The biology and ecology of polymorphic Lake Trout, *Salvelinus namaycush*, in Great Bear Lake, Northwest Territories.

by

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Abstract

Post-glacial lakes, a common feature in northern landscapes, provide favorable ecosystems for studying intra-specific diversity in fishes. Great Bear Lake, with its large size and virtually pristine, recently colonized cold water habitats, provides unique opportunities for Lake Trout (*Salvelinus namaycush*) diversification. This thesis presents a new case of exceptional intraspecific diversity of Lake Trout in Great Bear Lake, featuring four co-existing shallow-water morphotypes. In chapter 2, I combined classical morphometric/meristic measures with shape analysis (geometric morphometrics) to quantify morphological differences among adult and juvenile shallow-water Lake Trout. Head and fin measurements best discriminated the adult morphotypes whereas little differentiation was found in body shape. No consistent patterns of variation were found among juveniles, suggesting that divergence develops at a later stage.

The lack of body shape variation among morphs combined with the size the lake, led me to investigate geographic-based morphological patterns within the five arms of Great Bear Lake in Chapter 3. Within each of the three more common morphotypes, morphological measures, particurlaly body shape differences, were found to vary among lake arms. Genetic and morphological distance matrices were also compared to investigate potential parallel patterns, and suggested observed morphological variation is a phenotypically plastic response to distinct environments.

In Chapter 4, I analyzed stomach contents and fatty acids to investigate diet partitioning among the four sympatric shallow-water morphs of Lake Trout as a potential explanatory mechanism for diversification since trophic polymorphism is common among post-glacial fishes. Results suggested that polymorphism in the Lake Trout of Great Bear Lake is partially maintained by diet differences and by some habitat partitioning, but some overlap and seasonality in resource use were also found among morphs in this northern lake.

Finally, in Chapter 5, I investigated potential variation in life history traits among the four morphotypes, a commonly observed response to inhabiting different freshwater habitats and exploiting different resources. Growth rate, age-at-maturity, size-at-maturity, and survival differed among morphs, representing trade-offs between reproduction and somatic growth. However, unexpected results, such as high proportions of resting individuals, early maturation of Morph 2 (piscivorous form), and a lack of variation in fecundity, were also found, some of which reflect the complexity of making predictions in any specific case.

Great Bear Lake is a distinctive case that will be used as a benchmark for intraspecific diversity in Lake Trout, and for sympatric polymorphism and parallel adaptive radiation more generally. With its exceptional diversity and pristine environment exempt from problems that typically confound investigations (e.g., declines in fish diversity and anthropogenic impacts), Great Bear Lake provides a reference against which to compare other lakes, such as the Laurentian Great Lakes. This thesis addressed some key concepts (e.g., mode of diversification, ecological relationships) related to phenotypic diversity in northern Lake Trout and the extent of their polymorphism that can occur in large northern Canadian lakes. However, several gaps in our knowledge, e.g. the mechanism(s) of intraspecific diversity and its geographic context, remain in understanding polymorphism.

Preface

Some of the research conducted for this thesis forms part of an international research collaboration, led by Kimberly Howland at the Department of Fisheries and Ocean, with Professor William Tonn being the lead collaborator at the University of Alberta. The data analysis in chapter 3, 4, and 5, are my original work, as well as the literature review in chapter 1 and 6. Contribution to laboratory work and analysis in chapter 3 was done by Les Harris. Contribution to laboratory work in chapter 4 was done by Collin Gallagher. Contribution to analysis in chapter 5 was done by Assistant Professor Paul Venturelli and Benjamin Kissinger.

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Chapter 1: General Introduction

Ecology has always been considered integral to the processes of intraspecific divergence and speciation (Orr and Smith, 1998) and, despite on-going research ever since Darwin inaugurated the study of speciation, two important themes remain today: the mechanism(s) of speciation and its geographic context (Hendry *et al*., 2009). New cases of intraspecific diversity, which may be at the initial stages of speciation (Bush, 1994; Skúlason and Smith, 1995), provide opportunities to examine one or both of these fundamental topics to improve current knowledge.

Northern freshwater fauna have interesting ecological and evolutionary characteristics, including substantial diversification even within individual lakes (e.g., MacDonald *et al*., 2005). Northern freshwater fishes, in particular, have been productive for studying the origin of intraspecific diversity and divergence (McPhee *et al*., 2012). Circumpolar areas, including Canada, are characterized by recently glaciated areas (10 000-15 000 years ago), thus, the extant freshwater fish fauna has developed entirely by recent and on-going recolonization from non-glaciated refugia. The resulting depauperate postglacial systems are characterized by open niches and a relaxation of interspecific competition, conditions that favour the development of sympatric polymorphism (Smith and Skulason 1996). New northern examples of intraspecific diversity are being reported because of increased sampling effort, often related to resource development, and the associated increases in monitoring and assessment of ecosystems.

In general, northern freshwater fishes from postglacial environments show a greater degree of phenotypic variability than genetic diveristy (Bernatchez and Wilson, 1998). Nevertheless, sympatric polymorphism in fish can involve morphological divergence dramatic enough to result in misidentification as distinct species (Skulason and Smith, 1995). The most common cases of intraspecific divergence observed within lacustrine environments are linked with their predictably discrete habitats, i.e., littoral (benthic) vs. limnetic (pelagic) regions. In addition, significant differences associated with diet, life-history (e.g., growth, age-at-maturity) and/or behaviour have also been demonstrated (Schluter and McPhail, 1992).

Modes of resource polymorphism other than benthic-pelagic divergence are also possible in post-glacial fishes although they are not as frequent. For example, although depth partioning is typically the main driver of segregation between shallow and deep-water morphs of Lake Trout (*Salvelinus namaycush*), studies identified intraspecific diversity within the shallow-water regions of Great Bear Lake. Blackie et al. (2003) and Alfonso (2004) both identified "insectivore-like" and a "piscivore-like" morph co-existing in Great Bear Lake. However, their morphological analyses were limited and little information on other aspects of ecology were presented. Morevoer, Howland et al. (2008) suggested that the intraspecific diversity of Lake Trout in Great Bear Lake may have been underestimated with only the two previously described morphs. This system can thus offer new perspectives on the current models of polymorphism for northern fishes generally and within Lake Trout specifically.

From these unique observations of intraspecific diversity within Great Bear Lake and limited information from other northern lakes, many questions can be generated regarding the evolution of these sympatric forms of Lake Trout with respect to their morphology, feeding ecology, life-history, and behaviour. To address some of these questions, I conducted an extensive and detailed study of Lake Trout polymorphism in Great Bear Lake (2008-2013) in collaboration with Fisheries and Oceans Canada (DFO) and Sahtu Renewable Resource Board. This multi-year study involved the collection of data from each of the five arms of Great Bear

Lake, but was further complemented by existing data that had been collected by DFO since 2002. Data were collected in shallow-water habitat that had depths equal or less than 30 m where productivity is higher, and from a baseline (<50 m) established from previous Lake Trout studies (Johnson, 1975; Zimmerman *et al*., 2006, 2007, and 2009).

To begin the study, I combined classical morphometric and meristic measures with shape analysis (geometric morphometrics) to quantify lake-wide morphological differences among shallow-water Lake Trout from Great Bear Lake in Chapter 2. In Chapter 3, I further compared inter-arm morphological differentiation within Lake Trout morphs to provide insights into the relative importance of spatial and ecological factors in intraspecific diversity. Genetic and morphological distance matrices were compared among morphotypes to assess associations in the inter-arm variation patterns among morphotypes. In Chapter 4, I used stomach contents and fatty acids analysis to investigate diet partitioning, among the four sympatric shallow-water morphs of Lake Trout as a potential explanatory mechanism for diversification because trophic polymorphism is common among post-glacial fishes (Skúlason and Smith, 1995; Smith and Skúlason, 1996). The complementary methods proved valuable for elucidating the prey of this opportunistic feeder, given the diverse and variable diet of Lake Trout in Great Bear Lake. Finally, in Chapter 5, I compared life-histories of divergent morphotypes to further assess the implications of this diversity on traits of Lake Trout in this system. Age, back-calculated growth, length, weight, maturity, and reproductive output were used to compare length-age and weight-length relationships, age frequency, size- and age-at-maturation, egg diameter and total fecundity among morphotypes.

Currently, few of the measures developed to assess biodiversity of a community include intraspecific components but these elements are becoming essential in evaluating diversity in ecology (Pavoine and Izsák, 2014). Through intraspecific variation, one species can significantly contribute to the biodiversity of a system (Faith, 1994; Pavoine and Izsák, 2014), especially in nominally depauperate environments. Moreover, intraspecific functional diversity has been associated with ecosystem resilience to habitat modifications, including short-term disturbances and long-term human-driven changes (Whitman et al. 2003; Pachepsky et al. 2007).

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Chapter 2: Sympatric polymorphism in Lake Trout: The coexistence of multiple shallow-water morphotypes in Great Bear Lake.

Abstract

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

Introduction

The circumpolar north is characterized by recently de-glaciated areas (8 000-12 000 ybp), with correspondingly young aquatic ecosystems. Thus, the extant freshwater fish fauna has developed through relatively recent and on-going recolonization from non-glaciated refugia. The resulting postglacial systems are depauperate and characterized by open niches and a relaxation of interspecific competition or predation, conditions that favour the development of intraspecific sympatric polymorphism (Smith and Skulason 1996). Salmonids commonly show evidence of sympatric polymorphism promoted by the ecological opportunities found in these northern areas (Robinson and Wilson 1994). Although morphological variation can sometimes be subtle, on other occasions, differences are dramatic enough to have caused misidentification of morphs as distinct species, e.g., Arctic char, *Salvelinus alpinus*, where phenotypes vary considerably within and across localities, a situation known as the ”char problem” (Nordeng 1983; Skulason and Smith 1995; Jonsson and Jonsson 2001). Typically, cases of sympatric polymorphism involve a resource-based variation in a fish population, where significant differences in morphology, life-history, and behaviour are associated with differences in diet and habitat use (Schluter and McPhail 1992).

Lake Trout, *Salvelinus namaycush*, is a cold-stenothermic freshwater salmonid that is widely distributed in previously glaciated regions of North America. Lake trout was thought to be relatively stable morphologically (Benhke 1972; Eshenroder 2008), especially compared to other Salmonidae, such as Arctic char (e.g., Jonsson and Skulason 2000) and whitefishes, *Coregonus spp*. (e.g., Kahilainen and Ostbye 2006). An important exception to the morphological stability of Lake Trout has been depth-related diversification in Lake Superior

(Moore and Bronte 2001), with the siscowet and the humper recognized as the two principal forms inhabiting deeper waters, and the lean (piscivore) occupying shallow-water habitats (Eshenroder 2008). The availability of an open deep-water niche associated with emerging trophic differences may have provided the selection pressure contributing to phenotypic diversification (Henderson and Anderson 2002; Zimmerman et al. 2006; Eshenroder 2008). Unfortunately, additional diversity in Lake Trout may have declined or disappeared from the highly impacted Laurentian Great Lakes (Brown et al. 1981; Goodier 1981), which has limited investigations of Lake Trout intraspecific variation in this system (Eschenroder 2008; but see Bronte and Moore 2007).

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

A recent report proposing up to four forms of Lake Trout co-occur in shallow-water habitats (≤ 30 m) of Great Bear Lake (Howland et al., 2008) suggests this is an exceptional system in which to investigate Lake Trout diversification, independent of depth-based segregation, in a large, pristine northern lake. Our aim in the present study is to describe the morphological diversity of Lake Trout found in shallow (≤ 30m) waters of Great Bear Lake. Specifically, our objectives were to (1) determine how many distinct shallow-water morphs exist,

(2) quantitatively summarize the morphological variation among these shallow-water morphs using a combination of morphometric and traditional linear measures, and (3) determine if differences among morphs are equally strong in juveniles versus adults.

Study site

Great Bear Lake is located in the northeast portion of the Northwest Territories, between 65° and 67° N latitude, 250 km south of the Arctic Ocean. With a surface area of 31 790 km^2, Great Bear Lake is the 4th largest surface area lake in North America; together with a maximum depth of 450 m, it is truly one of the Great Lakes of North America (Evans 2000). The lake has characteristics typical of an arctic lake: it is ultra-oligotrophic, remains mostly isothermal during summer, and has a simple food web, e.g., despite its size, it supports only 15 fish species (Johnson 1975; Alfonso 2004; MacDonald et al. 2004). Adjacent terrestrial areas of Great Bear Lake include the southern Arctic ecozone to the north, the taiga plains to the west and south, and the taiga shield to the east (MacDonald et al. 2004). Great Bear Lake lacks a commercial fishery but plays an important role in the local economy, supporting both a fly-in sport fishery and a subsistence fishery for the small community of Déline.

Material and methods

Data collection

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

Morphology

We used the digital images to quantify morphological characteristics, employing a combination of traditional and geometric morphometrics (Zelditch et al. 2004). Twenty three landmarks (pre-determined homologous points) were selected to measure body shape (Fig. 2-1.) and twelve linear measurements (Fig. 2-2.) were selected based on their relationship to foraging (e.g., jaw size) and swimming (e.g., fin lengths and caudal peduncle depth; Webb 1984; Kristjansson et al. 2002; Kahilainen et al. 2004). Landmarks used in this study were comparable to those used previously for Lake Trout (e.g., Zimmerman et al. 2006, 2007, 2009). We also used 20 semi-landmarks (Fig. 2-3.) to measure important variation in head shape that was not well captured by landmarks. Semi-landmarks are non-homologous points that can be used to capture and analyze shape information on curved areas of a body lacking distinct landmarks (Green 1996; Bookstein 1997; Zelditch et al. 2004).

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

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

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

Results

Approximately 200 Lake Trout were sampled per year (3 year totals: 558 adults and 55 juveniles) for analysis. For adults, three major groups were identified with the UPGMA cluster analyses (Fig. 2-4.), referred to here as Group 1 (n=175), Group 2 (n=267), and Group 3 (n=94). Discriminant analysis showed that the three groups differed significantly despite some observed overlap (λ=0.16, N=555, $p \leq 0.01$). Group 1, Group 2, and Group 3 were classified correctly 90%, 93%, and 88% of the time, respectively, with the jackknife procedure. Groups were better distinguished by traditional measurements and head shape (Fig. 2-5a.); separation by body shape was not apparent (Fig. 2-6a.). Based on the PCA, adult members of Group 2 had bigger heads (quantified as longer head lengths, longer snout-eye lengths, and longer upper and lower jaws), which contrasted with Group 1 (smaller heads and jaws). Group 3 was distinguished by longer fins (pectoral, dorsal, caudal, anal, and pelvic) and caudal peduncle depths, in contrast to Group 2 (smaller fins and caudal peduncle depths). Least square means and their standard errors for a given standardized body size of 62.2 cm for head and fin measurements among morphotypes also showed clear distinctions (Table 2-1).

A fourth morph (n=22), although visually distinct due to a curved-arched lower jaw (Fig. 2-7.), was not classified as a distinct cluster in the UPGMA analysis. However, some traits (head depth and length of caudal fin) of this morph (Group 4) differed significantly from Groups 1-3 (Table 2-1), while the remaining traits formed a unique combination, relative to Groups 1-3. For the juvenile UPGMA, the three cluster level was not particularly successful in identifying distinct morphological groups, because two of the three groups were rare ($N < 5$), leaving most fish together in the same large cluster. Although discriminant analysis suggested that the groups were distinct (λ=0.14, N=55, $p < 0.01$), Jackknife cross-classification rates were lower for the two rare groups (73% and 0% classification success). In addition, no clear discrimination of the three groups could be made in either of the PCAs, using traditional measurements and head shape (Fig. 2-5b.), or body shape (Fig. 2-6b.).

Discussion

Based on an analysis of >600 fish from the shallow-water habitat of Great Bear Lake, our study demonstrated that there are at least three and possibly four morphologically distinct groups of Lake Trout. These findings expand and quantify this singular, contemporary case of Lake Trout polymorphism within shallow-water habitat (Blackie et al. 2003; Alfonso 2004; but see Brown et al. (1981) and Goodier (1981) for qualitative descriptions of historical stocks or “breeds” of shallow-water trout recalled by old-time commercial fishers from Lakes Michigan and Superior). Our study thus extends our knowledge of Lake Trout diversification, generally associated with depth (Moore and Bronte 2001; Zimmerman et al. 2007; Eschenroder 2008). Great Bear Lake remains isothermal throughout the open-water season, which may provide a variety of cold shallow-water habitats. Furthermore, the lake has a depauperate fish fauna, which may result in low interspecific competition. Consequently, Great Bear Lake likely provides different resource opportunities to Lake Trout within a narrow range of depths (MacDonald et al. 2004; Alfonso 2004). Interestingly, the different forms in our study were usually found mixed together in the same net catches.

Head and fin measurements of Lake Trout differed among the groups more than body shape. Previous studies of sympatric Lake Trout morphotypes, although usually based on limited sampling (n=72-99 fish), have generally shown that head and fin measurements better reflect differences in diet, with which these morphotypes are linked or inferred, than does body shape (Blackie et al. 2003; Alfonso 2004; Zimmerman et al. 2006, 2007). Body shape differences in this context are thought more to reflect adaptations to buoyancy, which is related to depth distribution and vertical migration (including feeding on vertically migrating prey) (Eshenroder

2008; Zimmerman et al. 2006, 2007, 2009). Because we focused on shallow-water morphotypes, it is perhaps not surprising that we observed a reduced importance of body shape.

Differences in the relative importance of head shape and fin measurements versus overall body shape have also been found in other fishes (e.g., Fryer and Iles, 1972; Maderbacher et al. 2007). Populations evolve in ways that allow better exploitation of their resources (Smith and Skulason 1996), and morphological differentiation in several fishes has been related to differences in feeding-related traits and swimming ability (Bouton et al. 2002; Kristjansson et al. 2002; Kahilainen et al. 2004). The stronger discrimination of head and fin measurements versus body shape we observed may reflect the way(s) in which selection favored the development of different shallow-water morphs (e.g., Susnik et al. 2006). In contrast, body shape differentiation might become more important where depth segregation among morphs is involved.

Morphological properties can suggest the ecological role of a fish in its community and thus provide the basis for niche predictions (Bronte et al. 1999). In general, head characteristics (i.e., shape and dimension) have been linked to foraging efficiency associated with particular prey and/or environments (e.g., Jonsson and Jonsson 2001; Adams et al. 2003). More specifically, diversification of fish via trophic specialization tends to reveal itself through differences in the trophic apparatus, particularly the mouth, which has direct contact with prey and/or substrate (Barlow and Munsey, 1976; Maderbacher et al. 2007). In our study, for example, Group 2 individuals were characterized by longer heads and longer jaws relative to Group 1, corresponding, respectively, to previously described piscivorous and insectivorous morphs in other Salmonidae (e.g., Proulx and Magnan 2004; Keeley et al. 2005, 2007; Janhunen et al. 2009).

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

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

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

Possible scenarios to explain the different degrees of morphological varition between adults and juveniles include phenotpically plastic responses observed in adults, a genetic variation expressing phenotypic differences only in adults and/or differences in juvenile vs. adult ecologies. The expression of morphological differences that parallels an ontogenic niche shift is common in arctic *Salvelinus* (Jonsson and Jonsson 2001). For example, the development of an individual Arctic char into a one specific morph or another may be a conditional strategy influenced by the growth of an individual at a specific development stage (Reist et al. 2012).

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

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

Morphological variation within a species has generally been associated with variation in life-history (Nordeng, 1983; Jonsson and Jonsson 2001), and life-history diversity has already been suggested for Lake Trout in Great Bear Lake (Blackie et al. 2003; Alfonso 2004). Life-history data are critical to the development of sustainable management strategies, and thus are essential for the maintenance of Lake Trout diversity in Great Bear Lake. Blackie et al. (2003), for example, suggested growth-rate differences between insectivorous and piscivorous morphs, which could lead to differential harvest rates in the Great Bear Lake fisheries and ultimately have important consequences for maintenance of the observed intraspecific variation (Moles et al. 2010). Life-history diversity should also increase stability and resistance of the ecosystem to perturbation, especially from anthropogenic impacts, such as climate change, that are increasing in northern aquatic systems (Reist et al. 2012). Further investigation of life-history diversity in Lake Trout from Great Bear Lake is needed both to better understand the origin and maintenance of this diversity of forms and to improve management of this exceptional example of arctic biodiversity.

Conclusion

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

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

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Table 2-1. Comparison of Least-Squared (LS) means of traditional morphological measurements for a standardized size (62.2 cm) of adult Lake Trout Groups 1-4 from Great Bear Lake. LS means ± 1 SE were calculated in a general linear model. Also, a comparison of traditional and geometric morphometric measurements based on MANOVA; Tukey HSD *post hoc* test results are represented in parentheses. Groups with the same upper case letter are not significantly different ($P > 0.05$).

Traits	**LS means ± 1 SE (Tukey HSD results)**				
	Group 1	**Group 2**	**Group 3**	**Group 4**	**P-value**
Upper jaw	6.61 ± 0.05 (A)	7.88 ± 0.04 (B)	7.65 ± 0.06 (C)	7.90 ± 0.14 (B)	≤ 0.01
Lower jaw	6.57 ± 0.05 (A)	7.83 ± 0.04 (B)	7.38 ± 0.06 (C)	7.15 ± 0.14 (C)	≤ 0.01
Head Depth	7.08 ±0.04 (A)	7.59 ± 0.03 (B)	7.91 ± 0.05 (C)	8.19 ± 0.10 (D)	≤ 0.01
Head Length	11.92 ± 0.06 (A)	13.15 ± 0.05 (B)	13.27 ± 0.08 (AB)	13.61 ± 0.18 (AB)	0.01
Snout-Eye	4.53 ± 0.04 (A)	5.42 ± 0.03 (B)	5.39 ± 0.05 (B)	5.63 ± 0.11 (B)	≤ 0.01
Dorsal Fin	9.31 ± 0.07 (A)	8.69 ± 0.06 (B)	10.76 ± 0.10 (C)	8.97 ± 0.21(AB)	≤ 0.01
Caudal Fin	10.67 ± 0.07 (A)	10.80 ± 0.06 (A)	12.27 ± 0.10 (B)	11.57 ± 0.21 (C)	≤ 0.01
Caudal Depth	6.55 ± 0.04 (A)	6.31 ± 0.03 (B)	6.86 ± 0.05 (C)	6.63 ± 0.10 (AC)	≤ 0.01
Anal Fin	8.94 ± 0.06 (A)	8.60 ± 0.05 (B)	10.37 ± 0.08 (C)	9.13 ± 0.17 (A)	≤ 0.01
Pelvic Fin	8.01 ± 0.06 (A)	7.73 ± 0.05 (B)	9.64 ±0.08 (C)	7.63 ± 0.17 (AB)	≤ 0.01
Pectoral Fin	11.12 ± 0.09 (A)	10.87 ± 0.07 (B)	14.01 ± 0.12 (C)	10.86 ± 0.26 (AB)	≤ 0.01
Head shape PC1	--- (A)	--- (B)	--- (C)	--- (AC)	≤ 0.01
Head shape PC2	--- (A)	--- (B)	--- (A)	--- (AB)	≤ 0.01
Body shape PC1	--- (A)	--- (A)	--- (A)	--- (A)	0.51
Body shape PC2	--- (A)	--- (A)	--- (A)	--- (A)	0.76

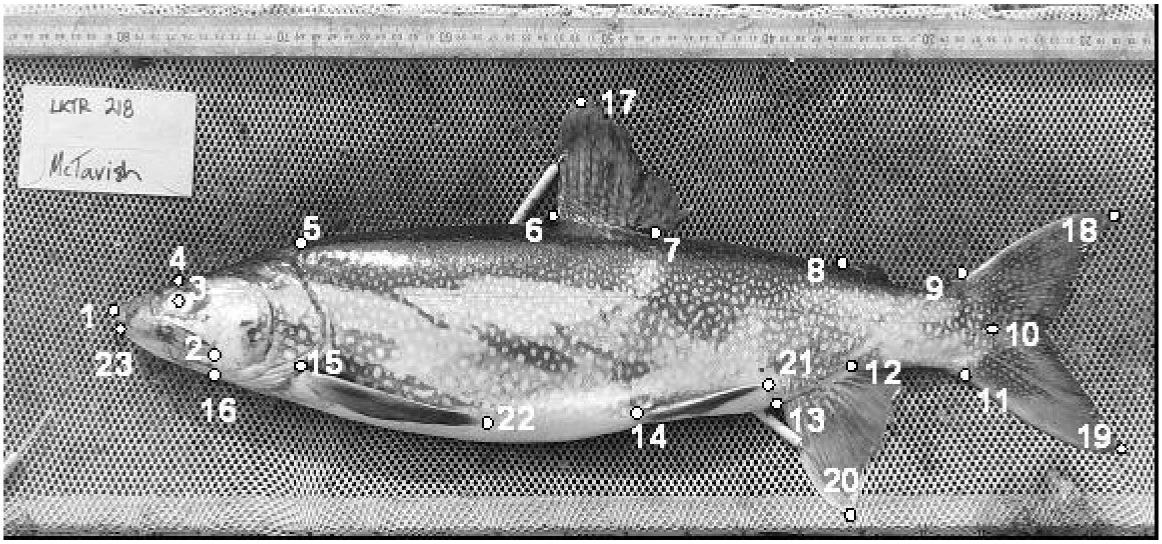


Fig. 2-1. Landmarks used to measure body shape and linear measurements of Lake Trout from Great Bear Lake: (1) anterior tip of the snout, (2) posterior tip of maxilla, (3) center of eye, (4) top of cranium at middle point of eye, (5) posterior of neurocranium above tip of opercle, (6) dorsal fin anterior insertion, (7) dorsal fin posterior insertion, (8) adipose fin anterior insertion, (9) caudal fin dorsal insertion, (10) hypural plate midpoint, (11) caudal fin ventral insertion, (12) anal fin anterior insertion, (13) anal fin posterior insertion, (14) pelvic fin insertion, (15) pectoral fin insertion, (16) ventral surface of head below maxilla tip, (17) dorsal fin tip, (18-19) caudal fin tips, (20) anal fin tip, (21) pelvic fin tip, (22) pectoral fin tip, and (23) anterior tip of lower jaw. Landmarks 1-16 and 23 were used for body shape analysis.

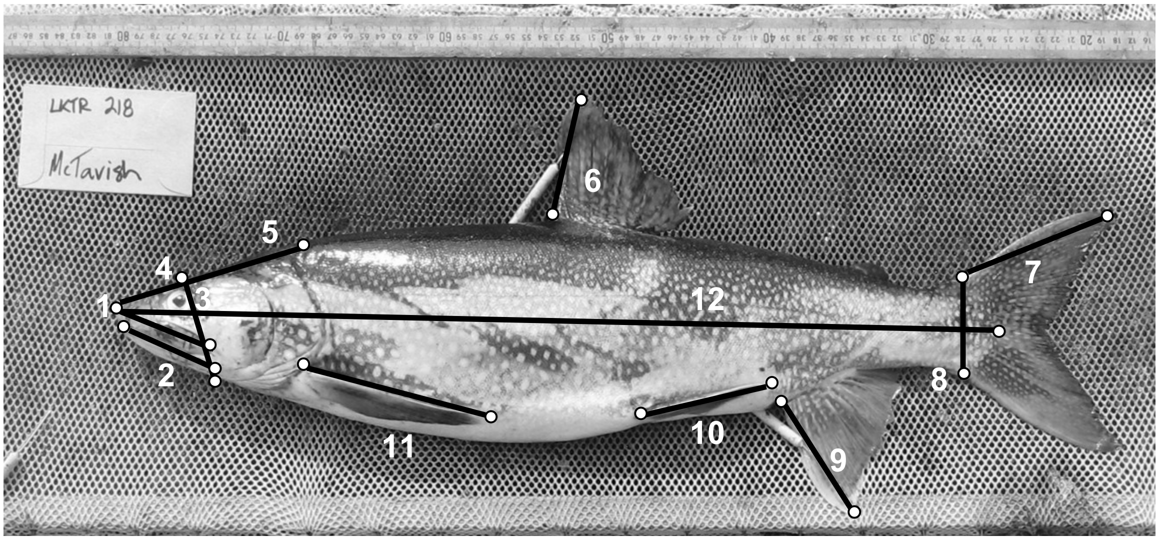


Fig. 2-2. Fin and body length measurements of Lake Trout from Great Bear Lake: (1) upper jaw, (2) lower jaw, (3) head depth, (4) snout-eye, (5) head, (6) dorsal fin, (7) caudal fin, (8) caudal peduncle depth, (9) anal fin, (10) pelvic fin, (11) pectoral fin, and (12) standard body length; standard body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

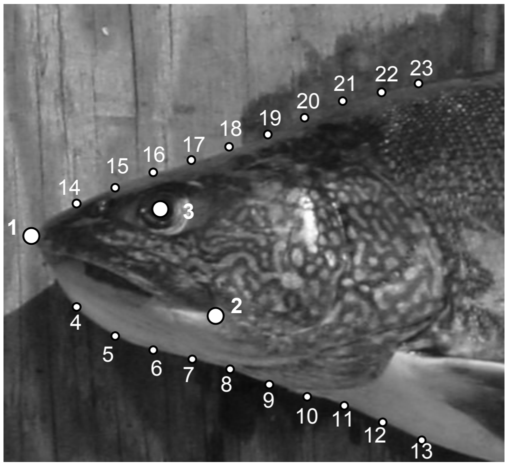


Fig. 2-3. Landmarks and semi-landmarks used to measure head shape of Lake Trout from Great Bear Lake. 1-3 represent the following landmarks: (1) anterior tip of snout, (2) posterior tip of maxilla, (3) center of eye; 4-13 and 14-23 represent ten ventrally and dorsally evenly spaced semi-landmarks, respectively.

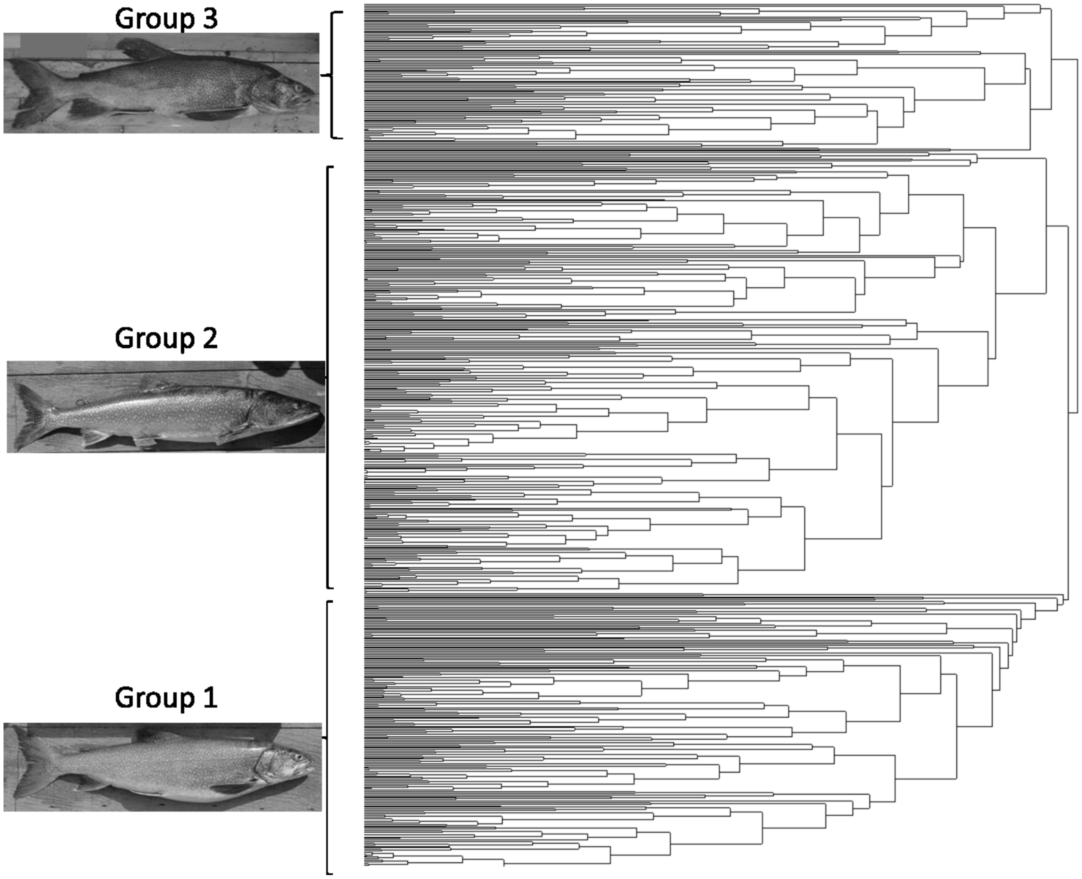
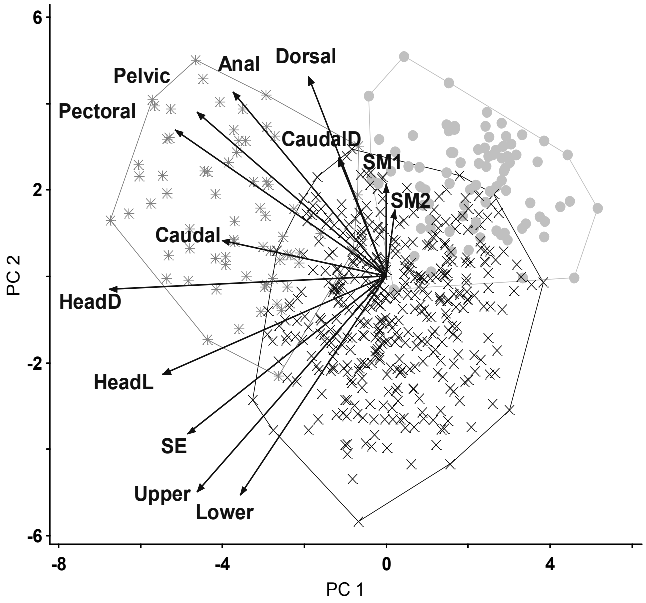
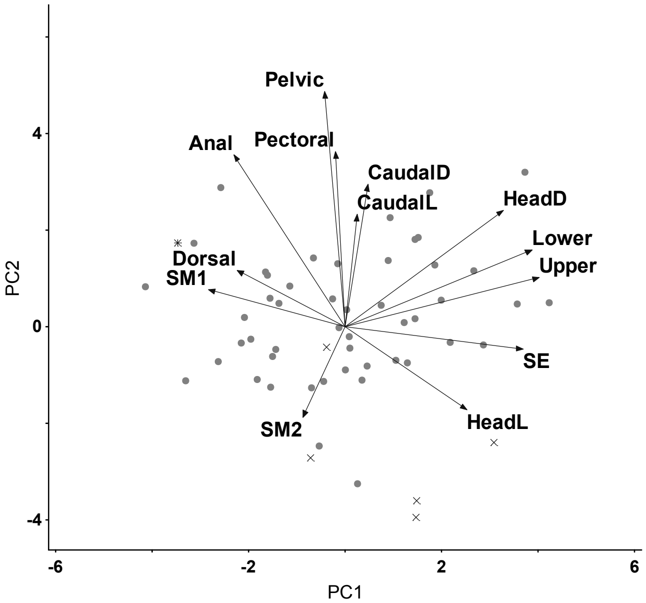


Fig. 2-4. The dendogram resulting from a UPGMA cluster analysis of 558 adult Lake Trout from shallow (≤30m) waters of Great Bear Lake. Three major groups of trout were identified based on traditional morphometric measurements and principal component scores of head shape and body shape measurements.

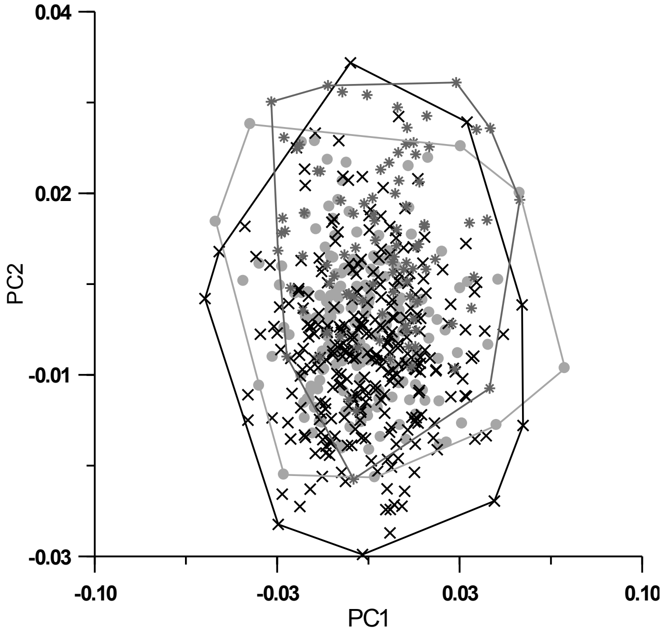


a)

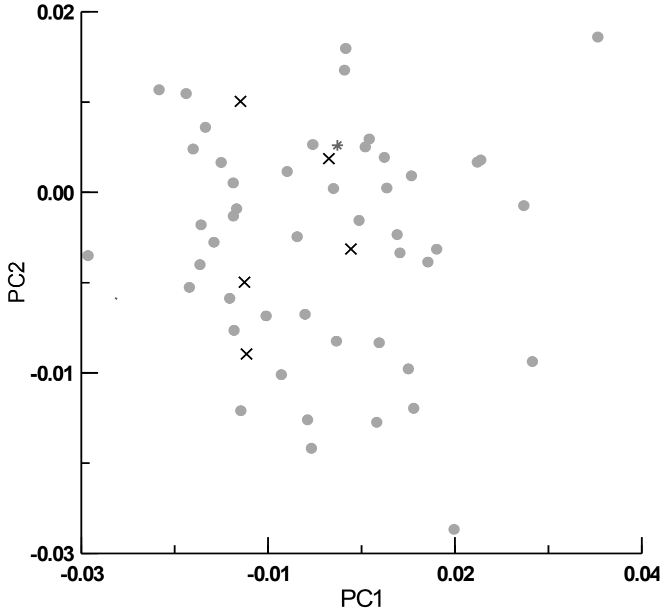


b)

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



a)



b)

Fig. 2-6. PCA ordinations of adult (a) and juvenile (b) Lake Trout body shape. PC1 and PC2 of adults explained 41.5 % and 13.5 % of the variance, respectively, whereas PC1 and PC2 of juveniles explained 45.8% and 14.2% of the variance. Groups identified by UPMGA cluster analysis are represented as follows: ● = Group1, x = Group 2, and * = Group 3; adults groups are outlined by convex hulls.

a)

b)

Fig. 2-7. Example of a Group 4 Lake Trout: full body profile (a), and close-up of head (b). Arrows indicate lower jaw, the visually distinctive trait that differentiates this group from the other groups of Lake Trout.

Chapter 3: Polymorphism in Lake Trout in Great Bear Lake: intra-lake morphological diversification at two spatial scales.

Abstract

Great Bear Lake is the most northerly lake of its size and provides unique opportunities for intra-specific diversification. Despite increasing attention to intraspecific polymorphism, several knowledge gaps remain, e.g., determining the extent of intra-specific diversification in large relatively pristine lakes and at which spatial scale it can occur. We focused on geographic patterns of morphological differentiation within Lake Trout (*Salvelinus namaycush*) to describe two levels of intra-lake diversification in Great Bear Lake. We used a combination of geometric and traditional linear measurements to quantify differences in body shape, head shape, and fin and body lengths among 910 adult Lake Trout from the five distinct arms of Great Bear Lake. Whereas head and fin linear measurements discriminated the three common morphotypes at the whole-lake level, inter-arm variation in body shape was observed within each morphotype. A comparison of genetic and morphological distance matrices revealed a lack of association between the two sets of data but both comparisons revealed association in the inter-arm variation patterns among morphotypes, suggesting a phenotypically plastic response to distinct environments. The whole-lake and inter-arm morphological variation observed within Lake Trout demonstrates the importance of considering scale, especially across large lakes that exhibit marked complexity and a variety of freshwater habitats.

Introduction

Intraspecific variability contributes significantly to biodiversity in northern freshwater fish faunas. Salmonid, gastererosteid, and osmerid fishes, in particular, represent some of the best examples of adaptative intraspecific radiation among freshwater fishes. In northern post-glacial lakes, these groups of fishes display variation in morphology, life-history, ecology, and habitat use, not only across their geographical ranges but sympatrically within single systems (i.e., sympatric resource polymorphism; Sandlund *et al*., 1992; Keeley *et al*., 2007; Adams *et al*., 2006). Sympatric divergence can occur (but is not limited to) when populations experience disruptive selection associated with different ecological environments containing alternative resources (Schluter, 2000; Crispo *et al*., 2006). Under the standard resource polymorphism model, a subset of individuals within a population switches to a novel and/or sub-optimal resource, which reduces intraspecific competition and facilitates morphological divergence (Olsson *et al*., 2006; Moles *et al*., 2010). These "evolutionarily young" polymorphic fishes, exhibiting varying degrees of repoductive isolation, may represent initial stages in speciation (Bush, 1994; Skúlason and Smith, 1995; Hendry, 2009).

Morphotypes are defined as groups of individuals within a species that are distinguished by a composite of traits (e.g., body shape), representing adaptations to a number of environmental and resource variables across different environments (Robinson and Parson, 2002; Lowry, 2012). The high degree of niche differentiation, often referred to as "ecological opportunity" (Schutler and Rambaut, 1996; Schutler, 2000), found in northern lake environments, is associated with low inter-specific competition and predation, and open niches (e.g., Smith and Skúlason, 1996) that promote adaptative radiation. Environmental heterogeneity is another important component enhancing intraspecific diversity. Lakes can represent a rich source of environmental gradients (e.g., depth, temperature, light, shoreline development, wave exposure, substrate) associated with different prey species and habitat characteristics that have the potential to promote ecological segregation (Smith and Todd, 1984; Taylor, 1991).

Lake Trout, *Salvelinus namaycush*, has been previously associated with low intraspecific variation, especially when compared to its congener Arctic Char (*Salvelinus alpinus*) (i.e. Hindar and Jonsson, 1993; Jonsson and Jonsson, 2001; Adam *et al*., 2007). However, Lake Trout can exhibit some sympatric diversification, at least in large deep lakes (Zimmerman *et al*., 2006, 2007, 2009; Eshenroder, 2008), or in a newly colonized lake (Stafford *et al*., 2014) where 2-3 different morphotypes vary in diet and in their use of habitat (depth). Chavarie *et al*. (2013) recently identified one rare and three common shallow-water morphotypes of Lake Trout in Great Bear Lake (an additional deep-water form is also thought to exist). Great Bear Lake might exhibit greater diversity than expected, but historical anecdotal observations have suggested similar levels of variation occurring in other large aquatic systems (Brown et al., 1981; Goodier 1981). Due to significant anthropogenic impacts in the Laurentian Great Lakes, however, Lake Trout diversity has greatly decreased (Zimmerman *et al*., 2007), limiting quantitative investigations or comparisons with Great Bear Lake. Consequently, Great Bear Lake may currently be the only lake of its size in which to investigate natural levels of Lake Trout sympatric diversity.

Morphological discrimination within Great Bear Lake was mostly associated with differences in head and fins among morphs. Morph 1 was characterized by a smaller head and jaws and intermediate fin sizes, Morph 2 had a longer head and jaws but smaller fins, whereas Morph 3 had the deepest head and caudal peduncle and longest fins. In contrast to the noticeable differences in head and fin measurements among morphotypes, variation in body shape was not observed at the whole-lake level in Great Bear Lake, despite being one of the main distinguishing features among the depth-related morphotypes in other large lakes. Given the large size and complex shape of this lake, we hypothesized that body-shape variation within a single morphotype could exist among the lake's five arms, which may have obscured differentiation at the whole-lake scale. If supported, this microgeographic variation and its driving mechanism could fundamentaly alter ecological and evolutionary dynamics in the lake, although research has not sufficently investigated smaller spatial scale adaptation (Richardson *et al.*, 2014).

Great Bear Lake is one of the largest and deepest lakes in the world (Alfonso, 2004). Five somewhat isolated arms with diverse aquatic habitats are connected to a central basin (Fig. 3-1). This complex morphometry, combined with the generally limited movement of Lake Trout within a system (e.g., Schmalz *et al.*, 2002), suggests that the Lake Trout "populations" of each arm could experience at least some degree of isolation and/or differences in habitats. Since isolation-by-distance and/or adaptive opportunities independent of geographic distance, e.g., isolation-by-adaptation, can result in differentiation among fish (e.g. Schluter and Nagel, 1995; Kristjánsson *et al.*, 2002; Nosil *et al.* 2007), we hypothesized that there could be geographical patterns of morphological divergence among arms, each of which is the size of a lake, associated with the "Lake Trout complex" of Great Bear Lake.

To test this hypothesis, our objectives here were to (1) determine if (and how many of) the three common morphotypes of Lake Trout display variation among arms in Great Bear Lake, (2) quantitatively summarize the morphological variation within morphotypes by using a combination of geometric morphometric and traditional linear measures, and (3) relate the inter-arm morphological variation to any differences in the physical and/or trophic information for the morphs among arms. Given a parallel study of genetic variation among and within morphotypes across arms (Harris *et al*., 2014), we also (4) compared the similarity of morphological and genetic patterns among arms as an indicator of potential adaptive patterns. Such information will be relevant for documenting intra-specific biodiversity in one of North America's few remaining pristine large lake systems in a region expected to be significantly altered by climate change. Furthermore, our results will be important for understanding the evolution of morphological and ecological variation in species occupying recently colonized, post-glacial habitats, particularly large lakes.

Material and Methods

Study area

At 31,790 km^2 and with a maximum depth of 446 m (mean depth = 90 m), Great Bear Lake is the ninth largest and fifteenth deepest freshwater lake in the world (Johnson 1975, Fig.3-1). Great Bear Lake was formed by the scouring action of the Laurentide ice-sheet during the Pleistocene and was originally part of glacial Lake McConnell 8,000–10,000 yr BP (Johnson, 1975; Pielou, 1991). The lake and its catchment (ca. 145 000 km^2) straddle two major physiographic regions: the metamorphic Precambrian shield to the north and east (Dease and McTavish arms), and sedimentary Paleozoic deposits of the Mackenzie Lowlands to the south and west (McVicar, Keith and Smith arms) (MacDonald *et al*. 2004). Three terrestrial ecozones surround Great Bear Lake, the Southern Arctic along the northern shore (Dease Arm), the Taiga

Plains to the west and south (McVicar, Keith and Smith arms), and the Taiga Shield to the east (McTavish Arm) (MacDonald *et al*. 2004, Fig.3-1).

Correspondingly diverse aquatic habitats can be found among the different arms of the lake, and along the 2719 km of shoreline (with an additional 824 km contributed by islands) (Johnson, 1975; Alfonso, 2004). These include offshore and nearshore shoals, dropoffs of varying depths, bays, islands, as well as river and stream mouths that can be very sheltered from open water. Great Bear Lake has two main inflows, the Camsell and the Johnny Hoe rivers in McTavish and McVicar arms, respectively, and one major outflow, the Great Bear River in Keith Arm. The Johnny Hoe River has its origin in an extensive area of muskeg (acidic peatland soil) to the south, resulting in McVicar Arm having the least transparent water (Johnson, 1975). Being the smallest, shallowest, most isolated, and southernmost arm, McVicar is also generally warmer than the rest of the lake (Riley, 1935). Its eastern shore is characterized by extensive marshy bays while the western side has sandy beaches. McTavish arm is characterized by a complex shoreline and numerous offshore islands (Riley, 1935). McTavish is deeper than the other arms, has the largest volume, and has the clearest water (maximum Secchi depth = 30 m; Johnson, 1975). Dease, Smith, and Keith arms have intermediate transparencies, with the majority of Secchi depths being 12-16 m. Dease is the most northerly arm, intersecting the Arctic circle, while Keith arm has the largest surface area. Fifteen fish species are reported from Great Bear Lake but only half were commonly caught in our nets (noted by *): Arctic Grayling* (*Thymallus arcticus*), Burbot (*Lota lota*), Chum Salmon (*Oncorhynchus keta*), Fourhorn Sculpin (*Myoxocephalus quadricornis*), Inconnu (*Stenodus leucichthys*), Cisco* (*Coregonus artedi*), Lake Trout*, Lake Whitefish* (*Coregonus clupeaformis*), Longnose Sucker (*Catostomus catostomus*), Ninespine Stickleback* (*Pungitius pungitius*), Northern Pike* (*Esox lucius*), Round Whitefish* (*Prosopium *cylindraceum*), Trout Perch (*Percopsis omiscomaycus*), Slimy Sculpin* (*Cottus cognatus*), Walleye (*Sander vitreus*) (Johnson 1975; Alfonso 2004; MacDonald *et al*. 2004)

Data collection

We analyzed 910 adult Lake Trout captured from all five arms of Great Bear Lake between 2002 and 2010: Keith (2002 and 2003), McVicar (2003 and 2008), McTavish (2009), Dease (2005 and 2010), and Smith (2006). All fish were caught at depths < 30 m, using paired bottom sets (ca. 24 h) of a 14-cm and a multi-mesh (3.8-14 cm) gill net during July and August. Multiple locations within each arm were sampled to spatially represent the arm, with similar net locations used if multiple years were sampled; surface water temperature was measured at each net location at the same time sampling. A lateral full-body digital image was taken of each trout, with extended fins, as described in Chavarie *et al*. (2013). For each trout, fork length, round weight, sex, and stage of maturity were recorded and stomachs were preserved if they were not empty. Our analyses focused on adults (> 450 mm), since they display greater diversity in morphological characteristics than juveniles (Chavarie *et al*. 2013).

Morphology

Analyses of digital images combined classical with geometric morphometrics (Bookstein 1991). Selected morphological characteristics focused on fins, head, and body shape, due to their direct and indirect relationships to foraging and swimming and because they are traits that are most likely subject to rapid change in fishes (Webb 1984; Kristjánsson *et al*. 2002; Kahilainen *et al*. 2004). Twenty-three homologous points, or landmarks, identical to those in Chavarie *et al*. (2013), were used. Seventeen landmarks covered the outline of the body to extract body shape information, while 18 were used to measure 12 linear distances (Fig. 3-2a). Linear and shape measures from the landmarks were comparable, to varying degrees, to those used in previous Lake Trout studies in Great Bear Lake (Blackie *et al*. 2003), Great Slave Lake (Zimmerman *et al*., 2006, 2009), Lake Mistassini (Zimmerman *et al*., 2007), and Lake Superior (Moore and Bronte, 2001). We also used 20 semi-landmarks (Green 1996; Bookstein 1997, Zelditch *et al.* 2004) around the head (Fig. 3-2b) to capture more detailed shape information (Zimmerman *et al*. 2007, 2009; Chavarie *et al*. 2013).

Landmarks and semi-landmarks were digitized in x and y coordinates using TPSDig2 software (http://life.bio.sunysb.edu/morph). Subsequently, digitized landmarks and semi-landmarks were processed in a series of Integrated Morphometrics Programs (IMP) (http://www2.canisius.edu/;sheets/morphsoft); morphological methods and programs are described in Zelditch *et al*. (2004) and morphological procedures described in further detail in Chavarie *et al*. (2013). Body and head shape analyses used geometric information from landmarks and semi-landmarks after differences in location, scale, and rotational effects were removed by CoordGen6f, producing procrustes distances. Because they are not homologous points, semi-landmarks were digitized by positioning points on a grid of ten equally spaced lines between the snout and the operculum using MakeFan software (Fig. 3-2b). Semi-landmarks were then "slid" using Semiland6. Standard6 was used to remove size-dependant variation on shape data via a regression of landmarks on centroid size (Zelditch *et al*. 2004). Traditional linear measurements were calculated with Tmorphgen6 and were then $\log_{10}$-transformed. Measurements were regressed against the standard length of the fish to obtain residuals that exhibit minimal size effects and could be used in the following analyses among and within morphotypes (Reist 1985).

Analyses

All body- and head-shape analyses were performed by IMP programs using partial warp scores, which are thin-plate spline coefficients (Zelditch *et al*. 2004). They were used in all subsequent conventional statistical analyses since they have the correct number of degrees of freedom (Zelditch *et al*. 2004). We performed principal component analyses (PCA) on body- and head-shape data using PCAGen (IMP software). This ordination technique constructs a reduced number of (multivariate) variables that maximizes the explained variance of the unreduced data set. SYSTAT V. 12 software was used (Systat Software Inc., Chicago, IL, USA) to perform a PCA on the traditional linear measurements. Based on the most discriminating traits found among morphotypes (Chavarie *et al*. 2013), morphological groups were identified using head and fin linear measurements with a MClust V.4 cluster analysis in R (http://www.stat.washington.edu/mclust/). MClust is a method that combines model-based hierarchical clustering, Expectation Maximization (EM) for maximum-likelihood estimation in parameterized Gaussian mixture models, and an estimation of the optimal number of clusters based on Bayesian Information Criteria (BIC) (Fraley and Raftery, 2006, 2007). The BIC is the value of the maximized log-likelihood, with a penalty on the number of model parameters, and allows comparison of models with differing parameterizations and/or differing numbers of clusters (Fraley and Raftery, 2006, 2007). A G-test (Sokal and Rohlf, 1981) was performed on the morphotypes identified with MClust to determine if the proportion of each morphotype, based on our net catches, differed among arms. G-test was also used to test if sampling locations were sex-biased, by comparing female : male ratios within a morphotype among arms.

Canonical Variate Analyses (CVA) and validation procedures were conducted on all morphological data, including body shape, head shape, and linear measurements, within morphotypes across the five arms of Great Bear Lake to assess inter-arm morphological differences. Body and head shape were analysed using CVAGen from the IMP software. Jacknife validation procedures included a test of the functioning of the assignment, with 1000 Jackknife sets using 20% of our data as unknowns (Zelditch *et al*., 2004). For linear measurements, CVA was analysed with SYSTAT, with the same Jackknife validation procedure performed in MATLAB (The MathWorks, Inc., Natick, Ma, USA). To visualize the influence of the spatial scale (whole lake or among arms) in the body shape data, a series of NMS analyses (nonmetric multidimensional scaling) was conducted, using Nmmds7_14 from IMP programs, to compare the three morphs in each arm.

Single Factor Permutation MANOVA with 10 000 permutations was performed with CVAGen to test if body shape means differed among morphs within an arm, and among arms within a morph. If MANOVA indicated differences, partial procrustes distance means (PPDMs) were calculated for pairwise comparisons of morphological distance using TwoGroup6h sofware from IMP as Post-hoc tests (Garcia-Rodriguez *et al*. 2011). A boostrapped F-test (n=1600 bootstraps) was used to determine if the calculated PPDMs were significantly different. Pairwise distances among arms were also used to construct an unrooted Neighbor-Joining tree using Phylip v 3.69 (Felsenstein, 2005), which was plotted with Fig Tree v 14 (http://tree.bio.ed.ac.uk/software/figtree/).

Finally, to test if there was any association between morphological variation and genetic variation, morphological distances produced using the TwoGroup6h software were compared to genetic distances among Lake Trout morphotypes. Briefly, pairwise estimates of Cavalli-Sforza and Edward's (1963) chord distance (DCE) (appendix 3-1), based on microsatellite DNA variation using 22 loci, were calculated to assess population structure (Harris *et al.*, 2014). This was done using using the GENDIST module in the PHYLIP software package (vers. 3.69, Felsenstein 1995). To assess any association between morphological and genetic variation (genotype-to-phenotype association) among Great Bear Lake morphotypes, partial Mantel tests (Mantel, 1967; Legendre and Fortin, 2010) were used to compare morphological and genetic distance matrices. Mantel tests were also performed within the morphological and genetic datasets to assess similarity in the among-arm patterns between Morph 1 (n=16-121 individuals per arm for morphology and n=20-59 for genetics) and Morph 2 (n=61-175 individuals per arm for morphology and n=20-45 for genetics). Mantel tests were perfomed using the PCORD program V.6 software (McCune and Mefford. 2011) and were limited to Morphs 1 and 2 due to sample size limitations in genetic analyses (Harris *et al.*, 2014).

Ecological data: stomach contents and surface water temperature

In the laboratory, random sub-samples of stomachs were opened (n=42, 32, and 16 for Morphs 1-3 respectively) and contents were sorted by prey type and weighed. Depending on the degree of digestion of prey items, identification ranged from species to family for both fishes and invertebrates. To facilitate data presentation, prey were pooled into the following groups: Fish (Burbot, fish remains, Cisco, Lake Trout, Lake Whitefish, otoliths, Northern Pike, Round Whitefish, Sculpin, Stickleback), Malacostraca, Mollusca, Orthoptera, Lepidoptera, Aranea, Diptera, Hemiptera, Hymenoptera, Trichoptera, Coleoptera, Plecoptera, and unknown invertebrates. Diet composition was summarized by morphotype using frequency of occurrence

(*%O)*, and percentage by abundance (*%N*) and mass (*%M)*. To scale the importance of each prey category among morphotypes, *%O*, *%N*, and *%M* were used to calculate the Relative Importance Index (RI) at the population level (morphotype) but also at the individual level, for which %O was excluded (George and Hadley 1979). Dietary differences among morphotypes and area captured (arm) were tested with a two-way PERMANOVA with 9999 permutations using Bray-Curtis measures (Anderson & ter Braak, 2003) followed by post-hoc pairwise comparisons among morphotype and arms using the program PAST V. 3 (Hammer *et al*., 2001). A multi-group SIMPER analysis using Bray-Curtis measures in PAST V.3 was also used to assess which prey categories were primarily responsible for an observed difference between morphotypes. A two-way ANOVA was also performed with SYSTAT on surface water temperature across arms, years and their interaction.

Results

We sampled 910 Lake Trout captured throughout the five arms of Great Bear Lake (Table 3-1). Mclust models showed a strong support for a division of the data into three clusters (morphs), which had a ΔBIC value of approximately 8 (Neumann *et al*., 2008). The 3-cluster Mclust model calculated uncertainties of classification at 17.5% (Morph 1), 18.5% (Morph 2), and 19.1% (Morph 3). The distribution of trout among the morphs differed among arms (G=258.72, df=8, p<0.01) (Table 3-1). Morph 2 was relatively more abundant in McVicar, McTavish, and Smith arms, while Dease was the only arm with a substantive proportion of Morph 3 (Table 3-1). The distribution of females vs. males within a morph was not significantly different among arms (Morph 1: G=5.82, p>0.05, Morph 2: G=6.41, p>0.05, and Morph 3: G=1.39, p>0.05) (Table 3-1).

CVAs suggested inter-arm variation in head and especially body shape for all three morphotypes (Fig. 3-3). For Morph 1, trout from Dease Arm had deeper heads, higher mouth and eye positions, and deeper and longer trunks, but were more streamlined than Keith and Smith Arm trout (deeper bodies), whereas trout from Smith Arm had greater body depth relative to other arms (body shape: Axis 1 $\lambda= 0.05$, $p<0.01$ and Axis 2 $\lambda = 0.24$, $p<0.01$; head shape: Axis 1 $\lambda= 0.061$, $p<0.01$ and Axis 2 $\lambda = 0.24$, $p<0.01$) (Fig. 3-3 and 3-4). For Morph 2, inter-arm analyses revealed longer heads and higher mouth positions for McTavish and Smith arms, and a deeper body for Keith Arm trout, whereas trout from Dease Arm expressed shorter body depths, but deeper heads and caudal peduncles and higher eye positions; Morph 2 trout from McTavish and Smith arms were streamlined, and McTavish Arm trout also had longer trunks relative to the other four arms (body shape: Axis 1 $\lambda= 0.063$, $p<0.01$ and Axis 2 $\lambda= 0.18$, $p<0.01$; head shape: Axis 1 $\lambda= 0.16$, $p<0.01$ and Axis 2 $\lambda= 0.43$, $p<0.01$) (Fig. 3-3 and 3-4). For Morph 3, deeper heads and bodies, including longer and deeper peduncles, and higher eye positions were found in Dease Arm compared to trout from the other arms (body shape: Axis 1 $\lambda= 0.083$, $p<0.01$ and Axis 2 = 0.27, $p<0.01$; head shape: Axis 1 $\lambda= 0.021$, $p<0.01$ and Axis 2 $\lambda= 0.087$, $p<0.01$) (Fig. 3-3 and 3-4). Jackknife classification on body shape had the highest rates of correct arm-assignments (77.1 %, 69.3%, and 66.9%, respectively, for Morphs 1-3), while the head shape analysis had correct assignment rates of 70.0%, 59.3 %, and 52.8% for Morphs 1-3, respectively.

In contrast, within-morphotype CVAs suggested less variation among arms for linear measurements. Although linear-measurement CVA's were significant for Morphs 1-3 ($p<0.01$), ƛs were generally larger (0.27-0.33) than those for body and head shape, indicating less discrimination and more similar centroids. Indeed, correct Jackknife classifications on traditional linear measurements were relatively low for Morphs 1 and 2 (55.1%, and 51.2%, respectively), although classification success was higher (65.7%) for Morph 3.

Variation in body shape among morphs was also observed within individual arms using NMS (Fig. 3-5). Morphs 1 and 2 were distinct for Smith and McTavish arms, whereas Morph 3 could be distinguished from Morph 1-2 in McVicar and Dease arms. Keith Arm displayed less among-morph distinction in body shape. Permutation MANOVA confirmed the difference in body-shape means among the three morphs in each arm ($p \leq 0.01$). Permutation MANOVA also confirmed within-morph body shape differences among arms ($p \leq 0.05$). All pairwise comparisons in each arm were significantly different (F-tests; $p \leq 0.05$), except for Morph 1 vs. 3 in Smith Arm and Morph 2 vs. 3 in Keith Arm. All among-arm pairwise comparisons for Morphs 1 and 2 were significant (F-tests; $p \leq 0.05$) except for McVicar-McTavish in Morph 1, which was marginally different (p=0.06) (Fig.3-4). For Morph 3, the only pair that differed was McVicar-Dease (PPDM=0.016, p=0.01).

Morphological matrices of Morphs 1 and 2 were significantly related (Mantel test; r=0.84, $p < 0.01$), indicating similarity in the patterns of inter-arm variation for these two morphotypes. However, despite analogous genetic associations in the patterns of inter-arm variation between Morphs 1 and 2 (r=0.96, p<0.01), there was no significant relationship between genetic and morphological datasets for either Morph 1 (r=0.31, p=0.19) or Morph 2 (r=0.12, p=0.76).

Significant dietary differences were found among the three morphotype diets (PERMANOVA: *df*=2, *F*= 1.01, *p*<0.02) and also among the arms of Great Bear Lake (*df*=4, *F*= 1.97, *p*<0.01), but the interaction between morphotype and arm was not significant (*p*>0.05). All pairwise comparisons indicated that Morph 2 had a significantly greater importance of fish in their diets than Morph 1 (*p*<0.05). Pairwise comparisons identified Dease and Smith arms as being different from the rest of the lake (p<0.05). Diet among arms was mainly differentiated by Trichoptera, fish, Malacostraca, Hymenoptera, and Mollusca with SIMPER-calculated contributions to arm differences of 30.95%, 25.74%, 13.81%, 11.43%, and 5.7%, respectively. The spatial difference resulted from difference in importance of specific food items between the following arms (in order of mean importance): Dease and Smith arms for Trichoptera, McTavish, Keith, and McVicar for fish, Keith, McTavish and McVicar for Malacostra, Dease, McTavish, and Smith for Hymenoptera, and McVicar for Mollusca (Table 3-2). Surface water temperature also differed among arms (two-way ANOVA; p≤0.01) (Fig. 3-6) but neither year nor the arm*year interaction were significant (p>0.05). The lowest and highest temperatures were found in McTavish and Smith arms, respectively.

Discussion

Using a robust classification method, and based on an analysis of >900 trout, our current study supported and extended our previous work (Chavarie *et al.* 2013), identifying multiple forms of Lake Trout in the shallow-water habitats of Great Bear Lake. Interestingly, for the 553 Lake Trout used in the UPGMA cluster analyses of Chavarie *et al.* (2013), agreement between UPGMA and Mclust was high (83-97%). These morphological results, reinforced by diet data, correspond to morphs described in other Salmonidae as piscivorous (Morph 2) and insectivorous (Morphs 1 and 3) (e.g., Proulx and Magnan 2004; Keeley *et al.*, 2005; Janhunen *et al.*, 2009).

Beyond this, however, our CVA, NMS, and Procrustes distance means analyses also identified inter-arm variation within the three common morphotypes, with significant similarity in the inter-arm morphological pattern for the two most common morphotypes that could be tested. Although the driving mechanism(s) behind this inter-arm variation remain unknown, our results suggest multiple levels of diversification that challenges the presumption that in sympatry, the pattern of diversification is system wide (e.g., Hindar and Jonsson, 1993; Orr and Smith, 1998; Bolnick and Fitzpatrick, 2007).

Freshwater habitats are often characterized as patchy, fragmented environments that can promote intraspecific variation in body shape (Carvalho, 1993). Salmonids, especially, can form local populations across contrasting environments over a variety of geographical scales, and represent some of the best examples of diversification in freshwater fishes (Taylor, 1991; Keeley *et al*. 2007; Vonlanthen *et al*., 2009). Selection can operate to promote divergence among fish inhabiting the near shore, littoral vs. off-shore, open water habitats, that differ in resource composition and availability, and thermal regime (Clabaut *et al*. 2007; McPhee et al., 2012; Woods *et al*., 2013). Indeed, specialization for benthic and pelagic food has frequently been proposed as a driving mechanism for many post-glacial adaptive radiations (Vonlanthen *et al*., 2009; McPhee *et al*., 2012).

Lake morphometry can also predict the likelihood of habitat coupling between littoral and pelagic zones by a mobile predator such as Lake Trout (Dolson *et al*. 2009). Subsequently, among-arm variation in depth, substrate, temperature, and the aquatic network of shoals, dropoffs, bays, islands and open water areas, together with the relative isolation among arms, could have induced further morphological responses within individual morphotypes, assuming there is a phenotype-environment relationship (Schluter, 2000). Although we lack a direct demonstration of local adaptation, diet differences among arms found within a morphotype likely reflect variability in resources that supports the possibility of morphological adaptations to diverse habitats among arms of Great Bear Lake.

Overall, four general morphological shifts were observed in Great Bear Lake within a given morphotype, in relation to their area of capture: 1) head depth and 2) maximum body depth, 3) caudal peduncle depth, and 4) eye position. From these relationships, inferences on functional roles, responses to selective pressures, growth processes, and mophogenesis can be made (Medina *et al*., 2008).

Lake Trout from Dease Arm typically exhibited larger heads, deeper caudal peduncles and higher eye positions whereas Keith Arm trout had deeper bodies. A deeper body is generally associated with manoeuverability to exploit structurally complex habitat, since greater body depth should reduce slip and promote better performance when searching for cryptic prey (Kristjánsson *et al*. 2002). A deeper body is also associated with burst swimming, improving fast-start capacity that is generally needed in habitats where prey are relatively large and fast, and where predators deploy ambush tactics (Robinson and Parson, 2002). The caudal peduncle is the primary structure driving energy efficiency and power during swimming, and a deeper peduncle provides better burst swimming needed in structurally complex environments. Finally, eye position can reflect the fish's vertical position in the water column, with higher position related to benthic exploitation (Gatz 1979, Hugueny and Pouilly, 1999). The consistent morphological variations we observed among the three morphotypes in Dease and Keith arms thus seem to reflect local adaptations that may be linked to resource exploitation in complex habitats (littoral and/or benthic habitats). This hypothesis is partially supported by the importance of benthic prey in the stomach contents from Keith Arm, although our sample size is relatively small and stomach contents are a “snapshot” that can reflect opportunistic feeding on a pulse of prey (Chavarie *et al*., in press (b)).

Furthermore, the relative abundance of each morphotype among arms suggests differences in the prevalence of different habitats. Prevalence among morphs was relatively equitable in Dease and Keith arms, suggesting that habitats in those arms have characteristics (e.g., greater habitat complexity) that favor Morphs 1 and/or 3 relative to the three other arms. In contrast, McTavish, McVicar and Smith arms were dominated by the more piscivorous Morph 2, which generally displayed traits better suited to pelagic habitats (Webb 1984; Pakkasmaa and Piironen 2001; Gillespie and Fox, 2003). Indeed, all three morphs of Lake Trout from McTavish Arm had relatively streamlined, longer bodies, and narrower peduncles, traits associated with sustained swimming in more open/pelagic environments; correspondingly, McTavish Arm contains the most deep-water/pelagic environment. McVicar Arm trout were intermediate in these traits, leading us to suggest no dominance of any specific habitat in that arm.

Benthic and pelagic environments tend to differ in several components (e.g., thermal regime), and McPhee *et al*. (2012) hypothesized morphologically divergent ecotypes might arise initially as a plastic response to heterogeneous thermal regimes. Although our data are limited in terms of habitat structure associated with thermal regime, McTavish had the coldest surface temperature during our sampling. This suggests a possible developmental influence on the external morphology of its residents, perhaps at the juvenile stage, as slow-developing fish can resemble a pelagic ecotype (Vila-Gispert et al. 2007; McPhee *et al*., 2012). In contrast, Smith arm was the warmest arm, and Morph 1 exhibited a more robust body shape that could be associated with fast-developing fishes and littoral habitat (McPhee *et al*., 2012). Such difference in thermal regime in Great Bear Lake is unexpected, since Great Bear Lake was thought to be an isothermal lake during summer, which illustrates how poorly understood this system is (MacDonald *et al*., 2004). Few empirical data on the habitat of each arm are currently available, thus, more effort is needed to investigate and validate the link between habitat characteristics and the morphological variation we have documented.

Variation in other ecological factors, such as predation, can also promote local adaptation (Kristjansson *et al*. 2002, Ólafsdottir *et al*. 2007; Hendry *et al*. 2009; Collin and Fumagalli, 2011), even in situations with considerable gene flow (Smith *et al*. 2001; Hendry and Taylor, 2004; Crispo *et al*. 2006; Eklöv and Svanbäck, 2006). For example, greater body depth, as seen for Morph 1 only in Smith Arm, can have defensive value against predators (Webb 1984; Webb and Fairchild 2001; Medina *et al*. 2008). This might be especially important for fish from arms with a high prevalence of Morph 2 (McVicar, McTavish, and Smith) and, in turn, might increase morphological differences between Morphs 1 and 2, as seen in NMS results for Smith and McTavish arms. Indeed, because cannibalism has been observed in Great Bear Lake (Chavarie *et al*., in press (b)), predation could impact Lake Trout at smaller sizes by influencing habitat selection (littoral vs. pelagic), and subsequently promoting morphological variation later in life (Claessen *et al*. 2002; Persson *et al*. 2004; Moles *et al*. 2010). It is not unreasonable to suspect that predation pressure differs among arms, influencing each population differently, especially if the availability of different habitats differs among arms.

Intraspecific diversity occurs at multiple levels, as seen in our study. If different characteristics, e.g., body shape, have a different degree of plasticity than others, e.g., head and fins, they could react differently in a heterogeneous environment such as Great Bear Lake via phenotypic plasticity, isolation-by-adaptation, and/or isolation-by-distance (Nosil *et al*., 2007; Collin and Fumagalli, 2011). For example, Sharpe *et al*. (2008) found that body shape had a strong genetic component in lake vs stream Threespine Stickleback (*Gasterosteus aculeatus*), whereas the environmental component was stronger for linear traits. The relative importance of genetic and environmental influences can vary both spatially and temporally (Schluter *et al*. 2004; Sharpe *et al*. 2008; Kristjánsson *et al*. 2011; 2012).

A concordant pattern of morphological variation among morphs but not between morphological and genetic patterns within a morph across arms suggests more of a phenotypically plastic response. Of course, the capacity for plasticity might be a heritable trait (Mittelbach *et al*. 1999) or there may be localized selection in the genome (Nosil *et al*. 2007). Nonetheless, Harris *et al*. (2013) found no genetic structure among arms despite large geographic distances, which is not surprising in "evolutionarily young" systems such as Great Bear Lake. The limited time is further exacerbated by the long generation time of northern Lake Trout (~15 years), which suggests that only about 330 generations have passed since the last glaciation for trout to have diverged genetically (Harris *et al*. 2013). The lack of morphological differentiation found in juvenile Lake Trout of Great Bear Lake (Chavarie *et al*., 2013) further supports the idea of induced phenotypic plasticity in this system.

Regardless of ecological influences, the differences in scale (whole-lake, among arms) influenced the success of the different morphological metrics used in Chavarie *et al*. (2013) and this study. Even though both linear measurements and geometric techniques can discriminate populations, Maderbacher *et al*. (2007) found that geometric techniques were more effective at visualizing and quantifying variations when comparing closely related entities (i.e., biological groups). Thus, when viewed at the whole-lake level, inter-arm variation in body shape within a morphotype can introduce "noise" that obscures the distinctiveness of the three basic morphotypes when using geometric techniques (Chavarie *et al*., 2013). However, when focusing on the smaller, among-arm scale, this morphometric tool had the appropriate resolution and sensitivity to capture variation within a morphotype. Conversely, limited differences in fins and body lengths ratios within a morph could have meant less noise at the larger scale, allowing traditional linear measurements to be more successful at capturing the whole-lake variation.

Conclusion

Three striking examples of sympatric variability and parallel adaptive radiation in post-glacial settings, associated with new habitat and vacant niches (Snorrason *et al*. 1994; Reist *et al*. 2013), are the Three-spined Stickleback (e.g. Nagel and Schulter, 1998; Mckinnon and Rundle 2002), Lake Whitefish (e.g., Kahilainen and Ostbyes, 2006; Hudson *et al*., 2007), and Arctic Char (e.g., Jonsson & Jonsson, 2001; Alekseyev *et al*. 2002). Our results suggest an analoguous case of extensive intra-lake morphological diversification within the Lake Trout of Great Bear Lake, extending recent observations in other large lakes (e.g., Eshenroder, 2008) or in introduced populations (e.g., Stafford *et al*., 2014). Indeed, we have detected two scales of diversification within Great Bear Lake, at the whole-lake level, and among arms within the lake-scale morphotypes. Our findings emphasize the importance of considering spatial scale in studies of large "Great" lakes, to adequately capture intraspecific differentiation. The relative importance of spatial and ecological factors, and their interaction, in adaptive radiation are not well understood despite recent theoretical advances (Vonlanthen *et al*., 2009). More research will be needed to investigate the phenotypic plasticity and genetic links to habitat heterogeneity and other ecological factors to more fully understand this adaptive radiation scenario.

In the face of substantive and pervasive threats (e.g., climate change), the importance of investigating diversity and exploring factors regarding its origin and maintenance is increasing. Ecological and evolutionary forces are interconnected and can act over surprisingly similar time scales (Kristjánsson *et al*. 2012), but as this study highlights, they also can act at different spatial scales. This study indicates rapid intra-specific diversification of Lake Trout occurring at both smaller and larger scales. The Lake Trout of Great Bear Lake thus represent one of the most extensive cases of sympatric intraspecific diversity in North America; combined with the relatively pristine environment of Great Bear Lake, this confers a special biological significance to this lake and its resident organisms. Therefore, conservation initiatives aimed at preserving both ecological and evolutionary processes within this system should be considered.

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Table 3-1. Number of each of three common morphotypes of Lake Trout captured in our gillnets in each of the five arms of Great Bear Lake and used in our morphological analyses. Females and males are reprented in brackets, respectively.

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

Table 3-2. Relative importance of prey items in stomachs of Lake Trout from Great Bear Lake for each Morph among the five arms.

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

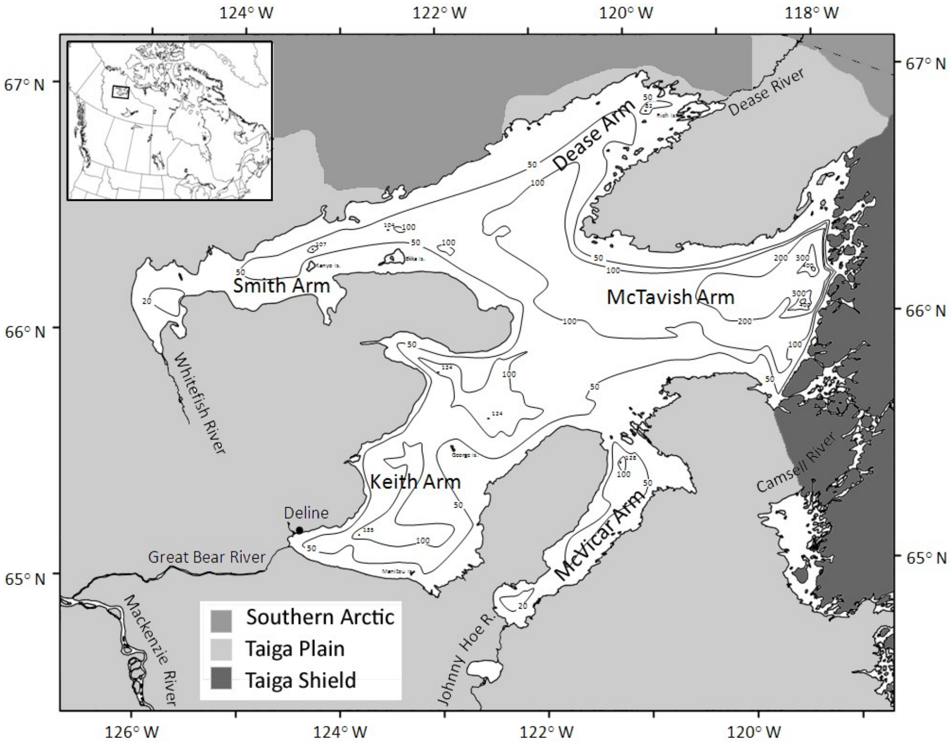


Fig. 3-1. Map of Great Bear Lake, Northwest Territories, Canada, adapted from Johnson (1975), indicating general bathymetry, the terrestrial ecozones adjacent to the lake, and its major rivers. Insert: location of study area within Canada.

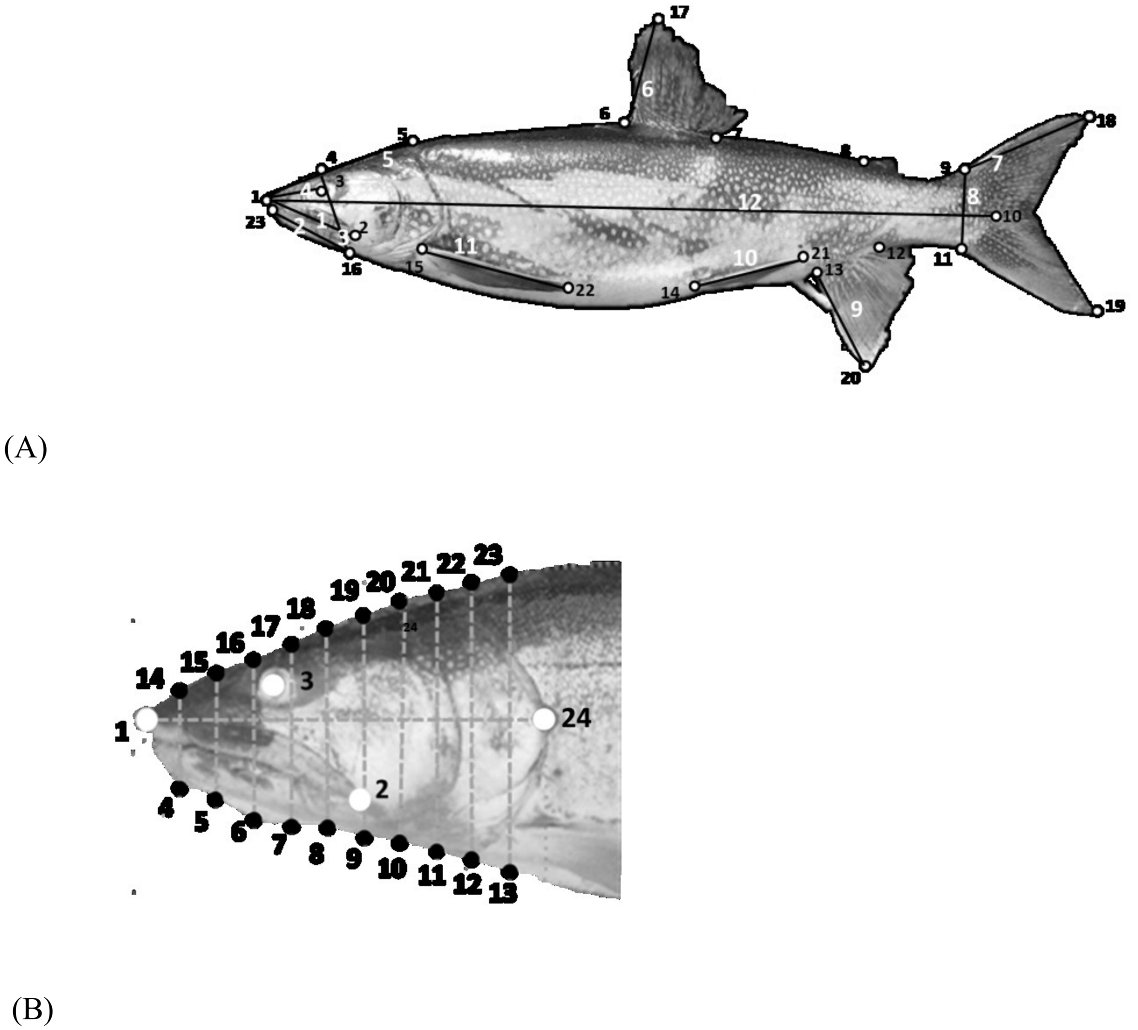


Fig. 3-2. (A) Twenty-three landmarks (white circles, black numbers) used to measure body shape and linear measurements of Lake Trout from Great Bear Lake: (1) anterior tip of the snout, (2) posterior tip of maxilla, (3) center of eye, (4) top of cranium at middle point of eye, (5) posterior of neurocranium above tip of opercle, (6) dorsal fin anterior insertion, (7) dorsal fin posterior insertion, (8) adipose fin anterior insertion, (9) caudal fin dorsal insertion, (10) hypural plate midpoint, (11) caudal fin ventral insertion, (12) anal fin anterior insertion, (13) anal fin posterior insertion, (14) pelvic fin insertion, (15) pectoral fin insertion, (16) ventral surface of head below maxilla tip, (17) dorsal fin tip, (18-19) caudal fin tips, (20) anal fin tip, (21) pelvic fin tip, (22) pectoral fin tip, and (23) anterior tip of lower jaw. Fin and body length measurements of Lake Trout from Great Bear Lake are represented by black lines and white numbers: (1) upper jaw, (2) lower jaw, (3) head depth, (4) snout-eye, (5) head, (6) dorsal fin, (7) caudal fin, (8) caudal depth,

(9) anal fin, (10) pelvic fin, (11) pectoral fin, and (12) standard body length; standard body length was used to standardize fin and body lengths and depths. (B) 20 semi-landmarks (black circles and numbers, 4-23) were used along with one marker (24), and three landmarks (1-3, as in (a), to determine head shape.

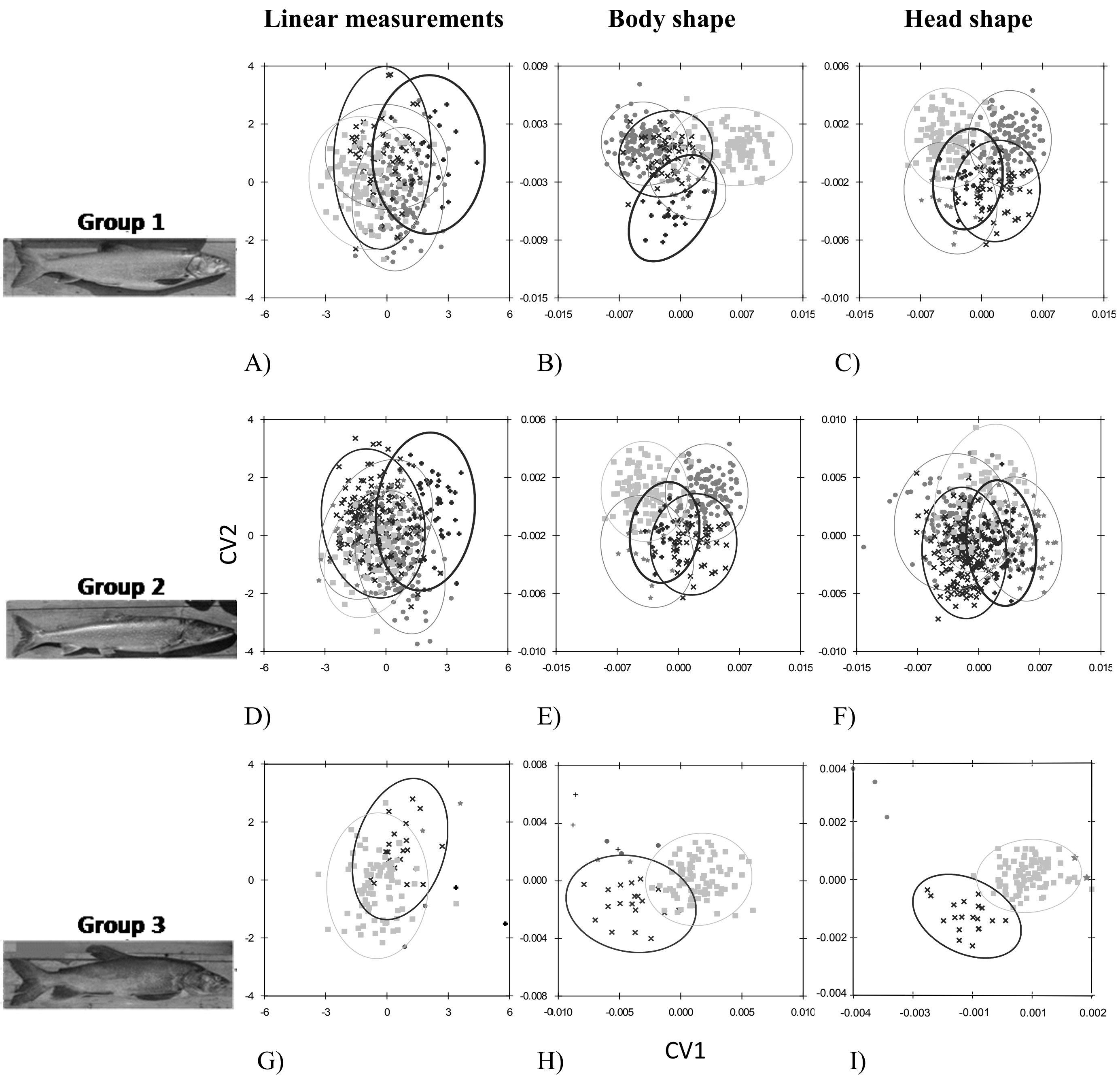
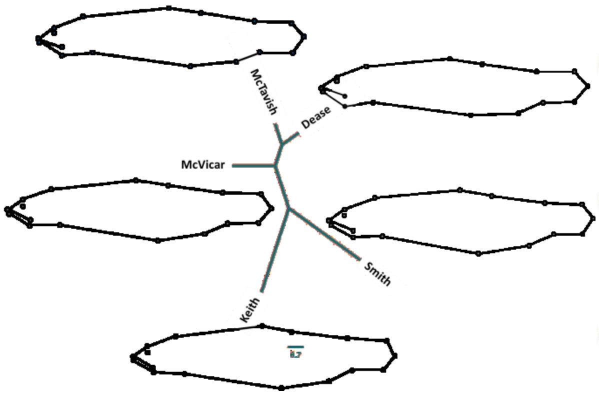
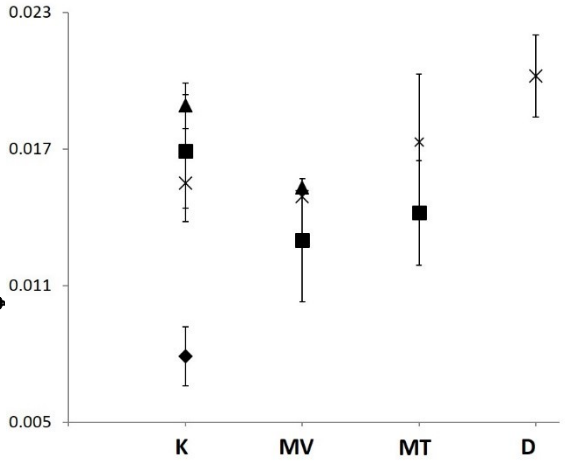


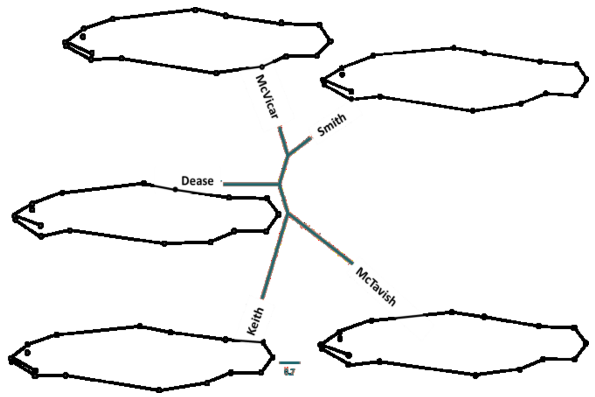
Fig. 3-3. Canonical Variate Analyses (CVAs) of linear measurements (a, d, g), body shape (b, e, h), and head shape (c, f, i) of 910 adult Lake Trout from Great Bear Lake, divided into three morphs. For each CVA, fish from different arms of Great Bear Lake are represented as follows: ● = Keith, x = McVicar, ★ = McTavish, ■ = Dease, and + = Smith. Each arm is also outlined by a 95% confidence ellipse.


McTavish
Dease
McVicar
Smith
Keith
0.7

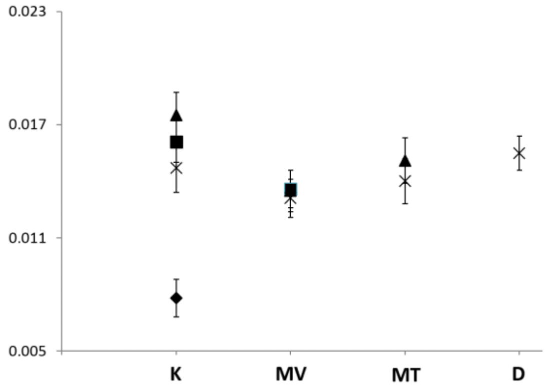
A)


0.023
0.017
0.011
0.005
K
MV
MT
D

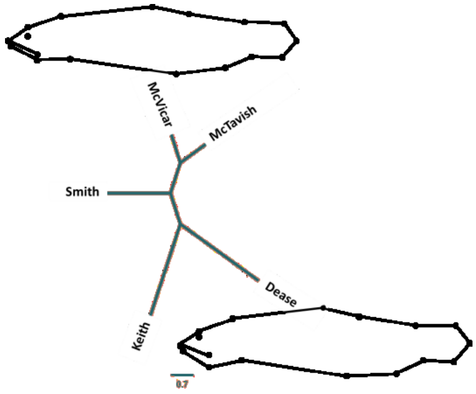
B)


McVicar
Smith
Dease
McTavish
Keith
0.7

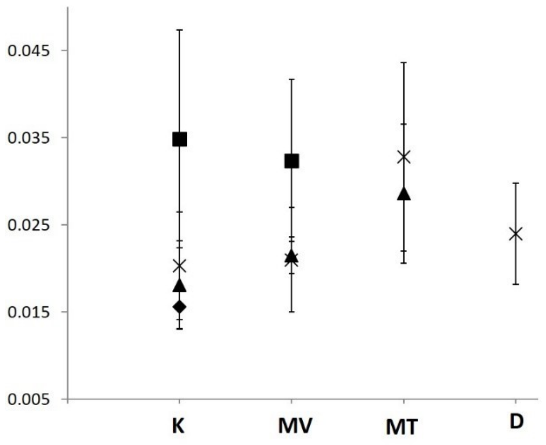
C)


0.023
0.017
0.011
0.005
K
MV
MT
D

D)

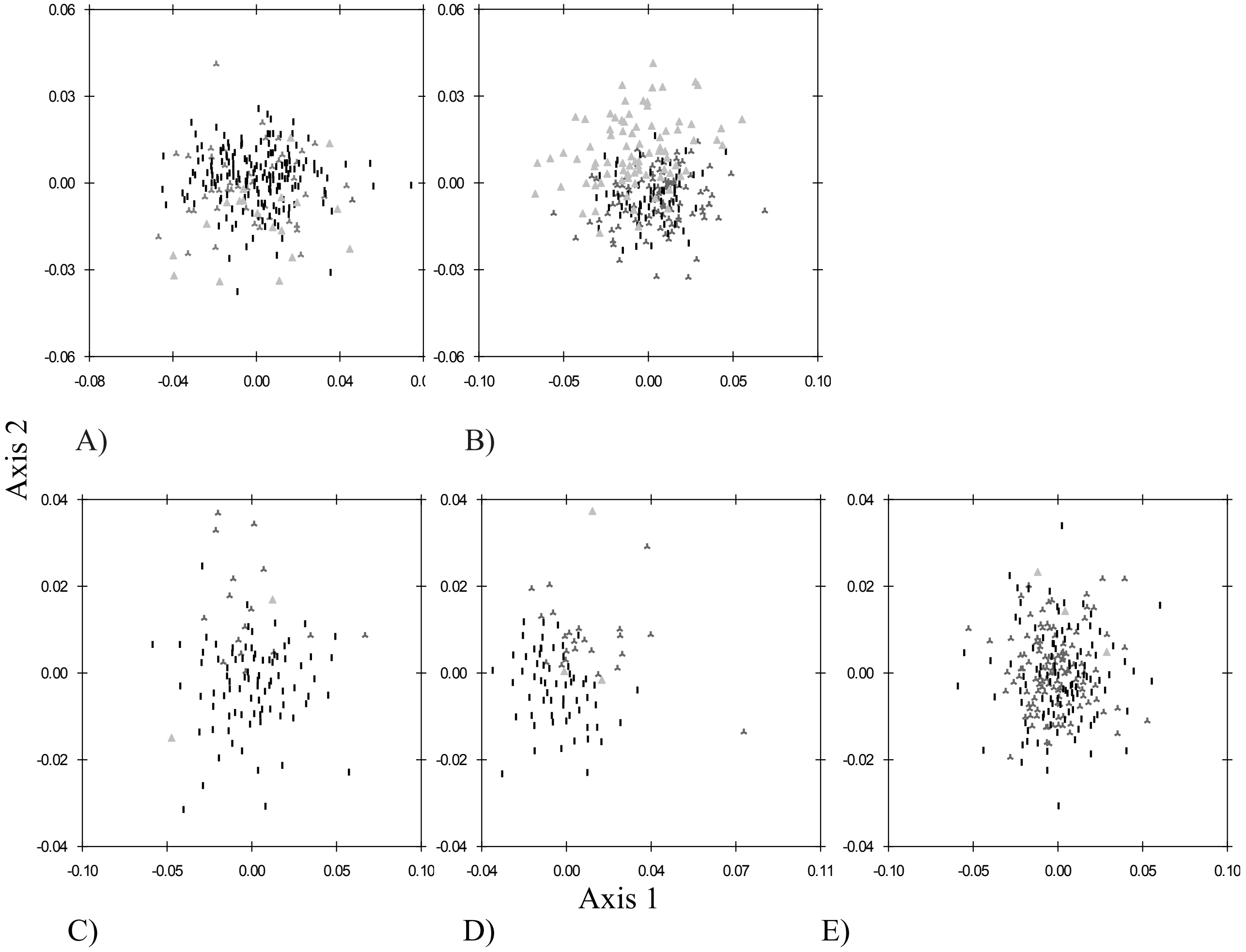

McVicar
McTavish
Smith
Dease
Keith
0.7

E)


0.045
0.035
0.025
0.015
0.005
K
MV
MT
D

F)

Fig. 3-4. Unrooted trees of Lake Trout body shape divergence and configurations of procrustes means of each arm of Great Bear Lake. Inter-arm distances from the body-shape mean and their respective Procrustes pairwise means (y-axis; ± 1 SE derived from 1600 boostraps) are presented for Morph 1 A-B), Morph 2 C-D), and Morph 3 E-F), where ◆ = McVicar, ■ = McTavish, ▲ = Dease, and **X** = Smith.



A) B)

C) D) E)

Fig. 3-5. NMS ordination of body shape byArm of capture: A) McVicar, B) Dease, C) McTavish, D) Smith, and E) Keith arms. Three morphs are represented as follows: Morph 1=⅄, Morph 2=|, and Morph 3=▲.

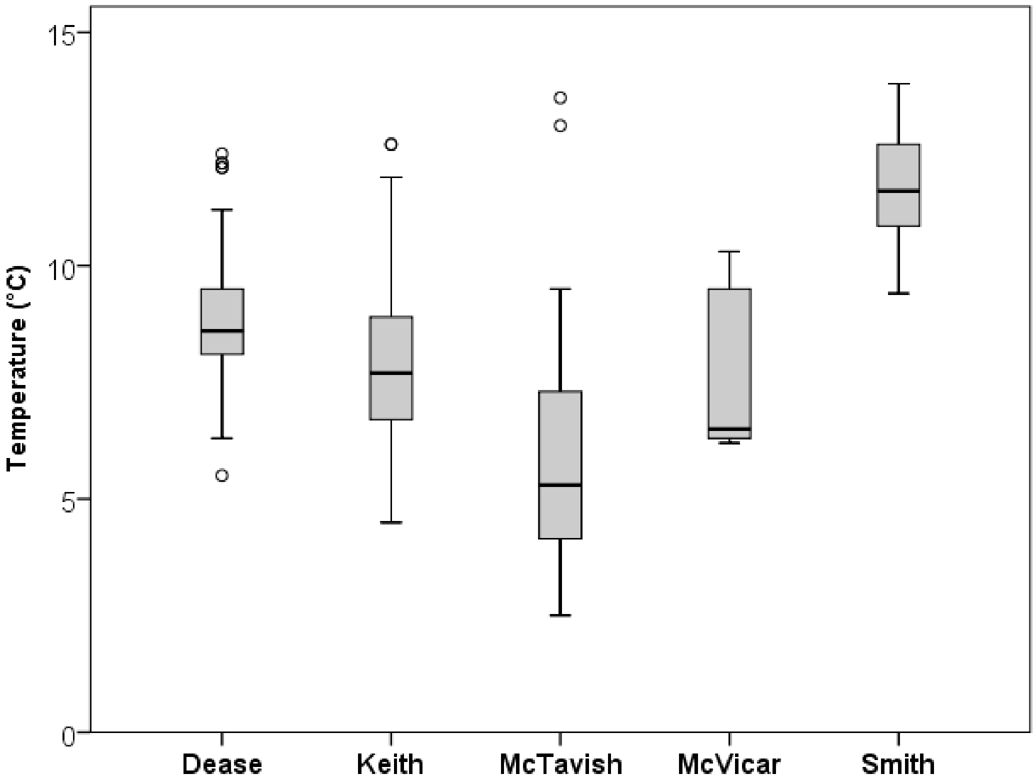


Fig. 3-6. Boxplots of July-August surface water temperatures (°C) sampled at our net locations in each of the five arms of Great Bear Lake. See Methods (*Data collection*) for years in which each arm was sampled. Horizontal lines represent median values, boxes enclose the two middle quartiles, whiskers represent 1.5 of the interquartile range, and empty circles indicate outliers beyond the interquantile range.

Chapter 4: Fatty acid signatures and stomach contents of four sympatric Lake Trout: assessment of trophic patterns among morphotypes in Great Bear Lake.

Abstract

Sympatric diversification in Lake Trout is generally linked to habitat use (especially depth), as a result of foraging on certain prey items. However, extensive sympatric divergence has taken place in the shallow waters (≤ 30 m) of Great Bear Lake, with multiple Lake Trout morphs varying in head and fin characteristics. To investigate diet partitioning as a potential explanatory mechanism for this diversification, we assessed trophic characteristics and relationships among four sympatric shallow-water morphs of Lake Trout via analyses of fatty acids and stomach contents. Fatty acids and stomach contents both identified Lake Trout, Cisco, and *Mysis* as key prey items in the diets. Interestingly, terrestrial invertebrates were also seasonally important among morphs, reflecting temporal variability of available prey in this Arctic lake. Some diet partioning was observed among morphs; Morph 1 was characterized as a generalist, Morph 3 was more benthic-oriented, Morphs 2 and 4 were mainly pelagic feeders. Of the latter, Morph 4 was the most specialized, whereas Morph 2 exhibited alternative feeding tactics between benthic cannibalistic and pelagic piscivorous feeding. Our findings demonstrate that complementary dietary methods can elucidate habits of opportunistic feeders, a task that can often be problematic, given the complex and variable diets. Our results add new information and perspectives on the current model of Lake Trout differentiation, demonstrating niche partioning based on benthic versus pelagic habitat use and generalist versus specialist feeding tactics.

Introduction

Resource polymorphism, the occurrence of discrete intraspecific morphs differing in their niches (especially feeding or habitat use), is a product of ecological adaptations associated with divergent selection (Smith and Skúlason, 1996). Sympatric resource polymorphism can arise rapidly, especially in novel environments such as newly-formed lakes or remote islands, where many of the most striking examples have been documented. Examples among fishes include Arctic Char (*Salvelinus alpinus*), whitefishes (*Coregonus spp.*), and Threespine Stickleback (*Gasterosteus aculeatus*) (Schluter & Rambaut, 1996; Jonsson & Jonsson, 2001; Mckinnon & Rundle 2002; Kahilainen *et al*., 2007). As a consequence of its glacial history, the Canadian freshwater fish fauna has a number of interesting examples of ecological and evolutionary characteristics resulting from geologically recent or on-going events, thus providing opportunities to study processes linked to resource polymorphism (Schluter, 2000; Guiguer *et al*., 2002; Ruzzante *et al*., 2003).

Investigating the relationship between morphological variation and diet is broadly accepted as an important feature for understanding the origin and maintenance of Lake Trout phenotypic diversity (Zimmerman *et al*. 2006, 2007, and 2009; Stafford *et al*., 2014). Conventional dietary methods include stomach content analysis (SCA), which provides a "snapshot" of the diet. However, SCA is known to have limitations and biases, including regurgitation during capture, variable rates of digestion of food items, identification of partly digested material, underestimation of prey size, and lack of temporal representation (Phillips *et al*., 2001; Krahn *et al*., 2007; Vinson & Budy, 2011). As a result, SCA should not be used alone to characterize diet (Kear, 1992) and should be complemented with an alternative method (Beaudoin *et al*., 1999).

Complementary methods to SCA, such as molecular biomarkers, have more recently been developed to elucidate dietary composition and trophic links of organisms over longer time periods (Iverson, *et al*., 1997; Budge *et al*., 2002; Bradshaw *et al*., 2003). Fatty acids (FA) are one set of dietary biomarkers, representing a large group of molecules that comprise the majority of lipids found in all organisms (Budge *et al*., 2006). The principle behind FA analysis is that consumers derive their lipids either from their diet or by endogenous lipogenesis from dietary protein or carbohydrate precursors (Howell *et al*., 2003). However, a relatively limited number of FA can be biosynthesized by animals, facilitating the distinction between dietary vs. non-dietary FA (Cook, 1991; Iverson *et al*., 2004). Thus, FA analysis assumes that dietary lipids are broken down into their constituent FA and incorporated relatively unchanged into the consumer tissues (Howell et al., 2003; Iverson *et al*., 2004). Both qualitative and quantitative FA analyses have been used to compare diet composition between organisms, and examine their spatial and temporal variations (Iverson, 2009). FA analysis is commonly used in studies of top predators, such as marine mammals, bears, and seabirds (Budge *et al*., 2006), but is increasingly receiving attention in freshwater ecosystems (Ahlgren *et al*., 2009; Iverson, 2009; Eloranta *et al*., 2013).

Morphology can also reflect diet of an organism; for example, gill-rakers are commonly used to infer foraging behavior in fishes (Kahilainen *et al*., 2011). The gill-raker apparatus plays a role in prey retention efficiency, with the gill-rakers functioning as a cross flow filter (Sanderson *et al*., 2001; Smith & Sanderson, 2008). Longer and more gill-rakers enhance cross flow filtering and improve retention of small prey whereas shorter and fewer gill-rakers are linked with larger prey and/or benthic habitat (Wright *et al*., 1983; Kahilainen *et al*., 2011). Characteristics such as these that can be linked with phenotype-environment associations can be valuable tools for determining feeding habits of morphotypes.

Despite some evidence of both piscivory and insectivory (Blackie *et al*., 2003; Alfonso, 2004; Chavarie *et al*., 2013; Chavarie *et al*., in press (a)), the nature of the ecological processes driving this phenotypic diversity remains unknown. The current study was undertaken to advance our understanding of the mechanisms for the extensive Lake Trout morphological variation found previously at Great Bear Lake (Blackie *et al*., 2003; Alfonso, 2004, Chavarie *et al*., 2013, Chavarie *et al*., in press (a)). The main objective is to compare diet composition among Lake Trout morphotypes by evaluating short-term diet composition from SCA in combination with longer-term patterns from FA analysis. We also examine gill-raker structure among Lake Trout morphotypes as an indicator of diet differences (e.g. Amundsen *et al*., 2004; Vila-Gispert *et al*., 2007). This study should advance our understanding of the niche relationships among Lake Trout morphotypes by assessing the link between morphological and ecological variation within a species.

Materials and Methods

Study system

A recently described Canadian post-glacial example of sympatric polymorphism is Lake Trout (*Salvelinus namaycush*) from Great Bear Lake, (N66° 06' W120° 35'). Great Bear Lake is the largest lake entirely within Canada; its surface area (31 790 km^2) is divided into five semi-isolated ″arms″. Maximum depth is 446 m, although mean depth is ca. 90 m (MacDonald *et al*. 2004). Four distinct morphotypes co-exist in the shallow-water zone (≤30m) of the lake

(Chavarie *et al.*, 2013). Morph 1 was characterized by a smaller head and intermediate fins, Morph 2 had the largest head and jaws but smallest fins, Morph 3 had the longest fins and a robust body shape, whereas Morph 4 had a thick curved lower jaw and the smallest caudal peduncle (Chavarie *et al.*, 2013, Chavarie *et al.*, in press (a)). An additional level of morphological differentiation within some of these morphs was demonstrated among the five arms of Great Bear Lake, mainly in relation to body shape (Chavarie *et al.*, in press (a)).

Field sampling

For this study, fish were caught at depths ≤ 30 m using paired bottom sets (ca. 24 h) of a 14-cm and a multi-mesh (3.8-14 cm) gill net during July and August. Sampling occurred in all five arms over multiple years: Dease (2005 and 2010), McVicar (2003 and 2008), Keith (2002, 2003, 2004, 2006, 2007, and 2010), McTavish (2009) and Smith (2006). Sampling procedures on captured Lake Trout included recording fork length, weight, sex, and stage of maturity, which was divided into juvenile, mature, and resting categories (see Chavarie *et al.*, 2013). For each fish captured, a piece of dorsal muscle, the first left gill-arch, and the stomach (if it was not empty) were removed and frozen.

Stomach content analysis

In the laboratory, stomachs were opened (n=42, 32, 16, and 2 for Morphs 1-4, respectively) and contents were sorted by prey type and weighed. Since Morph 4 is a rarer morph combined with a high rate of empty stomachs (n=20), only two stomachs were sorted through, resulting in a low sample size for that specific morph. Depending on the degree of digestion of prey items, identification ranged from species to family for both fishes and invertebrates. To facilitate data presentation, prey were pooled into the following groups: 1) fish, 2) Malacostraca,

3) Mollusca, 4) Orthoptera, 5) Lepidoptera, 6) Aranea, 7) Diptera, 8) Hemiptera, 9) Hymenoptera, 10) Trichoptera, 11) Coleoptera, 12) Plecoptera, and 13) unknown invertebrates. Prey were also categorized as invertebrate or fish, and by prey habitat (terrestrial, benthic, pelagic, littoral, and surface), based on Scott and Crossman (1973), Triplehorn and Johnson (2005), and Merritt *et al*., (2008). Diet composition was summarized by morphotype using frequency of occurrence (*%O)*, and percentage by abundance (*%N*) and mass (*%M)*. To scale the importance of each prey category among morphotypes, *%O*, *%N*, and *%M* were used to calculate the Relative Importance Index (RI) at the morphotype level but also at the individual level, where %O was excluded (George & Hadley 1979).

Using our data on prey mass, individual specialization was estimated across all individuals, but also within a morphotype, using DIETA and Indspec1 programs (produced by D. Bolnick, http://web.biosci.utexas.edu/bolnick_lab/styled-5/index.html), calculating, respectively, the E (mean pairwise diet dissimilarity between individuals) and WIC/TNW (Within-Individual Component)/(Total Niche Width) indexes (Bolnick *et al*., 2007; Bolnick *et al*., 2010). WIC/TNW is the ratio of the average individual niche width to the population niche width, and ranges from zero (strong specialization) to one (generalization) (Bolnick *et al*., 2002). We calculated morphotype diet proportions by averaging across individuals to obtain a measure of electivity (the proportion of decision making events that resulted in capturing resource type *j*) (Bolnick, 2002). To ensure that WIC/TNW was not sensitive to the particular measure of individual specialization, I also calculated a second index, E. E is the mean pairwise diet dissimilarity between individuals, where a value of zero implies an absence of inter-individual niche variation, increasing towards one with an increase of inter-individual variation (Araujo *et* *al*., 2008; Bolnick *et al*., 2010). Finally, to compare overall diet overlap among morphotypes, we calculated Schoener's proportional similarity, an index ranging from zero to one, for each pair of morphotypes; values higher than 0.6 represent significant biological diet overlap (Schoener 1968; Wallace, 1981).

Fatty Acids analysis

Dorsal muscle samples (Budge *et al*., 2011) were stored at -20 °C (Budge *et al*., 2006; Loseto et al., 2008, 2009; Kavanagh *et al*., 2010). Overall, FA analysis procedures, using 41 fatty acids (Appendix 4-1), followed the methods of Iverson *et al*. (1999) and Budge *et al*. (2006). Muscle samples were taken from indivuals sampled for SCA and from supplementary Lake Trout identified by Chavarie *et al*. (2013) to corresponding morphotypes (Morph 1 = 32, Morph 2 = 35, Morph 3 = 38, Morph 4 = 21, and Juvenile = 13). Initially, individuals were selected for both FA and SCA anlysis, but due to high rates of empty stomachs, it was not possible to match all samples for both analysis (empty stomachs were replaced by other samples afterward). Therefore, only 58 individuals across the 4 morphotypes were sampled for both FA and SCA anlysis. Muscle samples and prey items collected from stomachs and from gillnet by-catch (fish only) were freeze-dried, then homogenized with a mortar and pestle. Smaller fish and invetebrates were homogeneized whole to give the best representation of their FA signatures. Lipids were extracted from 1 g of the homogenate material using 2:1 chloroform-methanol containing 0.01% BHT (v/v/w) (Folch *et al*., 1957). After passive overnight extraction (at -20) in 2:1 chloroform:methanol samples were filtered through Whatman Grade 1 Qualitative filter paper and the filter paper/sample was rinsed twice with 2 mLs of 2:1 chloroform:methanol. Sample extract was collected in a test tube and 7 mLs 0.88 NaCl solution was added since NaCl encourages FAs 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 determination. The extracted lipid was used to prepare the fatty acid methyl esters (FAME) by transesterification with Hilditch reagent (0.5 N H_2SO_4 in methanol) (Morrison *et al., 1964).* The 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 ºC. Hydrogen was used as carrier gas flowing at 1.25 mLs/min for 14 minutes, and increased to 2.5 mLs/min for 5 minutes. The split/splitless injector was heated to 260 ºC and run in splitless mode. The oven program was as follows: 60 ºC for 0.66 min, increasing by 22.82 ºC/min to 165 ºC with a 1.97 min hold; increasing by 4.56 ºC/min to 174 ºC and by 7.61 ºC/min to 200 ºC with a 6 min hold. Peak areas were quantified using Agilent Technologies ChemStation software. FA standards were obtained from Supelco (37 component FAME mix) and Nuchek (54 component mix GLC-463). Seventy three FAME were identified via retention time and known standard mixtures and are reported as percentage of total FA.

All FA 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 FA, 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). FAs suggested by Iverson et al. (2004) as important dietary FAs, that to transfer from prey to predator, were used in our analyses. FA profiles were log-transformed to obtain normality and were explored with PC-ORD version 6 (McCune & Mefford 2011) using a principal component analysis (PCA) to provide inferences about patterns of habitat use (aquatic vs. terretrial and benthic vs. pelagic habitats defined based on both FA literature and prey ecology) and feeding ecology among the four Lake Trout morphotypes. Discriminant analyses and a jacknife validation procedure were also performed with SYSTAT V. 12 (Systat Software Inc., Chicago, IL, USA) on the FA signature among the four morphotypes to determine if their FA profiles differed.

Finally, gill-arches and gill-rakers were measured (±0.01 mm) with an occular micrometer at 64X magnification and gill-rakers were counted. We measured and then averaged the longest and shortest gill-rakers from the upper and lower gill-arch, along with one gill-raker from the middle of the arch, defined as the confluence of the ceratobranchial and epibranchial bones (Bodaly, 1979). Gill-rakers were measured from the center of the base, at the point of emergence from the gill-arch, to the tip of the raker. The three measurement locations were highly correlated, and thus, all measurements were averaged for each fish. A Multivariate Analysis of Variance (MANOVA) was performed with SPSS V. 21 on gill-raker count and length and arch-length among morphotypes, with length of fish as a co-variate, followed by a LSD post-hoc comparison with Bonferroni correction.

Results

Lake Trout diets in Great Bear Lake comprised of a variety of prey, both within and among morphotypes (see Appendix 4-2 for proportions and scientific names for taxa). Overall, Lake Trout, Round Whitefish, Burbot, and Sculpin were the most common fish prey (>10% by abundance and/or mass), whereas the most common invertebrate prey were Mysidae, Gammaridae, Formicidae, Hymenoptera, and Trichoptera (Appendix 4-2). Interestingly, diets of all morphs included a large proportion and diverse array of terrestrial invertebrates, varying between 28% to 50% of their diet (Fig. 4-1). Strong individual specialization was found overall and within morphotypes with relatively low WIC/TNW values (between 0.34 and 0.57), and relatively high E values (between 0.68 and 0.99) (Table 4-1). However, most Schoener overlap indices were higher than 0.6, indicating substantial diet overlap among morphotypes, except for Morph 4, where values were equal vs. Morphs 1 and 3 (0.061 and 0.056 respectively) and lower vs. Morph 2 (0.39) (Table 4-2).

The first two axes of the FA PCA explained 48.6% of the variation among the diets of the four adult morphs and juveniles. The first axis separated pelagic vs. benthic fish, based on FAs that have been previously associated with those two habitats (Dalsgaard *et al*., 2003; Budge *et al*., 2006; Tucker *et al*., 2008; Iverson, 2009) (Fig. 4-2). Individuals of Morph 4 were clustered together and positioned as pelagic fish, whereas those of Morph 2 appeared to be divided into two groups (pelagic and benthic). The benthic individuals from Morph 2 overlapped with juveniles and a few individuals of Morphs 1 and 3. The first two axis of a second FA PCA, using the four adult morphs, juvenile trout, and trout prey, explained 37.6% of the variation. Lake Trout and their prey were positioned on the X axis by different FA signatures associated with aquatic vs. terrestrial habitats (Dalsgaard *et al*., 2003; Gladyshev *et al*., 2009), with almost no FA overlap between those two habitats (Fig. 4-3). There was also some division between pelagic and benthic habitats along the Y-axis, based on Lake Trout individuals identified in previous PCA as benthic being higher on the Y-axis compared to pelagic Lake Trout. Cisco (adults and juveniles), and Northern Pike overlapped with Lake Trout FA signatures, while Arctic Grayling, Lake Whitefish, and *Mysis* partially overlapped with Lake Trout.

Pelagic Lake Trout (Morphs 2 in part, and 4) contained higher concentrations of the FAs 14:0, 18:2n-6, 18:3n-3, 18:4n-3, 18:1n-9, 20:1n-7 and 22:1n-9, whereas Morph 2 (benthic) and juveniles had higher concentrations of 16:0, 18:0; 20:4n-6, and 22:6n-3 (Fig. 4-2). Many individuals of Morphs 1 and 3 were more dispersed, but revealed a general pattern driven by 16:1n-7, 16:2n-4, 16:3n-4, 18:1n7, 18:2n4, 18:3n6, and 22:1n7. Morph 2 (benthic and pelagic) was also categorized by FA 22:5n-6, which was positioned to the lower part of the PCA (Fig. 4-2). Terrestrial invertebrates had generally higher concentrations of 18:2n-6, 18:3n-1, and 18:3n-3, whereas aquatic organisms, fish in particular, had higher concentrations of 20:4n-6, 20:5n-3, and 22:6n-3 (Fig. 4-3).

Discriminant analysis of the FA data showed significant differences among adult morphs and juveniles ($\lambda = 0.05$, $p<0.01$), especially for Morphs 2 and 4, whereas Morphs 1, 3, and juveniles overlapped (Fig. 4-4). Jackknife classification success was the highest for Morph 4 (86%) while Morphs 1, 2, 3, and juveniles had success rates of 56, 57, 55, and 61%, respectively.

Finally, gill-raker length differed among morphotypes ($p<0.01$) (Fig. 4-5), but no differences were observed in total counts of gill-rakers ($p=0.36$) or gill-arch length ($p=0.17$). Morph 3 had significantly longer gill-rakers than Morph 2 and 4 ($p\leq0.05$), Morph 1 was intermediate (and significantly longer than Morph 2; $p=0.02$), whereas Morphs 2 and 4 had the shortest gill-rakers. Length of fish, as a covariate, was significant only for gill-arch length ($p<0.01$).

Discussion

Our study demonstrated significant differences in prey exploitation among the four Lake Trout morphotypes inhabiting shallow-water of Great Bear Lake based on FA analysis and SCA.

Differences in gill-raker length also suggest that some feeding specialization has evolved (Kahilainen *et al*., 2007). However, by including an integrative approach, our analysis revealed overlaps in habitat use and prey items among the Lake Trout morphotypes. While Lake Trout have the reputation of being a voracious predator, they are also recognized as being opportunistic feeders and like many aquatic consumers, demonstrate flexible feeding habits both within and among populations (Vander Zanden *et al*., 2000). This appeared to be the case within and among the four morphotypes of Lake Trout in Great Bear Lake, each of which were found to exploit a range of prey from diverse environments.

One of the unexpected findings of this study was the importance of terrestrial insects in the diet, which contributed close to half of the stomach contents of each morph. In smaller lakes, Lake Trout are conventionally thought to feed predominately on fish, with some invertebrates contributing to the diet in the spring and summer (Martin, 1952; Jude *et al*., 1987). In many instances when invertebrates are found in the diet, they are usually aquatic (Martin, 1970; Madenjian, *et al*., 1998; Roseman *et al*., 2009). However, Zimmerman *et al*. (2007; 2009) found that in Mistassini and Great Slave Lakes, also large and deep northern lakes, terrestrial insects contributed considerably to the diets of both deep- and shallow-water morphs. Several large individuals of the shallow-water morph, a piscivorous form, appeared to have specialized on terrestrial insects in Great Slave Lake (Zimmerman *et al*., 2009). Similar to our study, Zimmerman *et al*. (2007, 2009) found terrestrial Coleoptera, Diptera, and Hymenoptera, but abundances were lower. Our results, together with Zimmerman *et al*. (2007; 2009), suggest that in northern aquatic systems, Lake Trout use temporal pulses of food, such as by surface feeding on flying insects (Martin, 1952).

While SCA demonstrated the importance of terrestrial prey during the summer (when our samples were collected), the disparity in FA signatures between Lake Trout and terrestrial insects suggest the latter's seasonal nature as prey. FA 18:2n-6 and 18:3n-3 are useful terrestrial biomarkers at lower trophic levels because they are common in terrestrial plants (Sargent *et al*., 1995; Brett & Müller-Navarra, 1997). Terrestrial omnivorous insects are also unique in possessing the Δ12 desturase and thus are able to convert 18:1n-9 to 18:2n-6 (Dalsgaard *et al*., 2003; Gladyshev *et al*., 2009). Both of these biomarkers were generally lower in Lake Trout, compared to terrestrial invertebrates, suggesting terrestrial invertebrates were a small component of Lake Trout diet over the longer period represented by FA. Insect availability is strongly seasonal in the Arctic, since their growth, development, and emergence are temperature dependent, thus linked to summer (Danks, 1992; Danks *et al*., 1994; Strathdee & Bale, 1998). Overall, terrestrial insects are incorporated into Arctic freshwater foodwebs to a greater degree than might be expected, since lacustrine productivity is thought to be mostly benthic oriented (Jonsson et al., 1988; MacDonald et al., 2004).

In general, feeding strategies in fishes are divided between generalist and specialist (Amundsen *et al*., 1996; Smith *et al*., 2011). The high overlap in diet observed among Lake Trout morphotypes from Great Bear Lake suggests that they are opportunistically taking advantage of short but substantial pulses of prey. Using a large resource spectrum may be an adaptive strategy of fishes living in environments where food availability is unpredictable (Dill, 1983; Smith *et al*., 2011) and niche expansion has been commonly observed in depauperate environments with few competitors, such as post-glacial lakes (Bolnick *et al*., 2010). Variation in resource use among individuals (high values of E) might be the result of environmental differences in resource availability across time and space (Bolnick *et al*., 2003; Pires *et al*., 2011), which is supported by diet differences among the different arms of Great Bear Lake (Chavarie *et al.*, in press (a)).

Nonetheless, PCA and discriminant analysis on FA profiles confirmed the persistence of diet overlap between Morphs 1 and 3. This seems to differ from the standard sympatric resource polymorphism model, where a subset of individuals within a population switches to a novel and/or sub-optimal resource, reducing intraspecific competition (Olsson *et al.*, 2006; Moles *et al.*, 2010). The nature of the diversification between Morphs 1 and 3 remains unclear, but is not necessarily associated with different alternative diets. Although there was overlap among the FA signatures, a high proportion of Morph 3 FA profiles were driven by 16:1n7 and 18:1n7, known to be diatom biomarkers and to be found in high concentrations in benthic invertebrates and/or fish (Virtue *et al.*, 2000; Budge *et al.*, 2002; Tucker *et al.*, 2008; Stowasser *et al.*, 2009; Mariash *et al.*, 2011). Indeed, *Mysis*, gastropod, and amphipod FA profiles were driven by 16:1n7 and 18:1n7 and SCA supported the importance of *Mysis* in the Morph 3 diet. The high relative mass of Slimy Sculpin in Morph 3 stomach contents further indicated their benthic habitat niche, although their long gill-rakers is not a typical characteristic of benthic exploitation (Amundsen *et al.*, 2004; Kahilainen *et al.*, 2011). In contrast, Morph 1's more dispersed FA signatures, combined with intermediate gill-rakers, suggested a more generalized diet. Thus, differences in habitat use, rather than specific prey types, might be part of the selective pressures operating on Lake Trout diversity in Great Bear Lake.

Although discrimination of Morph 4 based on morphology was not as apparent (Chavarie *et al.*, 2013), this morph was clearly distinct with respect to its long-term diet. FA analysis indicated diet specialization for Morph 4, with a single distinctive cluster of FA signatures among individuals. Similarly, Morph 2 individuals showed some distinction in their FA profiles, but were divided into two clusters, one of which was slightly overlapping with Morph 4. The overlapping Morph 2 and 4 individuals were characterized by C_{20} and C_{22} monounsaturates that can be used as biomarkers of food webs based on pelagic copepods (Ahlgren *et al*, 2009; Loseto *et al*., 2009; Stowasser *et al*., 2009). Specifically, 20:1n-9 and 22:5n-6 are well known indicators of diets based on calanoid copepods, which are particularly important in northern pelagic food webs (Kattner *et al*., 1998; Budge *et al*., 2006; Ahlgren *et al*., 2009; Loseto *et al*., 2009). Interestingly, both Morph 2 and 4 were characterized by shorter gill-rakers, an indicator of feeding on larger prey (Wright *et al*., 1983; Kahilainen *et al*., 2011). These shorter gill-rakers suggest that, rather than pelagic copepods per se, it is the pelagic, zooplanktivorous Cisco (Howland *et al*., 2013) that is important to both predator morphs, which is supported by their overlaping fatty acids signatures with Cisco. The FA signatures of *Mysis* was also overlapping with Morph 4, suggesting importance to their diet, which was supported by SCA (although sample number was limited).

The individuals of Morph 2 that did not exhibit pelagic FA signatures overlapped with juvenile Lake Trout and some Morph 1 individuals, with FAs associated with benthic environments (Budge *et al*., 2002; Käkelä *et al*., 2005). These fish had high concentrations of 20:4n-6 and 22:6n-3, found in in diatoms and dinoflagellates, respectively. The former reflects a benthic feeding mode through benthic invertebrates to fish (Tucker *et al*., 2008; Stowasser *et al*., 2009). The latter FA has been reported in pennate diatoms (Iverson, 2009) and in filter feeders, linking planktonic dinoflagellates to benthic filter feeding bivalves (Virtue *et al*., 2000; Alfaro *et al*., 2006). The overlap between these more benthic Morph 2 individuals, juveniles and some Morph 1 individuals, suggests a significant trophic interaction, most likely cannibalistic, since stomach contents showed Lake Trout to be the most important fish prey for Morph 2. Cannibalism is also supported by relatively high concentrations of FA 16:0, 18:0 and 22:6n-3 and low concentrations of 16:1n-7 and 20:5n-3 (Dalsgaard *et al*., 2003; Iverson *et al*., 2004; Piché *et al*., 2010). Overall, it appears that the piscivorous Morph 2 of Lake Trout in Great Bear Lake has alternative feeding tactics, showing either a cannibalistic pattern in benthic habitats or preying on fishes, mainly Cisco, in pelagic environments.

Conclusion

Our study demonstrates the benefits of combining dietary methods (FA and SCA) to clarify trophic habits of an opportunistic feeder, a task that can be problematic due to complex and variable diet patterns. The "snapshot" of stomach contents and the longer time frame of FA allowed us to capture both the seasonality in Lake Trout diets and validate the importance of cannibalism in a subset of the piscivorous trout. Important terrestrial inputs to each morph demonstrated a link between terrestrial and aquatic systems in the Arctic, suggesting that northern Arctic Lake Trout can specialize and/or respond rapidly to short temporal pulses in potential prey.

Overall, the integrated results of our study suggest that polymorphism in the Lake Trout of Great Bear Lake is maintained not only by diet differences, but also by shallow-water habitat partitioning. Morph 1 appears to be the most generalized of the four morphotypes, Morph 3 is mainly benthic while Morph 4 is pelagic. Morph 2 exhibited alternative feeding tactics of benthic cannibalism and pelagic piscivory; because only adults were examined, this dichotomy should be independant of an ontogenic shift. Our results offer new perspectives on the current model of depth as the major driver of Lake Trout differentiation (Eshenroder, 2008). We add a new layer of information in the context of shallow-water habitat exploitation and demonstrate the role of benthic versus pelagic habitat segregation. However, the overlap and seasonality found among diets of different morphs brings into question the degree to which diet and habitat partitioning are involved as drivers of divergent selection. Thus, future studies will be necessary to increase our understanding of the mechanisms that form the basis of, and maintain shallow-water Lake Trout polymorphism in Great Bear Lake.

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Table 4-1. Ratio of the average individual niche width to the population niche width (Within Individual Component/ Total Niche Width), based on stomach contents, ranging from zero (individual specialization) to one (generalization) and mean pairwise diet dissimilarity between individuals indices (E), ranging from zero (absence of inter-individual niche difference) to one (complete inter-individual variation) for the four shallow-water morphtypes of Lake trout from Great Bear Lake.

	Overall	**Morph 1**	**Morph 2**	**Morph 3**	**Morph 4**
WIC/TNW	0.49	0.45	0.34	0.42	0.57
E	0.73	0.71	0.68	0.69	0.99

Table 4-2. Schoener index of niche overlap for the four shallow-water morphotypes of Lake Trout from Great Bear Lake, based on the relative importance of prey taxa in their diet (stomach content). Values higher than 0.6 represent significant biological diet overlap (Schoener 1968; Wallace, 1981).

	Morph 1	**Morph 2**	**Morph 3**
Morph 2	0.72		
Morph 3	0.89	0.73	
Morph 4	0.61	0.39	0.56

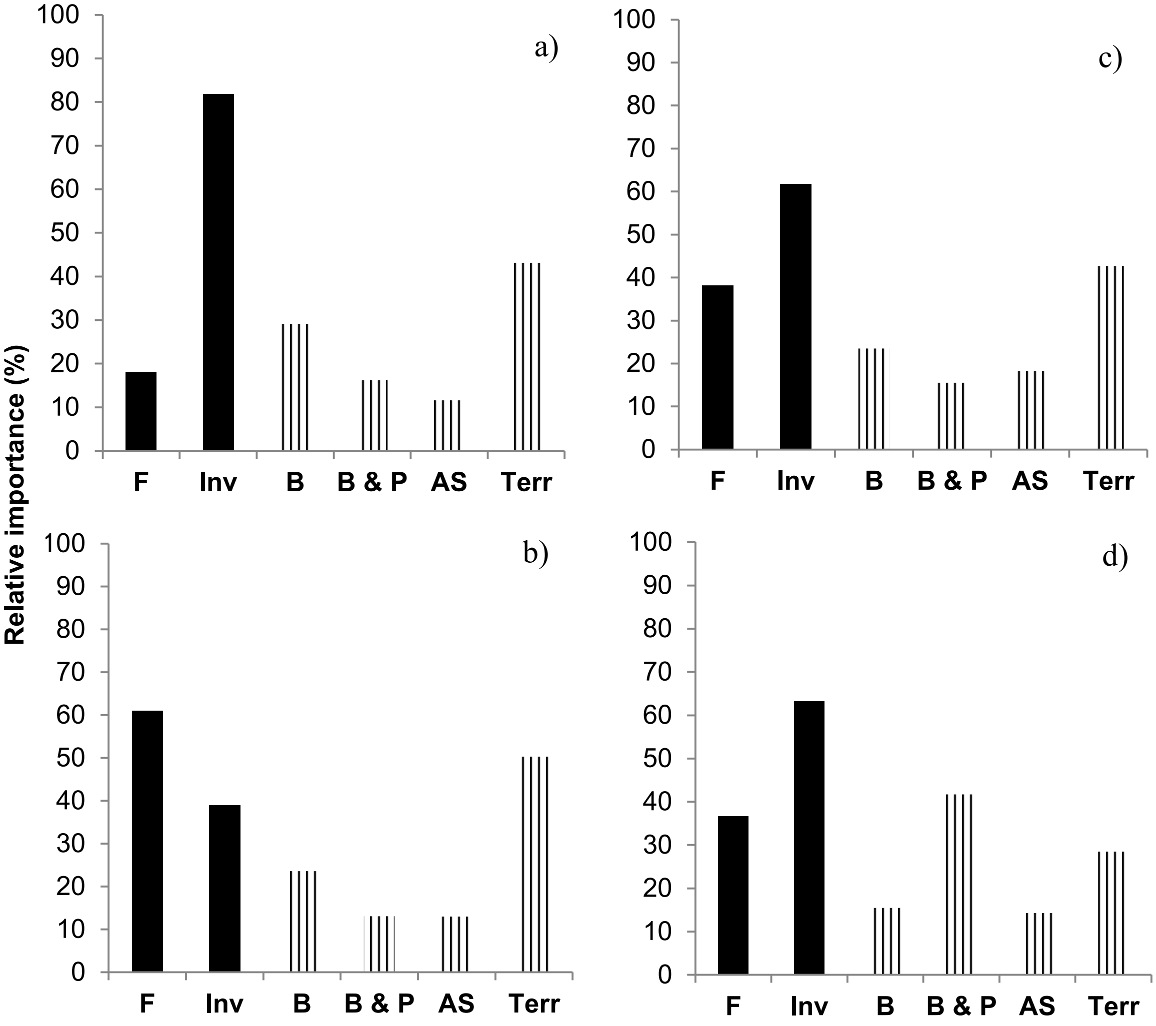

Fig. 4-1. Relative importance (%) of prey items in stomachs of Lake Trout from Great Bear Lake for Morph 1 (a), Morph 2 (b), Morph 3 (c), and Morph 4 (d). Prey are classified as: fish (F) or invertebrates (Inv) (solid bars), and as habitat categories (striped bars): benthic (B), Benthic & Pelagic (organisms that have vertical migration, e.g. *Mysis*) (B & P), aquatic surface (AS), and terrestrial (Terr). See Appendix 4-2 for identity and habitat categories of individual taxa.

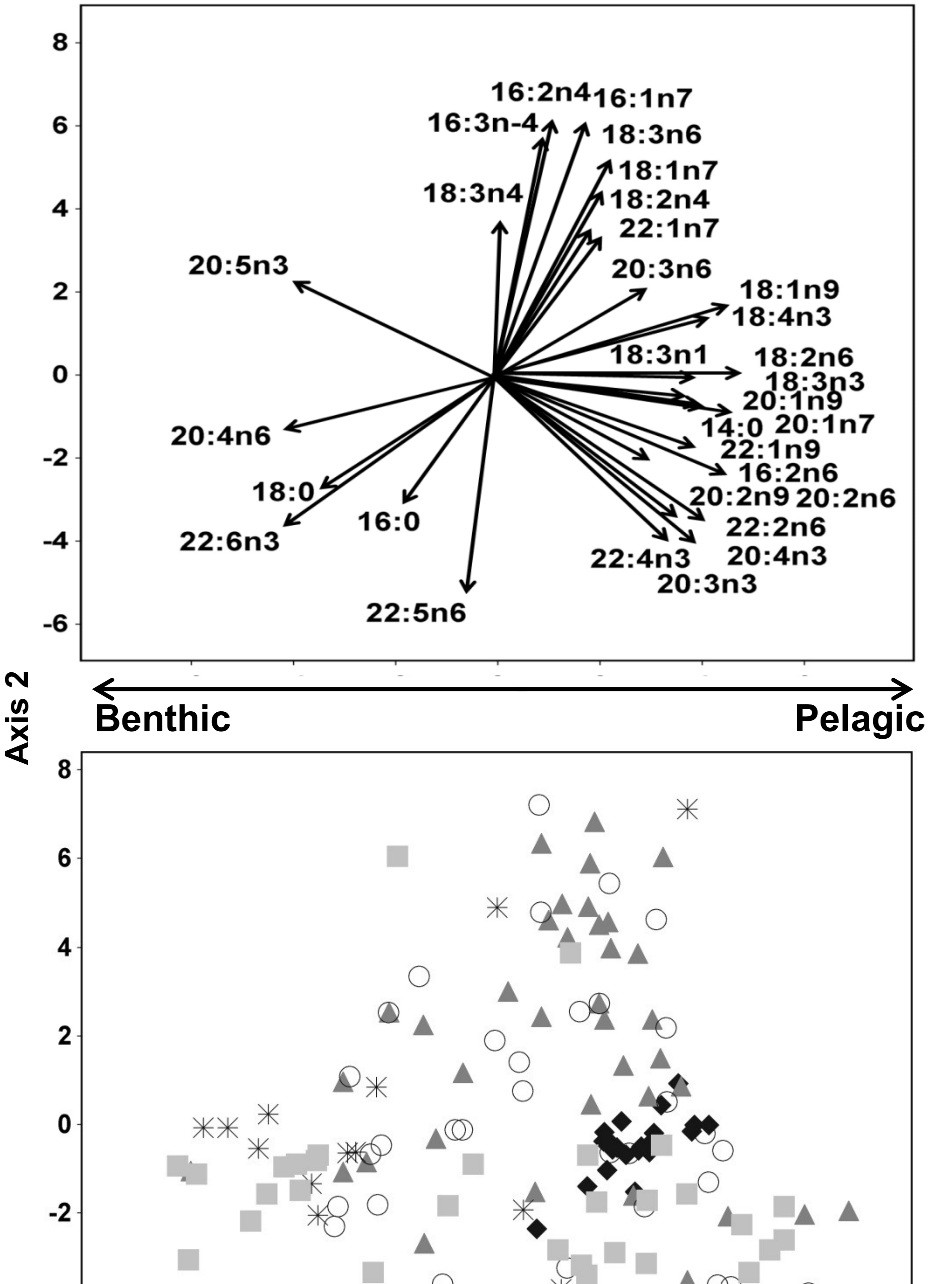

Fig. 4-2. PCA of four morphs of Lake Trout and their juveniles from Great Bear Lake, based on the abundance of 41 fatty acids in dorsal muscle tissue (PC1: 30.1%; PC2: 18.5% of total variance). Top: major vectors of individual FAs contributing to the positioning of morphs and

juveniles; Bottom: individual adult and juvenile Lake Trout, represented as: open circle =Morph 1, light grey square = Morph 2, dark grey triangle= Morph 3, black diamond= Morph 4, and star=juveniles. Angles and lengths of arrows represent the direction and the strength of relationship between variables and the principal components.

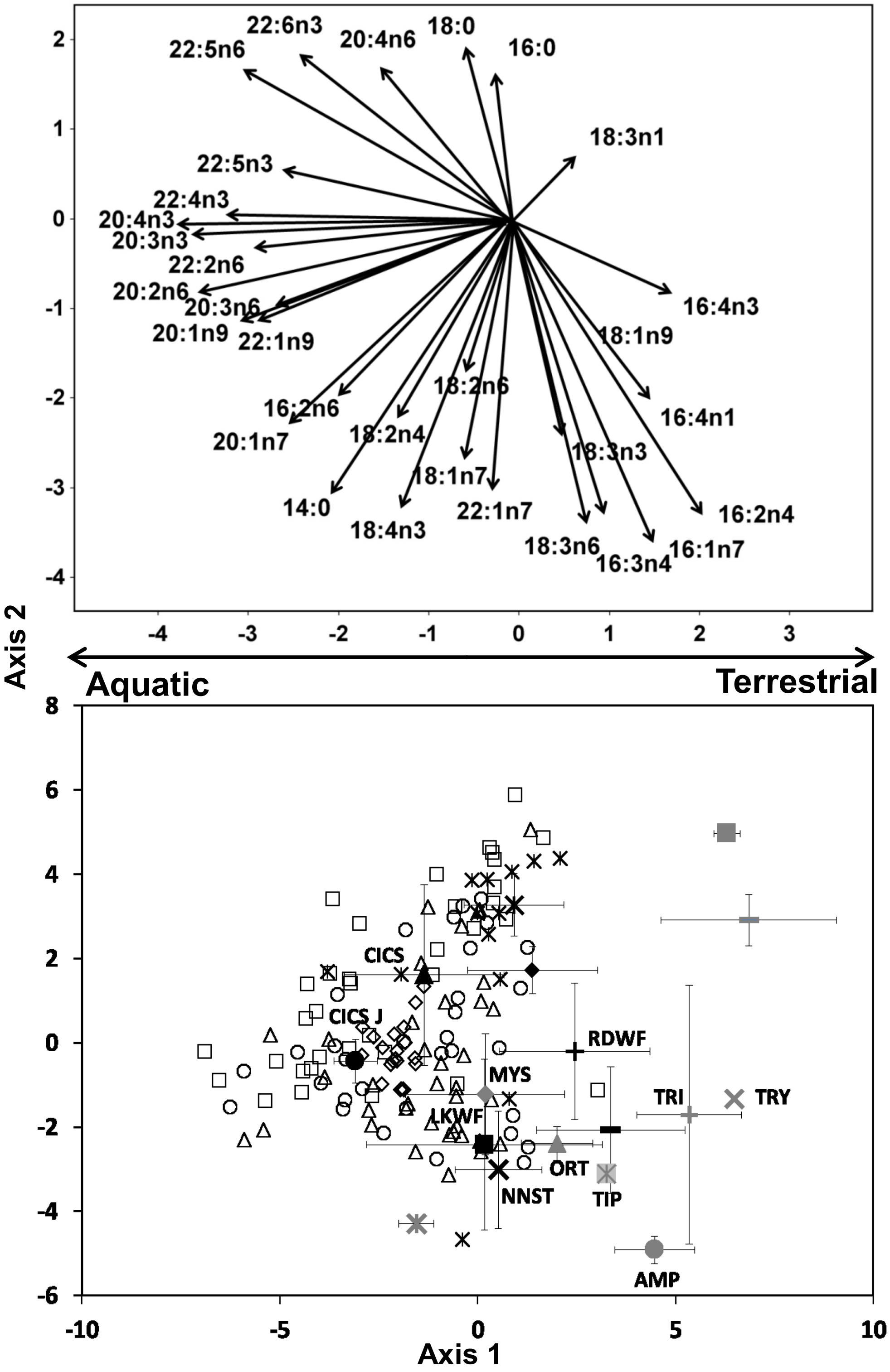

Fig. 4-3. PCA of four morphs for Lake Trout from Great Bear Lake, their juveniles, and potential prey based on 41 fatty acids (PC1: 21.6%; PC2: 16.0 % of total variance). Top: individual FAs

contributing to the position of Lake Trout and prey; Bottom: individual adult and juvenile Lake Trout are represented in open shapes as: circle = Morph 1, square = Morph 2, triangle= Morph 3, diamond= Morph 4, and star=juveniles. Prey (solid shapes) are represented as mean scores ± standard error; black are fish prey and grey are invertebrate prey. Prey are identified on the graph as follows: ARGR=Arctic Graying, CISC= Cisco, CISC J= Cisco juvenile, LKWF=Lake Whitefish, NRPK=Northern Pike, RDWF=Round Whitefish, SLSC=Slimy Sculpin, NNST= Ninespine Stickleback, AMP=Amphipods, FOR=Formacidae, GAS=Gastropoda, LEP=Lepidptera, MYS=*Mysis*, ORT= Orthoptera, TIP=Tipula, TRI= Trichoptera, and TRY= Tryphoninae. See appendix 4-2 for scientific name of each taxon. Angles and lengths of arrows represent the direction and the strength of relationship between variables and the principal components.

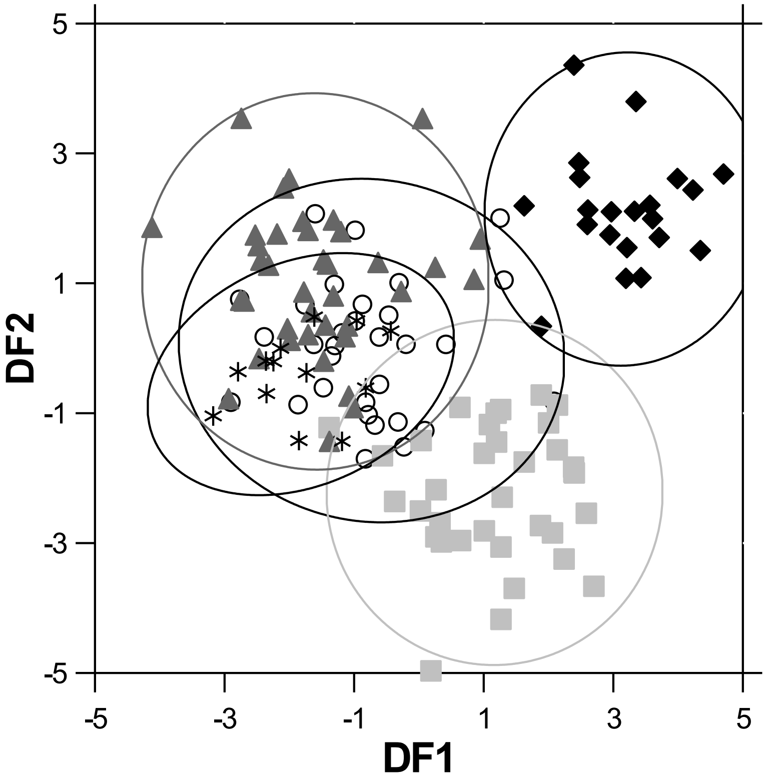

Fig. 4-4. Discriminant analysis for four morphs of Lake Trout and their juveniles from Great Bear Lake, based on the abundance of 41 fatty acids in dorsal muscle tissue. Open circle = Morph 1, light grey square = Morph 2, dark grey triangle= Morph 3, black diamond= Morph 4, and star=juveniles. Each group is outlined by a 95% confidence ellipse.

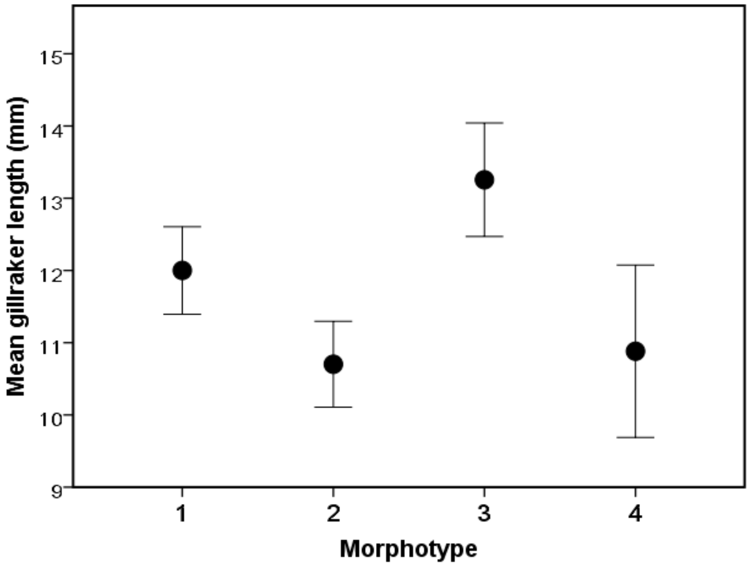

Fig. 4-5. Mean length (mm) ± standard error of gill-rakers for Morphs1-4 of the shallow-water morphotypes of Lake Trout from Great Bear Lake.

Chapter 5: Life history attributes of a sympatric case of Lake Trout: differentiation between four morphotypes from Great Bear Lake, NT.

Abstract

Phenotypic variation within populations, including life-history differentiation, within populations is a common feature of many species of salmonids, especially when inhabiting northern postglacial systems with a diversity of freshwater habitats. Thus, we compared the life-history attributes among four distinct Lake Trout morphs co-existing in the shallowwaters of Great Bear Lake, NWT. Juvenile and adult growth rate, age-at-maturity, size-at-maturity, and survival differed among morphs, supporting several predictions of life-history outcomes based on optimal foraging theory and degree of foraging specialization, including reduced somatic growth associated with higher investment in reproduction in the generalist morph, high growth throughout the life time of the piscivorous morph, and slower early growth stage but greater longevity and a large adult body size in the more benthic-oriented morph. However, other traits, such as the high proportion of resting individuals, suggest life-history adaptations to northern latitudes. In particular, morph 2 seems to take advantage of longer resting periods, to invest in post-maturation growth rather than reproduction. Fecundity and egg size varied among morphs with larger eggs for Morph 3 and higher fecundity for Morph 4. Overall, Lake Trout from Great Bear Lake demonstrated remarkable longevity and exceptional asymptotic sizes, even for a northern freshwater ecosystem, that have contributed to its reputation as a world renowned trophy fishery. Moreover, our study supports resource partitioning in Lake Trout, with insights on life-history evolution among morphs utilizing different food sources and habitats, contributing

to our understanding this lake ecosystem that exhibits one of the highest recorded levels of intraspecific diversity among freshwater fish.

Introduction

Numerous salmonid species are widely distributed in North America and maintain populations in a diversity of aquatic habitats (Braaten and Guy, 2002). For many of those species, variation in resource use, among but also within populations, is common. Within a given aquatic ecosystem, such variation can take the form of resource polymorphism or continuous niche variation (individual specialisation) (Bolnick et al., 2003; Morbey et al., 2006). For example, natural environmental gradients found in aquatic habitats, especially in lacustrine systems (e.g., pelagic-littoral, shallow-deep water), significantly influence phenotypic characteristics in salmonids, including life-history (Robinson and Parson, 2002; Braaten and Guy, 2002; Goetz et al., 2011).

Conspecific populations and morphs in salmonid species often show large differences in growth rate, adult size, age-at-maturity, and various other life-history attributes (e.g., Jonsson and Jonsson, 2001; Chavarie et al., 2010). Regardless of whether they originate from genetic and/or phenotypic divergence (Panfili et al., 2004), these differences can have population-level consequences, particularly when size is involved, since it is a key feature of their life-history (Baglinière and Maisse, 2002; Nicola and Almodóvar, 2004; Quince et al., 2008a). Individual growth rate, starting at early stages and continuing throughout life, plays a pivotal role in shaping life-history strategies (e.g., survival, longevity and reproduction) within a population (Rikardsen and Elliott, 2000; Loewen et al., 2010; Sogard et al., 2012).

Lake Trout, *Salvelinus namaycush*, is a widespread salmonid in North American lakes, where it is a dominant predator (Eshenroder, 2008; Jastrebski and Morbey, 2009). Although Lake Trout is not generally considered to be a *Salvelinus* species displaying much resource polymorphism (e.g., Snorasson and Skúlason, 2004; Hansen et al., 2012), recent studies have indicated that Lake Trout can display remarkable diversity. Across many lakes, including the Laurentian Great Lakes and those on the Canadian Shield, Lake Trout frequently specialize between shallow and deep water habitats and exhibit associated differences in body shape, life-history, lipid and trophic levels, buoyancy, and genetics (Moore and Bronte, 2001; Zimmerman et al., 2006, 2007, 2009; Hansen et al., 2012; Goetz et al., 2010).

A recent study of polymorphism in Lake Trout from Great Bear Lake established a benthic-pelagic gradient, independent of depth, as a driver of Lake Trout differentiation (Chavarie et al., 2013; Chavarie et al, in press (a), (b)). Four distinct morphs exhibited habitat and diet partitioning all within the shallow-water zone, suggesting a new environmental gradient by which Lake Trout morphotypes can arise (Chavarie et al, in press (a)). Differences in life history characteristics have not been investigated among these morphotypes. Therefore, this case of polymorphism offers the opportunity to quantify and test predictions of life-history from resource polymorphism theory (Fraser et al., 2008). The combination of related traits associated with resource partitioning should result in a coordinated life-history strategy among specialized individuals. For example, individuals with rapid growth generally exhibit a larger size at maturity, delayed maturity, high reproductive investment upon maturation, and longer life span, conversely, those with slow growth rates typically display the opposite suite of life-history traits (Hendry et al., 2004, Loewen et al., 2010).

The aim of this study is to compare life-history tactics of the four shallow-water morphs from Great Bear Lake, with a larger goal being to improve our knowledge of the cause-effect relationships in this case of sympatric intraspecific diversity. To test for life-history differences among morphs, we compared age, growth, maturity, and reproductive output among morphs. Variation (or lack thereof) in life-history patterns among morphs should reflect their ecological opportunities and niche spaces.

Materials and methods

Study system

Great Bear Lake is one of the largest and deepest freshwater systems in North America with a surface area of 31 790 km^2 and a maximum depth of 446m (MacDonald et al., 2004). Located in northeastern Northwest Territories (N66° 06’ W120° 35’), 250 km south of the Arctic Ocean, its limnological features are similar to a typical Arctic freshwater system associated with low productivity (Johnson, 1975). The lake and its inhabitants have remained relatively isolated and unexploited, except for a Dene community of approximately 650 people, Déline, which has a small subsistence fishery, and a fly-in sport fishing lodge. Great Bear Lake is a post-glacial system characterized by considerable intra-specific diversity (Chavarie et al., 2013, in press (a);

Howland et al., 2013). Polymorphism in Lake Trout (*Salvelinus namaycush*), includes four different morphs co-existing in the shallow-water (≤30m) zone. There is a generalist morph, with a smaller head and intermediate fins (Morph 1), a piscivorous morph with the largest head and jaws but smallest fins (Morph 2), a benthic morph with the longest fins and a robust body shape (Morph 3), and a pelagic morph with a thick curved jaw and the smallest caudal peduncle (Morph 4) (Chavarie et al., 2013; Chavarie et al, in press (a)). Great Bear Lake is divided in five "arms" (Keith, McVicar, McTavish, Dease, and Smith), and additional morphological differentiation in body shape was demonstrated within morphs among arms (Chavarie et al., in press (a)).

Data collection

For this study, fish were caught in depths ≤ 30 m using paired bottom sets of a 14-cm and a multi-mesh (3.8-14 cm) gill net, soaked for approximately 24 h periods, during July and August. Sampling of the 902 Lake Trout used in this study occurred in all five arms over multiple years: Dease (2005 and 2010), McVicar (2003 and 2008), Keith (2002, 2003, 2004, 2006, 2007, and 2010), McTavish (2009) and Smith (2006 and 2011). For each fish, a lateral full-body digital image was taken and morphs were assigned using a multivariate assignment method based on morphological traits (i.e., body and head shape, and linear measurements) (see Chavarie et al., in press (a)). Measurements and tissues/structures for determination of biological characteristics related to life-history were sampled, including otoliths, fork length, somatic weight, sex, stage of maturity (current year spawner, resting), gonad weight, and ovaries of female current-year spawners. Following the maturity stages and descriptions used for other northern iteroparous salmonids (Bond, 1985; Howland, 1997), current year spawners included all individuals expected to spawn in the fall of the year they were captured and were distinguished by having gonads that were fully developed and enlarged (females with eggs at or near full size and ovaries filling body cavity, males with large lobate testes that are white to purplish colour), whereas resting individuals were defined as adults that were recovering from a previous spawning event and were discerned as follows: females with ovaries that fill up to 50% of body cavity and contain small seed eggs, occasional atretic eggs and a loose membrane, males with more tubular testes that are mottled and purplish colour. Overall, 286, 434, 158, and 26 individuals of Morphs 1 to 4, respectively, were sampled, and ovaries of 150 mature females, representing the four morphs, were preserved. In all analysis, Morph 4 had lower sample size compared to the three other morphs due to its rarity.

Otolith processing

Lake Trout were aged from embedded and thin-sectioned otoliths (n=829). Each otolith was embedded in Cold Cure Epoxy Resin (System Three Resins, Inc.) for approximately a week, during which air bubbles around the otolith or in the sulcus were removed using a needle probe. Embedded otoliths were then viewed sulcus side down under a dissecting microscope with cross hairs, and the desired sectioning plane intersecting the nucleus was marked. The sectioning plane was chosen by selecting an area on the dorsal lobe of the otolith where annuli were clearly visible and widely spaced. Marked otoliths were then sectioned transversely through the core with a Buehler Isomet Low speed saw outfitted with two Buehler Diamond Wafering blades, separated by a 0.5 mm spacer. Sections were polished using a series of lapping films (30 and 12 micron) when they were wet, followed by 0.3 micron when they were dry. Ages were determined by an experienced reader from Fisheries and Oceans Canada using a Leica M125 dissecting microscope at 40x and 80x magnifications. An annulus was considered to consist of a wide, light, opaque zone and an adjacent narrow, dark, translucent, hyaline zone, as seen when the sectioned otolith was viewed under reflected light (Jearld 1983; Casselman and Gunn 1992; Secor et al. 1992). A second reader independently re-aged a randomly selected sub-sample (15%). Any structure yielding differences in ages was re-read independently by both readers, and finally looked at together, if disagreement persisted, to arrive at a final age. Crystalline otoliths were excluded.

Subsets of otoliths of each Lake Trout morph, selected to include a range of fish lengths and ages observed in our dataset, were used to back-calculate length-at-age (Morph 1: n=37, 484-745 mm and 12-43 years; Morph 2 : n= 44, 545-1136 mm and 15-45 years; Morph 3: n = 45, 554-751 mm and 16-53 years; and Morph 4 n= 22, 545-803 mm and 14-39 years). Lake Trout otolith sections were viewed at 40x and 80x magnification on a Leica M125 dissecting microscope and photographs calibrated to a 1 mm scale bar were taken. Increment measurements were taken from the photographs using Image-Pro® Express 6.0. All measurements were made on the ventral sagittal otolith lobe. Increment measures started at the center of the nucleus and were measured perpendicular to each annulus until reaching the outer ventral edge. Growth increments representative of one year's growth were then used to estimate length at age via the biological intercept back-calculation model (Campana, 1990). The measures used for Lake Trout length and sagittal otolith width at age 0 were 21.7 mm and 0.137 mm, respectively, based on newly hatched wild lake trout from Lake Superior (Bronte et al., 1995). Sagital otolith width at age-0 was divided by two since measures for back-calculation were taken from the center of the nucleus representing half the otolith width at age-0.

Ovary processing

Ovaries of female current year spawners were frozen in the field and later thawed and preserved in a 5% formalin solution to maintain integrity during subsequent handling in the lab. Following formalin preservation, ovaries were rinsed with water, neutralized with Formalex and total oocytes were counted (total fecundity). Egg diameter was then measured by lining up ten haphazardly selected eggs along a ruler and dividing the total diameter by 10 (Morin et al., 1982); an average egg diameter was obtained from three such replicates.

Life-history analyses

From our dataset of 902 Lake Trout, medians and distributions of ages and lengths were compared between females and males within a morphotype, to test for sexual dimorphism, using Mann-Whitney and Two Sample Kolmogorov-Sminorv tests, respectively, performed in PAST V. 3 (Hammer et al., 2001). Median ages and lengths were also compared among the four morphs with a Kruskal-Wallis test followed by a post-hoc Mann-Whitney pairwise comparisons with Bonferroni corrected p-values and distributions were compared with a Bonferroni corrected pairwise Two Sample Kolmogorov-Sminorv test; tests were performed in SYSTAT V. 12 (Systat Software Inc., Chicago, IL, USA) and PAST V. 3.

Growth parameters were estimated from a biphasic model for each morph, which includes a pre-maturity and a post-maturity phase (Lester et al., 2004; Quince et al., 2008a, 2008b; Giacomini and Shuter, 2013). The generic biphasic model can be described as follows (Lester et al., 2004, 2014):

$$l_t=h(t-\tau) \text{ (pre maturity)}$$

$$l_t = (l_\infty (1-e^{-k(t-t0)}) \text{ (post-maturation)}$$

The linear pre-maturity relationship of length (l_t) as a function of age (t) assumes all surplus energy is allocated to somatic growth with h as net rate of energy acquisition expressed in terms of somatic growth rate (i.e. mm/year), t as the x-intercept of immature growth, and τ as the theoretical age when length equal zero. The post-maturation growth curve is described by a von Bertalanffy growth equation (Lester *et al.*, 2014). The parameters h (immature growth), L_∞ (von Bertalanffy Length at infinity for adults), k (von Bertalanffy K for adults), t_0 (von Bertalanffy t_0 for adults), g (investment in reproduction as proportion of somatic mass), and M (instantaneous natural mortality rate) were estimated for each morph using following equations:

$$l_\infty=3h/g$$

$$k=\ln(1+g/3)$$

$$t_0 = T + \ln (1-g(T-t_1)/3)/\ln(1+g/3)$$

$$g \approx 1.18\ (1-e^{-M}).$$

Since morphotypes are difficult to identify at early ages (Chavarie et al., 2013), we used mean back-calculated length-at-age across individuals from our subset (n=159) to predict immature growth in our biphasic model. Because age-at-maturity (T) is unknown for the back-calculated sub-sample, biphasic models were fit to length-at-age data for a range of T values**.** Small-sample AIC was then used to identify the 'best' model among T values. Because the minimum sizeof current year spawning Lake Trout from Great Bear Lake is known to be ~450 mm (Chavarie et al., 2013), we assumed that the average Lake Trout did not begin to invest in reproduction until 350 mm. This lower bound (ranging from 6-9 years) also ensured that we had at least two immature age classes with which to describe immature growth. Estimates of k were constrained to the interval $[0,\ln(1/(T-t1)+1)]$ as a result of a logarithmic bound in the equation for describing adult growth.

Weight-length relationships were estimated for current year spawners and resting individuals from weight (g) and fork length (mm) measurements among Lake Trout morphotypes following the general approach of Hansen et al. (2012), with equations from Quinn and Deriso, (1999) as follows:

$$W=\alpha L^{\beta}e^{\varepsilon}$$

where weight (W) is a function of length (L), condition factor (α), the rate at which shape changes with length (β), and error (ε). The parameters α and β were estimated from a linear regression using the $\log_e$-transformed model:

$$\log_e (W) = \log_e (\alpha) + \beta \log_e (L) + \varepsilon.$$

To compare shape parameters between morphotypes, a class variable (morphotype) was introduced and an ANCOVA was performed in PAST V. 3 to test the homogenity of slopes among morphotypes (Zar, 1999). If differences were found, post-hoc Tukey pairwise comparisons of slopes, as demonstrated in Zar (1999), were calculated among morphs as follows:

$$q= \beta_B - \beta_A/SE.$$

A G-test (Sokal and Rohlf, 1981) was performed to test if the proportion of females versus males, as well as current year spawners versus resting, differed among morphotypes. Total fecundity and egg size were log-transformed and analyzed with an ANCOVA among morphotypes as functions of log-transformed fork length, weight and age with PAST V. 3 followed by Tukey post-hoc pairwise comparisons of size-adjusted means with Bonferroni corrected p-values. Finally GSI values were divided into two datasets, current year spawners and resting individuals, where a two-way ANOSIM was performed with PAST V. 3 within each dataset to test the effects of sex and morphotype. Post-hoc pairwise comparisons with Bonferroni corrected p-values were performed if differences among morphotypes were detected.

Results

There were no significant differences in length and age medians (Mann-Whitney U Tests, all $p > 0.07$ and $p > 0.1$ respectively) or distributions (Kolmogorov-Smirnov $p > 0.08$ and $p > 0.1$ respectively) between mature females and males within a morph. Therefore sexes were pooled for subsequent analyses of length and age. However, median age and length differed significantly among morphs (Kruskal-Wallis=87.05, *df*=3, $p < 0.001$; Kruskal-Wallis=27.33, *df*=3, $p < 0.001$, respectively) (Fig. 5-1). All pairwise comparisons were significantly different for age except for all combinations involving Morph 4 ($p > 0.05$). Morphs 1 vs. 2 and Morphs 2 vs. 3 differed significantly for length ($p < 0.01$). Length distributions also differed significantly among morphs ($p \leq 0.05$) except for Morph 1 vs. Morph 3 (p=0.4) and Morph 2 vs. Morph 4 (p=0.1). Age distributions differed significantly among morphs ($p \leq 0.01$) except for Morph 3 vs. Morph 4, Morph 1 vs. Morph 2, and Morph 2 vs. Morph 4 ($p \geq 0.05$).

Overall, the youngest mature Lake Trout was 9 years whereas the oldest was 60 years; lengths ranged between 450 and 1136 mm. Individuals of Morph 3 were oldest (median ± SE, 29.0 ± 0.86, range=11-60 years), individuals of Morph 1 were youngest (20.0 ± 0.45, range=11-45 years), while individuals of Morph 2 and Morph 4 were intermediate (22.0 ±0.39, range=9-53, and 26.0 ± 1.51, range=14-53 years, respectively). In contrast, individuals of Morph 4 and Morph 2 were longer (median ± SE, 683.0 ± 11.89, range 476-981 mm and, 670.8 ± 5.16, range=450-1136 mm, respectively) and individuals of Morph 1 were smaller (641.7 ± 4.97, range=508-1010 mm), while individuals of Morph 3 were intermediate (644.0 ± 5.12, range 476-981 mm).

For the biphasic model, T values (age-at-maturity) for the ‘best’ fit model based on AIC weightings ranged from 16.6 to 19.1 (Table 5-1, Fig. 5-2). Growth parameters generated from the ‘best’ fit biphasic models differed among morphs (Table 5-1, Fig. 5-2). Immature growth rate was estimated to range from 14.55 mm/year (Morph 3) to 25.3 mm/year (Morph 2), whereas length-at-maturity trends were from 508.76 mm (Morph 3) to 655.45 mm (Morph 2) (Table 5-1).

Annual investment in reproduction was highest in Morph 1 and lowest in morphs 2 and 3, whereas instantaneous natural mortality rate ranged from 0.036 (Morph 3) to 0.082 (Morph 1). Finally, von Bertalanffy k for adults was the lowest for morphs 2 and 3 and the highest for Morph 1, with asymptotic lengths ranging from 651.3 mm (Morph 1) to 1406.9 mm (Morph 2) (Table 5-1). Morph 4 was intermediate in all parameters.

No differences in weight-length slopes were observed between males and females within a morphotype ($p > 0.05$); data were thus pooled. For all morphotypes, current year spawners grew allometrically, as the βs from their weight-length relationship were all less than 3.0. The shape parameter β of current year spawners differed among morphotypes marginally ($F_{3,520}=2.61$, $p = 0.051$, Fig. 5-3), mostly due to a lower slope for Morph 4. Resting individuals grew allometrically but differed significantly in β among the four morphotypes ($F_{3,372}=3.81$, $p= 0.010$). More specifcically, the slope of Morph 1 was greater than those of morphs 3 and 4, while the slope for Morph 2 was greater than Morph 3 ($p\leq 0.05$) (Fig. 5-3).

Proportions of current year spawners vs. resting females and males, differed among morphotypes ($G = 62.40$, $df = 9$, $p < 0.01$), with Morph 3 differing significantly from morphs 1, 2, and 4, due to a higher proportions of current year spawning males (Fig. 5-4). Higher proportions of resting females and mature males were also generally found across morphotypes. Slopes of egg size vs. trout length and weight were marginally different across morphotypes ($F_{3,145} = 2.74$, $p=0.046$; $F_{3,145} = 2.36$, $p=0.074$, respectively) and mean egg sizes differed significantly ($F_{3,145} = 5.89$, $p \leq 0.01$ and $F_{3,145} = 5.33$, $p \leq 0.01$, respectively) (Fig. 5-5 a), with

Morph 3 having significantly larger eggs than morphs 1 and 2 ($p \leq 0.01$). For total fecundity vs. length and weight respectively, slopes were similar ($F_{3,148} = 1.08$, p=0.36 and $F_{3,145} = 2.39$, p= 0.07, respectively), and adjusted mean sizes differed among morphotypes ($F_{3,148} = 3.83$, $p = 0.01$ and $F_{3,145} = 3.23$, $p = 0.02$) (Fig. 5-5b). Slopes of egg size and number vs. age and age adjusted means did not differ among morphs (p>0.05). Finally, GSI values were significantly different between sexes (R=0.75, $p \leq 0.01$) but not among morphs (R= ≤0.01, p=0.50) within the current year spawners dataset. However, within the resting dataset, GSI values differed between sexes (R=0.54, $p \leq 0.01$) and among morphs (R=0.07, $p \leq 0.01$). GSI differed between Morph 1 and 2 and Morph 2 and 3, with Morph 2 the lowest GSI values at the resting stage for both males and females.

Discussion

Overall, Lake Trout from Great Bear Lake demonstrated remarkable longevity, up to 60 years, and exceptional asymptotic sizes, as large as 1407 mm. Consistent with other Lake Trout studies (e.g., Martin and Olver, 1980; Smith et al., 2008; McDermid et al., 2010), there were no sex-biases in length or age. Lake Trout is known to acheive greater longevity and asymptotic length at higher latitudes (especially in large, deep lakes) by growing more slowly, maturing at an older age, and experiencing lower total mortality (Jonhston, 1975; McDermid et al. 2010; Hansen et al, 2012). This trend, in combination with limited fishing pressure, results in Lake Trout that are among the oldest and longest ever recorded, which contribute to Great Bear Lake's reputation as a world class trophy fishery.

Our results demonstrated significant differences in life-histories among shallow-water morphotypes, differences that were generally consistent with trade-offs likely linked to the exploitation of different resources and environments (Schluter, 1995; Jonsson and Skúlason, 2000; Blackie et al., 2003; Fraser et al., 2008). Differences were evident not only in adults, but also in the early life history stages, where morphological tools had previously failed to detect differences (Chavarie et al., 2013). Early life-history can have important impacts on fishes both in the immediate and long-term, and is a key period in intraspecific life-history divergence (Skúlason et al., 1996; Hendry et al., 2004; Jonsson and Jonsson, 2014). However, results from our biphasic models need to be taken with precaution since sample size was low, resulting in difficulty to identify dimorphism in otolith, problem that is likely to exist since fish-otilith relationship does vary systematically with growth rate of fish (Campana, 1990).

In this study, immature growth patterns varied among morphs, which likely resulted in subsequent impacts on further critical life-history traits, such as age-at-maturity, size-at-maturity, and survival (e.g., Nordeng, 1983; Wootton, 1990; Parra et al., 2009). For example, the generalist Morph 1 had faster initial growth, associated with early maturation, which decreased considerably after maturation (Forseth et al., 1995; Skúlason et al., 1996; Jonhston and Post, 2009). Morph 1 seemed to trade off a high investment in reproduction (proportion of somatic mass investment) with reduced lifespan (higher adult mortality) and reduced somatic growth, resulting in the lowest asymptotic length (Thorpe, 1986; Jonsson et al., 1988; Wootton, 1998). Moreover, differences in feeding can affect growth rate, such as cost-benefit ratios for generalist foragers are likely to place a size constraint on this morph, if these fish are restricted to smaller prey and/or have lower feeding rates (Jonsson and Jonsson 2001; Fraser et al., 2008). Our results from both the biphasic model and age and length distributions also agreed with the typical insectivorous life-history traits observed in other lakes with sympatry, where smaller adult individuals often occur (Jonsson and Jonsson 2001; Woods et al., 2013).

The piscivorous Morph 2 was the earliest to achieve 50% maturation (T=16.6 years) according to our biphasic model, an unexpected finding for a piscivore (Thorpe, 1986; Jonsson et al. 1988; Skúlason et al., 1996), but it had the greatest length-at-maturity, as is usually observed (Jonsson and Jonsson 2001; Fraser et al., 2008). Morph 2 had the highest immature growth which was maintained over its life-span, a not uncommon phenomenon in salmonids associated with early maturation (Thorpe et al., 1998; Taborsky and Brockmann, 2010; Sogard et al., 2012). Although age is clearly a critical factor in maturation, size also plays an important role, and both are linked in a relationship known as the maturation reaction norm (Heino et al., 2002; Hutchings, 2011; Morbey and Shuter, 2013). In salmonid fishes, gonadal maturation is controlled by developmental decisions that are threshold-based and dependent on body size or condition at critical times of the year (Thorpe, 2007; Wright 2007; Morbey and Shuter, 2013). Consequently, it appears that because of the high immature growth rate, threshold size is reached relatively quickly triggering maturation in this piscivorous morph (Bell, 1980; Johnston and Post, 2009). Morph 2 adults also seem to invest relatively little in annual reproduction, which corresponds with their low natural mortality rate, large asymptotic length, and more similar weight-length relationships among current year spawners and resting individuals, traits that correspond with those observed for piscivorous forms in other cases of polymorphism (Fraser et al., 2008; Reist et al., 2012).

In contrast, the benthic Morph 3 had the lowest immature growth and the oldest age-at-maturity, but like the piscivorous Morph 2, adults seemed to invest relatively little in reproduction annually, had a low natural mortality rate, and relatively high adult growth rates, reaching large asymptotic lengths. Benthic morphs are generally smaller and mature earlier (Malmquist *et al.*, 1992). However, in Thingvallavatn, a large benthic morph of Arctic char (*Salvelinus alpinus*) was similar in growth and maturity to the piscivorous morph after a slower early growth stage, comparable to our results (Jonsson et al., 1988; Sandlund et al., 1992; Skúlason et al., 1996). Productivity in Arctic lakes is generally benthic oriented (Jonsson et al., 1988), thus the presence of large benthivorous char feeding on large benthic prey (littoral fish and benthic invertebrates, Chavarie et al, in press (b)) is perhaps not surprising for population in a large Arctic lake. Consistent with the common pattern that larger individuals live longer, and with its low annual reproductive investment, Morph 3 had the greatest longest longevity (Sandlund et al., 1992; Jonsson and Jonsson, 2001).

Finally, the pelagic Morph 4, which is the most specialized in diet feeding mostly on mysis or/and cisco (Chavarie et al, in press (b)) would therefore be expected to possess distinct adaptations or trade-offs to their different resource environment (Parker et al., 2001; Hendry et al., 2009; Taborsky and Brockmann, 2010). In other lakes, pelagic forms (i.e. zooplanktivores) usually display higher growth and delayed maturity compared to small benthic-oriented morphs

(Jonsson et al., 1988; Gillespie and Fox, 2003; Woods et al., 2013). However, Morph 4 was intermediate in all life-history characteristics, demonstrating no explicit adaptations as usually observed in foraging specialists (Fraser et al., 2008). Intermediate phenotypes should not be as effective as specialists when exploiting available resources (Taborsky and Brockmann, 2010). However, an intermediate phenotype might be an adaptation itself to the pelagic zone (feeding specialization). This specialization might then be related to other traits (e.g., their unique lower curved jaw).

Interestingly, almost half of the adult Lake Trout captured over nine years of sampling in Great Bear Lake were resting individuals, which suggests a programmed life-history of "constant skipping" (Healy, 1978; Secor, 2008; Goetz et al., 2011). Anecdotal observations of similar results were given by Kennedy (1954) and Johnson (1972, 1973) for Lake Trout populations from Great Slave and Keller lakes, respectively, both resource-poor, high-latitude lakes with short growing seasons. Lake Trout from Great Bear Lake have been hypothesized to spawn every second or third year (Miller and Kennedy, 1948). Interestingly, Goetz et al. (2011) found a significant proportion of Lake Trout in a resting stage in Lake Superior, a lower latitude system, for both siscowet and lean morphotypes. The causes of skipped spawning in Lake Trout are not fully understood, especially in northern populations, however some speculations can be made. The most common is poor nutrition (Rideout et al., 2005). Trout from Great Bear Lake became more streamlined as body length increased more than the average reported for both southern and northern populations (McDermid et al., 2010; Hansen et al., 2012), suggesting lower condition. Similar to the incidence of anadromy, the occurrence of skipped spawning may increase in northern populations, inversely correlated to aquatic productivity (Gross et al., 1988; McDowall, 1987; Doucett et al., 1999; Swanson et al., 2010). Although less likely in a cold-water species such as Lake Trout, low temperatures may also reduce fecundity or prevent gamete development by directly affecting biochemical processes or indirectly influencing energy budgets of the fish (Hodder, 1965; Rideout et al., 2005). Skipped spawning has also been associated with species having moderate to high longevity (>15 years), such as Lake Trout (Secor, 2008). Given that Great Bear Lake is characterized by low temperatures and the Lake Trout within this system have high longevity, they are likely subject to such influences.

Lake Trout with insufficient energy reserves can also interrupt gamete development, allowing fish to regulate fecundity (Rideout et al., 2005; Goetz et al., 2011). In general, females had higher proportions of resting individuals than males, consistent with their having higher reproductive investment (Johnston and Post, 2009; Morbey and Shuter, 2013). This has also been observed in Lake Trout from Lake Superior where 42-54% of females and 19-20% of males of siscowet and lean morphs were in a resting condition (Goetz et al., 2011). Conversely, based on the principle of fecundity regulation (Johnston and Post, 2009; Morbey and Shuter, 2013), we hypothesise that by reducing post-maturation investment in reproduction by extending resting period, the piscivorous Morph 2 is able to achieve improved compensatory growth despite an early maturation. In contrast, Morph 3 might have a higher frequency of spawning to compensate for delayed maturation, which is supported by the lower proportions of resting individuals in both sexes. However, discrepancy with the biphasic model results for Morph 3 challenges this hypothesis (or alternatively the validity of the estimated parameter).

Variation in reproductive tactics among different morphs has been observed in salmonids (Jonsson and Jonsson, 2001; Morbey and Hendry, 2008), but its absence is not necessarily rare (Jonsson and Jonsson, 1997; Goetz et al., 2011; Loewen et al., 2012). For example, egg size can show tremendous variation among and within populations (Morbey and Hendry, 2008). In this study, egg size varied among morphs, but most notably with larger eggs for the benthic Morph 3. Large eggs can increase fitness in salmonids by increasing survivorship (Hutching, 1991; Ojamguren et al. 1996). Thus, to compensate for delayed maturation, Morph 3 may be increasing maternal investment by increasing egg size without a major reduction in egg numbers. In contrast, higher egg numbers for the pelagic Morph 4 could compensate for smaller eggs. Finally, differences among morphs in their weight-length and GSI-length relationships for resting individuals but converging among spawners, also indicate different levels of reproductive investment.

Conclusion

Overall, species are affected through mechanisms that are connected to longevity and reproductive tactics (Allendorf and Luikart, 2007; Östergren and Nilsson, 2012). Growth rate, which has many fitness consequences in fish (Schluter, 1995), plays a crucial role in the life-history diversity among the four morphotypes of Lake Trout from Great Bear Lake. Indeed, morphological differentiation is often associated with growth rate (Jonsson and Jonsson, 1997), but distinguishing cause and effect is not a simple task when ecological polymorphism is considered. Several predictions of life-history outcomes based on classical optimal foraging theory were supported in our study, including higher investment in reproduction associated with reduced somatic growth in the generalist morph, high growth throughout the life time of the piscivorous morph, and slower early growth stage but greater longevity and a large adult body size in the more benthic-oriented morph. However unexpected findings also arose, such as early maturation in Morph 2 and an intermediate life-history for the diet specialist Morph 4, reflecting the complexity in making precise predictions of life-history in any specific case (Fraser et al., 2008), especially in an ecosystem with high degree of intraspecific diversity and little ecological information. The proportion of resting vs. current year spawners was generally high, suggesting a life-history adaptation for a northern environment, allowing to increased investment in adult growth; this was particularly evident in Morph 2 which had high proportion of resting individuals. As expected, reproduction strategies varied among morphs, with larger eggs for Morph 3 and higher fecundity for Morph 4.

This study extends the work of Blackie et al. (2003) and Alfonso (2004) and further demonstrates that Great Bear Lake provides an opportunity to study ecological and evolutionary mechanisms of intraspecific divergence in postglacial fishes. While this study complements those on morphological and diet variation (Chavarie et al., 2013, in press (a), (b)), several questions on the origin and the maintenance of such diversity remain. These are especially complex in this case of polymorphism, where a novel environmental gradient (littoral-pelagic) is combined with other resource gradients (e.g., prey items) and habitat and diet overlap among morphs (Chavarie et al., in press (b)). Finally, since morphological diversity has been linked with difference in diet, habitat use, and particularly life-history tactics for Lake Trout in Great Bear Lake, management will need to account for those differences to conserve such evolutionary significant unit.

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Table 5-1. Biphasic model parameters for each morph of Lake Trout from Great Bear Lake (both sexes combined). Parameters include the following: T= age-at-maturity (first investment in reproduction), L=length-at-maturity (first investment in reproduction), h=immature growth rate (mm/yr), t_1= x-intercept of immature growth, k=von Bertalanffy K for adults, g=investment in reproduction (proportion of somatic mass), L_{inf}= von Bertalanffy Length at infinity for adults, t_0 = von Bertalanffy t_0 for adults, M=instantaneous natural mortality rate, n=sample size, wi=AICc weighting for the 'best' model among T values. Parameters estimates of southern and northern population are based on McDermid *et al*. (2010).

Morph	**T**	**L**	**h**	**t_1**	**k**	**g**	**Linf**	**t_0**	**M**	**n**	**wi**
1	17.5	573.53	20.19	-10.91	0.031	0.093	651.29	-52.11	0.082	37	0.031
2	16.6	655.45	25.30	-9.31	0.018	0.054	1406.89	-18.59	0.047	44	0.015
3	19.1	508.76	14.55	-15.87	0.014	0.042	1041.35	-29.22	0.036	45	0.021
4	17.6	564.86	19.41	-11.51	0.021	0.063	925.05	-27.83	0.055	33	0.077
South	7.3	454	64				647				
North	10.4	439	45				647				

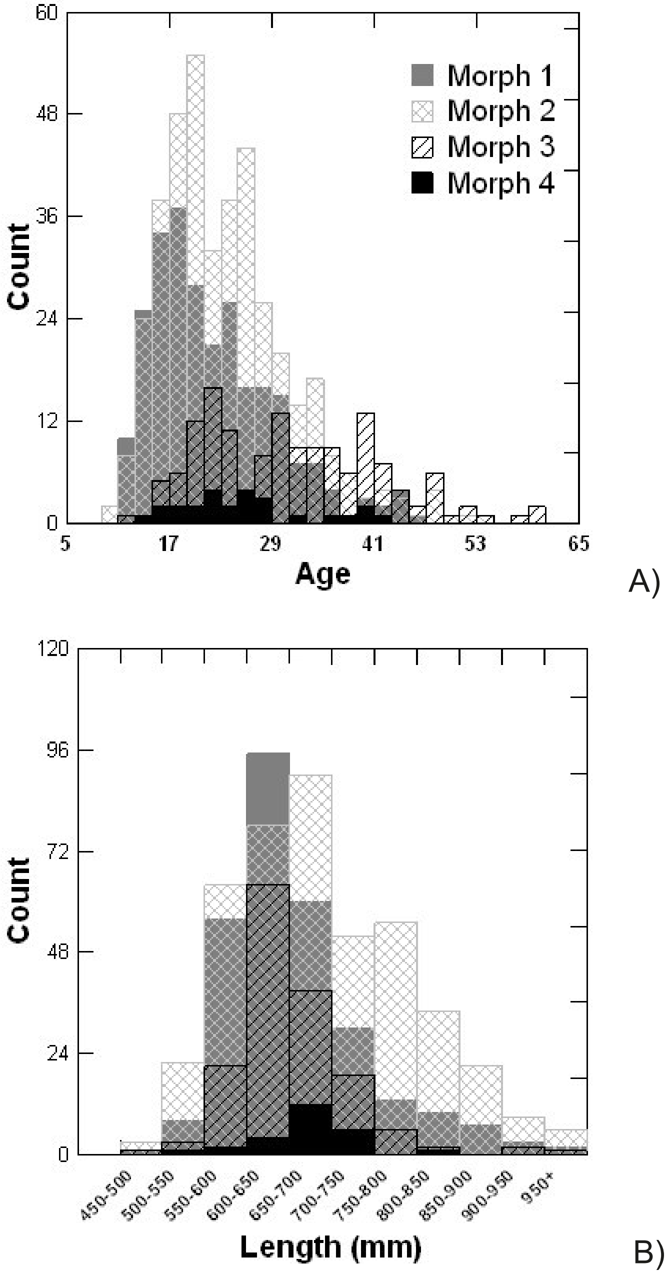

Fig. 5-1. Age (A) and length (B) distributions for 902 Lake Trout from Great Bear Lake, classified into four shallow-water morphotypes.

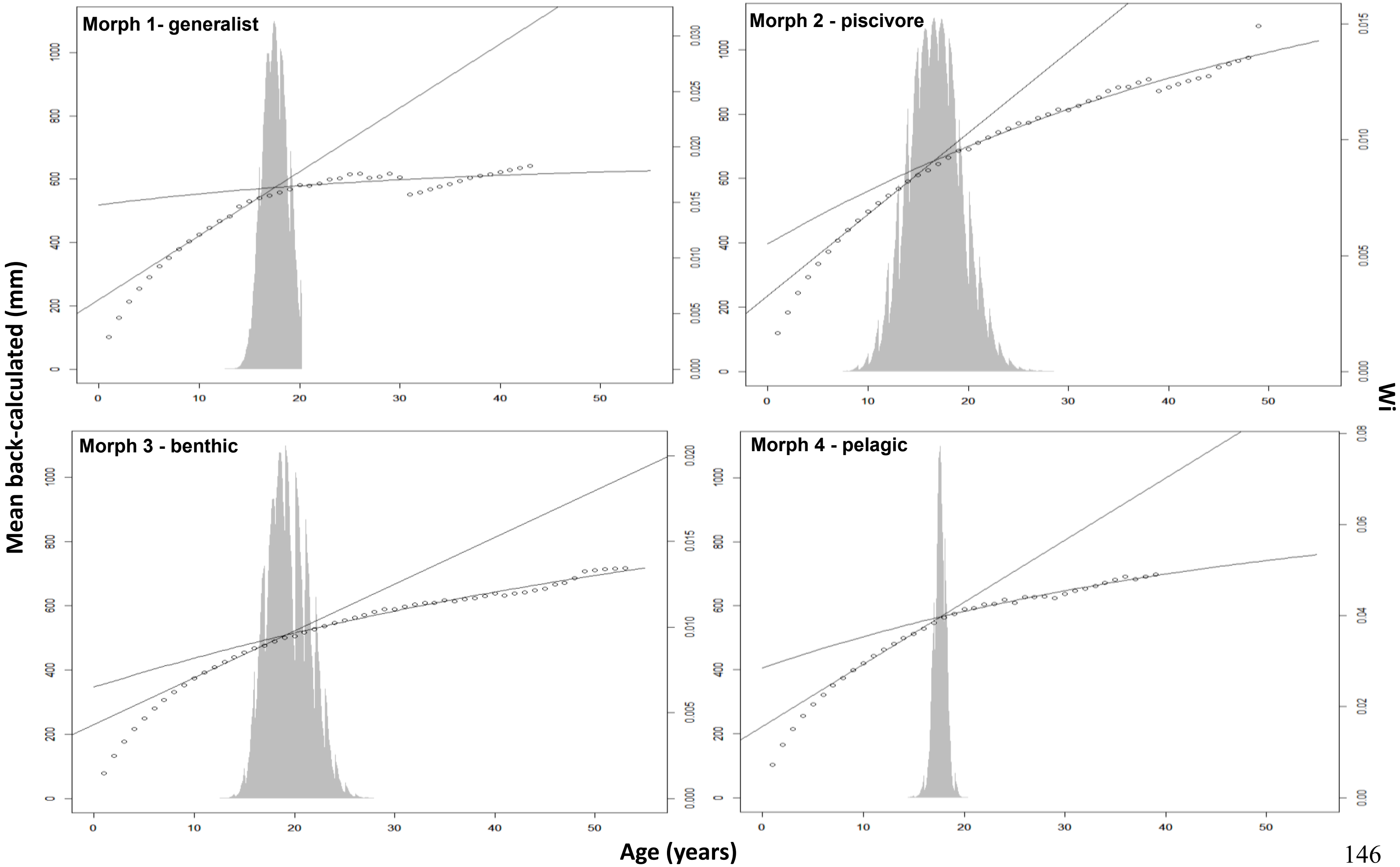
Morph 1- generalist
Morph 2 - piscivore
Morph 3 - benthic
Morph 4 - pelagic
Mean back-calculated (mm)
Age (years)
Wi
0
200
400
600
800
1000
0
10
20
30
40
50
0.000
0.005
0.010
0.015
0.020
0.025
0.030
0.00
0.02
0.04
0.06
0.08

Fig. 5-2. Results of biphasic models (see Table 1) for the four shallow-water morphs of Lake Trout from Great Bear Lake with predicted immature growth to the left and predicted adult growth to the right. Open circles represent mean observed back-calculated length-at-age from subsamples, whereas shaded area are AIC weights associated with each T value.

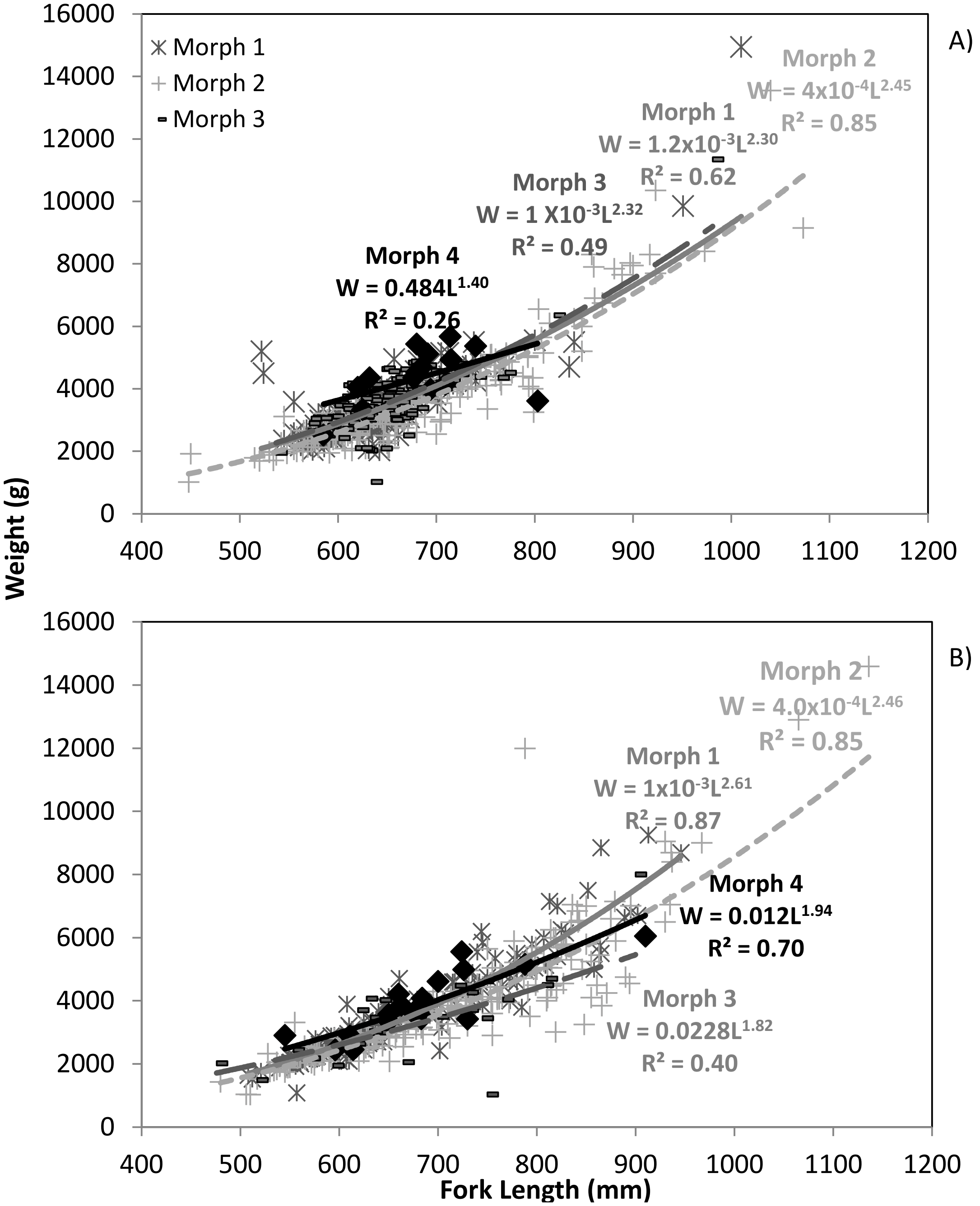

Fig. 5-3. Weight-length relationships in a) current year spawners and in b) resting Lake Trout according to their respective morph classification (Morph 1= - - - -, Morph 2= ——, Morph 3= — -, and Morph 4= ——).

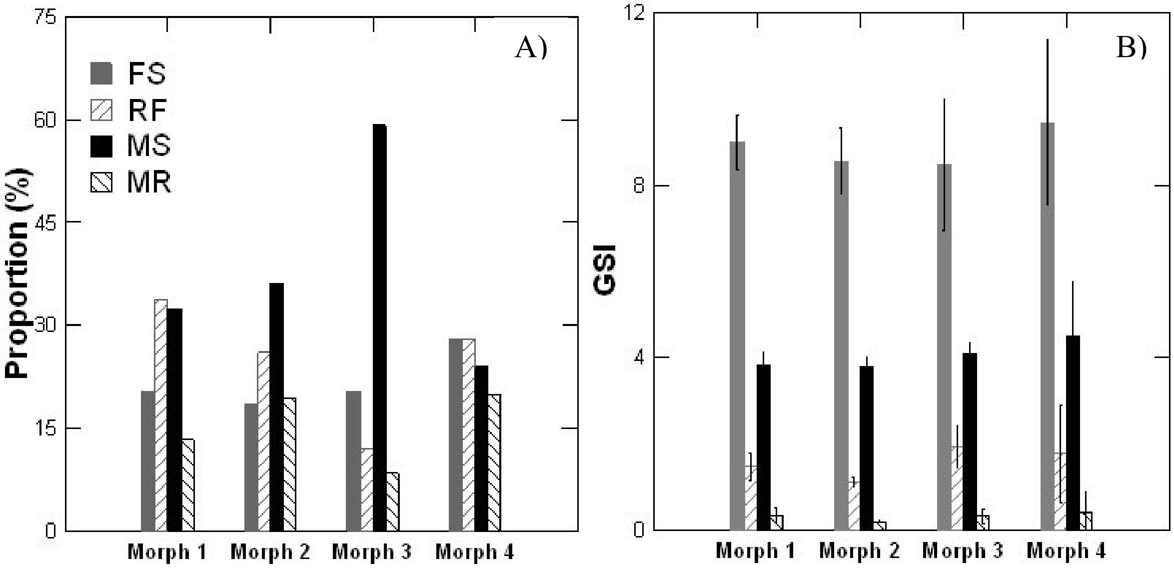

Fig. 5-4. Proportion in A) and GSI ± SE in B) of female current year spawners (FS), resting female (RF), male current year spawners (MS), and resting male (RM) among Lake Trout morphotypes of Great Bear Lake.

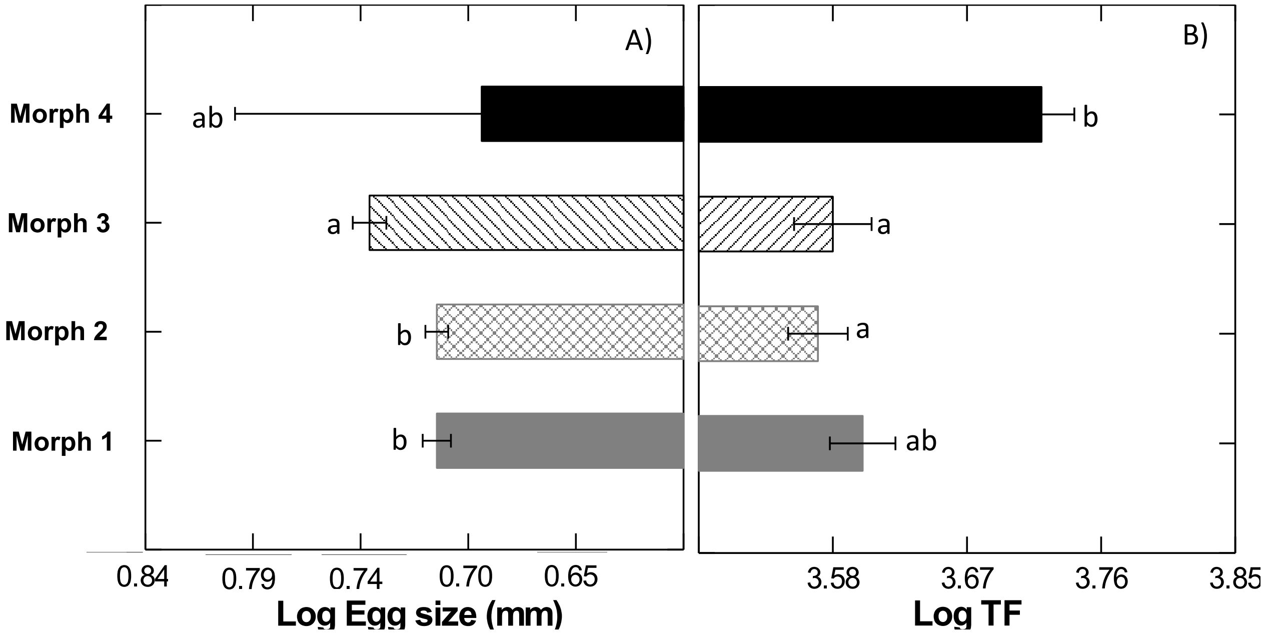

Fig. 5-5. Length-adjusted mean log egg size ± 1S.E. in a) and log total fecundity (TF) per individual ± standard error in b) among morphotype of Lake Trout from Great Bear Lake. Significant post-hoc pairwise comparisons are represented by different letters.

Chapter 6: General conclusion

This thesis presents a new case of intraspecific diversity in Lake Trout, adding new data to the limited information known at present about the extent to which Lake Trout polymorphism occurs in large northern Canadian lakes. Great Bear Lake is the most northerly lake of its size and, provides unique opportunities to study Lake Trout diversity in a relatively pristine environment. Although the main mechanism of Lake Trout diversification has generally been reported to be depth-related (Eshenroder, 2008), Chapter 2 established the presence of four morphs within the shallow-water habitats of Great Bear Lake, thereby requiring an expansion of the existing model (e.g., Zimmerman et al., 2006, 2007, 2009). One rare and three common morphs were categorized by differences in head and fin measurements, whereas body shape was less distinctive. These patterns are consistent with many evolutionary adaptations in fish that involve traits associated with feeding and swimming (e.g., Proulx and Magnan 2004; Keeley *et al*., 2005; Janhunen *et al*., 2009). However, no consistent patterns of variation were found among juveniles, suggesting that divergence develops at a later stage, although sample size was limited. This unusual degree of endemic diversity matches the striking example of Arctic Char in Lake Thingvallavatn (Jonsson and Jonsson, 2001), which exhibit the highest level of sympatric intraspecific diversity known to date in freshwater fishes, and might even exceed it if a fifth deep-water morph exists (unpublished data).

The unexpected lack of body and head shape variation led me to investigate the importance of considering scale in a lake exhibiting such marked morphometric complexity and variety of freshwater habitats. Chapter 3 demonstrated geographic patterns of morphological differentiation within individual Lake Trout morphs that were associated with the very large size of Great Bear Lake characterized by somewhat isolated arms, each of which is the size of a large lake. In contrast to the whole-lake pattern, intra-lake diversification within morphs was found in body shape, whereas linear measurements were more uniform. These results suggest two scales of diversification and challenge the presumption that in sympatry, the pattern of diversification is system wide (e.g., Hindar and Jonsson, 1993; Orr and Smith, 1998; Bolnick and Fitzpatrick, 2007). The lack of association between the morphological and genetic datasets in the inter-arm variation patterns among morphotype suggests a phenotypically plastic response to distinct environments.

A logical next step in this study was to investigate the relationship between morphological variation and diet, since sympatric diversification in Lake Trout is generally linked to habitat and diet partitioning (Smith and Skúlason, 1996; Stafford *et al*., 2014). Because Lake Trout is an opportunistic feeder with complex and variable diet patterns (Vander Zanden *et al*., 2000), a combination of dietary methods (fatty acids and stomach content) was beneficial in Chapter 4 for characterizing feeding habits between morphs. Overall, my study suggested that polymorphism in the Lake Trout of Great Bear Lake is partially maintained by diet differences but also by some habitat partitioning. Morph 1 had the most generalized feeding habits and Morph 3 was more benthic-oriented, but there was overlap between these two. Morph 2 exhibited both benthic cannibalism and pelagic piscivory independent of an ontogenic shift. Interestingly, Morph 4's pelagic diet was the most specialized and distinct, even though discrimination of Morph 4 based on morphology (Chapter 2) was not as apparent. The seasonality and the overlap found among the diets of different morphs may call into question the degree to which diet and habitat partitioning are involved as drivers of divergent selection, and also which other drivers have been or continue to be involved.

Finally, life-history strategies affect a species through mechanisms that are connected to survival and reproductive tactics (Allendorf and Luikart, 2007; Östergren and Nilsson, 2012). Morphological differentiation is often associated with growth rate (Jonsson and Jonsson, 1997), but distinguishing cause and effect is not a simple task when ecological polymorphism is considered. Indeed, growth rate, age-at-maturity, size-at-maturity, and survival differed among morphs, representing trade-offs between reproduction and somatic growth associated with the exploitation of different resources and environments. However, other traits, such as early maturation in Morph 2, reflect the challenge to making specific predictions of final life-history (Fraser et al., 2008). I also found that the ratio of current year spawners vs. resting individuals was high overall. This suggests a life-history adaptation of northern populations, of which Morph 2 in particular may use to increase investment in adult growth. Overall, Lake Trout from Great Bear Lake demonstrated remarkable longevity and exceptional asymptotic sizes, characteristics which contribute to this system's reputation as a world renowned trophy fishery.

My thesis extends our understanding of the origin and maintenance of Lake Trout phenotypic diversity and significantly advances our understanding of polymorphism in northern fish. The four Lake Trout morphs examined are unique components of Canadian biodiversity and their conservation should be a management goal in the face of substantive and pervasive threats (e.g., climate change, overfishing, habitat destruction), to avoid extinction, similar to what likely occurred in other large lakes of Canada, such as the Laurentian Great Lakes (Zimmerman *et al*., 2006). Intraspecific variability contributes significantly to biodiversity in northern freshwater fish faunas, where the few species living there profit from the depauperate postglacial systems by colonizing open niches.

Although no commercial fisheries occur in Great Bear Lake, a large population decline was previously observed (Howland *et al*., 2005) mainly within McTavish arm (Falk *et al.,* 1973) where Plummer's Lodge had their main base of operation for an intensive sport fishery without any catch-and-release policy as they have now adopted. This incident took place fifty years ago but population recovery has only been recent, which demonstrates that these Lake Trout are particularly susceptible to over-exploitation (Howland, *unpublished data*). Biological diversity stabilizes ecosystem processes and population diversity within exploited species can contribute to their long-term sustainability (Schindler *et al*., 2010). In recent decades, management has introduced the subspecific "evolutionarily significant unit", recognizing the importance of spatial, temporal, and genetic complexities within species, and works to conserve such units (Smedbol and Stephenson, 2001; Moritz, 2002). Consequently, with the new knowledge that this thesis provides on morphological diversity linked with difference in diet, habitat use, and particularly life-history tactics of Lake Trout in Great Bear Lake, management will need to account for those differences, e.g., to avoid targeting a particular morph in subsistence or/and sport fisheries (i.e. for shore lunches). For example, different habitat use can lead to differences in susceptibility and vulnerability to fishing gear, and differences in life-histories can affect the maximum sustainable yield in fisheries (Hilborne and Walters, 2001).

This project has addressed important ecological questions and created important partnerships between academic research, applied fisheries science, and local community knowledge. This study has also contributed to the long-term monitoring of Great Bear Lake by Fisheries and Oceans Canada to detect changes in fish stocks, and thus will be valuable for its management as well as its scientific perspective.

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Appendices

Appendix 3-1

Pairwise Cavalli-Sforza and Edward's (1963) chord distance (DCE), based on microsatellite DNA variation using 22 loci (Harris et al., 2014), used in Mantel tests to test association with morphological pairwise distances of Morph 1 and Morph 2.

	Keith		**McVicar**		**McTavish**		**Dease**		**Smith**	
	Morph 1	*Morph 2*	*Morph 1*	*Morph 2*	*Morph 1*	*Morph 2*	*Morph 1*	*Morph 2*	*Morph 1*	*Morph 2*
Keith	0	0	0.0005	0.004	0.0015	0.0031	-0.0007	0.0025	0.0041	0.0097
McVicar	0.0005	0.004	0	0	0.0015	0.0072	-0.0053	0.0053	0.006	0.0066
McTavish	0.0057	0.0031	0.0015	0.0072	0	0	-0.0005	0.0071	0.009	0.0169
Dease	-0.0007	0.0025	-0.0053	0.0053	-0.0005	0.0071	0	0	0.0046	0.0081
Smith	0.0041	0.0097	0.006	0.0066	0.009	0.0169	0.0046	0.0081	0	0

Appendix 4-1

List of 41 fatty acids considered as “dietary” fatty acids or “extended-dietary” fatty acids used in this study (see Iverson *et al*., 2004) and the component they are associated with, in this study, based on literature: Sargent *et al*., 1995; Brett & Müller-Navarra, 1997; Kattner *et al*., 1998; Virtue *et al*., 2000; Budge et al., 2002; Dalsgaard *et al*., 2003; Iverson *et al*., 2004; Käkelä *et al*., 2005; Alfaro *et al*., 2006; Tucker *et al*., 2008; Ahlgren *et al*., 2009; Gladyshev *et al*., 2009; Loseto *et al*., 2009; Stowasser *et al*., 2009; ; Piché *et al*., 2010; Mariash *et al*., 2011.

Fatty acids	**Fatty acids biomarkers**
14:0	Pelagic (Zooplankton) + diatom
16:0	Cannibalism or/and carnivorous
16:1n7	Benthic (bacterial synthesis + diatoms) Cannibalism or/and carnivorous
16:2n6	
16:2n4	Diatom
17:0	
16:3n-4	
16:4n3	
16:4n1	Diatom
18:0	Cannibalism or/and carnivorous
18:1n9	Pelagic (Zooplankton)
18:1n7	Benthic (bacterial synthesis + algal)
18:2n6	Terrestrial
18:2n4	
18:3n6	
18:3n4	
18:3n3	Terrestrial
18:3n1	
18:4n3	Pelagic (Zooplankton)
18:4n1	
20:0	
20:1n11	Copepod (Iverson, 2009)
20:1n9	Pelagic (Calanoid copepods diet based)
20:1n7	Pelagic (Zooplankton)
20:2n9	
20:2n6	
20:3n6	

20:4n6	Benthic (diatom)
20:3n3	
20:4n3	
20:5n3	Cannibalism or/and carnivorous
22:1n11	Copepod
22:1n9	Pelagic (Zooplankton)
22:1n7	
22:2n6	
21:5n3	
22:4n6	
22:5n6	Pelagic (Calanoid copepods diet based)
22:4n3	
22:5n3	
22:6n3	Benthic (Pennate diatoms + dinoflagellates + bivalves) Cannibalism

Appendix 4-2

Prey items in stomach contents of each shallow-water morphotype of Lake Trout from Great Bear Lake and for all trout combined (overall). Prey are presented by relative number (%n) and mass (%m), and are classified by habitat (T=terrestrial, B=benthic, P=pelagic, L=littoral, AS= aquatic surface), and by categorical identification (O. = Order, s.O. suborder, sp.F. superfamily F.= Family, sb. F.=Subfamily, t.=Tribe, sb. t = Subtribe, G.=Genus, sb. G.=Subgenus, and s.s.= Sub section). Numbers in bold represent >10% by abundance and/or mass.

		Overall		**Morph 1**		**Morph 2**		**Morph 3**		**Morph 4**	
	Habitat	**%n**	**%m**	**%n**	**%m**	**%n**	**%m**	**%n**	**%m**	**%n**	**%m**
Fish		0.94	**58.39**	0.53	**29.40**	1.61	**84.07**	1.61	**43.20**	0.16	**12.19**
Salvelinus namaycush	B,P	≤0.01	**13.46**	0.00	0.00	0.03	**27.35**	0.00	0.00	0.00	0.00
Coregonus clupeaformis	B,P	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Coregonus artedi	P	0.02	6.17	0.00	0.00	0.09	8.59	0.04	12.09	0.00	0.00
Prosopium cylindraceum	B,L	0.01	**17.82**	0.01	23.46	0.09	**19.98**	0.00	0.00	0.00	0.00
Exos lucius	B,L	≤0.01	2.36	0.00	0.00	0.03	4.79	0.00	0.00	0.00	0.00
Lota lota		≤0.01	5.54	0.00	0.00	0.03	**11.25**	0.00	0.00	0.00	0.00
Cottus cognatus	B,L	0.36	4.11	0.19	2.45	0.15	0.66	0.85	**18.39**	0.00	0.00
Pungitius pungitius	B,L	≤0.01	0.01	0.01	0.02	0.00	0.00	0.00	0.00	0.00	0.00
Otoliths		0.58	0.02	0.37	0.03	0.29	0.01	1.20	0.06	0.00	0.00
Fish remains		0.25	8.90	0.15	3.49	1.05	**11.42**	0.12	**12.55**	0.16	**12.19**
Invertebrate		**97.94**	**37.23**	**98.32**	**59.15**	**98.16**	**15.69**	**96.87**	**54.80**	**99.84**	**87.72**
Malacostraca	B,P	**33.35**	7.84	**40.10**	**17.48**	0.06	0.01	**29.09**	**10.13**	**80.47**	**36.98**
Mysidae	B,P	**18.38**	6.82	**26.56**	**15.94**	0.06	0.01	3.50	7.01	**79.53**	**36.77**
Gammaridae	B	**14.97**	1.02	**13.54**	1.54	0.00	0.00	**25.59**	3.11	0.94	0.20
Mollusca	B	0.78	1.13	0.25	0.50	3.80	1.85	0.26	0.15	5.67	3.82
Gasteropoda	B	0.60	1.10	0.20	0.47	3.80	1.85	0.06	0.13	1.26	1.59
Bivalve	B	0.18	0.02	0.05	0.01	0.00	0.00	0.20	0.01	4.41	2.23

Orthoptera		0.06	0.28	0.04	0.44	0.20	0.11	0.04	0.47	0.00	0.00
Caelifara (s. O.)	T	0.02	0.27	0.02	0.44	0.09	0.10	0.01	0.47	0.00	0.00
Tetrix ornata	T	≤0.01	0.01	0.00	0.00	0.03	0.01	0.00	0.00	0.00	0.00
Lepidoptera		0.32	1.28	0.01	0.02	2.63	2.57	0.04	0.05	0.00	0.00
Lepidoptera (O.)	T	0.32	1.27	0.01	0.00	2.63	2.57	0.04	0.05	0.00	0.00
Noctuidae (F.)	T	≤0.01	0.01	0.01	0.02	0.00	0.00	0.00	0.00	0.00	0.00
Aranea		0.01	0.00	0.01	0.01	0.03	0.00	0.00	0.00	0.00	0.00
Aranea (O.)	T	0.01	0.00	0.01	0.01	0.03	0.00	0.00	0.00	0.00	0.00
Xysticus triangulosus	T	≤0.01	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.00	0.00
Diptera		0.97	0.60	0.99	0.81	0.64	0.45	1.08	0.59	0.79	0.11
Diptera Adult (O.)	T	0.04	0.02	0.05	0.05	0.03	0.01	0.01	0.01	0.00	0.00
Diptera Pupae (O.)	AS	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chironomidae (adult) (F.)	T	0.02	0.20	0.00	0.00	0.15	0.40	0.00	0.00	0.00	0.00
Chironomidae (larvae)(F.)	B	0.14	0.09	0.14	0.25	0.00	0.00	0.15	0.01	0.47	0.07
Chironomidae (pupae) (F.)	AS	0.29	0.04	0.27	0.03	0.23	0.03	0.37	0.10	0.31	0.06
Diamesinae (sb. F.)	T	0.00	0.00	0.01	≤0.01	0.00	0.00	0.00	0.00	0.00	0.00
Dryomyzidae (F.)	T	0.00	0.00	0.01	≤0.01	0.00	0.00	0.00	0.00	0.00	0.00
Tabanidae (F.)	T	0.02	0.05	0.02	0.06	0.06	0.03	0.02	0.09	0.00	0.00
Oxycerini (t.)	T	0.00	0.00	0.01	≤0.01	0.00	0.00	0.00	0.00	0.00	0.00
Aecothea sp. (G.)	T	0.00	0.00	0.01	≤0.01	0.00	0.00	0.00	0.00	0.00	0.00
Crinurina sp. (G.)	T	0.41	0.15	0.42	0.25	0.18	0.02	0.50	0.37	0.00	0.00
Orbellia sp. (G.)	T	0.01	0.00	0.01	≤0.01	0.00	0.00	0.00	0.00	0.00	0.00
Sericomyia sp. (G.)	T	0.01	0.01	0.01	0.02	0.00	0.00	0.00	0.00	0.00	0.00
Syrphus sp. (G.)	T	0.00	0.00	0.01	≤0.01	0.00	0.00	0.00	0.00	0.00	0.00
Acalyptratae (s.s.)	T	0.00	0.00	0.00	≤0.01	0.00	0.00	0.00	0.00	0.00	0.00
Amphipogon hyperboreus	T	0.01	0.00	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.00
Curtonotum helvum	T	0.02	0.04	0.02	0.12	0.00	0.00	0.02	0.01	0.00	0.00
Hemiptera		0.08	0.03	0.11	0.07	0.00	0.00	0.06	0.03	0.00	0.00
Hemiptera (O.)	T	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.00	0.00
Lygaeidae (F.)	T	0.01	0.00	0.01	≤0.01	0.00	0.00	0.00	0.00	0.00	0.00
Miridae (F.)	T	0.01	0.00	0.01	≤0.01	0.00	0.00	0.04	0.01	0.00	0.00

Nabidae (F.)	T	0.00	0.00	0.01	≤0.01	0.00	0.00	0.00	0.00	0.00	0.00
Pentatomidae (F.)	T	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.00	0.00
Scutelleridae (F.)	T	0.01	≤0.01	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.00
Deraeocoris sp. (G.)	T	0.01	≤0.01	0.01	≤0.01	0.00	0.00	0.00	0.00	0.00	0.00
Lygidea sp. (G.)	T	0.01	0.01	0.01	0.02	0.00	0.00	0.00	0.00	0.00	0.00
Nabicula sp. (G.)	T	0.03	0.01	0.05	0.02	0.00	0.00	0.00	0.00	0.00	0.00
Perillus sp. (G.)	T	0.01	≤0.01	0.01	≤0.01	0.00	0.00	0.00	0.00	0.00	0.00
Hymenoptera		**11.08**	4.32	**11.33**	7.33	**14.37**	1.13	9.00	5.83	**12.76**	**46.78**
Hymenoptera (adult) (O.)	T	1.14	0.06	1.39	≤0.01	2.60	0.11	0.04	0.02	0.00	0.00
Apoidea (super F.)	T	0.00	0.01	0.00	0.00	0.00	0.00	0.01	0.07	0.00	0.00
Aulacidae (F.)	T	0.01	0.01	0.00	0.00	0.06	0.02	0.00	0.00	0.00	0.00
Formicidae (F.)	T	9.46	4.01	9.65	7.15	9.96	0.80	8.56	5.31	**12.76**	**46.78**
Banchinae (sb. F.)	T	0.04	0.01	0.05	0.01	0.00	0.00	0.04	0.02	0.00	0.00
Campopleginae (sb. F.)	T	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ctenopelmatinae (sb. F.)	T	0.01	≤0.01	0.01	0.00	0.00	0.00	0.01	0.01	0.00	0.00
Cyllocerinae (sb. F.)	T	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Diplazontinae (sb. F.)	T	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.00	0.00
Opiinae (sb. F.)	T	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Pimplinidae (s. F.)	T	0.19	0.09	0.00	0.00	1.58	0.18	0.02	0.01	0.00	0.00
Phygadeuontidae (sb. F.)	T	0.01	≤0.01	0.02	0.01	0.00	0.00	0.01	0.01	0.00	0.00
Tryphoninae (sb. F.)	T	0.01	≤0.01	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.00
Vespoidea (sb. F.)	T	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Xenosphecinae (sb. F)	T	0.02	0.03	0.02	0.06	0.00	0.00	0.01	0.05	0.00	0.00
Xoridinae (sb. F.)	T	0.01	≤0.01	0.01	0.00	0.00	0.00	0.02	0.02	0.00	0.00
Phaeogenini (t.)	T	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Platyabini (t.)	T	0.01	≤0.01	0.01	0.00	0.00	0.00	0.01	0.01	0.00	0.00
Amblytelina (sb. t.)	T	0.01	≤0.01	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00
Cratichneumonina (sb.t.)	T	0.02	0.01	0.00	0.00	0.06	≤0.01	0.05	0.03	0.00	0.00
Ichneumonina (sb. t.)	T	0.01	≤0.01	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.00
Protichneumonina (sb. t.)	T	0.01	≤0.01	0.00	0.00	0.06	0.01	0.00	0.00	0.00	0.00
Adrena sp. (G.)	T	≤0.01	0.01	0.00	0.00	0.00	0.00	0.01	0.04	0.00	0.00

Cylloceria sp. (G.)	T	0.08	0.05	0.09	0.05	0.00	0.00	0.10	0.19	0.00	0.00
Enicospilus sp. (G.)	T	0.01	≤0.01	0.00	0.00	0.06	0.01	0.00	0.00	0.00	0.00
*Ichneumonida*e sp. (G.)	T	0.01	≤0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Oxytorus sp. (G.)	T	0.01	≤0.01	0.01	0.00	0.00	0.00	0.04	0.01	0.00	0.00
Pimpla sp (G.)	T	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.00	0.00
Chelostomoides (sb. G.)	T	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Trichoptera		**50.20**	**20.55**	**44.67**	**31.38**	**73.22**	**8.21**	**56.39**	**36.28**	**0.16**	0.11
Caddisfly (adult) (O.)	AS,T	**49.07**	**19.93**	**43.05**	**29.52**	**73.16**	8.23	**55.81**	**36.33**	0.00	0.00
Caddisfly (larvae) (O.)	B	1.06	0.71	1.53	1.97	0.03	0.01	0.56	0.20	0.16	0.11
Caddisfly (pupae) (O.)	B	0.04	≤0.01	0.07	0.01	0.00	0.00	0.00	0.00	0.00	0.00
Apatania sp. (G.)	T	0.02	0.01	0.02	0.01	0.00	0.00	0.02	0.02	0.00	0.00
Phanocelia sp. (G.)	T	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Agrypnia sp. (G.)	T	0.00	0.00	0.00	0.00	0.03	≤0.01	0.00	0.00	0.00	0.00
Coleoptera		0.50	0.55	0.21	0.65	1.64	0.44	0.70	0.73	0.00	0.00
Coleoptera (O.)	AS	0.08	0.19	0.02	0.23	0.64	0.22	0.00	0.00	0.00	0.00
Buprestidae (F.)	T	0.02	0.03	0.02	0.04	0.06	≤0.01	0.01	0.05	0.00	0.00
Cerambycidae (F.)	T	0.01	0.02	0.00	0.00	0.00	0.00	0.02	0.11	0.00	0.00
Corixidae (F.)	AS	0.21	0.19	0.06	0.26	0.61	0.17	0.39	0.16	0.00	0.00
Gyrinidae (F.)	AS	0.04	0.02	0.02	0.01	0.18	0.02	0.05	0.02	0.00	0.00
Carabini (t.)	T	0.06	0.04	0.02	0.02	0.00	0.00	0.19	0.21	0.00	0.00
Harpalini (t.)	S	0.00	0.00	0.00	0.00	0.03	0.01	0.00	0.00	0.00	0.00
Aphodius sp. (G.)	T	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Arhopalus sp. (G.)	T	0.01	0.04	0.01	0.04	0.00	0.00	0.02	0.16	0.00	0.00
Diacheila sp (G.)	L	0.01	0.01	0.00	0.00	0.06	0.01	0.01	0.01	0.00	0.00
Dromaelus sp. (G.)	T	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ellychnia sp. (G.)	T	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Macrovatellus sp. (G.)	T	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Stenotrachelus sp. (G.)	T	0.01	0.01	0.02	0.02	0.00	0.00	0.00	0.00	0.00	0.00
Aclypea opaca	T	0.00	0.00	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.00
Adalia bipunctata	T	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Cosmosalia chrysocoma	T	0.00	0.00	0.00	0.00	0.03	≤0.01	0.00	0.00	0.00	0.00

Hydrobius fuscipes	L,B	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Orsodacne atra	T	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Pachyta lamed liturata	T	0.00	0.00	0.00	0.00	0.03	≤0.01	0.00	0.00	0.00	0.00
Plecoptera		0.11	0.12	0.11	0.18	0.00	0.00	0.19	0.38	0.00	0.00
Plecoptera (adult) (O.)	B	0.11	0.11	0.10	0.17	0.00	0.00	0.17	0.34	0.00	0.00
Diura sp. (G.)	T	0.01	0.00	0.01	≤0.01	0.00	0.00	0.01	0.02	0.00	0.00
Skwala sp. (G.)	T	0.00	0.00	0.00	0.00	0.00	0.00	≤0.01	0.02	0.00	0.00
Unidentified invertebrates		1.12	4.38	1.14	11.44	0.23	0.28	1.53	2.18	0.00	0.00
rocks		0.48	0.53	0.50	0.30	1.58	0.88	0.00	0.00	0.00	0.00