Polymorphism in lake trout in Great Bear Lake: intra-lake morphological diversification at two spatial scales

LOUISE CHAVARIE¹*, KIMBERLY HOWLAND², LES HARRIS² and WILLIAM TONN¹

¹Department of Biological Sciences, University of Alberta, Edmonton, AB, T6G 2E9, Canada
²Fisheries and Oceans Canada, 501 University Crescent, Winnipeg, MB, R3T 2N6, Canada

Received 22 May 2014; revised 23 July 2014; accepted for publication 24 July 2014

Great Bear Lake is the most northerly lake of its size and provides unique opportunities for intraspecific diversification. Despite increasing attention to intraspecific polymorphism, several knowledge gaps remain (e.g. determining the extent of intraspecific diversification in large relatively pristine lakes and at which spatial scale it can occur). We focused on geographical patterns of morphological differentiation within lake trout (Salvelinus namaycush) to describe two levels of intralake diversification in Great Bear Lake. We used a combination of geometric and traditional linear measurements to quantify differences in body shape, head shape, and fin and body lengths among 910 adult lake trout from the five distinct arms of Great Bear Lake. Although head and fin linear measurements discriminated the three common morphotypes at the whole-lake level, inter-arm variation in body shape was observed within each morphotype. A comparison of genetic and morphological distance matrices revealed the lack of an association between the two sets of data, although both comparisons revealed an association in the inter-arm variation patterns among morphotypes, suggesting a phenotypically plastic response to distinct environments. The whole-lake and inter-arm morphological variation observed within lake trout demonstrates the importance of considering scale, especially across large lakes that exhibit marked complexity and a variety of freshwater habitats. © 2014 The Linnean Society of London, Biological Journal of the Linnean Society, 2014, ••, ••–••.


INTRODUCTION

Intraspecific variability contributes significantly to biodiversity in northern freshwater fish faunas. Salmonid, gastererosteid, and osmerid fishes, in particular, represent some of the best examples of adaptative intraspecific radiation among freshwater fishes. In northern post-glacial lakes, these groups of fishes display variation in morphology, life history, ecology, and habitat use not only across their geographical ranges, but also sympatrically within single systems (i.e. sympatric resource polymorphism; Sandlund et al., 1992; Adam et al., 2006; Keeley, Parkinson & Taylor, 2007). Sympatric divergence can occur (but is not limited to) when populations experience disruptive selection associated with different ecological environments containing alternative resources (Schluter, 2000; Crispo et al., 2006). Under the standard resource polymorphism model, a subset of individuals within a population switches to a novel and/or sub-optimal resource, which reduces intraspecific competition and facilitates morphological divergence (Olsson et al., 2006; Moles et al., 2010). These ‘evolutionarily young’ polymorphic fishes, exhibiting varying degrees of reproductive isolation, may represent initial stages in speciation (Bush, 1994; Skúlason & Smith, 1995; Hendry et al., 2009).

Morphotypes are defined as groups of individuals within a species that are distinguished by a composite of traits (e.g. body shape), representing adaptations to a number of environmental and resource variables across different environments (Robinson & Parson, 2002; Lowry, 2012). The high degree of niche
differentiation (often referred to as ‘ecological opportunity’; Schluter & Rambaut, 1996; Schluter, 2000) found in northern lake environments is associated with low interspecific competition and predation, and open niches (Smith & Skúlason, 1996) that promote adaptive radiation. Environmental heterogeneity is another important component enhancing intraspecific diversity. Lakes can represent a rich source of environmental gradients (e.g. depth, temperature, light, shoreline development, wave exposure, substrate) associated with different prey species and habitat characteristics that have the potential to promote ecological segregation (Smith & Todd, 1984; Taylor, 1991).

Lake trout, *Salvelinus namaycush*, has been previously associated with low intraspecific variation, especially when compared to its congner Arctic char (*Salvelinus alpinus*) (Hindar & Jonsson, 1993; Jonsson & Jonsson, 2001; Adam et al., 2007). However, lake trout can exhibit some sympatric diversification, at least in large deep lakes (Zimmerman, Krueger & Eshenroder, 2006, 2007; Eshenroder, 2008; Zimmerman et al., 2009), or in a newly colonized lake (Stafford et al., 2014) where two or three different morphotypes vary in diet and in their use of habitat (depth). Chavarie, Howland & Tonn (2013) recently identified one rare and three common shallow-water morphotypes of lake trout in Great Bear Lake (an additional deep-water form is also assumed to exist). Great Bear Lake might exhibit greater diversity than expected, although historical anecdotal observations have suggested similar levels of variation occurring in other large aquatic systems (Brown et al., 1981; Goodier, 1981). As a result of significant anthropogenic impacts in the Laurentian Great Lakes, however, lake trout diversity has greatly decreased (Zimmerman et al., 2007), limiting quantitative investigations or comparisons with Great Bear Lake. Consequently, Great Bear Lake may currently be the only lake of its size in which to investigate natural levels of lake trout sympatric diversity.

Morphological discrimination within Great Bear Lake was mostly associated with differences in head and fins among morphs. Morph 1 was characterized by a smaller head and jaws and intermediate fin sizes; Morph 2 had a longer head and jaws but smaller fins; and Morph 3 had the deepest head and caudal peduncle and longest fins. By contrast to the noticeable differences in head and fin measurements among morphotypes, variation in body shape was not observed at the whole-lake level in Great Bear Lake, despite being one of the main distinguishing features among the depth-related morphotypes in other large lakes. Given the large size and complex shape of this lake, we hypothesized that body-shape variation within a single morphotype could exist among the lake’s five arms, which may have obscured differentiation at the whole-lake scale. If supported, this microgeographical variation and its driving mechanism could fundamentally alter ecological and evolutionary dynamics in the lake, although research has not sufficiently investigated smaller spatial scale adaptation (Richardson et al., 2014).

Great Bear Lake is one of the largest and deepest lakes in the world (Alfonso, 2004). Five somewhat isolated arms with diverse aquatic habitats are connected to a central basin (Fig. 1). This complex morphometry, combined with the generally limited movement of lake trout within a system (Schmalz et al., 2002), suggests that the lake trout ‘populations’ of each arm could experience at least some degree of isolation and/or differences in habitats. Because isolation-by-distance and/or adaptive opportunities independent of geographical distance (e.g. isolation-by-adaptation) can result in differentiation among fish (Schluter & Nagel, 1995; Kristjánsson, Noakes & Skúlason, 2002; Nosil, Egan & Funk, 2007), we hypothesized that there could be geographical patterns of morphological divergence among arms, each of which is the size of a lake, associated with the ‘lake trout complex’ of Great Bear Lake.

To test this hypothesis, the present study aimed to: (1) determine whether (and how many of) the three common morphotypes of lake trout display variation among arms in Great Bear Lake; (2) quantitatively summarize the morphological variation within morphotypes by using a combination of geometric morphometric and traditional linear measures; and (3) relate the inter-arm morphological variation to any differences in the physical and/or trophic information for the morphs among arms. Given a parallel study of genetic variation among and within morphotypes across arms (Harris et al., 2014), we also (4) compared the similarity of morphological and genetic patterns among arms as an indicator of potential adaptive patterns. Such information will be relevant for documenting intraspecific biodiversity in one of North America’s few remaining pristine large lake systems in a region expected to be significantly altered by climate change. Furthermore, our results will be important for understanding the evolution of morphological and ecological variation in species occupying recently colonized, post-glacial habitats, particularly large lakes.

**MATERIAL AND METHODS**

**STUDY AREA**

At 31 790 km² and with a maximum depth of 446 m (mean depth = 90 m), Great Bear Lake is the ninth
largest and fiftieth deepest freshwater lake in the world (Johnson, 1975) (Fig. 1). Great Bear Lake was formed by the scouring action of the Laurentide ice-sheet during the Pleistocene and was originally part of glacial Lake McConnell, 8000–10 000 years BP (Johnson, 1975; Pielou, 1991). The lake and its catchment (approximately 145 000 km²) straddle two major physiographical regions: the metamorphic Precambrian shield to the north and east (Dease and McTavish arms) and the sedimentary Paleozoic deposits of the Mackenzie Lowlands to the south and west (McVicar, Keith, and Smith arms) (MacDonald et al., 2004). Three terrestrial ecozones surround Great Bear Lake, the Southern Arctic along the northern shore (Dease Arm), the Taiga Plains to the west and south (McVicar, Keith, and Smith arms), and the Taiga Shield to the east (McTavish Arm) (MacDonald et al., 2004) (Fig. 1).

Correspondingly diverse aquatic habitats can be found among the different arms of the lake, and along the 2719 km of shoreline (with an additional 824 km contributed by islands) (Johnson, 1975; Alfonso, 2004). These include offshore and nearshore shoals, dropoffs of varying depths, bays, islands, as well as river and stream mouths that can be very sheltered from open water. Great Bear Lake has two main inflows, the Camsell and the Johnny Hoe rivers in McTavish and McVicar arms, respectively, as well as one major outflow, the Great Bear River in Keith Arm. The Johnny Hoe River has its origin in an extensive area of muskeg (acidic peatland soil) to the south, resulting in McVicar Arm having the least transparent water (Johnson, 1975). Being the smallest, shallowest, most isolated, and southernmost arm, McVicar is also generally warmer than the rest of the lake (Riley, 1935). Its eastern shore is characterized by extensive marshy bays, whereas the western side has sandy beaches. McTavish arm is characterized by a complex shoreline and numerous offshore islands (Riley, 1935). McTavish is deeper than the other arms, has the largest volume, and has the clearest water (maximum Secchi depth = 30 m; Johnson, 1975). Dease, Smith, and Keith arms have intermediate transparencies, with the majority of Secchi depths being 12–16 m. Dease is the most northerly arm, intersecting the Arctic circle, whereas Keith arm has the largest surface area. Fifteen fish species are reported from Great Bear Lake but only half were commonly caught in our nets (as indicated by an asterisk): Arctic grayling* (Thymallus arcticus), burbot (Lota lota), chum salmon (Oncorhynchus keta), fourhorn sculpin (Myoxocephalus quadricornis),
inconnu (Stenodus leucichthys), cisco* (Coregonus artedi), lake trout*, lake whitefish* (Coregonus clupeaformis), longnose sucker (Catostomus catostomus), ninespine stickleback* (Pungitius pungitius), northern pike* (Esox lucius), round whitefish* (Prosopium cylindraceum), trout perch (Percopsis omiscomaycus), slimy sculpin* (Cottus cognatus), walleye (Sander vitreus) (Johnson, 1975; Alfonso, 2004; MacDonald et al., 2004).

**DATA COLLECTION**

We analyzed 910 adult lake trout captured from all five arms of Great Bear Lake between 2002 and 2010: Keith (2002 and 2003), McVicar (2003 and 2008), McTavish (2009), Dease (2005 and 2010), and Smith (2006). All fish were caught at depths < 30 m, using paired bottom sets (approximately 24 h) of a 14-cm and a multi-mesh (3.8–14 cm) gill net during July and August. Multiple locations within each arm were sampled to spatially represent the arm, with similar net locations used if multiple years were sampled; surface water temperature was measured at each net location at the same time of sampling. A lateral full-body digital image was taken of each trout, with extended fins, as described in Chavarie et al. (2013). For each trout, fork length, round weight, sex, and stage of maturity were recorded and stomachs were preserved if they were not empty. Our analyses focused on adults (> 450 mm) because they display greater diversity in morphological characteristics than juveniles (Chavarie et al., 2013).

**MORPHOLOGY**

Analyses of digital images combined classical with geometric morphometrics (Bookstein, 1991). Selected morphological characteristics focused on fins, head, and body shape, as a result of their direct and indirect relationships to foraging and swimming and because they are traits that are most likely subject to rapid change in fishes (Webb, 1984; Kristjánsson et al., 2002; Kahlainen, Alajarvi, & Lehtonen, 2005). Twenty-three homologous points, or landmarks, identical to those in Chavarie et al. (2013), were used. Seventeen landmarks covered the outline of the body to extract body shape information, whereas 18 were used to measure 12 linear distances (Fig. 2A). Linear and shape measures from the landmarks were comparable (by varying degrees) to those used in previous lake trout studies in Great Bear Lake (Blackie, Weese & Noakes, 2003), Great Slave Lake (Zimmerman et al., 2006, 2009), Lake Mistassini (Zimmerman et al., 2007), and Lake Superior (Moore & Bronte, 2001). We also used 20 semi-landmarks (Bookstein 1991; Green, 1996; Zelditch et al., 2004) around the head (Fig. 2B) to capture more detailed shape information (Zimmerman et al., 2007, 2009; Chavarie et al., 2013).

Landmarks and semi-landmarks were digitized in x- and y-coordinates using TPSDIG2 (http://life.bio.sunysb.edu/morph). Subsequently, digitized landmarks and semi-landmarks were processed in a series of Integrated Morphometrics Packages (IMP) (http://www3.canisius.edu/~sheets/); morphological methods and the software are described in Zelditch et al. (2004) and morphological procedures are described in further detail in Chavarie et al. (2013).

Body and head shape analyses used geometric information from landmarks and semi-landmarks after differences in location, scale, and rotational effects were removed by CoordGen6f, producing the Procrustes distances. Because they are not homologous points, semi-landmarks were digitized by positioning points on a grid of ten equally spaced lines between the snout and the operculum using MAKEFAN software (Fig. 2B). Semi-landmarks were then ‘slid’ using SEMILAND6. STANDARD6 was used to remove size-dependant variation on shape data via a regression of landmarks on centroid size (Zelditch et al., 2004). Traditional linear measurements were calculated with TMORPHGEN6 and were then log10-transformed. Measurements were regressed against the standard length of the fish to obtain residuals that exhibit minimal size effects and could be used in the following analyses among and within morphotypes (Reist, 1985).

**ANALYSIS**

All body- and head-shape analyses were performed using IMP software using partial warp scores, which are thin-plate spline coefficients (Zelditch et al., 2004). They were used in all subsequent conventional statistical analyses because they have the correct number of degrees of freedom (Zelditch et al., 2004). We performed principal component analyses (PCA) on body- and head-shape data using PCAGEN (IMP software). This ordination technique constructs a reduced number of (multivariate) variables that maximizes the explained variance of the unreduced data set.

SYSTAT, version 12 software was used (Systat Software Inc.) to perform a PCA on the traditional linear measurements. Based on the most discriminating traits found among morphotypes (Chavarie et al., 2013), morphological groups were identified using head and fin linear measurements with MCLUST (version 4) cluster analysis in R (http://www.stat.washington.edu/mclust/). MCLUST is a method that combines model-based hierarchical clustering, expectation maximization for maximum-likelihood estimation in parameterized Gaussian
mixture models, and an estimation of the optimal number of clusters based on Bayesian information criteria (BIC) (Fraley & Raftery, 2006, 2007). The BIC is the value of the maximized log-likelihood, with a penalty on the number of model parameters, and allows comparison of models with differing parameterizations and/or differing numbers of clusters (Fraley & Raftery, 2006, 2007). A G-test (Sokal & Rohlf, 1981) was performed on the morphotypes identified with MCLUST to determine whether the proportion of each morphotype, based on our net catches, differed among arms. A G-test was also used to test whether sampling locations were sex-biased, by comparing female: male ratios within a morphotype among arms.

Canonical variate analyses (CVA) and validation procedures were conducted on all morphological data, including body shape, head shape, and linear measurements, within morphotypes across the five arms of Great Bear Lake to assess inter-arm morphological differences. Body and head shape were analyzed using CVAGen from the IMP software. Jackknife validation procedures included a test of the functioning of the assignment, with 1000 jackknife sets using 20% of our data as unknowns (Zelditch et al., 2004). For linear measurements, CVA was analyzed with SYSTAT, with the same jackknife validation procedure performed in MATLAB (The MathWorks, Inc.). To visualize the influence of the spatial scale (whole lake or among arms) in the body shape data, a series of nonmetric multidimensional scaling (NMS) analyses was conducted (using Nmmds7_14 from the IMP software) to compare the three morphs in each arm.

Figure 2. A, twenty-three landmarks (white circles, black numbers) used to measure body shape and linear measurements of lake trout from Great Bear Lake: (1) anterior tip of the snout, (2) posterior tip of maxilla, (3) center of eye, (4) top of cranium at middle point of eye, (5) posterior of neurocranium above tip of opercle, (6) dorsal fin anterior insertion, (7) dorsal fin posterior insertion, (8) adipose fin anterior insertion, (9) caudal fin dorsal insertion, (10) hypural plate midpoint, (11) caudal fin ventral insertion, (12) anal fin anterior insertion, (13) anal fin posterior insertion, (14) pelvic fin insertion, (15) pectoral fin insertion, (16) ventral surface of head below maxilla tip, (17) dorsal fin tip, (18–19) caudal fin tips, (20) anal fin tip, (21) pelvic fin tip, (22) pectoral fin tip, and (23) anterior tip of lower jaw. Fin and body length measurements of lake trout from Great Bear Lake are represented by black lines and white numbers: (1) upper jaw, (2) lower jaw, (3) head depth, (4) snout-eye, (5) head, (6) dorsal fin, (7) caudal fin, (8) caudal depth, (9) anal fin, (10) pelvic fin, (11) pectoral fin, and (12) standard body length; standard body length was used to standardize fin and body lengths and depths. B, 20 semi-landmarks (black circles and numbers, 4–23) were used along with one marker (24), and three landmarks (1–3), as in (A), to determine head shape.
Single-factor permutation multivariate analysis of variance (MANOVA) with 10 000 permutations was performed with CVAGen to test whether body shape means differed among morphs within an arm, and among arms within a morph. If MANOVA indicated differences, partial procrustes distance means (PPDMs) were calculated for pairwise comparisons of morphological distance using TWOGROUP6H from the IMP software as post-hoc tests (García-Rodríguez et al., 2011). A bootstrapped F-test ($N = 1600$ bootstraps) was used to determine whether the calculated PPDMs were significantly different. Pairwise distances among arms were also used to construct an unrooted Neighbor-joining tree using PHYLIP, version 3.69 (Felsenstein, 2005), which was plotted with FIGTREE, version 14 (http://tree.bio.ed.ac.uk/software/figtree/).

Finally, to test whether there was any association between morphological variation and genetic variation, morphological distances produced using the TWOGROUP6H software were compared with genetic distances among lake trout morphotypes. Briefly, pairwise estimates by Cavalli-Sforza & Edwards (1967) of chord distance, based on microsatellite DNA variation using 22 loci, were calculated to assess population structure (Harris et al., 2014). This was conducted using using the GENDIST module in the PHYLIP, version 3.69 (Felsenstein, 2005). To assess any association between morphological and genetic variation (genotype-to-phenotype association) among Great Bear Lake morphotypes, partial Mantel tests (Mantel, 1967; Legendre & Fortin, 2010) were used to compare morphological and genetic distance matrices. Mantel tests were also performed within the morphological and genetic datasets to assess similarity in the among-arm patterns between Morph 1 ($N = 16–121$ individuals per arm for morphology and $N = 20–59$ for genetics) and Morph 2 ($N = 61–175$ individuals per arm for morphology and $N = 20–45$ for genetics). Mantel tests were performed using PCORD, version 6 (McCune & Mefford, 2011) and were limited to Morphs 1 and 2 as a result of sample size limitations in the genetic analyses (Harris et al., 2014).

**RESULTS**

We sampled 910 lake trout captured throughout the five arms of Great Bear Lake (Table 1). MCLUST models showed a strong support for a division of the data into three clusters (morphs), which had a ΔBIC value of approximately 8 (Neumann, Cramon & Lohmann, 2008). The three-cluster MCLUST model calculated uncertainties of classification at 17.5% (Morph 1), 18.5% (Morph 2), and 19.1% (Morph 3). The distribution of trout among the morphs differed among arms ($G = 258.72$, $d.f. = 8$, $P < 0.01$) (Table 1). Morph 2 was relatively more abundant in McVicar, McTavish, and Smith arms, whereas Dease was the only arm with a substantive proportion of Morph 3 (Table 1). The distribution of females versus males within a morph was not significantly different among arms (Morph 1: $G = 5.82$, $P > 0.05$, Morph 2: $G = 6.41$, $P > 0.05$, and Morph 3: $G = 1.39$, $P > 0.05$) (Table 1).

CVAs suggested inter-arm variation in head and especially body shape for all three morphotypes (Fig. 3). For Morph 1, trout from Dease Arm had deeper heads, higher mouth and eye positions, and deeper and longer trunks, although they were more streamlined than Keith and Smith Arm trout (deeper bodies), whereas trout from Smith Arm had greater body depth relative to other arms (body shape: Axis 1 $\lambda = 0.05$, $P < 0.01$ and Axis 2 $\lambda = 0.24$, $P < 0.01$; head shape: Axis 1 $\lambda = 0.061$, $P < 0.01$ and Axis 2 $\lambda = 0.24$,...
Table 1. Number of each of three common morphotypes of lake trout captured in our gillnets in each of the five arms of Great Bear Lake and used in the morphological analyses

<table>
<thead>
<tr>
<th></th>
<th>Keith</th>
<th>McVicar</th>
<th>McTavish</th>
<th>Dease</th>
<th>Smith</th>
<th>Overall</th>
</tr>
</thead>
<tbody>
<tr>
<td>Morph 1</td>
<td>121 (73,48)</td>
<td>48 (25,23)</td>
<td>16 (6,10)</td>
<td>99 (47,52)</td>
<td>23 (14,9)</td>
<td>307</td>
</tr>
<tr>
<td>Morph 2</td>
<td>106 (58,48)</td>
<td>175 (69,106)</td>
<td>85 (36,49)</td>
<td>66 (29,37)</td>
<td>61 (27,34)</td>
<td>493</td>
</tr>
<tr>
<td>Morph 3</td>
<td>3 (1,2)</td>
<td>19 (5,14)</td>
<td>2 (0,2)</td>
<td>83 (26,57)</td>
<td>3 (1,2)</td>
<td>110</td>
</tr>
<tr>
<td>Overall</td>
<td>230</td>
<td>242</td>
<td>103</td>
<td>248</td>
<td>87</td>
<td>910</td>
</tr>
</tbody>
</table>

Females and males are presented in parenthesis, respectively.

Figure 3. Canonical variate analyses (CVAs) of linear measurements (A, D, G), body shape (B, E, H), and head shape (C, F, I) of 910 adult lake trout from Great Bear Lake, divided into three morphs. For each CVA, fish from different arms of Great Bear Lake are represented: •, Keith; x, McVicar; *, McTavish; ||, Dease; +, Smith. Each arm is also outlined by a 95% confidence ellipse.
For Morph 2, inter-arm analyses revealed longer heads and higher mouth positions for McTavish and Smith arms, and a deeper body for Keith Arm trout, whereas trout from Dease Arm expressed shorter body depths but deeper heads and caudal peduncles and higher eye positions; Morph 2 trout from McTavish and Smith arms were streamlined, and McTavish Arm trout also had longer trunks relative to the other four arms (body shape: Axis 1 $\lambda = 0.063, P < 0.01$ and Axis 2 $\lambda = 0.18, P < 0.01$; head shape: Axis 1 $\lambda = 0.16, P < 0.01$ and Axis 2 $\lambda = 0.43, P < 0.01$) (Figs 3, 4). For Morph 3, deeper heads and bodies, including longer and deeper peduncles, and higher eye positions were found in Dease Arm compared to trout from the other arms (body shape: Axis 1 $\lambda = 0.083, P < 0.01$ and Axis 2 $= 0.27, P < 0.01$; head shape: Axis 1 $\lambda = 0.021, P < 0.01$ and Axis 2 $\lambda = 0.087, P < 0.01$) (Figs 3, 4). Jackknife classification on body shape had the highest rates of correct arm-assignments (77.1%, 69.3%, and 66.9%, respectively, for Morphs 1–3), whereas the head shape analysis had correct assignment rates of 70.0%, 59.3%, and 52.8% for Morphs 1–3, respectively.

By contrast, within-morphotype CVAs suggested less variation among arms for linear measurements. Although linear-measurement CVAs were significant for Morphs 1–3 ($P < 0.01$), $\lambda$s were generally larger (0.27–0.33) than those for body and head shape, indicating less discrimination and more similar centroids. Indeed, correct jackknife classifications on traditional linear measurements were relatively low for Morphs 1 and 2 (55.1% and 51.2%, respectively), although classification success was higher (65.7%) for Morph 3.

Variation in body shape among morphs was also observed within individual arms using NMS (Fig. 5). Morphs 1 and 2 were distinct for Smith and McTavish arms, whereas Morph 3 could be distinguished from Morph 1–2 in McVicar and Dease arms. Keith Arm displayed less among-morph distinction in body shape. Permutation MANOVA confirmed the difference in body-shape means among the three morphs in each arm ($P \leq 0.01$). Permutation MANOVA also confirmed within-morph body shape differences among arms ($P \leq 0.05$). All pairwise comparisons in each arm were significantly different ($F$-tests; $P \leq 0.05$), except for Morph 1 versus 3 in Smith Arm and Morph 2 versus 3 in Keith Arm (Fraley & Raftery, 2006, 2007). All among-arm pairwise comparisons for Morphs 1 and 2 were significant ($F$-tests; $P \leq 0.05$) except for McVicar-McTavish in Morph 1, which was marginally different ($P = 0.06$) (Fig. 4). For Morph 3, the only pair that differed was McVicar–Dease (PPDM = 0.016, $P = 0.01$).

Morphological matrices of Morphs 1 and 2 were significantly related (Mantel test; $r = 0.84, P < 0.01$), indicating similarity in the patterns of inter-arm variation for these two morphotypes. However, despite analogous genetic associations in the patterns of inter-arm variation between Morphs 1 and 2 ($r = 0.96, P < 0.01$), there was no significant relationship between genetic and morphological datasets for either Morph 1 ($r = 0.31, P = 0.19$) or Morph 2 ($r = 0.12, P = 0.76$).

Significant dietary differences were found among the three morphotype diets (PERMANOVA: d.f. = 2, $F = 1.01, P < 0.02$) and also among the arms of Great Bear Lake (d.f. = 4, $F = 1.97, P < 0.01$), although the interaction between morphotype and arm was not significant ($P > 0.05$). All pairwise comparisons indicated that Morph 2 had a significantly greater importance of fish in their diets than Morph 1 ($P < 0.05$). Pairwise comparisons identified Dease and Smith arms as being different from the rest of the lake ($P < 0.05$). Diet among arms was mainly differentiated by Trichoptera, fish, Malacostraca, Hymenoptera, and Mollusca with SIMPER-calculated contributions to arm differences of 30.95%, 25.74%, 13.81%, 11.43%, and 5.7%, respectively. The spatial difference resulted from difference in importance of specific food items between the arms (in order of mean importance): Dease and Smith arms for Trichoptera; McTavish, Keith, and McVicar for fish; Keith, McTavish, and McVicar for Malacostraca; Dease, McTavish, and Smith for Hymenoptera; and McVicar for Mollusca (Table 2). Surface water temperature also differed among arms (two-way ANOVA; $P \leq 0.01$) (Fig. 6) but neither year, nor the arm × year interaction were significant ($P > 0.05$). The lowest and highest temperatures were found in McTavish and Smith arms, respectively.

**DISCUSSION**

Using a robust classification method, and based on an analysis of more than 900 trout, the present study supports and extends our previous work (Chavarie et al., 2013), identifying multiple forms of lake trout in the shallow-water habitats of Great Bear Lake. Interestingly, for the 553 lake trout used in the unweighted pair group method with arithmetic mean (UPGMA) cluster analyses of Chavarie et al. (2013), agreement between UPGMA and MCLUST was high. These morphological results, reinforced by some diet data, correspond to morphs described in other Salmonidae as piscivorous (Morph 2) and insectivorous (Morphs 1 and 3) (Proulx & Magnan, 2004; Keeley, Parkinson & Taylor, 2005; Janhunen et al., 2009). Beyond this, however, our CVA, NMS, and Procrustes distance means analyses also identified inter-arm variation within the three common morphotypes, with significant similarity in the inter-arm morphological pattern for the two most common
Figure 4. Unrooted trees of lake trout body shape divergence and configurations of procrustes means of each arm of Great Bear Lake. Inter-arm distances from the body-shape mean and their respective Procrustes pairwise means (y-axis; ± 1 SE derived from 1600 bootstraps) are presented for Morph 1, A, B), Morph 2, C, D), and Morph 3, E, F), where ◆, McVicar; ■, McTavish; ▲, Dease; ×, Smith.

© 2014 The Linnean Society of London, Biological Journal of the Linnean Society, 2014, ••, ••••••
morphotypes that could be tested. Although the driving mechanism(s) behind this inter-arm variation remain unknown, our results suggest multiple levels of diversification, challenging the presumption that, in sympatry, the pattern of diversification is system wide (Hindar & Jonsson, 1993; Orr & Smith, 1998; Bolnick & Fitzpatrick, 2007).

Freshwater habitats are often characterized as patchy, fragmented environments that can promote intraspecific variation in body shape (Carvalho, 1993). Salmonids, especially, can form local populations across contrasting environments over a variety of geographical scales, and represent some of the best examples of diversification in freshwater fishes (Taylor, 1991; Keeley et al., 2007; Vonlanthen et al., 2009). Selection can operate to promote divergence among fish inhabiting the near shore, littoral versus off-shore, open water habitats, that differ in resource composition and availability, and thermal regime (Clabaut et al., 2007; McPhee, Noakes & Allendorf, 2012; Woods et al., 2013). Indeed, specialization for benthic and pelagic food has frequently been proposed as a driving mechanism for many post-glacial adaptive radiations (Vonlanthen et al., 2009; McPhee et al., 2012).

Lake morphometry can also predict the likelihood of habitat coupling between littoral and pelagic zones by a mobile predator such as lake trout (Dolson et al., 2009). Subsequently, among-arm variation in depth, substrate, temperature, and the aquatic network of shoals, drop-offs, bays, islands and open water areas, together with the relative isolation among arms, could have induced further morphological responses within individual morphotypes, assuming there is a phenotype–environment relationship (Schluter, 2000). Although we lack a direct demonstration of local adaptation, diet differences among arms found within a morphotype likely reflect variability in resources.

Figure 5. NMS ordination of body shape divided per arm of capture. A, McVicar. B, Dease. C, McTavish. D, Smith. E, Keith arms. Three morphological morphs are presented: ⊖, Morph 1; |, Morph 2; ⊔, Morph 3.
that supports the possibility of morphological adaptations to diverse habitats among arms of Great Bear Lake.

Overall, four general morphological shifts were observed in Great Bear Lake within a given morphotype, in relation to their area of capture: (1) head depth, (2) maximum body depth, (3) caudal peduncle depth, and (4) eye position. From these relationships, inferences on functional roles, responses to selective pressures, growth processes, and morphogenesis can be made (Medina, Brêthes & Sévigny, 2008).

Lake trout from Dease Arm typically exhibited larger heads, deeper caudal peduncles and higher eye positions whereas Keith Arm trout had deeper bodies. A deeper body is generally associated with maneuverability to exploit structurally complex habitat because greater body depth should reduce slip and promote better performance when searching for cryptic prey (Kristjánsson et al., 2002). A deeper body is also associated with burst swimming, improving fast-start capacity that is generally needed in habitats where prey are relatively large and fast, and where predators deploy ambush tactics (Robinson & Parson, 2002). The caudal peduncle is the primary structure driving energy efficiency and power during swimming, and a deeper peduncle provides better burst swimming needed in structurally complex environments. Finally, eye position can reflect the vertical position of a fish in the water column, with higher position related to benthic exploitation (Gatz, 1979; Hugueny & Pouilly, 1999). The consistent morphological variations that we
observed among the three morphotypes in Dease and Keith arms thus appear to reflect local adaptations that may be linked to resource exploitation in complex habitats (littoral and/or benthic habitats). This hypothesis is partially supported by the importance of benthic prey in the stomach contents from Keith Arm, although our sample size is relatively small and stomach contents are a ‘snapshot’ that can reflect opportunistic feeding on a pulse of prey (Chavarie et al., in press).

Furthermore, the relative abundance of each morphotype among arms suggests differences in the prevalence of different habitats. Prevalence among morphs was relatively equitable in Dease and Keith arms, suggesting that habitats in those arms have characteristics (e.g. greater habitat complexity) that favour Morphs 1 and/or 3 relative to the other three arms. By contrast, McTavish, McVicar and Smith arms were dominated by the more piscivorous Morph 2, which generally displayed traits better suited to pelagic habitats (Webb, 1984; Pakkasmaa & Piironen, 2001; Gillespie & Fox, 2003). Indeed, all three morphs of lake trout from McTavish Arm had relatively streamlined, longer bodies, and narrower peduncles, which are traits associated with sustained swimming in more open/pelagic environments; correspondingly, McTavish Arm contains the most deep-water/pelagic environment. McVicar Arm trout were intermediate in these traits, suggesting that there was no dominance of any specific habitat in that arm.

Benthic and pelagic environments tend to differ in several components (e.g. thermal regime) and McPhee et al. (2012) hypothesized that morphologically divergent ecotypes might arise initially as a plastic response to heterogeneous thermal regimes. Although our data are limited in terms of habitat structure associated with thermal regime, McTavish had the coldest surface temperature during our sampling. This suggests a possible developmental influence on the external morphology of its residents, perhaps at the juvenile stage, because slow-developing fish can resemble a pelagic ecotype (Vila-Gispert et al., 2007; McPhee et al., 2012). By contrast, Smith arm was the warmest arm, and Morph 1 exhibited a more robust body shape that could be associated with fast-developing fishes and littoral habitat (McPhee et al., 2012). Such a difference in thermal regime in Great Bear Lake is unexpected because Great Bear Lake was considered to be an isothermal lake during summer, which illustrates the poor understanding of this system (MacDonald et al., 2004). Few empirical data on the habitat of each arm are currently available, thus, more effort is needed to investigate and validate the link between habitat characteristics and the morphological variation that we have documented.

Variation in other ecological factors, such as predation, can also promote local adaptation (Kristjánsson et al., 2002; Ólafsdóttir et al., 2007; Hendry et al., 2009; Collin & Fumagalli, 2011), even in situations with considerable gene flow (Smith, Schneider & Holder, 2001; Hendry & Taylor, 2004; Crispo et al., 2006; Eklöv & Svanbäck, 2006). For example, greater body depth, as seen for Morph 1 only in Smith Arm, can have defensive value against predators (Webb, 1984; Webb & Fairchild, 2001; Medina et al., 2008). This might be especially important for fish from arms with a high prevalence of Morph 2 (McVicar, McTavish, and Smith) and, in turn, might increase morphological differences between Morphs 1 and 2, as seen in NMS results for Smith and McTavish arms. Indeed, because cannibalism has been observed in Great Bear Lake (Chavarie et al., in press), predation could impact lake trout at smaller sizes by influencing habitat selection (littoral versus pelagic), and subsequently promoting morphological variation later in life (Claessen et al., 2002; Persson et al., 2004; Moles et al., 2010). It is not unreasonable to suspect that predation pressure differs among arms, influencing each population differently, especially if the availability of different habitats differs among arms.

Intraspecific diversity occurs at multiple levels, as seen in the present study. If different characteristics (e.g. body shape) have a different degree of plasticity than others (e.g. head and fins), they could react differently in a heterogeneous environment such as Great Bear Lake via phenotypic plasticity, isolation-by-adaptation, and/or isolation-by-distance (Nosil et al., 2007; Collin & Fumagalli, 2011). For example, Sharpe et al. (2008) found that body shape had a strong genetic component in lake versus stream threespine stickleback (Gasterosteus aculeatus), whereas the environmental component was stronger for linear traits. The relative importance of genetic and environmental influences can vary both spatially and temporally (Schluter et al., 2004; Sharpe et al., 2008; Kristjánsson et al., 2011, 2012).

A concordant pattern of morphological variation among morphs but not between morphological and genetic patterns within a morph across arms suggests more of a phenotypically plastic response. Of course, the capacity for plasticity might be a heritable trait (Mittelbach, Osenberg & Wainwright, 1999) or there may be localized selection in the genome (Nosil et al., 2007). Nonetheless, Harris et al. (2013) found no genetic structure among arms despite large geographical distances, which is not surprising in ‘evolutionarily young’ systems such as Great Bear Lake. The limited time is further exacerbated by the long generation time of northern lake trout (approximately 15 years), which suggests that...
only approximately 330 generations have passed since the last glaciation for trout to have diverged genetically (Harris et al., 2013). The lack of morphological differentiation found in juvenile lake trout of Great Bear Lake (Chavarie et al., 2013) further supports the idea of induced phenotypic plasticity in this system.

Regardless of ecological influences, the differences in scale (whole-lake, among arms) influenced the success of the different morphological metrics used in the study by Chavarie et al. (2013), as well as the present study. Even though both linear measurements and geometric techniques can discriminate populations, Maderbacher et al. (2007) found that geometric techniques were more effective at visualizing and quantifying variations when comparing closely related entities (i.e. biological groups). Thus, when viewed at the whole-lake level, inter-arm variation in body shape within a morphotype can introduce ‘noise’ that obscures the distinctiveness of the three basic morphotypes when using geometric techniques (Chavarie et al., 2013). However, when focusing on the smaller, among-arm scale, this morphometric tool had the appropriate resolution and sensitivity to capture variation within a morphotype. Conversely, limited differences in fins and body lengths ratios within a morph could have meant less noise at the larger scale, allowing traditional linear measurements to be more successful at capturing the whole-lake variation.

CONCLUSIONS

Three striking examples of sympatric variability and parallel adaptive radiation in post-glacial settings, associated with new habitat and vacant niches (Snorrason et al., 1994; Reist, Power & Dempson, 2013), are the three-spined stickleback (Nagel & Schluter, 1998; Mckinnon & Rundle, 2002), lake whitefish (Kahilainen & Ostbye, 2006; Hudson et al., 2007), and Arctic char (Jonsson & Jonsson, 2001; Alekseyev et al., 2002). Our results suggest an analogous case of extensive intra-lake morphological diversification within the lake trout of Great Bear Lake, extending recent observations in other large lakes (Eshenroder, 2008) or in introduced populations (Stafford et al., 2014). Indeed, we have detected two scales of diversification within Great Bear Lake, at the whole-lake level, and among arms within the lake-scale morphotypes. Our findings emphasize the importance of considering spatial scale in studies of large ‘Great’ lakes, to adequately capture intraspecific differentiation. The relative importance of spatial and ecological factors, as well as their interaction, in adaptive radiation is not well understood despite recent theoretical advances (Vonlanthen et al., 2009). More research will be needed to investigate the phenotypic plasticity and genetic links to habitat heterogeneity and other ecological factors to more fully understand this adaptive radiation scenario.

In the face of substantive and pervasive threats (e.g. climate change), the importance of investigating diversity and exploring factors regarding its origin and maintenance is increasing. Ecological and evolutionary forces are interconnected and can act over surprisingly similar time scales (Kristjánsson et al., 2012), although, as highlighted in the present study, they also can act at different spatial scales. The present study indicates rapid intra-specific diversification of lake trout occurring at both smaller and larger scales. The lake trout of Great Bear Lake thus represents one of the most extensive cases of sympatric intraspecific diversity in North America; combined with the relatively pristine environment of Great Bear Lake, this confers a special biological significance to this lake and its resident organisms. Therefore, conservation initiatives aimed at preserving both ecological and evolutionary processes within this system should be considered.

ACKNOWLEDGEMENTS

We thank Déline Renewable Resources Council, Déline Lands and Finance Corporation, the community of Déline, DFO in Hay River, and the Department of Environment and Natural Resources in Déline, who all provided valuable help with field planning and logistics. We especially thank J. Chavarie, G. Lafferty, Z. Martin, S. Wiley, and Chris Yukon who helped lead sampling teams and coordinate logistics, along with the following individuals who helped conduct field sampling in various years: J. Baptiste, D. Baton, L. Dueck, R. Eshenroder, M. Lennie, M. Lindsay, G. Menacho, I. Neyelle, L. Neyelle, M. Smirle, A. Vital, M. Yukon, and Charity, Cameron, and Cyre Yukon. We thank Adam Harrison for his MATLAB support. Financial support was provided by Fisheries and Oceans Canada (DFO), Natural Sciences and Engineering Research Council of Canada, Sahtu Renewable Resource Board, Association of Canadian Universities for Northern Studies, Canadian Circumpolar Institute’s Circumpolar/Boreal Alberta Research and Northern Scientific Training Program, Alan Birdshall Memorial Scholarship, and Aboriginal Affairs and Northern Development Canada Northwest Territories Cumulative Impacts Monitoring Program grants. Logistical support was provided by the Polar Continental Shelf Program. We thank three anonymous reviewers for their helpful comments.
REFERENCES


© 2014 The Linnean Society of London, Biological Journal of the Linnean Society, 2014, ••–••


Reist JD, Power M, Dempson JB. 2013. Arctic charr (Salvelinus alpinus): a case study of the importance of understanding biodiversity and taxonomic issues in northern fishes. Biodiversity 14: 45–56.


© 2014 The Linnean Society of London, Biological Journal of the Linnean Society, 2014, ••, ••–••


