Trophic variation within a piscivorous lake trout morph from Great Bear Lake, Canada: The initial step toward ecological specialization?

Running title: Among-individual ecological specialization: lake trout polymorphism

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Abstract:

Ecological opportunities present during colonization of novel environments can drive divergent selection on traits, resulting in specialization of morphs to enhance efficient use of resources. Thus, in an ecologically polymorphic species, differences in resource specialization should be found among morphs, and homogeneity in resource use expected within a morph. Using one of four morphs in Great Bear Lake, we investigate whether specialization of trophic resources among individuals occurs within this single morph, which could indicate a potential for continued divergence. Four distinct dietary patterns of resource use within the lake trout morph were detected from fatty acid composition. Feeding habits of different groups within the morph were not associated with detectable morphological or genetic differentiation, suggesting that behavioral plasticity may have caused the trophic variation within this morph. A low level of genetic differentiation was detected between exceptionally large-sized individuals and other individuals. Investigating a geologically young system that displays high levels of intraspecific diversity and focusing on dietary patterns of resource use variation of individuals suggested that individual specialization can occur within a morph.

Keywords: Among-individual resource specialization, polymorphism, fatty acids, genetic, morphology.

Introduction:

Intraspecific diversity within fish species that have colonized post-glacial lakes may represent early stages of ecological speciation (Snorrason and Skúlason 2004). Given a novel environment and new ecological opportunity, a monomorphic population may begin to diverge on a variety of evolutionary trajectories. Intraspecific diversity can begin with adaptive variation along selection gradients in the absence of reproductive isolation, and potentially progress to adaptive differentiation and reproductive isolation (Hendry 2009; Seehausen and Wagner 2014; Snorrason and Skúlason 2004; Svanbäck et al. 2009a). Many fishes that have colonized post-glacial freshwater systems may be considered generalists (i.e., flexible in use of habitat and food resources) (Snorrason and Skúlason 2004). If recently colonized systems become stable and predictable, foraging and habitat specialization may lead to eco-morphological diversification, which has potential to promote reproductive isolation, further divergence, and ultimately speciation (Skúlason et al. 1999; Snorrason and Skúlason 2004; Van Kleunen and Fischer 2005). Phenotypic plasticity, the capacity for one genotype to produce different phenotypes in response to environmental cues, could be a character (the capacity) subject to selection, facilitating evolution (De Jong 2005). Despite uncertainties of how phenotypic plasticity promotes diversification and its role in speciation, plasticity appears to serve as an important element in early phases of diversification (Handelsman et al. 2013; Nonaka et al. 2015; Snorrason and Skúlason 2004).

Phenotypic plasticity in temporally and spatially varying environments has been demonstrated repeatedly within and among populations, but whether niche expansion of a population is achieved by a general increase in niche widths for all individuals overall or by an increase of among-individual variation (i.e., expression of multiple individual specializations

within a population), is a question that has been raised repeatedly (Bolnick et al. 2003; Roughgarden 1972; Svanbäck and Persson 2004; Svanbäck and Schluter 2012). Several apparent generalist populations have been reported to be composed of a combination of specialized individuals using several narrow niches that in combination yield an overall wide population niche (Araújo et al. 2008; Svanbäck and Persson 2004; Svanbäck and Schluter 2012; Woo et al. 2008). Characterization of niche use among individuals is necessary to understand the role that individual variation can play at the beginning of adaptive divergence and in potentially promoting polymorphism and speciation (Klemetsen 2010; Svanbäck and Persson 2004; Svanbäck and Bolnick 2005; Svanbäck et al. 2015).

The mechanisms underlying variation in the magnitude and effect of individual specialization in different freshwater systems, species, and trophic positions are poorly understood (Cloyed and Eason 2016; De León et al. 2012; Svanbäck et al. 2015). Depauperate ecosystems, with low interspecific competition provide ecological opportunities favoring niche expansion (Bolnick et al. 2010b; Costa et al. 2008; Parent et al. 2014). Flexibility within colonizing species with high levels of genetic variation and phenotypic plasticity, in which individuals have the potential to exploit a wide range of resources, provides potential for the evolution of individual resource specialization and population divergence. The trophic position of a species may also affect the degree of individual variation and diversification within a population as evidence suggests that among-individual variation in diet may be greatest at intermediate trophic positions (Collar et al. 2009; Svanbäck et al. 2015).

Great Bear Lake (Northwest Territories, Canada) straddling the Arctic Circle provides an excellent opportunity to investigate the role of among-individual variation in diversification. Lake trout, *Salvelinus namaycush*, with this lake show a high degree of intraspecific diversity

within a geologically young system (8,000–10,000 yr BP) (Johnson 1975; Pielou 2008). Specifically, extensive sympatric divergence occurs for this species within the shallow-water (≤ 30 m) zone of Great Bear Lake (Chavarie et al. 2013; Chavarie et al. 2015; Chavarie et al. 2016b; Harris et al. 2015). Morph 1 is characterized by a small head and intermediate-sized fins. Morph 2 has the largest head and jaws but smallest fins of the morphs. Morph 3 has the longest fins and a robust body shape (i.e., deep body depth). Morph 4 has a thick curved lower jaw and the smallest caudal peduncle depth of the morphs (Fig. A1) (Chavarie et al. 2013; Chavarie et al. 2015). Three of these four shallow-water lake trout morphs are described as trophic generalists with differing degrees of omnivory along a weak benthic-pelagic gradient (Chavarie et al. 2016a; Chavarie et al. 2016b). Despite habitat and dietary overlap, significant differences in morphological, genetic, and life-history variation have been reported (Chavarie et al. 2013; Chavarie et al. 2016 ; Harris et al. 2015), suggesting that rather than two or more discrete phenotypes specialized for different resources and habitats, these morphs function as trophic generalists (Chavarie et al. 2016b; Svanbäck et al. 2009b).

Furthermore, fatty acid and stomach content analyses of the four lake trout morphs suggested homogenous resource use among morphs, but this observation could be caused by the combination of specializations by individuals along a resource continuum (Chavarie et al. 2016a). In other words, whereas morph resource use may appear similar, individuals within a morph may differ in their resource use. One morph (Morph 2; generalist with a tendency to consume more fish than other morphs, referred to here as the piscivorous morph; Fig. 1) showed at least two different feeding strategies, benthic cannibalism and interspecific piscivory in the pelagic zone. Overall, the piscivorous morph had a streamlined body shape, large gape, and high growth rates throughout life, characteristics indicative of piscivory (Chavarie et al. 2013;

Chavarie et al. 2015; Chavarie et al. 2016). Finally, the piscivorous morph displayed a modest level of genetic differentiation from the three other morphs (Harris et al. 2015).

To characterize individual variation within a morph in relation to observed differentiation of feeding strategies, the current study focused solely on the piscivorous lake trout morph. Samples from previous collections (Chavarie et al. 2016a; Harris et al. 2015), plus some additional fish, were analyzed for fatty acid composition. Fatty acids analysis assumes that dietary lipids are broken down into their constituent fatty acids and incorporated relatively unchanged into the consumer tissues (Howell et al. 2003; Iverson 2009; Iverson et al. 2004), allowing spatial and temporal diet comparison between organisms (Duerksen et al. 2014; Eloranta et al. 2011; Hoffmann 2017; Iverson 2009; Scharnweber et al. 2016). Due to their lack of ability to modify fatty acids, overall modification of dietary fatty acids in fish is probably related to dietary deposition, resulting in a robust tool to represent lake trout diet (Happel et al. 2017a; Happel et al. 2016; Happel et al. 2017b; Iverson 2009). Thus, fatty acids were used as trophic bio-indicators to better understand dietary patterns of piscivorous lake trout and investigate whether individual specialization may be contributing to trophic breadth and variation observed among individuals in this morph. Specifically, our aims were to 1) compare resource use among piscivorous lake trout individuals (Morph 2) by characterizing their fatty acids profiles, 2) determine whether resource-use differences were influenced by life-history traits (e.g., size and age), 3) characterize the extent of morphological variation individuals present among groups expressing different feeding strategies, and 4) determine if genetic differences existed among groups. In addition, we examined a sub-set of large lake trout from our collections ($\geq$ 900 mm in fork length) referred to locally as “Giants” (Fig. 1), to determine if they showed any ecological and genetic differences. These exceptionally large individuals

comprise < 1% of the lake trout population in Great Bear Lake, and are among the largest lake trout in the world (Chavarie et al. 2016). Except for their large body-size, these individuals exhibit no major morphological or spatial and temporal distribution differences relative to other co-occurring piscivorous lake trout. By focusing on trophic variation within a specific morph, we aimed to advance our understanding of ecological and evolutionary processes operating within a geologically young ecosystem that provides resource potential sufficient for promoting intraspecific divergence (Bhat et al. 2014; Coyne and Orr 2004; Hudson et al. 2016).

Methods

Study area and field sampling

Great Bear Lake is an oligotrophic Arctic freshwater system, 250 km south of the Arctic Ocean, in Northwest Territories, Canada (N66° 06' W120° 35') (Johnson 1975). As the world's ninth largest and 19th deepest lake, the lake has a complex, multi-armed surface area of 31,790 km^2 and a maximum depth of 446 m (mean depth = 90 m). Great Bear Lake was formed by scouring from the Laurentide ice-sheet during the Pleistocene and was originally part of glacial Lake McConnell 8,000–10,000 yr BP (Johnson 1975; Pielou 2008). The lake has characteristics typical of an arctic lake: ultra-oligotrophic, short ice-free season, and a simple food web supporting only 15 fish species (Alfonso 2004; Johnson 1975; MacDonald et al. 2004). Great Bear Lake lacks a commercial fishery but plays an important role in the local economy, supporting a fly-in sport fishery for tourists and a subsistence fishery for the small Sahtu community of Déline. Great Bear Lake has considerable intraspecific diversity within lake trout, lake whitefish (*Coregonus clupeaformis*), and cisco (*C. artedi*) (Chavarie et al. 2013; Howland et al. 2013).

Piscivorous lake trout were caught at depths ≤ 30 m using paired bottom sets (ca. 24 h) of 140-mm and multi-mesh (38–140 mm) stretched-mesh gill nets during end of July and August over multiple years (2002–2011) among all five arms of the lake (Chavarie et al. 2013; Chavarie et al. 2015; Chavarie et al. 2016a). During 2012-2014, multi-mesh gill nets (38 to 140 mm), with a typical soak time of 24 hours, were distributed across random depth-stratified sites (0–150 m) among Keith, McVicar, and McTavish arms (Table A1). We focused on adult trout due to the difficulty of classifying juveniles into morphs (Chavarie et al. 2013; Zimmerman et al. 2006; Zimmerman et al. 2007) and to avoid the confounding effects of ontogenetic shifts in morphology and diet. Of 79 fish analyzed herein, 35 piscivourous lake trout (Morph 2) were previously analyzed for fatty acids by Chavarie et al. (2016a) and 44 fish were new to the current diet analysis. Fish were randomly selected from the collections analyzed morphologically by Chavarie et al. (2015) to include a range of sizes and ages within the piscivorous morph. For the Giant individuals, lake trout with fork length ≥ 900 mm were targeted. A left lateral full-body digital image was taken for each lake trout caught according to the procedures in Muir et al. (2012). Measurements, tissues, and structures were sampled for determination of biological characteristics related to life-history, including otoliths, fork length, somatic weight, sex, and stage of maturity (i.e., immature, current year spawner, or resting) (Chavarie et al. 2013; Chavarie et al. 2016). A dorsal muscle sample was removed and frozen at −20ºC for fatty acids analysis (Budge et al. 2006; Kavanagh et al. 2010; Loseto et al. 2009) and tissue from pectoral fins was collected and preserved in ethanol for genetic analyses.

Fatty Acids

Analysis of 41 dietary fatty acids was carried out using procedures described by Chavarie et al. (2016a) (Table 1) . Muscle samples were freeze-dried, and subsequently homogenized with

a mortar and pestle. Lipids were extracted overnight from 1 g of the homogenate in a 2:1 chloroform-methanol solution containing 0.01% BHT (v/v/w) at −20ºC (Folch et al. 1957). After extraction, samples were filtered through Whatman Grade 1 Qualitative filter paper and the filter paper/sample was rinsed twice with 2 ml of the 2:1 chloroform:methanol. Sample extract was collected in a test tube and 7 ml of 0.88 N NaCl solution was added to encourage fatty acids to move into the organic (chloroform) layer. The aqueous layer was discarded after which the chloroform was dried with sodium sulfate prior to total lipid measurement. The extracted lipid was used to prepare fatty acid methyl esters (FAME) by transesterification with Hilditch reagent (0.5 N H_2SO_4 in methanol) (Morrison and Smith 1964). Samples were heated for 1 h at 100 °C. Gas chromatographic (GC) analysis was performed on an Agilent Technologies 7890N GC equipped with a 30 m J&W DB-23 column (0.25 mm I.D; 0.15 µm film thickness). The GC was coupled to a Flame Ionization Detector operating at 350 ^{o}C. Hydrogen was used as carrier gas flowing at 1.25 ml/min for 14 minutes, and increased to 2.5 ml/min for 5 min. The split/splitless injector was heated to 260 ^{o}C and run in splitless mode. The oven program was as follows: 60 ^{o}C for 0.66 min, increasing by 22.82 ^{o}C/min to 165 ^{o}C with a 1.97 min hold; increasing by 4.56 ^{o}C/min to 174 ^{o}C and by 7.61 ^{o}C/min to 200 ^{o}C with a six min hold. Peak areas were quantified using Agilent Technologies ChemStation software. Fatty acids standards were obtained from Supelco (37 component FAME mix) and Nuchek (54 component mix GLC-463).

All fatty acids values were converted to a mass percentage of the total array, and were named according the IUPAC nomenclature as X:Y n-z, where X is the number of carbon atoms in the fatty acids, Y is the number of methylene-interrupted double bonds in the chain, and n-z denotes the position of the last double bond relative to the methyl terminus (Ronconi et al. 2010). Fatty acids suggested by Iverson et al. (2004) as important dietary fatty acids, which transfer

from prey to predator, were used in our analyses. Fatty acids profiles (% of fatty acids) were transformed using arcsin square-root function. Fatty acids groups were identified using a multivariate analysis R Package (Team 2017), FactoMineR, using a hierarchical clustering analysis based on principal components (Husson et al. 2012). To reduce the number of variables used, A SIMPER (similarity percentage routine) was used to assess which fatty acids primarily were responsible for observed differences among groups (King and Jackson 1999). A principal component analysis (PCA) was performed on the fatty acids profiles with PC-ORD version 6 (McCune and Mefford 2011) among piscivorous groups to provide inferences about patterns of resource use as defined by Chavarie et al. (2016a). Permutational Multivariate Analysis of Variance (PERMANOVA), a non-parametric analog of Multivariate analysis of variance (MANOVA), was used to test for differences in fatty acid composition among the groups identified by the hierarchal cluster analysis process. PERMANOVA was performed in Primer 7 (Primer E, Plymouth, UK) using 9999 permutations. Pairwise *post-hoc* comparison followed to test differences among groups. Finally, the fatty acid groups were tested for differences in depth of capture using one way analysis of similarities (ANOSIM) with 9999 permutations using PAST 3 (Hammer et al. 2001).

Life-history

To determine if fatty acid groups differed in size-at-age, length vs. age was modeled using the Von Bertalanffy length-age model fit to length at age-of-capture of individual fish (Quinn and Deriso 1999):

$$L_t = L_\infty \left(1 - e^{-K(t-t_0)}\right)^{\varepsilon}$$

The length-age model describes length L_t at age-of-capture t as a function of theoretical maximum length (L_∞ = mm), instantaneous rate at which L_t approaches L_∞ (K = 1/year),

theoretical age-at-zero length (t_0 = years), and multiplicative error (ε). Model parameters, L_∞, K, and t_0, and associated standard errors were estimated using nonlinear regression. Residual sums-of-squares were compared between a full model (separate models for each group) to a reduced model (a single model for all groups) in a likelihood-ratio test (Hosmer Jr et al. 2000). If the likelihood-ratio test was significant ($P \leq 0.05$), we concluded that growth differed among groups identified by fatty acids (79 lake trout). If the likelihood-ratio test was not significant ($P > 0.05$), we concluded that growth did not differ among groups. The same test was repeated for each pair of groups, with and without the Giant form (fork length ≥900 mm) included in each group, to isolate the influence of this sub-set in our size-at-age comparison due to the prevalence of Giants in Group 3.

Genetic analyses

To determine if genetic differences existed among individuals expressing different feeding strategies, 79 lake trout classified by fatty acid composition into four groups were genotyped to determine genetic variation and structure within and among groups. To allow a sample size sufficient for making a genetic comparison of the Giant to the other dietary groups, 22 additional individuals determined non-randomly by their size (≥ 900 mm ; Giant sub-set) from the 2002-2015 collections were added to the Giant processed for fatty acids, for a total of 39 Giants for genetic analysis. Lake trout DNA was extracted from pectoral fin tissue preserved in ethanol using DNEasy extraction kits (Qiagen Inc., Valencia, CA) following manufacturer protocols. Piscivorous groups were assayed using a suite of 23 putatively neutral microsatellite markers amplified in four multiplexes previously described in Harris et al. (2015). Amplified microsatellite fragments were analyzed using an automated sequencer (ABI 3130xl Genetic Analyzer; Applied Biosystems, Foster City, CA). The LIZ 600 size standard was incorporated

for allele base-size determination. All genotypes were scored using GeneMapper software ver. 4.0 (Applied Biosystems) and then manually inspected to ensure accuracy.

The program MICROCHECKER ver. 2.2.0.3 (Van Oosterhout et al. 2004) was used to identify genotyping errors, specifically null alleles and large allele dropout. Observed and expected heterozygosity (H_E and H_O) were calculated using GENEPOP ver. 4.2 (Rousset 2008). The program HP-RARE ver. 1.1 (Kalinowski 2005) was used to determine the number of alleles, allelic richness, and private allelic richness for each group, sampling 22 genes in each sample. Tests of departure from Hardy-Weinberg equilibrium and genotypic linkage disequilibrium within each sample (i.e., for each fatty acid grouping and the Giant sub-set) were conducted in GENEPOP using default values for both. Results from all tests were compared with an adjusted alpha ($\alpha = 0.05$) following the False Discovery Rate procedure (Narum 2006).

We used the POWSIM V. 4.1 analysis to assess the statistical power of our microsatellite data set given the observed allelic frequencies within our samples in detecting significant genetic differentiation between sampling groups (Ryman and Palm 2006). For POWSIM analyses, we assumed that Lake Trout within our study diverged from a common baseline population with the same allelic frequencies as observed in our contemporary samples. Simulations were performed with an effective population size of 5000 to yield values of F_{ST} of 0.01, 0.005 and 0.001. The significance of tests in POWSIM were evaluated using Fisher's exact test and the $\chi 2$ test and the statistical power was determined as the proportion of simulations for which these tests showed a significant deviation from zero. All simulations were performed with 1000 iterations.

Genetic structuring was tested among lake trout groups using several different methods. First, genotypic differentiation among lake trout groups was calculated using log-likelihood (G) based exact tests (Goudet et al. 1996) implemented in GENEPOP. Global F_{ST} (θ) (Weir and

Cockerham 1984) was calculated in FSTAT ver. 2.9.3 (Goudet 1995) and pairwise comparisons of F_{ST} between groups were calculated in ARLEQUIN ver. 3.5 (Excoffier et al. 2005) using 10,000 permutations. We then employed the Bayesian clustering program STRUCTURE V. 2.3.2 (Pritchard et al. 2000) to resolve the putative number of populations (i.e., genetic clusters (K)) within our samples. Owing to the remarkably low levels of genetic differentiation among lake trout in the Great Bear Lake (Harris et al. 2013; Harris et al. 2015), we employed the LOCPRIOR algorithm (Hubisz et al. 2009). The LOCPRIOR algorithm considered the location/sampling information as a prior in the model, which may perform better than the traditional STRUCTURE model when the genetic structure is weak (Hubisz et al. 2009). We also incorporated an admixture model with correlated allelic frequencies and the model was run with a burn-in period of 500,000 iterations and 500,000 Markov chain Monte Carlo iterations. We varied the potential number of populations (K) from 1 to 10 and we ran 20 iterations for each value of K. The STUCTURE output was first processed in the program STRUCTURE HARVESTER (Earl 2012), followed by the combination of results of independent runs of the program and compilation of results based on lnP(D) and the post hoc ΔK statistic of Evanno et al. (2005), to infer the most likely number of clusters. The best alignment of replicate runs was assessed with CLUMPP V. 1.1 (Jakobsson and Rosenberg 2007) and DISTRUCT V. 1.1 (Rosenberg 2004) was then used to visualize the results. For STRUCTURE analyses, we reported both lnP(D) and the post hoc ΔK statistic.

Finally, Discriminant Analysis of Principal Components (DAPC) (Jombart et al. 2010) was implemented in the Adegenet package (Jombart 2008) in R (Team 2015). The number of clusters was identified using the *find.clusters* function (a sequential K-means clustering algorithm) and subsequent Bayesian Information Criterion (BIC), as suggested by Jombart et al.

(2010). Stratified cross-validation (carried out with the function *xvalDapc*) was used to determine the optimal number of principal components to retain in the analysis.

Morphology

Morphological variation was quantified for the 79 lake trout to compare fatty acid groupings (different feeding strategies) to morphological variation within the piscivorous morph. Twenty-three landmarks, 20 semi-landmarks based on Chavarie et al. (2015), and fourteen linear measurements based on Muir et al. (2014), were used to characterize body and head shape from photographed fish. The combination of traditional and geometric morphometrics was used because of the empirical relationships of phenotype with foraging (e.g., jaw size) and swimming (e.g., fin lengths and caudal peduncle depth) (Kahilainen et al. 2004; Kristjánsson et al. 2002; Webb 1984). Landmarks and semi-landmarks were digitized in x and y coordinates using TPSDig2 software (http://life.bio.sunysb.edu/morph). Subsequently, digitized landmarks and semi-landmarks were processed in a series of Integrated Morphometrics Programs (IMP) version 8 (http://www2.canisius.edu/;sheets/morphsoft), using partial warp scores, which are thin-plate spline coefficients. Morphological methods and programs are described in Zelditch et al. (2012) and specific procedures were described in further detail in Chavarie et al. (2013). All morphological measurements were size-free, using centroid sizes or residuals from regressions on standard length (Zelditch et al. 2012).

Canonical Variate Analyses (CVA) were conducted on all morphological data, including body shape, head shape, and linear measurements, to determine relationships among groups identified by fatty acid composition. Body and head shape were analysed using CVAGen8 from the IMP software (Zelditch et al. 2012) and for linear measurements, CVA was analyzed with SYSTAT (Systat Software Inc., Chicago, IL, USA). Single Factor Permutation MANOVA with

10 000 permutations tested for differences among groups and determined the percentage of variation explained for a grouping if a CVA was significant. For linear measurements, a Bonferroni-corrected post-hoc test followed MANOVA to identify measurements that differed among group. Principal component analyses (PCA) were performed on body- and head-shape data using PCAGen8 (IMP software) among groups to visualize morphological variation within the dataset. PC-ORD version 6 software (McCune and Mefford 2011) was used to perform a PCA on the linear measurements.

Results

Fatty acids

On the basis of fatty acid composition, piscivorous lake trout were divided along a resource use axis into four groups (Fig. 2 and A2; Table 1). Overall, 14 individuals were assigned in Group 1, 16 individuals in Group 2, 21 individuals in Group 3, and 28 individuals in Group 4. Average dissimilarity was 14.61 from the SIMPER analysis, whereas the most discriminating 26 fatty acids, explaining together ~89% of the separation among groups, were: 22:6n-3 (12.5 %), 18:1n-9 (10.8 %), 16:1n-7 (6.8 %), 20:5n-3 (5.0 %), 20:4n-6 (3.9 %), 18:2n-6 (3.8 %), 22:4n-3 (3.7 %), 16:0 (3.5%), 20:4n-3 (3.3%), 18:1n7 (3.3%), 20:2n-6 (3.1%), 14:0 (2.8%), 20:1n-9 (2.7%), 22:5n-6 (2.7%), 20:3n-3 (2.3%), 22:2n-6 (2.1%), 18:0 (2.0%), 18:3n-3 (1.9%), 18:4n-3 (1.8%), 22:4n-6 (1.7%), 20:1n-7 (1.5%), 22:5n-3 (1.4%), 21:5n-3 (1.3%), 22:1n-11 (1.2%), 20:0 (1.2%), 16:4n-3 (1.2%), and 16:2n-4 (1.1%) (Table 1). The first two axes of the fatty acids PCA explained 65.2 % of the variation in diet and the four groups were supported by PERMANOVA ($F_{3,76} = 39.4$, $P < 0.01$) and pairwise comparisons between all pairs (all $P < 0.01$). Finally, depth of capture did not differ among groups identified by fatty acids profiles ($p \geq 0.05$). For all groups, the majority of lake trout were caught between 0-20 m (Fig. A3).

Life-history

Overall, life history parameters did not differ among lake trout groups identified by fatty acid composition. Length-age models did not differ among fatty acid groups, based on overall likelihood-ratio tests (Fig. 3; $F_{9, 63}$ = 1.58; P = 0.141). With the Giant sub-set included, growth differed between Group 3 and Group 4 ($F_{3, 41}$ = 3.958; P = 0.014), but not between Groups 1 and 2 ($F_{3, 22}$ = 0.408; P = 0.749), Groups 1 and 3 ($F_{3, 27}$ = 0.410; P = 0.747), Groups 1 and 4 ($F_{3, 34}$ = 0.930; P = 0.437), Groups 2 and 3 ($F_{3, 29}$ = 1.820; P = 0.166), or Groups 2 and 4 ($F_{3, 36}$ = 1.058; P = 0.379). Without Giants included (prevalence of Giants was higher in Group 3 than Group 1, Group 2, and Group 4), none of the paired groups (morphs) differed for length-at-age: Groups 1 vs. 2 ($F_{3, 16}$ = 0.353; P = 0.787); Groups 1 vs. 3 ($F_{3, 13}$ = 0.958; P = 0.441); Groups 1 vs. 4 ($F_{3, 30}$ = 1.458; P = 0.246); Groups 2 vs. 3 ($F_{3, 17}$ = 1.254; P = 0.321); Groups 2 vs. 4 ($F_{3, 34}$ = 1.431; P = 0.251); and Groups 3 vs. 4 ($F_{3, 31}$ = 2.062; P = 0.126).

Genetic differentiation

Little genetic differentiation was evident among piscivorous lake trout groups, except for the Giant sub-set, which differed slightly from other groups defined by fatty acids. The program MICROCHECKER identified two loci (OtsG253b and Sco102) that contained null alleles. These loci, along with non-variable loci Sco218 and SSOSL456, were removed, leaving 19 informative loci for subsequent analyses. Descriptive statistics of genetic variation were similar among groups. The number of alleles per locus ranged from four (Smm21) to 41 (SnaMSU10) and averaged 28.75 across all loci. Observed heterozygosity averaged across all loci ranged from 0.78 (Giant) to 0.83 (Group 1) while expected heterozygosity ranged from 0.84 (all groups with the exception of Group 1) to 0.85 (Group 1; Table 2). Allelic richness ranged from 9.57 (Group 2 and 4) to 9.87 (Group 1), while expected private allelic richness ranged from 0.87 (Group 3) to

1.08 (Group 2; Table 2). Departures from Hardy-Weinberg equilibrium were found in 15 of 95 tests (at $\alpha = 0.05$), but only five (all of which involved different loci) were significant after adjustment for False Discovery Rate (adjusted $\alpha = 0.01$). Of those five, all were heterozygote deficits and three of five departures involved the Giant sub-set. Significant linkage disequilibrium was evident in 14 of 885 tests ($\alpha = 0.05$), but only nine were significant after adjusting for False Discovery Rate (adjusted $\alpha = 0.0068$). No locus-pair linkage disequilibrium combinations were consistently significant, but seven of nine departures were in the Giant sub-set.

Using our microsatellite data set, the POWSIM analysis indicated a 100% power of detecting a F_{ST} value as low of 0.01 and 0.005. However, power was reduced to 77% when assessing genetic differentiation at a F_{ST} of 0.001. Overall our microsatellite data set (including the number of loci, alleles per locus, and sample sizes) had sufficient power to detect relatively low levels of genetic differentiation.

Global genetic differentiation was extremely low ($\theta = 0.001$, 95% c.i. = −0.002−0.005) among groups of piscivorous lake trout assessed. Pairwise F_{ST} ranged from -0.004 to 0.016 (Table 3) whereas comparisons that included Giants always differed the most from the other fatty acid groups, and were also the only significant pairwise comparisons ($P < 0.05$, Table 3). The F_{ST} value for the Giant vs. Group 1 and 4 were similar to genetic differentiation previously observed among four lake trout morphs in Great Bear Lake (Table 3), with the exception of Morph 1 vs Morph 2 [32]. Bayesian clustering implemented in STRUCTURE provided evidence for two genetic clusters when evaluating both lnP(D) or ΔK (Table A2). The admixture plot based on K=2 showed no clear genetic structure among groups defined by fatty acid analysis, however, some differentiation of the Giant sub-set from the fatty acid groups was observed (Fig. 4).

Finally, the Bayesian information criterion in the DAPC analysis (BIC = 185.42, Table A3, Fig. A5 A) suggested that two clusters best explained genetic structure in our study (30 PCs retained as suggested by the cross-validation procedure; Fig. A5 B). A compoplot (barplot showing the probabilities of assignment of individuals to the different clusters) for K=2 revealed no clear genetic structure between two groups identified by the DAPC analysis with the exception of the Giant group which appeared to have more individuals assigned to cluster two (Fig 4). Density plots of the discriminant function, however, do show that the two clusters identified through the DAPC analysis are mostly non-overlapping (Fig. A5 C).

Morphology

Morphological variation was low among four dietary groups within the piscivorous morph. The first canonical axis for body shape CVA was significant (P>0.05), but head shape CVA revealed no significant canonical axes (P>0.05) in groupings (Fig. 5 a, b, c). MANOVAs for body and head shape were not significant (P>0.05). Linear measurements CVA revealed one significant canonical axis (P>0.05). MANOVA permutation tests confirmed differences in linear measurements among groups for linear measurements (P = 0.047). Most distinctions were related to linear measurements of heads, whereas upper and lower jaws, head depth, and snout-eye lengths differed between Group 3 and Group 4 ($P \leq 0.05$), and head length differed between Group 1 and 4 (P = 0.03; Fig. 6). Caudal peduncle length and anal fin length differed marginally between Group 2 vs 3 (P = 0.068) and Group 1 vs 3 (P = 0.075), respectively. The first two PCA axes explained 44.3% and 12.3 % of variation for body shape, 35.1% and 30.7 % of variation for head shape, and 39.6 % and 20.9 % for linear measurements (Fig. 5 d, e, f).

Discussion

A common assumption in polymorphic species is that partitioning and variability of resource use will occur predominantly among morphs rather than within morphs. Homogeneity of resource use is anticipated to occur within morphs and represent selection for specialization (Amundsen et al. 2008; Knudsen et al. 2010; Svanbäck and Persson 2004). However, this study provided evidence that instead of homogeneity, variation occurred within a trophic morph due to individual specialization, possibly a precursor to further population diversification via fine scale ecological selection (Richardson et al. 2014; Vonlanthen et al. 2009). Based on dietary fatty acids, we identified four patterns of resource use within the piscivorous morph. Size-at-age did not explain observed variation in resource use within the piscivorous individuals, even though size-based trophic structure has been frequently observed in fishes (Layman et al. 2005; Mittelbach et al. 2014; Scharf et al. 2000; Svanbäck and Eklöv 2002; Wainwright et al. 1991). Feeding habits were also not linked with differences in morphology (except for minor variations linked to the caudal peduncle) nor were they related to differentiation based on neutral genetic markers, thereby suggesting that behavioral plasticity may cause the variation in resource use. Giant individuals as a sub-set displayed some genetic differentiation relative to other piscivorous lake trout in our analyses. The co-existence of multiple generalist morphs in Great Bear Lake, demonstrated by Chavarie et al. (2016b), combined with individual specialization shown herein within one of the generalist morphs identified previously, expands our understanding of niche expansion, plasticity, individual specialization, and intraspecific diversity in evolutionarily young populations.

Using fatty acids as dietary biomarkers, four distinct patterns of resource use were identified within the piscivorous lake trout of Great Bear Lake (Fig. 2). Groups 3 and 4 had the most overlap and these groups were characterized by C20 and C22 monounsaturates, biomarkers of a

food web based on pelagic or deep-water copepods (Ahlgren et al. 2009; Happel et al. 2017b; Hoffmann 2017; Loseto et al. 2009; Stowasser et al. 2006). Specifically, 20:1n-9 is associated with calanoid copepods known to be particularly important in northern pelagic food webs (Ahlgren et al. 2009; Budge et al. 2006; Kattner et al. 1998; Loseto et al. 2009). High levels of 14:0, 18:3n-3 and 18:4n-3 fatty acids within groups 3 and 4 are also associated with pelagic environments (Scharnweber et al. 2016; Tucker et al. 2008), although high levels of 18:2n-6 and 18:3n-3 have also been associated with terrestrial markers (Budge et al. 2001; Budge and Parrish 1998; Hoffmann 2017). Groups 1 and 2 were characterized by higher concentrations of 16:4n-3, 20:4n-6 and 22:6n-3 found in diatom and dinoflagellate-based food webs, respectively. The fatty acid 20:4n-6 reflects a benthic feeding strategy (from benthic invertebrates to fish) (Stowasser et al. 2006; Tucker et al. 2008), whereas 22:6n-3 in pennate diatoms (Iverson 2009) and filter feeders links planktonic dinoflagellates to benthic filter-feeding bivalves in a food web (Alfaro et al. 2006; Virtue et al. 2000). Relatively high concentrations of 16:0, 18:0 and 22:6n-3 and low concentrations of 16:1n-7 supported the interpretation of carnivorous (or cannibalistic) dietary patterns (Dalsgaard et al. 2003; Iverson 2009; Iverson et al. 2004; Piché et al. 2010). Individuals positioned between ends of principal components suggests a clinal pattern of resource use or habitat coupling (Vonlanthen et al. 2009), where borders among groups are neither abrupt nor obvious as they are part of a continuum (Hendry et al. 2009b). Overall, observed trophic patterns could reflect prey associated with different microhabitat patches; however, the key assumption of disparity of prey associated with habitat heterogeneity (Bolnick et al. 2010a; Chavarie et al. 2016b; Collar et al. 2009; Skulason and Smith 1995; Svanbäck and Bolnick 2005) may not be applicable to Great Bear Lake (Chavarie et al. 2016b).

Sympatric divergence, in which barriers to gene flow are driven by selection between ecological niches, has been implicated in the evolution of ecological and morphological variation in fishes (Chavarie et al. 2016c; Harris et al. 2015; Hendry et al. 2007; Præbel et al. 2013; Schluter 1996). Despite the limited ability of neutral microsatellite markers to detect patterns of functional divergence (Berg et al. 2016; Lamichhaney et al. 2016; Roesti et al. 2015), the significant genetic differentiation based on comparisons with Giant sub-set suggests some deviation from panmixis within the piscivorous morph. Such a genetic pattern displayed by the Giant sub-set, despite a lack of ecological discreteness, perhaps resulted from size-assortative mating and/or differences in timing and location of spawning (Nagel and Schluter 1998; Rueger et al. 2016; Servedio et al. 2011). Great Bear Lake is not the only lake in North America with an apparent divergence in lake trout body size; in Lake Mistassini, "Giant" individuals also differed genetically from other lake trout groups (Marin et al. 2016). The similarity based on lake trout body size between both lakes suggests analogous variables favoring partial reproductive isolation. Although alternative causes of genetic differentiation may be possible, due to the short time since the onset of divergence post-zygotic isolation seems unlikely in this system (e.g., prezygotic isolation generally evolves more rapidly Coyne and Orr 2004) and we therefore favor size and location assortative mating as an explanation for the low level genetic divergence observed. Nonetheless, putative partial reproductive isolation within a morph further adds to the complexity of diversification and speciation processes potentially occurring within lake trout in Great Bear Lake (Hendry 2009; Nosil et al. 2009).

A central question arising from our analysis is what are the mechanisms behind these patterns of variation? As individual specialization can result in dietary sub-groups and perhaps differences in habitat use among sections of a population, such inter-individual variation within

ecological sub-groups could have substantial influence on processes of diversification (Araújo et al. 2008; Cloyed and Eason 2016). Among-individual resource specialization within a morph in a species-poor ecosystem like Great Bear Lake could reflect the diversifying force of intraspecific competition, lack of constraining effects of interspecific competition, the abundance and distribution of space and food resources (e.g., temporal and spatial variation of resources), or some combination of these processes (Bolnick et al. 2007; Cloyed and Eason 2016; Winkelmann). Multiple patterns of resource specialization within a single lake trout morph in Great Bear Lake contrasts with the expected pattern of trophic divergence among morphs and homogenization in habitat use or diet within a morph, a key assumption guiding development of functional ecological theory (Svanbäck and Persson 2004; Violle et al. 2012). Expression of intraspecific divergence through habitat and foraging specialization is thought to drive selection on traits that enable more efficient use of resources (Schluter 2000; Skulason and Smith 1995; Snorrason and Skúlason 2004).

In Great Bear Lake, multiple trophic generalists (which include piscivores studied herein) coexist with one specialist lake trout morph. This contrasts with the more commonly reported observation, the co-occurrence of multiple specialist morphs (Chavarie et al. 2016b; Elmer 2016; Kassen 2002). Apparent generalist population, however, can be composed of several subsets of specialized individuals that result in broad use of resources by the population (Bolnick and Paull 2009; Bolnick et al. 2007; Bolnick et al. 2002; Bolnick et al. 2003; Chavarie et al. 2016a). This broad distribution of trophic variation within a population appears to be the case within the Great Bear Lake piscivorous morph. Among-individual specialization, reported in this study, may result from variable use of spatially separated resources and/or resources in different seasons and years (temporal variation), both of which could be expected in the depauperate environment of a

large northern lake (Fig. A4; Chavarie et al. 2016b; Costa et al. 2008; Cusa et al. 2019; Quevedo et al. 2009). Ecologically, among-individual resource specialization is another form of diversity that is contained within a morph (Araújo et al. 2008; Bolnick et al. 2003; Pires et al. 2011), which may increase stability and persistence of a morph within a system where energy resources are scarce and ephemeral, such as in Great Bear Lake (Cloyed and Eason 2016; Davies et al. 2016; Okuyama 2008; Pfennig and Pfennig 2012; Smith et al. 2011). Whether among-individual resource use within this morph is stable or is an initial divergent step that with enough time will fully differentiate evolutionary units is a question that cannot be answered with our data.

Realized niche expansions are often linked to individuals of different morphologies and body sizes, with evidence of efficiency trade-offs among different resources (Cloyed and Eason 2016; Parent et al. 2014; Roughgarden 1972; Svanbäck and Persson 2004). When a resource gradient exists, niche expansion can be achieved via genetic differentiation, phenotypic plasticity, or a combination of these processes (Parent et al. 2014). The apparent segregation of resource use based on fatty acid analyses, despite a lack of major morphological, body size, and neutral genetic differentiation among the four dietary groups within the piscivorous morph, suggests that behavioral plasticity in resource exploitation is causing the observed patterns of dietary differentiation. Plasticity may promote evolution of diversification by expanding the range of phenotypes on which selection can act (Nonaka et al. 2015; Pfennig et al. 2010; West-Eberhard 2003). Theoretical models suggest that exploiting a wide range of resources is either costly or limited by constraints, but plasticity is favored when 1) spatial and temporal variation of resources are important (i.e., highly present in Great Bear Lake; Fig. A4), 2) dispersal is high, 3) environmental cues are reliable, 4) genetic variation for plasticity is high and 5) cost/limits of plasticity are low (Ackermann et al. 2004; Hendry 2016).

The expression of plasticity in response to particular ecological conditions (e.g., habitat structure, prey diversity) can be evolutionarily beneficial (i.e., result in increases in fitness). While most studies of diet variation focus on morphological differences among morphs in a population, diet variation can also arise from behavioral, biochemical, cognitive, and social-rank differences that cause functional ecology to be expressed at a finer scale rather than at the morph level (McGill et al. 2006; Svanbäck and Bolnick 2005; Violle et al. 2012; Zhao et al. 2014). Indeed, behavioral plasticity likely has a temporal evolutionary advantage relative to morphological plasticity due to relatively reduced reliance on ecologically beneficial structural and morphological adaptation (Smith et al. 2011; Svanbäck et al. 2009b). The only detectable morphological differences among the piscivorous groups in Great Bear Lake were associated with jaw lengths, snout-eye distance, and head length and depth, which are strongly related to foraging opportunities (Adams and Huntingford 2002; Sušnik et al. 2006; Wainwright and Price 2016). Some morphological characters likely express different degrees of plastic responses (adaptive or not), and thus may be expressed differently depending on the magnitude and time of exposure to heterogeneous environments (Hendry 2016; Sharpe et al. 2008). For example, environmental components (e.g., habitat structure) appear to have stronger and faster effects on linear characters (e.g., jaw length) than on body shape (Chavarie et al. 2015; Sharpe et al. 2008). Trophic level might also limit the scope for morphological variation in lake trout because piscivory can limit diversification of feeding morphology in fishes (Collar et al. 2009; Svanbäck et al. 2015).

Conclusion

Understanding ecological mechanisms of diversification is a challenging aspect of evolutionary ecology (Ackermann et al. 2004). Diversification occurs along a continuum of differentiation and

in early stages, morphological and dietary differences may not always result from genetic divergence (Hendry 2016; Nosil et al. 2009). Considering that processes of speciation continue to be debated, disagreement on when intraspecific divergence starts and what processes are involved is not surprising (De Queiroz 2005, 2007; Venton 2017). The debate around diversification sequence, (which diverges first, behaviour, morphology, or ecology?) highlights the mosaic nature of speciation (Hendry et al. 2009a). In this study, we asked whether diversification could be occurring within a morph by examining the fine-scale trophic variation, at a presumed early stage of sympatric evolutionary divergence of lake trout in Great Bear Lake (i.e., postglacial, representing ~350 generations) (Harris et al. 2015). Rapid evolution in nature on an "ecological time scale", within relatively few generations, has demonstrated that rapid differentiation can be a strong driver of population dynamics (Ashley et al. 2003; Fussmann et al. 2007; Hendry 2016; Turcotte et al. 2011). Due to presumed homogeneity, few studies have investigated dietary patterns and groupings within a morph. However, in this study, we found evidence that among-individual resource specialization occurred within a piscivorous lake trout morph, with four different patterns of resource use identified by fatty acids composition of muscle tissue. These groups did not differ in depth of capture or life history parameters, showed a lack of morphological differentiation (i.e., except for caudal peduncle), and only the Giant sub-set was weakly genetically distinctive from others. The lack of non-neutral markers in the analyses may have prevented us from detecting multiple genetic populations. However, the trophic patterns shown within this morph suggested that ecological drivers (i.e., habitat use, prey diversity) could have important effects on plasticity expression and perhaps on initial or early stages of divergence. By focusing on a postglacial ecosystem, the confounding effects of time, which can influence (and obscure observation of) mechanisms of divergence (Seehausen and

Wagner 2014), were reduced in this study. But whether we have identified a stable polymorphism or the first step in diversification on a trajectory of divergence and speciation, remains unknown (Seehausen et al. 2008). Nonetheless, the observed trophic specialization within a morph, compared to the previously reported generality among morphs (Chavarie et al. 2016b), suggests that individual specialization can occur within a trophic morph. Future research should focus on the role of among-individual differences within evolutionary units such as morphotypes.

List of abbreviations:

BP = before present

m = meter

mm = millimeter

h = hour

ca. = around

i.e., = stands for

e.g., = for example

NaCl = Sodium Chloride

FAME = fatty acid methyl esters

H_2SO_4 = Sulfuric acid

GC = Gas chromatographic

^{o}C = degree Celsius

^{o}C/min = degree Celsius/minutes

UPGMA = Unweighted Pair Group Method with Arithmetic Mean

PCA = principal component analysis

PERMANOVA = Permutational Multivariate Analysis of Variance

MANOVA = Multivariate analysis of variance

SIMPER= similarity percentage routine

ANOSIM = analysis of similarities

N =Number of individuals genotyped

N_A = number of alleles

H_E=expected heterozygosity

H_O = observed heterozygosity

A_R= allelic richness

PA_R = private allelic richness

A = alpha

FCA = Factorial correspondence analysis

k=number of alleles

DAPC = Discriminant Analysis of Principal Components

IMP = Integrated Morphometrics Programs

CVA = Canonical Variate Analyses

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Declarations:

Authors' contributions

LC, KH, WT, CK, and AM conceived and funded the study. LC and CG carried out the field work. LC, CG, LH, and MH participated in the data analyses. LC wrote the manuscript. All authors read and approved the final manuscript.

Competing interests

The authors declare that they have no competing interests.

Availability of data and materials

The datasets supporting the conclusions of this article are included within the article. Raw data are available from the corresponding author upon reasonable request.

Consent to publish

Not applicable.

Ethics approval and consent to participate

We declare that our experiments were performed in the respect of ethical rules. This protocol was approved by Department of Fisheries and Ocean Canada, Freshwater Institute Animal Care Committee Science Laboratories.

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Table 1. Mean composition (±SD) of the 41 fatty acids profile (%) for the Group 1, Group 2, Group 3, and Group 4 of piscivorous Lake Trout morph identified from Great Bear Lake.

Fatty acids	Group 1	Group 2	Group 3	Group 4
14:0	6.8 ± 1.0	7.0 ± 1.0	9.2 ± 1.0	9.9 ± 1.1
16:0	28.1 ± 1.0	28.13 ± 1.7	24.2 ± 1.7	26.1 ± 1.2
16:1n-7	15.9 ± 3.7	10.1 ± 2.0	19.5 ± 3.4	15.6 ± 2.1
16:2n-6	2.0 ± 0.5	2.4 ± 0.6	2.6 ± 0.2	3.1 ± 0.2
16:2n-4	2.6 ± 0.7	1.5 ± 0.4	2.7 ± 0.9	2.3 ± 0.4
17:0	2.7 ± 0.5	2.8 ± 0.3	2.4 ± 0.4	2.8 ± 0.2
16:3n-4	1.5 ± 0.7	1.4 ± 0.5	1.9 ± 0.6	1.8 ± 0.9
16:4n-3	2.6 ± 1.2	0.8 ± 0.3	1.3 ± 0.6	1.2 ± 0.4
16:4n-1	1.6 ± 0.7	1.5 ± 0.8	0.9 ± 0.6	1.0 ± 0.6
18:0	14.2 ± 1.6	13.1 ± 0.8	11.6 ± 0.7	11.7 ± 0.5
18:1n-9	20.6 ± 4.1	18.5 ± 3.4	32.3 ± 3.9	27.9 ± 3.5
18:1n-7	11.9 ± 2.4	9.5 ± 1.0	13.9 ± 1.2	12.5 ± 0.8
18:2n-6	8.6 ± 1.5	9.2 ± 1.6	12.4 ± 1.2	12.9 ± 1.0
18:2n-4	2.0 ± 0.4	1.5 ± 0.2	2.1 ± 0.2	2.1 ± 0.2
18:3n-6	2.2 ± 0.8	1.5 ± 0.4	2.5 ± 0.4	2.3 ± 0.2
18:3n-4	2.2 ± 0.7	1.5 ± 0.3	2.4 ± 0.4	2.0 ± 0.3
18:3n-3	6.6 ± 1.4	6.9 ± 0.9	7.9 ± 0.6	8.7 ± 0.7
18:3n-1	1.2 ± 0.7	1.2 ± 0.3	1.1 ± 0.3	1.5 ± 0.3
18:4n-3	3.5 ± 0.7	4.0 ± 1.2	4.9 ± 0.7	5.6 ± 0.7
18:4n-1	1.3 ± 0.6	0.4 ± 0.5	0.9 ± 0.5	1.2 ± 0.6
20:0	2.1 ± 0.7	2.8 ± 0.7	3.1 ± 0.6	2.8 ± 0.8
20:1n-11	1.7 ± 1.0	0.8 ± 0.5	1.9 ± 0.8	1.4 ± 0.4
20:1n-9	6.0 ± 1.4	4.2 ± 0.8	7.9 ± 0.9	7.1 ± 0.9
20:1n-7	2.5 ± 0.4	2.5 ± 0.3	3.8 ± 0.4	4.1 ± 0.6
20:2n-9	0.8 ± 0.6	1.4 ± 0.8	1.3 ± 0.4	1.2 ± 0.4
20:2n-6	3.8 ± 0.9	4.7 ± 0.9	6.8 ± 1.3	7.5 ± 1.0
20:3n-6	3.4 ± 0.5	3.6 ± 0.4	4.4 ± 0.5	4.0 ± 0.4
20:4n-6	13.8 ± 1.7	14.2 ± 1.3	10.1 ± 1.1	10.0 ± 1.2
20:3n-3	3.5 ± 0.7	4.5 ± 0.9	5.1 ± 0.6	6.6 ± 0.7
20:4n-3	6.1 ± 1.2	8.2 ± 1.3	8.8 ± 1.1	10.8 ± 0.9
20:5n-3	18.0 ± 2.9	15.7± 1.2	11.8 ± 2.1	12.2 ± 1.8
22:1n-11	1.8 ± 1.7	0.9 ± 0.5	1.0 ± 1.3	0.9 ± 0.4
22:1n-9	2.2 ± 0.5	2.4 ± 0.4	3.3 ± 0.4	3.1 ± 0.4
22:1n-7	1.2 ± 0.6	1.0 ± 0.5	1.1 ± 0.3	1.6 ± 0.4
22:2n-6	1.4 ± 0.5	1.7 ± 0.6	3.0 ± 0.5	4.0 ± 0.8
21:5n-3	0.9 ± 0.6	1.8 ± 0.6	2.2 ± 0.6	1.6 ± 0.9
22:4n-6	0.2 ± 0.5	1.0 ± 1.6	0.3 ± 0.6	1.6 ± 1.7
22:5n-6	7.6 ±1.1	10.7 ± 1.4	7.7 ± 0.7	9.6 ± 1.4
22:4n-3	2.3 ± 0.9	4.2 ± 1.3	5.1 ± 0.9	7.2 ± 1.7
22:5n-3	10.4 ± 0.9	10.8 ± 0.6	10.4 ± 2.4	11.1 ± 0.7
22:6n-3	33.9 ± 5.6	38.9 ± 4.3	23.1 ± 3.7	26.3 ± 4.7

Table 2. Number of individuals genotyped (N), number of alleles (N_A), expected heterozygosity (H_E), observed heterozygosity (H_O), allelic richness (A_R) and private allelic richness (PA_R) within fatty acid groups identified within a piscivorous morphotype of Lake Trout from Canada's Great Bear Lake.

	N	**N_A**	**H_E**	**H_O**	**A_R**	**PA_R**
Group 1	12	10.16	0.85	0.83	9.87	1.08
Group 2	16	11.26	0.84	0.82	9.57	0.99
Group 3	20	12.32	0.84	0.81	9.70	0.87
Group 4	28	14.11	0.84	0.81	9.57	0.98
Giant	39	15.95	0.84	0.78	9.69	1.05

Table 3. Pairwise F_{ST} based on variation at microsatellite loci among Lake Trout morphs from Harris et al. (2015) and piscivorous fatty acids dietary groups from Great Bear Lake. Significant results are represented as follow: * values are significant at an initial α of 0.05 and ** values are significant at an α of 0.02 subsequent False Discovery Rate adjustments for multiple comparisons.

	Morph 1	**Morph 2**	**Morph 3**		**Group 1**	**Group 2**	**Group 3**	**Group 4**
Morph 1				**Group 1**				
Morph 2	0.063**			**Group 2**	0.003			
Morph 3	0.004**	0.007**		**Group 3**	0.001	-0.01		
Morph 4	0.012**	0.017**	0.009**	**Group 4**	0.005	-0.004	-0.002	
				Giant	0.016**	0.001	-0.002	0.006**

List of Figures:

Fig. 1. Example of a piscivorous (64 cm) and a Giant (100 cm standard length) Lake Trout, respectively, from Great Bear Lake (NT).

Fig. 2. Principal Component Analysis of fatty acids of 79 individual Lake Trout classified as piscivorous morph from Great Bear Lake, based on the most discriminating 26 fatty acids from SIMPER analysis, explaining together ~89% of the separation among groups. A) Vectors of individual fatty acids contributing to the positioning of piscivorous individuals and the convex hull delimitating group's position are shown. B) Individual Lake Trout are represented as circle = Group 1, square = Group 2, triangle = Group 3, and diamond = Group 4. To visualize their variation within and among groups, large symbols were used to depict individuals longer than 900 mm fork length, which were identified as the Giant sub-set in this study. Groups were defined by FactoMineR using fatty acids and they are outlined by convex hulls.

Fig. 3. Fork length (mm) at age (years) for four piscivorous groups of Lake Trout sampled from Great Bear Lake in 2002–2015 (Group 1 = squares; Group 2 = circles; Group 3 = triangles; diamond = Group 4). Large symbols depict Giants (FL > 900 mm) within each group. The von Bertalanffy length-age model is depicted as a solid line without Giants and a dashed line with Giants.

Fig. 4. Results of the Bayesian clustering analysis implemented in the program STRUCTURE (B) and the compoplot of percent membership assignment revealed from the DAPC analysis (B) for piscivorous Lake Trout form Great Bear Lake. Shown is the admixture coefficient/percent membership assignment plot where each individual is represented as a vertical line partitioned into colored segments representative of an individual's fractional membership in any given cluster (K). The most likely number of genetic clusters was two in both the STRUCTURE

analysis (based on lnP[D] and the ΔK statistic of Evanno et al. (2005)) and DAPC analysis (based on the lowest BIC score and with 30 PCs retained.

Fig. 5. Canonical Variate Analyses (95% ellipses) and Principal Component Analysis of body shape (a, d), head shape (b, e) and linear measurements (c, f), respectively, of piscivorous Lake Trout represented as: square = Group 1, circle = Group 2, triangle = Group 3, and diamond = Group 4. The first two PCA axes explained 44.3% and 12.3 % of variation for body shape, 35.1% and 30.7 % of variation for head shape, and 39.6 % and 20.9 % for linear measurements (Fig. 6 d, e, f). To visualize their variation within and among groups, larger symbols were used to depict individuals longer than 900 mm FL, which are considered the Giant sub-set in this study.

Fig. 6. Residuals of mean (± 95%CI) size-standardized upper and lower jaw lengths, head depth and length, and snout-eye length among piscivorous Lake Trout groups. Grouping symbols are as follow: square = Group 1, circle = Group 2, triangle = Group 3, and diamond = Group 4.

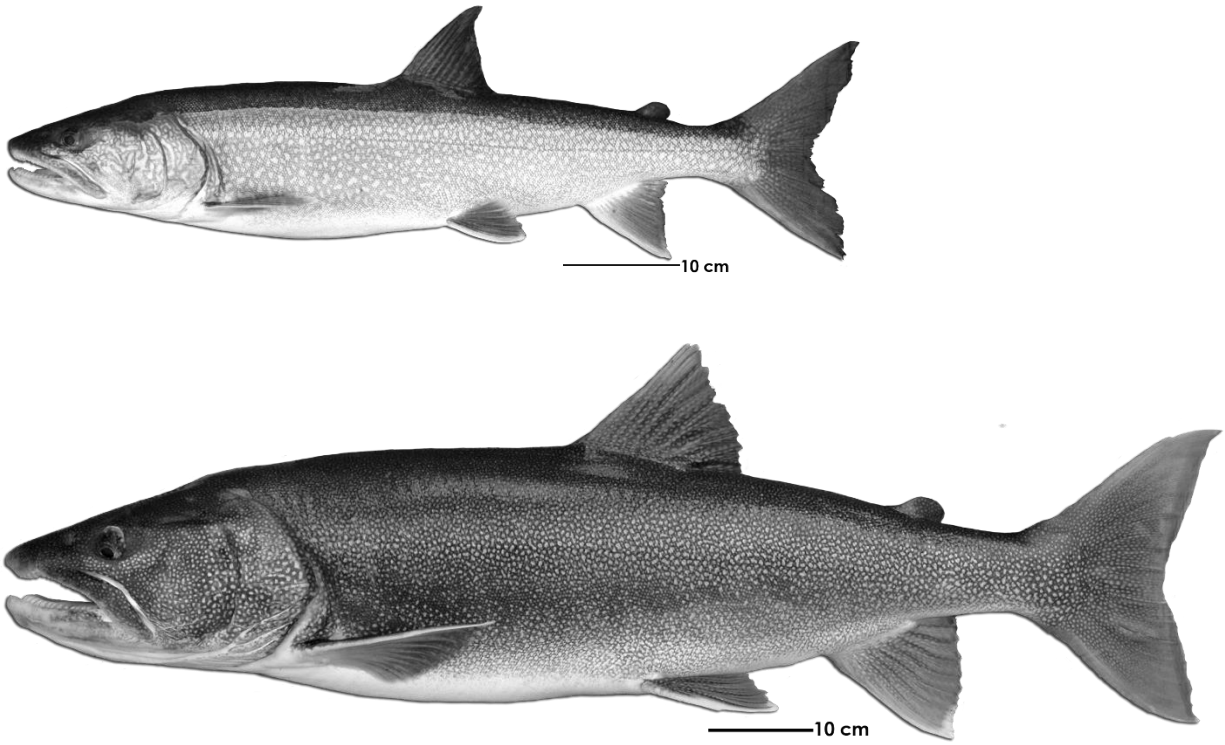


Fig. 1.

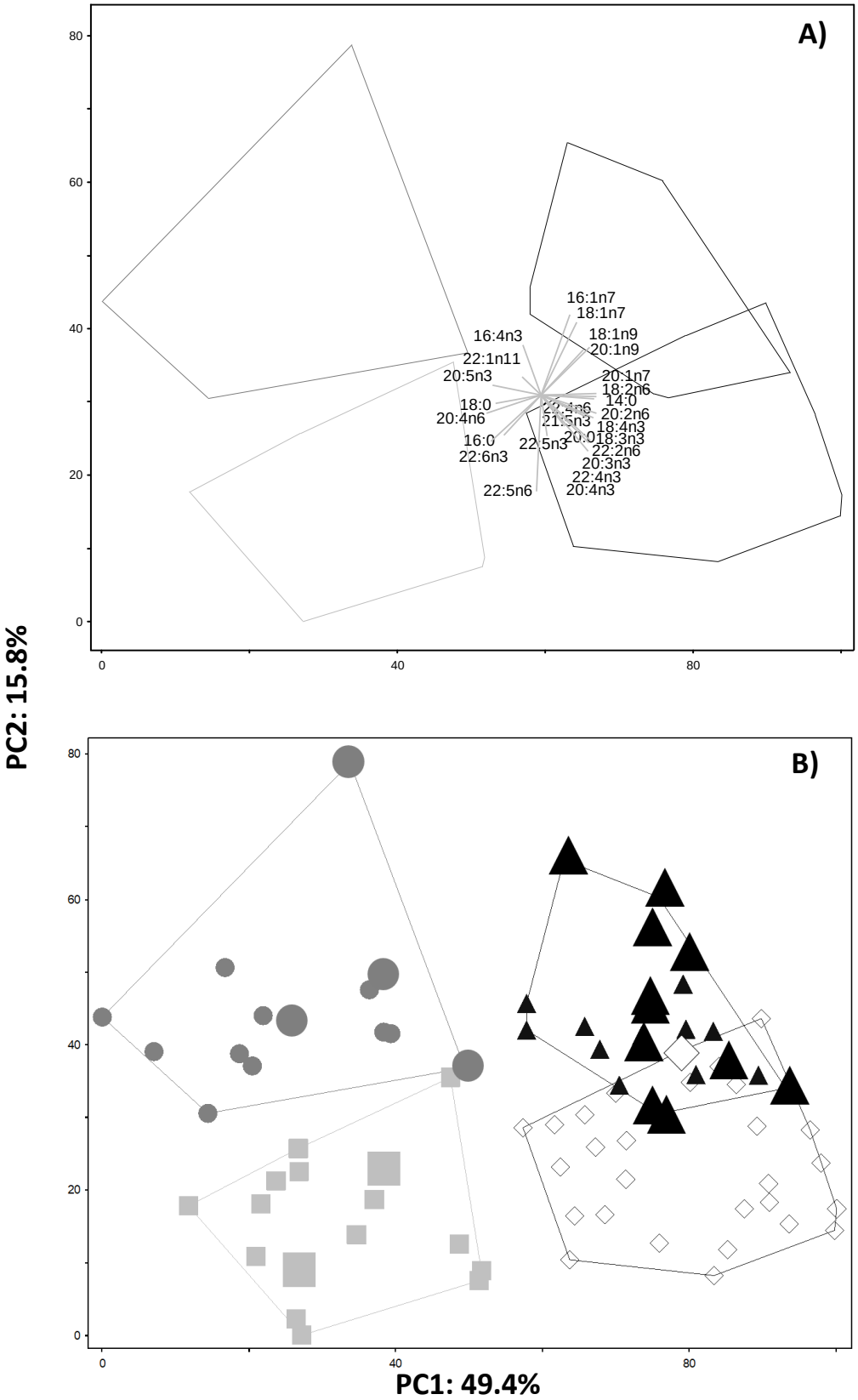

A)
16:1n7
18:1n7
18:1n9
20:1n9
16:4n3
22:1n11
20:5n3
20:1n7
18:2n6
14:0
18:0
20:4n6
20:2n6
18:4n3
16:0
22:6n3
22:5n3
18:3n3
22:2n6
20:3n3
22:4n3
20:4n3
22:5n6
B)
PC2: 15.8%
PC1: 49.4%

Fig. 2

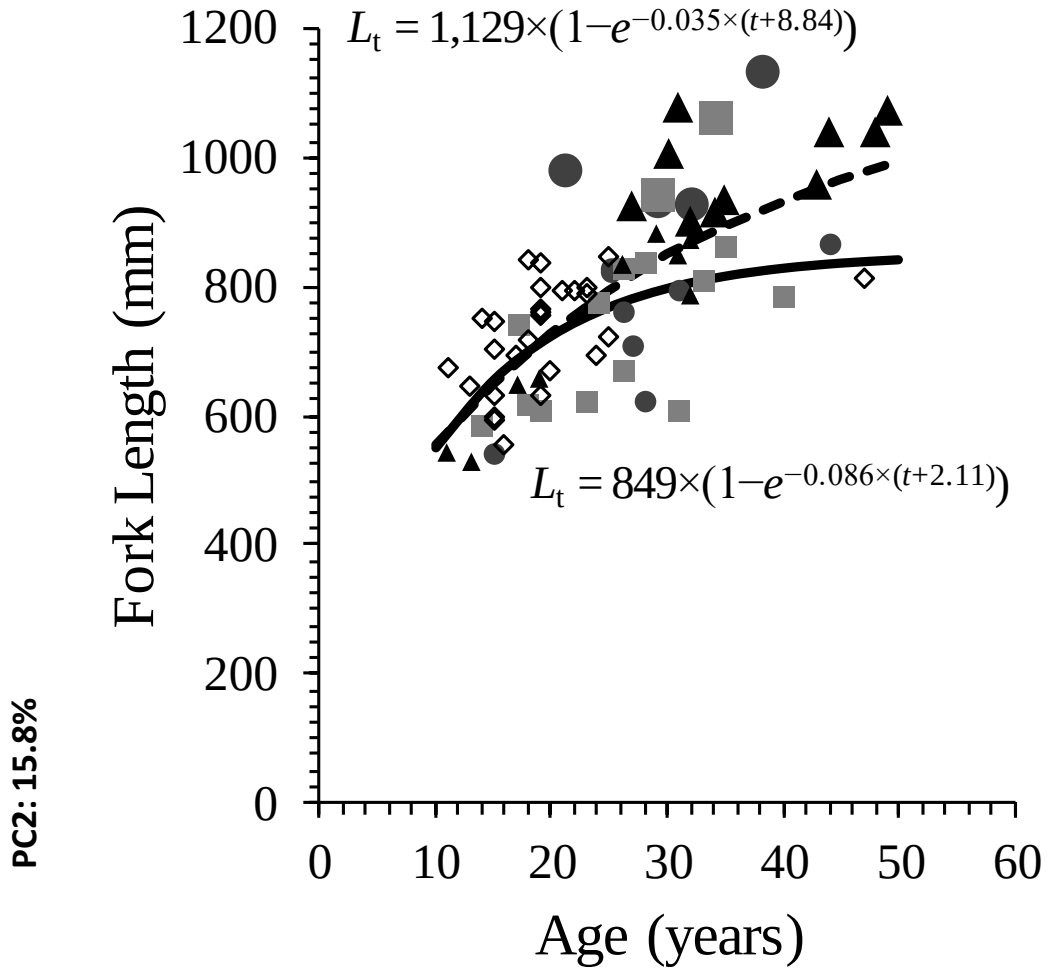

$L_t = 1{,}129\times(1-e^{-0.035\times(t+8.84)})$
$L_t = 849\times(1-e^{-0.086\times(t+2.11)})$
Fork Length (mm)
Age (years)
0
200
400
600
800
1000
1200
0
10
20
30
40
50
60
PC2: 15.8%

Fig. 3.

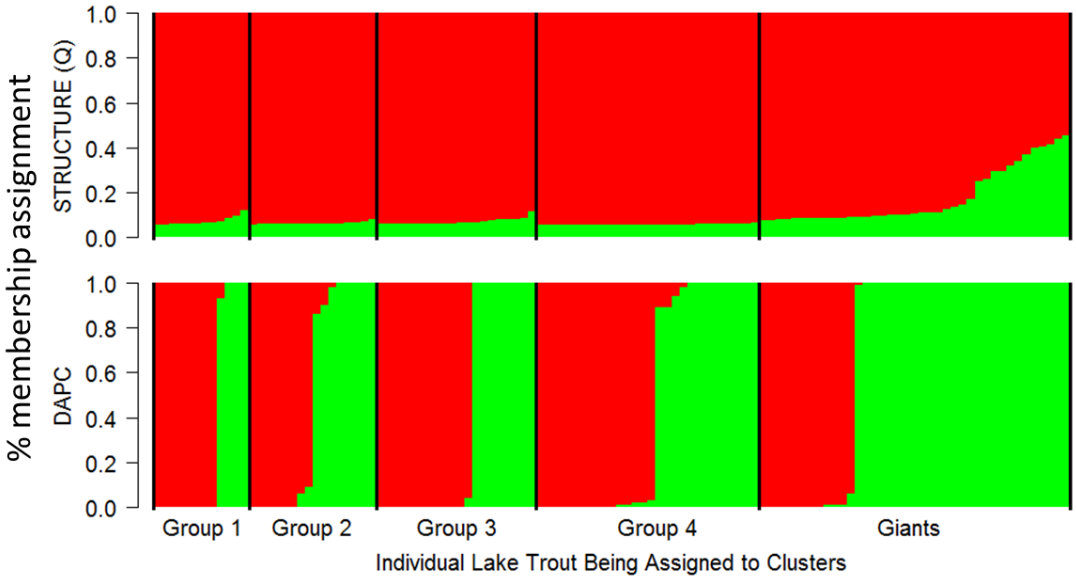

% membership assignment
STRUCTURE (Q)
DAPC
1.0
0.8
0.6
0.4
0.2
0.0
Group 1
Group 2
Group 3
Group 4
Giants
Individual Lake Trout Being Assigned to Clusters

Fig. 4.

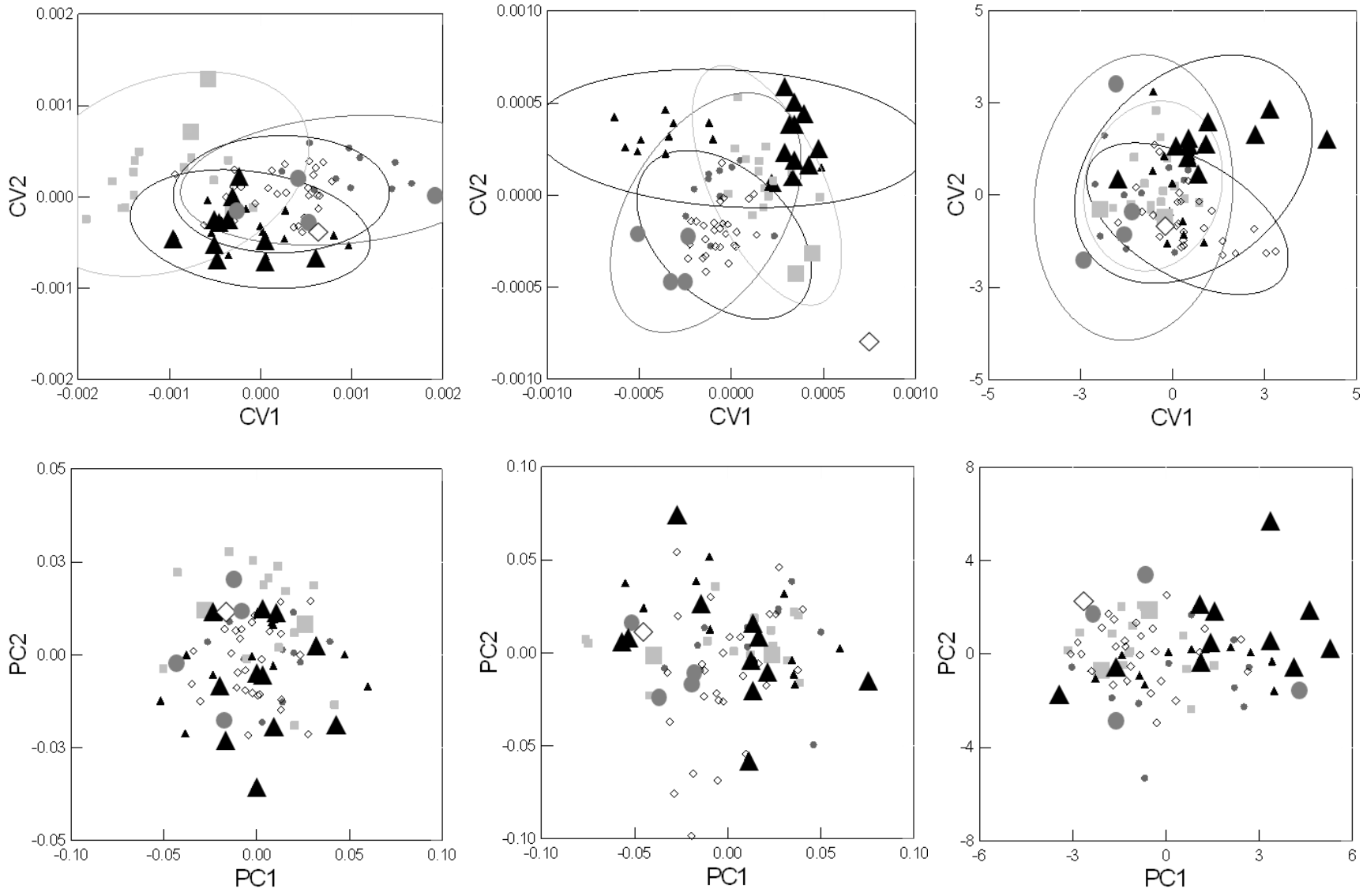


Fig. 5

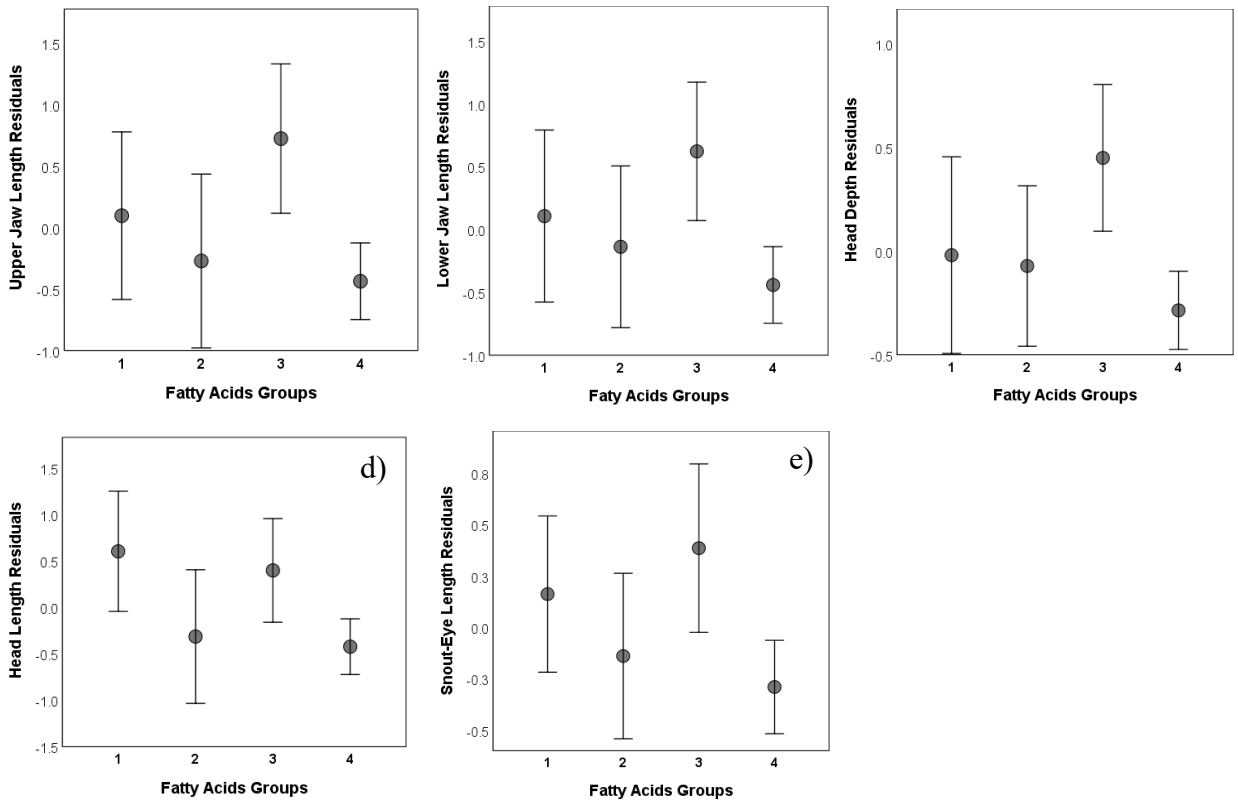

Upper Jaw Length Residuals
Fatty Acids Groups
Lower Jaw Length Residuals
Faty Acids Groups
Head Depth Residuals
Fatty Acids Groups
d)
Head Length Residuals
Fatty Acids Groups
e)
Snout-Eye Length Residuals
Fatty Acids Groups

Fig. 6

Appendix:

Table A1. Spatial and temporal information for the 79 Lake Trout classified as piscivorous morph from Great Bear Lake and analyzed for fatty acids. Sample sizes are in brackets.

	Sample information	
Group 1 (14)	Dease 2005 (1)	Smith 2011 (1)
	Dease 2010 (1)	
	McTavish 2009 (6)	
	McVicar 2008 (1)	
	Smith 2006 (4)	
Group 2 (16)	Dease 2010 (4)	Smith 2006 (1)
	Keith 2012 (2)	Smith 2011 (5)
	McTavish 2009 (1)	
	McTavish 2014 (2)	
	McVicar 2008 (1)	
Group 3 (21)	Dease 2005 (2)	McVicar 2003 (2)
	Dease 2010 (3)	McVicar 2008 (2)
	Keith 2012 (3)	McVicar 2013 (3)
	McTavish 2004 (1)	Smith 2006 (1)
	McTavish 2014 (2)	Smith 2011 (2)
Group 4 (28)	Dease 2005 (5)	McTavish 2014 (1)
	Dease 2010 (2)	McVicar 2003 (2)
	Keith 2002 (4)	McVicar 2008 (5)
	Keith 2003 (4)	Smith 2006 (1)
	MCTavish 2004 (2)	Smith 2011 (1)
	McTavish 2009 (1)	

Table A2. Bayesian clustering (i.e., STRUCTURE, Pritchard et al. 2000) results for piscivorous morphotypes of lake trout from Great Bear Lake assessed using variation at 19 microsatellite markers. Shown are the mean log likelihood values (LnP[D]) for different hypothesized

numbers of genetic populations (K) and the mean value of ΔK statistic of Evanno et al. (2005). Bold values represent the most likely number of genetic groups indicated by ΔK. Dashes = not applicable given that ΔK cannot be calculated for these values of K. For all STRUCTURE analyses, we employed an admixture model with the LOCPRIOR algorithm, correlated allelic frequencies, 100,000 burn-in and MCMC iterations and 10 iterations per K value were completed.

K	Reps	Mean LnP(D)	Delta K
1	10	-10271.83	—
2	10	**-10266.25**	**9.26**
3	10	-10572.68	0.03
4	10	-10868.33	1.39
5	10	-10739.53	0.45
6	10	-10806.97	0.84
7	10	-10678.37	0.66
8	10	-10739.90	0.13
9	10	-10862.98	1.09
10	10	-10553.04	—

Table A3. Results of the discriminant analysis of principal components (DAPC, Jombart et al. 2010) implemented in the Adegenet package (Jombart et al. 2008) to determine the most likely

number of genetic clusters (K) within the piscivorous Lake Trout form Great Bear Lake. The number of groups was identified using the find.clusters function (a sequential K-means clustering algorithm) and subsequent Bayesian Information Criterion (BIC), as suggested by Jombart et al. (2010). Stratified cross-validation carried out with the function *xvalDapc* was employed to determine the optimal number of PCs to retain in the analysis.

K	BIC
1	185.98
2	185.42
3	185.89
4	186.51
5	187.40
6	189.10
7	190.64
8	191.99
9	193.61
10	195.67

Table A4. Microsatellite loci used in this study and F_{is} values for each group per locus.

Locus	Group 1	Group 2	Group 3	Group 4	Giant
OtsG83b	-0.021	0.017	0.046	0.090	-0.013
Sco215	0.061	0.042	-0.011	-0.029	0.071
Smm17	-0.433	-0.069	-0.038	-0.304	-0.012
Smm21	-0.143	-0.286	-0.266	0.023	0.028
SnaMSU1	0.012	-0.069	-0.024	-0.028	-0.074
SnaMSU8	-0.031	0.002	0.048	0.023	0.081
OMM1105	0.094	-0.075	-0.041	-0.098	-0.065
Smm22	-0.014	0.055	0.082	-0.088	0.137
SnaMSU13	-0.105	0.053	0.136	-0.073	-0.049
SnaMSU5	0.088	0.065	-0.032	0.039	0.159
Sco19	-0.082	0.190	0.067	-0.009	0.051
Sco202	0.107	-0.166	0.047	0.115	-0.080
SnaMSU10	-0.108	-0.030	0.086	0.096	0.203
SnaMSU12	0.122	0.069	0.123	0.201	0.072
SnaMSU6	0.008	-0.090	0.002	0.007	0.207
Sal38	-0.056	0.121	-0.016	-0.012	0.041
Sco200	-0.015	0.098	-0.096	0.041	0.244
SnaMSU11	-0.060	-0.108	-0.012	0.083	-0.011
SnaMSU3	0.059	-0.019	0.065	0.012	0.085
Overall	-0.027	-0.011	0.009	0.005	0.057

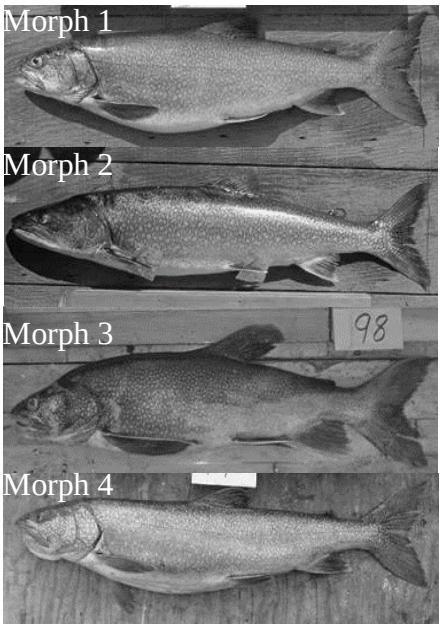


Fig. A1. The four shallow-water morphotypes of Lake Trout from Great Bear Lake identified in Chavarie et al. (2013, 2015, 2016a, 2016b): the generalist, the piscivore, the benthic-oriented, and the pelagic specialist, Morphs1-4, respectively.

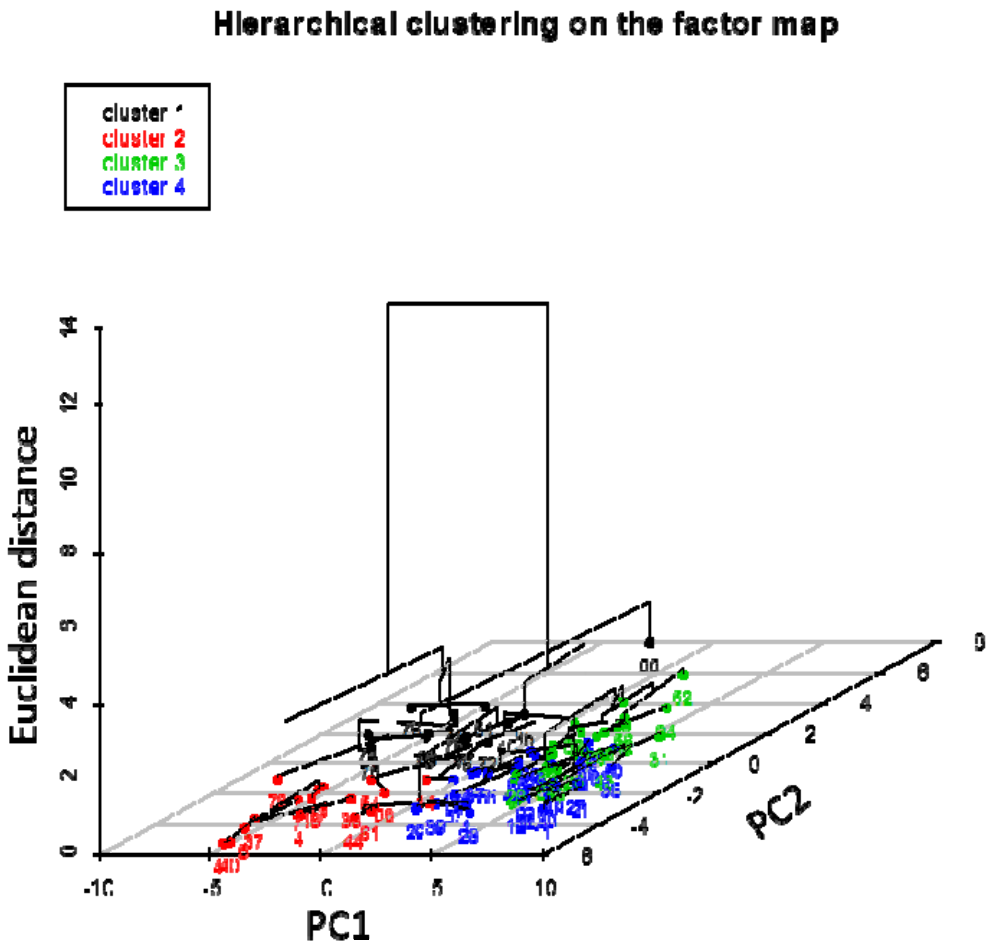


Fig. A2. Hierarchical clusters of Great Bear Lake Lake Trout fatty acids profiles overlaid on the first two principal component axes (PCA) using FactoMineR.

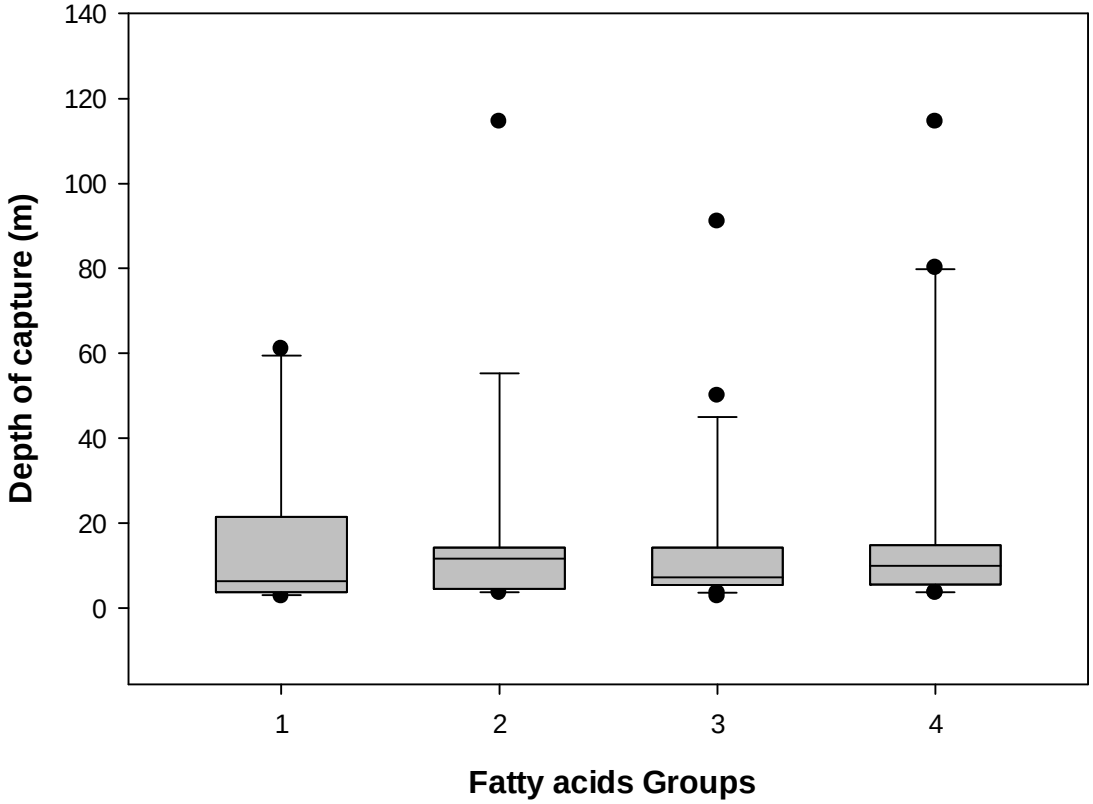
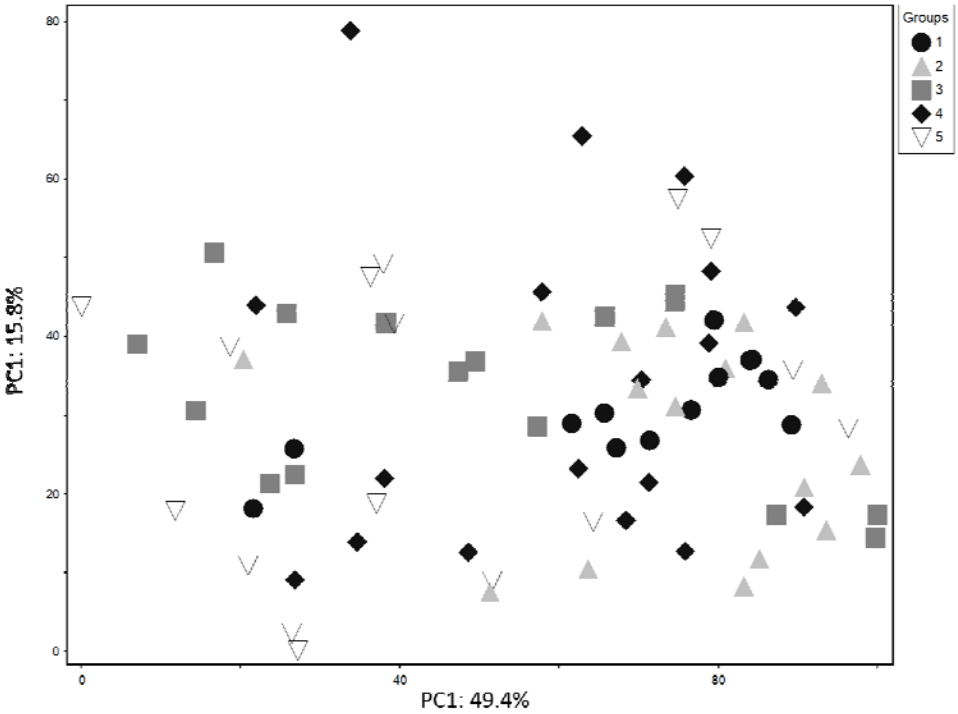
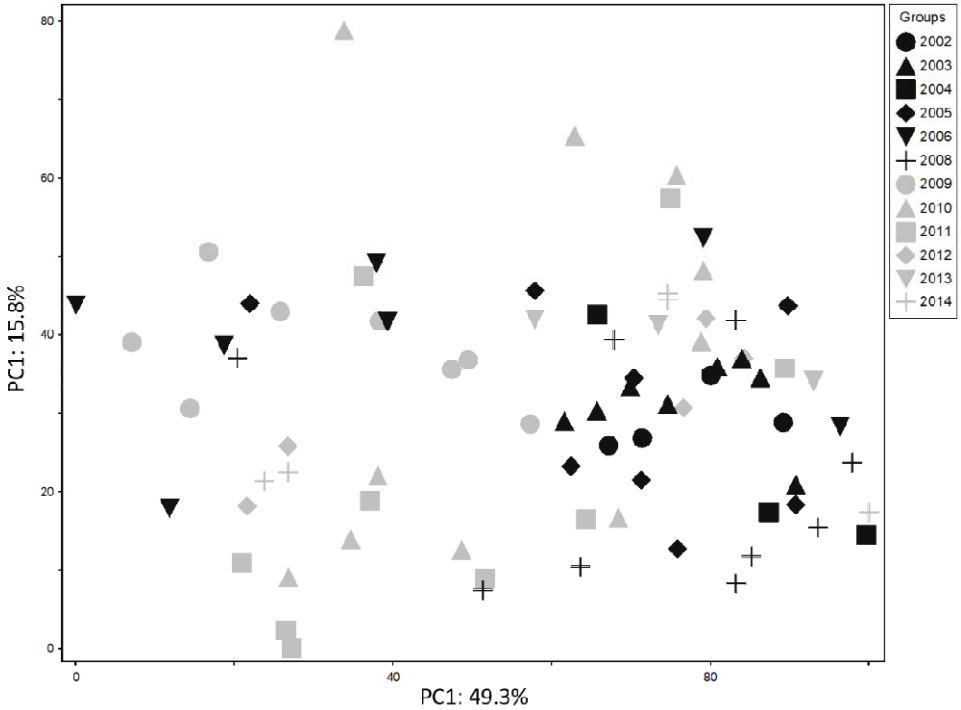


Fig. A3. Depth of capture for four groups of piscivorous Lake Trout from Great Bear Lake (Groups identified by fatty acids profiles of individuals). Outliers are represented by a circle.



a)



b)

Fig. A4. Principal Component Analysis (PCA) of fatty acids of 79 Lake Trout classified as piscivorous morph from Great Bear Lake, based on the proportions of 41 fatty acids in dorsal muscle tissue. Spatial variations (5 arms; 1=Keith, 2=McVicar, 3=McTavish, 4=Dease, and 5=Smith) are represented in a) and temporal (12 years) variations are represented in b), based on the fatty acids profile of each lake trout analyzed in this study.

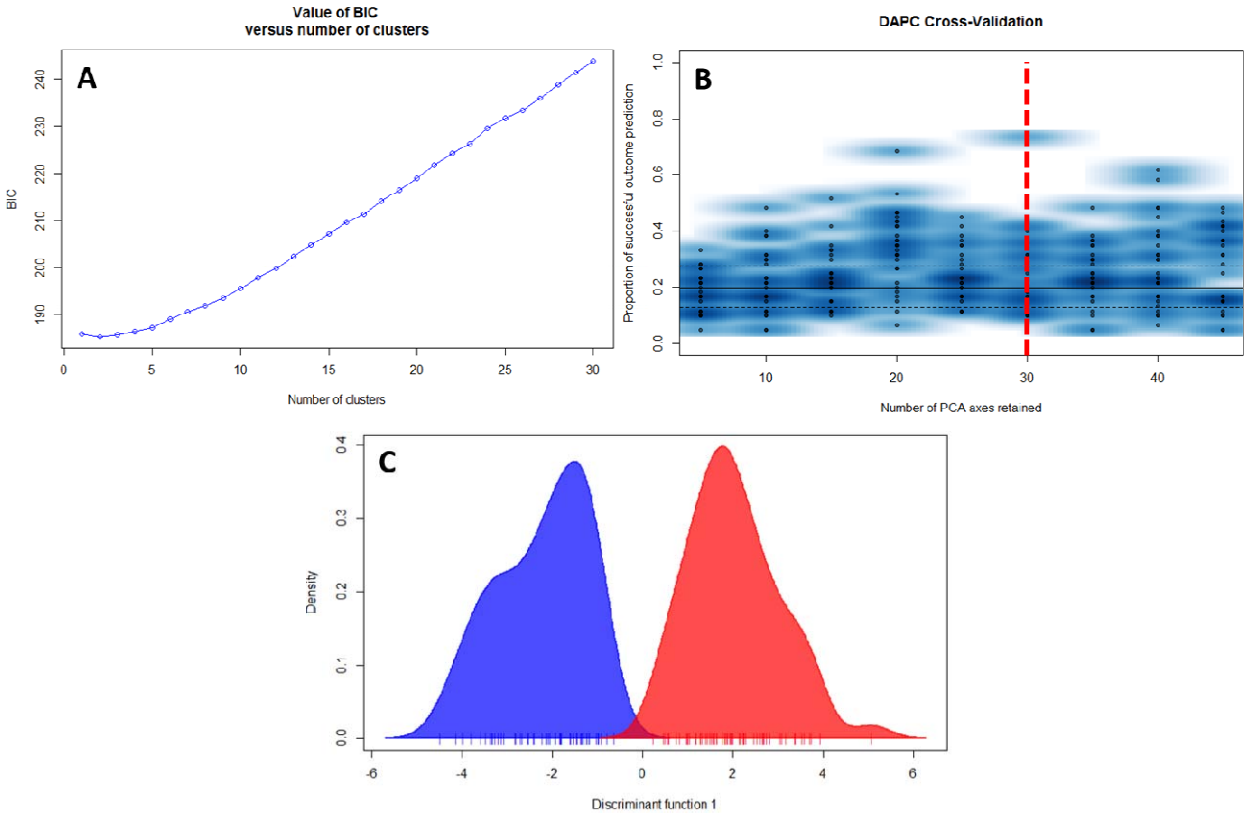


Fig. A5. Summary of the DAPC analysis. (A) Results of the cross-validation analysis used to determine the number of PCs to retain in the DAPC analysis. Cross-validation analysis determined the most appropriate number of PCs retained was 30. (B) Inference of the number of clusters in the DAPC performed on piscivorous Lake Trout from Great Bear Lake. The function find.clusters was run with a maximum number of clusters of 10 to identify the optimal number of clusters based on the BIC values. A K value of 2 (the lowest BIC value) represents the best summary of the data (most probable number of (K)). (C) The results of the discriminant function that shows that the two clusters are mostly non-overlapping.