



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

LOUISE CHAVARIE^{1*}, 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, ••, ••–••.

ADDITIONAL KEYWORDS: arctic – morphology – *Salvelinus namaycush* – sympatric.

INTRODUCTION

Intraspecific variability contributes significantly to biodiversity in northern freshwater fish faunas. Salmonid, gasterosteid, 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 expe-

rience 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

*Corresponding author. E-mail: chavarie@ualberta.ca

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 congener 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

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; Kahilainen, 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

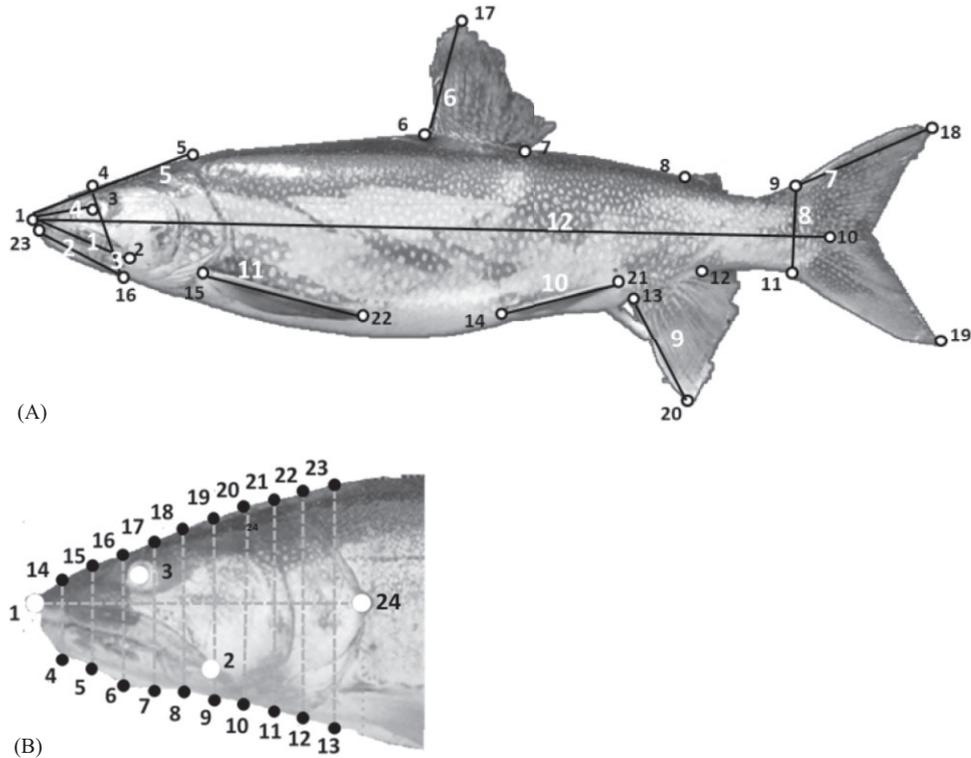


Figure 2. A, twenty-three landmarks (white circles, black numbers) used to measure body shape and linear measurements of lake trout from Great Bear Lake: (1) anterior tip of the snout, (2) posterior tip of maxilla, (3) center of eye, (4) top of cranium at middle point of eye, (5) posterior of neurocranium 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.

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 Nmmnds7_14 from the IMP software) to compare the three morphs in each arm.

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 (Garcia-Rodriguez *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 FIG TREE, 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 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).

ECOLOGICAL DATA: STOMACH CONTENTS AND SURFACE WATER TEMPERATURE

In the laboratory, random sub-samples of stomachs were opened ($N = 42$, 32, and 16 for Morphs 1–3, respectively) and contents were sorted by prey type and weighed. Depending on the degree of digestion of prey items, identification ranged from species to family for both fishes and invertebrates. To facilitate data presentation, prey were pooled into the groups: Fish (= burbot, fish remains, cisco, Lake

Trout, lake whitefish, otoliths, northern pike, round whitefish, sculpin, stickleback), Malacostraca, Mollusca, Orthoptera, Lepidoptera, Aranea, Diptera, Hemiptera, Hymenoptera, Trichoptera, Coleoptera, Plecoptera, and unknown invertebrates. Diet composition was summarized by morphotype using frequency of occurrence (%*O*), and percentage by abundance (%*N*), and mass (%*M*). To scale the importance of each prey category among morphotypes, %*O*, %*N*, and %*M* were used to calculate the relative importance index not only at the population level (morphotype), but also at the individual level, for which %*O* were excluded (George & Hadley, 1979). Dietary differences among morphotypes and area captured (arm) were tested with a two-way PERMANOVA with 9999 permutations using Bray–Curtis measures (Anderson & Ter Braak, 2003) followed by post-hoc pairwise comparisons among morphotype and arms using PAST, version 3 (Hammer *et al.*, 2001). A multigroup SIMPER analysis using Bray–Curtis measures in PAST, version 3, was also used to assess which prey categories were primarily responsible for an observed difference between morphotypes. A Two-way ANOVA was also performed with SYSTAT on surface water temperature across arms, years, and their interaction.

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 Δ BIC 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

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

Females and males are presented in parenthesis, respectively.

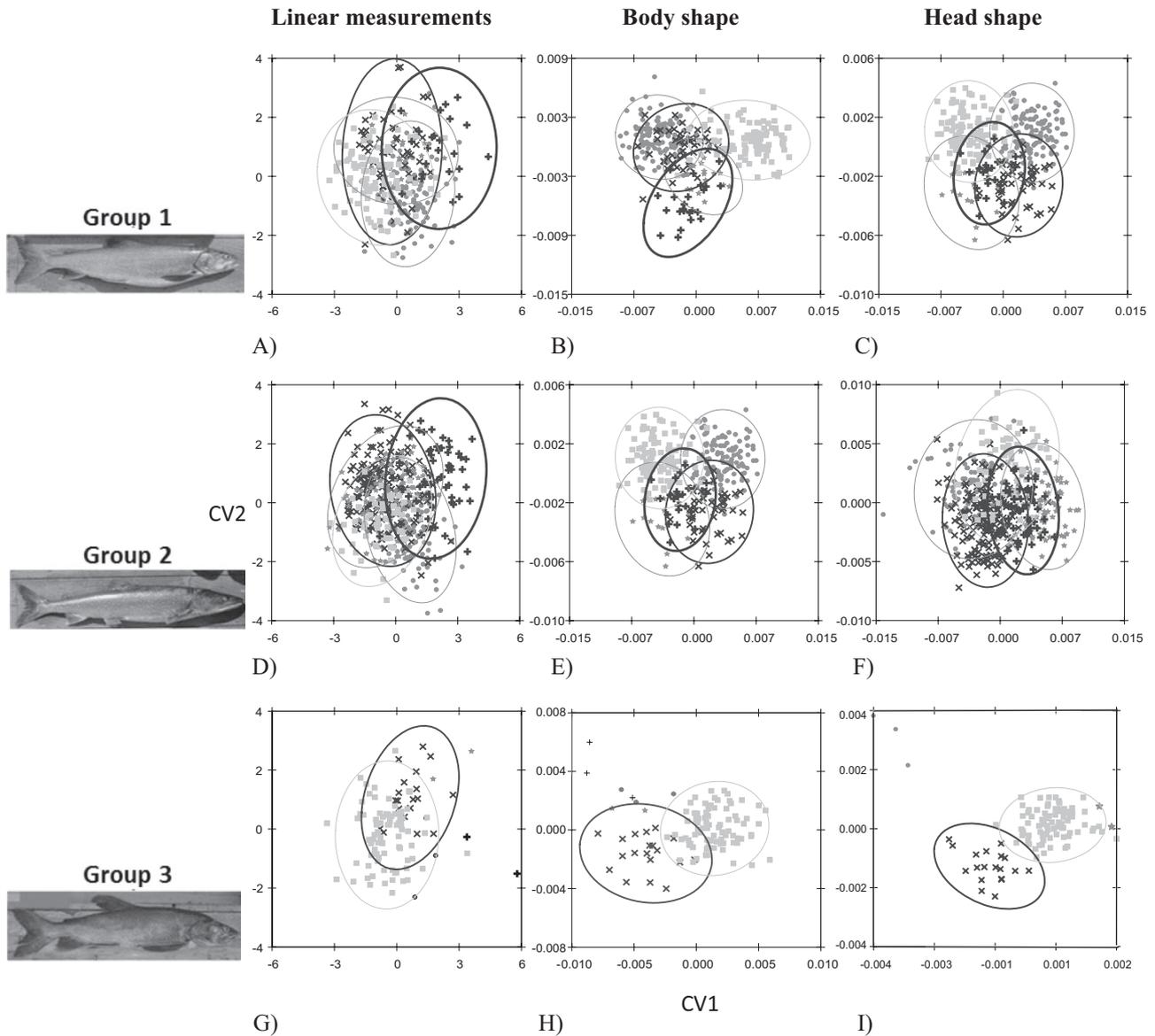


Figure 3. Canonical variate analyses (CVAs) of linear measurements (A, D, G), body shape (B, E, H), and head shape (C, F, I) of 910 adult lake trout from Great Bear Lake, divided into three morphs. For each CVA, fish from different arms of Great Bear Lake are represented: ●, Keith; ×, McVicar; ★, McTavish; ■, Dease; +, Smith. Each arm is also outlined by a 95% confidence ellipse.

$P < 0.01$) (Figs 3, 4). 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 ($P < 0.01$), λ 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 (Fralely & 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 vari-

ation 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 \times 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

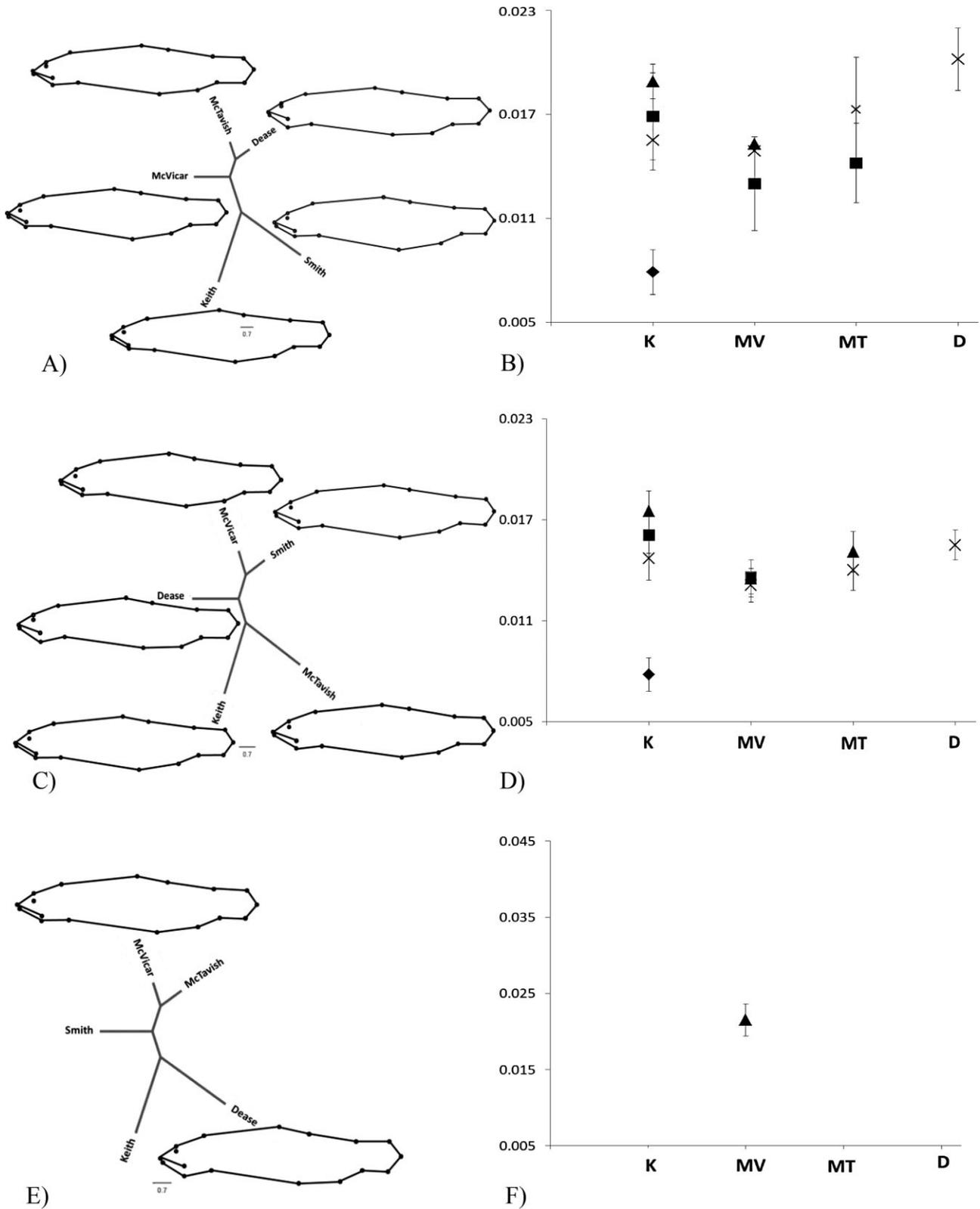


Figure 4. Unrooted trees of lake trout body shape divergence and configurations of procrustes means of each arm of Great Bear Lake. Inter-arm distances from the body-shape mean and their respective Procrustes pairwise means (y-axis; ± 1 SE derived from 1600 bootstraps) are presented for Morph 1, A, B), Morph 2, C, D), and Morph 3, E, F), where \blacklozenge , McVicar; \blacksquare , McTavish; \blacktriangle , Dease; \times , Smith.

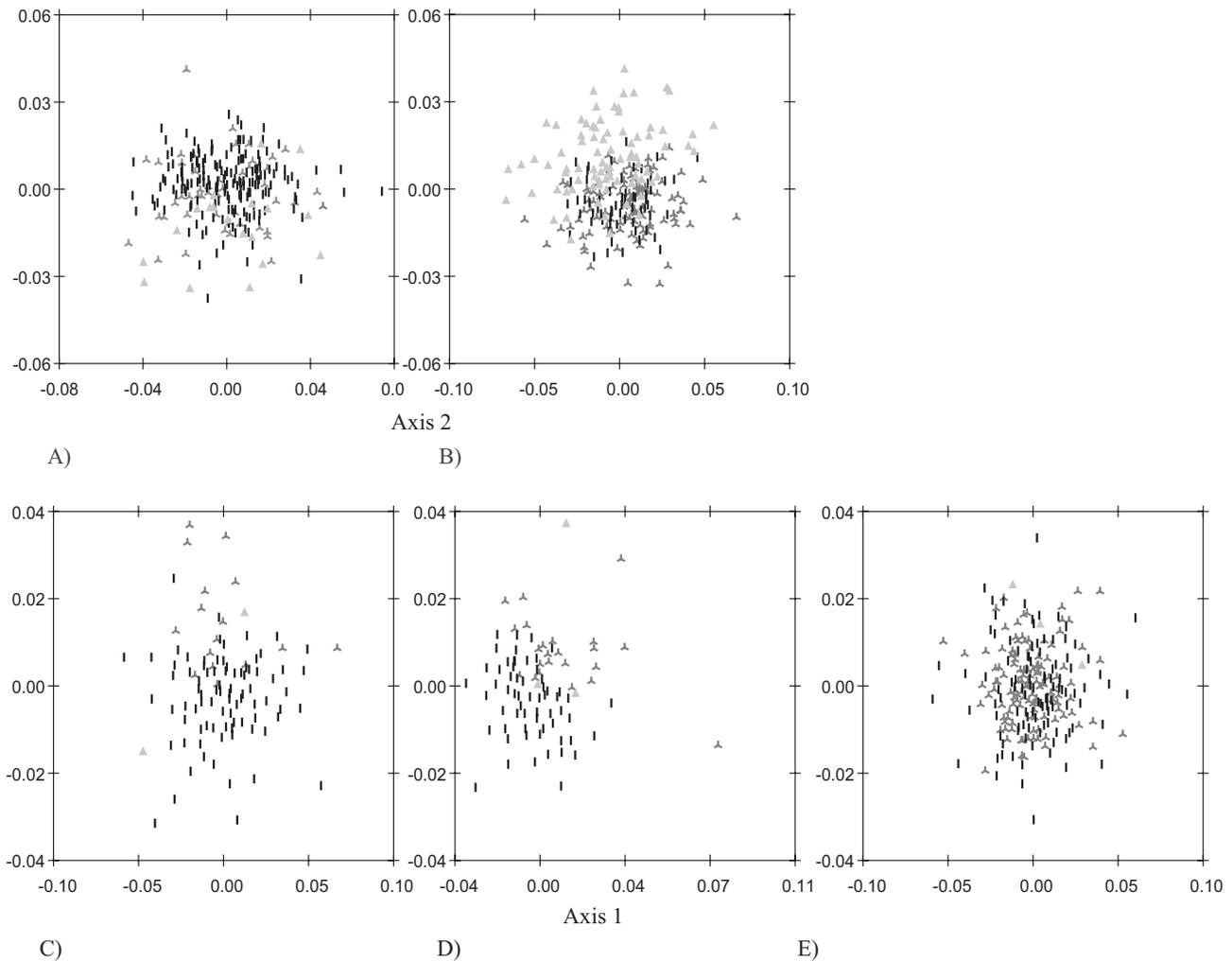


Figure 5. NMS ordination of body shape divided per arm of capture. A, McVicar. B, Dease. C, McTavish. D, Smith. E, Keith arms. Three morphological morphs are presented: ∇ , Morph 1; |, Morph 2; \blacktriangle , Morph 3.

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

Table 2. Relative importance of prey items in stomachs of lake trout from Great Bear Lake for each Morph among the five arms

	Fish	Araneae	Coleoptera	Diptera	Gasteropoda	Hemiptera	Hymenoptera	Lepidoptera	Malacostraca	Orthoptera	Plecoptera	Trichoptera	unknown inv.
Morph 1													
Dease	0.10	<0.01	0.01	0.04	<0.01	≤0.01	0.16	≤0.01	0.05	0.00	<0.01	0.60	0.03
Keith	0.27	0	0.03	<0.01	<0.01	0	0.04	≤0.01	0.39	0.09	0	0.17	0
McTavish	0	0	0	0.10	0.03	0	0	0	0.85	0	0	0.02	0
McVicar	0	0	0.07	0.05	0.18	<0.01	0.10	0	0.21	0.04	0	0.34	0
Smith	0.16	<0.01	0.01	0.01	0.04	0	0.01	0	0.14	<0.01	<0.01	0.58	0.04
Morph 2													
Dease	0.00	0	0.14	0	0	0	0.08	0	<0.01	0	0	0.65	0.13
Keith	0.60	0	0.01	<0.01	0	0	0.05	0.16	0	0.01	0	0.17	0
McTavish	0.76	0	0	0.07	0	0	0.17	0	0	0	0	0	0
McVicar	0.68	0	<0.01	0.06	0.10	0	0	0	0	0	0	0.15	0
Smith	0.12	<0.01	0.04	<0.01	0.09	0	0.20	<0.01	0	0.01	0	0.52	0.01
Morph 3													
Dease	0.12	0.00	0.07	0.03	<0.01	<0.01	0.10	<0.01	0.10	0.01	<0.01	0.56	0
Keith	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
McTavish	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
McVicar	0.46	0	0	<0.01	0.04	0	0	0	0.50	0	0	0	0
Smith	0.34	0	0	0	0.10	0	0	0	0	0.04	0	0.52	0

NA, not available.

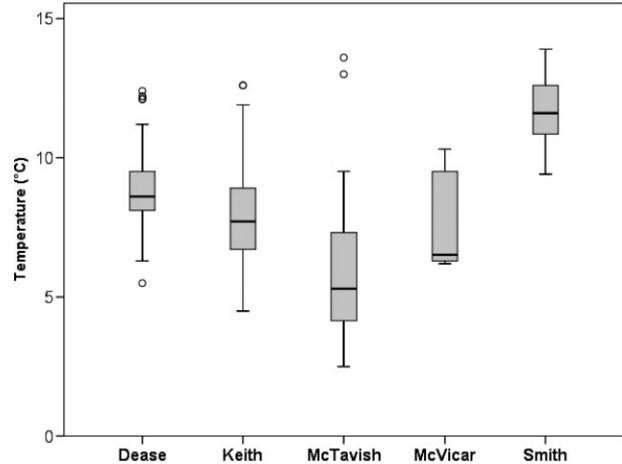


Figure 6. Boxplots of July to August surface water temperatures (°C) sampled at our net locations in each of the five arms of Great Bear Lake. For years in which each arm was sampled, see Material and methods (data collection). Horizontal lines represent median values, boxes enclose the two middle quartiles, whiskers represent 1.5 of the interquartile range, and empty circles indicate outliers beyond the interquartile range.

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 manoeuvrability 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 three other 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 Birdsall 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

- Adam CE, Fraser D, Wilson AJ, Alexander G, Ferguson MM, Skúlason S. 2007. Patterns of phenotypic and genetic variability show hidden diversity in Scottish Arctic charr. *Ecology of Freshwater Fish* **16**: 78–86.
- Adam CE, Hamilton DJ, McCarthy I, Wilson AJ, Grant A, Alexander G, Waldron S, Snorrason SS, Ferguson MM, Skúlason S. 2006. Does breeding site fidelity drive phenotypic and genetic sub-structuring of a population of Arctic charr? *Evolutionary Ecology* **20**: 11–26.
- Alekseyev SS, Samusenok VP, Matveev AN, Pichugin MY. 2002. Diversification, sympatric speciation, and trophic polymorphism of Arctic charr, *Salvelinus alpinus* complex, in Transbaikalia. *Developments in Environmental Biology of Fishes* **22**: 97–114.
- Alfonso NR. 2004. Evidence for two morphotypes of lake charr, *Salvelinus namaycush*, from Great Bear Lake, Northwest Territories, Canada. *Environmental Biology of Fishes* **71**: 21–32.
- Anderson MJ, Ter Braak CJ. 2003. Permutation tests for multi-factorial analysis of variance. *Journal of Statistical Computation and Simulation* **73**: 85–113.
- Blackie CT, Weese DJ, Noakes DLG. 2003. Evidence for resource polymorphism in the lake charr (*Salvelinus namaycush*) population of Great Bear Lake, Northwest Territories, Canada. *Ecoscience* **10**: 509–514.
- Bolnick DI, Fitzpatrick BM. 2007. Sympatric speciation: models and empirical evidence. *Annual Review of Ecology and Systematics* **38**: 459–487.
- Bookstein FL. 1991. *Morphometric tools for landmark data: geometry and biology*. New York, NY: Cambridge University Press.
- Brown E, Eck GW, Foster NR, Horrall RM, Coberly CE. 1981. Historical evidence for discrete stocks of lake trout (*Salvelinus namaycush*) in Lake Michigan. *Canadian Journal of Fish Aquatic Sciences* **38**: 1747–1758.
- Bush GL. 1994. Sympatric speciation in animals: new wine in old bottles. *Trends in Ecology and Evolution* **9**: 285–288.
- Carvalho GR. 1993. Evolutionary aspects of fish distribution: genetic variability and adaptation. *Journal of Fish Biology* **43**: 53–73.
- Cavalli-Sforza LL, Edwards AWF. 1967. Phylogenetic analysis models and estimation procedures. *The American Journal of Human Genetics* **19**: 233–257.
- Chavarie L, Howland K, Gallagher C, Tonn W. *In press*. Fatty acid signatures and stomach contents of four sympatric lake trout: assessment of trophic patterns among morphotypes in Great Bear Lake. *Ecology of Freshwater Fish*. EFF-14-0084.R1.
- Chavarie L, Howland KL, Tonn W. 2013. Sympatric polymorphism in lake trout: the coexistence of multiple shallow-water morphotypes in Great Bear Lake. *Transactions of the American Fisheries Society* **142**: 814–823.
- Clabaut C, Bunje PME, Salzburger W, Meyer A. 2007. Geometric morphometric analyses provide evidence for the adaptive character of the Tanganyikan cichlid fish radiation. *Evolution* **61**: 560–578.
- Claessen D, Van Oss C, De Roos AM, Persson L. 2002. The impact of size-dependent predation on population dynamics and individual life history. *Ecology* **83**: 1660–1675.
- Collin H, Fumagalli L. 2011. Evidence for morphological and adaptive genetic divergence between lake and stream habitats in European minnows (*Phoxinus phoxinus*, Cyprinidae). *Molecular Ecology* **20**: 4490–4502.
- Crispo E, Bentzen P, Reznick DN, Kinnison MT, Hendry AP. 2006. The relative influence of natural selection and geography on gene flow in guppies. *Molecular Ecology* **15**: 49–62.
- Dolson R, McCann K, Rooney N, Ridgway M. 2009. Lake morphometry predicts the degree of habitat coupling by a mobile predator. *Oikos* **118**: 1230–1238.
- Eklöv P, Svanbäck R. 2006. Predation risk influence adaptive morphological variation in fish populations. *The American Naturalist* **167**: 440–452.
- Eshenroder RL. 2008. Differentiation of deep-water lake charr *Salvelinus namaycush* in North American lakes. *Environmental Biology of Fishes* **83**: 77–90.
- Felsenstein J. 2005. Evolutionary trees from DNA sequences: a maximum likelihood approach. *Journal of Molecular Evolution* **17**: 368–376.
- Fraley C, Raftery AE. 2006. *Mclust Version 4 for R: normal mixture modeling and model-based clustering, classification, and density estimation*. Technical Report 597, University of Washington, Department of Statistics, Seattle.
- Fraley C, Raftery AE. 2007. Model-based methods of classification: using the Mclust software in chemometrics. *Journal of Statistical Software* **18**: 1–13.
- García-Rodríguez FJ, García-Gasca S, De La Cruz-Agüero J, Cota-Gómez VM. 2011. A study of the population structure of the Pacific sardine *Sardinops sagax* (Jeyns, 1842) in Mexico based on morphometric and genetic analyses. *Fisheries Research* **107**: 169–176.
- Gatz AJ Jr. 1979. Ecological morphology of freshwater stream fishes. *Tulane Studies in Zoology and Botany* **21**: 91–124.
- George EL, Hadley WF. 1979. Food and habitat partitioning between rock bass (*Ambloplites rupestris*) and smallmouth bass (*Micropterus dolomieu*) young of the year. *Transactions of the American Fisheries Society* **108**: 253–261.
- Gillespie GJ, Fox MG. 2003. Morphological and life-history differentiation between littoral and pelagic forms of pumpkinseed. *Journal of Fish Biology* **62**: 1099–1115.
- Goodier JL. 1981. Native lake trout (*Salvelinus namaycush*) stocks in the Canadian waters of Lake Superior prior to 1955. *Canadian Journal of Fish Aquatic Sciences* **38**: 1724–1737.
- Green WDK. 1996. The thin-plate spline and images with curving features. In: Mardia KV, Gill CA, Dryden IL, eds. *Image fusion and shape variability*. Leeds: University of Leeds Press, 79–87.
- Harris LN, Chavarie L, Bajno R, Howland KL, Wiley SH, Tonn W, Taylor EB. 2014. Evolution and origin of sympatric shallow-water morphotype of Lake trout, *Salvelinus namaycush*, in Canada's Great Bear Lake. *Heridity*. doi:10.1038/hdy.2014.74.

- Harris LN, Howland KL, Kowalchuck MW, Bajno R, Lindsay MM, Taylor EB. 2013.** Microsatellite and mtDNA analysis of lake trout, *Salvelinus namaycush*, from Great Bear Lake, Northwest Territories: impacts of historical and contemporary evolutionary forces on Arctic ecosystems. *Ecology and Evolution* **3**: 145–161.
- Hammer Ø, Harper DAT, Ryan PD. 2001.** PAST: Paleontological statistics software package for education and data analysis. *Palaeontologia Electronica* **4**: 1–9.
- Hendry AP, Bolnick DI, Berner D, Peichel CL. 2009.** Along the speciation continuum in sticklebacks. *Journal of Fish Biology* **75**: 2000–2036.
- Hendry AP, Taylor EB. 2004.** How much of the variation in adaptive divergence can be explained by gene flow? An evaluation using lake-stream sticklebacks pairs. *Evolution* **58**: 2319–2331.
- Hindar K, Jonsson B. 1993.** Ecological polymorphism in Arctic charr. *Biological Journal of the Linnean Society* **48**: 63–74.
- Hudson AG, Vonlanthen P, Müller R, Seehausen O. 2007.** Review: the geography of speciation and adaptive radiation in Coregonines. *Journal Advances in Limnology* **60**: 111–146.
- Hugueny B, Pouilly M. 1999.** Morphological correlates of diet in an assemblage of West African freshwater fishes. *Journal of Fish Biology* **54**: 1310–1324.
- Janhunen M, Peuhkuri N, Piironen J. 2009.** Morphological variability among three geographically distinct Arctic charr (*Salvelinus alpinus* L.) populations reared in a common hatchery environment. *Ecology of Freshwater Fish* **18**: 106–116.
- Johnson L. 1975.** Distribution of fish species in Great Bear Lake, Northwest Territories, with reference to zooplankton, benthic invertebrates, and environmental conditions. *Journal of Fisheries Research Board of Canada* **32**: 1989–2004.
- Jonsson B, Jonsson K. 2001.** Polymorphism and speciation in Arctic charr. *Journal of Fish Biology* **58**: 605–638.
- Kahilainen K, Alajarvi E, Lehtonen H. 2005.** Planktivory and diet-overlap of densely rakered whitefish (*Coregonus lavaretus* L.) in a subarctic lake. *Ecology of Freshwater Fish* **14**: 50–58.
- Kahilainen K, Ostbye K. 2006.** Morphological differentiation and resource polymorphism in three sympatric whitefish *Gasterosteus aculeatus* (L.) forms in a subarctic lake. *Journal of Fish Biology* **68**: 63–79.
- Keeley ER, Parkinson EA, Taylor EB. 2005.** Ecotypic differentiation of native rainbow trout (*Oncorhynchus mykiss*) populations from British Columbia. *Canadian Journal Fish Aquatic Sciences* **62**: 1523–1539.
- Keeley ER, Parkinson EA, Taylor EB. 2007.** The origins of ecotypic variation of rainbow trout: a test of environmental vs. genetically based differences in morphology. *Journal of Evolutionary Biology* **20**: 725–736.
- Kristjánsson BK, Malmquist HJ, Ingimarsson F, Antonsson T, Snorrason SS, Skúlason S. 2011.** Relationships between lake ecology and morphological characters in Icelandic Arctic charr, *Salvelinus alpinus*. *Biological Journal of the Linnean Society* **103**: 761–771.
- Kristjánsson BK, Noakes DLG, Skúlason S. 2002.** Morphological segregation of Icelandic threespine stickleback (*Gasterosteus aculeatus* L.). *Biological Journal of the Linnean Society* **76**: 247–257.
- Kristjánsson BK, Skúlason S, Snorrason SS, Noakes DLG. 2012.** Fine-scale parallel patterns in diversity of small endemic Arctic charr (*Salvelinus alpinus*) in relation to the ecology of lava groundwater habitats. *Ecology and Evolution* **2**: 1099–1112.
- Legendre P, Fortin M-J. 2010.** Comparison of the Mantel test and alternative approaches for detecting complex multivariate relationships in the spatial analysis of genetic data. *Molecular Ecology Resources* **10**: 831–844.
- Lowry DB. 2012.** Ecotypes and the controversy over stages in the formation of new species. *Biological Journal of the Linnean Society* **106**: 241–257.
- MacDonald DD, Levy DA, Czarnecki A, Low G, Richea N. 2004.** State of the aquatic knowledge of Great Bear Lake watershed. Report to Indian and Northern Affairs Canada, Water Resources Division, MacDonald Environmental Sciences, Nanaimo, British Columbia.
- Maderbacher M, Bauer C, Herler J, Post L, Makasa L, Sturbauer C. 2007.** Assessment of traditional versus geometric morphometrics for discriminating populations of the *Tropheus moorii* species complex (Teleostei: Cichlidae), a Lake Tanganyika model for allopatric speciation. *Journal of Zoological Systematics and Evolutionary Research* **46**: 153–161.
- Mantel N. 1967.** The detection of disease clustering and a generalized regression approach. *Cancer Research* **27**: 209–220.
- McCune B, Mefford MJ. 2011.** *PC-ORD. Multivariate analysis of ecological data*, Version 6. Glenden Beach, OR: MM Software Design.
- McKinnon JS, Rundle DR. 2002.** Speciation in nature: the threespine stickleback model systems. *Trends in Ecology and Evolution* **17**: 480–488.
- McPhee MV, Noakes DL, Allendorf FW. 2012.** Developmental rate: a unifying mechanism for sympatric divergence in postglacial fishes? *Current Zoology* **58**: 21–34.
- Medina A, Brêthes J-C, Sévigny J-M. 2008.** Habitat fragmentation and body shape variation of African hind *Cephalopholis taeniops* (Valenciennes) in an archipelago system (Cape Verde, eastern Atlantic Ocean). *Journal of Fish Biology* **73**: 902–925.
- Mittelbach GG, Osenberg CW, Wainwright PC. 1999.** Variation in feeding morphology between pumpkinseed populations: phenotypic plasticity or evolution? *Evolutionary Ecology Research* **1**: 111–128.
- Moles MD, Robinson BW, Johnston TA, Cunjak RA, Jardine TD, Casselman JM, Leggett WC. 2010.** Growth, body form, and trophic ecology of walleye (*Sander vitreus*) morphotypes in Lake Winnipeg, Canada. *Canadian Journal of Zoology* **88**: 950–960.

- Moore SA, Bronte CR. 2001. Delineation of sympatric morphotypes of lake trout in Lake Superior. *Transactions of the American Fisheries Society* **130**: 1233–1240.
- Nagel L, Schluter D. 1998. Body size, natural selection, and speciation in sticklebacks. *Evolution* **52**: 209–218.
- Neumann J, Cramon DY, Lohmann G. 2008. Model-based clustering of meta-analytic functional imaging data. *Human Brain Mapping* **29**: 177–192.
- Nosil P, Egan SP, Funk DJ. 2007. Heterogeneous genomic differentiation between walking-stick ecotypes: 'Isolation by adaptation' and multiple roles for divergent selection. *Evolution* **62**: 316–336.
- Ólafsdóttir GA, Snorrason SS, Ritchie MG. 2007. Postglacial intra-lacustrine divergence of Icelandic threespine stickleback morphs in three neovolcanic lakes. *Journal of Evolutionary Biology* **20**: 1870–1881.
- Olsson IC, Greenberg LA, Bergman E, Wysujack K. 2006. Environmentally induced migration: the importance of food. *Ecology Letters* **9**: 645–651.
- Orr M, Smith TB. 1998. Ecology and speciation. *Trends in Ecology and Evolution* **13**: 502–506.
- Pakkasmaa S, Piironen J. 2001. Morphological differentiation among local trout (*Salmo trutta*) populations. *Biological Journal of the Linnean Society* **72**: 231–239.
- Persson L, Claessen D, DeRoos AM, Byström P, Sjögren S, Svanbäck R, Wahlström E, Westman E. 2004. Cannibalism in a size structured population: energy extraction and control. *Ecological Monographs* **74**: 135–157.
- Pielou EC. 1991. *After the Ice Age: the return of life to glaciated North America*. Chicago, IL: University of Chicago Press.
- Proulx R, Magnan P. 2004. Contribution of phenotypic plasticity and heredity to the trophic polymorphism of lacustrine brook charr (*Salvelinus fontinalis* M.). *Evolutionary Ecology Research* **6**: 503–522.
- Reist JD. 1985. An empirical evaluation of several univariate methods that adjust for size variation in morphometric data. *Canadian Journal of Zoology* **63**: 1429–1439.
- Reist JD, 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.
- Richardson JL, Urban MC, Bolnick DI, Skelly DK. 2014. Microgeographic adaptation and the spatial scale of evolution. *Trends in Ecology and Evolution* **29**: 165–176.
- Riley C. 1935. The granite-porphyrries of Great Bear Lake, Northwest Territories, Canada. *Journal of Geology* **43**: 497–523.
- Robinson BW, Parson KJ. 2002. Changing times, spaces, and faces: tests and implications of adaptive morphological plasticity in the fishes of northern post glaciated lakes. *Canadian Journal Fish Aquatic Sciences* **59**: 1819–1833.
- Sandlund OT, Gunnarsson K, Jónasson PM, Jonsson B, Torfinn L, Magnússon KP, Malmquist HJ, Sigurjónsdóttir H, Skúlason S, Snorrasson SS. 1992. The Arctic charr *Salvelinus alpinus* in Thingvallavatn. *Oikos* **64**: 305–351.
- Schluter D. 2000. *The ecology of adaptive radiation*. Oxford Series in Ecology and Evolution. Oxford: Oxford University Press.
- Schluter D, Clifford EA, Nemethy M, McKinnon JS. 2004. Parallel evolution and inheritance of quantitative traits. *The American Naturalist* **163**: 809–822.
- Schluter D, Nagel LM. 1995. Parallel speciation by natural selection. *The American Naturalist* **146**: 292–301.
- Schluter D, Rambaut A. 1996. Ecological speciation in postglacial fishes (and discussion). *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences* **351**: 807–814.
- Schmalz PJ, Hansen MJ, Holey ME, McKee PC, Toney ML. 2002. Lake trout movements in Northwestern Lake Michigan. *North American Journal of Fisheries Management* **22**: 737–749.
- Sharpe DMT, Räsänen K, Berner D, Hendry AP. 2008. Genetic and environmental contributions to the morphology of lake and stream stickleback: implications for gene flow and reproduction isolation. *Evolutionary Ecology Research* **10**: 849–866.
- Skúlason S, Smith TB. 1995. Resource polymorphism in vertebrates. *Trends in Ecology and Evolution* **10**: 366–370.
- Smith GR, Todd TN. 1984. Evolution of fish species flocks in north-temperate lakes. In: Echelle AA, Kornfield I, eds. *Evolution of fish species flocks*. Orono, ME: University of Maine. Orono Press, 47–68.
- Smith TB, Schneider CJ, Holder K. 2001. Refugial isolation versus ecological gradients. *Genetica* **112**: 383–398.
- Smith TB, Skúlason S. 1996. Evolutionary significance of resource polymorphisms in fishes, amphibians, and birds. *Annual Review of Ecology and Systematics* **27**: 111–133.
- Snorrason SS, Skúlason S, Jonsson B, Malmquist HJ, Jonasson PM, Sandlund OT, Lindem T. 1994. Trophic specialization in Arctic charr *Salvelinus alpinus* (Pisces: Salmonidae): morphological divergence and ontogenetic niche shifts. *Biological Journal of the Linnean Society* **52**: 1–18.
- Sokal RR, Rohlf FJ. 1981. *Biometry, 2nd edn*. San Francisco, CA: WH Freeman.
- Stafford CP, McPhee MV, Eby LA, Allendorf FW. 2014. Introduced lake trout exhibit life-history and morphological divergence with depth. *Canadian Journal of Fisheries and Aquatic Sciences* **71**: 10–20.
- Taylor EB. 1991. A review of local adaptation in Salmonidae, with particular reference to Pacific and Atlantic salmon. *Aquaculture* **98**: 185–207.
- Vila-Gispert A, Fox MG, Zamora L, Moreno-Amich R. 2007. Morphological variation in pumpkinseed *Lepomis gibbosus* introduced into Iberian lakes and reservoirs; adaptations to habitat type and diet? *Journal of Fish Biology* **71**: 163–181.
- Vonlanthen P, Roy D, Hudson AG, Largiadèr CR, Bittner D, Seehausen O. 2009. Divergence along a steep ecological gradient in lake whitefish (*Coregonus* sp.). *Journal of Evolutionary Biology* **22**: 498–514.
- Webb PW. 1984. Body form, locomotion and foraging in aquatic vertebrate. *American Zoologist* **24**: 107–120.

- Webb PW, Fairchild AG. 2001.** Performance and maneuverability of three species of teleostean fishes. *Canadian Journal of Zoology* **79**: 1866–1877.
- Woods PJ, Skúlason S, Snorrason SS, Kristjánsson BK, Ingimarsson F, Malmquist HJ. 2013.** Variability in the functional role of Arctic charr *Salvelinus alpinus* as it relates to lake ecosystem characteristics. *Environmental Biology of Fishes* **96**: 1361–1376.
- Zelditch ML, Swiderski DL, Sheets HD, Fink WL. 2004.** *Geometric morphometrics for biologists: a primer*. San Diego, CA: Elsevier.
- Zimmerman MS, Krueger CC, Eshenroder RL. 2006.** Phenotypic diversity of lake trout in Great Slave Lake: differences in morphology, buoyancy, and habitat depth. *Transactions of the American Fisheries Society* **135**: 1056–1067.
- Zimmerman MS, Krueger CC, Eshenroder RL. 2007.** Morphological and ecological differences between shallow- and deep-water trout in Lake Mistassini, Quebec. *Journal of Great Lakes Research* **33**: 156–169.
- Zimmerman MS, Schmidt SN, Krueger CC, Vander Zanden MJ, Eshenroder RL. 2009.** Ontogenetic niche shifts and resource partitioning of lake trout morphotypes. *Canadian Journal Fish Aquatic Sciences* **66**: 1007–1018.