Phenotypic Diversity of Lake Trout in Great Slave Lake: Differences in Morphology, Buoyancy, and Habitat Depth

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Abstract.—Little is known about the phenotypic diversity of lake trout Salvelinus namaycush in large North American lakes outside the Laurentian Great Lakes. This study tested the hypothesis that phenotypic diversity in Great Slave Lake, Northwest Territories, Canada, is associated with water depth, as was observed during similar studies of lake trout in Lake Superior. We describe the association of body size with color, buoyancy, and morphology; compare these phenotypic traits among depth strata; and establish whether lake trout phenotypes occur as discrete groups. Phenotypic diversity increased among fish longer than 43 cm standard length. In water less than 50 m deep, large lake trout (>43 cm) were light in color, buoyantly heavy, and streamlined and possessed short pectoral fins. In water deeper than 50 m, large lake trout were dark in color, buoyantly light, and deep bodied (less streamlined) and had long pectoral fins. Without assigning descriptions to individuals before the analysis, we identified two phenotypic groups. These groups represented nondiscrete phenotypes; lake trout of intermediate shape had intermediate fin lengths, capture depths, and buoyancies. The phenotypic patterns observed in Great Slave Lake were similar to the lean and siscowet forms that currently exist in Lake Superior. Deepwater forms, previously believed to be endemic to the Great Lakes, are more geographically widespread and may represent diversity typical of this species in large, deep lakes. We suggest that the lake trout phenotype associated with deep water (buoyantly light, long pectoral fins) is adaptive for daily vertical migrations.

Diversification of fish body form has been reported from lakes across Asia (Bronte et al. 1999), Africa (Greenwood 1974), and North America (Behnke 1972; Smith and Todd 1984). The prevalence of multiple intraspecific phenotypes, reflecting intralacustrine radiations in recently formed lakes, has been attributed to the abundance of niches available under lessened competitive and predation pressures (Schluter 1993, 1995; Robinson and Wilson 1994).

In the Laurentian Great Lakes, morphologically distinct forms of lake trout Salvelinus namaycush occupy different depths (Moore and Bronte 2001; Bronte et al. 2003). Deepwater forms of lake trout, rare in small lakes, are believed to have been historically widespread in the Great Lakes (Brown et al. 1981; Eshenroder et al. 1995); however, over the past century, these forms disappeared outside of Lake Superior and are not the focus of ongoing restoration efforts (Burnham-Curtis et al. 1995; Krueger et al. 1995; Eshenroder and Burnham-Curtis 1999). The most common forms of Lake Superior lake trout are the lean and siscowet (fat) lake trout (Khan and Qadri 1970; Lawrie and Rahrer 1973; Moore and Bronte 2001). Although leans and siscowets are less distinct at small sizes (Eschmeyer and Phillips 1965; Harvey et al. 2003), large leans (>60 cm) are more streamlined, have a lower lipid content, and typically occupy shallower depths (<70 m) than large siscowets, which are deep bodied, have high lipid content, and typically occupy deeper habitats (>100 m). A third, less-common form, the humper (banker), is smaller in size and has thinner abdominal walls than the other two forms, is intermediate in lipid content, and is restricted in distribution to isolated offshore shoals (≥50-m depths surrounded by ≥100-m depths).

The relatively high lipid content of siscowet lake trout in Lake Superior gives them an advantage over lean lake trout for buoyancy regulation in deepwater habitats (Henderson and Anderson 2002). Fish with high lipid content weigh less in water at a given mass, a characteristic associated with reduced swimming costs in fishes without swim bladders (Corner et al. 1969; Bone 1972; Eastman 1988). High lipid content also occurs in vertically migrating fishes whose swim bladders are compressed after rapid descents (Alexander 1972; Krause et al. 2002). Buoyancy regulation,
therefore, is a potentially important selection pressure contributing to phenotypic diversity of lake trout in Lake Superior (Henderson and Anderson 2002) and could be expected to select for novel phenotypes in deepwater lakes similar to the Laurentian Great Lakes.

Until recently, North American lakes of comparable area and depth to the Laurentian Great Lakes have received little attention with regard to descriptions of lake trout phenotypic diversity. Two recent studies from Great Bear Lake reported multiple forms of lake trout coexisting in shallow-water habitats (Blackie et al. 2003; Alfonso 2004). These discoveries challenged the long-held belief that lake trout phenotypic diversity was endemic to the Laurentian Great Lakes (Behnke 1972; Burnham-Curtis and Smith 1994).

Herein, we describe the phenotypic diversity of lake trout in another large, deep lake, Great Slave Lake, Northwest Territories, which is considered to be one of the Great Lakes of Canada (Evans 2000). Because its size and bathymetry are comparable to those of Lake Superior, we hypothesized that the lake trout community in Great Slave Lake would be phenotypically diverse and that this diversity would be associated with water depth. The objectives of our study were (1) to determine whether an association exists between lake trout body size and four phenotypic traits (buoyancy, color, fin length, and body shape) and establish the body size at which phenotypic diversification becomes apparent; (2) to identify relationships between capture depth and lake trout phenotype; and (3) to establish whether lake trout phenotypes occur as discrete groups or as a continuum among extremes.

Methods

Study area.—Great Slave Lake, located in the Northwest Territories, is the fifth largest lake in North America (Rawson 1950). It has a surface area of 28,568 km² and a maximum depth of 614 m, which are comparable to those of Lake Superior (82,410 km² and 358 m) and Great Bear Lake (31,320 km² and 452 m) (Christie and Regier 1988; Evans 2000). The historic composition of aquatic communities in all three lakes is also comparable (Keleher 1972; Johnson 1975; Bailey and Smith 1981). The lake comprises two distinct physiographic regions, the Western Interior Lowland (West Arm) and the Canadian Shield (East Arm). The West Arm has relatively shallow depths and soft substrates, whereas the East Arm is characterized by abundant deepwater habitats and rocky substrates (Evans 2000). Lake trout were collected for this study from Christie Bay, which is one of two bays in the East Arm. In comparison to Lake Superior, fish communities in Great Slave Lake have been less influenced by human activities. Fishery harvests in the East Arm include subsistence fishing and limited levels of sports angling (Low et al. 1999); this area has been closed to commercial fishing since 1974 (Evans 2000). Exotic fishes have not become established (Keleher 1972; Stewart 1997).

Field procedures.—Lake trout were caught in the East Arm of Great Slave Lake during August of 2001 and 2002 with gill nets and by angling (Table 1). Gill-net mesh sizes varied from 64 to 114 mm (stretch measure). Five gill-net sets were made in 2001, and eight were made in 2002. Depth strata for the gill-net sets were chosen based on known depths of lake trout forms in Lake Superior (Moore and Bronte 2001; Bronte et al. 2003). Of the 13 gill-net sets, 4 were conducted within the 0–50-m depth stratum, 7 were conducted within the 50–100-m stratum, and 2 were conducted at depths greater than 100 m. Nets were in the water overnight for about 24 h. An additional four fish were angled from the 0–50-m depth stratum in 2001. Data collected from each fish included a full-body photograph (for shape and fin measures), weight in air, and weight in water with the swim bladder deflated (for estimating buoyancy).

Full-body photographs were taken of each fish lying on its side with pectoral and pelvic fins extended parallel to the body and with dorsal, caudal, and anal fins in an open position (Figures 1, 2). Each fish was positioned on a cradle strung with seine netting. The cradle reduced the distortion caused by curvature if individuals had been laid on a flat surface. Photographs were taken with a 35-mm camera equipped with an 80-mm lens, a strobe light, cable release, tripod, and super-fine-grain transparency film (Fujichrome Provia 100F). Transparencies were scanned and converted to digital format. The digital-image files were used to quantify morphology and color.

Measures of lake trout phenotype.—Body coloration of each image was quantified along a 255-unit brightness scale using ImageJ version 1.32j software (http://rsb.info.nih.gov/ij). This scale was converted to a scale of 0 (black) to 1 (white) for ease of interpretation. Brightness was averaged for six measurements taken from each lake trout based on a 40 × 40 pixel square placed over six general regions of the lateral body image (cheek, three dorsal, and two ventral). Lake trout were excluded from further color analysis if their body coloration was noticeably altered after collection.

Percent buoyancy (water weight divided by air weight; Krause et al. 2002) is an approximation of gravitational pull when a fish has descended to a depth where its swim bladder is completely compressed. The percent buoyancy of each lake trout was calculated after expelling the gas from its swim bladder. Weight
was obtained using a Pesola spring scale calibrated using a standard set of weights (Jennings 1989). Each fish was suspended from the spring scale with a hook and weighed to the nearest gram in air and then in water. The water:air weight ratio was converted to a percentage. The weight-in-water method accounts for all physiological differences (soft and hard tissues) that affect buoyancy.

Fin lengths and body shape were measured from each digital image using \((x, y)\) coordinates (Figures 1, 2). The coordinates were digitized using tpsDIG software available from the State University of New York at Stony Brook morphometric website (http://life.bio.sunysb.edu/morph). Five fins were measured using 10 landmarks associated with the first ray of each fin and the sites of fin insertion (Figure 1). Body shape was measured using 16 landmarks that covered the entire lake trout body form (Figure 2). These landmarks included all of the anatomical structures used by Moore and Bronte (2001) in their study of Lake Superior lake trout.

Fins were measured as one-dimensional linear distances. Fin lengths and standard length (SL) were log\(_{10}\) transformed for the statistical analyses. Body shapes were measured as two-dimensional geometric forms and compared using landmark-based geometric morphometrics (Bookstein 1991; Parsons et al. 2003; Zimmerman 2004). The geometric morphometric method calculated shape variables from digitized coordinates of our 16 landmarks (Figure 2). This technique removed information pertaining to scale, rotation, and position from the digitized coordinates (Zelditch et al. 2004). Shape differences among individuals were represented by relative differences in

### Table 1

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**FIGURE 1**.—Fin length, body depth, and body length (SL) of lake trout from Great Slave Lake. First-ray length was measured for the dorsal fin (1), anal fin (3), pelvic fin (4), and pectoral fin (5). The caudal fin (2) measure was the longest ray on the dorsal side of the fin. Head depth (HD) intersected the top edge of the opercular flap. Midbody depth (MBD) was the maximum depth of the midbody. Caudal depth (CD) intersected the posterior insertion of the anal fin.
landmark positions. The CoordGen program was used to calculate shape variables. CoordGen is one of a series of integrated morphometrics programs (IMPs) produced in Matlab6 (Mathworks 2000) by H.D. Sheets (http://www2.canisius.edu/sheets/morphsoft.html).

Ontogeny of phenotypic traits.—Separate linear regression models were used to determine whether phenotypic traits (buoyancy, brightness, fin lengths, and shape) were correlated with SL. Shape was represented as a procrustes distance. Procrustes distance is a univariate measure, calculated from shape variables, that represents the magnitude of difference between each individual and a reference shape. The reference shape used was the average shape of the shortest three lake trout in our collection (see Zelditch et al. 2004 for calculation). All data were log_{10} transformed before analysis. Individual fins were analyzed separately. An α value of 0.05 was used in all statistical tests. Unless otherwise noted, all statistical tests were conducted with SPSS 12.0 (SPSS 2003).

To determine the SL at which phenotypic variation becomes apparent, we first determined which of the measured characters become more variable with increased size and then identified the approximate SL when diversification appears. Character variation was represented by residuals from the regression of each trait on SL. Residuals represented the magnitude of difference between an individual measure and the predicted measure for a given SL (Reist 1985), and thus represented phenotypic variation with size effects removed. The relationship between character variation and size was determined by regressing the absolute value of the calculated residuals on SL. If phenotypic diversity increases with body size, the absolute value of the residuals will be positively correlated with SL. If phenotypic diversity remains constant over ontogeny, residuals and SL will not be correlated. For traits with a positive correlation, we inspected the trait–SL plot to determine whether trait diversification begins at a common size for all traits.

Phenotype differences between depth strata.—Four separate fixed-effects models were used to determine whether lake trout color, buoyancy, fin lengths, and shape differed between depth strata. To interpret the results of these analyses, we assumed that capture depth was a good measure of living depth for the collected individuals. In each statistical model, depth stratum was the categorical explanatory variable. Standard length was the covariate for color, buoyancy, and fin length analyses, and centroid size (log_{10} transformed) was the covariate for shape analysis. Centroid size is a geometric measure of size, is highly correlated with SL, and is appropriate for shape analysis (Zelditch et al. 2004). An analysis of covariance (ANCOVA) model was used to determine whether color and buoyancy were associated with depth stratum and length. A MANCOVA model was used to determine whether fin lengths and shape were associated with depth stratum and length. Fin lengths were represented by linear measurements of all five fins (Figure 1). Shape variables were represented by principal components (PC) scores to reduce the number of dependent variables used for analysis. Principal component scores were used from axes explaining 90%
of the variation in shape. Significant multivariate differences from the MANCOVA analyses were further analyzed with a discriminant function analysis (DFA) to determine which dependent variables contributed to the significant differences. The DFA for shape was conducted using the CVAGen6i, a program in the IMP series.

Where character–SL regression slopes differed among depth strata, measures were size adjusted before the analysis using within-depth-strata regression slopes (Reist 1985) and were analyzed with a MANOVA model. Size-adjusted scores for buoyancy, brightness, and fin lengths were calculated from the regression of each character on SL. Residuals from the regression were added to the predicted trait measure for a 55-cm lake trout. Size adjustment for shape variables followed a similar technique and was performed with Standard6, a program in the IMP series.

Groupings of lake trout phenotypes.—An unweighted pair-group method with arithmetic averages (UPGMA) cluster analysis was used to examine groups of lake trout phenotypes. Measures used for this analysis were buoyancy, head depth, midbody depth, caudal depth (Figure 1), and pectoral, caudal, and dorsal fin lengths. Buoyancy and body depth measures were included because they were known to differ between shallow-water and deepwater forms in Lake Superior (Eschmeyer and Phillips 1965; Moore and Bronte 2001) and were associated with capture depth in Great Slave Lake (this study). Pectoral, caudal, and dorsal fins were included because they were associated with depth of capture in Great Slave Lake (this study). Measures were size adjusted to 55 cm SL and standardized to a z-distribution prior to the analysis. Euclidean distance was the resemblance coefficient used to calculate clusters with MVSP version 3.12 (Kovach Computing Services 2001). The robustness of groups identified by the cluster analysis was tested with a DFA. Classification of individuals into groups was cross validated using a jackknifing procedure that sequentially removed individuals and determined group membership based on a recalculated discriminate function (Johnson 1998; Moore and Bronte 2001; Alfonso 2004).

A two-block partial-least-squares analysis (2B-PLS) explored the covariation among the measured aspects of lake trout phenotype. This analysis allowed us to inspect for groupings and for a continuum of phenotypic expression. We used continuous measures of depth (maximum depth of the net in which each fish was captured) rather than the depth strata used in the previous analyses. Brightness was not included because it restricted sample size too much. The 2B-PLS tested for covariance patterns between shape variables (block 1) and pectoral, caudal, and dorsal fin lengths, depth of capture, and buoyancy (block 2; standardized to z-distributions) (Rohlf and Corti 2000; Rüber and Adams 2001). The 2B-PLS calculated vector pairs that best explained the covariation between the two sets of variables (shape versus fin depth–buoyancy). Each fin depth–buoyancy vector was weighted for the five measures (similar to PC coefficients), and each individual had a single composite fin depth–buoyancy score along each vector.

Permutation tests determined whether each identified vector pair explained more covariance between the blocks than expected by chance and whether the correlation among individual scores for each vector pair was greater than expected by chance. One hundred permutations randomly reshuffled the data; this destroyed the covariation but retained the sample size of the original data set. The vector pair was considered to have identified a significant pattern if the singular value (equivalent to eigenvalue in PC analysis) of the original data set was greater than 95% of those calculated from the permutation tests. The correlation for a given vector pair was considered significant if the correlation among axis scores was greater than 95% of those calculated from the permutation test. The 2B-PLS and permutation tests were performed using PLSMaker, an IMP program.

Results

Data were analyzed for 72 lake trout. The mean catch per unit effort was eight lake trout per set (minimum, 0; maximum, 27). A total of 26 lake trout, ranging in length from 27 to 71 cm SL (mean, 50.2 cm; SD, 9.9), were caught in the 0–50-m depth stratum. Forty-six lake trout, ranging in length from 25 to 58 cm SL (mean, 45.5 cm; SD, 10.3), were caught in the 50–100-m depth stratum. No lake trout were caught in the two sets made in the 100–150-m depth stratum.

Ontogeny of Phenotypic Traits

As lake trout body length increased, percent buoyancy decreased ($R^2 = 0.18, F_{1,69} = 14.8, P < 0.001$), color became darker ($R^2 = 0.33, F_{1,33} = 15.9, P < 0.001$), and midbody profile depth increased ($R^2 = 0.40, F_{1,70} = 46.4, P < 0.001$). All five fin lengths were positively correlated with SL ($R^2 > 0.71, P < 0.001$). Variation in buoyancy ($R^2 = 0.20, F_{1,69} = 17.2, P < 0.001$), shape ($R^2 = 0.11, F_{1,70} = 8.3, P = 0.005$), and pectoral fin length ($R^2 = 0.11, F_{1,70} = 8.2, P = 0.005$) were positively correlated with SL. No correlation between trait variation and SL existed for brightness and dorsal, caudal, anal, and pelvic fin lengths ($R^2 < 0.05, P > 0.06$).

Buoyancy, shape, and pectoral fin length were similar among small lake trout but varied widely
Diversification of each trait began at an approximate length of 43 cm SL. In fish longer than 43 cm SL, trait ontogeny appeared to follow one of two trajectories, which were more apparent when individuals were coded by depth stratum (Figure 3). The trajectory of all lake trout collected in the 0–50-m stratum followed a similar slope across all sizes. The trajectory of lake trout from the 50–100-m stratum, however, differed in slope for lake trout smaller and larger than the 43-cm threshold. Subsequent analyses, therefore, were conducted separately for small (N = 18) and large lake trout (N = 54). Separate comparisons for small and large fish allowed for the trait size adjustments necessary for statistical analyses.

Phenotype Differences between Depth Strata

Large lake trout caught at 50–100-m depth were darker than those caught at 0–50-m depth (F₁,22 = 56.8, P < 0.001), and larger lake trout were darker than smaller individuals (F₁,22 = 35.7, P < 0.001). Brightness of small lake trout was not correlated with length (F₁,6 = 0.35, P = 0.58) or depth (F₁,5 = 0.61, P = 0.47). No length × depth interaction existed for small (F₁,5 = 2.2, P = 0.2) or large lake trout (F₁,21 = 0.11, P = 0.75). Sample size for the color comparisons was low, as many individuals were not in suitable condition for this measure. The brightness measure of one large fish (GSL 4–9), collected at a depth of 76 m, was 3.0 standard deviations whiter than the predicted score for a lake trout of its size in the 50–100-m depth stratum. Including this fish in the ANCOVA model for large lake trout produced a depth × length interaction (F₁,22 = 6.19, P = 0.02) that changed how these data were interpreted. Further analysis (see below) indicated that, in addition to color, this individual was more similar to the body, fin, and buoyancy measures found in lake trout collected from shallow water (50 m). This fish may have been caught as the net descended to the bottom, ascended to the surface, or it may actually have been swimming at 76-m depth. Regardless, this lake trout was removed from the analysis of brightness because of its singular effect on the statistical outcome.

Large lake trout were buoyantly lighter in the 50–100-m depth stratum (mean percent buoyancy, 2.09%; SD, 1.31) than in the 0–50-m depth stratum (mean, 5.04%; SD, 0.89) (F₁,52 = 85.2, P < 0.001). Buoynancies of large lake trout were size adjusted before analysis because buoyancy–SL correlations differed between depth strata (depth × length interaction: F₁,46 = 4.2, P = 0.05). Percent buoyancy of small lake trout was not correlated with length (F₁,14 = 0.03, P = 0.86) or depth stratum (F₁,14 = 0.003, P = 0.96), and no depth × length interaction existed for small fish (F₁,13 = 0.92, P = 0.36).

The average 55-cm lake trout caught in the 50–100-m depth stratum had a pectoral fin that was 1.2 cm (14%) longer, a caudal fin that was 1.1 cm (12%) longer, and a dorsal fin that was 1.1 cm (14%) shorter than those of a similar-sized fish caught in the 0–50-m stratum.
depth stratum. Fin lengths of large lake trout were correlated with SL \((F_{5,47} = 26.5, P < 0.001)\) and depth stratum \((F_{5,47} = 10.7, P < 0.001)\). Differences between depth strata were largely influenced by the pectoral, dorsal, and caudal fins (DFA: Wilk’s \(\lambda = 0.41, df = 5, P < 0.001\)). The standardized canonical discriminant function coefficients were 0.84 for the pectoral fin, 0.55 for the dorsal fin, 0.30 for the anal fin, and 0.04 for the pelvic fin. Fin lengths of small lake trout were positively associated with SL \((F_{5,11} = 61.1, P < 0.001)\) but did not differ between depth strata \((F_{5,11} = 0.81, P = 0.57)\). Fin–SL correlations were similar between depth strata for small \((F_{5,10} = 2.15, P = 0.14)\) and large lake trout \((F_{5,46} = 0.33, P = 0.89)\).

Large lake trout shape was associated with length \((F_{8,44} = 12.2, P = 0.01)\) and differed between depth strata \((F_{8,44} = 15.8, P < 0.001)\). The function discriminating the shape of large lake trout between depth strata (Wilk’s \(\lambda = 0.105, df = 28, P < 0.001)\) indicated that lake trout in the 50–100-m depth stratum had deeper head, midbody, and caudal profiles than those collected from the 0–50-m depth stratum (Figure 4). The shape of small fish was not correlated with length \((F_{7,9} = 2.08, P = 0.15)\) or depth stratum \((F_{7,9} = 1.01, P = 0.49)\). Correlations of shape with size did not differ between depth strata in small \((F_{7,8} = 0.98, P = 0.51)\) or large \((F_{8,43} = 1.38, P = 0.23)\) lake trout.

**Groupings of Lake Trout Phenotypes**

At least two phenotypic groups were identified based on measurements of lake trout longer than 43 cm SL collected from Great Slave Lake (Figure 5). Compared to group 1, lake trout in group 2 were, on average, 66% lighter (percent buoyancy) with a 15% increase in head depth, 32% increase in midbody depth, and 9% increase in caudal depth (Table 2). Pectoral fin length of group 2 was, on average, 16% longer than that of group 1. Caudal and dorsal fins were 3% longer and 5% shorter, respectively, in group 2 than in group 1. A single discriminant function best differentiated these groups (Wilk’s \(\lambda = 0.14, df = 7, P < 0.001)\). Individuals in groups 1 and 2 had jackknifed cross validation rates of 100% and 96.4%, respectively. Phenotypic groupings were examined only for lake trout longer than 43 cm SL because phenotypic diversity was notable for this size-group when compared to smaller lake trout (Figure 3).

Ninety-two percent of the covariation between shape and fin depth–buoyancy measures was explained by a single pair of axes (Figure 6) and differed from that expected by chance (permutation test: \(P < 0.001)\). Deep midbody profiles were associated with long pectoral fins, deep water, and low percent buoyancies, and streamlined bodies were associated with short pectoral fins, shallow water, and high percent buoyancies \((R = 0.88; \text{permutation test: } P < 0.001; \text{Figure 6})\). The contribution of pectoral fin, depth of capture, and buoyancy measures to the fin depth–buoyancy scores were relatively equivalent in magnitude (coefficients were \(-0.57\) for pectoral fin, \(-0.54\) for depth, and \(-0.56\) for buoyancy) and represented the correlation

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**FIGURE 4.**—Shape differences of large lake trout between depth strata in Great Slave Lake. Outlines connect selected landmarks to illustrate shape differences and were drawn from vector plots. The (A) average shape of all large fish was weighted to accommodate for numerical differences from each depth stratum. Changes in landmark positions for lake trout in the (B) 0–50 m and (C) 50–100 m depth strata are shown relative to the average shape of all large lake trout (gray outlines).

**FIGURE 5.**—Dendrogram produced by a UPGMA cluster analysis based on seven measures of the large (≥43 cm SL) lake trout phenotype in Great Slave Lake. Selected images represent lake trout from the two major groups in the cluster analysis. Clusters were determined using Euclidean distances of size-adjusted measures of buoyancy, pectoral fin length, caudal fin length, dorsal fin length, head depth, midbody depth, and caudal depth.
between them. Caudal fin length was negatively correlated and dorsal fin length was positively correlated with increasing values along the fin depth–buoyancy axis (coefficients were −0.20 and 0.17, respectively). Intermediate shapes occurred and were associated with intermediate fin, body depth, and buoyancy values. The apparent break in scores along the fin–body-depth–buoyancy axis (Figure 6) reflected a gap in sampling at a depth of around 50 m (an artifact of our sampling).

Lake trout belonging to groups 1 and 2, as identified by the cluster analysis (Figure 5), were represented at opposite ends of the shape and fin depth–buoyancy axes and overlapped among intermediate values (Figure 6). The deep-bodied group (group 2) had longer pectoral fins, occurred in deeper water, and was buoyantly lighter than the streamlined body group (group 1). The most streamlined lake trout within the deep-bodied group (group 2) were the intermediate shapes, as were the most deep-bodied fish within the streamlined group (group 1).

### Discussion

The expression of lake trout phenotypic diversity in Great Slave Lake was associated with body size and water depth and resembled that seen in the lean and siscowet lake trout of Lake Superior. The large lean-like lake trout in Great Slave Lake used shallower waters, were more streamlined in shape, and were buoyantly heavier than lake trout from deep waters. Similarly, the lean form in Lake Superior is more prevalent in shallow-water habitats (Bronte et al. 2003), is more streamlined in shape (Khan and Qadri 1970; Lawrie and Rahrer 1973; Moore and Bronte 2001), and has lower lipid content (Thurston 1962; Eschmeyer and Phillips 1965) than the siscowet form. Likewise, large lake trout from deepwater habitat in Great Slave Lake were similar in shape (deep-body profile) and buoyancy (light) to the siscowet phenotype in Lake Superior. The low variation among small lake trout (<43 cm SL) in Great Slave Lake was also consistent with the ontogeny of lean and siscowet fish in Lake Superior. Small lean and siscowet lake trout are more similar in tissue composition and trophic position than large individuals of each form (Eschmeyer and Phillips 1965; Harvey et al. 2003).

Our study and the Lake Superior studies differed in emphasis from those on Great Bear Lake, which focused on lake trout collected in water less than 50 m deep (Blackie et al. 2003; Alfonso 2004) and which attributed morphological differences to alternate shallow-water foraging strategies (Blackie et al. 2003). Based on our sampling effort, phenotypic variation in Great Slave Lake appeared to be greater between than within depth strata. In this respect, the phenotypic differences between lake trout from deep and shallow waters of Great Bear Lake are unknown.

We conclude that the phenotypic characteristics that differentiate large lake trout do not apply to small lake trout in Great Slave Lake. A physiological association

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**Table 2.—Descriptive statistics of two groups of large (>43 cm SL) lake trout identified in Great Slave Lake by use of a UPGMA cluster analysis (see Figure 5).** Percent buoyancy, pectoral fin length, caudal fin length, dorsal fin length, head depth, mid body depth, and caudal depth are reported for each group. All measures have been size-adjusted to 55 cm SL. Statistical differences between groups are reported.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Group 1 (Mean [SD])</th>
<th>Group 2 (Mean [SD])</th>
<th>Wilk's $\lambda$</th>
<th>$F_{1,52}$</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Buoyancy (%)</td>
<td>5.0 (0.9)</td>
<td>1.7 (0.9)</td>
<td>0.23</td>
<td>173.2</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Pectoral fin length (cm)</td>
<td>8.9 (0.7)</td>
<td>10.3 (1.1)</td>
<td>0.63</td>
<td>30.8</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Caudal fin length (cm)</td>
<td>9.7 (0.5)</td>
<td>10.0 (0.6)</td>
<td>0.90</td>
<td>6.0</td>
<td>0.018</td>
</tr>
<tr>
<td>Dorsal fin length (cm)</td>
<td>7.7 (0.4)</td>
<td>7.3 (0.6)</td>
<td>0.90</td>
<td>6.1</td>
<td>0.017</td>
</tr>
<tr>
<td>Head depth (cm)</td>
<td>10.1 (0.6)</td>
<td>11.6 (0.6)</td>
<td>0.37</td>
<td>90.6</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Mid body depth (cm)</td>
<td>13.2 (1.2)</td>
<td>17.4 (1.1)</td>
<td>0.22</td>
<td>184.7</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Caudal depth (cm)</td>
<td>5.5 (0.3)</td>
<td>6.0 (0.4)</td>
<td>0.76</td>
<td>16.6</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>
may exist between lake trout shape (i.e., body depth) and buoyancy because variation in their expression increased in apparent synchrony with body size. Deeper body shapes may accommodate more lipid storage, which increases at around 43 cm SL (inferred from our buoyancy measurements). The existence of a threshold length associated with lipid accumulation may represent a high energetic cost for small lake trout that are investing in length growth followed by an ontogenetic shift of larger fish to high-lipid prey (such as deepwater ciscoes Coregonus spp.). Phenotypic groupings of small lake trout may exist; however, they were not detectable with our sample size \((N = 18)\). Further investigation of the early ontogeny of phenotypes in Great Slave Lake will also need to consider that the depth distributions of small lake trout will probably not be similar to those of large lake trout (Eschmeyer 1956; Peck 1982).

**Phenotypic Differentiation: Groupings of Lake Trout**

The results of our study contrast with those of studies on Lake Superior, where intermediate phenotypes are rarely mentioned. This contrast may reflect a lower frequency of intermediates in Lake Superior or may result from different analytic methods. Qualitative assignment of lake trout forms has been the precedent in Lake Superior (Brown et al. 1981; Goodier 1981) even when the stated purpose of the study was to quantify differences among forms (Dehring et al. 1981; Burnham-Curtis and Smith 1994; Page et al. 2004). Morphological studies using this approach have demonstrated both differences and overlap among Lake Superior forms (Khan and Qadri 1970; Moore and Bronte 2001), suggesting that intermediates occur in this lake as well. The subjective assignment of forms used in previous comparative studies assumes that intermediate phenotypes are rare. We made no such assumption, which probably accounts for the continuous distribution of phenotypes revealed in our study. Intermediate phenotypes may reflect incomplete differentiation among forms, other undescribed forms, or weak isolating mechanisms. Alternatively, they may result from environmental contributions to phenotypic expression (i.e., phenotypic plasticity).

**Ecological Differentiation: Buoyancy, Lift, and Habitat Use**

In deepwater habitats, long pectoral fins and low percent buoyancy should give the deepwater phenotype in Great Slave Lake a functional advantage over the shallow-water phenotype. Long paired fins and high-lipid tissues improve buoyancy regulation in fishes with no swim bladder or with a compressed swim bladder (Alexander 1972; Gee 1983). A fish undergoing daily vertical migrations, as inferred for deepwater lake trout in Lake Superior (Henderson and Anderson 2002), is unlikely to inflate its swim bladder when descended (Alexander 1972, 1993) because gas secretion into swim bladders is too slow (Wittenberg et al. 1964; Alexander 1972). When swim bladders are absent or compressed, fish are negatively buoyant (they are denser than the water they displace) and, as such, must either rest on the bottom or continually swim upwards to overcome a tendency to sink (Alexander 1966). Sinking can be overcome with long pectoral fins that, when angled upwards, provide hydrodynamic lift while swimming, as seen in some sharks, sturgeons, and tunnies (Alexander 1965, 1993; Magnuson 1970). The sinking tendency can also be overcome with high-lipid (low-density) tissues, as seen in Lake Baikal’s pelagic sculpins Comephorus spp. (Sideleva 1996; Eshenroder et al. 1999b) and Antarctic pelagic nototheniids Dissostichus mawsoni and Pleuragramma antarcticum (Eastman 1988, 1993). High-lipid tissues also occur in deepwater ciscoes (Krause et al. 2002), which are physisostomus fishes known to undergo daily vertical migrations in the Great Lakes (Eshenroder et al. 1998; TeWinkel and Fleischer 1999).

In shallow-water habitat, at least three different costs associated with phenotype may result in deep-bodied lake trout having a competitive disadvantage compared with the streamlined form. First, the deep-bodied shape, being less streamlined, creates more drag thus increasing swimming costs. Second, the energy used in producing excess body fat necessary for buoyancy regulation could be channeled instead into increased length, muscle development, or gamete production, as seen in more streamlined fish. Third, the costs of accumulating extra fat should be higher in shallow-water habitat because prey lipid content, associated with prey type, changes with depth. Diets of siscowet and lean lake trout in Lake Superior differ substantially (Conner et al. 1993; Harvey and Kitchell 2000; Harvey et al. 2003). Siscowet fish in deepwater habitats consumed western slimy sculpins Cottus cognatus gracilis, deepwater sculpins Myoxocephalus thompsonii, and deepwater ciscoes, whereas lean lake trout in nearshore habitats consumed mainly rainbow smelt Osmerus mordax, an introduced fish, and ciscoes Coregonus artedi (Conner et al. 1993). Shortjaw ciscoes Coregonus zenithicus, part of the deepwater cisco complex in Lake Superior, also occur in Great Slave Lake (Todd 2003). Deepwater coregonines have higher lipid content than their shallow-water relative, the cisco (Rowan and Rasmussen 1992; Krause et al. 2002). Lipid deposition, therefore, should be less costly for siscowet lake trout than lean lake trout because
siccowet individuals gain greater caloric value per prey item than do lean lake trout.

**Genetic Differentiation**

Whether the groups of lake trout identified in this study are genetically distinct awaits further investigation. Some insight into this issue, however, can be inferred from past studies of Lake Superior lean and siccocowet lake trout. Several studies have described a genetic basis for lake trout traits (reviewed in Krueger and Ihssen 1995) such as lipid composition (Eschmeyer and Phillips 1965) and swim bladder gas retention (Ihssen and Tait 1974), which are associated with the use of different habitat depths. In addition, populations of siccocowet lake trout in Lake Superior are genetically distinct from lean populations (Page et al. 2004), although this difference is not always greater than that between geographically separate lean populations (Dehring et al. 1981; Krueger et al. 1989). An interaction between genes and environment, such as that observed in Arctic char *Salvelinus alpinus* (Johnson 1980; Nordeng 1983; Hindar and Jonsson 1993; Skúlason et al. 1996), is probable. We expect that lake trout with a genetic tendency toward storing more lipids in their tissues should be better at vertical migration and, in deepwater habitats, should have access to more lipid-rich prey such as shrimp *Mysis* spp. and deepwater coregonines, which are less available at shallower depths. Such diet differences should reinforce existing buoyancy differences.

**Management Implications**

The distinctive morphological features of lake trout in Great Slave Lake are associated with their ecology (i.e., capture depth) and, potentially, their behavior (i.e., daily vertical migrations). This finding may be relevant to restoration programs elsewhere. Current lake trout restoration programs in Lakes Huron, Michigan, and Ontario have introduced the lean morphological form best adapted for life at less than 50-m depths (Krueger and Ebener 2004). Other forms, however, were historically present in these lakes, and deepwater areas and offshore shoals were originally the predominant and most productive lake trout habitats in the Great Lakes (Eshenroder et al. 1995). Fifty-five percent of the area of Lake Huron and 65% of the areas of Lakes Michigan and Ontario are deeper than 50 m (Christie and Regier 1988). Thus, the current reintroduction program focuses on historically less productive areas and on less than half of the available habitat in these three lakes. Lake trout management strategies should be revised to consider restoration of the full phenotypic diversity of the species so as to use the full breadth of habitats available in the Great Lakes.

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**References**


