

# Life history differences between fat and lean morphs of lake charr (*Salvelinus namaycush*) in Great Slave Lake, Northwest Territories, Canada

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**Abstract** Life history characteristics (size, age, plumpness, buoyancy, survival, growth, and maturity) were compared between fat and lean morphs of lake charr *Salvelinus namaycush* in Great Slave Lake, Canada, to determine if differences may reflect effects of resource polymorphism. Lake charr were sampled using graded-mesh gill nets set in three depth strata. Of 236 lake charr captured, 122 were a fat morph and 114 were a lean morph. Males and females did not differ from each other in any attributes for either fat or lean

morphs. The fat morph averaged 15 mm longer, 481 g heavier, and 4.7 years older than the lean morph. The fat morph averaged 26% heavier and 48% more buoyant at length than the lean morph. Survival of the fat morph was 1.7% higher than that of the lean morph. The fat morph grew at a slower annual rate to a shorter asymptotic length than the lean morph. Fat and lean morphs matured at similar lengths and ages. We concluded that the connection between resource polymorphism and life histories in lean versus fat lake charr suggests that morph-specific restoration objectives may be needed in lakes where lake charr diversity is considered to be a restoration goal.

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## Introduction

Sympatric populations of fish may have multiple morphs that use different food or habitat resources, known as resource polymorphisms, which are often expressed as differences in life history characteristics, such as growth, age structure, survival, and size at maturity among sympatric morphs (Smith & Skúlason, 1996; Skúlason et al., 1996). Numerous sympatric lake charr *S. namaycush* morphs were recognized centuries ago in the Laurentian Great Lakes of North America by aboriginal people (Agassiz, 1850), early

Jesuit missionaries (Goodier, 1981), and French voyageurs (Roosevelt, 1865), and lean, fat, humper, and redfin morphs are presently recognized (Muir et al., 2014, 2015). The lean morph typically uses shallow waters <50 m in depth, is streamlined in form, low in fat content, and is often a piscivore when >460 mm in length (Krueger & Ihssen, 1995; Muir et al., 2015). The fat (siscowet) morph is deep bodied with a rounded snout, inhabits deep waters >80 m in depth, is high in fat content (Thurston, 1962; Khan & Qadri, 1970; Burnham-Curtis & Smith, 1994), and often feeds by following diel vertical movements in the water column of *Mysis relicta* and *Coregonus* species (Hrabik et al., 2006). The humper morph has a small head, short snout, short maxilla, large eye, short and narrow caudal peduncle, and uses isolated offshore reefs surrounded by water >90 m in depth or steep-sided sloping banks in Lake Superior (Burnham-Curtis & Smith, 1994; Krueger & Ihssen, 1995; Muir et al., 2015). The redfin morph is the most robust morph, with the largest head, snout, eyes, longest and deepest caudal peduncle, and longer pelvic and pectoral fins than other morphs (Muir et al., 2014). Lean, fat, and humper morphs are genetically differentiated (Dehring et al., 1981; Krueger et al., 1989; Page et al., 2004). Physiological differences between lean and fat morphs are heritable, including fat or oil content (Eschmeyer & Phillips, 1965; Goetz et al., 2010), swim bladder gas retention (Ihssen & Tait, 1974), and developmental rates of fertilized eggs and fry (Horns, 1985). Heritability of traits, especially fat and swim bladder gas that affect the ability to regulate depth through buoyancy compensation (Henderson & Anderson, 2002), indicates that the presence of sympatric morphs in the Great Lakes is not just a result of phenotypic plasticity (sensu Hindar & Jonsson, 1993).

Sympatric morphs of the lake charr resembling those from the Laurentian Great Lakes have also been described from other lakes in North America (Muir et al., 2015). In Great Bear Lake, several morphologically distinct morphs of shallow-water lean lake charr have been described (Blackie et al., 2003; Alfonso, 2004; Chavarie et al., 2013, 2014, 2015a). In Great Slave Lake, a fat morph occupied mostly deep waters, ate mostly invertebrates, especially opossum shrimp, had a narrow caudal peduncle, light body color, greater buoyancy, and deep anterior body, whereas a sympatric lean morph occupied mostly shallow

waters, ate mostly fish, were streamlined in shape, darker in color, and less buoyant (Zimmerman et al., 2006, 2009). In Lake Mistassini, Quebec, a deep-water light-colored humper-like morph was distinct from a dark, shallow-water lean morph (Zimmerman et al., 2007; Hansen et al., 2012). The presence of lean, fat, and humper morphs across North America suggests that common selection pressures and ecological opportunities have resulted in multiple morphs that are more widespread than just in the Laurentian Great Lakes (Eshenroder, 2008; Muir et al., 2015). Differences in life history (age, growth, and maturity) among sympatric lake charr morphs from the Laurentian Great Lakes (e.g., Rahrer, 1965; Burnham-Curtis & Bronte, 1996) and other North American lakes (Hansen et al., 2012; Chavarie et al., 2015b; Muir et al., 2015) may reflect unique use of ecological opportunities and niche space by sympatric morphs, and suggest a possible need for different management strategies for each morph.

We compared size, age, plumpness, buoyancy, survival, growth, and maturity between fat and lean morphs of lake charr in Great Slave Lake, Northwest Territories, Canada, to determine if differences may reflect effects of resource polymorphism. From otoliths, lengths, and weights collected from the same fish used in their original description (Zimmerman et al., 2006, 2009), we compared length and age frequencies, and weight–length, water–air weight, survival, length–age, and maturity–age relationships between fat and lean morphs. We expected to find that differences between fat and lean morphs in population characteristics (i.e., size, age, plumpness (weight at length), buoyancy, survival, growth, and maturity) would be similar to those in the Laurentian Great Lakes (Miller & Schram, 2000; Sitar et al., 2014), but that fat and lean morphs in the relatively lightly exploited eastern arm of Great Slave Lake (closed to fishing since 1972; Low et al., 1999; Evans, 2000) would be older, slower growing, and later maturing than exploited populations (Johnson, 1972, 1976).

## Methods

Great Slave Lake is located in the Northwest Territories, Canada, between latitudes 61 and 63° north and longitude 109 and 117° east. Great Slave Lake is the fifth largest (surface area = 28,568 km<sup>2</sup>) and the

deepest (maximum depth = 614 m) lake in North America (Rawson, 1950; Christie & Regier, 1988; Evans, 2000). The West Arm lies in the Western Interior Lowland and is relatively shallow, with soft substrate, whereas the East Arm lies in the Canadian Shield and is deeper (maximum depth = 614 m), with rocky substrate (Evans, 2000). Glacial processes formed the deep bays of the East Arm and the gradually shallower western main body. Great Slave Lake is considered a fairly young lake in geologic terms, with estimates of ice being present between 7500 and 9000 years ago (Rawson, 1950). The Hay, Buffalo, Little Buffalo, Taltson, Snowdrift, Lockhart, Yellowknife, and Snare rivers drain into Great Slave Lake from all sides (Rawson, 1950). Trophic conditions range from moderately oligotrophic in the southwest to extremely oligotrophic in the northwest (Kennedy, 1954). Fishery harvest in the East Arm, where fish were collected for this study, includes subsistence fishing and limited recreational angling (Low et al., 1999), whereas commercial fishing has been closed since 1974 (Evans, 2000). The cold-water fish community includes slimy sculpin (*Cottus cognatus*), spoonhead sculpin (*Cottus ricei*), deepwater sculpin (*Myoxocephalus thompsonii*), ninespine stickleback (*Pungitius pungitius*), burbot (*Lota lota*), cisco (*Coregonus artedii*) and shortjaw cisco (*Coregonus zenithicus*), lake whitefish (*Coregonus clupeaformis*), and lake charr (Rawson, 1951; Keleher, 1972; Stewart, 1997). Opossum shrimp (*Mysis relicta*) and a benthic amphipod (*Diporeia affinis*) are also abundant (Rawson, 1951). Non-native fishes have not been established (Keleher, 1972; Stewart, 1997).

Lake charr were sampled from Christie Bay in the East Arm of Great Slave Lake during 1–3 August 2002, 6–11 August 2005, and 26 July–3 August 2010 with gill nets and angling. Of the 48 gill-net sets, two were in depths of 0–50 m, 17 were in 50–100 m, and 29 were in 100–150 m. Ten fish caught by angling were from water less than 30 m deep. Deep-water (>50 m) nets were often set within 100 m of the steeply sloped shoreline. Gill-net mesh sizes ranged from 64 to 114 mm stretch measure. Based on relationships between girth and total length (TL) for lake charr caught in gill nets (Hansen et al., 1997), the range of mesh sizes used would enable wedging of lake charr ranging from 260 to 827 mm TL. Eight gangs were fished in 2002, 17 were fished in 2005, and 23 were fished in 2010. Depth strata for gill-net sets

were chosen based on known depths of lake charr morphs in Lake Superior (Moore & Bronte, 2001; Bronte et al., 2003). Nets were in the water overnight for about 24 h. Data collected from each fish included a full-body photograph (for shape and fin measures), total length (mm), weight in air (grams), weight in water (grams) with the swim bladder deflated (for buoyancy), sex (male or female), and maturity status (immature or mature; Zimmerman et al., 2006, 2009). From full-body photographs (Muir et al., 2012b), most fish were assigned to a morph using a combination of statistical analysis of head and body measures and visual assignment, as described by Muir et al. (2014). However, for some fish, statistical assignments differed between head and body measures, and visual consensus was not reached, so these fish were classified by visual comparison to the library of statistical and visual assignments (Hansen et al., 2012).

Sagittal otoliths were removed during field collections, placed in small tubes, and allowed to dry. Sagittal otoliths were used because they have been validated for age estimation of lake charr to an age of at least 50 years (Campana et al., 2008). One otolith from each fish was embedded in epoxy, and a thin transverse section (400  $\mu$ m) was cut, mounted on glass slides, polished, and photographed for age and growth assessment (Hansen et al., 2012). Annuli were counted by three independent readers using criteria described by Casselman & Gunn (1992), and specimens were excluded from analysis if the coefficient of variation (CV) of age estimates was more than 5% (Campana, 2001). Age estimates were used to inform demarcation of growth increments, measured from the nucleus to the maximum ventral radius of the otolith, and radial measurements at each annulus were used to back-calculate length at age using the biological intercept back-calculation model (Campana, 1990). The biological intercept (sagittal otolith width = 0.137 mm; age-0 lake charr length = 21.7 mm; Hansen et al., 2012) was based on equations describing relationships between length, age, and sagittal otolith width of age-0 lake charr (Bronte et al., 1995). The final back-calculated age was used for all analyses.

Length, weight, and age were first compared between males and females within morphs, and next between lean and fat morphs using single-factor ANOVA (Zar, 1999). We assumed that mean length, weight, or age differed between sexes or morphs if the

main effect was significant ( $P \leq 0.05$ ). Weight–length relationships were estimated from field measurements of weight (grams) and length (mm) of individual fish at the time of their capture (Quinn & Deriso, 1999):

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

$$\log_{10}(W) = \log_{10}(\alpha) + \beta \log_{10}(L) + \varepsilon$$

$$\log_{10}(W) = \log_{10}(\alpha) + \beta \log_{10}(L) + b_2(X \times \log_{10}(L)) + \varepsilon.$$

The power model (first equation) describes weight,  $W$ , as a function of length,  $L$ , the intercept,  $\alpha$ , the rate at which weight changes with length,  $\beta$ , and multiplicative error,  $\varepsilon$ . Model parameters,  $\alpha$  and  $\beta$ , and their standard errors were estimated using linear regression on the  $\log_{10}$ -transformed model (second equation; Zar, 1999). To determine if slopes differed between sexes or morphs, we included morph,  $X$ , as a class variable in an expanded model (third equation; Zar, 1999). If the interaction term was significant ( $P \leq 0.05$ ), we concluded that weight changed at different rates with length between sexes or morphs. If sexes did not differ in body condition, morphs were compared using the same approach. Buoyancy was compared between sexes and morphs using the same approach (without transforming mass in water or air), with mass in water as the dependent variable and mass in air as the independent variable.

Survival was estimated for each morph from the number of fish in each age class caught during gill-net sampling using the Robson–Chapman estimator (Robson & Chapman, 1961):

$$S = \frac{T}{n + T - 1}.$$

In the Robson–Chapman estimator,  $T$  is the sum of products of coded age (age—minimum age recruited to the sample) and the number in each age group, and  $n$  is the number of fish in the sample. We used all ages captured because all fish were vulnerable to wedging in the range of gill-net mesh sizes used for sampling (see above). Samples from all three years of sampling were pooled within each age class, because samples from individual years were too small to reliably estimate survival, and to smooth inter-annual variation in the age frequency caused by random variation in recruitment and mortality, as suggested by Ricker (1975). We compared survival between morphs using

an unpaired  $Z$  test for comparing two proportions (Eq. 24.58 in Zar, 1999), with the variance of  $S$  estimated for each morph from  $n$  and  $T$ , as described by Chapman & Robson (1961).

Growth in length with age was modeled using two versions of the Von Bertalanffy length–age model fit to back-calculated length at age of individual fish (Mooij et al., 1999; Quinn & Deriso, 1999):

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

$$L_t = L_\infty - (L_\infty - L_0) \left( 1 - e^{-(\omega/L_\infty) \times t} \right) + \varepsilon.$$

These length–age models describe back-calculated length  $L_t$  at age  $t$  as a function of theoretical maximum length ( $L_\infty$  = years), instantaneous rate at which  $L_t$  approaches  $L_\infty$  ( $K$  = 1/year), age at length = 0 ( $t_0$  = years), early growth rate ( $\omega = L_\infty \times K$  = mm/year; Gallucci & Quinn, 1979), length at age = 0 ( $L_0$  = mm), and additive error ( $\varepsilon$ ). Model parameters,  $L_\infty$ ,  $K$ ,  $t_0$ ,  $L_0$ , and  $\omega$  were estimated using nonlinear mixed-effect models (package ‘nlme’ in R; R Core Team, 2014), with a fixed population effect, random individual effects, and sex or morph as a fixed factor (Vigliola & Meekan, 2009). If sexes did not differ significantly in growth parameters, morphs were compared using the same approach.

Length and age at maturity were estimated using logistic regression based on the maturity status of individual fish sampled at each length or age (immature = 0; mature = 1):

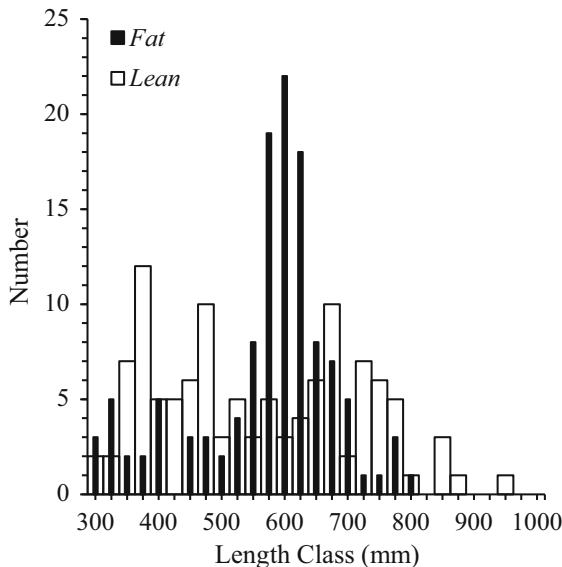
$$F(x) = \frac{1}{1 + e^{-(b_0 + b_1 x)}}.$$

The model describes the likelihood  $F(x)$  that an individual fish was sexually mature at age or length  $x$ , as a function of an intercept  $b_0$  and the rate of increase in the probability of maturity with increasing age or length  $b_1$ . Model parameters  $b_0$  and  $b_1$  and their standard errors were estimated using logistic regression on the logit transformation of the logistic equation (Hosmer & Lemeshow, 2000). To determine if maturity models differed between sexes and morphs, we compared log likelihoods of full models (separate models for each sex, or each morph) to reduced models (a single model for both sexes, or both morphs) in likelihood ratio tests (Hosmer & Lemeshow, 2000). If the likelihood ratio test was significant ( $P \leq 0.05$ ), we concluded that maturity models differed between

sexes or morphs. If maturity models did not differ between sexes, morphs were compared using the same approach. Length and age at 50% maturity ( $L_{50}$  and  $A_{50}$ ) were estimated for each morph from the intercept and slope,  $|b_0/b_1|$ .

## Results

Of 236 lake charr captured from Great Slave Lake that were assigned to a morph, 122 charr were classified as the fat morph (27 in 2002, 60 in 2005, and 35 in 2010) and 114 charr were classified as the lean morph (2 in 2002, 61 in 2005, and 51 in 2010). Males and females of both fat (48 females, 73 males, and 1 unknown) and lean (53 females, 60 males, and 1 unknown) morphs did not differ in mean TL (fat,  $F_{1,119} = 1.169$ ,  $P = 0.282$ ; lean,  $F_{1,111} = 0.0124$ ,  $P = 0.91$ ) or mean weight (fat,  $F_{1,119} = 1.234$ ,  $P = 0.27$ ; lean,  $F_{1,111} = 0.348$ ;  $P = 0.56$ ). On average, fat and lean morphs differed by only 15 mm TL ( $F_{1,234} = 0.800$ ;  $P = 0.37$ ), but the fat morph was 481 g heavier ( $F_{1,234} = 7.933$ ;  $P = 0.005$ ) than the lean morph (Fig. 1; Table 1). The fat morph averaged 583 mm TL (SE = 12.1 mm; range = 308–802 mm) and 2319 g in weight (SE = 119 g; range = 182–7200 g),



**Fig. 1** Length frequency of 122 fat (solid bars) and 114 lean (open bars) lake charr captured in Great Slave Lake, Northwest Territories, Canada, during 1–3 August 2002, 6–11 August 2005, and 26 July–3 August 2010

whereas the lean morph averaged 568 mm TL (SE = 12.5 mm; range = 323–959 mm) and 1838 g in weight (SE = 123 g; range = 232–7000 g).

The fat morph was 26% heavier at length than the lean morph in Great Slave Lake (Fig. 2; Table 1). Males and females did not differ in length-specific weight for either the fat morph (interaction between sex and length;  $F_{1,117} = 1.478$ ;  $P = 0.23$ ) or the lean morph ( $F_{1,109} = 0.055$ ;  $P = 0.81$ ). Fat and lean morphs differed in body condition because their weight–length relationships differed in both shape parameters  $\beta$  (interaction between morph and length;  $F_{1,232} = 24.2$ ;  $P < 0.001$ ) and intercepts  $\log_{10}(\alpha)$  (main effect of morph;  $F_{1,232} = 19.6$ ;  $P < 0.001$ ). The fat morph was heavier at length than the lean morph, because the shape parameter of the weight–length relationship  $\beta$  was larger for the fat morph (3.508; SE = 0.0641) than for the lean morph (3.145; SE = 0.0396), although the intercept  $\log_{10}(\alpha)$  was lower for the fat morph (−6.395; SE = 0.177) than for the lean morph (−5.498; SE = 0.109).

The fat morph was 48% lighter in water (more buoyant) than the lean morph in Great Slave Lake (Fig. 3; Table 1). Males and females did not differ in buoyancy for either the fat morph (interaction between sex and length;  $F_{1,117} = 0.260$ ;  $P = 0.61$ ) or the lean morph ( $F_{1,109} = 0.099$ ;  $P = 0.75$ ). Fat and lean morphs differed in buoyancy because their relationships between weight in air and water differed in both slopes (interaction between morph and length;  $F_{1,232} = 195.3$ ;  $P < 0.001$ ) and intercepts (main effect of morph;  $F_{1,232} = 10.7$ ;  $P = 0.001$ ). The fat morph was more buoyant than the lean morph, because the slope of the relationship between weight in air and water was smaller for the fat morph (0.0203; SE = 0.00237) than for the lean morph (0.0580; SE = 0.00141), although the intercept was higher for the fat morph (20.259; SE = 6.154) than for the lean morph (−1.735; SE = 3.296).

The fat morph was older on average than the lean morph in Great Slave Lake (Fig. 4; Table 1). Males and females did not differ in mean age for either the fat morph ( $F_{1,119} = 0.0112$ ;  $P = 0.92$ ) or the lean morph ( $F_{1,111} = 0.0007$ ;  $P = 0.98$ ). The fat morph averaged 4.7 years older (24.9 years; SE = 0.806 years; range = 7–43 years) than the lean morph (20.2 years; SE = 0.834 years; range = 8–46 years;  $F_{1,234} = 16.4$ ;  $P < 0.001$ ). Fat and lean morphs differed in annual survival  $S$  ( $Z$  test = 2.207;  $P = 0.03$ ). Annual

**Table 1** Total length (TL = mm), weight (g), age (years), intercept and slope of  $\log_{10}$ -transformed weight–length relationships (condition), intercept and slope of wet-weight versus dry-weight relationships (buoyancy), average growth parameters [age at length zero ( $t_0$  = years), length at age zero ( $L_0$  = mm), early growth rate ( $\omega$  = mm/year), instantaneous growth rate ( $K$  = years<sup>-1</sup>), and asymptotic length ( $L_\infty$  = mm)], and intercept and slope of logit functions for length and age at maturity for two Lake Charr morphs captured in Great Slave Lake, Northwest Territories, Canada, during 1–3 August 2002, 6–11 August 2005, and 26 July–3 August 2010

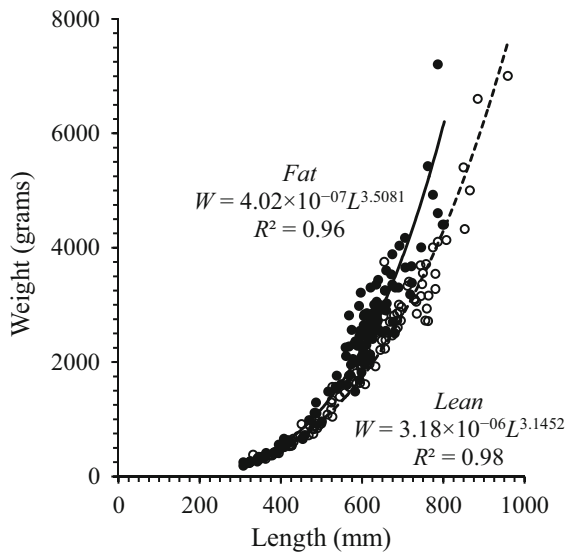
Attribute	Parameter	Fat	Lean	<i>F</i> ratio	<i>P</i>
Demography	TL				
	Estimate	583	568	0.80	0.372
	SE	12.1	12.5		
	Range	308–802	323–959		
	Weight				
	Estimate	2319	1838	7.93	0.005
	SE	119	123		
	Range	182–7200	232–7000		
	Age				
	Estimate	24.9	20.2	16.37	<0.001
Condition	SE	0.806	0.834		
	Range	7–43	8–46		
	Intercept				
	Estimate	−6.395	−5.498	19.60	<0.001
	SE	0.177	0.109		
Buoyancy	Slope				
	Estimate	3.508	3.145	24.24	<0.001
	SE	0.0642	0.0396		
	Intercept				
	Estimate	20.259	−1.735	10.69	0.001
Survival	SE	6.155	3.296		
	Slope				
	Estimate	0.0203	0.0580	195.31	<0.001
	SE	0.00237	0.00141		
	<i>S</i>				
Growth	Estimate	0.947	0.930	2.21 <sup>a</sup>	0.035
	SE	0.00465	0.00635		
	$t_0$				
	Estimate	−0.751	−0.760	0.00	0.996
	SE	0.0596	0.0619		
	$L_0$				
	Estimate	36.5	37.7	2.77	0.096
	SE	2.89	3.02		
	$\omega$				
	Estimate	54.1	58.4	7.53	0.006
	SE	1.09	1.14		
	$K$				
	Estimate	0.077	0.082	2.30	0.129
	SE	0.00254	0.00270		
	$L_\infty$				
	Estimate	726	756	15.90	<0.001
	SE	17.1	18.1		
Maturity–length	Intercept				
	Estimate	−25.0	−20.6	−0.535 <sup>a</sup>	0.593
	SE	6.72	4.84		



**Table 1** continued

Attribute	Parameter	Fat	Lean	<i>F</i> ratio	<i>P</i>
Maturity–age	Slope				
	Estimate	0.0496	0.0393	0.649 <sup>a</sup>	0.516
	SE	0.0128	0.0094		
	Intercept				
	Estimate	−17.8	−13.4	−0.627 <sup>a</sup>	0.531
	SE	6.29	3.15		
	Slope				
	Estimate	1.116	0.827	0.656 <sup>a</sup>	0.512
	SE	0.390	0.202		

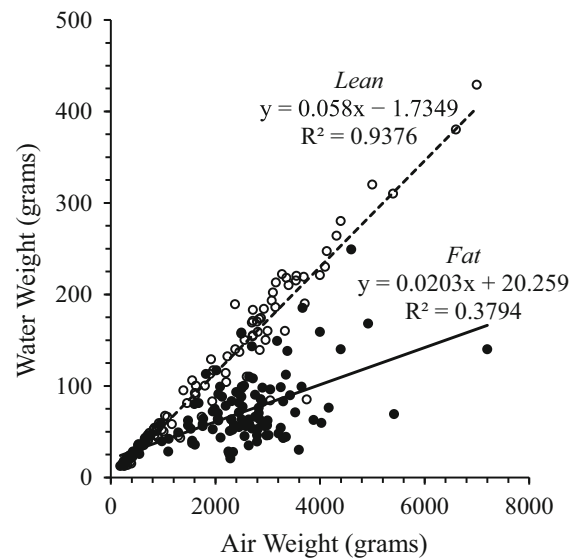
<sup>a</sup> The test statistic is a Z test, rather than an *F* ratio



**Fig. 2** Weight–length relationships of 122 fat (solid circles and line) and 114 lean (open circles, dashed line) lake charr captured in Great Slave Lake, Northwest Territories, Canada, during 1–3 August 2002, 6–11 August 2005, and 26 July–3 August 2010

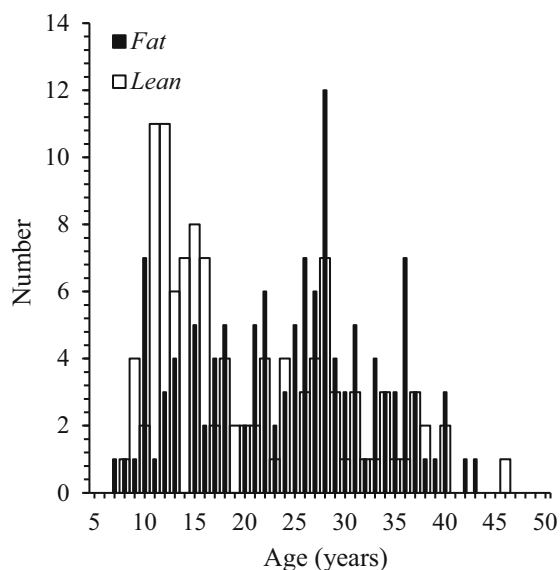
survival (age-7 +) was higher for the fat morph ( $S = 94.7\%$ ; 95% CI 93.8–95.6%) than for the lean morph ( $S = 93.0\%$ ; 95% CI 91.7–94.3%).

The fat morph grew at a slower early growth rate to a shorter average asymptotic length than the lean morph in Great Slave Lake (Fig. 5; Table 1). Fat and lean morphs did not differ in average age at length zero ( $t_0$  ( $F_{1,232} < 0.001$ ;  $P = 0.996$ ), length at age zero  $L_0$  ( $F_{1,232} = 2.769$ ;  $P = 0.096$ ), or instantaneous growth rate  $K$  ( $F_{1,232} = 2.304$ ;  $P = 0.129$ ). Early growth rate  $\omega$  ( $F_{1,232} = 7.531$ ;  $P = 0.006$ ) and asymptotic length  $L_\infty$  ( $F_{1,232} = 9.27$ ;  $P = 0.002$ ) differed between fat and lean morphs. Fat and lean morphs grew from similar ages at length zero (fat:  $t_0 = -0.7505$  years,

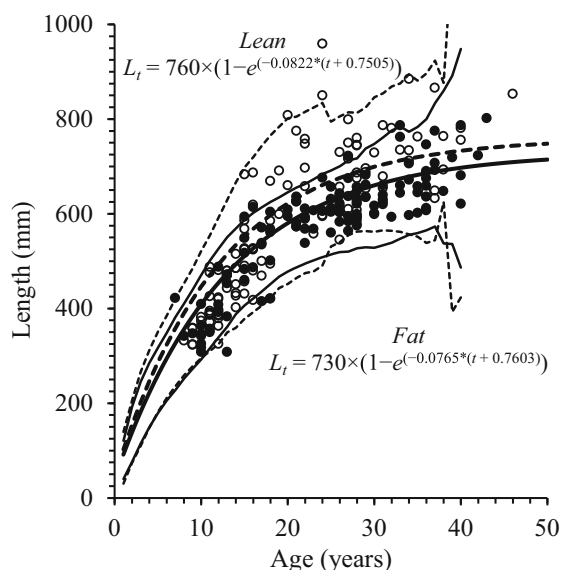


**Fig. 3** Relationships between mass in water and air for 122 fat (solid circles and line) and 114 lean (open circles, dashed line) lake charr captured in Great Slave Lake, Northwest Territories, Canada, during 1–3 August 2002, 6–11 August 2005, and 26 July–3 August 2010

$SE = 0.0596$  years; lean:  $t_0 = -0.7603$  years,  $SE = 0.0619$  years) and lengths at age zero (fat:  $L_0 = 36.5$  mm/year,  $SE = 2.89$ ; lean:  $L_0 = 37.7$  mm/year,  $SE = 3.02$ ) at similar instantaneous growth rates (fat:  $K = 0.0765$ /year  $SE = 0.00254$ /year; lean:  $K = 0.0822$ /year,  $SE = 0.00270$ /year). In contrast, the fat morph grew at a 4.3 mm/year slower early growth rate ( $\omega = 54.1$  mm/year;  $SE = 1.09$  mm/year) than the lean morph ( $\omega = 58.4$  mm/year;  $SE = 1.14$  mm/year) toward a 30 mm shorter mean asymptotic length ( $L_\infty = 730$  mm;  $SE = 15.9$  mm) than the lean morph ( $L_\infty = 760$  mm;  $SE = 16.8$  mm).



**Fig. 4** Age frequency of 122 fat (solid bars) and 114 lean (open bars) lake charr captured in Great Slave Lake, Northwest Territories, Canada, during 1–3 August 2002, 6–11 August 2005, and 26 July–3 August 2010



**Fig. 5** Length–age relationships for 122 fat (solid circles and line) and 114 lean (open circles, dashed line) lake charr captured in Great Slave Lake, Northwest Territories, Canada, during 1–3 August 2002, 6–11 August 2005, and 26 July–3 August 2010

Fat and lean morphs matured at similar lengths and ages in Great Slave Lake (Fig. 6; Table 1). Fewer immature lake charr were collected ( $n = 75$ ; length range 193–594 mm) than mature lake charr ( $n = 156$ ;

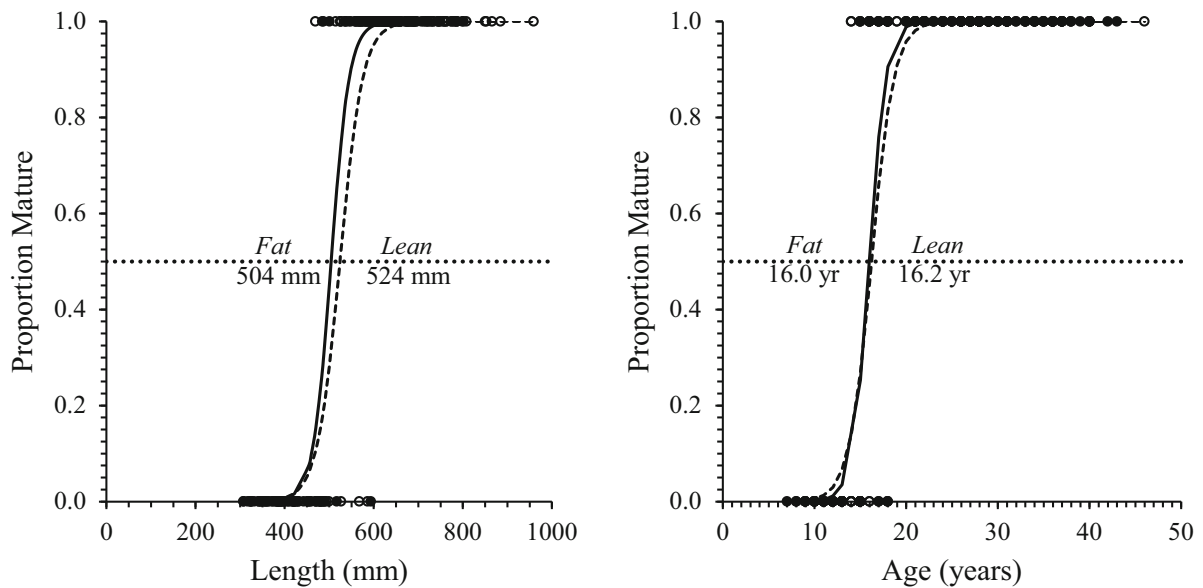
length range 196–959 mm; maturity was not diagnosed for five fish). Males and females did not differ in maturity–length relationships for either the fat morph ( $\chi^2 = 0.081$ ;  $df = 2$ ;  $P = 0.96$ ) or the lean morph ( $\chi^2 = 0.620$ ;  $df = 2$ ;  $P = 0.73$ ). Similarly, males and females did not differ in maturity–age relationships for either the fat morph ( $\chi^2 = 0.244$ ;  $df = 2$ ;  $P = 0.885$ ) or the lean morph ( $\chi^2 = 0.393$ ;  $df = 2$ ;  $P = 0.821$ ). Maturity of the fat morph was related to length ( $\chi^2 = 99.2$ ;  $df = 1$ ;  $P < 0.001$ ) and age ( $\chi^2 = 100.9$ ;  $df = 1$ ;  $P < 0.001$ ). Maturity of the lean morph was also related to length ( $\chi^2 = 123.7$ ;  $df = 1$ ;  $P < 0.001$ ) and age ( $\chi^2 = 115.4$ ;  $df = 1$ ;  $P < 0.001$ ). Length at 50% maturity was 504 mm (SE = 15.6 mm) for the fat morph and 524 mm (SE = 13.8 mm) for the lean morph. Age at 50% maturity was 16.0 years (SE = 0.735 years) for the fat morph and 16.2 years (SE = 0.610 years) for the lean morph.

## Discussion

In Great Slave Lake, lean lake charr were lighter, slimmer, less buoyant, younger, and faster growing than fat lake charr, but matured at a similar size and age, which is consistent with a connection between life history and resource polymorphism observed more broadly for fishes in recently glaciated areas of the northern hemisphere (at least 21 species reviewed by Smith & Skúlason, 1996). For example, in Lake Mistassini, Quebec, a deep-water humper morph grew slower to a shorter mean asymptotic length, was older, and matured at an older age and larger size than a shallow-water lean morph (Hansen et al., 2012). Similarly, in Lake Superior, a deep-water fat morph grew slower to a smaller asymptotic size, was plumper, lighter, shorter, older, and matured at shorter lengths and older ages than a shallow-water lean morph (Miller and Schram, 2000; Sitar et al., 2014). Last, in Great Bear Lake, Northwest Territories, Canada, four lean lake charr morphs differed in mean length, mean age, growth, and maturity (Chavarie et al., 2015b).

Previous life history studies of lake charr from Great Slave Lake likely included fat and lean morphs, although multiple morphs were not identified. Early sampling in Great Slave Lake prior to opening commercial fishing (1944–1947) included gill-net mesh sizes (38–140 mm stretch measure), depths





**Fig. 6** Maturity versus length (*left panel*) and age (*right panel*) for 118 fat (solid circles and line) and 113 lean (open circles, dashed line) lake charr captured in Great Slave Lake, Northwest

Territories, Canada, during 1–3 August 2002, 6–11 August 2005, and 26 July–3 August 2010

(2–300 m), and regions (multiple locations in the western and eastern basins) that would likely have caught both lean and fat morphs, but lake charr were all treated as a single morph (Rawson, 1949, 1951). In early studies, lake charr were third most numerically abundant, behind lake whitefish and cisco, but were the largest biomass of all 21 species sampled, with an estimated yield similar to the upper Laurentian Great Lakes and Lake Nipigon (Rawson, 1949, 1951). During early years of exploitation (1948–1952), lake charr were much younger (mean age = 11.2 years; range = 6–25 years), mortality was much higher ( $A = 33\%$  at age 10;  $49\%$  at age 20), and maturity was at a much younger age ( $A_{50} = 8.8$  years) and smaller body size ( $L_{50} = 467$  mm; Kennedy, 1954) than in our study, possibly because the population was being fished, mostly in the productive western basin, or because age was estimated from scales rather than otoliths. For long-lived species like lake charr, age is underestimated from scales, because scale growth slows after sexual maturity while otoliths continue to grow (Dubois & Legueux, 1968; Simard & Magnin, 1972; Sharp & Bernard, 1988; Burnham-Curtis & Bronte, 1996). Nonetheless, over-exploitation caused lake charr relative abundance to decline 93% from 1945 to 1964, as average weight of harvested fish

declined 28–49% among areas in the lake (Keleher, 1972). By 1972, after fishery quotas were substantially reduced and commercial fishing was eliminated in the East Arm, otolith ages of lake charr in the recreational fishery were higher than earlier scale ages (mean = 16.2 years, range = 5–33 years; Falk et al., 1973; Healey, 1978), but still much lower than in our study.

Life history characteristics of sympatric fat and lean morphs from Great Slave Lake were generally similar to those of sympatric fat and lean morphs in Lake Superior (Miller & Schram, 2000; Sitar et al., 2014). For example, fat morphs in Great Slave Lake were heavier, older, and grew slower toward a shorter asymptotic length than lean morphs, like sympatric fat and lean morphs in Lake Superior (Miller & Schram, 2000). In contrast, length and age at maturity did not differ between fat and lean morphs in Great Slave Lake, whereas the fat morph matured at shorter length ( $L_{50} = 443$  mm) and older age ( $A_{50} = 11.4$  years) than the lean morph ( $L_{50} = 605$  mm;  $A_{50} = 8.8$  years) in Lake Superior (Sitar et al., 2014). The phenotypic differences we observed between lean and fat morphs in Great Slave Lake, such as body condition and buoyancy, persist in lean and fat morphs from Lake Superior when reared under identical conditions, which suggests that these differences have

**Table 2** Slope of log<sub>10</sub>-transformed weight–length relationships ( $\beta$ ), predicted weight of a 500-mm fish ( $W_{500}$  = kg), annual survival ( $S$ ), asymptotic length ( $L_{\infty}$  = mm), early growth rate ( $\omega$  = mm/year), length at 50% maturity ( $L_{50}$  = mm), and age at 50% maturity ( $A_{50}$  = years) for native lake trout populations from North America (mean, standard deviation = SD, coefficient of variation = CV, and number of populations =  $N$ ; Dubois & Lageaux, 1968; Healey,

1978; Piccolo et al., 1993; Trippel, 1993; Martin & Olver, 1980; Shuter et al., 1998; Mills et al., 2002; McDermid et al., 2010; Hansen et al., 2012) and percentiles of each metric's cumulative North American distribution for lean and fat lake trout morphs captured in Great Slave Lake, Northwest Territories, Canada, during 1–3 August 2002, 6–11 August 2005, and 26 July–3 August 2010 (Table 1; this study)

Source	Statistic/Morph	$\beta$	$W_{500}$	$S$	$L_{\infty}$	$\omega$	$L_{50}$	$A_{50}$
North America	Mean	3.228	1.136	60%	639.6	107.2	421.9	8.9
	SD	0.258	0.143	77%	139.3	27.1	80.9	3.3
	CV	8%	13%	58%	22%	25%	19%	37%
	$N$	48	48	70	186	56	132	132
Great Slave	Lean	37%	14%	67%	80%	4%	90%	99%
	Fat	86%	63%	68%	73%	2%	85%	98%

a genetic basis (Eschmeyer & Phillips, 1965; Goetz et al., 2010). Fat and lean morphs occupy overlapping depths in both lakes, although the fat morph occurs at much greater depth than the lean morph (Sitar et al., 2008), largely because the fat morph invests in lipids (Miller & Schram, 2000; Goetz et al., 2014) that allow them to expend less energy to remain buoyant at great depth (Henderson & Anderson, 2002). High lipids also enable the fat morph to migrate vertically in pursuit of invertebrate (*Mysis diluviana*) and fish (cisco) prey (Ahrenstorff et al., 2011; Gamble et al., 2011; Isaac et al., 2012; Hrabik et al., 2014). In Lake Superior, diets of fat and lean morphs overlap greatly (Fisher & Swanson, 1996; Zimmerman et al., 2009), likely because the fat morph exploits prey in both deep and shallow water (Harvey et al., 2003), although trophic overlap was low between fat and lean morphs (Harvey & Kitchell, 2000; Zimmerman et al., 2009).

Demographic and life history attributes of fat and lean lake charr morphs in Great Slave Lake were consistent with lightly exploited lake trout populations elsewhere in North America (Healey, 1978; Martin & Olver, 1980). Body condition of the lean morph was low in Great Slave Lake, because the exponent of the weight–length relationship was higher than only 37% and the predicted weight of a 500-mm fish ( $W_{500}$ ) was higher than only 14% of 48 other lake trout populations in North America (Table 2). In contrast, body condition of the fat morph was high in Great Slave Lake, because the exponent of the weight–length relationship was higher than 86% and the predicted weight of a 500-mm fish ( $W_{500}$ ) was higher than 63%

of 48 other populations in North America (Table 2), as expected for a fish that invests energy in body fat rather than length (Goetz et al., 2014). Annual survival of lake charr in Great Slave Lake was higher than 67% (lean morph) and 68% (fat morph) of 70 other populations in North America (Table 2). Lake charr in Great Slave Lake grew slower than all but 4% (lean morph) and 3% (fat morph) of 56 other populations in North America, but toward an asymptotic length that was higher than 80% (lean morph) and 73% (fat morph) of 186 other populations in North America (Table 2). Length and age at maturity of lean and fat lake charr in Great Slave Lake were higher than nearly all of 132 other populations in North America (Table 2). In contrast, four lean lake charr morphs matured at larger sizes and older ages in Great Bear Lake ( $L_{50}$  = 582–704 mm,  $A_{50}$  = 17.4–20.2 years, Chavarie et al., 2015b) than we found in Great Slave Lake. Collectively, these life history attributes suggest that lean and fat lake charr populations in Great Slave Lake were lightly exploited (high survival) and therefore lived at high density relative to prey supply (low body condition), so grew slowly to a large asymptotic length, and to a large size and old age at maturity (Rose et al. 2001).

Length and age at maturity did not differ between fat and lean lake charr morphs in Great Slave Lake, which may reflect their ontogeny up to the point of maturation, as in other lake charr populations (Van Oosten & Deason, 1938; Dryer et al., 1965; Fisher & Swanson, 1996). The onset of maturity in many lake charr populations is related to both body size and age

(Martin & Olver, 1980). In Great Slave Lake, lean and fat morphs shift from benthic to pelagic feeding with increasing body size: small lake charr (<430 mm TL) are benthic feeders that overlap in depth distribution, but partition resources within depths, whereas large lake charr (>430 mm TL) are pelagic feeders that occupy shallow (lean) or deep (fat) depths, and partition resources in depths they inhabit (Zimmerman et al., 2009). Therefore, physical and chemical features of a shared environment (pH, oxygen, salinity, diurnal and annual light cycles, temperature; Boeuf & Le Bail, 1999) affected growth and maturation of both morphs similarly in years prior to maturity, which may partly explain the observed lack of differences in length and age at maturation, although similar pre-maturation growth rates (22 mm/year) preceded different lengths and ages at maturity among four lean morphs in Great Bear Lake (Chavarie et al., 2015b). After sexual maturity is reached, growth usually slows as fish allocate more energy to reproductive tissue and behavior associated with reproduction, such as migration and courtship (Roff, 1983). Lacking a clear difference in age at maturity, the subsequent differences observed in asymptotic length between morphs in Great Slave Lake were likely due to differences in processing of energy after sexual maturity was reached, as also seen for fat and lean morphs in Lake Superior (Goetz et al., 2014). Similarly, in Lake Vangsvatnet, Norway, sympatric dwarf and normal morphs of Arctic char differed in growth but not age at maturity (Jonsson & Hindar, 1982), and growth differences were genetically determined (Hindar & Jonsson, 1993).

Discrete intraspecific morphs can arise in a single population from phenotypic plastic adaptations to environmental conditions, genetic isolation, or both (Skúlason et al., 1996) and, therefore, cause differences in life history, behavior, body shape, and color (Schluter & McPhail, 1992; Robinson & Wilson, 1994; Smith & Skúlason, 1996). In Great Slave Lake, fat and lean morphs partition resources within deep benthic habitats when small, and between shallow and deep pelagic habitats when large (Zimmerman et al., 2009), rather than partitioning between benthic and pelagic habitats as in many Arctic charr systems (Fraser et al., 2008). Nonetheless, differences in morphology and growth between lean and fat morphs in Lake Superior reared under the same environmental conditions were genetically determined, rather than

attributable to resource plasticity (Goetz et al., 2010). Differences in growth between fat and lean morphs in Great Slave Lake may be caused by differences in the dynamics of energy processing and storage metabolism between fat and lean morphs, as in Lake Superior (Goetz et al., 2014). The decrease in metabolic output of the fat morph compared to the lean morph in Lake Superior may be related to temperature, food availability, predator–prey interactions, food predictability, or reproductive investment (Goetz et al., 2014). Although lipid storage may offer a functional advantage for inhabiting high-pressure, deep-water environments (Henderson & Anderson, 2002), lipid storage itself may be part of a genetically driven life history strategy, rather than a response to environmental conditions (Goetz et al., 2014). Low biological productivity and diversity of deep oligotrophic lakes may enable specialization in feeding and habitat depth that ultimately facilitates morphological divergence (Eshenroder, 2008) and genetic differentiation (Goetz et al., 2010) that may translate into the observed differences in life history between the fat and lean lake charr morphs in Great Slave Lake.

The presence of multiple lake charr morphs in large Canadian lakes enables comparison of life history attributes, such as growth, survival, and maturity, among morphs in relatively unperturbed large lakes to the same morphs in Lake Superior and other Laurentian Great Lakes that have been perturbed by invasive species, fishing, and habitat degradation. For this reason, we previously suggested that instead of relying solely on life history measures from disturbed stocks in Lake Superior (the current practice), measures from undisturbed populations, like the fat morph in Great Slave Lake, could be used to guide development of restoration objectives for a fat morph of the lake charr in the Laurentian Great Lakes (Hansen et al., 2012). Until recently, lake charr restoration in the Laurentian Great Lakes ignored deep-water forms (fat and humper) in favor of the more economically valuable and accessible shallow-water lean form (Hansen, 1999; Krueger & Ebener, 2004; Muir et al., 2012a). Recent versions of lake charr restoration plans now include strategies to reintroduce a humper morph into deep waters of Lakes Michigan (Bronte et al., 2008) and Erie (Markham et al., 2008), although plans have not yet included reintroduction of a fat morph. To that end, life history characteristics we found for the fat morph in Great Slave Lake could be used to set goals

and measure progress of population recovery for a reintroduced fat lake charr morph in the Laurentian Great Lakes. Further, consideration of life history differences between deep-water and shallow-water lake charr morphs will help promote re-establishment of lake charr diversity in the Laurentian Great Lakes. Remaining questions include (1) how similar are lake charr life histories among lakes and (2) to what extent do environment and genetics determine life history variation? Further studies of lake charr morphs elsewhere in North America will be useful for answering these questions and for understanding the generality of our findings for fat and lean lake charr morphs in Great Slave Lake.

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