

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

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

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30 **Abstract:**

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

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

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53 **Introduction:**

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

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

76 within a population), is a question that has been raised repeatedly (Bolnick et al. 2003;
77 Roughgarden 1972; Svanbäck and Persson 2004; Svanbäck and Schluter 2012). Several apparent
78 generalist populations have been reported to be composed of a combination of specialized
79 individuals using several narrow niches that in combination yield an overall wide population
80 niche (Araújo et al. 2008; Svanbäck and Persson 2004; Svanbäck and Schluter 2012; Woo et al.
81 2008). Characterization of niche use among individuals is necessary to understand the role that
82 individual variation can play at the beginning of adaptive divergence and in potentially
83 promoting polymorphism and speciation (Klemetsen 2010; Svanbäck and Persson 2004;
84 Svanbäck and Bolnick 2005; Svanbäck et al. 2015).

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

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

99 within a geologically young system (8,000–10,000 yr BP) (Johnson 1975; Pielou 2008).
100 Specifically, extensive sympatric divergence occurs for this species within the shallow-water (\leq
101 30 m) zone of Great Bear Lake (Chavarie et al. 2013; Chavarie et al. 2015; Chavarie et al.
102 2016b; Harris et al. 2015). Morph 1 is characterized by a small head and intermediate-sized fins.
103 Morph 2 has the largest head and jaws but smallest fins of the morphs. Morph 3 has the longest
104 fins and a robust body shape (i.e., deep body depth). Morph 4 has a thick curved lower jaw and
105 the smallest caudal peduncle depth of the morphs (Fig. A1) (Chavarie et al. 2013; Chavarie et al.
106 2015). Three of these four shallow-water lake trout morphs are described as trophic generalists
107 with differing degrees of omnivory along a weak benthic-pelagic gradient (Chavarie et al. 2016a;
108 Chavarie et al. 2016b). Despite habitat and dietary overlap, significant differences in
109 morphological, genetic, and life-history variation have been reported (Chavarie et al. 2013;
110 Chavarie et al. 2016 ; Harris et al. 2015), suggesting that rather than two or more discrete
111 phenotypes specialized for different resources and habitats, these morphs function as trophic
112 generalists (Chavarie et al. 2016b; Svanbäck et al. 2009b).

113 Furthermore, fatty acid and stomach content analyses of the four lake trout morphs
114 suggested homogenous resource use among morphs, but this observation could be caused by the
115 combination of specializations by individuals along a resource continuum (Chavarie et al.
116 2016a). In other words, whereas morph resource use may appear similar, individuals within a
117 morph may differ in their resource use. One morph (Morph 2; generalist with a tendency to
118 consume more fish than other morphs, referred to here as the piscivorous morph; Fig. 1) showed
119 at least two different feeding strategies, benthic cannibalism and interspecific piscivory in the
120 pelagic zone. Overall, the piscivorous morph had a streamlined body shape, large gape, and high
121 growth rates throughout life, characteristics indicative of piscivory (Chavarie et al. 2013;

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

124 To characterize individual variation within a morph in relation to observed differentiation
125 of feeding strategies, the current study focused solely on the piscivorous lake trout morph.
126 Samples from previous collections (Chavarie et al. 2016a; Harris et al. 2015), plus some
127 additional fish, were analyzed for fatty acid composition. Fatty acids analysis assumes that
128 dietary lipids are broken down into their constituent fatty acids and incorporated relatively
129 unchanged into the consumer tissues (Howell et al. 2003; Iverson 2009; Iverson et al. 2004),
130 allowing spatial and temporal diet comparison between organisms (Duerksen et al. 2014;
131 Eloranta et al. 2011; Hoffmann 2017; Iverson 2009; Scharnweber et al. 2016). Due to their lack
132 of ability to modify fatty acids, overall modification of dietary fatty acids in fish is probably
133 related to dietary deposition, resulting in a robust tool to represent lake trout diet (Happel et al.
134 2017a; Happel et al. 2016; Happel et al. 2017b; Iverson 2009). Thus, fatty acids were used as
135 trophic bio-indicators to better understand dietary patterns of piscivorous lake trout and
136 investigate whether individual specialization may be contributing to trophic breadth and
137 variation observed among individuals in this morph. Specifically, our aims were to 1) compare
138 resource use among piscivorous lake trout individuals (Morph 2) by characterizing their fatty
139 acids profiles, 2) determine whether resource-use differences were influenced by life-history
140 traits (e.g., size and age), 3) characterize the extent of morphological variation individuals
141 present among groups expressing different feeding strategies, and 4) determine if genetic
142 differences existed among groups. In addition, we examined a sub-set of large lake trout from
143 our collections (≥ 900 mm in fork length) referred to locally as “Giants” (Fig. 1), to determine if
144 they showed any ecological and genetic differences. These exceptionally large individuals

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

152 **Methods**

153 *Study area and field sampling*

154 Great Bear Lake is an oligotrophic Arctic freshwater system, 250 km south of the Arctic
155 Ocean, in Northwest Territories, Canada (N66° 06' W120° 35') (Johnson 1975). As the world's
156 ninth largest and 19th deepest lake, the lake has a complex, multi-armed surface area of 31,790
157 km² and a maximum depth of 446 m (mean depth = 90 m). Great Bear Lake was formed by
158 scouring from the Laurentide ice-sheet during the Pleistocene and was originally part of glacial
159 Lake McConnell 8,000–10,000 yr BP (Johnson 1975; Pielou 2008). The lake has characteristics
160 typical of an arctic lake: ultra-oligotrophic, short ice-free season, and a simple food web
161 supporting only 15 fish species (Alfonso 2004; Johnson 1975; MacDonald et al. 2004). Great
162 Bear Lake lacks a commercial fishery but plays an important role in the local economy,
163 supporting a fly-in sport fishery for tourists and a subsistence fishery for the small Sahtu
164 community of Déline. Great Bear Lake has considerable intraspecific diversity within lake trout,
165 lake whitefish (*Coregonus clupeaformis*), and cisco (*C. artedi*) (Chavarie et al. 2013; Howland et
166 al. 2013).

167 Piscivorous lake trout were caught at depths ≤ 30 m using paired bottom sets (ca. 24 h) of
168 140-mm and multi-mesh (38–140 mm) stretched-mesh gill nets during end of July and August
169 over multiple years (2002–2011) among all five arms of the lake (Chavarie et al. 2013; Chavarie
170 et al. 2015; Chavarie et al. 2016a). During 2012–2014, multi-mesh gill nets (38 to 140 mm), with
171 a typical soak time of 24 hours, were distributed across random depth-stratified sites (0–150 m)
172 among Keith, McVicar, and McTavish arms (Table A1). We focused on adult trout due to the
173 difficulty of classifying juveniles into morphs (Chavarie et al. 2013; Zimmerman et al. 2006;
174 Zimmerman et al. 2007) and to avoid the confounding effects of ontogenetic shifts in
175 morphology and diet. Of 79 fish analyzed herein, 35 piscivorous lake trout (Morph 2) were
176 previously analyzed for fatty acids by Chavarie et al. (2016a) and 44 fish were new to the current
177 diet analysis. Fish were randomly selected from the collections analyzed morphologically by
178 Chavarie et al. (2015) to include a range of sizes and ages within the piscivorous morph. For the
179 Giant individuals, lake trout with fork length ≥ 900 mm were targeted. A left lateral full-body
180 digital image was taken for each lake trout caught according to the procedures in Muir et al.
181 (2012). Measurements, tissues, and structures were sampled for determination of biological
182 characteristics related to life-history, including otoliths, fork length, somatic weight, sex, and
183 stage of maturity (i.e., immature, current year spawner, or resting) (Chavarie et al. 2013;
184 Chavarie et al. 2016). A dorsal muscle sample was removed and frozen at -20°C for fatty acids
185 analysis (Budge et al. 2006; Kavanagh et al. 2010; Loseto et al. 2009) and tissue from pectoral
186 fins was collected and preserved in ethanol for genetic analyses.

187 *Fatty Acids*

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

190 a mortar and pestle. Lipids were extracted overnight from 1 g of the homogenate in a 2:1
191 chloroform-methanol solution containing 0.01% BHT (v/v/w) at -20°C (Folch et al. 1957). After
192 extraction, samples were filtered through Whatman Grade 1 Qualitative filter paper and the filter
193 paper/sample was rinsed twice with 2 ml of the 2:1 chloroform:methanol. Sample extract was
194 collected in a test tube and 7 ml of 0.88 N NaCl solution was added to encourage fatty acids to
195 move into the organic (chloroform) layer. The aqueous layer was discarded after which the
196 chloroform was dried with sodium sulfate prior to total lipid measurement. The extracted lipid
197 was used to prepare fatty acid methyl esters (FAME) by transesterification with Hilditch reagent
198 (0.5 N H_2SO_4 in methanol) (Morrison and Smith 1964). Samples were heated for 1 h at 100°C .
199 Gas chromatographic (GC) analysis was performed on an Agilent Technologies 7890N GC
200 equipped with a 30 m J&W DB-23 column (0.25 mm I.D; 0.15 μm film thickness). The GC was
201 coupled to a Flame Ionization Detector operating at 350°C . Hydrogen was used as carrier gas
202 flowing at 1.25 ml/min for 14 minutes, and increased to 2.5 ml/min for 5 min. The split/splitless
203 injector was heated to 260°C and run in splitless mode. The oven program was as follows: 60°C
204 for 0.66 min, increasing by $22.82^{\circ}\text{C}/\text{min}$ to 165°C with a 1.97 min hold; increasing by 4.56
205 $^{\circ}\text{C}/\text{min}$ to 174°C and by $7.61^{\circ}\text{C}/\text{min}$ to 200°C with a six min hold. Peak areas were quantified
206 using Agilent Technologies ChemStation software. Fatty acids standards were obtained from
207 Supelco (37 component FAME mix) and Nuchek (54 component mix GLC-463).

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

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

229 *Life-history*

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

$$233 \quad L_t = L_\infty \left(1 - e^{-K(t-t_0)}\right)^e$$

234 The length-age model describes length L_t at age-of-capture t as a function of theoretical
235 maximum length ($L_\infty = \text{mm}$), instantaneous rate at which L_t approaches L_∞ ($K = 1/\text{year}$),

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

246 *Genetic analyses*

247 To determine if genetic differences existed among individuals expressing different
248 feeding strategies, 79 lake trout classified by fatty acid composition into four groups were
249 genotyped to determine genetic variation and structure within and among groups. To allow a
250 sample size sufficient for making a genetic comparison of the Giant to the other dietary groups,
251 22 additional individuals determined non-randomly by their size (≥ 900 mm ; Giant sub-set)
252 from the 2002-2015 collections were added to the Giant processed for fatty acids, for a total of
253 39 Giants for genetic analysis. Lake trout DNA was extracted from pectoral fin tissue preserved
254 in ethanol using DNEasy extraction kits (Qiagen Inc., Valencia, CA) following manufacturer
255 protocols. Piscivorous groups were assayed using a suite of 23 putatively neutral microsatellite
256 markers amplified in four multiplexes previously described in Harris et al. (2015). Amplified
257 microsatellite fragments were analyzed using an automated sequencer (ABI 3130xl Genetic
258 Analyzer; Applied Biosystems, Foster City, CA). The LIZ 600 size standard was incorporated

259 for allele base-size determination. All genotypes were scored using GeneMapper software ver.
260 4.0 (Applied Biosystems) and then manually inspected to ensure accuracy.

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

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

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

282 Cockerham 1984) was calculated in FSTAT ver. 2.9.3 (Goudet 1995) and pairwise comparisons
283 of F_{ST} between groups were calculated in ARLEQUIN ver. 3.5 (Excoffier et al. 2005) using
284 10,000 permutations. We then employed the Bayesian clustering program STRUCTURE V.
285 2.3.2 (Pritchard et al. 2000) to resolve the putative number of populations (i.e., genetic clusters
286 (K)) within our samples. Owing to the remarkably low levels of genetic differentiation among
287 lake trout in the Great Bear Lake (Harris et al. 2013; Harris et al. 2015), we employed the
288 LOCPRIOR algorithm (Hubisz et al. 2009). The LOCPRIOR algorithm considered the
289 location/sampling information as a prior in the model, which may perform better than the
290 traditional STRUCTURE model when the genetic structure is weak (Hubisz et al. 2009). We also
291 incorporated an admixture model with correlated allelic frequencies and the model was run with
292 a burn-in period of 500,000 iterations and 500,000 Markov chain Monte Carlo iterations. We
293 varied the potential number of populations (K) from 1 to 10 and we ran 20 iterations for each
294 value of K. The STRUCTURE output was first processed in the program STRUCTURE
295 HARVESTER (Earl 2012), followed by the combination of results of independent runs of the
296 program and compilation of results based on $\ln P(D)$ and the post hoc ΔK statistic of Evanno et
297 al. (2005), to infer the most likely number of clusters. The best alignment of replicate runs was
298 assessed with CLUMPP V. 1.1 (Jakobsson and Rosenberg 2007) and DISTRICT V. 1.1
299 (Rosenberg 2004) was then used to visualize the results. For STRUCTURE analyses, we
300 reported both $\ln P(D)$ and the post hoc ΔK statistic.

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

305 (2010). Stratified cross-validation (carried out with the function *xvalDapc*) was used to
306 determine the optimal number of principal components to retain in the analysis.

307 *Morphology*

308 Morphological variation was quantified for the 79 lake trout to compare fatty acid
309 groupings (different feeding strategies) to morphological variation within the piscivorous morph.
310 Twenty-three landmarks, 20 semi-landmarks based on Chavarie et al. (2015), and fourteen linear
311 measurements based on Muir et al. (2014), were used to characterize body and head shape from
312 photographed fish. The combination of traditional and geometric morphometrics was used
313 because of the empirical relationships of phenotype with foraging (e.g., jaw size) and swimming
314 (e.g., fin lengths and caudal peduncle depth) (Kahilainen et al. 2004; Kristjánsson et al. 2002;
315 Webb 1984). Landmarks and semi-landmarks were digitized in x and y coordinates using
316 TPSDig2 software (<http://life.bio.sunysb.edu/morph>). Subsequently, digitized landmarks and
317 semi-landmarks were processed in a series of Integrated Morphometrics Programs (IMP) version
318 8 (<http://www2.canisius.edu/~sheets/morphsoft>), using partial warp scores, which are thin-plate
319 spline coefficients. Morphological methods and programs are described in Zelditch et al. (2012)
320 and specific procedures were described in further detail in Chavarie et al. (2013). All
321 morphological measurements were size-free, using centroid sizes or residuals from regressions
322 on standard length (Zelditch et al. 2012).

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

328 10 000 permutations tested for differences among groups and determined the percentage of
329 variation explained for a grouping if a CVA was significant. For linear measurements, a
330 Bonferroni-corrected post-hoc test followed MANOVA to identify measurements that differed
331 among group. Principal component analyses (PCA) were performed on body- and head-shape
332 data using PCAGen8 (IMP software) among groups to visualize morphological variation within
333 the dataset. PC-ORD version 6 software (McCune and Mefford 2011) was used to perform a
334 PCA on the linear measurements.

335 **Results**

336 *Fatty acids*

337 On the basis of fatty acid composition, piscivorous lake trout were divided along a resource use
338 axis into four groups (Fig. 2 and A2; Table 1). Overall, 14 individuals were assigned in Group 1,
339 16 individuals in Group 2, 21 individuals in Group 3, and 28 individuals in Group 4. Average
340 dissimilarity was 14.61 from the SIMPER analysis, whereas the most discriminating 26 fatty
341 acids, explaining together ~89% of the separation among groups, were: 22:6n-3 (12.5 %), 18:1n-
342 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 %),
343 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%),
344 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%),
345 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%),
346 16:4n-3 (1.2%), and 16:2n-4 (1.1%) (Table 1). The first two axes of the fatty acids PCA
347 explained 65.2 % of the variation in diet and the four groups were supported by PERMANOVA
348 ($F_{3,76} = 39.4$, $P < 0.01$) and pairwise comparisons between all pairs (all $P < 0.01$). Finally, depth
349 of capture did not differ among groups identified by fatty acids profiles ($p \geq 0.05$). For all
350 groups, the majority of lake trout were caught between 0-20 m (Fig. A3).

351 *Life-history*

352 Overall, life history parameters did not differ among lake trout groups identified by fatty
353 acid composition. Length-age models did not differ among fatty acid groups, based on overall
354 likelihood-ratio tests (Fig. 3; $F_{9, 63} = 1.58$; $P = 0.141$). With the Giant sub-set included, growth
355 differed between Group 3 and Group 4 ($F_{3, 41} = 3.958$; $P = 0.014$), but not between Groups 1 and
356 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 ($F_{3, 34} =$
357 0.930 ; $P = 0.437$), Groups 2 and 3 ($F_{3, 29} = 1.820$; $P = 0.166$), or Groups 2 and 4 ($F_{3, 36} = 1.058$;
358 $P = 0.379$). Without Giants included (prevalence of Giants was higher in Group 3 than Group 1,
359 Group 2, and Group 4), none of the paired groups (morphs) differed for length-at-age: Groups 1
360 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 ($F_{3, 30}$
361 $= 1.458$; $P = 0.246$); Groups 2 vs. 3 ($F_{3, 17} = 1.254$; $P = 0.321$); Groups 2 vs. 4 ($F_{3, 34} = 1.431$; $P =$
362 0.251); and Groups 3 vs. 4 ($F_{3, 31} = 2.062$; $P = 0.126$).

363 *Genetic differentiation*

364 Little genetic differentiation was evident among piscivorous lake trout groups, except for
365 the Giant sub-set, which differed slightly from other groups defined by fatty acids. The program
366 MICROCHECKER identified two loci (OtsG253b and Sco102) that contained null alleles. These
367 loci, along with non-variable loci Sco218 and SSOSL456, were removed, leaving 19 informative
368 loci for subsequent analyses. Descriptive statistics of genetic variation were similar among
369 groups. The number of alleles per locus ranged from four (Smm21) to 41 (SnaMSU10) and
370 averaged 28.75 across all loci. Observed heterozygosity averaged across all loci ranged from
371 0.78 (Giant) to 0.83 (Group 1) while expected heterozygosity ranged from 0.84 (all groups with
372 the exception of Group 1) to 0.85 (Group 1; Table 2). Allelic richness ranged from 9.57 (Group 2
373 and 4) to 9.87 (Group 1), while expected private allelic richness ranged from 0.87 (Group 3) to

374 1.08 (Group 2; Table 2). Departures from Hardy-Weinberg equilibrium were found in 15 of 95
375 tests (at $\alpha = 0.05$), but only five (all of which involved different loci) were significant after
376 adjustment for False Discovery Rate (adjusted $\alpha = 0.01$). Of those five, all were heterozygote
377 deficits and three of five departures involved the Giant sub-set. Significant linkage
378 disequilibrium was evident in 14 of 885 tests ($\alpha = 0.05$), but only nine were significant after
379 adjusting for False Discovery Rate (adjusted $\alpha = 0.0068$). No locus-pair linkage disequilibrium
380 combinations were consistently significant, but seven of nine departures were in the Giant sub-
381 set.

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

387 Global genetic differentiation was extremely low ($\theta = 0.001$, 95% c.i. = $-0.002-0.005$)
388 among groups of piscivorous lake trout assessed. Pairwise F_{ST} ranged from -0.004 to 0.016
389 (Table 3) whereas comparisons that included Giants always differed the most from the other fatty
390 acid groups, and were also the only significant pairwise comparisons ($P < 0.05$, Table 3). The F_{ST}
391 value for the Giant vs. Group 1 and 4 were similar to genetic differentiation previously observed
392 among four lake trout morphs in Great Bear Lake (Table 3), with the exception of Morph 1 vs
393 Morph 2 [32]. Bayesian clustering implemented in STRUCTURE provided evidence for two
394 genetic clusters when evaluating both $\ln P(D)$ or ΔK (Table A2). The admixture plot based on
395 $K=2$ showed no clear genetic structure among groups defined by fatty acid analysis, however,
396 some differentiation of the Giant sub-set from the fatty acid groups was observed (Fig. 4).

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

405 *Morphology*

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

418

419 **Discussion**

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

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

443 food web based on pelagic or deep-water copepods (Ahlgren et al. 2009; Happel et al. 2017b;
444 Hoffmann 2017; Loseto et al. 2009; Stowasser et al. 2006). Specifically, 20:1n-9 is associated
445 with calanoid copepods known to be particularly important in northern pelagic food webs
446 (Ahlgren et al. 2009; Budge et al. 2006; Kattner et al. 1998; Loseto et al. 2009). High levels of
447 14:0, 18:3n-3 and 18:4n-3 fatty acids within groups 3 and 4 are also associated with pelagic
448 environments (Scharnweber et al. 2016; Tucker et al. 2008), although high levels of 18:2n-6 and
449 18:3n-3 have also been associated with terrestrial markers (Budge et al. 2001; Budge and Parrish
450 1998; Hoffmann 2017). Groups 1 and 2 were characterized by higher concentrations of 16:4n-3,
451 20:4n-6 and 22:6n-3 found in diatom and dinoflagellate-based food webs, respectively. The fatty
452 acid 20:4n-6 reflects a benthic feeding strategy (from benthic invertebrates to fish) (Stowasser et
453 al. 2006; Tucker et al. 2008), whereas 22:6n-3 in pennate diatoms (Iverson 2009) and filter
454 feeders links planktonic dinoflagellates to benthic filter-feeding bivalves in a food web (Alfaro et
455 al. 2006; Virtue et al. 2000). Relatively high concentrations of 16:0, 18:0 and 22:6n-3 and low
456 concentrations of 16:1n-7 supported the interpretation of carnivorous (or cannibalistic) dietary
457 patterns (Dalsgaard et al. 2003; Iverson 2009; Iverson et al. 2004; Piché et al. 2010). Individuals
458 positioned between ends of principal components suggests a clinal pattern of resource use or
459 habitat coupling (Vonlanthen et al. 2009), where borders among groups are neither abrupt nor
460 obvious as they are part of a continuum (Hendry et al. 2009b). Overall, observed trophic patterns
461 could reflect prey associated with different microhabitat patches; however, the key assumption of
462 disparity of prey associated with habitat heterogeneity (Bolnick et al. 2010a; Chavarie et al.
463 2016b; Collar et al. 2009; Skulason and Smith 1995; Svanbäck and Bolnick 2005) may not be
464 applicable to Great Bear Lake (Chavarie et al. 2016b).

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

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

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

501 In Great Bear Lake, multiple trophic generalists (which include piscivores studied herein)
502 coexist with one specialist lake trout morph. This contrasts with the more commonly reported
503 observation, the co-occurrence of multiple specialist morphs (Chavarie et al. 2016b; Elmer 2016;
504 Kassen 2002). Apparent generalist population, however, can be composed of several subsets of
505 specialized individuals that result in broad use of resources by the population (Bolnick and Paull
506 2009; Bolnick et al. 2007; Bolnick et al. 2002; Bolnick et al. 2003; Chavarie et al. 2016a). This
507 broad distribution of trophic variation within a population appears to be the case within the Great
508 Bear Lake piscivorous morph. Among-individual specialization, reported in this study, may
509 result from variable use of spatially separated resources and/or resources in different seasons and
510 years (temporal variation), both of which could be expected in the depauperate environment of a

511 large northern lake (Fig. A4; Chavarie et al. 2016b; Costa et al. 2008; Cusa et al. 2019; Quevedo
512 et al. 2009). Ecologically, among-individual resource specialization is another form of diversity
513 that is contained within a morph (Araújo et al. 2008; Bolnick et al. 2003; Pires et al. 2011),
514 which may increase stability and persistence of a morph within a system where energy resources
515 are scarce and ephemeral, such as in Great Bear Lake (Cloyed and Eason 2016; Davies et al.
516 2016; Okuyama 2008; Pfennig and Pfennig 2012; Smith et al. 2011). Whether among-individual
517 resource use within this morph is stable or is an initial divergent step that with enough time will
518 fully differentiate evolutionary units is a question that cannot be answered with our data.

519 Realized niche expansions are often linked to individuals of different morphologies and
520 body sizes, with evidence of efficiency trade-offs among different resources (Cloyed and Eason
521 2016; Parent et al. 2014; Roughgarden 1972; Svanbäck and Persson 2004). When a resource
522 gradient exists, niche expansion can be achieved via genetic differentiation, phenotypic
523 plasticity, or a combination of these processes (Parent et al. 2014). The apparent segregation of
524 resource use based on fatty acid analyses, despite a lack of major morphological, body size, and
525 neutral genetic differentiation among the four dietary groups within the piscivorous morph,
526 suggests that behavioral plasticity in resource exploitation is causing the observed patterns of
527 dietary differentiation. Plasticity may promote evolution of diversification by expanding the
528 range of phenotypes on which selection can act (Nonaka et al. 2015; Pfennig et al. 2010; West-
529 Eberhard 2003). Theoretical models suggest that exploiting a wide range of resources is either
530 costly or limited by constraints, but plasticity is favored when 1) spatial and temporal variation
531 of resources are important (i.e., highly present in Great Bear Lake; Fig. A4), 2) dispersal is high,
532 3) environmental cues are reliable, 4) genetic variation for plasticity is high and 5) cost/limits of
533 plasticity are low (Ackermann et al. 2004; Hendry 2016).

534 The expression of plasticity in response to particular ecological conditions (e.g., habitat
535 structure, prey diversity) can be evolutionarily beneficial (i.e., result in increases in fitness).
536 While most studies of diet variation focus on morphological differences among morphs in a
537 population, diet variation can also arise from behavioral, biochemical, cognitive, and social-rank
538 differences that cause functional ecology to be expressed at a finer scale rather than at the morph
539 level (McGill et al. 2006; Svanbäck and Bolnick 2005; Violle et al. 2012; Zhao et al. 2014).
540 Indeed, behavioral plasticity likely has a temporal evolutionary advantage relative to
541 morphological plasticity due to relatively reduced reliance on ecologically beneficial structural
542 and morphological adaptation (Smith et al. 2011; Svanbäck et al. 2009b). The only detectable
543 morphological differences among the piscivorous groups in Great Bear Lake were associated
544 with jaw lengths, snout-eye distance, and head length and depth, which are strongly related to
545 foraging opportunities (Adams and Huntingford 2002; Sušnik et al. 2006; Wainwright and Price
546 2016). Some morphological characters likely express different degrees of plastic responses
547 (adaptive or not), and thus may be expressed differently depending on the magnitude and time of
548 exposure to heterogeneous environments (Hendry 2016; Sharpe et al. 2008). For example,
549 environmental components (e.g., habitat structure) appear to have stronger and faster effects on
550 linear characters (e.g., jaw length) than on body shape (Chavarie et al. 2015; Sharpe et al. 2008).
551 Trophic level might also limit the scope for morphological variation in lake trout because
552 piscivory can limit diversification of feeding morphology in fishes (Collar et al. 2009; Svanbäck
553 et al. 2015).

554 **Conclusion**

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

557 in early stages, morphological and dietary differences may not always result from genetic
558 divergence (Hendry 2016; Nosil et al. 2009). Considering that processes of speciation continue
559 to be debated, disagreement on when intraspecific divergence starts and what processes are
560 involved is not surprising (De Queiroz 2005, 2007; Venton 2017). The debate around
561 diversification sequence, (which diverges first, behaviour, morphology, or ecology?) highlights
562 the mosaic nature of speciation (Hendry et al. 2009a). In this study, we asked whether
563 diversification could be occurring within a morph by examining the fine-scale trophic variation,
564 at a presumed early stage of sympatric evolutionary divergence of lake trout in Great Bear Lake
565 (i.e., postglacial, representing ~350 generations) (Harris et al. 2015). Rapid evolution in nature
566 on an “ecological time scale”, within relatively few generations, has demonstrated that rapid
567 differentiation can be a strong driver of population dynamics (Ashley et al. 2003; Fussmann et al.
568 2007; Hendry 2016; Turcotte et al. 2011). Due to presumed homogeneity, few studies have
569 investigated dietary patterns and groupings within a morph. However, in this study, we found
570 evidence that among-individual resource specialization occurred within a piscivorous lake trout
571 morph, with four different patterns of resource use identified by fatty acids composition of
572 muscle tissue. These groups did not differ in depth of capture or life history parameters, showed
573 a lack of morphological differentiation (i.e., except for caudal peduncle), and only the Giant sub-
574 set was weakly genetically distinctive from others. The lack of non-neutral markers in the
575 analyses may have prevented us from detecting multiple genetic populations. However, the
576 trophic patterns shown within this morph suggested that ecological drivers (i.e., habitat use, prey
577 diversity) could have important effects on plasticity expression and perhaps on initial or early
578 stages of divergence. By focusing on a postglacial ecosystem, the confounding effects of time,
579 which can influence (and obscure observation of) mechanisms of divergence (Seehausen and

580 Wagner 2014), were reduced in this study. But whether we have identified a stable
581 polymorphism or the first step in diversification on a trajectory of divergence and speciation,
582 remains unknown (Seehausen et al. 2008). Nonetheless, the observed trophic specialization
583 within a morph, compared to the previously reported generality among morphs (Chavarie et al.
584 2016b), suggests that individual specialization can occur within a trophic morph. Future research
585 should focus on the role of among-individual differences within evolutionary units such as
586 morphotypes.

587 **List of abbreviations:**

588 BP = before present

589 m = meter

590 mm = millimeter

591 h = hour

592 ca. = around

593 i.e., = stands for

594 e.g., = for example

595 NaCl = Sodium Chloride

596 FAME = fatty acid methyl esters

597 H₂SO₄ = Sulfuric acid

598 GC = Gas chromatographic

599 °C = degree Celsius

600 °C/min = degree Celsius/minutes

601 UPGMA = Unweighted Pair Group Method with Arithmetic Mean

602 PCA = principal component analysis

603 PERMANOVA = Permutational Multivariate Analysis of Variance

604 MANOVA = Multivariate analysis of variance

605 SIMPER= similarity percentage routine

606 ANOSIM = analysis of similarities

607 N =Number of individuals genotyped

608 N_A = number of alleles

609 H_E =expected heterozygosity

610 H_O = observed heterozygosity

611 A_R = allelic richness

612 PA_R = private allelic richness

613 A = alpha

614 FCA = Factorial correspondence analysis

615 k =number of alleles

616 DAPC = Discriminant Analysis of Principal Components

617 IMP = Integrated Morphometrics Programs

618 CVA = Canonical Variate Analyses

619

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632 **Declarations:**

633 **Authors' contributions**

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

637 **Competing interests**

638 The authors declare that they have no competing interests.

639 **Availability of data and materials**

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

642 **Consent to publish**

643 Not applicable.

644 **Ethics approval and consent to participate**

645 We declare that our experiments were performed in the respect of ethical rules. This protocol
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654

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1089 differences between shallow- and deep-water lake trout in Lake Mistassini, Quebec.
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1091

1084 Table 1. Mean composition (\pm SD) of the 41 fatty acids profile (%) for the Group 1, Group 2,
 1085 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 \pm 1.0	7.0 \pm 1.0	9.2 \pm 1.0	9.9 \pm 1.1
16:0	28.1 \pm 1.0	28.13 \pm 1.7	24.2 \pm 1.7	26.1 \pm 1.2
16:1n-7	15.9 \pm 3.7	10.1 \pm 2.0	19.5 \pm 3.4	15.6 \pm 2.1
16:2n-6	2.0 \pm 0.5	2.4 \pm 0.6	2.6 \pm 0.2	3.1 \pm 0.2
16:2n-4	2.6 \pm 0.7	1.5 \pm 0.4	2.7 \pm 0.9	2.3 \pm 0.4
17:0	2.7 \pm 0.5	2.8 \pm 0.3	2.4 \pm 0.4	2.8 \pm 0.2
16:3n-4	1.5 \pm 0.7	1.4 \pm 0.5	1.9 \pm 0.6	1.8 \pm 0.9
16:4n-3	2.6 \pm 1.2	0.8 \pm 0.3	1.3 \pm 0.6	1.2 \pm 0.4
16:4n-1	1.6 \pm 0.7	1.5 \pm 0.8	0.9 \pm 0.6	1.0 \pm 0.6
18:0	14.2 \pm 1.6	13.1 \pm 0.8	11.6 \pm 0.7	11.7 \pm 0.5
18:1n-9	20.6 \pm 4.1	18.5 \pm 3.4	32.3 \pm 3.9	27.9 \pm 3.5
18:1n-7	11.9 \pm 2.4	9.5 \pm 1.0	13.9 \pm 1.2	12.5 \pm 0.8
18:2n-6	8.6 \pm 1.5	9.2 \pm 1.6	12.4 \pm 1.2	12.9 \pm 1.0
18:2n-4	2.0 \pm 0.4	1.5 \pm 0.2	2.1 \pm 0.2	2.1 \pm 0.2
18:3n-6	2.2 \pm 0.8	1.5 \pm 0.4	2.5 \pm 0.4	2.3 \pm 0.2
18:3n-4	2.2 \pm 0.7	1.5 \pm 0.3	2.4 \pm 0.4	2.0 \pm 0.3
18:3n-3	6.6 \pm 1.4	6.9 \pm 0.9	7.9 \pm 0.6	8.7 \pm 0.7
18:3n-1	1.2 \pm 0.7	1.2 \pm 0.3	1.1 \pm 0.3	1.5 \pm 0.3
18:4n-3	3.5 \pm 0.7	4.0 \pm 1.2	4.9 \pm 0.7	5.6 \pm 0.7
18:4n-1	1.3 \pm 0.6	0.4 \pm 0.5	0.9 \pm 0.5	1.2 \pm 0.6
20:0	2.1 \pm 0.7	2.8 \pm 0.7	3.1 \pm 0.6	2.8 \pm 0.8
20:1n-11	1.7 \pm 1.0	0.8 \pm 0.5	1.9 \pm 0.8	1.4 \pm 0.4
20:1n-9	6.0 \pm 1.4	4.2 \pm 0.8	7.9 \pm 0.9	7.1 \pm 0.9
20:1n-7	2.5 \pm 0.4	2.5 \pm 0.3	3.8 \pm 0.4	4.1 \pm 0.6
20:2n-9	0.8 \pm 0.6	1.4 \pm 0.8	1.3 \pm 0.4	1.2 \pm 0.4
20:2n-6	3.8 \pm 0.9	4.7 \pm 0.9	6.8 \pm 1.3	7.5 \pm 1.0
20:3n-6	3.4 \pm 0.5	3.6 \pm 0.4	4.4 \pm 0.5	4.0 \pm 0.4
20:4n-6	13.8 \pm 1.7	14.2 \pm 1.3	10.1 \pm 1.1	10.0 \pm 1.2
20:3n-3	3.5 \pm 0.7	4.5 \pm 0.9	5.1 \pm 0.6	6.6 \pm 0.7
20:4n-3	6.1 \pm 1.2	8.2 \pm 1.3	8.8 \pm 1.1	10.8 \pm 0.9
20:5n-3	18.0 \pm 2.9	15.7 \pm 1.2	11.8 \pm 2.1	12.2 \pm 1.8
22:1n-11	1.8 \pm 1.7	0.9 \pm 0.5	1.0 \pm 1.3	0.9 \pm 0.4
22:1n-9	2.2 \pm 0.5	2.4 \pm 0.4	3.3 \pm 0.4	3.1 \pm 0.4
22:1n-7	1.2 \pm 0.6	1.0 \pm 0.5	1.1 \pm 0.3	1.6 \pm 0.4
22:2n-6	1.4 \pm 0.5	1.7 \pm 0.6	3.0 \pm 0.5	4.0 \pm 0.8
21:5n-3	0.9 \pm 0.6	1.8 \pm 0.6	2.2 \pm 0.6	1.6 \pm 0.9
22:4n-6	0.2 \pm 0.5	1.0 \pm 1.6	0.3 \pm 0.6	1.6 \pm 1.7
22:5n-6	7.6 \pm 1.1	10.7 \pm 1.4	7.7 \pm 0.7	9.6 \pm 1.4
22:4n-3	2.3 \pm 0.9	4.2 \pm 1.3	5.1 \pm 0.9	7.2 \pm 1.7
22:5n-3	10.4 \pm 0.9	10.8 \pm 0.6	10.4 \pm 2.4	11.1 \pm 0.7
22:6n-3	33.9 \pm 5.6	38.9 \pm 4.3	23.1 \pm 3.7	26.3 \pm 4.7

1086 Table 2. Number of individuals genotyped (N), number of alleles (N_A), expected heterozygosity
1087 (H_E), observed heterozygosity (H_O), allelic richness (A_R) and private allelic richness (PA_R) within
1088 fatty acid groups identified within a piscivorous morphotype of Lake Trout from Canada's Great
1089 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

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1092 Table 3. Pairwise F_{ST} based on variation at microsatellite loci among Lake Trout morphs from
 1093 Harris et al. (2015) and piscivorous fatty acids dietary groups from Great Bear Lake. Significant
 1094 results are represented as follow: * values are significant at an initial α of 0.05 and ** values are
 1095 significant at an α of 0.02 subsequent False Discovery Rate adjustments for multiple
 1096 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**

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1098 **List of Figures:**

1099 Fig. 1. Example of a piscivorous (64 cm) and a Giant (100 cm standard length) Lake Trout,
1100 respectively, from Great Bear Lake (NT).

1101 Fig. 2. Principal Component Analysis of fatty acids of 79 individual Lake Trout classified as
1102 piscivorous morph from Great Bear Lake, based on the most discriminating 26 fatty acids from
1103 SIMPER analysis, explaining together ~89% of the separation among groups. A) Vectors of
1104 individual fatty acids contributing to the positioning of piscivorous individuals and the convex
1105 hull delimitating group's position are shown. B) Individual Lake Trout are represented as circle
1106 = Group 1, square = Group 2, triangle = Group 3, and diamond = Group 4. To visualize their
1107 variation within and among groups, large symbols were used to depict individuals longer than
1108 900 mm fork length, which were identified as the Giant sub-set in this study. Groups were
1109 defined by FactoMineR using fatty acids and they are outlined by convex hulls.

1110 Fig. 3. Fork length (mm) at age (years) for four piscivorous groups of Lake Trout sampled from
1111 Great Bear Lake in 2002–2015 (Group 1 = squares; Group 2 = circles; Group 3 = triangles;
1112 diamond = Group 4). Large symbols depict Giants (FL > 900 mm) within each group. The von
1113 Bertalanffy length-age model is depicted as a solid line without Giants and a dashed line with
1114 Giants.

1115 Fig. 4. Results of the Bayesian clustering analysis implemented in the program STRUCTURE
1116 (B) and the compoplot of percent membership assignment revealed from the DAPC analysis (B)
1117 for piscivorous Lake Trout from Great Bear Lake. Shown is the admixture coefficient/percent
1118 membership assignment plot where each individual is represented as a vertical line partitioned
1119 into colored segments representative of an individual's fractional membership in any given
1120 cluster (K). The most likely number of genetic clusters was two in both the STRUCTURE

1121 analysis (based on $\ln P[D]$ and the ΔK statistic of Evanno et al. (2005)) and DAPC analysis (
1122 based on the lowest BIC score and with 30 PCs retained.

1123 Fig. 5. Canonical Variate Analyses (95% ellipses) and Principal Component Analysis of body
1124 shape (a, d), head shape (b, e) and linear measurements (c, f), respectively, of piscivorous Lake
1125 Trout represented as: square = Group 1, circle = Group 2, triangle = Group 3, and diamond =
1126 Group 4. The first two PCA axes explained 44.3% and 12.3 % of variation for body shape,
1127 35.1% and 30.7 % of variation for head shape, and 39.6 % and 20.9 % for linear measurements
1128 (Fig. 6 d, e, f). To visualize their variation within and among groups, larger symbols were used to
1129 depict individuals longer than 900 mm FL, which are considered the Giant sub-set in this study.

1130 Fig. 6. Residuals of mean (\pm 95%CI) size-standardized upper and lower jaw lengths, head depth
1131 and length, and snout-eye length among piscivorous Lake Trout groups. Grouping symbols are
1132 as follow: square = Group 1, circle = Group 2, triangle = Group 3, and diamond = Group 4.

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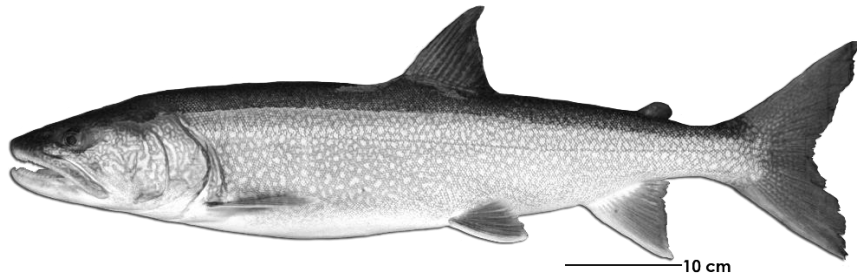
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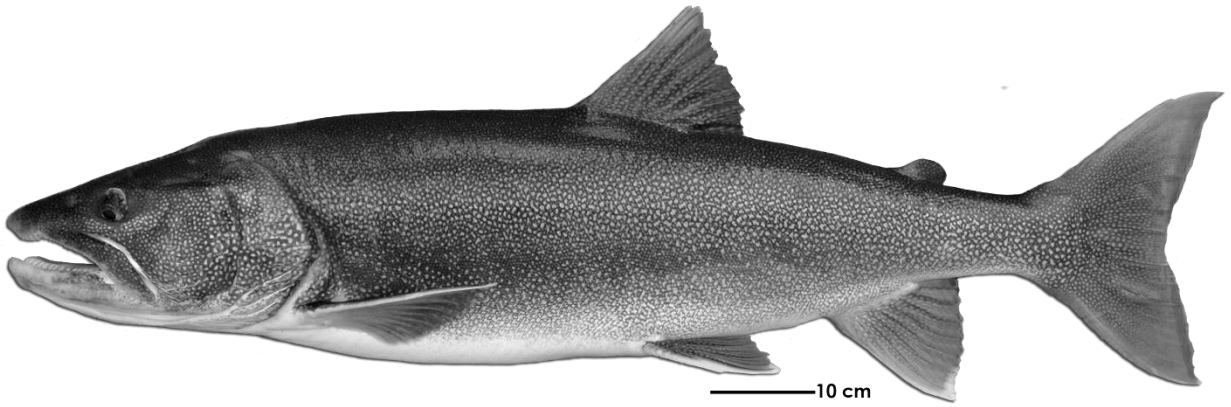
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1145 Fig. 1.

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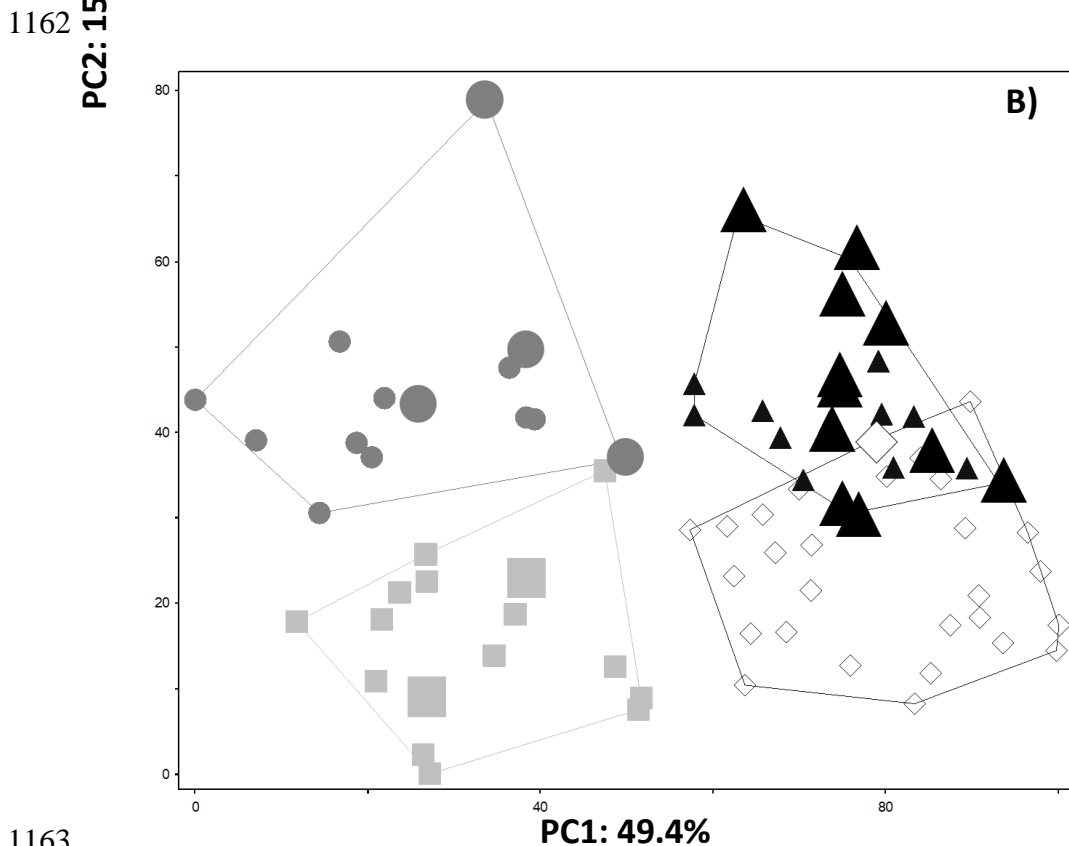
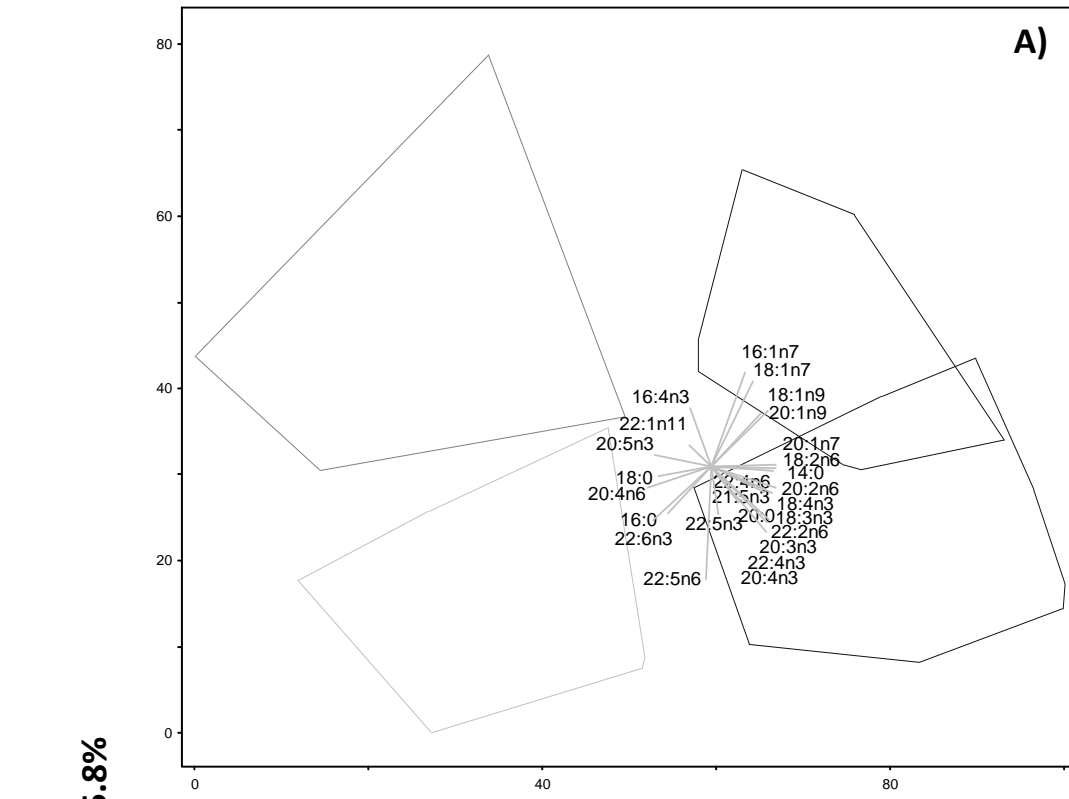
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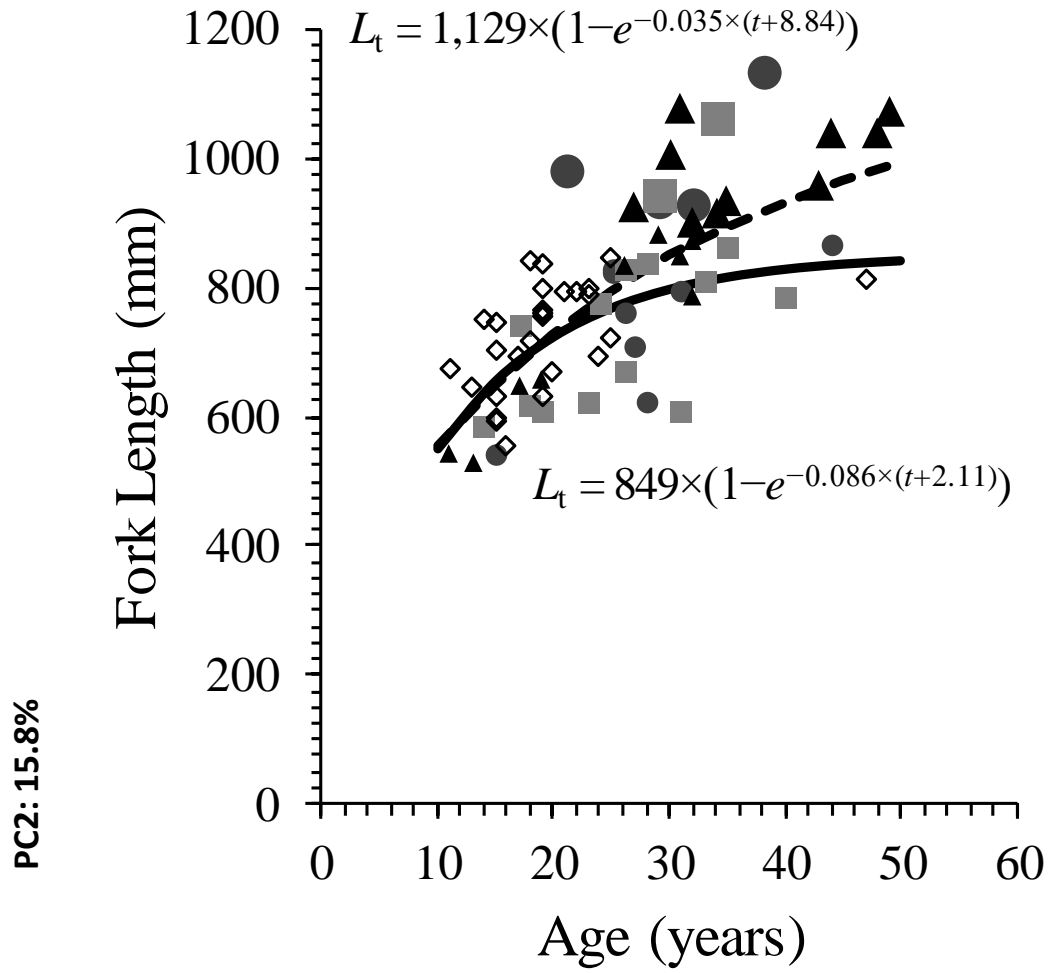
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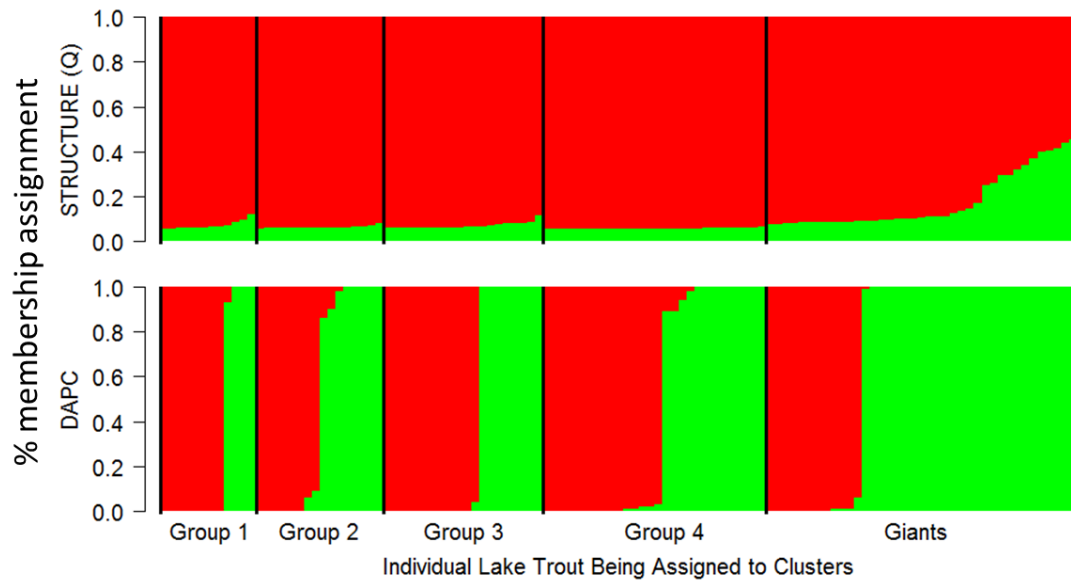
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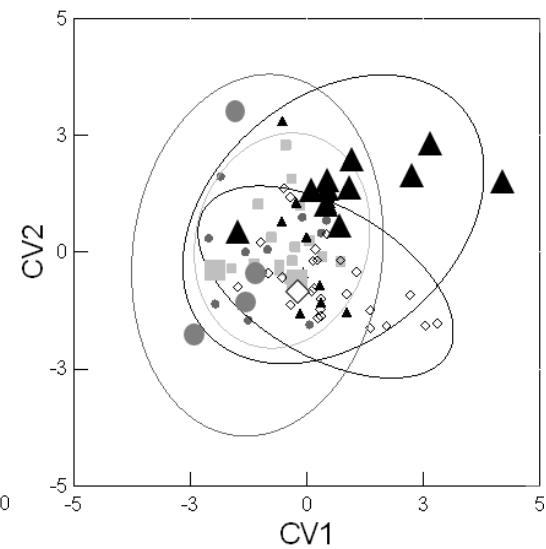
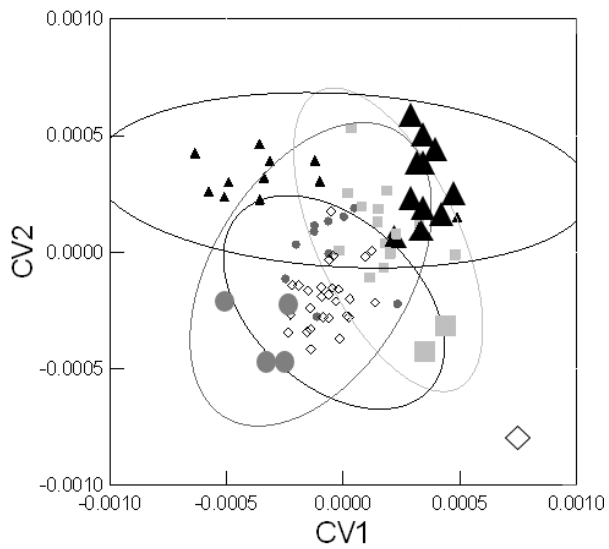
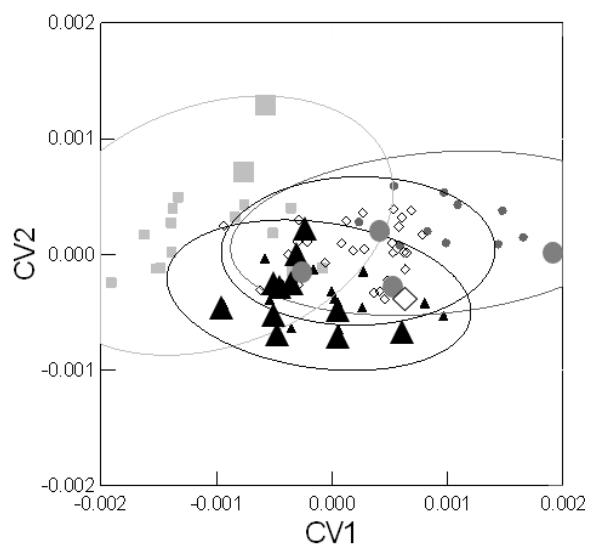
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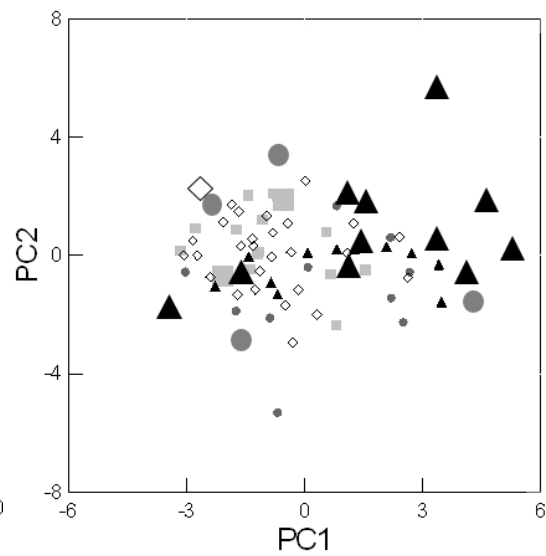
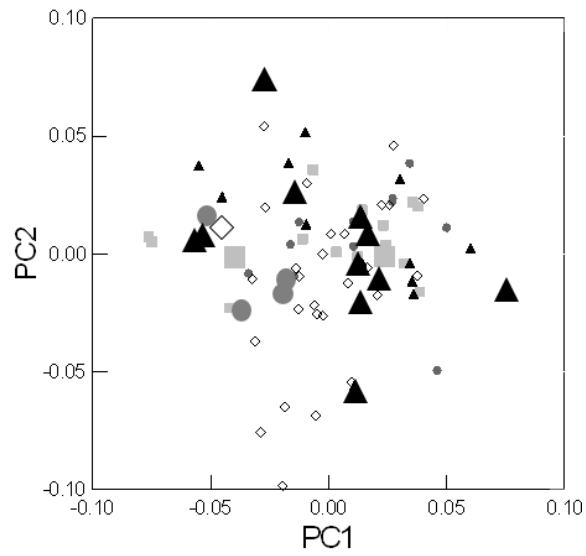
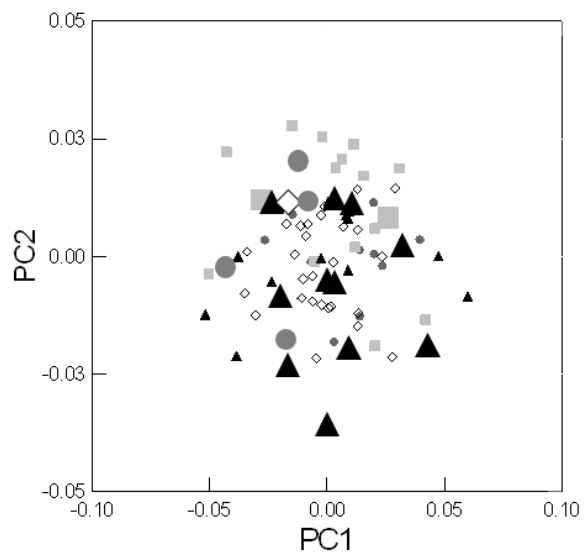
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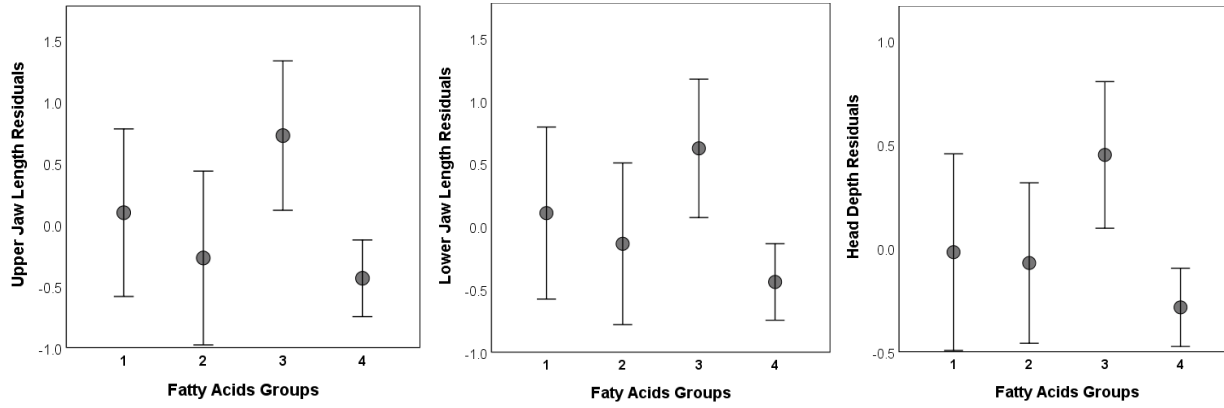


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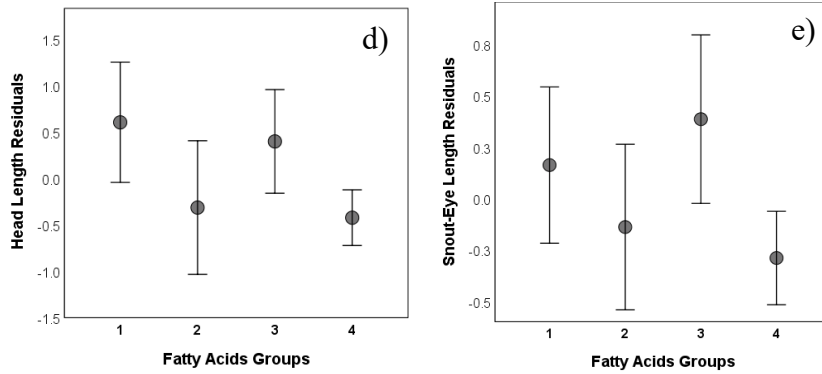


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1189 Fig. 5



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1192 Fig. 6

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1192 **Appendix:**

1193 Table A1. Spatial and temporal information for the 79 Lake Trout classified as piscivorous
 1194 morph from Great Bear Lake and analyzed for fatty acids. Sample sizes are in brackets.

Sample information

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

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1200 Table A2. Bayesian clustering (i.e., STRUCTURE, Pritchard et al. 2000) results for piscivorous
 1201 morphotypes of lake trout from Great Bear Lake assessed using variation at 19 microsatellite
 1202 markers. Shown are the mean log-likelihood values (LnP[D]) for different hypothesized

1203 numbers of genetic populations (K) and the mean value of ΔK statistic of Evanno et al. (2005).
1204 Bold values represent the most likely number of genetic groups indicated by ΔK . Dashes = not
1205 applicable given that ΔK cannot be calculated for these values of K. For all STRUCTURE
1206 analyses, we employed an admixture model with the LOCPRIOR algorithm, correlated allelic
1207 frequencies, 100,000 burn-in and MCMC iterations and 10 iterations per K value were
1208 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	—

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1226 Table A3. Results of the discriminant analysis of principal components (DAPC, Jombart et al.
1227 2010) implemented in the Adegenet package (Jombart et al. 2008) to determine the most likely

1228 number of genetic clusters (K) within the piscivorous Lake Trout form Great Bear Lake. The
1229 number of groups was identified using the `find.clusters` function (a sequential K-means
1230 clustering algorithm) and subsequent Bayesian Information Criterion (BIC), as suggested by
1231 Jombart et al. (2010). Stratified cross-validation carried out with the function `xvalDapc` was
1232 employed to determine the optimal number of PCs to retain in the analysis.
1233

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

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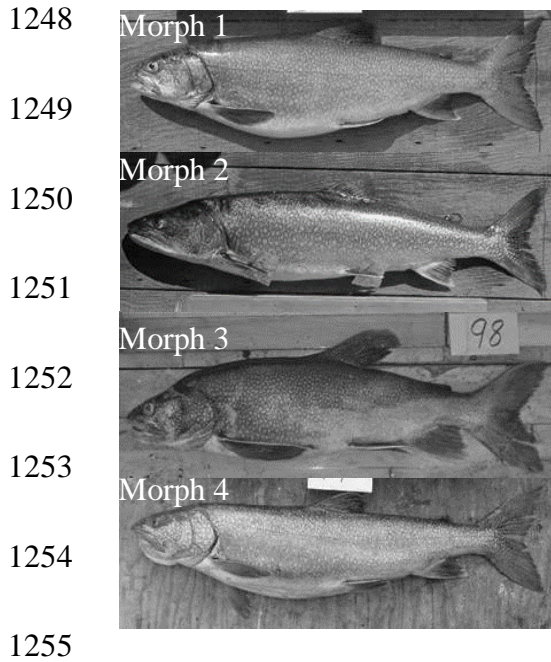
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1246 Table A4. Microsatellite loci used in this study and F_{is} values for each group per locus.

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



1256 Fig. A1. The four shallow-water morphotypes of Lake Trout from Great Bear Lake identified in
1257 Chavarie et al. (2013, 2015, 2016a, 2016b): the generalist, the piscivore, the benthic-oriented,
1258 and the pelagic specialist, Morphs1-4, respectively.

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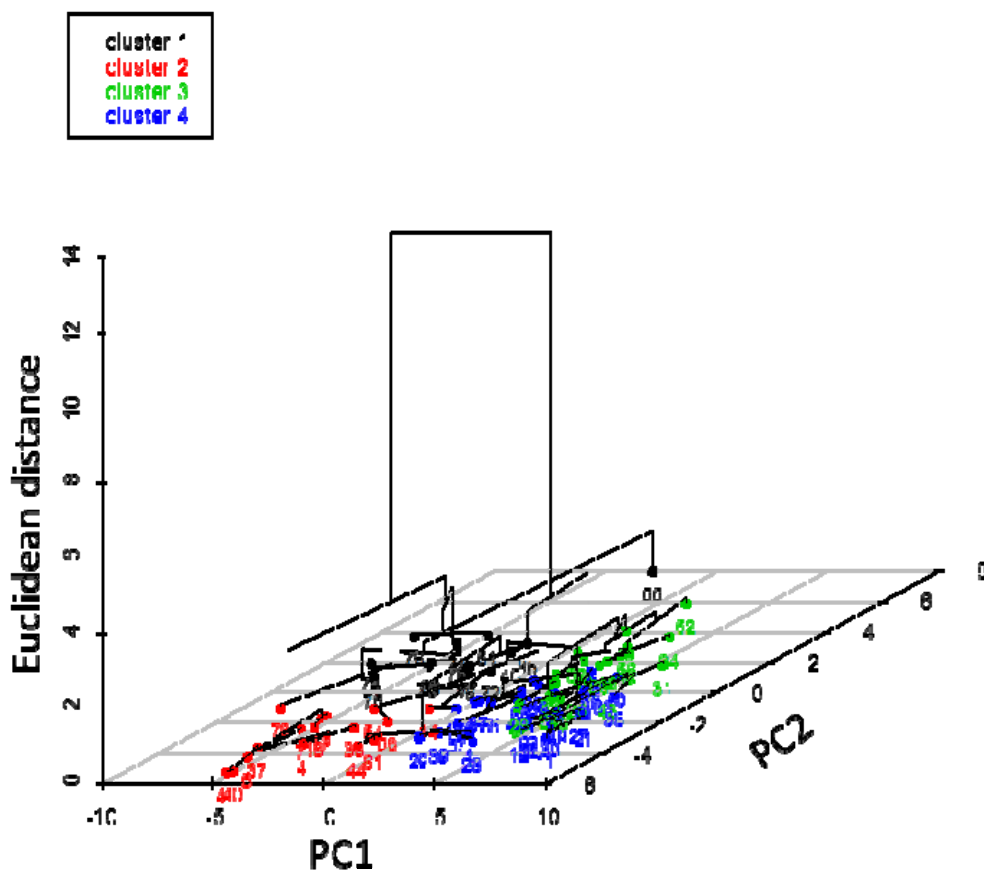
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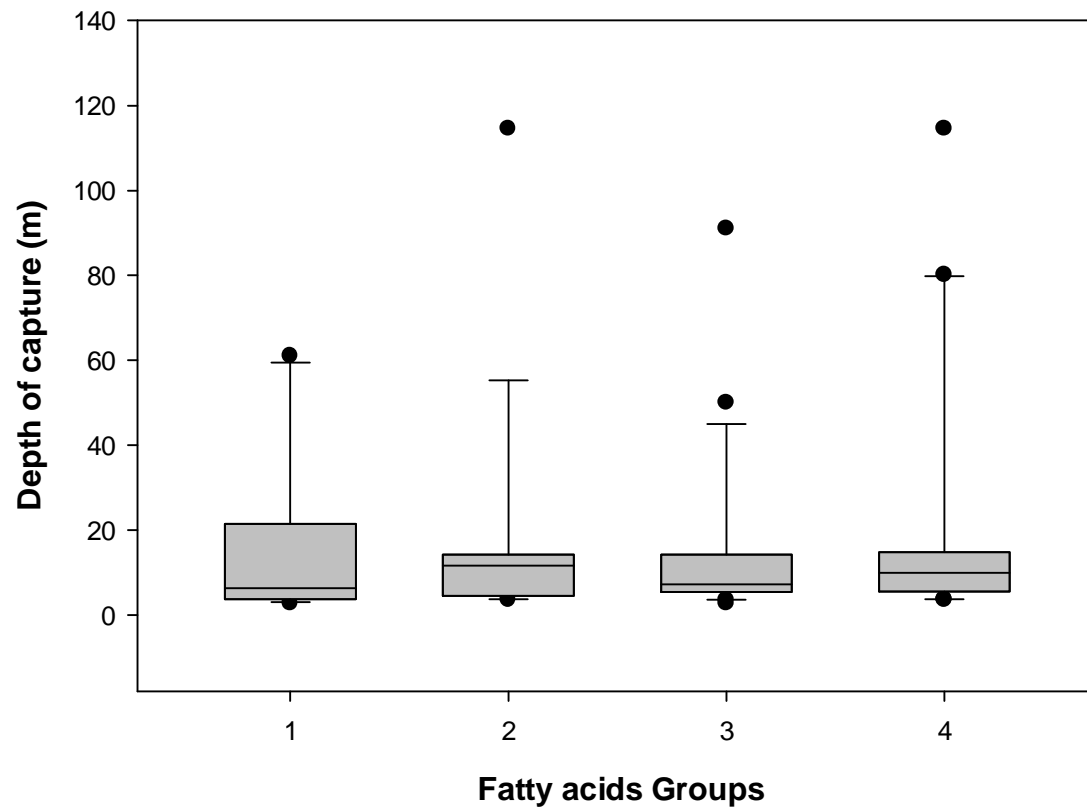
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Hierarchical clustering on the factor map



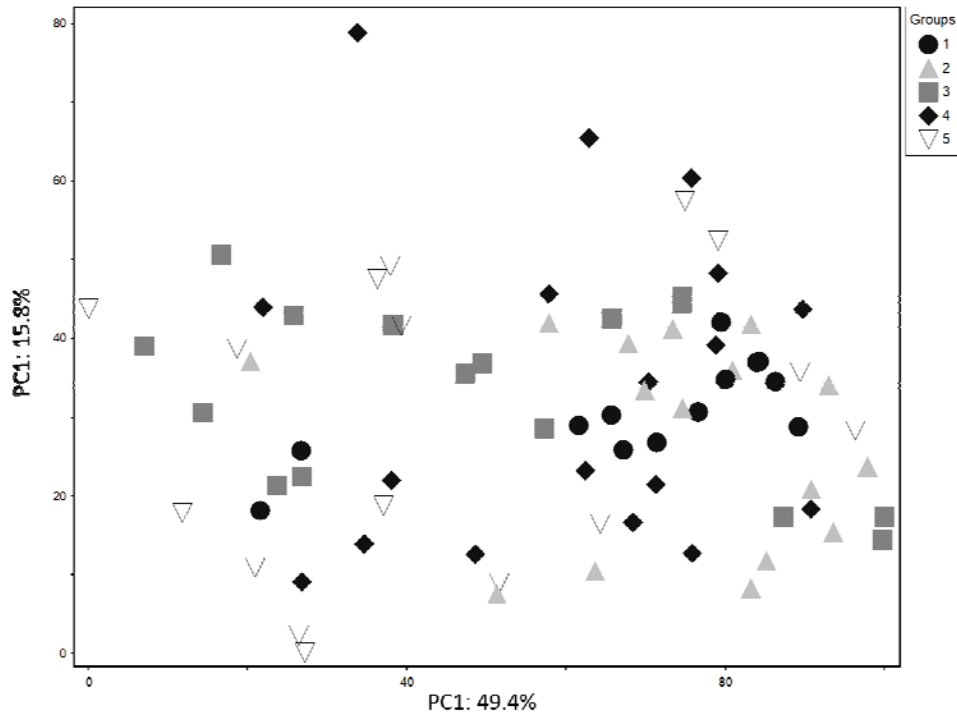
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Fig. A2. Hierarchical clusters of Great Bear Lake Lake Trout fatty acids profiles overlaid on the first two principal component axes (PCA) using FactoMineR.

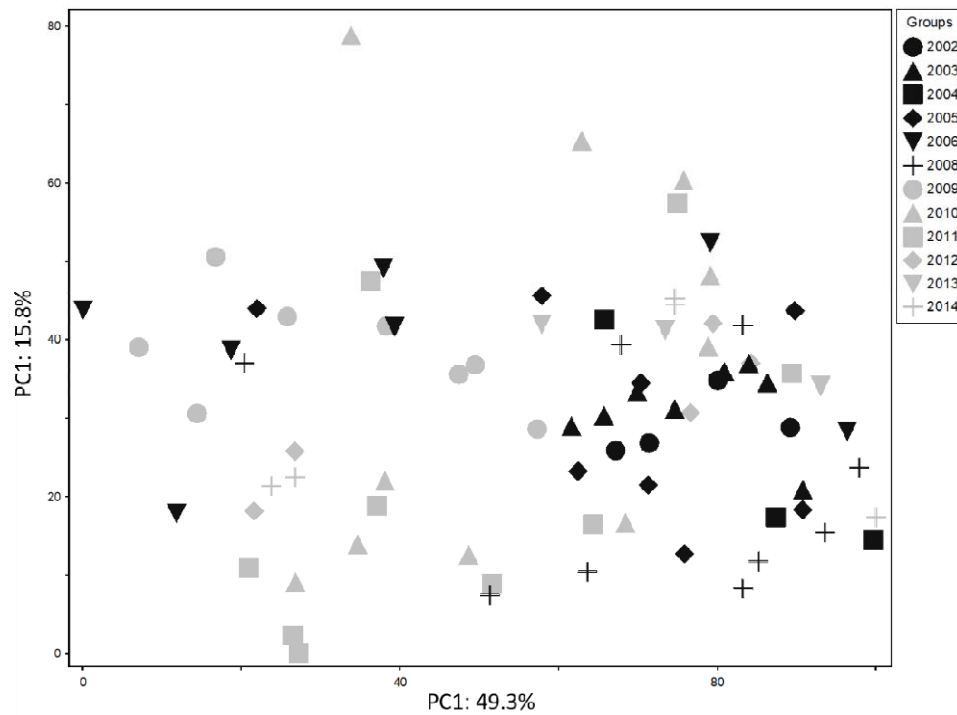


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Fig. A3. Depth of capture for four groups of piscivorous Lake Trout from Great Bear Lake (Groups identified by fatty acids profiles of individuals). Outliers are represented by a circle.



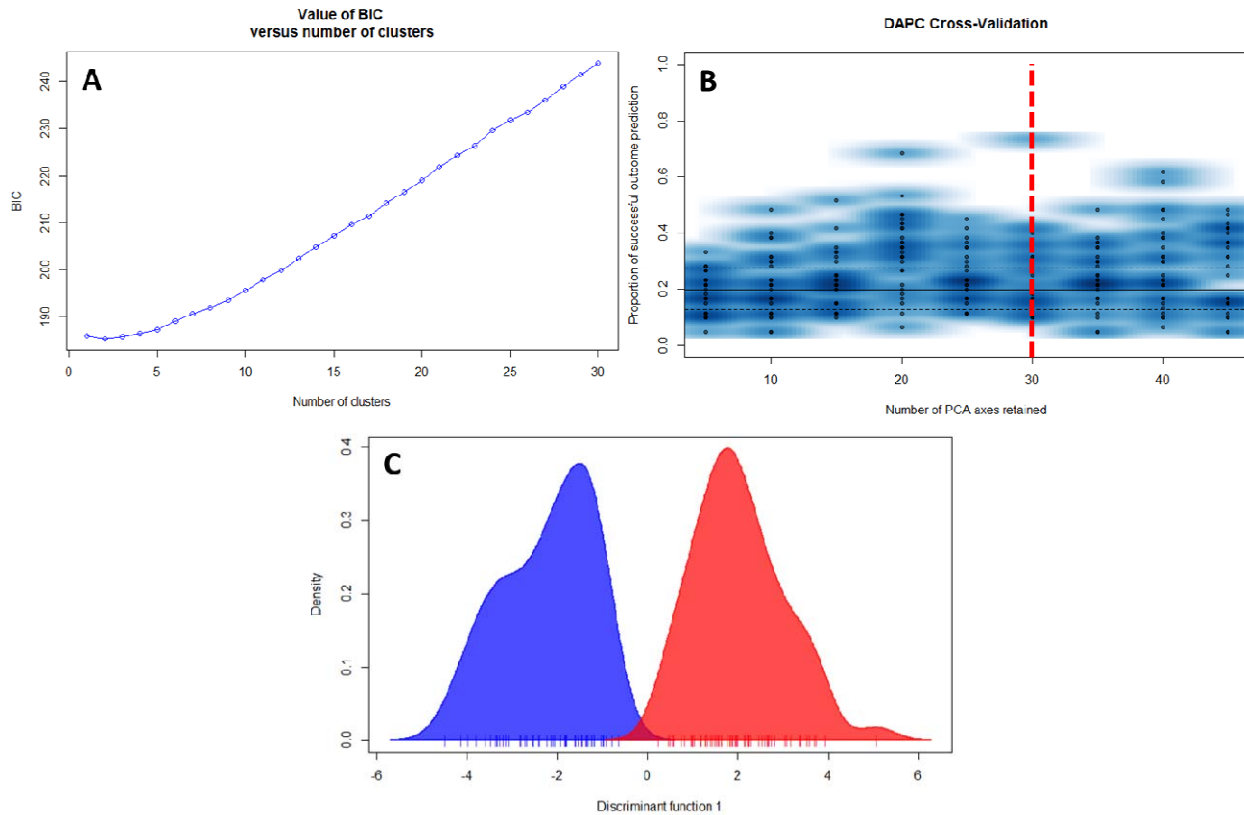
1299 a)



1300 b)

1301 Fig. A4. Principal Component Analysis (PCA) of fatty acids of 79 Lake Trout classified as
1302 piscivorous morph from Great Bear Lake, based on the proportions of 41 fatty acids in dorsal
1303 muscle tissue. Spatial variations (5 arms; 1=Keith, 2=McVicar, 3=McTavish, 4=Dease, and
1304 5=Smith) are represented in a) and temporal (12 years) variations are represented in b), based on
1305 the fatty acids profile of each lake trout analyzed in this study.

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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.