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Life-history variation among four shallow-water morphotypes of lake trout from Great Bear Lake, Canada

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ABSTRACT

Phenotypic variation within populations is common in many salmonids, especially when inhabiting northern postglacial systems. We compared life-history traits among four lake trout morphs co-existing in the shallow-waters of Great Bear Lake (Northwest Territories, Canada). Adult growth rate, age- and size-at-maturity, and survival differed among morphs, consistent with their degree of foraging specialization and predictions from foraging theory, e.g., reduced somatic growth and higher reproductive investment in the generalist morph, high growth throughout life in the piscivorous morph, and intermediate life-histories in the more benthic- and pelagic-oriented morphs. Fecundity and egg size also varied among morphs. However unexpected findings also arose, such as comparable immature growth rates among morphs. Other traits, such as a high proportion of resting individuals among all morphs, suggest life-history adaptations to northern latitudes. Longer resting periods are likely needed to obtain enough energy for reproduction, and may also allow greater investment in post-maturation growth. Overall, lake trout from Great Bear Lake demonstrated remarkable longevity and exceptional asymptotic sizes, even for a northern freshwater ecosystem. Our study provides new insights into life-history evolution among lake trout morphs that use different food sources and habitats. In addition, it contributes to our understanding of this complex aquatic ecosystem, which exhibits one of the highest known levels of intraspecific diversity among freshwater fish.

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Introduction

Numerous salmonid species are widely distributed in North America and occupy a diversity of aquatic habitats (Behnke, 2002). Natural environmental gradients found in aquatic habitats, especially in lacustrine systems (e.g., pelagic vs. littoral, shallow vs. deep water), significantly influence phenotypic characteristics in salmonids (Robinson and Parson, 2002; Goetz et al., 2011). For many salmonids, intraspecific variation in resource use, both among and 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).

Salmonid species can also show intraspecific differences in life-history traits, often linked to polymorphism and resource use variation (e.g., Jonsson and Jonsson, 2001; Parra et al., 2009; Chavarie et al., 2010). Regardless of whether these differences originate from genetic and/or phenotypic divergence (Panfili et al., 2004), they can have population-

level consequences, particularly when body size is involved (Baglinière and Maise, 2002; Nicola and Almodóvar, 2004; Quince et al., 2008a). For example, individual growth rate, can play a pivotal role in shaping other life-history traits (e.g., survival, longevity and reproduction) that can influence population-level processes (Rikardsen and Elliot, 2000; Loewen et al., 2010; Sogard et al., 2012).

Lake trout, *Salvelinus namaycush*, has a widespread distribution in northern North America, where it is a dominant predator within lakes (Martin and Olver, 1980; Behnke, 2002). Among species of *Salvelinus*, lake trout is generally considered to display limited resource polymorphism (e.g., Snorrason and Skúlason, 2004; Hansen et al., 2012), but recent studies have demonstrated remarkable morphological diversity (Muir et al., 2015). In the Laurentian Great Lakes and other large, deep lakes, lake trout morphs specialize between shallow and deep water habitats and exhibit associated differences in body shape, life-history, lipids and buoyancy, trophic levels, and/or genetics (Moore and Bronte, 2001; Zimmerman et al., 2006, 2007, 2009; Goetz et al., 2010; Hansen et al., 2012; Muir et al., 2014).

Recent studies of lake trout from Great Bear Lake, NWT, Canada, have established extensive polymorphism, independent of depth

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differentiation (Blackie et al., 2003; Alfonso, 2004; Chavarie et al., 2013, 2014a,b). Instead, lake trout morphotypes within shallow waters are associated with a benthic–pelagic gradient, combined with differential resource use (e.g., picivores vs. insectivores) (Chavarie et al., 2014b). This polymorphism offers the opportunity to examine predictions from resource polymorphism theory and consequent variation in life-history (Fraser et al., 2008). A combination of related traits associated with resource partitioning can result in a coordinated life-history strategy within a group of similarly specialized individuals. For example, piscivorous Arctic char (*Salvelinus alpinus*) exhibit a larger size at maturity, delayed maturity, low reproductive investment upon maturation, and longer life span; conversely, insectivorous char with slow growth rates typically display the opposite suite of life-history traits (Nordeng, 1983; Jonsson and Jonsson, 2001).

The aim of this study is to compare life-history tactics among the four shallow-water morphs from Great Bear Lake, to improve our understanding of this case of sympatric intraspecific diversity. To examine life-history differences among morphs, we compared age, growth, maturity, and reproductive output. Variation (or lack thereof) in life-history patterns among morphs is then discussed in the framework of ecological opportunities and niche space.

Materials and methods

Study system

Great Bear Lake (Fig. 1A) is one of the largest and deepest freshwater systems in North America, with a surface area of 31 790 km² and a maximum depth of 446 m (MacDonald et al., 2004). Located in northeastern Northwest Territories, 250 km south of the Arctic Ocean, its limnological features are similar to other Arctic freshwater systems associated with low productivity (Johnson, 1975). This post-glacial lake has remained relatively isolated and is lightly exploited by a small, subsistence fishery that supports a Dene community (Délina), and by a fly-in sport fishing lodge.

Several salmonids in the lake, including lake trout, cisco (*Coregonus artedii*), and lake whitefish (*Coregonus clupeaformis*), are characterized by considerable intra-specific diversity (Chavarie et al., 2013, 2014a;

Howland et al., 2013; and L. Chavarie, pers. obs.). In lake trout, polymorphism includes four morphs that co-exist in the shallow-water (≤ 30 m) zone (Chavarie et al., 2013). 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 lower jaw and the smallest caudal peduncle (Morph 4) (Chavarie et al., 2013, 2014a) (Fig. 1B). Great Bear Lake is divided into five “arms” (Keith, McVicar, McTavish, Dease, and Smith), and additional morphological differentiation in body shape was demonstrated within morphs among arms (Chavarie et al., 2014a).

Data collection

For this study, fish were caught at depths ≤ 30 m using paired bottom sets of a 14-cm and a multi-mesh (3.8–14 cm stretch mesh) gill net, with each set soaked for approximately 24 h, during July and August, 2002–2011. Sampling of the 902 adult lake trout used in this study occurred in all five arms, usually one arm per year: Dease (2005 and 2010), McVicar (2003 and 2008), Keith (2002–2004, 2006, 2007, and 2010), McTavish (2009) and Smith (2006 and 2011). We obtained lateral, full-body, digital images of each fish, and assigned each fish to a morph using a multivariate assignment method based on body and head shape, and linear measurements (see Chavarie et al., 2014a). Measurements of characteristics and tissues/structures related to life history were sampled, including fork length, somatic weight, sex, reproduction state (current year spawner or resting), gonad weight, ovaries of female current year spawners, and sagittal otoliths. Following the reproductive states and descriptions used for other northern iteroparous salmonids (Bond and Erickson, 1985; Howland, 1997), current year spawners included all individuals expected to spawn in the fall of the year in which they were collected. These individuals were distinguished as 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 of white to purplish in color), 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 $\leq 50\%$ of body cavity and contained small seed eggs, occasional atretic

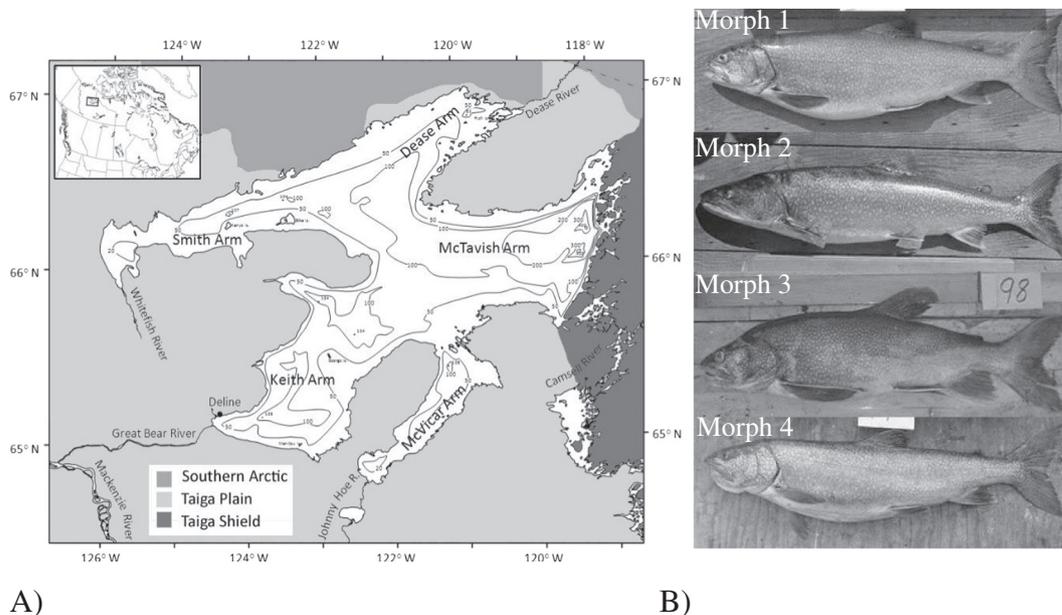


Fig. 1. A) Map of Great Bear Lake, Northwest Territories, Canada, adapted from Johnson (1975) and Chavarie et al. (2014a, 2014b), indicating general bathymetry, the terrestrial ecozones adjacent to the lake, and its major rivers. Insert: location of study area within Canada. B) The four shallow-water morphotypes of Lake Trout from Great Bear Lake: the generalist, the piscivore, the benthic, and the pelagic, Morphs 1–4, respectively.

eggs, and a loose membrane; males with more tubular testes of mottled and purplish color. Overall, 283, 431, 155, and 33 individuals of Morphs 1 to 4, respectively, were sampled, and ovaries of 150 mature females, representing the four morphs, were preserved. In all analyses, Morph 4 had lower sample sizes due to its rare occurrence in catches.

Otolith processing

Lake trout ($n = 829$) were aged from otoliths. Each otolith was embedded in Cold Cure Epoxy Resin (System Three Resins, Inc.) for approximately 1 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 μm) when they were wet, followed by a 0.3 μm film when dry. Ages were determined by an experienced reader from Fisheries and Oceans Canada Freshwater Institute Aging Lab using a Leica M125 dissecting microscope at 40 \times and 80 \times 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 (i.e., blind re-test with no reference to fish size or previous reader) re-aged a random 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. Vateric otoliths were excluded.

Subsets of otoliths of each lake trout morph, selected to include the range of fish lengths and ages observed, were used to back-calculate length-at-age (Morph 1: $n = 39$, 484–750 mm and 12–43 years; Morph 2: $n = 30$, 545–1136 mm and 15–49 years; Morph 3: $n = 40$, 554–751 mm and 17–53 years; and Morph 4: $n = 23$, 545–803 mm and 14–45 years). Otolith sections were viewed at 40 \times and 80 \times magnification on a Leica M125 dissecting microscope and from photographs calibrated to a 1 mm scale bar. Increment measurements were taken from the photographs using Image-Pro® Express 6.0 software. All measurements were made on the ventral lobe of the sagittal otolith. Measurements started at the centre of the nucleus and were made at a 90° angle between each subsequent annulus until reaching the outer edge, following close to the sulcus. These increments were then used to back-calculate length-at-age data.

The relationship between fish length and otolith length depended on morph. The Morph 2 relationship followed a realistic trend with the y-intercept (length-at-hatch) at a biologically realistic location, but y-intercepts were unrealistically large for morphs 1, 3, and 4. Therefore, back-calculated lengths for Morph 2 were estimated via the biological intercept method, whereas Morphs 1, 3 and 4 combined the biological intercept and Fraser–Lee methods (Campana, 1990; Campana et al., 1992). Prior to the divergence in the fish length: otolith length relationship, the biological intercept method was used assuming no dimorphism in otolith length at early stages. 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 “lean” lake trout from Lake Superior (Bronte et al., 1995). Sagittal otolith width at age-0 was divided by two because measures for back-calculation started at the center of the nucleus. Lengths after the divergence were then calculated assuming reduced otolith growth for Morphs 1, 3 and 4 and incorporated the Fraser–Lee model. This approach incorporated morph-specific y-intercepts that more accurately described observed reductions in fish growth after divergence (B. Kissinger, University of

Manitoba, unpublished data). Increased accuracy from the combination of the two methods was supported by a reduction in residuals when comparing estimated and true lengths, as well as by the elimination of Lee's Phenomenon (i.e., older fish predicting smaller lengths at a given age than younger fish).

Ovary processing

Ovaries of 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 all oocytes were counted (total fecundity). Egg diameter was measured by lining up ten haphazardly selected eggs along a ruler and dividing the total diameter by 10 (Morin et al., 1982); an egg diameter for an individual female was obtained from averaging three such measurements.

Life-history traits

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–Smirnov 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 post-hoc Mann–Whitney pairwise comparisons with Bonferroni corrected p-values and distributions were compared with a Bonferroni corrected pairwise two sample Kolmogorov–Smirnov test; tests were performed in SYSTAT V. 12 (Systat Software Inc., Chicago, IL, USA) and PAST V. 3.

Growth parameters for each morph were estimated by fitting a bi-phasic growth model (Lester et al., 2004; Quince et al., 2008a,b; Giacomini and Shuter, 2013). We fit the growth model to back-calculated lengths-at-age for each individual from our back-calculated subset ($n = 132$) because morphotypes are difficult to identify at early ages (Chavarie et al., 2013). The generic biphasic model can be described as follows (Lester et al., 2004):

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

$$l_t = (1 - e^{-k(t-t_0)}) \text{ (post-maturity).}$$

The linear pre-maturity relationship of length (l_t) as a function of age (t) assumes that all surplus energy is allocated to somatic growth, with h as the net rate of energy acquisition expressed in terms of somatic growth rate (mm/year), t as the x-intercept of immature growth, and τ as the theoretical age when length equal 0. The post-maturity growth curve is described by a von Bertalanffy growth equation (Lester et al., 2014). The parameters h (immature growth, mm/year), T (age-at-first investment in reproduction, years), L_∞ (mean maximum adult length, mm), k (rate of deceleration of growth), t_0 (x-intercept of adult growth), g (investment in reproduction as proportion of somatic mass), and M (instantaneous natural mortality rate) were estimated for each morph using the following equations:

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

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

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

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

Because T was unknown for the back-calculated sub-sample, biphasic models were fit to length-at-age data for a range of plausible T values in increments of 0.1. The lower bound of this range was between 7 and 10 years depending on the morph. We established this lower bound

based on a minimum length of ~450 mm for spawning lake trout in Great Bear Lake (Chavarie et al., 2013). To ensure at least two age classes with which to describe immature growth, we also assumed that the average lake trout did not begin to invest in reproduction until 350 mm. As a result of these lower bounds, we did not attempt to fit the biphasic growth model to length data from the first 6–9 years of life (depending on morph). We determined the upper bound for T via an iterative search for the maximum value of T for which our fitting procedure converged on a solution. The model failed to converge when T was so large that length-at-maturity was predicted to be greater than the observed length-at-age of adults. This maximum value of T is given by $(1 + t_1(e^k - 1))/t_1(e^k - 1)$ in the absence of variability and when growth conforms to theory.

After fitting the biphasic model to a range of plausible T values, we used small-sample AIC to identify the value of T that resulted in the highest AIC weight. We then approximated the 95% confidence interval around this T by finding the range of neighboring T values for which AIC weights summed to 0.95. Because both the sample size and number of model parameters were fixed, this approach to finding T is analogous to maximum likelihood profiling. Although the auto-correlated nature of back-calculated data means that growth models should be fit using repeated measures analysis (Jones, 2000) or mixed effects modeling (Vigliola and Meekan, 2009), biases are generally small and statistical techniques for two-stage fitting have yet to be developed.

To validate our approach to estimating growth parameters and associated life history traits, we used histograms to visually compare the estimated T and h values from the biphasic model to estimates from 129 North American lake trout populations in McDermid et al. (2010). We added 1 year to our estimates of T so that they were comparable to the McDermid et al. (2010) estimates of age-at-first-spawning. We then multiplied McDermid et al.'s and our values by mean annual degree-days above 0 °C to obtain degree-days (DD) at maturity, to account for among-population differences in climate. We estimated degree-days for each population from interpolated, mean monthly air temperatures for the 1971–2000 climate normals (McKenney et al., 2006). Immature growth values (h) from this study and from McDermid et al. (2010) were also divided by annual DD to obtain climate-corrected immature growth (mm/degree-day).

Weight-length relationships were estimated for current year spawners and resting individuals from weight (g) and fork length (mm) measurements for each morphotype 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 homogeneity of slopes among morphotypes (Zar, 1999). If differences were found, post-hoc Tukey pairwise comparisons of slopes for two groups (q), A and B, 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 used to assess if the proportion of females versus males, as well as current year spawners versus resting individuals, 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 with Bonferroni corrected p-values if significant values were found. Finally, trout were divided into current year spawners and resting individuals, and a two-way ANOSIM was performed on GSI values using PAST V. 3 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

The youngest and oldest mature lake trout were 9 years and 60 years, respectively; adult lengths ranged between 450 and 1136 mm. Length and age medians (Mann–Whitney U tests, all $p > 0.07$ and $p > 0.1$ respectively) and distributions (Kolmogorov–Smirnov $p > 0.08$ and $p > 0.1$ respectively) were similar between mature females and males within morphs. Therefore sexes were pooled for subsequent analyses of length and age. Median age differed among morphs (Kruskal–Wallis = 87.05, $df = 3$, $p < 0.001$) (Fig. 2, Table 1). All pairwise comparisons were significantly different except for all combinations involving Morph 4 ($p > 0.05$); individuals of Morph 3 were oldest, whereas individuals of Morph 1 were youngest. Age distributions also differed among morphs ($p \leq 0.01$) except for Morph 3 vs. Morph 4, Morph 1 vs. Morph 2, and Morph 2 vs. Morph 4 ($p \geq 0.05$). Median lengths differed among morphs (Kruskal–Wallis = 27.33, $df = 3$, $p < 0.001$) (Fig. 2, Table 1), and Morphs 1 vs. 2 and Morph 2 vs. 3 differed ($p < 0.01$). Individuals of Morph 4 and Morph 2 were longer and individuals of Morph 1 were shorter; individuals of Morph 3 were intermediate. Length distributions also differed among morphs ($p \leq 0.05$) except for Morph 1 vs. Morph 3 ($p = 0.4$) and Morph 2 vs. Morph 4 ($p = 0.1$).

According to the biphasic growth model, immature growth rates were similar, ca. 22.1 mm/year, but length-at-maturity ranged from 581.71 mm (Morph 3) to 703.70 mm (Morph 2). Age at maturity (T) ranged from 17.4 to 20.2 years and post-maturation growth parameters generally differed among morphs (Table 2, Fig. 3). Annual investment in reproduction was almost twice as high in Morph 1 (0.090) as in Morph 2 (0.048), paralleling annual instantaneous natural mortality rate, which ranged from 0.042 (Morph 2) to 0.079 (Morph 1). Finally, asymptotic lengths ranged from 740.8 mm (Morph 1) to 1371.9 mm (Morph 2) (Table 2). Morphs 3 and 4 were intermediate for most parameters. Degree-days-at-maturity from our biphasic model (22116.8 to 25482.4 °C-days) and immature growth rate (0.018 mm/°C-days) were within the range observed for other North American populations (McDermid et al., 2010), but in the right and left tails of these distributions, respectively (Fig. 4).

No differences in weight-length slopes were observed between males and females within a morphotype ($p > 0.05$); therefore data were pooled. For all morphotypes, current year spawners grew allometrically, as indicated by the β s < 3.0 . β s of current year spawners differed marginally among morphotypes ($F_{3,520} = 2.61$, $p = 0.051$, Fig. 5A), mostly due to a lower slope for Morph 4. Resting individuals also grew allometrically, and β s differed significantly among the four morphotypes ($F_{3,372} = 3.81$, $p = 0.010$). The slope for 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. 5B).

Proportions of current year spawners vs. resting females and males differed among morphotypes ($G = 62.40$, $df = 9$, $p < 0.01$), with Morph 3 having a higher proportion of current year spawning males (Fig. 6A). Higher proportions of current year spawning vs. resting males were found across all morphotypes whereas different patterns were found for females: Morphs 1 and 2 had fewer spawning vs. resting females, proportions were equal for Morph 4, and Morph 3 had more spawners. Slopes of egg size vs. trout length and weight differed marginally 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 among morphs when adjusted for covariates ($F_{3,145} = 5.89$, $p < 0.01$

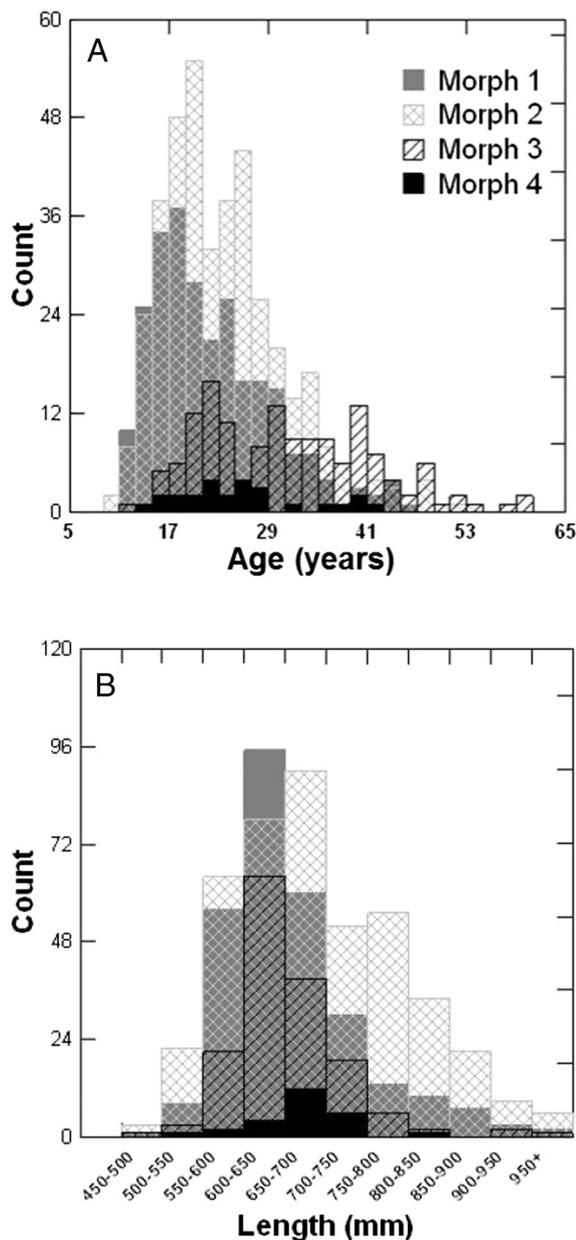


Fig. 2. Age (A) and length (B) distributions for 902 Lake Trout from Great Bear Lake, classified into four shallow-water morphotypes. Morphs are presented as follow: Morph 1 is a generalist (smaller head and intermediate fins), Morph 2 is piscivorous (largest head and jaws but smallest fins), Morph 3 is benthic oriented (longest fins and a robust body shape), and Morph 4 is pelagic (thick curved lower jaw and the smallest caudal peduncle).

with length covariate and $F_{3,145} = 5.33$, $p \leq 0.01$ with weight covariate) (Fig. 7A); Morph 3 had larger eggs than morphs 1 and 2 ($p \leq 0.01$). For total fecundity vs. length and weight, slopes were similar among morphotypes ($F_{3,148} = 1.08$, $p = 0.36$ and $F_{3,145} = 2.39$, $p = 0.07$,

respectively), but mean fecundity differed ($F_{3,148} = 3.83$, $p = 0.01$ for length covariate and $F_{3,145} = 3.23$, $p = 0.02$ for weight covariate) (Fig. 7B), with Morph 4 having highest fecundity. Egg size and number vs. age did not differ (slopes and means) among morphs ($p > 0.05$). Finally, GSI values for current year spawners were significantly different between sexes ($R = 0.75$, $p \leq 0.01$) but not among morphs ($R = \leq 0.01$, $p = 0.50$) (Fig. 6B). However, for resting fish, GSI values differed both between sexes ($R = 0.54$, $p \leq 0.01$) and among morphs ($R = 0.07$, $p \leq 0.01$), with Morph 2 having the lowest GSI values during the resting stage for both males and females.

Discussion

Lake trout from Great Bear Lake displayed remarkable longevity, up to 60 years, and exceptional asymptotic sizes, as large as 1372 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 are known to achieve greater longevity and asymptotic length at higher latitudes (especially in large, deep lakes) by growing more slowly, maturing at older ages, and experiencing lower total mortality (Johnson, 1975; McDermid et al., 2010; Hansen et al., 2012). This trend, in combination with limited fishing pressure, has resulted in lake trout in Great Bear Lake that are among the oldest and longest ever recorded, even relative to other northern populations (see Table 2; McDermid et al., 2010).

Among life history traits that varied among the different morphs, differences were generally consistent with trade-offs linked to the exploitation of different resources and environments (Schluter, 1995; Jonsson and Skúlason, 2000; Blackie et al., 2003; Fraser et al., 2008). However, as with morphological differences (Chavarie et al., 2013), life-history differences were primarily evident in adults rather than juveniles. In contrast, most studies of salmonids highlight differences in juvenile growth as a critical feature of the resource polymorphism model (Skúlason et al., 1996; Hendry et al., 2004; Noakes, 2008; Jonsson and Jonsson, 2014).

Although Blackie et al. (2003) showed differences in growth rate between the two shallow-water forms that he described through age 19, an examination of their Fig. 4 suggests that growth rate during this juvenile period become more similar after age 4. When reared under similar environmental conditions, juvenile growth rates of sympatric Arctic char morphs were almost identical despite differences in age-at-maturity and adult size (Hindar and Jonsson, 1993; Jonsson and Jonsson, 2001). The similar immature growth rates among the shallow-water morphs in Great Bear Lake might therefore reflect similar juvenile rearing environments and is consistent with prey size-spectrum theory (Andersen et al., 2009). Stabilizing selection on juvenile growth might be responsible for the lack of observed variation (Stearns, 1977; Tallman and Healy, 1991).

The generalist Morph 1 had an early age-at-maturation, which was associated with a subsequent decrease in somatic growth (see also Forseth et al., 1995; Skúlason et al., 1996; Johnston and Post, 2009) and higher adult mortality, resulting in the lowest asymptotic length among the four morphotypes (Thorpe, 1986; Jonsson et al., 1988; Wootton, 1998). Generalist foragers, such as Morph 1, can be restricted to smaller prey and/or have lower feeding efficiencies than specialists,

Table 1

Age and length medians (\pm SE) and ranges for each morphotype. Sample sizes are provided in Methods (Data collection).

	Age median	Age range	Length median	Length range
Morph 1 (generalist)	20.0 \pm 0.45 years	11–45 years	641.7 \pm 4.97 mm	508–1010 mm
Morph 2 (piscivores)	22.0 \pm 0.39 years	9–53 years	670.8 \pm 5.16 mm	450–1136 mm
Morph 3 (benthic)	29.0 \pm 0.86 years	11–60 years	644.0 \pm 5.12 mm	476–981 mm
Morph 4 (pelagic)	26.0 \pm 1.51 years	14–53 years	683.0 \pm 11.89 mm	476–981 mm

Table 2
Biphasic model parameters for each morph of Lake Trout from Great Bear Lake (sexes combined). Parameters include the following: T = age-at-maturity (years) \pm 95% CI, L = length-at-maturity (mm) (first investment in reproduction), h = immature growth rate (mm/year), t₁ = x-intercept of immature growth (years), k = von Bertalanffy growth parameter (adult), g = investment in reproduction (proportion of somatic mass), L_∞ = mean maximum adult length (mm), t₀ = von Bertalanffy age at which length is 0, M = instantaneous natural mortality rate (days⁻¹). Parameter estimates for southern and northern populations, based on McDermid et al. (2010), are also provided.

Morph	T	L	h	t ₁	k	g	L _∞	t ₀	M
1	17.4 \pm 2.3	593.40	22.23	-9.30	0.030	0.090	740.82	-37.21	0.079
2	20.2 \pm 7.3	703.70	22.16	-11.56	0.016	0.048	1371.94	-24.70	0.042
3	18.6 \pm 1.9	581.71	22.27	-7.52	0.028	0.086	773.69	-30.52	0.076
4	20.2 \pm 0.4	640.85	21.96	-8.99	0.027	0.081	809.56	-38.40	0.071
South	7.3	454	64						
North	10.4	439	45						

contributing to reduced growth (Jonsson and Jonsson, 2001; Fraser et al., 2008). Morph 1's life-history traits were consistent with other insectivorous morphs observed in sympatry, including early age-at-maturity and smaller adult size (Jonsson and Jonsson, 2001; Woods et al., 2013).

The piscivorous Morph 2 had highest growth that was maintained over its adult life-span; it also had among the oldest modeled age-at-maturity and the greatest length-at-maturity compared to the other morphs. All three traits are common in piscivorous salmonids (Thorpe et al., 1998; Taborsky and Brockmann, 2010; Sogard et al., 2012). Both age and size play important roles in maturation, and are linked in a relationship known as the maturation reaction norm (Heino et al., 2002; Hutchings, 2011; Morbey and Shuter, 2013). In salmonids, gonadal maturation is controlled by developmental decisions that are dependent on body size or condition thresholds at critical times of the year (Thorpe,

2007; Wright, 2007; Morbey and Shuter, 2013). Consequently, although immature growth rates were similar across morphs, threshold size may be a more important trigger of maturation than age in this piscivorous morph, which could explain its higher variation in modeled age-at-maturity (Bell, 1980; Johnston and Post, 2009). Morph 2 adults also invested relatively little in annual reproduction, which corresponds to their low natural mortality rate, large asymptotic length, and more similar weight-length relationships among current year spawners and resting individuals, traits that are consistent with greater piscivory (Fraser et al., 2008; Reist et al., 2013).

In contrast, the benthic Morph 3 and pelagic Morph 4 were intermediate for most life-history traits, but unlike the generalist Morph 1, they also combined a relatively high reproductive investment with a high natural mortality rate and relatively low adult growth rate. Morph 3 had the shortest length-at-maturity but intermediate age-at-maturity.

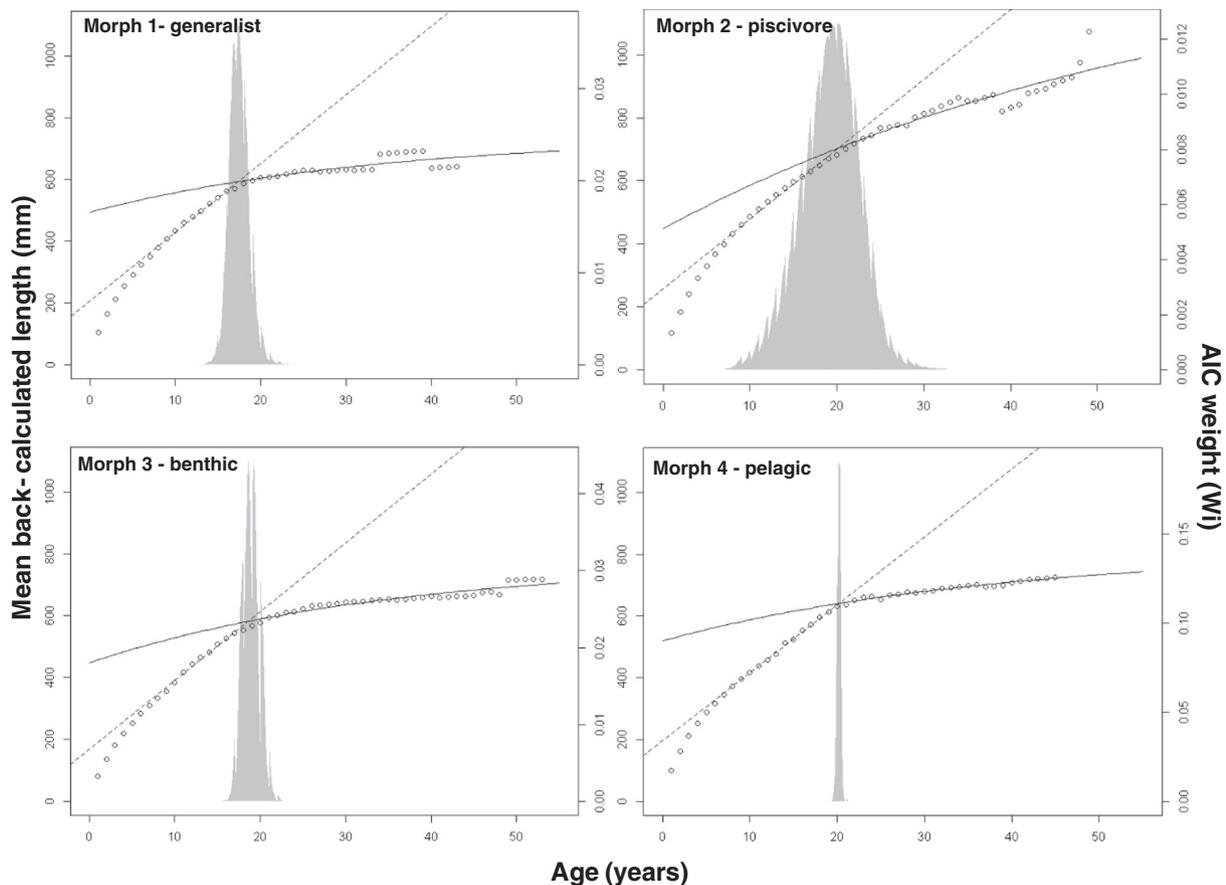


Fig. 3. Results of biphasic models (see Table 2) for the four shallow-water morphs of Lake Trout from Great Bear Lake, showing predicted immature (dashed line) and adult (solid line) growth. Open circles represent mean observed back-calculated length-at-age from subsamples, and the shaded area shows AIC weights over the range of plausible T values. We did not attempt to fit the growth model to length data from the first 6–9 years of life (depending on morph). The tendency of younger ages to deviate from linearity is common and indicative of ontogenetic shifts in ecology (Lester et al., 2004).

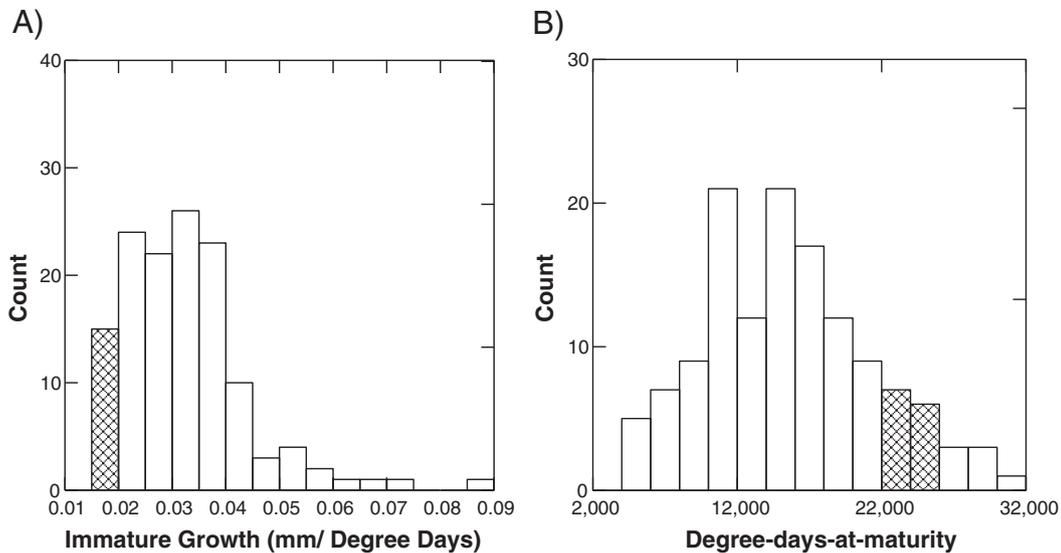


Fig. 4. Estimated immature growth rate (mm/degree-days) (A) and degree-days-at-maturity (B) of Lake Trout from Great Bear Lake (shaded bars) compared to estimated values from 129 North American Lake Trout populations (McDermid et al., 2010; open bars). Degree-days (≥ 0 °C) estimated from monthly average of air temperatures (1971–2000 climate normals) were used to standardize for climate differences across locations. The values of immature growth rate (mm/degree-days) and degree-days-at-maturity, respectively, are 0.018 and 22117 (Morph 1), 0.018 and 25482 (Morph 2), 0.018 and 23559 (Morph 3), and 0.018 and 25482 (Morph 4).

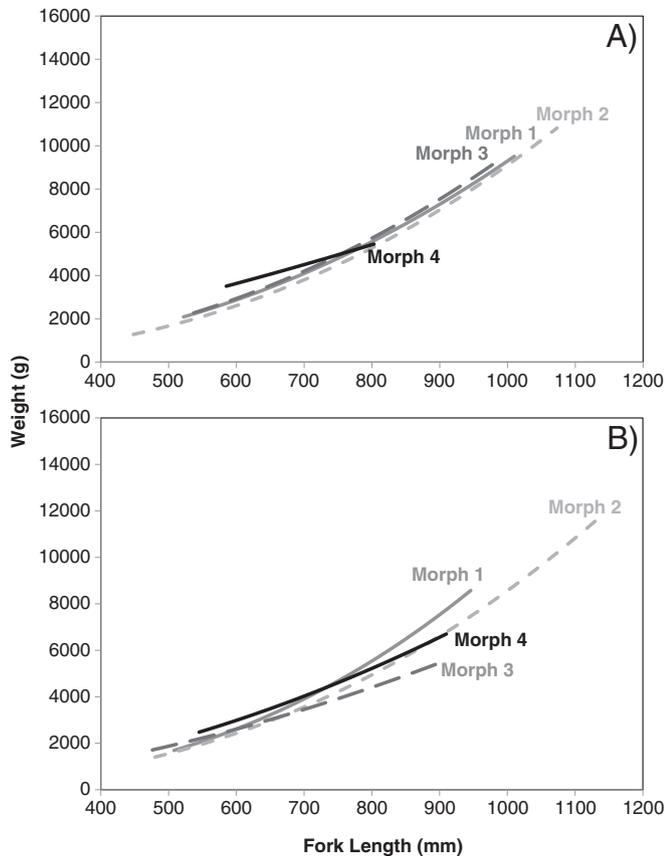


Fig. 5. Morph-specific weight–length relationships in current year spawners (A) and resting Lake Trout (B) in Great Bear Lake (Morph 1 = ----, Morph 2 = —, Morph 3 = - · -, and Morph 4 = ———). Equations for current spawners and resting individuals are, respectively: Morph 1: $W = 1.2 \times 10^{-3} L^{2.30}$, $R^2 = 0.62$, Morph 2: $W = 4 \times 10^{-4} L^{2.45}$, $R^2 = 0.85$, Morph 3: $W = 1 \times 10^{-3} L^{2.32}$, $R^2 = 0.49$, Morph 4: $W = 0.484 L^{1.40}$, $R^2 = 0.26$, and Morph 1: $W = 1 \times 10^{-3} L^{2.61}$, $R^2 = 0.87$, Morph 2: $W = 4.0 \times 10^{-4} L^{2.46}$, $R^2 = 0.85$, Morph 3: $W = 0.0228 L^{1.82}$, $R^2 = 0.40$, Morph 4: $W = 0.012 L^{1.94}$, $R^2 = 0.70$.

Nevertheless, this morph reached greater asymptotic lengths than generalist Morph 1, probably because it had greater longevity, as evidenced by the age–frequency distributions, despite the high mortality rates predicted by the biphasic growth model. Benthic morphs are generally smaller and mature earlier than other conspecific morphs (Adams et al., 1998; Snorrason and Skúlason, 2004; Arbour et al., 2011) although Thingvallavatn also has a large benthic morph of Arctic Char (Jonsson et al., 1988; Sandlund et al., 1992; Skulason et al., 1996). Primary productivity in Arctic lakes is generally benthic oriented (Jonsson et al., 1988), thus the presence of a large benthivorous morph feeding on large benthic prey (littoral fish and benthic invertebrates, Chavarie et al., 2014b) is perhaps not surprising for the shallow-water region of Great Bear Lake.

The pelagic Morph 4, which is the most specialized in diet, feeding mostly on Mysis and/or Cisco (Chavarie et al., 2014b), could be expected to possess distinct adaptations that reflect its specialized resource environment (Parker et al., 2001; Hendry et al., 2009; Taborsky and Brockmann, 2010). In other lakes, pelagic forms, generally piscivores or zooplanktivores, display higher growth and delayed maturity (Jonsson et al., 1988; Adams et al., 1998; Snorrason and Skúlason, 2004). Although not as common, small limnetic forms can also be found (Alekseyev et al., 2002; Power et al., 2005; Kristjansson, 2008; Woods et al., 2013). Age-at-maturity and asymptotic length of pelagic Morph 4 were similar to the piscivorous Morph 2, which may reflect their common use of the pelagic zone for foraging. Still, Morph 4 was less distinct morphologically, so the lack of a distinct life-history may simply reflect an intermediate phenotype adapted to the pelagic zone.

We observed almost half of the adult lake trout captured over nine years of sampling to be resting individuals, consistent with an earlier suggestion (Miller and Kennedy, 1948). Kennedy (1954) and Johnston (1972, 1973) observed similar patterns for populations from other resource-poor, high-latitude lakes, which suggests a programmed life-history of “constant skipping” (Healey, 1978; Secor, 2008). Interestingly, Goetz et al. (2011) recently found a significant proportion of lake trout in a resting stage in Lake Superior, a cold, oligotrophic system, albeit at a lower latitude, for both siscowet and lean morphotypes. The causes of skipped spawning in lake trout are not fully understood, although the most common hypothesis is poor nutrition (Rideout et al., 2005). Trout from Great Bear Lake become more streamlined as body length increases, relative to the average reported for both southern and northern populations (McDermid et al., 2010; Hansen et al.,

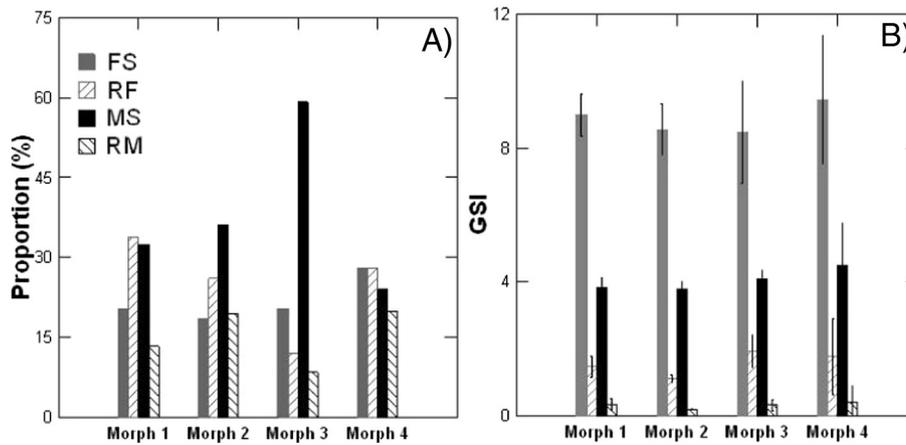


Fig. 6. Proportion (A) and GSI \pm SE at 95% confidence level (B) for female (FS) and male (MS) current year spawners, and resting females (RF) and males (RM) among Lake Trout morphotypes of Great Bear Lake. Sample sizes were as follows: Morph 1: FS = 58, RF = 96, MS = 92, and RM = 38; Morph 2 = FS = 80, RF = 113, MS = 157, and RM = 84; Morph 3: FS = 29, RF = 17, MS = 84, and RM = 12; and Morph 4: FS = 7, RF = 7, MS = 6, and RM = 5.

2012), suggesting lower condition. Skipped spawning may increase in northern populations, and be inversely correlated to freshwater productivity, similar to anadromy (Gross et al., 1988; McDowall, 1987; Doucett et al., 1999; Swanson et al., 2010). 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), although this seems less likely in a cold-water species such as lake trout. Skipped spawning has also been associated with moderate to high longevity (>15 years) (Secor, 2008). Given their environment and longevity, lake trout from Great Bear Lake are likely subject to such reproductive constraints.

Lake trout with insufficient energy reserves can interrupt gamete development, allowing fish condition to regulate fecundity (Rideout et al., 2005; Goetz et al., 2011). In lake trout from Lake Superior, females had higher proportions of resting individuals than males (Goetz et al., 2011; Sitar et al., 2014), consistent with their having higher reproductive investment (Johnston and Post, 2009; Morbey and Shuter, 2013). By having a high proportion of resting individuals, the piscivorous Morph 2 may be able to achieve improved growth during its life-time. In contrast, lower proportions of resting individuals in both sexes of benthic Morph 3 suggest higher frequencies of spawning.

Other traits related to reproductive investment in salmonids (Jonsson and Jonsson, 2001; Morbey and Hendry, 2008) differed among morphs. Despite similarities among lake trout morphs in weight-length and GSI-length relationships for current year spawners, differences among morphs for resting individuals suggest different levels of reproductive investment. The relatively greater difference in weight-length relationships between current year spawners and resting individuals for Morph 3 supports its higher investment in reproduction. Compared to Morphs 1 and 2, Morph 3 may also be increasing maternal investment by increasing egg size without a major reduction in egg numbers, which can increase survivorship in salmonids (Hutchings, 1991; Ojanguren et al., 1996). In contrast, higher egg numbers for the pelagic Morph 4 may compensate for their smaller eggs.

Conclusions

Life-history traits can directly and indirectly affect many aspects of a species' biology (Allendorf and Luikart, 2007; Östergren and Nilsson, 2012). Growth rate, which has many fitness consequences in fish (Schluter, 1995), plays a crucial role in life-history variation among fish morphotypes. Indeed, morphological differentiation is often

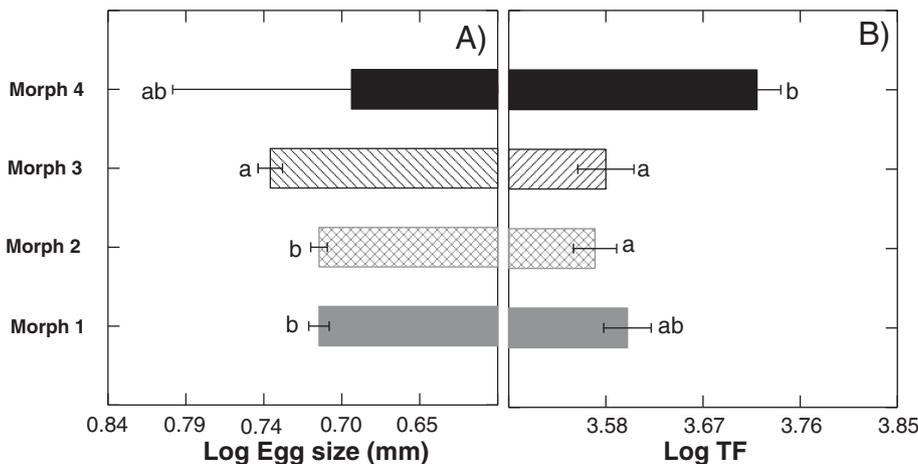


Fig. 7. Log-transformed length (covariate) adjusted mean egg size \pm SE (A) and log total fecundity (TF) per individual \pm SE (B) among morphotypes of Lake Trout from Great Bear Lake. Significant post-hoc pairwise comparisons are represented by different letters.

associated with differences in growth rate (Jonsson and Jonsson, 1997), but distinguishing cause-and-effect is difficult when considering ecological polymorphism (Fraser et al., 2008), especially in ecosystems with a high degree of intraspecific diversity and little ecological information. 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 adult life time of the piscivorous morph, and intermediate life-histories in the more benthic- and pelagic-oriented morphs. However, unexpected findings also arose, such as similar immature growth rates. The proportion of resting vs. current year spawners was generally high, suggesting a life-history adaptation for a cold, oligotrophic environment, allowing increased investment in adult growth; this was particularly evident in Morph 2.

This study extends the work of Blackie et al. (2003), Alfonso (2004) and Chavarie et al. (2013, 2014a,b), and confirms that Great Bear Lake provides an excellent opportunity to study ecological and evolutionary mechanisms of intraspecific divergence in postglacial fishes. While our study complements recent studies, several questions remain on the origin and the maintenance of this intraspecific diversity. These are especially complex in this case, where a novel environmental gradient (littoral-pelagic) is combined with other resource gradients (e.g., prey) and relatively high habitat and diet overlap (Chavarie et al., 2014b). Nevertheless, because these morphotypes represent a significant contribution to biodiversity, management will need to account for this complexity as northern aquatic systems face increasing anthropogenic stresses, such as climate change and industry development.

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