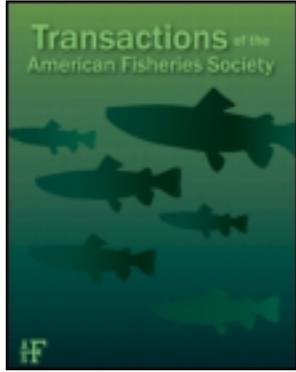


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Transactions of the American Fisheries Society

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/utaf20>

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Published online: 15 Apr 2013.

To cite this article: Louise Chavarie, Kimberly L. Howland & William M. Tonn (2013): Sympatric Polymorphism in Lake Trout: The Coexistence of Multiple Shallow-Water Morphotypes in Great Bear Lake, Transactions of the American Fisheries Society, 142:3, 814-823

To link to this article: <http://dx.doi.org/10.1080/00028487.2013.763855>

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ARTICLE

Sympatric Polymorphism in Lake Trout: The Coexistence of Multiple Shallow-Water Morphotypes in Great Bear Lake

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Abstract

Polymorphism in northern fishes is common, but the extent to which polymorphism occurs in Lake Trout *Salvelinus namaycush*, a species generally associated with low intraspecific variation, is not well known. This study examined the polymorphism of Lake Trout inhabiting the shallow-water zones (≤ 30 m) of Great Bear Lake, Northwest Territories. We combined an analysis of classical morphometric and traditional linear measures with shape analysis (geometric morphometrics) to quantify morphological differences in body shape, head shape, and fin and body length measurements among 558 adult and 55 juvenile shallow-water Lake Trout from Great Bear Lake. A UPGMA cluster analysis on adult Lake Trout distinguished three different morphs that coexist in the shallow-water habitat. The most important differences among adult morphotypes were associated with head and fin measurements, whereas body shape variation was less distinct. A fourth, albeit rarer, morph was supported by a multivariate ANOVA that indicated significant differences in head and fin characteristics among the four groups. The divergent morphologies among the shallow-water Lake Trout of Great Bear Lake are consistent with traits generally associated with feeding and swimming. In contrast to adult trout, no consistent patterns were found for juveniles, suggesting that phenotypic differences develop at a later stage. This unusual level of endemic diversity in the shallow-water habitat expands our knowledge of Lake Trout diversity beyond the predominant focus on shallow- versus deepwater forms.

The circumpolar north is characterized by recently deglaciated areas (10,000–15,000 years ago), with correspondingly young aquatic ecosystems. Thus, the extant freshwater fish fauna has developed through relatively recent and ongoing recolonization from nonglaciated refugia. The resulting postglacial systems are depauperate and characterized by open niches and a relaxation of interspecific competition or predation, conditions that favor the development of intraspecific sympatric polymorphism (Smith and Skúlason 1996). Salmonids commonly show evidence of sympatric polymorphism promoted by the ecological opportunities found in these northern areas (Robinson and Wilson 1994). Although morphological variation can sometimes

be subtle, on other occasions differences are dramatic enough to have caused misidentification of morphs as distinct species, e.g., Arctic Char *Salvelinus alpinus*, where phenotypes vary considerably within and across localities, a situation known as the “char problem” (Nordeng 1983; Skúlason and Smith 1995; Jónsson and Jónsson 2001). Typically, cases of sympatric polymorphism involve a resource-based variation in a fish population, where significant differences in morphology, life history, and behavior are associated with differences in diet and habitat use (Schluter and McPhail 1992).

Lake Trout *S. namaycush* is a cold-stenothermic freshwater salmonid that is widely distributed in previously glaciated

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Received July 16, 2012; accepted December 29, 2012

Published online April 15, 2013

regions of North America. Lake Trout was thought to be relatively stable morphologically (Behnke 1972; Eshenroder 2008), especially compared with other Salmonidae, such as Arctic Char (e.g., Jónsson and Skúlason 2000) and whitefishes, *Coregonus* spp. (e.g., Kahilainen and Østbye 2006). An important exception to the morphological stability of Lake Trout has been depth-related diversification in Lake Superior (Moore and Bronte 2001), with the siscowet and the humper recognized as the two principal forms inhabiting deeper waters, and the lean (piscivore) occupying shallow-water habitats (Eshenroder 2008). The availability of an open deepwater niche associated with emerging trophic differences may have provided the selection pressure contributing to phenotypic diversification (Henderson and Anderson 2002; Zimmerman et al. 2006; Eshenroder 2008). Unfortunately, additional diversity in Lake Trout may have declined or disappeared from the highly impacted Laurentian Great Lakes (Brown et al. 1981; Goodier 1981), which has limited investigations of Lake Trout intraspecific variation in this system (Eshenroder 2008; but see Bronte and Moore 2007).

Lake Superior still has the highest extant diversity of Lake Trout documented to date (Moore and Bronte 2001; Eshenroder 2008). However, discoveries of deepwater and shallow-water forms from Lake Mistassini, Quebec, (Zimmerman et al. 2007) and Great Slave Lake, Northwest Territories, (Zimmerman et al. 2006, 2009) and of a second shallow-water form (insectivorous) in Great Bear Lake, Northwest Territories, (Blackie et al. 2003; Alfonso 2004) have challenged any suggestions that Lake Trout diversity is endemic to the Laurentian Great Lakes and have demonstrated that additional research on Lake Trout diversification is needed.

A recent report proposing that up to four forms of Lake Trout co-occur in shallow-water habitats (≤ 30 m) of Great Bear Lake (Howland et al. 2008) suggests this is an exceptional system in which to investigate Lake Trout diversification, independent of depth-based segregation, in a large, pristine northern lake. Our aim in the present study is to describe the morphological diversity of Lake Trout found in shallow (≤ 30 m) waters of Great Bear Lake. Specifically, our objectives were to (1) determine how many distinct shallow-water morphs exist, (2) quantitatively summarize the morphological variation among these shallow-water morphs using a combination of morphometric and traditional linear measures, and (3) determine whether differences among morphs are equally strong in juveniles versus adults.

STUDY SITE

Great Bear Lake is located in the northeastern portion of the Northwest Territories, between 65° and 67° N latitude, 250 km south of the Arctic Ocean. With a surface area of 31,790 km², Great Bear Lake is the fourth largest lake in surface area in North America; together with a maximum depth of 450 m, it is truly one of the great lakes of North America (Evans 2000). The lake has characteristics typical of an arctic lake: it is ultraoligotrophic, remains mostly isothermal during summer, and has a simple food web; e.g., despite its size, it supports only 15 fish

species (Johnson 1975; Alfonso 2004; MacDonald et al. 2004). Adjacent terrestrial areas of Great Bear Lake include the southern Arctic ecozone to the north, the taiga plains to the west and south, and the taiga shield to the east (MacDonald et al. 2004). Great Bear Lake does not sustain a commercial fishery but plays an important role in the local economy, supporting both a fly-in sport fishery and a subsistence fishery for the small community of Déline.

METHODS

Data collection.—We collected Lake Trout from three of Great Bear Lake's five arms (Keith, McVicar, and Dease) in 2002, 2003, and 2005. Lake Trout were caught in shallow water (≤ 30 m) in July and August using paired bottom sets of a 14-cm-mesh gill net and a multimesh (3.8–14 cm mesh) gill net with a typical soak time of approximately 24 h. A lateral (left side) full-body digital image was taken of each trout, with caudal, pelvic, and pectoral fins extended and dorsal and anal fins pinned. A focal length of ≥ 50 mm was used to reduce parallax distortion, and a cradle made from seine netting was used to reduce curvature distortion caused by individuals resting on a plane surface (Zimmerman et al. 2006). For each fish captured, we recorded fork length, round weight, sex, and stage of maturity. Maturity was divided into two stages, juvenile and mature. To avoid confusion between juveniles and smaller resting adults, we set maximum juvenile length at 450 mm based on length-at-maturity information from captured Lake Trout spawners (K. Howland and L. Chavarie, unpublished data).

Morphology.—We used the digital images to quantify morphological characteristics, employing a combination of traditional and geometric morphometrics (Zelditch et al. 2004). Twenty-three landmarks (predetermined homologous points) were selected to measure body shape (Figure 1) and 12 linear

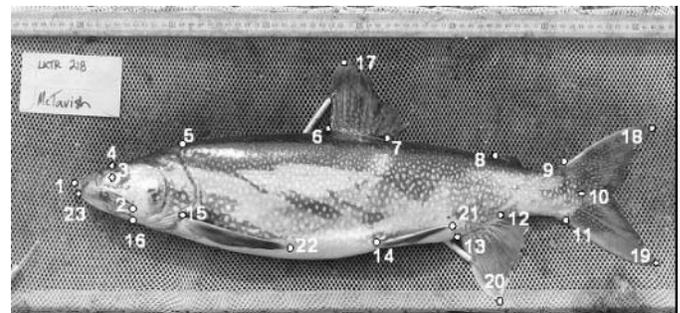


FIGURE 1. Landmarks used to measure body shape and linear measurements of Lake Trout from Great Bear Lake: (1) anterior tip of the snout, (2) posterior tip of maxilla, (3) center of eye, (4) top of cranium at middle point of eye, (5) posterior of neurocranium above tip of opercle, (6) dorsal fin anterior 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. Landmarks 1–16 and 23 were used for body shape analysis.

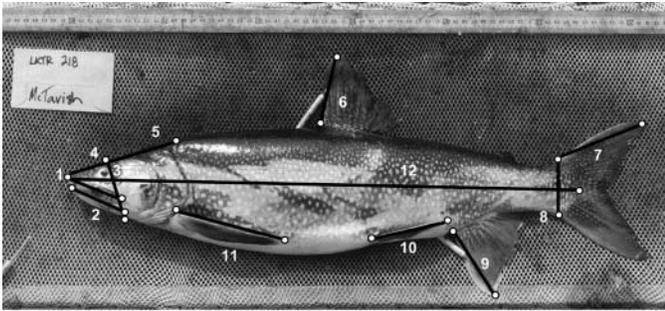


FIGURE 2. Fin and body length measurements of Lake Trout from Great Bear Lake: (1) upper jaw, (2) lower jaw, (3) head depth, (4) snout-eye, (5) head, (6) dorsal fin, (7) caudal fin, (8) caudal peduncle depth, (9) anal fin, (10) pelvic fin, (11) pectoral fin, and (12) standard body length; standard body length was used to standardize fin and body lengths and depths (see text). Landmarks 1, 2, 4, 5, 6, 9, 10, 11, 13–18, and 20–23 (in Figure 1) were used to calculate these traditional measurements.

measurements (Figure 2) were selected based on their relationship to foraging (e.g., jaw size) and swimming (e.g., fin lengths and caudal peduncle depth: Webb 1984; Kristjánsson et al. 2002; Kahilainen et al. 2005). Landmarks used in this study were comparable with those used previously for Lake Trout (e.g., Zimmerman et al. 2006, 2007, 2009). We also used 20 semilandmarks (Figure 3) to measure important variation in head shape that was not well captured by landmarks. Semilandmarks are nonhomologous points that can be used to capture

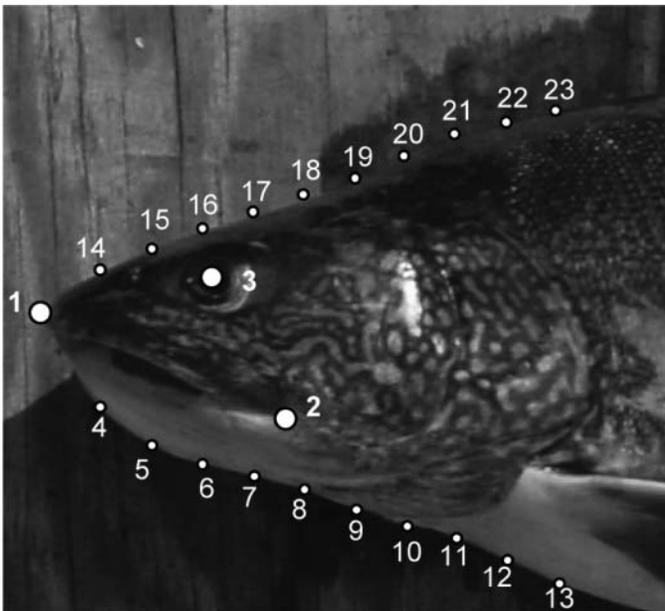


FIGURE 3. Landmarks and semilandmarks used to measure head shape of Lake Trout from Great Bear Lake. Landmarks 1–3 represent the following: (1) anterior tip of snout, (2) posterior tip of maxilla, (3) center of eye; semilandmarks 4–13 and 14–23 represent 10 ventrally and dorsally evenly spaced semilandmarks, respectively.

and analyze shape information on curved areas of a body lacking distinct landmarks (Green 1996; Bookstein 1997; Zelditch et al. 2004).

Morphological analyses were conducted using a thin-plate spline (TPS) method of geometric morphometrics (Adams et al. 2004). For each specimen, TPSDig2 software (<http://life.bio.sunysb.edu/morph>) was used to record X and Y coordinates of all landmarks used for body shape and traditional morphometric measurements. A series of integrated morphometrics programs (IMPs), produced in Matlab6 by H. D. Sheets (<http://www3.canisius.edu/~sheets/morphsoft.html>) and well described in Zelditch et al. (2004), was then used to process the X and Y coordinates. CoordGen generated Bookstein coordinates (BCs) superimposition data (Bookstein 1991), removing variation due to scale, rotation, and position. TMorphGen was used to calculate fin- and body-length measures based on paired coordinate measurements (BCs) and a baseline of known length. To adjust for size variation among individuals, fin- and body-length measurements were \log_{10} transformed prior to analysis and regressed against standard length. Residuals from these regressions were then used in subsequent analyses to minimize effects of size on character variation (Reist 1985). The software MakeFan was used to superimpose a reference grid between the snout and the opercle on each fish image producing 10 equally spaced regions. Semilandmarks were then “slided” along the upper and lower curves of the head bounded by the landmarks with the Semiland6 program to minimize the bending energy of deformation among individual points (Zelditch et al. 2004), resulting in an alignment of the semilandmarks on the target form along lines perpendicular to the curve (Bookstein 1997; Zelditch et al. 2004). All shape data were standardized for size before any further analyses by using the centroid size of all fish using Standard6.

All analyses were performed separately on adult and juvenile Lake Trout. Partial warp scores, which are coefficients indicating the position of an individual and generated by IMPs, were used to describe variation in body and head shape and were used in all subsequent conventional statistical analyses since they have the correct number of degrees of freedom (Zelditch et al. 2004). We conducted principal component analyses (PCAs) on body and head shape data using PCAGen (IMP software) for both adult and juvenile groups to capture the maximum amount of variation with the fewest number of variables. Morphological groups were initially identified with a UPGMA cluster analysis, using PC-ORD version 6 software (McCune and Mefford 2011), based on scores from the first two principal components (PCs) of the body shape and head shape PCAs, and 11 traditional measurements. Number of groups was imposed for the juvenile cluster analyses, based on that for the adult cluster analyses, for consistency among the two maturity stages. A PCA of head shape and traditional measurements (using PC-ORD) and of body shape (using PCAGen) was then conducted to quantify the importance of each variable to the ordination axes and

thus for summarizing the variation in the morphological groups identified by the cluster analysis.

Discriminant function analysis and jackknife validation procedures were performed with SYSTAT version 12 software (Systat Software, Chicago, Illinois) on groups defined by cluster analysis to determine whether they were significantly distinct (Oksanen et al. 2009). Finally, we performed a multivariate ANOVA (MANOVA) followed by Tukey honestly significant difference (HSD) post hoc comparisons (SPSS version 19; SPSS, Chicago, Illinois) on body and head and body shape PCs and linear measurements of adult Lake Trout, to complete the comparison among morphotypes, with a focus on a putative morphotype not identified in the cluster analysis. Subsequently, least-square means and their standard errors for each morphotype were calculated for each variable in a general linear model in SPSS version 19 software for a standardized body size of 62.2 cm (based on the mean length of fish in the data set) to illustrate their differences among morphs.

RESULTS

Approximately 200 Lake Trout were sampled per year (3-year totals: 558 adults and 55 juveniles) for analysis. For adults, three major groups were identified with the UPGMA cluster analyses (Figure 4), referred to here as group 1 ($n = 175$), group 2 ($n = 267$), and group 3 ($n = 94$). Discriminant analysis showed that the three groups differed significantly despite some observed overlap ($\lambda = 0.16$, $N = 555$, $P \leq 0.01$). Group 1, group 2, and group 3 were classified correctly 90, 93, and 88% of the time, respectively, with the jackknife procedure. Groups were better distinguished by traditional measurements and head shape (Figure 5a); separation by body shape was not apparent (Figure 6a). Based on the PCA, adult members of group 2 had bigger heads (quantified as longer head lengths, longer snout-to-eye lengths, and longer upper and lower jaws), which contrasted with group 1 (smaller heads and jaws). Group 3 was distinguished by longer fins (pectoral, dorsal, caudal, anal, and pelvic) and caudal peduncle depths, in contrast to group 2

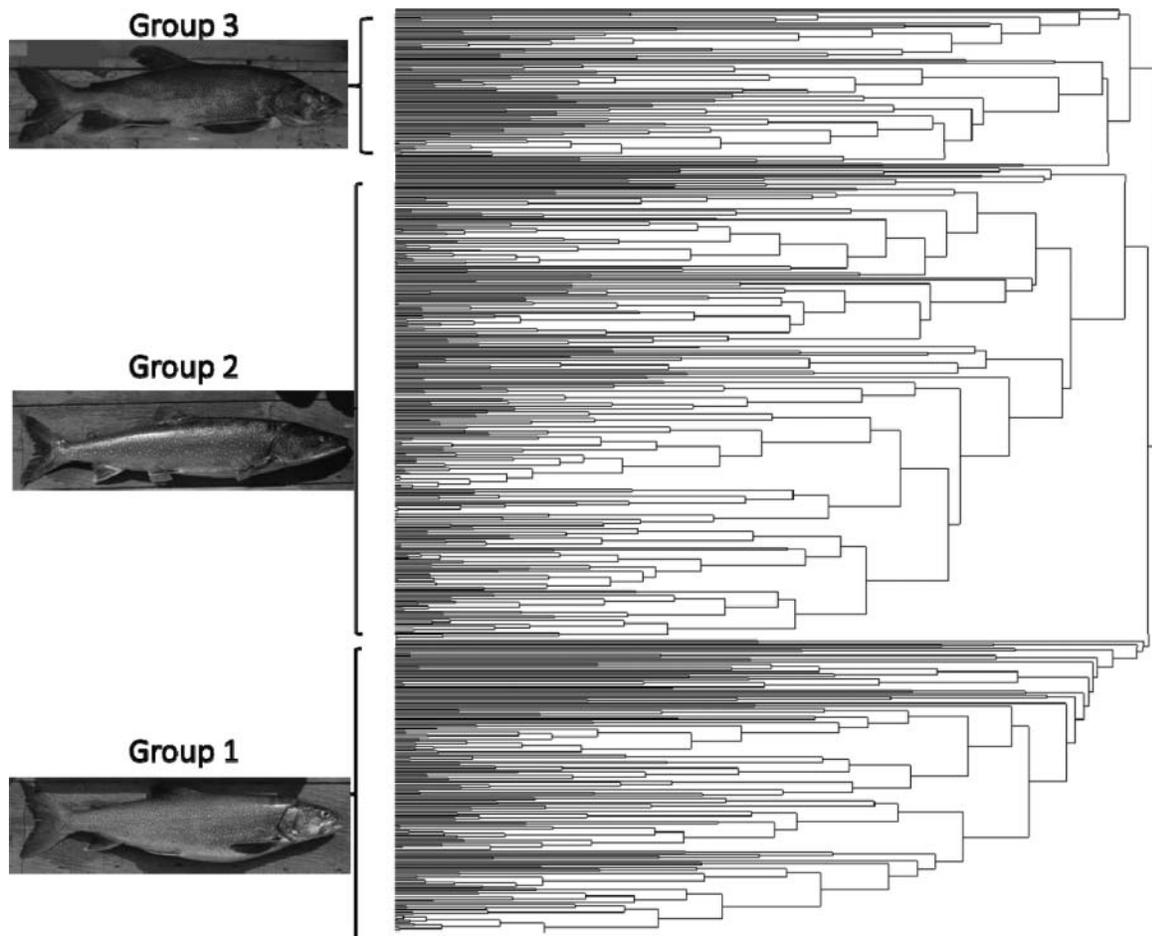


FIGURE 4. The dendrogram resulting from a UPGMA cluster analysis of 558 adult Lake Trout from shallow (≤ 30 m) waters of Great Bear Lake. Three major groups of trout were identified based on traditional morphometric measurements and principal component scores of head shape and body shape measurements.

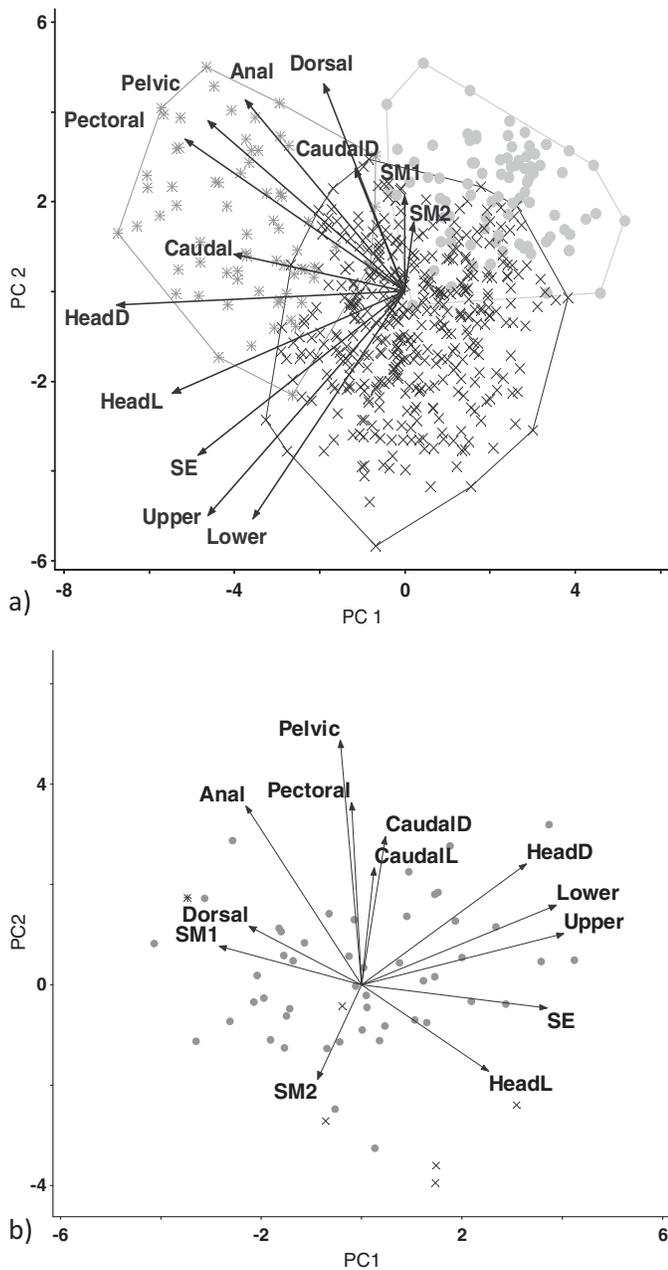


FIGURE 5. The PCA ordinations of traditional measurements and head shape of (a) adult and (b) juvenile Lake Trout. Traditional and head shape variables are defined in Figures 2 and 3 and are represented as follows: lower = lower jaw, upper = upper jaw, SE = snout-eye, HeadL = head length, HeadD = head depth, Dorsal = dorsal fin length, Caudal = caudal fin length, CaudalD = caudal peduncle depth, Pelvic = pelvic fin length, Anal = anal fin length, Pectoral = pectoral fin length, SM1 = first-axis PCA score of head shape from semilandmarks, SM2 = second-axis PCA score of head shape from semilandmarks. Principal components, PC1 and PC2, of adult Lake Trout explained 32.8% and 28.1% of the variance, respectively, whereas PC1 and PC2 of juvenile Lake Trout explained 28.3% and 18.1% of the variance. Angles and lengths of arrows represent the direction and the strength of relationship between variables and the principal components. Groups identified by UPGMA cluster analysis are represented as follows: ● = group 1, × = group 2, and * = group 3; adult groups are outlined by convex hulls.

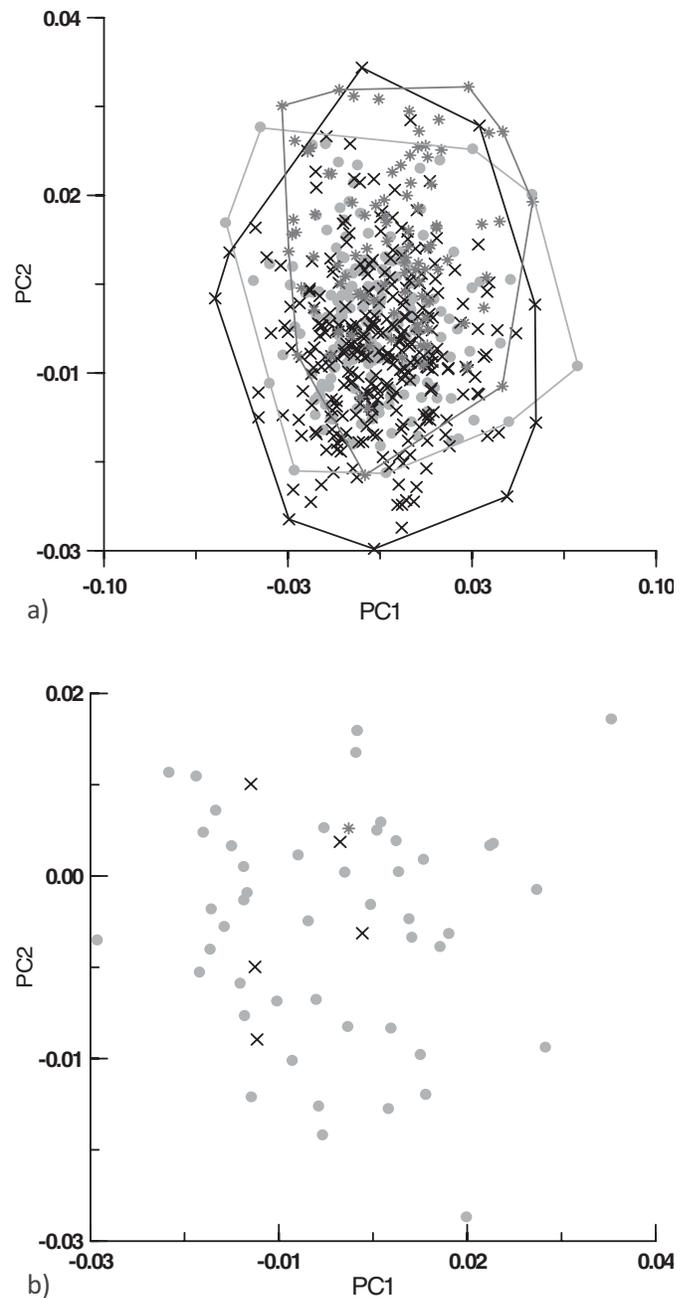


FIGURE 6. The PCA ordinations of (a) adult and (b) juvenile Lake Trout body shape. Principal components, PC1 and PC2, of adults explained 41.5% and 13.5% of the variance, respectively, whereas PC1 and PC2 of juveniles explained 45.8% and 14.2% of the variance. Groups identified by UPGMA cluster analysis are represented as follows: ● = Group 1, × = group 2, and * = group 3; adults groups are outlined by convex hulls.

(smaller fins and caudal peduncle depths). Least-square means and their standard errors for a given standardized body size of 62.2 cm for head and fin measurements among morphotypes also showed clear distinctions (Table 1).

A fourth morph ($n = 22$), although visually distinct due to a curved, arched lower jaw (Figure 7), was not classified as a

TABLE 1. Least-squares (LS) means \pm SEs of traditional morphological measurements for groups of adult Lake Trout from Great Bear Lake. The LS means were calculated in a general linear model for a standardized fish size (62.2 cm). Also presented are the results from MANOVA comparing the traditional morphological measurements and principal component (PC) scores for head and body shape among the groups. Groups with the same lowercase letter were not significantly different (Tukey's HSD post hoc test; $P > 0.05$). Least-squares means could not be calculated for the PC scores.

Traits	LS means \pm SE (Tukey HSD test results)				MANOVA <i>P</i> -value
	Group 1	Group 2	Group 3	Group 4	
Upper jaw	6.61 \pm 0.05 x	7.88 \pm 0.04 z	7.65 \pm 0.06 y	7.90 \pm 0.14 z	≤ 0.01
Lower jaw	6.57 \pm 0.05 x	7.83 \pm 0.04 z	7.38 \pm 0.06 y	7.15 \pm 0.14 y	≤ 0.01
Head depth	7.08 \pm 0.04 w	7.59 \pm 0.03 x	7.91 \pm 0.05 y	8.19 \pm 0.10 z	≤ 0.01
Head length	11.92 \pm 0.06 x	13.15 \pm 0.05 y	13.27 \pm 0.08 zy	13.61 \pm 0.18 zy	0.01
Snout-eye	4.53 \pm 0.04 y	5.42 \pm 0.03 z	5.39 \pm 0.05 z	5.63 \pm 0.11 z	≤ 0.01
Dorsal fin	9.31 \pm 0.07 y	8.69 \pm 0.06 x	10.76 \pm 0.10 z	8.97 \pm 0.21 yx	≤ 0.01
Caudal fin	10.67 \pm 0.07 x	10.80 \pm 0.06 x	12.27 \pm 0.10 z	11.57 \pm 0.21 y	≤ 0.01
Caudal peduncle depth	6.55 \pm 0.04 y	6.31 \pm 0.03 x	6.86 \pm 0.05 z	6.63 \pm 0.10 zy	≤ 0.01
Anal fin	8.94 \pm 0.06 y	8.60 \pm 0.05 x	10.37 \pm 0.08 z	9.13 \pm 0.17 y	≤ 0.01
Pelvic fin	8.01 \pm 0.06 y	7.73 \pm 0.05 x	9.64 \pm 0.08 z	7.63 \pm 0.17 yx	≤ 0.01
Pectoral fin	11.12 \pm 0.09 y	10.87 \pm 0.07 x	14.01 \pm 0.12 z	10.86 \pm 0.26 yx	≤ 0.01
Head shape PC1	z	x	y	zy	≤ 0.01
Head shape PC2	z	y	z	zy	≤ 0.01
Body shape PC1	z	z	z	z	0.51
Body shape PC2	z	z	z	z	0.76

distinct cluster in the UPGMA analysis. However, some traits (head depth and length of caudal fin) of this morph (group 4) differed significantly from groups 1–3 (Table 1), while the remaining traits formed a unique combination relative to groups 1–3. For the juvenile UPGMA, the three-cluster level was not particularly successful in identifying distinct morphological groups, because two of the three groups were rare ($N < 5$), leaving most fish together in the same large cluster. Although discriminant analysis suggested that the groups were distinct ($\lambda = 0.14$, $N = 55$, $P < 0.01$), jackknife cross-classification rates were lower for the two rare groups (73% and 0% classification success). In addition, no clear discrimination of the three groups

could be made in either of the PCAs using traditional measurements and head shape (Figure 5b) or body shape (Figure 6b).

DISCUSSION

Based on an analysis of more than 600 fish from the shallow-water habitat of Great Bear Lake, our study demonstrated that there are at least three and possibly four morphologically distinct groups of Lake Trout. These findings expand and quantify this singular, contemporary case of Lake Trout polymorphism within shallow-water habitat (Blackie et al. 2003; Alfonso 2004; but see Brown et al. 1981 and Goodier 1981 for qualitative

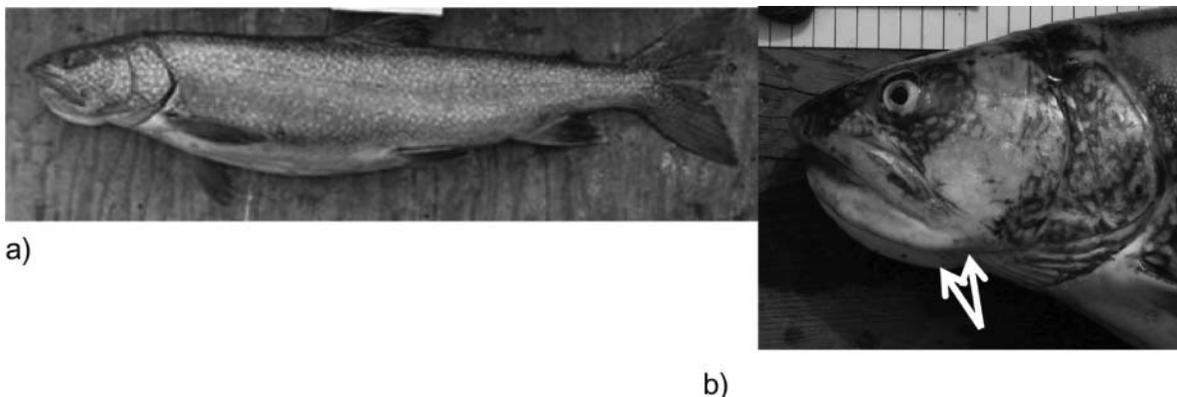


FIGURE 7. Example of a group 4 Lake Trout from Great Bear Lake: (a) full body profile and (b) close-up of head. Arrows indicate lower jaw, the visually distinctive trait that differentiates this group from the other groups of Lake Trout.

descriptions of historical stocks or “breeds” of shallow-water trout recalled by old-time commercial fishers from Lakes Michigan and Superior). Our study thus extends our knowledge of Lake Trout diversification, generally associated with depth (Moore and Bronte 2001; Zimmerman et al. 2007; Eshenroder 2008). Great Bear Lake remains isothermal throughout the open-water season, which may provide a variety of cold shallow-water habitats. Furthermore, the lake has a depauperate fish fauna, which may result in low interspecific competition. Consequently, Great Bear Lake probably provides different resource opportunities to Lake Trout within a narrow range of depths (Alfonso 2004; MacDonald et al. 2004). Interestingly, the different forms in our study were usually found mixed together in the same net catches.

Head and fin measurements of Lake Trout differed among the groups more than did body shape. Previous studies of sympatric Lake Trout morphotypes, although usually based on limited sampling ($n = 72\text{--}99$ fish), have generally shown that head and fin measurements better reflect differences in diet, with which these morphotypes are linked or inferred, than differences in body shape (Blackie et al. 2003; Alfonso 2004; Zimmerman et al. 2006, 2007). Body shape differences in this context are thought more to reflect adaptations to buoyancy, which is related to depth distribution and vertical migration (including feeding on vertically migrating prey) (Zimmerman et al. 2006, 2007, 2009; Eshenroder 2008). Because we focused on shallow-water morphotypes, it is perhaps not surprising that we observed a reduced importance of body shape.

Differences in the relative importance of head shape and fin measurements versus overall body shape have also been found in other fishes (e.g., Fryer and Iles 1972; Maderbacher et al. 2008). Populations evolve in ways that allow better exploitation of their resources (Smith and Skúlason 1996), and morphological differentiation in several fishes has been related to differences in feeding-related traits and swimming ability (Bouton et al. 2002; Kristjánsson et al. 2002; Kahilainen et al. 2005). The stronger discrimination of head and fin measurements versus body shape we observed may reflect the ways in which selection favored the development of different shallow-water morphs (e.g., Sušnik et al. 2006). In contrast, body shape differentiation may become more important where depth segregation among morphs is involved.

Morphological properties can suggest the ecological role of a fish in its community and thus provide the basis for niche predictions (Bronte et al. 1999). In general, head characteristics (i.e., shape and dimension) have been linked to foraging efficiency associated with particular prey, environment, or both (e.g., Jónsson and Jónsson 2001; Adams et al. 2004). More specifically, diversification of fish via trophic specialization tends to reveal itself through differences in the trophic apparatus, particularly the mouth, which has direct contact with prey and substrate (Barlow and Munsey 1976; Maderbacher et al. 2008). In our study, for example, group 2 individuals were characterized by longer heads and longer jaws relative to group 1, corresponding to

previously described piscivorous and insectivorous morphs, respectively, in other Salmonidae (e.g., Proulx and Magnan 2004; Keeley et al. 2005, 2007; Janhunen et al. 2009).

Lake Trout in group 3 were characterized by deeper heads and caudal peduncles and longer fins than those in groups 1 and 2. Fin lengths and caudal peduncle depth should reflect differences in locomotion, which are often associated with differences in habitat use or foraging modes (Kristjánsson et al. 2002). Longer fins are generally linked with more precise maneuvering but lower speed associated with prey capture in complex benthic habitat, whereas short pectoral fins, in particular, are related to cruising movements associated with pelagic predators in open water (Webb 1984; Pakkasmaa and Piironen 2001; Gillespie and Fox 2003). In addition, the relative body depth differences, e.g., between groups 2 and 3, suggest differences in swimming performance. A fusiform body shape associated with short fins, as seen in group 2, is known to provide a hydrodynamic advantage by minimizing drag and energy during extended swimming periods (Webb 1984).

Paired morphotypes in several species are commonly observed in northern aquatic systems and are associated with differences in foraging and habitat use (Robinson and Wilson 1994). Indeed, two of the groups we identified in Great Bear Lake can be linked to various names previously described in the literature. Blackie et al. (2003) described Lake Trout with traits comparable to our group 1 as “piscivores” and group 3 as “insectivores” whereas Alfonso (2004) identified group 1-like trout as “bluebacks” (piscivores) and group 3-like trout as “redfins” (benthic feeders). The morphological descriptions of these groups correspond in each study: shorter head measurements for group 1 and longer fin lengths and caudal peduncle depths for group 3. Limited diet information to date has made it difficult to draw definitive conclusions regarding these two morphs, but larger otolith increments for “piscivores” was consistent with faster growth expected of fish-eating Lake Trout (Blackie et al. 2003). That we were also able to describe two additional Lake Trout morphotypes (groups 2 and 4) may relate to our greater sample sizes and more extensive spatial and temporal coverage.

Although we analyzed fewer juveniles, which may have contributed to our inability to identify clear groups, the limited discrimination among juvenile groups using body shape and traditional head and fin characteristics also suggests that trait differences are expressed primarily at a later life stage, leading to larger and more measurable changes at the adult stage. Ontogenetic shifts later in life are common in fish, including polymorphic populations, with juveniles of two morphs often sharing habitats and resources and looking correspondingly similar (Meyer 1990; Snorrason et al. 1994; Mittelbach et al. 1999; Moles et al. 2010). However, other sympatric polymorphic species will have distinct groups of juveniles occupying the same distinct habitats and exploiting the same distinct prey as adults (e.g., Werner and Gilliam 1984; Robinson and Wilson 1996; Ruzzante et al. 2003; Morinville and Rasmussen 2008).

An important step, therefore, in understanding the polymorphism that we observed is to understand the ecological and evolutionary processes that led to the differences and the relative contribution of genetics and phenotypic plasticity (Robinson and Wilson 1996; Mittelbach et al. 1999).

Phenotypically plastic responses observed in adults, a genetic variation expressing phenotypic differences only in adults, or differences in juvenile versus adult ecologies are possible scenarios to explain the different degrees of morphological variation between adults and juveniles. The expression of morphological differences that parallels an ontogenetic niche shift is not uncommon in arctic *Salvelinus* species (Jónsson and Jónsson 2001). For example, the development of an individual Arctic char into one specific morph or another may be a conditional strategy influenced by the growth of an individual at a specific development stage (Reist et al. 2013).

In Lake Trout more specifically, Zimmerman et al. (2009) found marked morphological differences between smaller and younger lean- and siscowet-like fish in Great Slave Lake, especially in head profiles, snouts, and eye position. Although depth distributions still overlapped among these younger trout, they were already partitioning available food resources. We currently have little information on genetic differences among any of the morphotypes or on resource use patterns of juvenile Lake Trout in Great Bear Lake. As noted earlier, however, all Lake Trout, including juveniles and adults, were caught together in depths less than 30 m, which suggests differences in the pattern of diversification among shallow-water morphotypes of Great Bear Lake and the depth-stratified morphotypes of Great Slave Lake.

The inability to clearly identify the fourth morphotype in our cluster analysis tempers our conclusions about this potential morph. The fourth group was not as numerous in our data set and was less widespread compared with the other forms. The variation associated with this group, most notably related to the lower jaw, was probably limited in magnitude compared with the combination of other traits that primarily defined the first three groups, which explains its absence from the UPGMA analysis. Nevertheless, we found distinct differences in head shape and fin measurements between this group and the other groups, supporting its consideration as a fourth shallow-water morph. Head depth was most distinctive in this morph, reflecting a thicker, more curved, lower jaw. Lower jaw length in this group also differed from groups 1 and 2, but not group 3, probably due to the position of group 3's subterminal mouth. Although the small sample size may raise questions about the validity of this group, rare morphotypes can have fitness advantages over more common ones (Wimberger 1994; Skúlason and Smith 1995; Smith and Skúlason 1996). Further research is required to confirm the validity of this fourth group and to investigate whether its diet or other niche dimensions differ from other forms of Lake Trout.

Morphological variation within a species has generally been associated with variation in life history (Nordeng 1983; Jónsson and Jónsson 2001), and life history diversity has already been

suggested for Lake Trout in Great Bear Lake (Blackie et al. 2003; Alfonso 2004). Life history data are critical to the development of sustainable management strategies and thus are essential for the maintenance of Lake Trout diversity in Great Bear Lake. Blackie et al. (2003), for example, suggested growth-rate differences between insectivorous and piscivorous morphs, which could lead to differential harvest rates in the Great Bear Lake fisheries and ultimately have important consequences for maintenance of the observed intraspecific variation (Moles et al. 2010). Life history diversity should also increase stability and resistance of the ecosystem to perturbation, especially from anthropogenic impacts, such as climate change, that are increasing in northern aquatic systems (Reist et al. 2013). Further investigation of life history diversity in Lake Trout from Great Bear Lake is needed both to better understand the origin and maintenance of this diversity of forms and to improve management of this exceptional example of arctic biodiversity.

CONCLUSION

Lake Trout in northern lakes are expanding our knowledge and understanding of intraspecific diversity in recently deglaciated lakes (e.g., Schluter 1995; Smith and Skúlason 1996; Robinson and Parsons 2002; Zimmerman et al. 2009). Research on the ecology, life history, and genetics of the groups identified in our study is needed to investigate the mechanisms maintaining this diversity and its impacts on Lake Trout biology, ecology, and management in Great Bear Lake and elsewhere.

Lake Trout has been characterized as expressing low phenotypic variation compared with its congeneric relatives, especially Arctic char (Behnke 1972). Our demonstration of three or four shallow-water morphotypes, despite relatively limited sampling of this large North American lake, expands previous models of the origin and maintenance of Lake Trout diversity. Although the deep waters of Great Bear Lake are even less well studied, Eshenroder (2008) reported observing humper-like, deepwater Lake Trout, and additional present shallow-water sampling among all five arms of Great Bear Lake suggests interarm diversity occurs within each of the morphotypes described here (authors' unpublished data). Thus, it seems possible that the Lake Trout of Great Bear Lake could challenge the iconic diversity of Arctic char, e.g., of Thingvallavatn (Snorrason et al. 1994). Other recent discoveries of, for instance, anadromous behavior (Swanson et al. 2010) and ontogenetic shifts rather than a polymorphism between benthic and pelagic habitats (Zimmerman et al. 2009) illustrate how variability in northern Lake Trout populations is poorly understood and should receive further study.

ACKNOWLEDGMENTS

Financial support was provided by Fisheries and Oceans Canada (DFO), Natural Sciences and Engineering Research Council of Canada, Sahtu Renewable Resource Board, Canadian Circumpolar Institute's Circumpolar/Boreal Alberta Research

and Northern Scientific Training Program, and Aboriginal Affairs and Northern Development Canada Northwest Territories Cumulative Impacts Monitoring Program grants. Logistical support was provided by Polar Continental Shelf Program. Déline Renewable Resources Council, Déline Lands and Finance Corporation, the community of Déline, DFO in Hay River, and the federal Department of Environment and Natural Resources in Déline provided valuable help with field planning and logistics. We especially thank G. Lafferty, S. Wiley, and C. Yukon who helped lead field camps and coordinate logistics along with the following individuals who helped conduct field sampling in various years: J. Baptiste, D. Baton, L. Dueck, R. Eshenroder, G. Kenny, H. Kenny, M. Lindsay, G. Menacho, I. Neyelle, L. Neyelle, M. Smirle, A. Vital, and C. Yukon.

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