



Life history variation among four lake trout morphs at Isle Royale, Lake Superior



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ABSTRACT

Life history traits were compared among four morphs of lake trout at Isle Royale, Lake Superior. Of 738 lake trout caught at Isle Royale, 701 were assigned to a morph (119 humpers, 160 leans, 85 redfins, and 337 siscowets) using a combination of statistical analysis of head and body shape and visual assignment. On average, redfins were longer (544 mm), heavier (1481 g), heavier at length, more buoyant, and older (22 years) than siscowets (519 mm; 1221 g; 19 years), leans (479 mm; 854 g; 13 years), and humpers (443 mm; 697 g; 17 years). On average, leans grew from a younger age at length = 0 and shorter length at age = 0, at a faster early growth rate to a longer asymptotic length than the other three morphs, while redfins grew at a slower instantaneous rate and humpers grew to a shorter asymptotic length than other morphs. On average, leans were longer (562 mm) and older (15 years) at 50% maturity than redfins (427 mm, 12 years), siscowets (401 mm, 11 years), or humpers (394 mm, 13 years). Life history parameters did not differ between males and females within each morph. We conclude that differences in life history attributes of lean, humper, redfin, and siscowet morphs of lake trout are consistent with differential habitat use in waters around Isle Royale, Lake Superior.

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Introduction

Many visually-distinct and easily-identified sympatric morphs of the lake trout *Salvelinus namaycush* were recognized more than a century ago in the Laurentian Great Lakes of North America (Agassiz, 1850; Goodier, 1981; Roosevelt, 1865). However, much of this morphological diversity was lost in the middle of the 20th century when over-fishing, predation by the invasive sea lamprey *Petromyzon marinus*, and habitat degradation caused lake trout stocks to collapse throughout much of the basin (Hansen, 1999; Krueger and Ebener, 2004; Muir et al., 2012a). Subsequently, fishery managers attempted to restore lake trout stocks by stocking hatchery-reared fish, restricting fisheries, and controlling sea lamprey populations. However, hatchery production and stocking were focused on the lean form of lake trout that occupied shallow in-shore waters where fisheries were focused. Recently, lake trout recovery plans have expanded to include other forms that occupy deep

offshore waters (e.g., Lake Michigan, Bronte et al., 2008; Lake Erie, Markham et al., 2008).

Although lake trout morphological diversity in Lake Superior is currently reduced from historical conditions, lean, siscowet (fat), humper, and redfin morphs are currently recognized (Bronte et al., 2003; Burnham-Curtis and Smith, 1994; Khan and Qadri, 1970; Krueger and Ihssen, 1995; Moore and Bronte, 2001; Muir et al., 2014, 2015; Peck, 1975; Thurston, 1962). The lean morph uses shallow waters <50 m, is streamlined in form, relatively low in fat content, and mostly piscivorous when >460 mm in length (Conner et al., 1993; Dryer et al., 1965; Ray et al., 2007). The siscowet (fat) morph is deep bodied with a rounded snout, uses deep waters >80 m, is high in fat content, and feeds in pelagic habitat by following diel vertical movements of *Mysis diluviana* and *Coregonus* species (Hrabik et al., 2006) and in benthic habitat on sculpins (*Cottus* sp. and *Myoxocephalus thompsonii*) and burbot *Lota lota* (Conner et al., 1993; Ray et al., 2007). The humper morph has a small head, short snout, short maxilla, large eye, short and narrow caudal peduncle, and often uses isolated offshore reefs surrounded by water >90 m in depth or steep-sided sloping banks. The redfin morph is the most full-bodied, with the largest head, snout, and 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

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genetically distinct (Dehring et al., 1981; Goetz et al., 2010; Guinand et al., 2003, 2012; Krueger et al., 1989; Page et al., 2004), with heritable physiological differences in fat content (Eschmeyer and Phillips, 1965; Goetz et al., 2010; Thurston, 1962), swim bladder gas retention (Ihssen and Tait, 1974), and developmental rates of fertilized eggs and fry (Horns, 1985). Heritability of traits like fat metabolism (Goetz et al., 2010) and swim-bladder gas that affect the ability to regulate depth through buoyancy compensation (Henderson and Anderson, 2002; Ihssen and Tait, 1974) indicates that some of the sympatric morphological diversity of lake trout in the Great Lakes has genetic origins and does not reflect environmental plasticity (Hindar and Jonsson, 1993).

Similar morphological diversity of lake trout also occurs in other North American lakes, including Great Bear Lake (Alfonso, 2004; Blackie et al., 2003; Chavarie et al., 2013, 2014, 2015a), Great Slave Lake (Zimmerman et al., 2006, 2009), and Lake Mistassini, Quebec (Zimmerman et al., 2007). Morphological diversity in multiple lakes suggests that diversity is an important feature of the species that should be incorporated into recovery plans within the Laurentian Great Lakes (Hansen et al., 2012; Krueger and Ebener, 2004; Muir et al., 2015). Further, the presence of lean, fat (i.e. siscowet-like), and humper-like morphs across North America suggests that common selection pressures and ecological opportunities result 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 trout morphs from the Laurentian Great Lakes (e.g., Rahrer, 1965; Burnham-Curtis and Bronte, 1996) and other North American lakes (Chavarie et al., 2015b, in review; Hansen et al., 2012, in press) may reflect unique use of ecological opportunities and niche space by sympatric morphs that requires different management strategies for each morph.

In this study, multiple life history traits were compared among four morphs of lake trout at Isle Royale, Lake Superior, to determine if life history attributes differed among morphs. As part of an ongoing study of lake trout diversity in North America (Hansen et al., 2012; Muir

et al., 2014; Zimmerman et al., 2006, 2007, 2009), lake trout were sampled in the Isle Royale region of Lake Superior because of its remote offshore location, national park status, and historical and recent accounts of the occurrence of multiple morphs. Historically, the nearshore fishery for lean lake trout was significant in this region of Lake Superior, with less intensive fishing on deep-water morphs (Bronte and Sitar, 2008), although these fisheries caused abundance to decline (Wilberg et al., 2003; Bronte and Sitar, 2008). However, the rebound of lake trout abundance at Isle Royale in the 1970s suggested that this area was less perturbed than mainland areas. Remoteness of the island and recent relatively light fishery exploitation led us to expect that lake trout populations in waters surrounding Isle Royale would more closely resemble historical populations than those along the mainland shoreline where hatchery fish were stocked and fisheries were comparatively intense. Life history metrics from such lightly exploited populations could provide useful benchmarks for restoration and future management of lake trout biodiversity elsewhere in the Laurentian Great Lakes.

Methods

Lake trout were sampled at Isle Royale (48°00'N, 88°50'W) during 15–20 August 2006 and 6–8 August 2007 (Fig. 1). Three depth strata were sampled based on depths occupied by lean, humper, and siscowet lake trout morphs in Lake Superior (Moore and Bronte, 2001): 0–50-m = eight sets; 50–100-m = six sets; and 100–150-m = six sets (Muir et al., 2014). Gill nets were 183-m long by 1.8-m high, and made of multifilament nylon twine, with 30.5-m panels of stretch mesh sizes ranging from 50.8 to 114.3 mm, in 12.7-mm increments. Based on girth–total length (TL) relationships for lake trout caught in similar gill nets in Lake Superior (Hansen et al., 1997), the range of mesh sizes used would enable wedging of lake trout ranging from small juveniles (222 mm TL) to large adults (827 mm TL). Nets were set on the lake bottom for ~24 h. Data collected from each fish included total length (TL = mm), weight in air (W_a = grams), weight in water

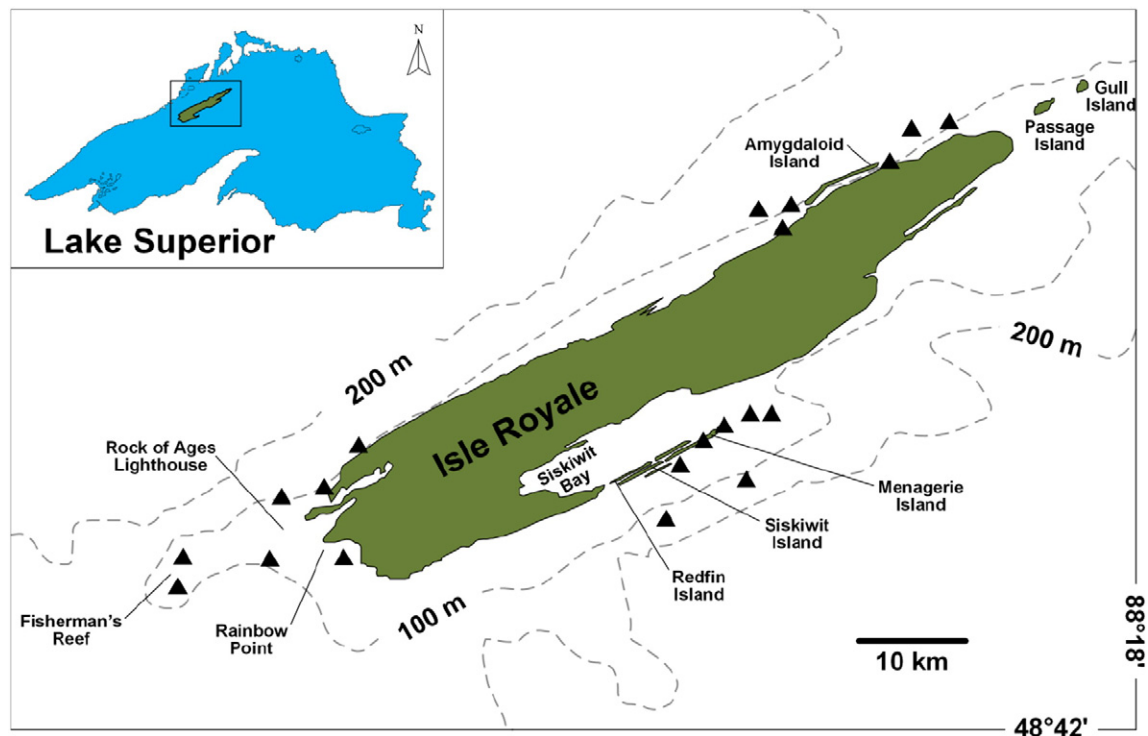


Fig. 1. Sampling locations for lake trout (solid triangles) at Isle Royale, Lake Superior, during 15–20 August 2006 and 6–8 August 2007. Reproduced from Muir et al. (2014).

(W_w = grams) with the swim bladder deflated (for buoyancy), sex (male or female), and maturity status (immature or mature; Muir et al., 2014; Zimmerman et al., 2006).

Digital full-body photographs of each specimen were captured in the field using methods described by Muir et al. (2012b). Specimens were assigned to a morph (Fig. 2) using a combination of statistical analysis of size-free head and body shape and visual assignment, as described by Muir et al. (2014). When head and body model assignments differed and visual consensus was not achieved on an individual fish, that individual was removed from further analyses (Muir et al., 2014). To use biological information from fish that were not classified by Muir et al. (2014), we assigned most remaining individuals to a morph by visual comparison to the library of statistical and visual assignments, as described by 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 trout 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 μ m) was cut, mounted on glass slides, polished, and imaged for age and growth assessment (Hansen et al., 2012). Annuli were counted by three independent readers using criteria described by Casselman and 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 trout length = 21.7 mm; Hansen et al., 2012) was based on equations describing relationships between length, age in days, and sagittal otolith width of age-0 lake trout (Bronte et al., 1995).

Catch/net, length, weight, relative body condition, relative buoyancy, and age were each compared between males and females for each morph separately, and then among morphs and depth strata for both sexes combined using general linear models (GLM), with main effects for morph and depth strata and the interaction between morphs and depths (Zar, 1999). To normalize residuals of the GLM, catch/net, length, and weight were transformed into logarithms prior to analysis. Least-squares means ($\pm$ SE) from the GLM were back-transformed from logarithms into original units of measure for catch/net, length, and weight. To correct for size-related trends in body condition and buoyancy, relative body condition was defined as residuals from the power relationship between $\log_{10}(W_a)$ and $\log_{10}(TL)$, and relative buoyancy was defined as residuals from the power relationship between $\log_{10}(W_w)$ and $\log_{10}(W_a)$. Mean catch/net, length, weight, relative body condition, relative buoyancy, and age were compared pairwise among morphs and depths with Tukey's honestly significant difference test (Zar, 1999). To enable comparison of the body condition of Isle Royale lake trout to other populations, the weight of a 500-mm fish (W_{500}), the median length of all fish sampled, was estimated from the weight-length relationship for each morph.

Growth in length with age was modeled using two parameterizations of the Von Bertalanffy length-age model, which express growth in terms of five, rather than only three, life history parameters (Mooij et al., 1999; Quinn and 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 (mm) at age t (years) as a function of age at length = 0 (t_0 = years; incubation time of embryos from fertilization to hatching), length at age = 0 (L_0 = mm; length at emergence from the egg), early annual growth rate ($\omega = L_{\infty} \times K$ = mm/year; Gallucci and Quinn, 1979), instantaneous growth rate ($K = 1/\text{year}$) at which L_t approaches the theoretical maximum length (L_{∞} = mm), and residual error (ε). Parameters L_{∞} , K , t_0 , L_0 , and ω were estimated using nonlinear mixed-effect models (package 'nlme' in R; R Core Team, 2014), with a fixed population effect (the average growth curve for the population from which individual fish were sampled), random individual effects (growth curves for individual fish sampled from the population), and sex or morph as a fixed factor (to compare average growth curves between sexes or among morphs; Vigliola and Meekan, 2009). Mixed-effects models are appropriate for modeling the within-group correlation of longitudinal, autocorrelated, and unbalanced data, such as back-calculated growth histories (Pinheiro and Bates, 2000). To compare growth between sexes and among morphs, log-likelihoods of full models (with sex or morph) were compared to reduced models (without sex or morph) in likelihood-ratio tests (Hosmer and Lemeshow, 2000). If a likelihood-ratio test was significant ($P \leq 0.05$), growth parameters were compared among morphs using single-factor ANOVA and Tukey's honestly significant difference test (Zar, 1999).

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

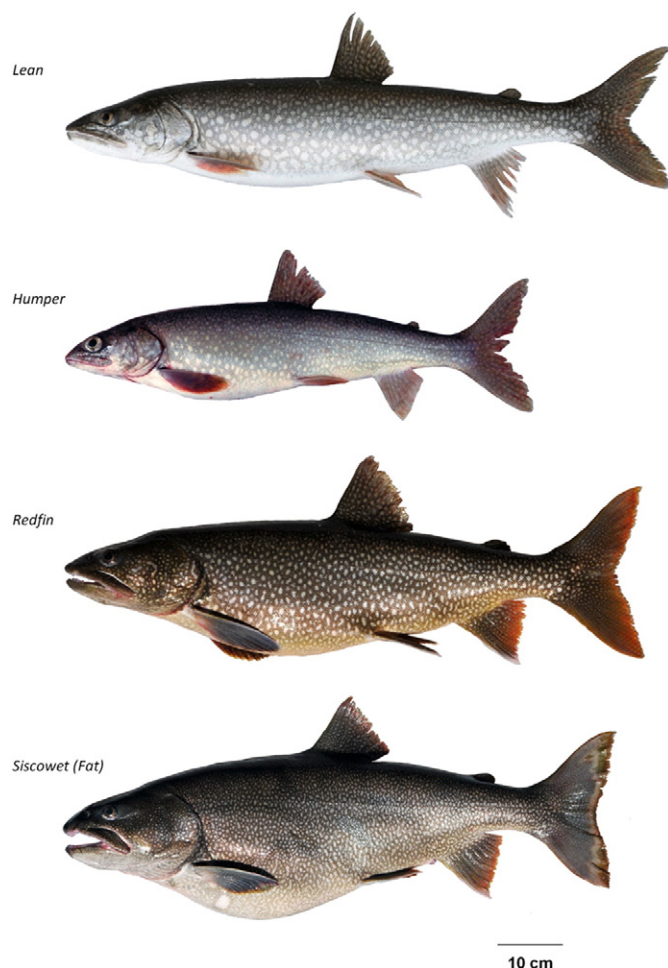


Fig. 2. Lean, humpback, redfin, and siscowet (fat) lake trout morphs from Lake Superior (images are scaled to the asymptotic length for each morph from Table 2).

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 and Lemeshow, 2000). To compare maturity between sexes and among morphs, log-likelihoods of full models (with sex or morph) were compared to reduced models (without sex or morph) in likelihood-ratio tests (Hosmer and Lemeshow, 2000). If the likelihood-ratio test was significant ($P \leq 0.05$), maturity was assumed to differ between sexes or among morphs. Length and age at 50% maturity (L_{50} and A_{50}) were estimated for each morph as the absolute value of the ratio of the intercept to the slope, $|b_0/b_1|$. To test for differences in length and age at maturity between morphs, log-likelihoods were compared between full and reduced models for pairs of morphs.

Results

Of 738 lake trout caught at Isle Royale, 701 were successfully assigned to a morph, which included 119 humpers (63 females, 56 males), 160 leans (83 females, 76 males, 1 unknown sex), 85 redfins (31 females, 54 males), and 337 siscowets (150 females, 185 males, 2 unknown sex). Otoliths were recovered from 685 fish for which a morph was assigned, of which age and growth could be estimated for 654 fish: 105 humpers, 151 leans, 79 redfins, and 319 siscowets. Otoliths from the remaining 31 fish were too deformed for age and growth analysis because of vaterite formations (see Bowen et al., 1999) in one or more otolith planes, including 15% of humpers, 10% of leans, 7% of redfins, and 8% of siscowets. Males and females did not differ in mean length, weight, relative weight, buoyancy, age, growth, length-at-

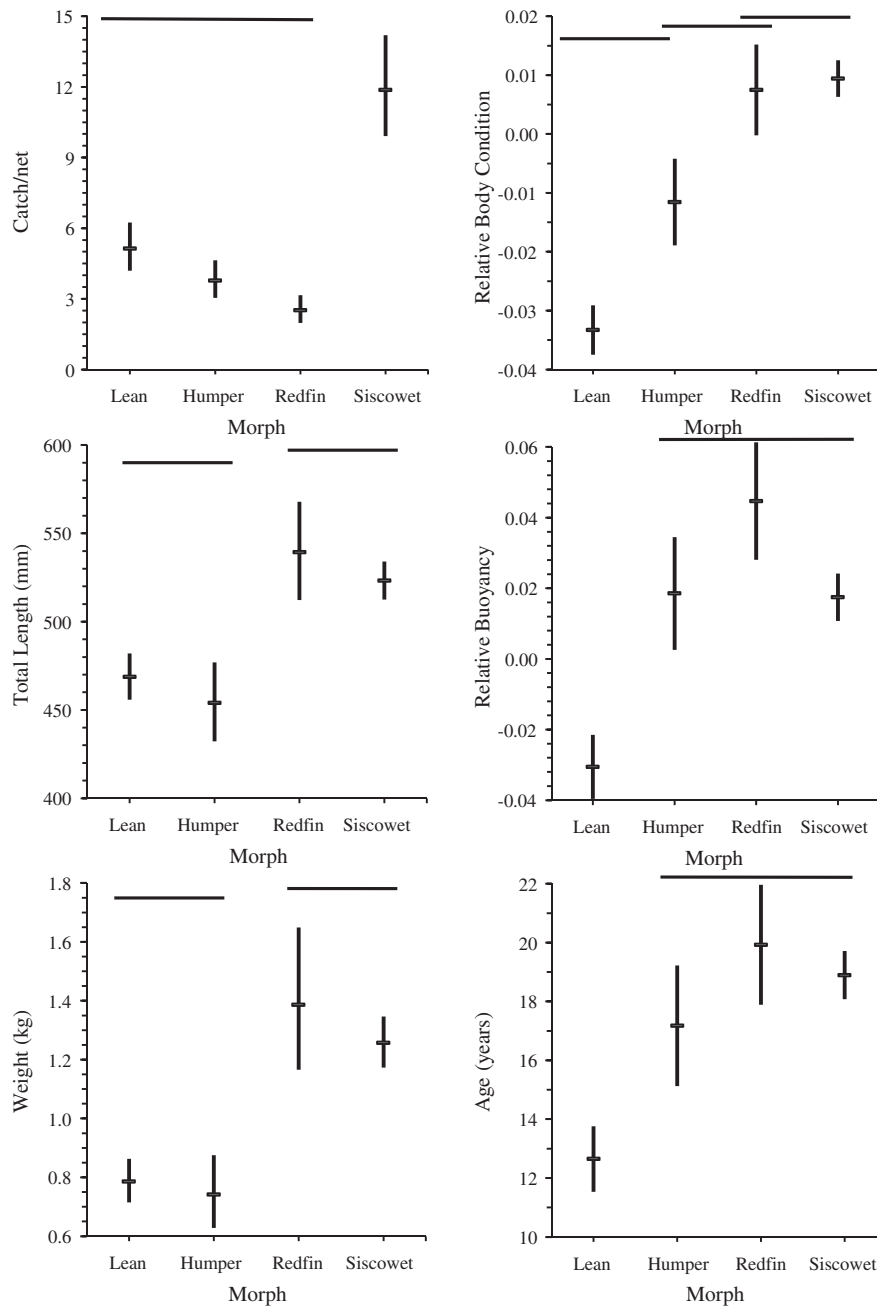


Fig. 3. Mean catch/net, total length, weight, relative body condition, relative buoyancy, and age (horizontal bars = mean; vertical bars = SE) of lean, humper, redfin, and siscowet lake trout morphs captured at Isle Royale, Lake Superior, during 15–20 August 2006 and 6–8 August 2007 (horizontal lines at the same position on the y-axis join means that do not differ, $P > 0.05$).

maturity, or age-at-maturity for any of the four morphs (Electronic Supplementary Material (ESM) Table S1), so males were combined with females for subsequent comparisons of metrics among morphs.

Siscowets were significantly more abundant (higher catch/net) than leans, humpers, or redfins at Isle Royale (Fig. 3; ESM Table S2). Leans did not vary significantly in abundance among depth strata, whereas humpers were more abundant in intermediate and deep strata than in the shallow stratum, redfins were more abundant in the intermediate stratum than in the deep stratum, and siscowets were more abundant in the intermediate stratum than in the shallow stratum (Fig. 4; ESM Table S3). Leans were more abundant than humpers in the shallow

stratum, and less abundant than siscowets in the intermediate stratum, whereas redfins were less abundant than siscowets in the deep stratum (Fig. 4; Table ESM S3).

Leans and humpers were significantly shorter and lighter, on average, than redfins and siscowets at Isle Royale (Table 1; Fig. 3; ESM Table S2). Mean length and weight of leans were greater in the shallow than the deep stratum, whereas mean length and weight of humpers, redfins, and siscowets did not vary significantly with depth (Fig. 4; ESM Table S3). Morphs did not differ significantly in mean length or weight in the shallow stratum (except leans were lighter than siscowets), whereas leans and humpers were shorter and lighter than redfins and siscowets

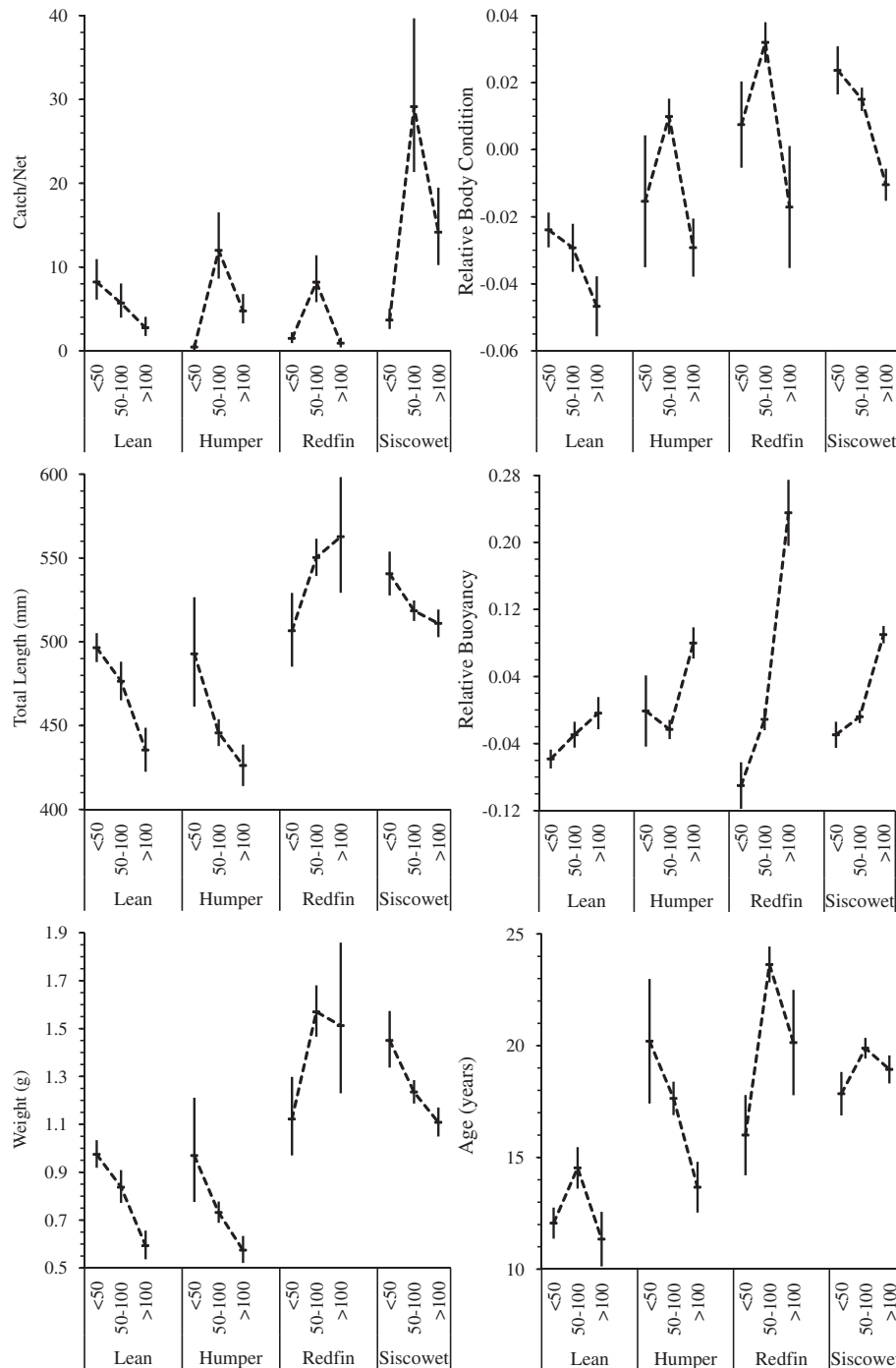


Fig. 4. Mean catch/net, total length, weight, relative body condition, relative buoyancy, and age (horizontal bars = mean; vertical bars = SE) of humper, lean, redfin, and siscowet lake trout morphs captured in three depth strata at Isle Royale, Lake Superior, during 15–20 August 2006 and 6–8 August 2007.

Table 1
Total length (TL = mm), weight in air (W_a = g), weight in water (W_w = g), age (years), relative body condition (condition = residuals of linear regression of $\log_{10}(W_a)$ against $\log_{10}(TL)$), relative buoyancy (buoyancy = residuals of regression of $\log_{10}(W_w)$ against $\log_{10}(W_a)$), age-at-length-zero (t_0 = years), length-at-age-zero (L_0 = mm), early growth rate (ω = mm/year), instantaneous growth rate (K = 1/years), asymptotic length (L_∞ = mm), length at 50% maturity (L_{50} = mm), and age at 50% maturity (A_{50} = years) for 119 humper, 160 lean, 85 redfin, and 337 siscowet lake trout morphs captured at Isle Royale, Lake Superior, during 15–20 August 2006 and 6–8 August 2007. Test statistics are F -ratios for TL, W_a , W_w , age, condition, and buoyancy, and Chi-squares (χ^2) for growth (t_0 , L_0 , ω , K , and L_∞) and maturity (L_{50} and A_{50}).

Trait	Parameter	Lean	Humper	Redfin	Siscowet	Test	P
TL	Estimate	469	454	539	523	21.07	0.000
	SE	6.6	11.3	14.0	5.5		
	Range	253–780	295–687	303–868	285–781		
W_a	Estimate	785	741	1386	1257	30.28	0.000
	SE	37.4	62.1	121.1	44.2		
	Range	125–4200	160–3250	200–5300	150–5100		
W_w	Estimate	63	55	57	54	1382.02	0.000
	SE	1.3	1.9	2.0	0.9		
	Range	8.0–220	5.5–132	11.0–234	8.5–200		
Age	Estimate	12.6	17.2	19.9	18.9	29.68	0.000
	SE	0.562	1.033	1.023	0.416		
	Range	4–43	4–46	5–48	6–47		
Condition	Estimate	−0.033	−0.012	0.007	0.009	23.47	0.000
	SE	0.004	0.007	0.008	0.003		
	Estimate	0.031	−0.019	−0.045	−0.017	8.40	0.000
Buoyancy	SE	0.009	0.016	0.017	0.007		
	Estimate	−0.665	−0.934	−1.094	−0.987	1.85	0.604
t_0	SE	0.0565	0.0688	0.0781	0.0390		
	Estimate	41.6	47.5	55.9	51.5	2.99	0.393
L_0	SE	2.45	2.90	3.30	1.65		
	Estimate	71.1	59.8	58.4	59.0	94.90	0.000
ω	SE	1.17	1.37	1.55	0.77		
	Estimate	0.105	0.110	0.089	0.095	70.93	0.000
K	SE	0.00253	0.00295	0.00323	0.00161		
	Estimate	715	556	675	639	132.59	0.000
L_∞	SE	11.7	13.2	15.2	7.5		
	Estimate	562	394	427	401	131.13	0.000
L_{50}	SE	25	53	24	28		
	Estimate	15.0	12.9	11.9	11.5	7.346	0.062
A_{50}	SE	0.9	2.9	2.2	1.4		

in intermediate and deep strata (except leans did not differ in mean length from siscowets in the intermediate stratum; Fig. 4; ESM Table S3).

Leans were significantly lower in mean relative body condition than redfins and siscowets, and humpers were lower than siscowets at Isle Royale (Table 1; Fig. 3; ESM Table S2). Leans and redfins did not differ significantly in mean body condition among depth strata, whereas humpers were higher in body condition in the intermediate stratum than in the deep stratum, and siscowets were higher in body condition in shallow and intermediate strata than in the deep stratum (Fig. 4; ESM Table S3). Leans were significantly lower in mean relative body condition than siscowets in all three depth strata, and leans were lighter than all three other morphs in the intermediate stratum (Fig. 4; ESM Table S3).

Leans were significantly less buoyant than redfins or siscowets at Isle Royale, whereas humpers did not differ in mean buoyancy from the other three morphs, and redfins and siscowets did not differ in mean buoyancy (Table 1; Fig. 3; ESM Table S2). Leans did not differ significantly in mean buoyancy among depth strata, whereas the other three morphs were more buoyant in the deep stratum than in the intermediate stratum, and redfins and siscowets were more buoyant in the deep stratum than in the shallow stratum (Fig. 4; ESM Table S3). Morphs did not differ significantly in mean buoyancy in either shallow or intermediate strata, whereas redfins were more buoyant than the other three morphs and siscowets were more buoyant than leans in the deep stratum (Fig. 4; ESM Table S3).

Leans were significantly younger than the other three morphs at Isle Royale, none of which differed significantly in mean age (Table 1; Fig. 3; ESM Table S2). Leans, humpers, and siscowets did not differ significantly in mean age among depth strata, whereas redfins were older in the intermediate stratum than in the shallow stratum (Fig. 4; ESM Table S3). Leans were significantly younger than siscowets in all three depth strata, redfins were older than the other three morphs in the intermediate stratum, and humpers were younger than redfins and leans were

younger than siscowets in the deep stratum (Fig. 4; Table ESM S3). The range in ages and the maximum ages observed were similar among all morphs (Table 2).

Morphs differed in growth at Isle Royale (Table 1; Figs. 5–6; ESM Table S2). Leans grew from a younger age at length = 0 (t_0) and shorter length at age = 0 (L_0), at a faster early growth rate (ω) to a longer asymptotic length (L_∞) than the other three morphs, while redfins grew at a slower instantaneous growth rate (K) and humpers grew to a shorter asymptotic length (L_∞) than other morphs at Isle Royale. Mean t_0 was higher for leans than for humpers, redfins, and siscowets. Mean L_0 was lower for leans than for redfins and siscowets, but not for humpers. Instantaneous growth rate K was

Table 2

Slope of $\log_{10}$ -transformed weight-length relationships (β), predicted weight of a 500-mm fish (W_{500} = kg), asymptotic length (L_∞ = mm), early growth rate (ω = 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 and Lagueux, 1968; Hansen et al., 2012; Healey, 1978; Martin and Olver, 1980; McDermid et al., 2010; Mills et al., 2002; Piccolo et al., 1993; Shuter et al., 1998; and Trippel, 1993) and percentiles of each metric's cumulative North American distribution for humper, lean, redfin, and siscowet lake trout morphs captured at Isle Royale, Lake Superior, during 15–20 August 2006 and 6–8 August 2007 (this table; this study).

Source	Statistic/Morph	β	W_{500}	L_∞	ω	L_{50}	A_{50}
North America	Mean	3.228	1.136	639.6	107.2	421.9	8.9
	SD	0.258	0.143	139.3	27.1	80.9	3.3
	CV	8%	13%	22%	25%	19%	37%
	N	48	48	186	56	132	132
	Lean	48%	14%	71%	9%	96%	97%
Isle Royale	Humper	92%	34%	27%	4%	36%	88%
	Redfin	78%	43%	60%	4%	52%	82%
	Siscowet	56%	35%	50%	4%	40%	78%

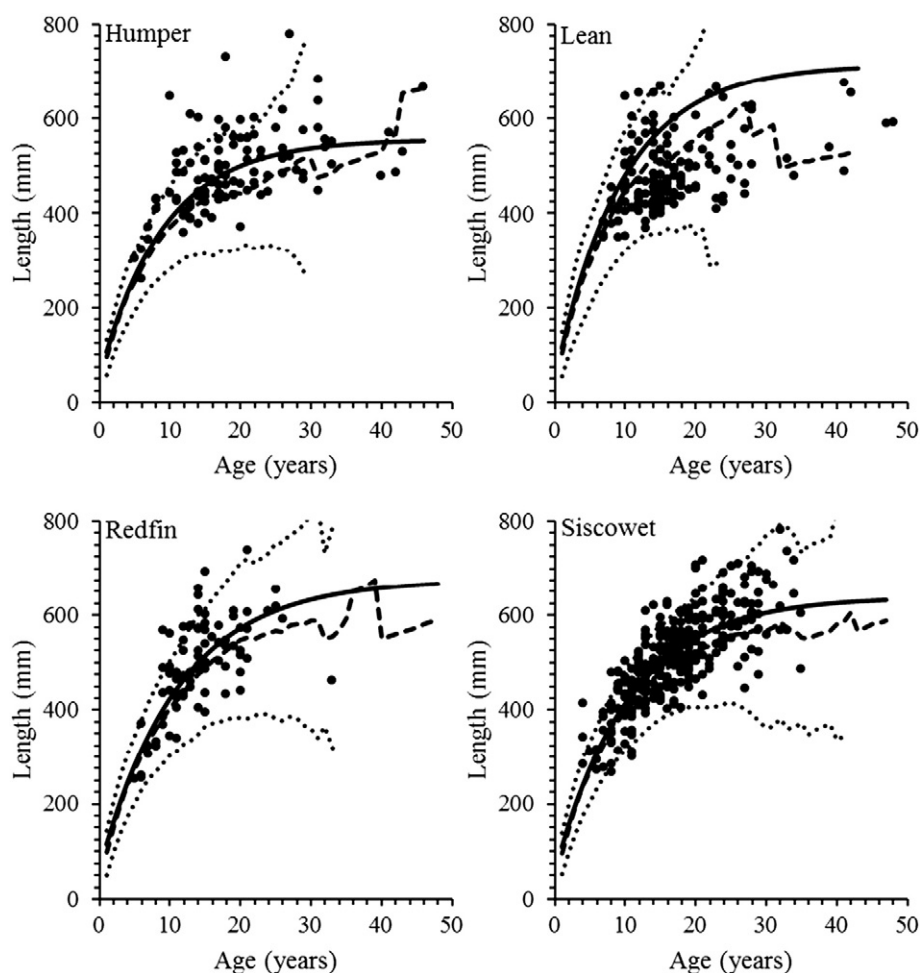


Fig. 5. Length versus age for humper, lean, redfin, and siscowet lake trout morphs captured at Isle Royale, Lake Superior, during 15–20 August 2006 and 6–8 August 2007 (solid circles = length at age of capture; dashed line = mean back-calculated length at age; dotted lines = 95% confidence limits for mean back-calculated length at age; solid lines = Von Bertalanffy length-age model estimated from individual back-calculated growth histories).

faster for humpers and leans than for redfins and siscowets. Early growth rate ω was faster for leans than for the other three morphs. Asymptotic length L_{∞} ranged from a low of $L_{\infty} = 556$ mm for humpers, to $L_{\infty} = 639$ mm for siscowets, $L_{\infty} = 675$ mm for redfins, and a high of $L_{\infty} = 715$ mm for leans.

Morphs differed in length and age at maturity at Isle Royale (Table 1; Fig. 7; Table ESM S1). Maturity was significantly related to length of leans ($\chi^2 = 24.5$; $df = 1$; $P < 0.001$), humpers ($\chi^2 = 7.90$; $df = 1$; $P = 0.005$), redfins ($\chi^2 = 31.4$; $df = 1$; $P < 0.001$), and siscowets ($\chi^2 = 27.2$; $df = 1$; $P < 0.001$). Leans were longer at 50% maturity (562 mm) than redfins (427 mm), siscowets (401 mm), and humpers (394 mm years). Maturity was also significantly related to age of leans ($\chi^2 = 36.6$; $df = 1$; $P < 0.001$), humpers ($\chi^2 = 10.8$; $df = 1$; $P = 0.001$), redfins ($\chi^2 = 25.4$; $df = 1$; $P < 0.001$), and siscowets ($\chi^2 = 40.5$; $df = 1$; $P < 0.001$). Leans were older at 50% maturity (15 years) than siscowets (11 years), but not humpers (13 years) or redfins (12 years).

Discussion

Differences in life history characteristics of humper, lean, and siscowet morphs of lake trout at Isle Royale were generally consistent with previous comparisons between pairs of these morphs elsewhere in Lake Superior and in North America. For example, a siscowet-like (i.e., fat) morph in Great Slave Lake, Northwest Territories (Hansen et al., in press) and in western Lake Superior (Miller and Schram, 2000) was also heavier, older, and grew more slowly toward a shorter

asymptotic length than the sympatric lean morph. Likewise, the siscowet-like morph in Great Slave Lake was older than the sympatric lean morph (Hansen et al., in press). By contrast, length and age at maturity did not differ between fat and lean morphs in Great Slave Lake (Hansen et al., in press), whereas the fat morph matured at a shorter length and older age than the lean morph in southern Lake Superior (Sitar et al., 2014) and a shorter length and younger age than the lean morph at Isle Royale (this study). In Lake Mistassini, Quebec, the humper morph was smaller bodied, older, and grew slower to a shorter asymptotic length than the lean morph (Hansen et al., 2012), similar to differences between humper and lean morphs at Isle Royale, Lake Superior (Burnham-Curtis and Bronte, 1996; Rahrer, 1965; this study). Among the three morphs that occur elsewhere (lean, humper, and siscowet), the siscowet morph is the plumpest and oldest, but sometimes intermediate in length, whereas the humper morph is the smallest, but intermediate in body condition and age, and the lean morph is often the longest, but leaner and younger than the other two morphs. This pattern appears to hold, even when a pair of morphs are relatively large bodied, such as siscowet-like and lean morphs in Great Slave Lake, Northwest Territories (Hansen et al., in press) or relatively small bodied, such as humper and lean morphs in Lake Mistassini, Quebec (Hansen et al., 2012).

We assumed that sampling represented the full range of life history attributes of lake trout populations around Isle Royale, because (1) spatial coverage of sampling included a wide range of depths from multiple areas around the island and (2) sampling gear included a wide range of mesh sizes to target the full range of possible lake trout sizes (Hansen

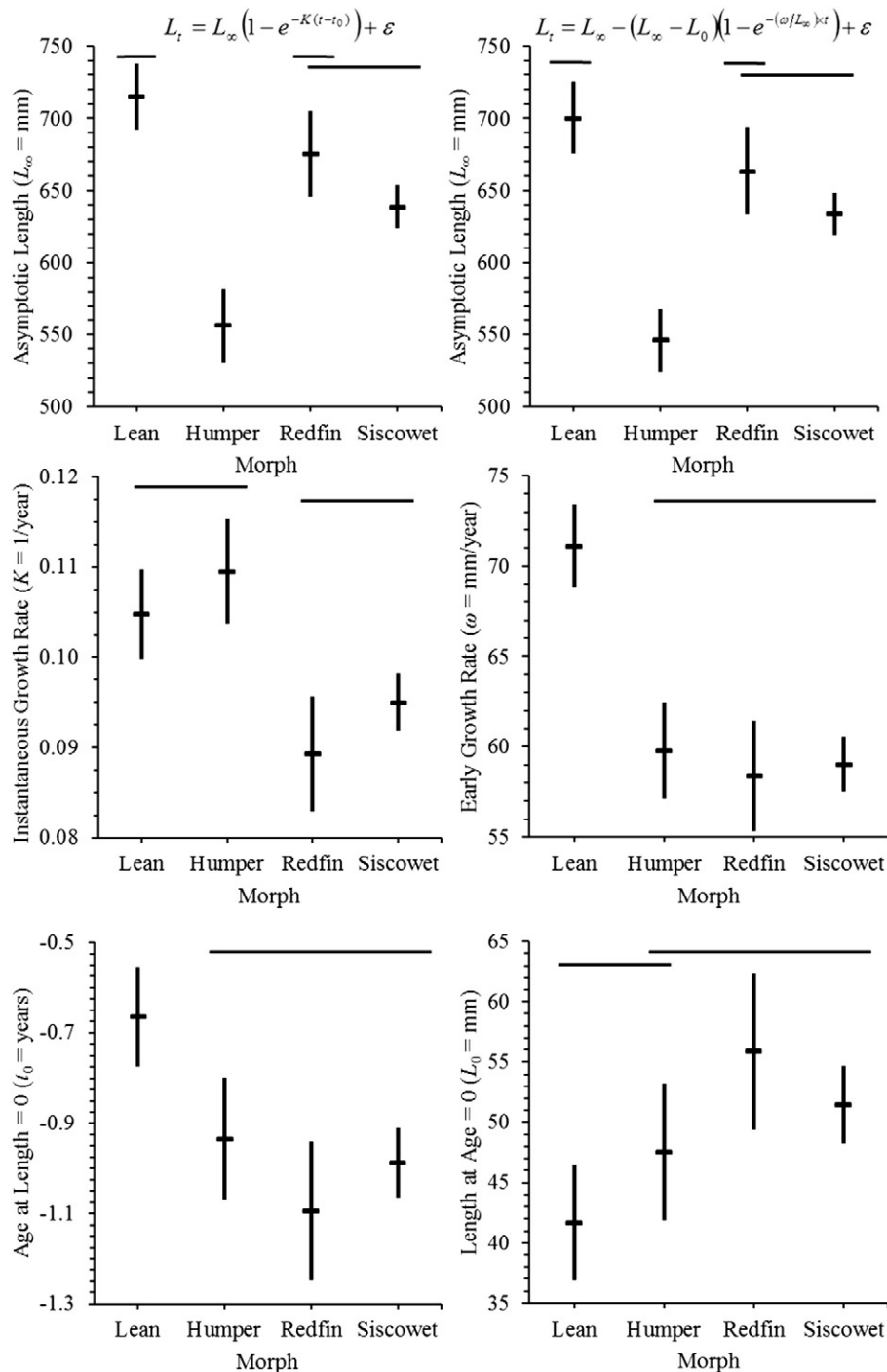


Fig. 6. Parameter estimates (horizontal bars = mean; vertical bars = 95% confidence limits) for two versions of the Von Bertalanffy length-age model estimated from individual back-calculated growth histories for humper, lean, redfin, and siscowet lake trout morphs captured at Isle Royale, Lake Superior, during 15–20 August 2006 and 6–8 August 2007 (horizontal lines at the same position on the y-axis join means that do not differ, $P > 0.05$).

et al., 1997). Nonetheless, sampling in late summer could have missed pelagic and migratory components of populations that were present in areas sampled at other times of the year or above nets. Such populations are currently unknown, and would require sampling throughout the year to identify. Further, although areal and bathymetric coverage of sampling was extensive, sampling locations were chosen opportunistically, rather than based on a statistical sampling design. Therefore, in an area as large and physically complex as Isle Royale, our sampling likely missed small local populations of morphs that would have been encountered by more spatially and temporally extensive sampling. For example, numerous lake trout morphs have been described anecdotally

from around Isle Royale (Coberly and Horrall, 1980; Goodier, 1981; Loftus, 1980; Organ et al., 1979; Rakestraw, 1968; Toupal et al., 2002; Stuart Siverson, Duluth Minnesota, personal communication), which suggests that we may have encountered only the most abundant or widespread morphs during our sampling. We therefore acknowledge that our samples reflect only the main forms of lake trout present at Isle Royale and that morphological diversity of lake trout may be greater than we describe herein.

Traits of the lean lake trout morph at Isle Royale were consistent with a lightly exploited fish population. Body condition of lean lake trout at Isle Royale was low, because the predicted weight of a 500-

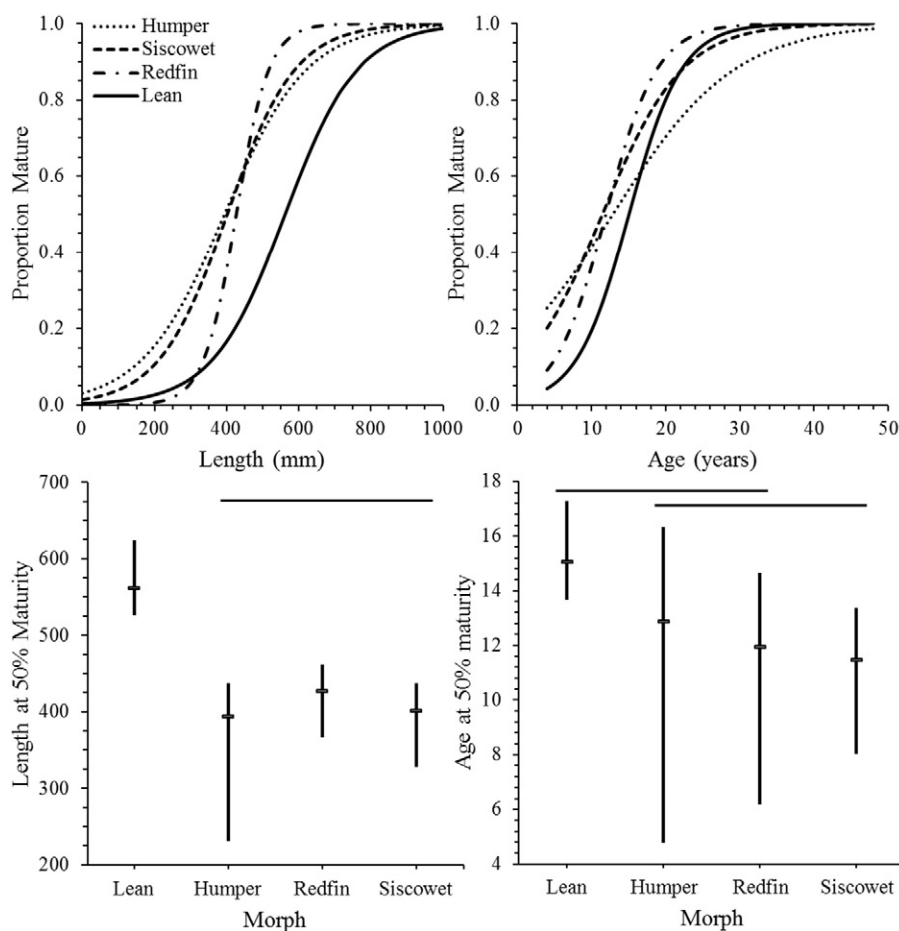


Fig. 7. Proportion mature versus length (upper-left panel) and age (upper-right panel), and length (lower-left panel; horizontal bars = mean; vertical bars = 95% confidence limits) and age (lower-right panel; horizontal bars = mean; vertical bars = 95% confidence limits) at 50% maturity for humper, lean, redfin, and siscowet lake trout morphs captured at Isle Royale, Lake Superior, during 15–20 August 2006 and 6–8 August 2007 (horizontal lines at the same position on the y-axis join means that do not differ, $P > 0.05$).E

mm fish (W_{500}) was lower than 86% of 48 lake trout populations in North America (Table 2). Lean lake trout at Isle Royale grew slower (ω) than 91% of 56 populations toward an asymptotic length (L_{∞}) that was longer than 71% of 186 populations in North America (Table 2), as expected for a high-density population (Rose et al., 2001). Length and age at maturity of lean lake trout at Isle Royale were higher than 96% of 132 populations in North America (Table 2), as expected for slow-growing populations (Healey, 1978). In contrast, lean lake trout at Isle Royale were not as large or as old at maturity as four shallow-water morphs in Great Bear Lake (L_{50} = 582–704 mm, A_{50} = 17.4–20.2 years, Chavarie et al. 2015b), as expected for a slow-growing population in an unproductive lake at a northerly latitude with a short growing season (McDermid et al., 2010). Collectively, life history attributes of lean lake trout at Isle Royale are consistent with low exploitation (old aged) and high density relative to prey supply (low body condition), which has been declining (Gorman et al., 2013), so growth is slow toward a large asymptotic size, and large size and old age at maturity (Rose et al., 2001).

Traits of the humper lake trout morph at Isle Royale were generally similar to the same morph elsewhere in North America. Size structure of the humper morph in our study was similar to an earlier study (1959–1963, mean = 442 mm; range = 376–742 mm; Rahrer, 1965) and in Lake Mistassini, Quebec (mean = 474 mm; range = 389–616 mm; Hansen et al., 2012), but larger than a humper morph in a relatively small lake adjacent to Lake Superior (Rush Lake, Michigan, USA, mean = 393 mm; range = 335–641 mm; Chavarie et al., in review). The humper morph was less plump in our study (W_{500} = 1.078 kg) than in 1959–1963 at Isle Royale (W_{500} = 1.231 kg; Rahrer,

1965), but intermediate between humper-like morphs in Lake Mistassini (W_{500} = 0.947 kg; Hansen et al., 2012) and Rush Lake (W_{500} = 1.133 kg; Chavarie et al., in review). The humper morph at Isle Royale in 2006–2007 (this study) was similar in mean age as in 1989–1992 (mean age = 16 years; range = 8–29 years; Burnham-Curtis and Bronte, 1996) and in Rush Lake (mean age = 16.8 years; range = 7–31 years; Chavarie et al., in review), but younger than in Lake Mistassini (mean age = 27 years; range = 13–49 years; Hansen et al., 2012). The humper morph at Isle Royale grew at a slower early rate (ω) to a similar asymptotic length (L_{∞}) in 2006–2007 (this study) as in 1989–1992 (ω = 116 mm/year, L_{∞} = 542 mm, SE = 13; Burnham-Curtis and Bronte, 1996), Lake Mistassini (ω = 52.3 mm/year, SE = 2.15; L_{∞} = 514 mm, SE = 14.1; Hansen et al., 2012), and Rush Lake (ω = 53.0 mm/year, SE = 2.33; L_{∞} = 489 mm, SE = 20.0; Chavarie et al., in review). The humper morph at Isle Royale in our study matured at a similar size and age as in Lake Mistassini, Quebec (L_{50} = 395 mm; A_{50} = 13 years; Hansen et al., 2012), has a smaller size and an older age than in Rush Lake (L_{50} = 423 mm; A_{50} = 10 years; Chavarie et al., in review), and has a larger size than at Isle Royale in 1959–1963 (L_{50} = 343–359 mm; Rahrer, 1965). Eshenroder (2008) theorized that a humper-like morph diverged postglacially in sympatry from the ancestral lean morph as a feeding specialist on *Mysis*.

The redfin morph recently described by Muir et al. (2014) was the largest, oldest, and slowest-growing morph at Isle Royale, Lake Superior, similar to early qualitative descriptions of lake trout morphological diversity from the Laurentian Great Lakes. A redfin morph was often included in early descriptions of lake trout morphological diversity from Lake Superior (Rakestraw, 1968; Organ et al., 1979), and also from

lakes Michigan and Huron (Coberly and Horrall, 1980; Loftus, 1980). As we found in this study, redfins in early accounts were described as being relatively large bodied in Lake Michigan (5–7 kg, Coberly and Horrall, 1980), Lake Huron (≥ 5 kg, Loftus, 1980), and at Isle Royale in Lake Superior (≤ 20 kg Toupal et al., 2002). The redfin morph described by Muir et al. (2014) was consistent in appearance with redfins described in early accounts: large bodied, with a big head and large pectoral fins, red flesh, red or red and yellow fins, sometimes spotted, and often dark dorsal coloration (Loftus, 1980; Goodier, 1981). The life history of redfins we quantified at Isle Royale may be maintained by reliance on a different (moderate) depth range than the other three morphs, as was described earlier for redfins in Lake Huron (Loftus, 1980). Redfins may also maintain distinct life history features by spawning at a different time of year than other morphs, as can be inferred from commercial fishery harvests of spawning redfins in late summer (August to mid-September), similar to the spawning season for humpers (Rahrer, 1965), but earlier than the late-autumn (October–November) spawning period of leans (Coberly and Horrall, 1980; Goodier, 1981; Loftus, 1980; Organ et al., 1979; Toupal et al., 2002). Similarly, a redfin-like morph was observed by the authors in mature and spent condition in August 2013 at Superior Shoal, a remote shoal 50 miles east of Isle Royale. In Lake Huron, redfins were believed to spawn in late summer over rocky substrate at depths of 1–18 m (Loftus, 1980), and in Lake Superior, redfins often spawned on the same shoals used by leans in autumn (Goodier, 1981). Redfins spawn around Isle Royale at Passage Island, Gull Island, and from Rainbow Point to Siskiwit Island over numerous shoals in 9–15 m of water, and were harvested at 13 areas around Isle Royale, including Redfin Island, named for the prevalence of the morph (Fig. 1; Toupal et al., 2002).

Traits of the siscowet lake trout morph at Isle Royale were generally similar to fat morphs elsewhere in North America and Lake Superior. Size structure of the siscowet morph at Isle Royale in our study was similar to the siscowet morph in southern Lake Superior (mean = 545 mm; range = 340–828 mm; Sitar et al., 2014) and a siscowet-like morph in Great Slave Lake, Northwest Territories (mean = 583 mm; range = 308–802 mm; Hansen et al., in press). Similarly, mean age of the siscowet morph at Isle Royale in our study was similar to the siscowet morph in southern Lake Superior (mean age = 19.0 years; Sitar et al., 2014), but younger than a siscowet-like morph in Great Slave Lake (mean age = 24.9 mm; Hansen et al., in press). The siscowet morph in our study was less plump ($W_{500} = 1.080$ kg) than in western Lake Superior ($W_{500} = 1.768$ kg; Miller and Schram, 2000), but similar to a siscowet-like morph in Great Slave Lake ($W_{500} = 1.182$ kg; Hansen et al., in press). The siscowet morph at Isle Royale grew to a shorter asymptotic length (L_{∞}) in our study than in western Lake Superior ($L_{\infty} = 850$ mm; Miller and Schram 2000), and at a slower early growth rate (ω) toward a longer asymptotic length than in Great Slave Lake ($\omega = 54.1$ mm/year, SE = 1.09; $L_{\infty} = 726$ mm, SE = 17.1; Hansen et al., in press). The siscowet morph at Isle Royale in our study matured at a similar size (L_{50}) and age (A_{50}) as in southern Lake Superior ($L_{50} = 443$ mm, 95% CI = 408–462; $A_{50} = 11$ years, 95% CI = 8–13; Sitar et al., 2014), but a smaller size and younger age than in Great Slave Lake ($L_{50} = 504$ mm, 95% CI = 467–529; $A_{50} = 16$ years, 95% CI = 14–17; Hansen et al., in press).

Lake trout morphs differed in life history attributes at Isle Royale, despite relatively small morphometric (Moore and Bronte, 2001; Muir et al., 2014) and genetic (Baillie et al., in review) differences among the same morphs. We therefore conclude that conservation of life history attributes is ecologically important for conserving morphometric and genetic differences. For example, phenotypic differences we observed between lean and siscowet morphs at Isle Royale, such as body condition and buoyancy, persisted in lean and siscowet morphs from Lake Superior when reared under identical (common garden) conditions, which indicates that these differences are at least partially under genetic control (Eschmeyer and Phillips, 1965; Goetz et al., 2010). Siscowet and lean morphs occupy overlapping depths in Lake Superior (Bronte et al.,

2003; Moore and Bronte, 2001; Bronte and Sitar, 2008), although the siscowet morph also occurs at much greater depth than the lean morph (Sitar et al., 2008), largely because the siscowet morph metabolizes lipids differently, such that high concentrations are retained within the flesh and organs (Goetz et al., 2010), which allow them to expend less energy to remain buoyant at great depth (Henderson and Anderson, 2002). High lipid content provides positive buoyancy that enables the siscowet morph to migrate vertically in pursuit of invertebrate (*M. diluviana*) and fish (cisco and sculpin) prey (Ahrenstorff et al., 2011; Gamble et al., 2011; Isaac et al., 2012; Hrabik et al., 2014). Diets of siscowet and lean morphs do not greatly overlap (Conner et al. 1993; Ray et al., 2007), because the siscowet morph exploits prey in both deep and shallow water (Harvey et al., 2003), thereby minimizing trophic overlap between the two morphs in Lake Superior when measured using stable isotopes (Harvey and Kitchell, 2000). Similar studies of humpers and redfin morphs, in relation to lean and siscowet morphs, are needed to confirm the roles of ecological and genetic differences in maintaining morphological and life history diversity of lake trout at Isle Royale and across Lake Superior.

Life history differences among lake trout morphs at Isle Royale suggest that lake trout restoration in the rest of the Laurentian Great Lakes should incorporate more than just a lean form. The remarkable diversity of lake trout forms at Isle Royale could serve as a reservoir for developing hatchery programs to support reintroduction of up to four morphs elsewhere in the Laurentian Great Lakes (Krueger et al., 1995). For example, rehabilitation plans for lake trout have recently aimed at reintroducing a humpers morph into Lake Michigan (Bronte et al., 2008) and Lake Erie (Markham et al., 2008), and are now being stocked in these lakes as well as in Lake Ontario. Lake trout restoration that has relied on stocking only the lean morph will use less than 40% of total available Great Lakes habitat (Eshenroder and Burnham-Curtis, 1999). Further, high historical diversity of lake trout morphology in waters around Isle Royale (Rakestraw, 1968; Toupal et al., 2002) suggests that Isle Royale is a unique area in the Laurentian Great Lakes basin that deserves careful consideration for conservation of lake trout diversity. Lastly, regulation of fisheries must acknowledge that harvest of mixed stocks (morphs), such as those around Isle Royale or in areas of the basin where multiple morphs are introduced, will require mixed-stock management to avoid over-exploitation of weak stocks (Ricker, 1958). Life history attributes of lightly exploited populations of lean, humpers, redfin, and siscowet lake trout morphs at Isle Royale can be used as benchmarks for restoration and management plans of such lake trout morphs elsewhere in the Laurentian Great Lakes.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.jglr.2015.12.011>.

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