbend” specimens. When position and

shape information were not expressed on different RW axes (based on thin-plate splines), discriminant function analysis of RW scores was used to examine which combinations of RW axes separated the two morphs.

Genetic analysis

DNA was extracted from the tissue samples according to the protocol given by Elphinstone et al. (2003). Individual specimens were genotyped using a polymerase chain reaction, as described by Bradbury et al. (2008). Allelic variation was examined at five microsatellite loci (Sco19, Sco202, Omm1105, OtsG83b, and OtsG253; supplementary Table S2⁴). Random subsampling was used to correct for the effect of sample size on allelic richness and mean diversity was determined from 1000 iterations for the large morph of Arctic char (L_{sub} ; Table 3) (Leberg 2002). Single locus estimates of F_{IS} , F_{ST} , and F_{IT} were calculated for each microsatellite locus using GENEPOP version 4.0.7. GENEPOP was used to test for deviations from Hardy–Weinberg equilibrium (HWE) at each locus, using a Markov chain method (dememorization = 10 000, batches = 20, iterations per batch = 5 000) to determine an unbiased estimate of the P values (Guo and Thompson 1992; Raymond and Rousset 1995). An exact G test of genotypic differentiation was used to examine population differentiation between the two morphs (Markov chain parameters: dememorization = 10 000, batches = 20, iterations per batch = 5 000). A Fishers method χ^2 test was used to assess the significance of the P values across all of the loci examined (Raymond and Rousset 1995).

The Bayesian analysis program Structure was used to probabilistically assign individuals to inferred groups based upon their genotype at multiple loci (50 000 burn-in period, 250 000 repetitions, and $k = 1, 2,$ or 3) (Pritchard et al. 2000). BAPS, a second Bayesian analysis program, was used to cluster groups of individuals based on expected HWE between loci within the defined groups (in this case the two morphs; Corander et al. 2003). A population mixture analysis based on clustering of groups of individuals was conducted on the five microsatellite loci, with a maximum number of clusters of 2.

Results

Morphometric analysis

Large morphs of Arctic char exhibited a greater maximum size and size range (22.5–73.5 cm) compared with the small morphs (31.5–49.5 cm), but the morphs did not differ in mean body size (large morphs = 41.3 ± 11.8 cm, small morphs = 38.9 ± 3.6 cm; Student’s t test: $P = 0.101$).

Head morphology

Three of the nine univariate measures of head morphology showed significant differences between the two morphs. Small morphs exhibited a greater head depth at the operculum ($P = 0.006$), a greater head depth at the eye ($P = 0.007$), and a longer upper jaw ($P = 0.023$) (supplementary Fig. S1).⁴

Given that PC1 (~63% of variation, Table 2) was characterized by positive factor loadings that were similar in range, high PC1 scores can be interpreted as representing individu-

Fig. 4. Curved outlines of pelvic (A) and anal (B) fins of specimens of Arctic char (*Salvelinus alpinus*). Dots indicate the position of landmarks established by resampling the curves by length.

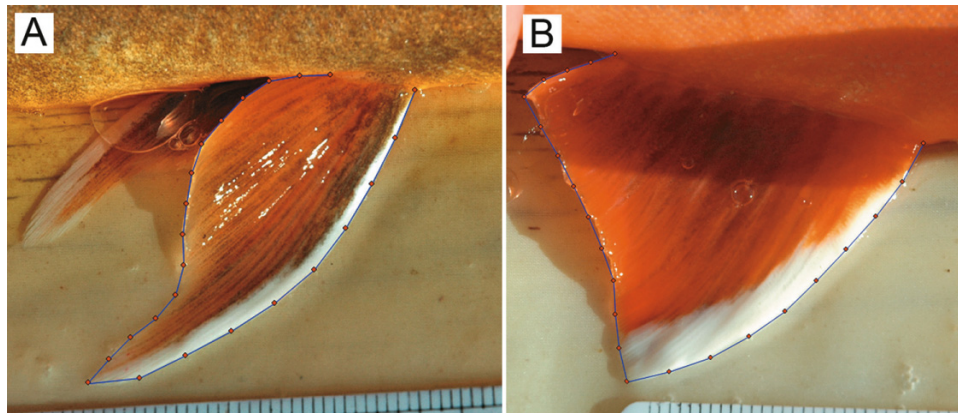


Table 2. Factor loadings for the first two principle components (PC1 and PC2) of head morphology for Lake Hazen Arctic char (*Salvelinus alpinus*).

Variable	Landmarks	PC1	PC2
Head depth (operculum)	1–3	0.273	0.403
Head depth (eye)	4–6	0.363	0.148
Head length	2–7	0.399	–0.065
Post eye length	2–5	0.355	0.217
Eye diameter	5–8	0.187	–0.711
Upper jaw length	7–9	0.389	–0.088
Maxilla width	10–11	0.198	0.406
Lower jaw length	12–13	0.388	–0.057
Snout length	4–7	0.364	–0.29
Variation explained (%)		62.70	12.60
<i>P</i> value (ANOVA by morph)		0.035	0.198

als with larger features (i.e., head depth, jaw length and width, eye size), whereas low PC1 scores corresponded to individuals with smaller features for a given body size. PC1 did not exhibit a significant relationship with body size ($R^2 \leq 0.021$ for both morphs, $P = 0.324$ – 0.807). PC1 was found to differ significantly between the two morphs, with small morphs having higher scores, on average (ANOVA: $F_{[1,122]} = 4.56$, $P = 0.035$). Small morphs of Arctic char possessed a more robust head morphology than large morphs of Arctic char. PC2 (Table 2) did not exhibit a significant relationship with body size ($R^2 = 0.007$ – 0.016 , $P = 0.399$ – 0.469). The mean PC2 scores also did not differ significantly between the two morphs (ANOVA: $F_{[1,122]} = 1.67$, $P = 0.198$).

Body shape

RW1 score explained 43.9% of the variation in the configuration of the body landmarks. Thin-plate splines revealed that the gradient from positive to negative RW1 scores described a transition in body shape from long and slender towards a longer, deeper head, a longer abdomen with a more angled dorsal fin base, and a shorter caudal peduncle for a given body size (Fig. 5A). RW1 exhibited a relationship with body size with the large morph's scores being more strongly correlated with log FL than those of the small morph ($R^2 = 0.601$ vs. $R^2 = 0.115$, $P \leq 0.02$ for both).

This is not unexpected, as the gradient from positive RW1 scores to negative RW1 scores reflected the typical transition in body shape from that of an immature individual to one that is mature (transition from a narrow body with a small head to a broad body with a steeper dorsal profile and a large head), which is observed in many salmonid species. The small morph also possessed a more negative regression coefficient than the large morph ($\beta = -0.157$ vs. $\beta = -0.148$). When FL was considered a covariate, a statistically significant difference in RW1 scores was observed between large and small morphs of Arctic char (ANCOVA; log FL: $F_{[1,118]} = 103.3$, $P = <0.001$; morph: $F_{[1,118]} = 7.24$, $P = 0.008$), with small morphs possessing lower RW1 (corresponding to a “mature” body form) than the large morph, on average (Fig. 5B).

RW2 score explained 17.2% of the variation in the configuration of the landmarks. Thin-plate splines revealed that the gradient from positive to negative RW2 scores described a transition from a fusiform body shape to a broad body shape (Fig. 5C). Small morph RW2 scores were not significantly correlated with body size ($R^2 = 0.049$, $P = 0.136$) and large morph RW2 scores were only weakly positively correlated with body size ($R^2 = 0.066$, $P = 0.03$). The mean RW2 scores differed significantly between the two morphs (ANOVA: $F_{[1,119]} = 11.92$, $P = 0.001$; Fig. 5D), with the small morph exhibiting higher RW2 scores than the large morph. On average, the small morphs expressed a broader lateral profile than the large morphs and this disparity in body shape between the morphs was consistent in spite of differences in body size.

Fin size and shape

The anal fins of the two morphs differed significantly in length (ANOVA: $F_{[1,122]} = 89.27$, $P < 0.001$) but did not exhibit a significant relationship with body size. On average, the anal fins of the small morph were 21% longer than those of the large morph (4.80 vs. 3.98 cm size-corrected length, respectively). RW1 score explained 54.1% of the variation in the configuration of the landmarks but described only a change in fin position and did not differ significantly between morphs (ANOVA: $F_{[1,122]} = 0.41$, $P = 0.521$; Fig. 6A). RW2 explained 27.2% of the variation in the configuration of the anal fin landmarks (or ~60% of variation after excluding RW1). Positive RW2 scores corresponded to

Fig. 5. Relative warps (RWs) from a geometric morphometric analysis of body shape in Lake Hazen Arctic char (*Salvelinus alpinus*). (A, C) Thin-plate splines (oriented with the head to the right) illustrating the complete range of RW1 and RW2 scores. (B, D) The 95% confidence intervals for the mean RW1 and RW2 scores from each morph.

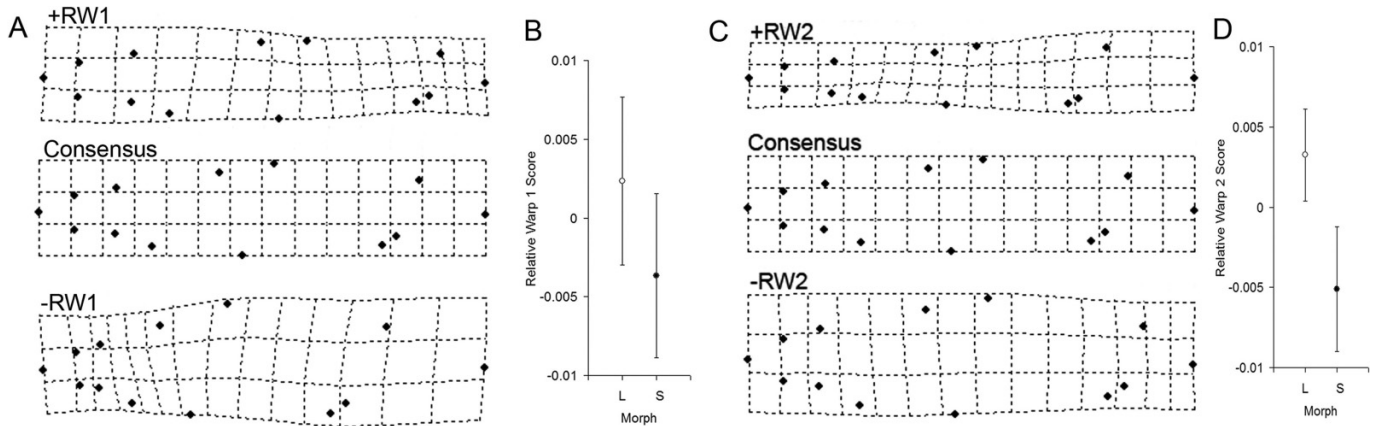
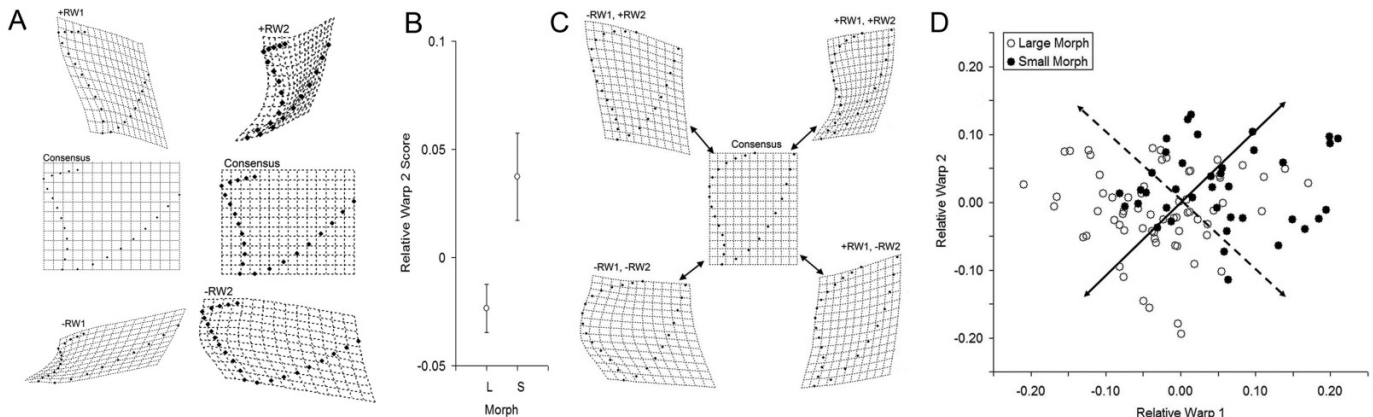


Fig. 6. A geometric morphometric analysis of anal fin shape in Lake Hazen Arctic char (*Salvelinus alpinus*). (A, C) Thin-plate splines illustrating the complete range of relative warp (RW) 1 (left) and RW2 (right) scores of anal and pelvic fin shapes. (B) The 95% confidence intervals for the mean RW2 scores for the shape of anal fins from each morph. (D) Distribution of RW1 and RW2 scores for the pelvic fin shape of large morphs (○) and small morphs (●) of Arctic char (*Salvelinus alpinus*). Solid line is the hypothesized “fin shape” subspace, whereas the broken line is the hypothesized “fin position” subspace.



individuals with an elongated, scythe-shaped anal fin, whereas negative RW2 scores corresponded to individuals with a broad triangular anal fin (Fig. 6A). The mean RW2 scores differed significantly between the two morphs (ANOVA: $F_{[1,122]} = 31.58, P < 0.001$), with the small morph possessing higher RW2 scores than the large morph (Fig. 6B). RW2 differed between the two morphs when considered in respect to body size (ANCOVA; log FL: $F_{[1,121]} = 7.24, P = 0.008$; morph: $F_{[1,121]} = 35.54, P < 0.001$). However, for both the large and small morphs, the correlation between RW2 and log FL was very weak ($R^2 = 0.058, P = 0.037$ and $R^2 = 0.142, P = 0.008$, respectively).

The length of the pelvic fins of the two morphs differed significantly (ANOVA: $F_{[1,122]} = 98.52, P < 0.001$), was not significantly correlated with body size for the large morph ($R^2 = 0.002, P = 0.733$), and was only weakly positively correlated with body size for the small morph ($R^2 = 0.086, P = 0.04$). On average, the pelvic fins of small morphs were 22% longer than those of large morphs (5.27 vs. 4.30 cm size-corrected length, respectively). RW1 score explained 49.0% of the variation and RW2 score explained 27.8% of the variation in the configuration of the pelvic fin land-

marks. The two groups differed significantly in both RW scores (RW1 score: $F_{[1,103]} = 27.16, P < 0.001$; RW2 score: $F_{[1,103]} = 7.80, P = 0.006$), with small morphs possessing higher scores, on average, across both axes (Fig. 6D). RW1 and RW2 scores appeared to each describe elements of both fin position and fin shape; based on the thin-plate splines produced as a combination of RW1 and RW2 scores (Fig. 6C), it appeared that information pertaining to fin shape was described along a subspace approximate to span $\left\{ \begin{bmatrix} 1 \\ 1 \end{bmatrix} \right\}$ (Fig. 6C, solid line), whereas information regarding fin position appeared to be described along a subspace approximate to span $\left\{ \begin{bmatrix} -1 \\ 1 \end{bmatrix} \right\}$ (Fig. 6C, broken line). A discriminant function analysis showed that both morphs were best explained along an axis with a regression coefficient (slope) of +0.81, which corresponds with the observed subspace of fin shape. The discriminant function analysis “accurately” predicted group membership (based on our observations) in 70% of small morphs and 76% of large morphs. Although fin shape is not an absolute predic-

Table 3. Allele richness of large (L and L_{sub} ; mean richness based on 1000 random subsamplings) and small (S) morphs of Lake Hazen Arctic char (*Salvelinus alpinus*), size range in base pairs, expected (H_e) and observed (H_o) heterozygosities, inbreeding coefficients (F_{IS} , F_{ST} , and F_{IT}), and P values for deviations from Hardy–Weinberg equilibrium (HWE) and genotypic differentiation.

Locus	Morph	Sco19	Sco202	Omm1105	OtsG83b	OtsG253	Overall
Number of alleles	L	25	8	9	8	9	
	L_{sub}	21	7.9	8.4	7.7	7.5	
	S	20	11	9	8	8	
	L + S	28	11	9	9	9	
Size range	L	184–258	121–185	138–170	148–176	114–150	
	S	186–260	121–189	142–170	144–176	114–150	
H_o	L	0.941	0.687	0.612	0.791	0.618	
	S	0.921	0.816	0.816	0.816	0.658	
H_e	L	0.918	0.782	0.612	0.784	0.716	
	S	0.891	0.824	0.768	0.774	0.742	
F_{IS}		–0.0288	0.0806	–0.0258	–0.0251	0.1295	0.0246
F_{ST}		0.0023	–0.0027	0.0402	–0.001	–0.0052	0.006
F_{IT}		–0.0264	0.0781	0.0155	–0.0262	0.1249	0.0304
P value (HWE)	L	0.3035	0.0439	0.2678	0.987	0.2065	0.153
	S	0.9938	0.0464	0.9039	0.5666	0.1363	0.322
P value (genotypic differentiation)		0.481	0.193	0.037	0.584	0.511	0.184

tor of morph type, the large and small morphs appear to be generally divergent in terms of pelvic fin shape. Similar to the anal fin, small morphs appear to possess fins that are elongated along the anterior margin compared with large morphs.

The shape of the caudal fins could not be analyzed using geometric morphometrics, as they were improperly placed in many full body photographs. However, a number of small morphs, in particular those that were especially large or exhibited the largest anal and pelvic fins compared with body size, possessed an extension of the most ventral fin rays on the lower lobe of the caudal fin (supplementary Fig. S2).⁴ Such an extension or elongation of fin rays was not observed on the upper lobe of the caudal fin or on any of the caudal fins of the large morphs.

Genetic analysis

Four of the five microsatellite loci examined were moderately polymorphic, with 9–11 alleles present at each locus over all the specimens sampled (supplementary Fig. S3).⁴ One locus (Sco19) was highly polymorphic, with a total of 28 alleles present across the specimens sampled. The composition of alleles at each locus was similar between the two morphs. The dominant alleles at each locus were typically conserved between the morphs, and for alleles unique to only one morph, the frequencies were typically low (<4%). At Omm1105, however, the frequency of the most common alleles differed substantially between the morphs; e.g., allele 2 (142): 8.21% for the large morph vs. 21.05% for the small morph, and allele 4 (150): 60.45% for the large morph vs. 39.47% for the small morph (supplementary Fig. S3).⁴ When the large morphs were subsampled to the same sample size as the small morphs, there were few differences in allelic richness between the two morphs. However, at Sco202, allelic richness was greater among small morphs than among large morphs (Table 3), both before and after corrections for sample size.

Overall, the H_e values of the five loci ranged from 0.618 (OtsG253, large morph) to 0.941 (Sco19, large morph). Sco202 was the only locus to exhibit a significant departure from HWE (both morphs; Table 3) and overall the two morphs did not exhibit significant departures from HWE, based on Fishers method ($P = 0.153$ for large morphs and $P = 0.322$ for small morphs). Although significant genotypic differentiation was observed at Omm1105 ($P = 0.037$), the morphs did not exhibit significant genotypic differentiation overall ($P = 0.184$).

No significant differences were observed in the allelic composition of the inferred groups produced from the genotype data in the program Structure. The probability of the inferred populations was maximized at a k of 1 (probability of one population > probability of two populations > probability of three populations). When groups were predefined in the program BAPS (i.e., morphs), the optimal clustering indicated no differences between large and small morphs of Arctic char.

Discussion

Arctic char exhibit some of the most impressive examples of resource polymorphisms (Wimberger 1994). Two morphs of Arctic char have been identified from Lake Hazen, Ellesmere Island, and these morphs have been shown to differ in life-history characteristics and trophic ecology (Reist et al. 1995; Babaluk et al. 1997, 2001; Guiguer et al. 2002). The present study showed that the large and small morphs differed significantly in body shape, head morphology, and fin length and shape, but they did not exhibit significant genetic differentiation across five microsatellite loci. The functional and ecological implications of these differences are discussed below.

Head morphology and trophic ecology

The Lake Hazen small morph exhibited a larger, predom-

inantly deeper, head proportional to body size when compared with that of the large morph. Similar trends in head morphology have been observed in other populations of Arctic char and other polymorphic populations of fish. Johnson (1980) noted, for example, that Arctic char consuming zooplankton and other pelagic prey exhibited a shallower head structure than those consuming benthic prey. Furthermore, morphs of stickleback (*Gasterosteus* spp.) specializing on pelagic prey such as zooplankton exhibit a longer, shallower head morphology than those specializing on benthic prey (McPhail 1984; Schluter 1993). Similar to our findings, Fraser et al. (1998) found that a benthic morph of Arctic char from Loch Ericht, Scotland, possessed a longer upper jaw and deeper body than a pelagic, planktivorous morph. Overall, the head morphologies of Lake Hazen Arctic char are consistent with trends observed in benthic and pelagic morphs (corresponding to the small and large morphs, respectively) from other populations of Arctic char and in other polymorphic fish.

Adaptation to steady vs. unsteady swimming

Fish body shapes are typically adapted towards steady swimming (high efficiency, long-range cruising or gliding) or unsteady swimming (high acceleration, low efficiency bursts and turns), with some intermediate shapes (Webb 1982). Steady swimming is constrained by minimizing frictional drag; steady swimmers tend to exhibit a streamlined (fusiform) shape, narrow caudal peduncle, and a high aspect ratio caudal fin (high height to width ratio; Lighthill 1977). Unsteady swimming is constrained by maximizing thrust; unsteady swimmers typically exhibit a deep caudal peduncle and increased body depth across the entire length of the fish.

Trade-offs in steady vs. unsteady swimming have been linked to diet preference and trophic ecology in fish and can characterize some resource polymorphisms (Webb 1982; Malmquist et al. 1992; Hjelm et al. 2001). Steady swimmers can cover large distances relative to their body size while using a minimal amount of energy, which is beneficial for preying on food that is highly dispersed or very mobile (e.g., plankton or fish). Unsteady swimmers cannot cover large distances efficiently but are capable of fast bursts of speed and tight manoeuvring, which is beneficial for preying on food that can be highly evasive (e.g., benthic prey). Eurasian perch (*Perca fluviatilis* L., 1758) confined to pelagic enclosures have been found to exhibit a fusiform body shape (streamlined with a narrow caudal peduncle), whereas those grown in benthic enclosures have been found to exhibit a deeper body morphology (Hjelm et al. 2001). Malmquist et al. (1992) found that both the planktivorous morph and the piscivorous morph from Thingvallavatn exhibited the streamlined body shape of a steady swimmer, whereas the benthic morphs exhibited a deeper body shape, typical of an unsteady swimmer. In our examination of body shape in the Lake Hazen morphs of Arctic char, the large morph possessed a more fusiform body shape, whereas the small morph possessed a deeper body shape.

Body shape and growth

The first axis of a geometric morphometric analysis of body shape (RW1) in Lake Hazen Arctic char may describe ontogenetic changes in body shape (allometry). In general,

the small morph exhibited a more “mature” body shape (deep body with a steep dorsal profile, a large head, and a proportionately short caudal peduncle relative to the positive extreme of RW1) than the large morph in terms of the RW1, although the relationship between body shape and size differed between the morphs. The difference in RW1 scores may reflect differences in growth rates, as higher rates have been observed in the large morph (Reist et al. 1995; Guiguer et al. 2002). This would not, however, explain why the strength of the correlation (of RW1 vs. body size) differed between the two morphs, especially when considering that the large morph exhibits greater variability in size at age than the small morph (Guiguer et al. 2002). It is also possible that the morphs are exhibiting heterochrony, or differential timing of developmental events (Gould 1966; Skúlason et al. 1989). The small morph may be achieving a “mature” body shape at a younger age than the large morph, which would be beneficial if the small morph is adapted to unsteady swimming (Webb 1982). Lacking specimen ages, it is impossible to fully differentiate the influences of resource-limited growth and heterochrony; however, the greater variability in the RW1 scores across body size for small morphs suggests that heterochrony may play a role in generating morphological differences between the morphs of Arctic char from Lake Hazen, as has been observed among morphs of Arctic char from Thingvallavatn (Skúlason et al. 1989).

Implications of differential fin size and shape

The median (dorsal, anal, and caudal) fins have been found to play an important role in acceleration for both steady and unsteady swimming (Lauder and Drucker 2004). Median fins in steady swimmers prevent lateral flow across the top and bottom of the body, reducing drag by delaying separation of flow (Weihs 1989). Unsteady swimmers may employ enlarged median fins to add to the surface area of the posterior body (i.e., towards the caudal peduncle), which consolidates flow, improving thrust and acceleration overall. In the large morph of Arctic char, the small anal fin would be beneficial in improving flow regimes across the caudal peduncle and fin, whereas the long anal fins of the small morph of Arctic char would increase the thrust-producing surface area of the caudal peduncle region, contributing to fast starts and manoeuvres.

The function of the pelvic fins in ray-finned fish is poorly understood compared with that of other fish fins (Lauder and Drucker 2004). Standen (2008) concluded that the pelvic fins in the salmonid rainbow trout (*Oncorhynchus mykiss* (Walbaum, 1792)) may dampen body oscillations and reduce drag during steady swimming. Furthermore, during manoeuvres (turns, sudden starts and stops), the pelvic fins act as trimming surfaces (Gosline 1980; Standen 2008). In the large morph, the small pelvic fins may dampen body oscillations (greater swimming efficiency), whereas the long pelvic fins of the small morph could improve turning radius and precision, as well as contribute to the overall area of the lateral profile.

There are several possible mechanisms by which the elongation of the anterior rays (that produces the observed scythe shape) in the pelvic and anal fins in the small morph could influence swimming dynamics. The elongated fins

rays may help to generate turbulent wake in front of the caudal fin or improve flexibility towards the distal end of the pelvic and anal fins, which would aid in precise manoeuvring (Greenwood et al. 1966; Webb 1982). The elongated tips of the pelvic and anal fins of the small morph may extend past the turbulent boundary layer produced around the fish as it accelerates, which would improve the effectiveness of the fins at controlling stability and manoeuvrability (Pavlov 2003). Alternatively, the elongation of the anterior rays of the anal and pelvic fins may function in some sort of substrate interaction in the small morph of Arctic char, as has been observed in the parr of Atlantic salmon (*Salmo salar* L., 1758) (Arnold et al. 1991). This would be supported by the observation that some small morph of Arctic char exhibited extensions of the most ventral rays of ventral lobe of the caudal fin, but never exhibited fin ray extensions of the dorsal lobe (supplementary Fig. S2).⁴

Genetic differentiation of Lake Hazen Arctic char

Our results suggest that the large and small morphs do not constitute genetically distinct populations. However, deviations in tests for HWE and differentiation occurred at individual loci, which may indicate a few weak genetic differences between the two morphs. Furthermore, it is possible that the variability of the five (assumedly) selectively neutral loci may not reflect the variation observed in encoding loci. Therefore, our estimates of genetic divergence between morphs of Lake Hazen Arctic char could underestimate the true level of divergence between the morphs. The present discussion will focus on interpreting the results of our analyses. However, given that the potential weaknesses of the approaches used in the present study may lead to an under-representation of the genetic divergence between the morphs, it must be noted that further genetic studies are necessary to confirm (or refute) our findings of no significant genetic differentiation between the morphs of Lake Hazen Arctic char.

Morphs of Arctic char in other lakes exhibit a wide range of genetic divergence. Genetic differentiation has been observed in populations of Arctic char from Loch Rannoch, Scotland (Hartley et al. 1992), as well as several Icelandic lakes, including Thingvallavatn (Volpe and Ferguson 1996), Svinavatn, and Lake Galtabol (Gíslason et al. 1999), whereas no differentiation has been observed in the populations from Vatnshlidarvatn and Stora Vidarvatn, Iceland (Gíslason et al. 1999). Considering the relatively recent time frame in which Arctic char could have colonized and been isolated in Lake Hazen, it may not be a surprise that genetic differences at (presumably) selectively neutral loci have not accumulated between the two morphs. Gíslason et al. (1999) noted that a maximum of 3000 generations of Arctic char may have lived in the Icelandic lakes since they were deglaciated 10000 years ago, making divergence between these morphs extremely rapid. Based on the geologic history of the region, it is likely that Lake Hazen was colonized much later, occurring 3300 to 5300 years ago (Smith 1999, 2002). It is also probable that the generation time of Lake Hazen Arctic char is greater than that of other polymorphic Arctic char. Lake Hazen Arctic char as old as 35 years of age have been collected (Guiguer et al. 2002), with a mean age of sampled adults often ranging between

18 and 22 years. By comparison, maximum ages of 15 and 18 years have been reported for Arctic char from Thingvallavatn and Loch Rannoch, respectively (Gardner et al. 1988; Sandlund et al. 1992; Adams et al. 1998).

Lacking genetic differences between the two Lake Hazen morphs, it is possible that phenotypic plasticity plays an important role in maintaining the morphological differences between the two morphs. Diet has been shown to regulate head morphology in polymorphic Arctic char from Loch Rannoch, despite significant genetic differences between the morphs (Hartley et al. 1992; Adams and Huntingford 2004). It has been suggested that heritable variation in foraging behaviours could be reinforced by plastic morphology and promote assortative mating; following reproductive isolation, such plasticity could be rapidly reduced (Wimberger 1994; Adams et al. 2003). It is possible that in genetically differentiated morphs of Arctic char, such as those observed in Thingvallavatn, morphological traits that exhibit a strong genetic basis may have originally been plastic and later become fixed. In this case, the Lake Hazen Arctic char could represent an example of the early stages of the divergence of Arctic char.

Resource polymorphism in Lake Hazen Arctic char

The results of this and previous studies on Lake Hazen Arctic char suggest that differences observed between large and small morphs of Arctic char are indicative of a resource polymorphism. The large morph has been found to feed at a higher trophic level than the small morph, with the large morph preying on juvenile Arctic char (<20–25 cm) and the small morph preying on benthic invertebrates (Reist et al. 1995; Babaluk et al. 1997; Guiguer et al. 2002). The coloration of the small morph is typical of a fish feeding near the substrate (dark dorsal coloration), whereas the coloration of the large morph is typical of a fish feeding in the water column (silvery dorsal and lateral coloration, pale ventral coloration). The two morphs, when visually assessed based on qualitative characteristics (e.g., coloration), were found to exhibit complex, quantitative morphological differences with important functional implications. The large morph appears to be adapted to steady swimming, whereas the small morph appears to be adapted to unsteady swimming. It has been repeatedly observed that such trade-offs in swimming dynamics are typical of morphs specializing on pelagic prey (steady swimming) or benthic prey (unsteady swimming; Webb 1982; Malmquist et al. 1992; Hjelm et al. 2001). A lack of genetic differentiation between the two morphs would not rule out resource polymorphism as playing a major role in the divergence of the two morphs observed in Lake Hazen, and may suggest a role for phenotypic plasticity in the maintenance of the different morphologies. The life histories, trophic ecology, and morphologies of the large and small morphs reported in the present study and in previous studies are consistent with previous reports of resource polymorphisms in Arctic char, other fish, and other vertebrate species (Wimberger 1994).

Genetic and ontogenetic studies have suggested that the piscivorous morphs from Thingvallavatn represent planktivorous individuals that have attained a sufficient size to prey on other fish and thus undergo an ontogenetic niche shift (Skúlason et al. 1989). The Thingvallavatn piscivore exhib-

its a streamlined, steady swimmer morphology which is consistent with that observed from the planktivorous morph. However, the piscivorous morph from Loch Ericht, Scotland, exhibits an unsteady swimmer morphology and lives epibenthically, preying on both fish and benthic invertebrates (Fraser et al. 1998). It appears that the piscivorous morphs in Arctic char may arise via several trophic and ontogenetic pathways. In the case of the Lake Hazen piscivorous (large) morph, it is possible that the morph may have arisen through an ontogenetic diet shift in juvenile Arctic char feeding on zooplankton, as has been previously suggested (Guiguer et al. 2002). The body and head morphology of the large morph is most similar to streamlined planktivorous morphs and the planktivore-originating piscivore from Lake Thingvallavatn, rather than the benthivore-originating piscivore from Loch Ericht. Therefore, the most appropriate classification of these two morphs may be the benthic morph (small morph) and the pelagic morph (large morph), rather than the benthivorous and piscivorous morphs.

From our results, it is evident that the Lake Hazen Arctic char do not currently represent a population diverging to a significant, measurable level (though see discussion of genetic results). However, the variety of Arctic char polymorphisms together may indicate one mechanism by which sympatric populations may diverge. The potential plastic morphology of the Lake Hazen Arctic char may represent a polymorphic population that is “primed” to take advantage of environmental (changing habitats), ecological (variation in resource availability), or genetic (appearance of novel traits or heritable behaviours) changes. The resource polymorphism exhibited by Lake Hazen Arctic char may represent an early stage along a gradient of ecological, spatial, and reproductive differentiation on a route towards speciation and adaptive radiations (Dieckmann et al. 2004; Butlin et al. 2008). This highlights the importance of long-term examinations of morphological differentiation and population dynamics of polymorphic populations, such as those exhibited by the Lake Hazen Arctic char, particularly in northern ecosystems that are anticipated to change significantly as a consequence of climate change.

Acknowledgements

The work could not have been undertaken without the generous logistic support provided by the Polar Continental Shelf Project (Natural Resources Canada), Parks Canada (notably Ross Glenfield, Park Manager, Quttinirpaaq National Park), the Grise Fiord Hunters and Trappers Association, and the Nunavut Research Institute (notably Rick Armstrong). We are grateful to Trina Peters for her technical assistance associated with the genetic analyses. Financial support for the work was provided by a Natural Sciences and Engineering Research Council of Canada Discovery Grant and associated Northern Research Supplement to J.A.H.

References

Adams, C.E., and Huntingford, F.A. 2004. Incipient speciation driven by phenotypic plasticity? Evidence from sympatric populations of Arctic charr. *Biol. J. Linn. Soc.* **81**(4): 611–618. doi:10.1111/j.1095-8312.2004.00314.x.

- Adams, C.E., Fraser, D., Huntingford, F.A., Greer, R.B., Askew, C.M., and Walker, A.F. 1998. Trophic polymorphism amongst Arctic charr from Loch Rannoch, Scotland. *J. Fish Biol.* **52**(6): 1259–1271. doi:10.1111/j.1095-8649.1998.tb00970.x.
- Adams, C.E., Woltering, C., and Alexander, G. 2003. Epigenetic regulation of trophic morphology through feeding behaviour in Arctic charr, *Salvelinus alpinus*. *Biol. J. Linn. Soc.* **78**(1): 43–49. doi:10.1046/j.1095-8312.2003.00126.x.
- Adams, C.E., Hamilton, D.J., McCarthy, I., Wilson, A.J., Grant, A., Alexander, G., Waldron, S., Snorasson, S.S., Ferguson, M.M., and Skúlason, S. 2006. Does breeding site fidelity drive phenotypic and genetic sub-structuring of a population of Arctic charr? *Evol. Ecol.* **20**(1): 11–26. doi:10.1007/s10682-005-2489-4.
- Alekseyev, S.S., Samusenok, V.P., Matveev, A.N., and Pichugin, M.Y. 2002. Diversification, sympatric speciation, and trophic polymorphism of Arctic charr, *Salvelinus alpinus* complex, in Transbaikalia. *Environ. Biol. Fishes.* **64**(1–3): 97–114. doi:10.1023/A:1016050018875.
- Arnold, G.P., Webb, P.W., and Holford, B.H. 1991. The role of the pectoral fins in station-holding of Atlantic salmon parr (*Salmo salar* L.). *J. Exp. Biol.* **156**(1): 625–629.
- Austin-Smith, P., Smith, S., Bondy, D., Caulkett, N., Festa-Bianchet, M., Hudson, R., McKay, D., O’Brien, M., Ripley, J., Schwantje, H., Shury, T., and Griffin, G. 2003. Guidelines on the care and use of wildlife. In *Guide to the Care and Use of Experimental Animals*. Vol. 2. Canadian Council on Animal Care. Ottawa, Ont.
- Babaluk, J.A., Halden, N.M., Reist, J.D., Kristofferson, A.H., Campbell, J.L., and Teesdale, W.J. 1997. Evidence for non-anadromous behaviour of arctic charr (*Salvelinus alpinus*) from Lake Hazen, Ellesmere Island, Northwest Territories, Canada, based on scanning proton microprobe analysis of otolith strontium distribution. *Arctic*, **50**: 224–233.
- Babaluk, J.A., Wissink, R., Troke, B.G., Clarke, D.A., and Johnston, J.D. 2001. Summer movements of radio-tagged Arctic charr (*Salvelinus alpinus*) in Lake Hazen, Nunavut, Canada. *Arctic*, **54**(4): 418–424.
- Bookstein, F.L. 1991. Morphometric tools for landmark data: geometry and biology. Cambridge University Press, Cambridge.
- Bookstein, F.L. 1997. Landmark methods for forms without landmarks: morphometrics of group differences in outline shape. *Med. Image Anal.* **1**(3): 225–243. doi:10.1016/S1361-8415(97)85012-8.
- Bradbury, I.R., Campana, S.E., and Bentzen, P. 2008. Low genetic connectivity in an estuarine fish with pelagic larvae. *Can. J. Fish. Aquat. Sci.* **65**(2): 147–158. doi:10.1139/F07-154.
- Butlin, R.K., Galindo, J., and Grahame, J.W. 2008. Sympatric, parapatric or allopatric: the most important way to classify speciation? *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **363**(1506): 2997–3007. doi:10.1098/rstb.2008.0076. PMID:18522915.
- Corander, J., Waldmann, P., and Sillanpää, M.J. 2003. Bayesian analysis of genetic differentiation between populations. *Genetics*, **163**(1): 367–374. PMID:12586722.
- Dieckmann, U., Tautz, D., Doebeli, M., and Metz, J.A.J. 2004. Epilogue. In *Adaptive speciation. Edited by U. Dieckmann, D. Tautz, M. Doebeli, and J. A. J. Metz*. Cambridge University Press, Cambridge. pp. 380–394.
- Elphinstone, M.S., Hinten, G.N., Anderson, M.J., and Nock, C.J. 2003. An inexpensive and high-throughput procedure to extract and purify total genomic DNA for population studies. *Mol. Ecol.* **3**(2): 317–320. doi:10.1046/j.1471-8286.2003.00397.x.
- Fraser, D., Adams, C.E., and Huntingford, F.A. 1998. Trophic polymorphism among Arctic charr, *Salvelinus alpinus* L., from Loch Ericht, Scotland. *Ecol. Freshwat. Fish.* **7**(4): 184–191. doi:10.1111/j.1600-0633.1998.tb00185.x.

- Gardner, A.S., Walker, A.F., and Greer, R.B. 1988. Morphometric analysis of two ecologically distinct forms of Arctic charr, *Salvelinus alpinus* (L.), in Loch Rannoch, Scotland. *J. Fish Biol.* **32**(6): 901–910. doi:10.1111/j.1095-8649.1988.tb05433.x.
- Gíslason, D., Ferguson, M.M., Skúlason, S., and Snorrason, S.S. 1999. Rapid and coupled phenotypic and genetic divergence in Icelandic Arctic char (*Salvelinus alpinus*). *Can. J. Fish. Aquat. Sci.* **56**(12): 2229–2234. doi:10.1139/cjfas-56-12-2229.
- Gosline, W.A. 1980. The evolution of some structural systems with reference to interrelationships of modern lower teleostean fish groups. *Jpn. J. Ichthyol.* **27**: 1–28.
- Gould, S.J. 1966. Allometry and size in ontogeny and phylogeny. *Biol. Rev. Camb. Philos. Soc.* **41**(4): 587–640. doi:10.1111/j.1469-185X.1966.tb01624.x. PMID:5342162.
- Greenwood, P.H. 1974. The cichlid fishes of Lake Victoria, East Africa: the biology and evolution of a species flock. *Bull. Br. Mus. (Nat. Hist.) Zool. Suppl.* **6**: 1–134.
- Greenwood, P.H., Rosen, D.E., Weitzman, S.H., and Myers, G.S. 1966. Phyletic studies of teleostean fishes, with a provisional classification of living forms. *Bull. Am. Mus. Nat. Hist.* **131**(Suppl.): 343–455.
- Guiguer, K.R.R.A., Reist, J.D., Power, M., and Babaluk, J.A. 2002. Using stable isotopes to confirm the trophic ecology of Arctic charr morphotypes from Lake Hazen, Nunavut, Canada. *J. Fish Biol.* **60**(2): 348–362. doi:10.1111/j.1095-8649.2002.tb00285.x.
- Guo, S.W., and Thompson, E.A. 1992. Performing the exact test of Hardy–Weinberg proportion for multiple alleles. *Biometrics*, **48**(2): 361–372. doi:10.2307/2532296. PMID:1637966.
- Halden, N.M., Mejia, S.R., Babaluk, J.A., Reist, J.D., Kristofferson, A.H., Campbell, J.L., and Teesdale, W.J. 2000. Oscillatory zinc distribution in Arctic char (*Salvelinus alpinus*) otoliths: the result of biology or environment? *Fish. Res.* **46**(1–3): 289–298. doi:10.1016/S0165-7836(00)00154-5.
- Hartley, S.E., McGowan, C., Greek, R.B., and Walker, A.F. 1992. The genetics of sympatric Arctic charr [*Salvelinus alpinus* (L.)] populations from Loch Rannoch, Scotland. *J. Fish Biol.* **41**(6): 1021–1031. doi:10.1111/j.1095-8649.1992.tb02729.x.
- Hjelm, J., Svanbäck, R., Bryström, P., Persson, L., and Wahlström, E. 2001. Diet-dependent morphology and ontogenetic reaction norms in Eurasian perch. *Oikos*, **95**(2): 311–323. doi:10.1034/j.1600-0706.2001.950213.x.
- Hunter, J.G. 1960. Hazen Lake. In Fisheries Research Board of Canada, Arctic Unit. Annual Report and Investigators Summaries (April 1, 1959 to March 31, 1960). Fisheries Research Board of Canada, Ottawa, Ont. pp. 18–20.
- Johnson, L. 1980. The Arctic charr, *Salvelinus alpinus*. In Charrs: salmonid fishes of the genus *Salvelinus*. Edited by E.K. Balon. Dr. W. Junk Publishers, The Hague, the Netherlands. pp. 15–98.
- Lauder, G.V., and Drucker, E.G. 2004. Morphology and experimental hydrodynamics of fish fin control surfaces. *IEEE J. Oceanic Eng.* **29**(3): 556–571. doi:10.1109/JOE.2004.833219.
- Leberg, P.L. 2002. Estimating allelic richness: effects of sample size and bottlenecks. *Mol. Ecol.* **11**(11): 2445–2449. doi:10.1046/j.1365-294X.2002.01612.x. PMID:12406254.
- Lighthill, M.J. 1977. Mathematical theories of fish swimming. In Fisheries mathematics. Edited by J.H. Steele. Academic Press, New York. pp. 131–144.
- Malmquist, H.J., Snorrason, S.S., Skúlason, S., Jonsson, B., Sandlund, O.T., and Jónasson, P.M. 1992. Diet differentiation in polymorphic Arctic charr in Thingvallavatn, Iceland. *J. Anim. Ecol.* **61**(1): 21–35. doi:10.2307/5505.
- McLaren, I.A. 1964. Zooplankton of Lake Hazen, Ellesmere Island, and a nearby pond, with special reference to the copepod *Cyclops scutifer* Sars. *Can. J. Zool.* **42**(4): 613–629. doi:10.1139/z64-053.
- McPhail, J.D. 1984. Ecology and evolution of sympatric sticklebacks (*Gasterosteus*): morphological and genetic evidence for a species pair in Enos Lake, British Columbia. *Can. J. Zool.* **62**(7): 1402–1408. doi:10.1139/z84-201.
- Oliver, D.R. 1963. Entomological studies in the Lake Hazen area, Ellesmere Island, including lists of species of arachnida, collembola and insecta. *Arctic*, **16**: 175–180.
- Pavlov, V.V. 2003. Wing design and morphology of the harbor porpoise dorsal fin. *J. Morphol.* **258**(3): 284–295. doi:10.1002/jmor.10135. PMID:14584030.
- Pritchard, J.K., Stephens, M., and Donnelly, P. 2000. Inference of population structure using multilocus genotype data. *Genetics*, **155**(2): 945–959. PMID:10835412.
- Raymond, M., and Rousset, F. 1995. GENEPOP (version 1.2): population genetics software for exact tests and ecumenicism. *J. Hered.* **86**(3): 248–249.
- Reist, J.D. 1985. An empirical evaluation of several univariate methods that adjust for size variation in morphometric data. *Can. J. Zool.* **63**(6): 1429–1439. doi:10.1139/z85-213.
- Reist, J.D., Gyselman, E., Babaluk, J.A., Johnson, J.D., and Wissink, R. 1995. Evidence for two morphotypes of Arctic char (*Salvelinus alpinus* (L.)) from Lake Hazen, Ellesmere Island, Northwest Territories, Canada. *Nord. J. Freshw. Res.* **71**: 396–410.
- Rohlf, F.J. 2002. Geometric morphometrics in phylogeny. In Morphology, shape and phylogeny. Chap. 9. Systematics Association Special Volume Series No. 64. Edited by N. MacLeod and P.L. Forey. Taylor and Francis, London. pp. 175–193.
- Rohlf, F.J. 2003. tpsRelw, relative warps analysis, version 1.36. Department of Ecology and Evolution, State University of New York at Stony Brook, Stony Brook, N.Y.
- Rohlf, F.J., and Slice, D. 1990. Extensions of the Procrustes method for the optimal superimposition of landmarks. *Syst. Zool.* **39**(1): 40–59. doi:10.2307/2992207.
- Sandlund, O.T., Gunnarsson, K., Jónasson, P.M., Jonsson, B., Lindem, T., Magnússon, K.P., Malmquist, H.J., Sigurjónsdóttir, H., Skúlason, S., and Snorrason, S.S. 1992. The arctic charr *Salvelinus alpinus* in Thingvallavatn. *Oikos*, **64**(1–2): 305–351. doi:10.2307/3545056.
- Schluter, D. 1993. Adaptive radiation in sticklebacks: size, shape and habitat use efficiency. *Ecology*, **74**(3): 699–709. doi:10.2307/1940797.
- Skúlason, S., and Smith, T.B. 1995. Resource polymorphisms in vertebrates. *Trends Ecol. Evol.* **10**(9): 366–370. doi:10.1016/S0169-5347(00)89135-1.
- Skúlason, S., Noakes, D.L.G., and Snorrason, S.S. 1989. Ontogeny of trophic morphology in four sympatric morphs of arctic charr *Salvelinus alpinus* in Thingvallavatn, Iceland. *Biol. J. Linn. Soc.* **38**(3): 281–301. doi:10.1111/j.1095-8312.1989.tb01579.x.
- Skúlason, S., Snorrason, S.S., and Jonsson, B. 1999. Sympatric morphs, populations and speciation in freshwater fish with an emphasis on Arctic charr. In Evolution of biological diversity. Oxford University Press, New York. pp. 70–92.
- Smith, I.R. 1999. Late quaternary glacial history of Lake Hazen Basin and eastern Hazen Plateau, northern Ellesmere Island, Nunavut, Canada. *Can. J. Earth Sci.* **36**(9): 1547–1565. doi:10.1139/cjes-36-9-1547.
- Smith, I.R. 2002. Diatom-based Holocene paleoenvironmental records from continental sites on northeastern Ellesmere Island, high Arctic, Canada. *J. Paleolimnol.* **27**(1): 9–28. doi:10.1023/A:1013514305420.
- Smith, T., and Skúlason, S. 1996. Evolutionary significance of resource polymorphisms in fishes, amphibians, and birds. *Annu. Rev. Ecol. Syst.* **27**(1): 111–133. doi:10.1146/annurev.ecolsys.27.1.111.

- Standen, E.M. 2008. Pelvic fin locomotor function in fishes: three-dimensional kinematics in rainbow trout (*Oncorhynchus mykiss*). *J. Exp. Biol.* **211**(18): 2931–2942. doi:10.1242/jeb.018572. PMID:18775930.
- Swanson, B.O., Gibb, A.C., Marks, J.C., and Hendrickson, D.H. 2003. Trophic polymorphism and behavioural differences decrease intraspecific competition in a cichlid, *Herichthys minckleyi*. *Ecology*, **84**(6): 1441–1446. doi:10.1890/02-0353.
- Thorpe, R.S. 1975. Quantitative handling of characters useful in snake systematics with particular reference to intraspecific variation in the Ringed Snake *Natrix natrix* (L.). *Biol. J. Linn. Soc.* **7**(1): 27–43. doi:10.1111/j.1095-8312.1975.tb00732.x.
- Volpe, J.P., and Ferguson, M.M. 1996. Molecular genetic examination of the polymorphic Arctic charr *Salvelinus alpinus* of Thingvallavatn, Iceland. *Mol. Ecol.* **5**(6): 763–772. doi:10.1111/j.1365-294X.1996.tb00372.x. PMID:8981767.
- Webb, P.W. 1982. Locomotor patterns in the evolution of actinopterygian fishes. *Am. Zool.* **22**: 329–342.
- Weihs, D. 1989. Design features and mechanics of axial locomotion in fish. *Am. Zool.* **29**: 151–160.
- Wimberger, P.H. 1994. Trophic polymorphisms, plasticity and speciation in vertebrates. *In* Theory and application of fish feeding ecology. Edited by D.J. Stouder, K.L. Fresh, and R.J. Feller. University of South Carolina Press, Columbia. pp. 19–43.
- Zelditch, M.L., Swiderski, D.L., and Fink, W.L. 2000. Discovery of phylogenetic characters in morphometric data. *In* Phylogenetic analysis of morphological data. Chap. 3. Edited by J.J. Wiens. Smithsonian Institution Press, Washington, D.C. pp. 37–83.