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Usefulness of Otolith Weight for Estimating Age-Based Life History Metrics of Lake Trout

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Abstract

To determine if otolith weight can be used to accurately and precisely estimate age-based life history metrics of Lake Trout *Salvelinus namaycush* populations, we quantified relationships between Lake Trout otolith age and weight sampled from a wide geographic and size range of North American lakes. Separate nonlinear age–weight models for each of 22 surveys (each year within each area or lake) described 82.8% of variation in the relationship between otolith age and weight, whereas separate age–weight models for each of 13 lakes or areas within lakes (years combined) described only 0.4% less variation. Over all surveys, age increased at an average rate of 1.13 years per milligram increase in otolith weight and the otolith weight–age relationship was significantly nonlinear. Age of individual fish could not be estimated accurately from otolith weight alone, although bias of mean age estimated from mean otolith weight was small, whether using survey-specific or general otolith age–weight relationships. Age at maturity and survival derived from indirect otolith age–weight relationships were estimated with less bias than growth parameters. We

conclude that a general model for estimating Lake Trout age from otolith weight may be more useful for maturity and survival analyses that are less susceptible to estimation error of individual (often old) fish than for growth analysis that can be susceptible to estimation error of individual (often old) fish.

Accurate age information is one of the most important biological variables in fishery science because age is required for estimating mortality, growth, and production (Campana 2001). For example, the frequency of ages in a fish population reflects the interplay of growth, recruitment, and survival and is therefore required for estimating mortality that underlays age-structured stock assessment models (Quinn and Deriso 1999). Similarly, age and size are needed to estimate growth as the change in body size (length and weight) with age, a rate that is a fundamental component of production models (Quinn and Deriso 1999). Assignment of age from bony structures often results in underestimates of true age, which can lead to overharvest by fisheries targeted on stocks that are slower growing, longer lived, and less productive than assumed (Campana 2001). For example, harvest management based on grossly underestimated longevity and growth led to overharvest of Orange Roughy *Hoplostethus atlanticus* off New Zealand and rockfishes *Sebastes* spp. off western Canada (Campana 2001).

Otoliths are often the most accurate and precise structures for estimating age of a wide range of fish species but require sacrifice of fish and typically require the most processing time among other available structures (e.g., Secor et al. 1995; Begg et al. 2005). Weight and age of otoliths are frequently strongly correlated, which engenders interest in using otolith weight as a less time-consuming, albeit still lethal, method for estimating fish age (Boehlert 1985). For example, a strong linear relationship between otolith weight and fish age has been used to accurately define mostly nonoverlapping age-groups of fast-growing, young-aged species such as Pilchard *Sardinops neopilchardus* (Fletcher 1991). Similarly, age-frequency distributions estimated from otolith weight–age relationships did not differ significantly from those estimated by counting annuli for longer-lived species, such as Plaice *Pleuronectes platessa* and Atlantic Cod *Gadus morhua* (Cardinale et al. 2000) and Sky Emperor *Lethrinus mahsena* (Pilling et al. 2003). However, accuracy of the estimated age frequency based on otolith age–weight models declined with geographic distance from the source population where the model was applied (e.g., Common Coral Trout *Plectropomus leopardus* at 24 coral reefs in four regions spanning seven degrees of latitude along the Great Barrier Reef of Australia; Lou et al. 2005). Further, simple relationships between otolith weight and age that are not accurate for predicting age of individual fish can often be improved by using multivariate models with other otolith dimensions (e.g., length or width; Boehlert 1985; Kasapoglu and Duzgunes 2013) or covariates for fish attributes (e.g., length, weight, or sex) and sampling dates (Fey and Linkowski 2006; Lepak et al. 2012).

Asking whether otolith weight can be used to estimate age of individual fish is often the wrong question because the ultimate purpose is usually to estimate the age frequency of a sample or some other population attribute, such as length at age or age at maturity (Francis and Campana 2004). Therefore, indirect estimation of fish age from otolith weight should first address the ultimate use or purpose of indirect estimates of age, before evaluating which predictors to use (e.g., otolith weight or fish length) for inferring age (e.g., individual age, age frequency, or population metric), and if indirect estimation of age is beneficial in its costs versus benefits (Francis and Campana 2004). This sequence of steps for developing indirect methods for estimating fish age is especially important for long-lived fish species or populations because the accuracy of otolith weight (or other features such as length) as a predictor of individual fish age is likely only possible for young age-classes that are clearly separated from older age-classes in age-frequency distributions (Francis and Campana 2004).

Lake Trout *Salvelinus namaycush* support important indigenous, commercial, and recreational fisheries in North America (Hansen 1999; Muir et al. 2013; Hansen et al. 2021; Lester et al. 2021). Age-based metrics, such as growth, age at maturity, and survival are used for monitoring status and managing harvest of Lake Trout populations across northern North America (e.g., Shuter et al. 1998; Lester et al. 2003, 2021; Lester and Dunlop 2004; Hansen et al. 2021). Our objective was to test whether otolith weight could be used to accurately and precisely estimate age-dependent life history metrics for Lake Trout, a relatively long-lived, late-maturing species. We first tested for a relationship between fish age and otolith weight of Lake Trout sampled from lakes across the species' range in North America. We then tested the accuracy and precision of otolith weight-based (indirect) estimates of age for estimating age-based life history parameters, including growth (length–age parameters), age at 50% maturity, and survival. Our aim was to identify age-dependent life history metrics of Lake Trout populations that could be accurately and precisely estimated from otolith weight, which would thereby be obtainable in less time at lower

material cost than is required for embedding, sectioning, and estimating age of a species that commonly lives to an age of 50 years or more (Campana et al. 2008).

METHODS

Lake Trout populations were sampled from multiple lakes within the native range of the species, multiple years within lakes, and multiple locations within Great Bear Lake and Lake Superior (Table 1; Hansen et al. 2012, 2016a, 2016b, 2021; Chavarie et al. 2017, 2018, 2019) to test for spatial and temporal variation in otolith weight–age relationships. Samples spanned the geographic range of the species (46°35.54′N to 66°45.29′N; 155°53.65′W to 73°32.33′W) and a wide range of lake surface areas (1.31–82,100 km^2), which we assumed to represent a comprehensive range of variation in biotic and abiotic variables that could influence the relationship between otolith weight and age.

Lake Trout were collected using graded-mesh gill nets set within three depth strata to cover the anticipated depth distribution of the species (0–50, 50–100, and 100–150 m; Moore and Bronte 2001). 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 should have enabled 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. Sampling in Dease Arm, Great Bear Lake, in 2015 used monofilament multimesh gill nets (11 panels, 38 to 140 mm stretch mesh, 275 m long and 1.8 m wide) set for 24 h in three depth zones (0–20, 21–50, and 51–150 m) on bottom (0–20, 21–50, and 51–150 m), at middepth (21–50 and 51–150 m), and just below the surface (0–20 and 21–50 m; Chavarie et al. 2019).

Sagittal otoliths were removed during field collections, cleaned of tissue and debris, placed in microcentrifuge tubes or scale envelopes, and allowed to air dry. One otolith from each fish was weighed to the nearest milligram (equivalent precision to years of age), embedded in epoxy, cut to form a thin transverse section (400 μm), mounted on a glass slide, polished, and imaged for age estimation (Hansen et al. 2012, 2016a, 2016b). Annuli were counted by 2–4 independent readers on otoliths or otolith images where translucent zones were proximal to adjacent opaque zones (as described by Casselman and Gunn 1992). Specimens were excluded from analysis if the coefficient of variation (CV; 100·SD/mean) of multiple 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, to back-calculate length at age for related studies (Hansen et al. 2012, 2016a, 2016b). The count of annuli marked on each otolith image was used as the final age for further analysis. We assumed our age estimates were unbiased because thin-sectioned sagittal otoliths have been validated for age estimation of Lake Trout to an age of at least 50 years (Campana et al. 2008).

Nonlinear power models were used to test for the relationship between fish age estimated directly from otoliths

TABLE 1. Lakes, locations within lakes, surface area, latitude, longitude, years sampled, number of gill nets lifted, and number of ages estimated (N) for Lake Trout sampled in three depth strata in North America. Latitude and longitude reflect mean locations of all gill nets lifted in each lake or location. Lakes and subareas within lakes are sorted from north to south. Surface area is not estimable for subareas (reef complexes) in Lake Superior. Years sampled are shown in Table 3.

Lake and area	Surface area (km^2)	Latitude	Longitude	Years	Lifts	N
Great Bear	31,790	66°33.06′N	119°24.61′W	3	62	364
Dease Arm	3,007	66°45.29′N	120°17.77′W	2	23	177
McTavish Arm	4,553	66°12.32′N	117°54.47′W	2	39	187
Great Slave	28,568	62°32.12′N	110°50.36′W	3	43	278
Skilak	99	60°25.77′N	150°19.76′W	1	9	132
Naknek	610	58°40.63′N	155°53.65′W	1	4	33
Mistassini	2,164	51°00.83′N	73°32.33′W	1	12	146
Superior	82,100	47°09.64′N	87°12.18′W	7	89	1,892
Isle Royale		47°58.55′N	88°54.38′W	2	20	688
Superior Shoal		47°12.55′N	87°11.77′W	1	12	383
Stannard Rock		47°11.74′N	87°12.44′W	2	21	343
Klondike Reef		47°05.29′N	85°51.27′W	1	2	91
Grand Marais		46°46.64′N	85°57.37′W	2	10	116
Big Reef		46°35.54′N	86°24.89′W	2	24	271
Rush	1.31	46°53.31′N	87°54.60′W	2	19	136

(years) and otolith weight (mg) of Lake Trout. Parameters were estimated from $\log_e$ transformation of the power model: $\log_e(\text{otolith age}) = \log_e(b_0) + b_1 \times \log_e(\text{otolith weight})$. To test whether other variables would increase accuracy of ages estimated from otolith weight–age models, we first measured the relative proportion of total variance explained by otolith weight, fish total length, sex, maturity, location, and morph as main effects in a general linear model. To further judge the relative importance of each variable, we then quantified the increase in agreement between ages estimated by models that included otolith weight with each individual variable and those estimated by a model with only otolith weight. Linearity of the otolith weight–age model was tested by comparing the exponent of the power model to a null hypothesis of $b_0 = 1.0$ ($P \le 0.0015$; Bonferroni-corrected $P \le 0.05$). To test the relative importance of temporal and spatial variation on the otolith weight–age relationship, models were constructed with (1) different slopes (b_0) and curvature (b_1) for each survey (hypothesis: each year in each area or lake differed from all other years in each area or lake), (2) different slopes and intercepts for each lake or area (hypothesis: years did not differ in each area or lake), and (3) a common slope and intercept across all surveys (hypothesis: all years and areas or lakes did not differ from one another). Models were ranked using the Akaike information criterion (AIC), where $\text{AIC} = n\log_e\left(\frac{\text{RSS}}{n}\right) + 2K + \left[\frac{2K(K+1)}{n-K-1}\right]$, AIC differences, where $\Delta_i = \text{AIC}_i - \text{AIC}_{\min}$, and AIC weights, where $w_i = \frac{e^{(-0.5\Delta_i)}}{\sum_{r=1}^{R} e^{(-0.5\Delta_r)}}$, to express the relative likelihood that a particular model was the best model among those considered (Burnham and Anderson 2002).

Fish age was estimated indirectly from otolith weight using geometric-mean functional regression models (Ricker 1975). Age was rounded to the nearest whole integer for further analysis (equivalent precision as milligram of otolith weight). Based on results of the preliminary analysis of other explanatory variables (see above and Results), age-bias plots (Campana et al. 1995) were used to test for bias of two model-based estimates of fish age: (1) age estimated for each fish using the otolith age–weight model for the survey in which the fish was caught (survey-specific models), and (2) age estimated for each fish using an otolith age–weight model from all other surveys except the survey in which the fish was caught (general models). Survey-specific age estimates were assumed to be the best possible indirect age estimates because they estimated age of each fish from the full set of available pairs of otolith weights and ages for each survey. In contrast, general age estimates for each survey were assumed to be the worst possible indirect age estimates because they were derived from all other pairs of otolith weights and ages not including the survey for which age was estimated. Mean estimated age was regressed against mean otolith age to test for overall bias of model-based mean age (H_0: $b_0 = 0.0$ and $b_1 = 1.0$; $P \le 0.05$; Campana et al. 1995) using functional regression parameters that account for measurement error of the predictor variable (Ricker 1975). Age-specific bias of the two model-based age estimates was also tested for significance using paired t-tests of each model-based age minus otolith age, under an assumption that direct estimates of age were unbiased (Campana et al. 1995). For age-specific tests of bias, ages 40 years and older were pooled because of small samples and a Bonferroni correction was used to account for 38 multiple age-specific comparisons ($P \le 0.05/38 = P \le 0.00135$).

Growth parameters (L_∞ and K), age at 50% maturity (A_{50}), and annual survival rate (S) were estimated from survey-specific and general otolith age–weight models for comparison to direct estimates of fish age. Average asymptotic length (L_∞) and instantaneous growth coefficient (K) of the Von Bertalanffy length–age model were estimated from length at age of capture for individual fish (with multiplicative errors) for Lake Trout sampled in each lake and area (Quinn and Deriso 1999). Age at 50% maturity (A_{50}) was estimated using logistic regression on the logit transformation of the logistic equation that describes the relationship between maturity status of individual fish (immature = 0, mature = 1) and age (Hosmer and Lemeshow 2000). Survival (S) was estimated for each lake and area from the number of fish in each mature age-class (A_{50} estimated from otolith ages) using the Robson–Chapman estimator (Robson and Chapman 1961). For estimates of L_∞, K, A_{50}, and S, bias was defined as the difference between each of the two indirect estimates and the direct estimate, under an assumption that direct estimates of age were unbiased (Campana et al. 2008). Significance of bias was tested by assuming the ratio of bias to the pooled average standard error of the two estimates followed a Student's t-distribution ($P \le 0.0033$; Bonferroni-corrected $P \le 0.05$).

RESULTS

Otolith weight and sampling location were the only two variables tested that were useful for estimating fish age indirectly. First, otolith weight explained nearly all (92.1%) of the modeled variance of fish age when fish length, location, sex, morph, and maturity were included as main effects in a general linear model (Figure 1). Second, sampling location was the only other potential explanatory variable that measurably increased the variance explained (+3.2%; 0.0–1.0% for all other potential explanatory variables) between observed and modeled estimates of age compared with ages estimated from otolith weight alone (9.6% agreement; Figure 2). Therefore,

further analysis was focused on comparisons between life history parameters derived from a general otolith weight–age model for all samples combined and survey-specific weight–age models (see Methods).

Age estimated directly from otoliths was strongly correlated with otolith weight for Lake Trout populations in North America, but relationships varied temporally within lakes and spatially within and among lakes. Different nonlinear otolith age–weight relationships (i.e., different slopes and curvatures) for each of 22 surveys described 82.8% of the variation in otolith age–weight relationships (Table 2). However, different linear relationships (i.e., different slopes and curvatures) for each of the 13 lakes or areas within lakes described only 0.4% less variation (82.4%) in otolith age–weight relationships (Figure 2; Table 2). The simplest model with only one slope and one curvature for all fish from all surveys described 76.0% of the variation in the otolith age–weight relationship (Table 2).

Over all surveys, estimated age increased at an average rate of 1.13 years per milligram increase in otolith weight (slope = b_0) and the slope increased nonlinearly at an average exponential rate of 1.02 (curvature = b_1) per milligram increase in otolith weight (Table 3; Figure 2). Among surveys, the rate of increase in estimated otolith age with otolith weight ranged from 0.30 years/mg at Grand Marais, Lake Superior, in 2002 to 2.08 years/mg in McTavish Arm, Great Bear Lake, in 2004. Among lakes or areas, the rate of increase in estimated otolith age with otolith weight ranged from 0.51 years/mg at Grand Marais, Lake Superior, to 2.05 years/mg in Great Slave Lake (Table 3; Figure 2). Among surveys, the otolith weight–age relationship was significantly nonlinear for 9 of 22 surveys ($P <$ 0.0015; Bonferroni corrected) and the nonlinearity coefficient ranged from 0.80 in Great Slave Lake in 2010 to 1.44 in Rush Lake in 2007 (Table 3). Among lakes or areas, the otolith weight–age relationship was significantly nonlinear for 11 of 15 lakes or areas and the nonlinearity coefficient ranged from 0.80 in Great Slave Lake to 1.27 in Lake Mistassini (Table 3; Figure 2).

Survey-specific otolith age–weight relationships were only slightly more accurate than general otolith age–weight relationships for estimating Lake Trout age. Across all individuals, mean-age estimates from survey-specific and general otolith age–weight relationships were free of bias and similar in precision (Figure 3, left panels). Model-based age-specific bias was significant and positive, albeit small, for 7 of 38 age-groups from both survey-specific models (ages 7–12 and 14; bias <1.0 year) and general models (ages 6–12; bias <1.4 years; Figure 3, right panels). The overall average bias of estimating age from otolith weight using survey-specific otolith age–weight relationships was negligible (mean = −0.03 years; SD = 4.3) and ranged from −1.9 years (SD = 4.6) for Rush Lake in 2018 to +0.1 years (SD = 4.3) for McTavish Arm in Great Bear Lake in 2012. The overall average bias of estimating age from otolith weight using general otolith age–weight relationships (age–weight relationships from all other surveys to estimate age of individuals from each survey) was also negligible (mean = 0.04 years; SD = 5.0) but ranged more broadly from −4.2 years (SD = 4.6) for Superior Shoal, Lake Superior, in 2013 to +4.4 years (SD = 3.6) for Great Slave Lake in 2002. However, only 14% of survey-specific age estimates agreed with direct age estimates (38% were within ±1 year and 84% were within ±5 years), whereas
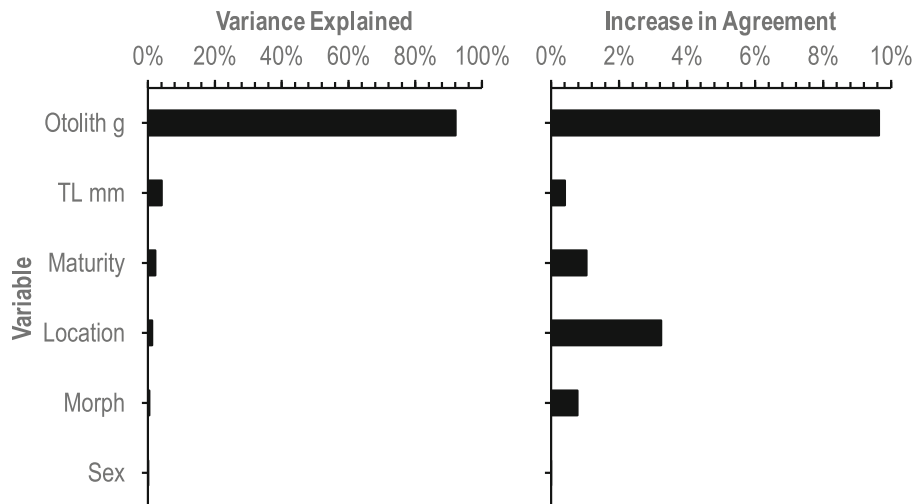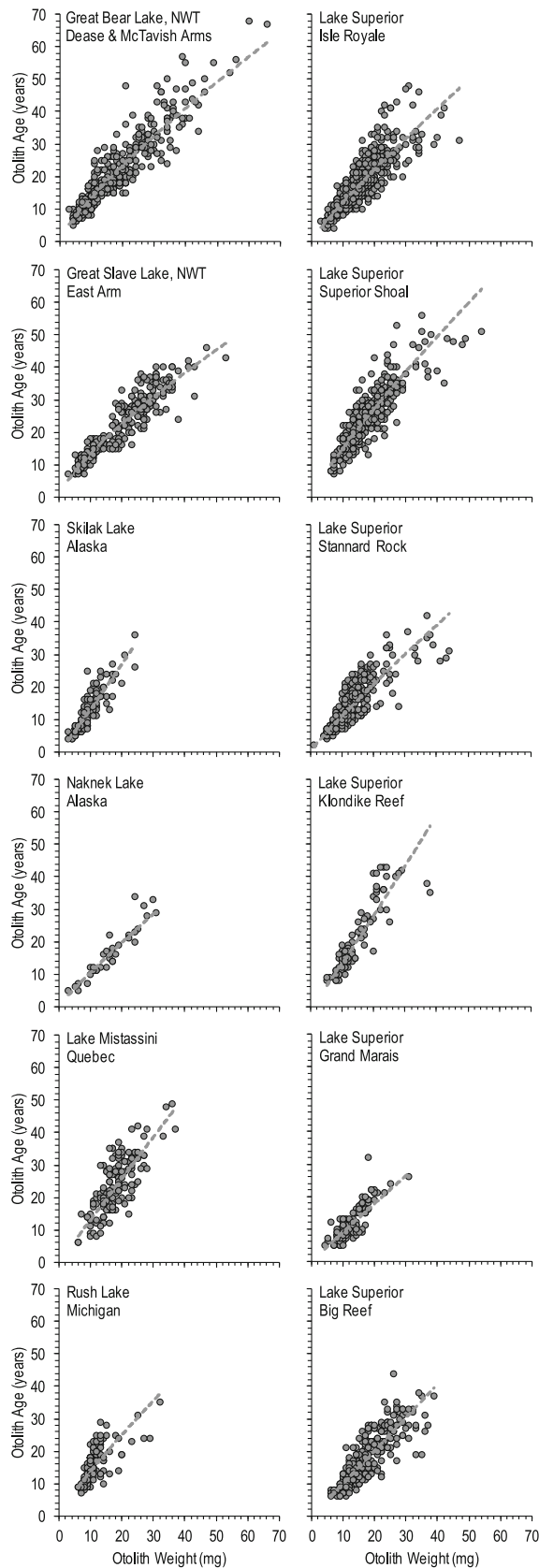

FIGURE 1. Variable importance for estimating Lake Trout age using a general linear model from otolith weight (mg), total length (mm), maturity (mature, immature), location from which an individual was collected (lake or location within Great Bear Lake or Lake Superior), morph (shape group), and sex of an individual (male or female). Model variance explained by each variable is shown in the left panel, and increase in agreement between direct and model-based estimates of age for each variable is shown in the right panel.

FIGURE 2. Power relationships between estimated otolith age (years) and otolith weight (mg) of Lake Trout sampled in North American lakes (left column of figures) and areas within Lake Superior (right column of figures) during 2001–2018. Multiple years of samples are not shown separately within lakes and areas within Lake Superior. See Table 1 for lake names, locations, and sampling information. See Table 2 for parameters of nonlinear relationships depicted for each lake or area.

only 11% of general age estimates agreed (31% were within ±1 year and 77% were within ±5 years).

Asymptotic length L_∞ derived from indirect age estimates was of relatively high precision but bias was large enough to be significant for nearly half of all estimates (Figure 4). Estimated L_∞ was of relatively high precision from survey-specific (mean CV = 0.062) and general (mean CV = 0.067) otolith age–weight estimates. Bias was significant for 6 of 15 lakes or areas from survey-specific age estimates (Great Bear, Skilak, Mistassini, Superior, Isle Royale, and Stannard Rock) and 7 of 15 lakes or areas from general-model age estimates (Skilak, Mistassini, Superior, Isle Royale, Stannard Rock, Klondike Reef, and Big Reef; Figure 4). Mean relative bias of estimated L_∞ was 18% from survey-specific age estimates (mean absolute bias = 29 mm; SD = 268; range = −857 to +305 mm) and 20% from general-model age estimates (mean absolute bias = 23 mm; SD = 282; range = −890 to +291 mm).

The instantaneous growth coefficient K derived from indirect age estimates was of relatively low precision, and bias was large and significant for half of all estimates (Figure 4). Estimated K was of lower precision than any other life history metric, whether from survey-specific (mean CV = 0.180) or general (mean CV = 0.186) otolith age–weight model age estimates. Bias was significant for 3 of 15 lakes or areas from survey-specific age estimates (Superior, Isle Royale, and Grand Marais; Figure 4) and for 9 of 15 lakes or areas from general-model age estimates (Great Bear, Dease Arm, Great Slave, Skilak, Mistassini, Superior, Superior Shoal, Big Reef, and Rush; Figure 4). Mean relative bias of K estimates was 64% from survey-specific age estimates (mean absolute bias = −0.016/year; SD = 0.056; range = −0.090 to +0.157/year) and 66% from general-model age estimates (mean absolute bias = −0.021/year; SD = 0.046; range = −0.091 to +0.105/year). Relative bias was much higher for K than L_∞ because K is exponentially related to L_∞ in the length–age model.

Age at 50% maturity A_{50} derived from indirect estimates of otolith age were of similar precision as the growth parameter L_∞ and higher precision than the growth parameter K, whereas bias of A_{50} was much lower than for L_∞ and K and not significant for most samples (Figure 4). Estimated A_{50} from survey-specific otolith age–weight models was relatively precise (mean CV = 0.114), and bias was significant for none of the 15 estimates

TABLE 2. Ranking of power models describing the relationship between estimated otolith age (years, dependent variable) and otolith weight (mg, independent variable) of Lake Trout sampled in North American lakes during 2001–2018 ($n = 2,981$ for all models, K = number of parameters, RSS = residual sum of squared residuals, AIC_c = corrected AIC statistic, Δ_i = AIC_c difference, w_i = relative likelihood of being the "best" model, and R^2 = goodness of fit).

Model (variables included)	K	RSS	AIC_c	Δ_i	w_i	$e^{(-0.5 \cdot \Delta i)}$	R^2 (%)
Surveys (multiple slopes and intercepts)	44	121.87	14,407	0.00	1.000	1	82.8
Lakes (multiple slopes and intercepts)	26	124.49	14,433	26.43	0.000	0.00000	82.4
Base model (1 slope, 1 intercept)	2	169.63	15,307	900.31	0.000	0.00000	76.0

TABLE 3. Parameters of power models (N = sample size, R = correlation coefficient, b_0 = slope, b_1 = curvature, and P = probability of $b_0 \neq 0$ or $b_1 \neq 1$) describing relationships between estimated otolith age (years, dependent variable) and otolith weight (mg, independent variable) of Lake Trout sampled in North American lakes (area = locations within Great Bear Lake and Lake Superior) during 2001–2018.

| Lake and area	Year	N	R	Slope b_0	Slope $P(b_0 \neq 0)$	Curvature b_1	Curvature $P(b_1 \neq 1)$
All		2,981	0.872	1.1279	<0.0001	1.0210	0.0221
Great Bear		364	0.929	1.7890	<0.0001	0.8659	<0.0001
Dease Arm		177	0.943	1.4898	<0.0001	0.9163	0.0004
	2014	22	0.951	1.9355	<0.0001	0.8483	0.0172
	2015	155	0.943	1.3954	<0.0001	0.9345	0.0098
McTavish Arm		187	0.899	1.8818	<0.0001	0.8590	<0.0001
	2004	86	0.892	2.0780	<0.0001	0.8081	<0.0001
	2012	101	0.911	1.7151	<0.0001	0.9053	0.0134
Great Slave, East Arm		278	0.945	2.0492	<0.0001	0.8040	<0.0001
	2002	30	0.868	0.8480	0.0130	1.0626	0.5348
	2005	130	0.934	2.0509	<0.0001	0.8094	<0.0001
	2010	118	0.957	2.0687	<0.0001	0.7991	<0.0001
Skilak	2006	132	0.887	0.8658	<0.0001	1.1858	0.0002
Naknek	2001	33	0.949	1.1297	<0.0001	0.9599	0.4663
Mistassini	2003	146	0.776	0.6039	0.0018	1.2705	0.0001
Superior		1,892	0.854	0.8538	<0.0001	1.1160	<0.0001
Isle Royale		688	0.885	1.1683	<0.0001	0.9974	0.8847
	2006	432	0.874	1.0688	<0.0001	1.0335	0.1678
	2007	256	0.903	1.3257	<0.0001	0.9465	0.0372
Superior Shoal	2013	383	0.871	1.4877	<0.0001	0.9810	0.4424
Stannard Rock		343	0.876	1.0036	<0.0001	1.0346	0.2019
	2012	110	0.893	1.1176	<0.0001	0.9835	0.6989
	2013	233	0.859	0.9472	<0.0001	1.0598	0.0945
Klondike Reef	2004	91	0.919	0.8821	<0.0001	1.1675	0.0009
Grand Marais		116	0.790	0.5074	0.0052	1.2311	0.0014
	2002	87	0.838	0.3035	0.1627	1.4097	<0.0001
	2003	29	0.698	1.0624	0.0020	0.9799	0.8830
Big Reef		271	0.850	0.5887	<0.0001	1.1889	<0.0001
	2006	138	0.769	0.7458	0.0001	1.0988	0.1180
	2014	133	0.899	0.5607	<0.0001	1.2128	<0.0001
Rush		136	0.741	0.9339	<0.0001	1.1595	0.0191
	2007	66	0.753	0.5040	0.0725	1.4423	0.0004
	2018	70	0.744	1.1832	<0.0001	1.0482	0.5723
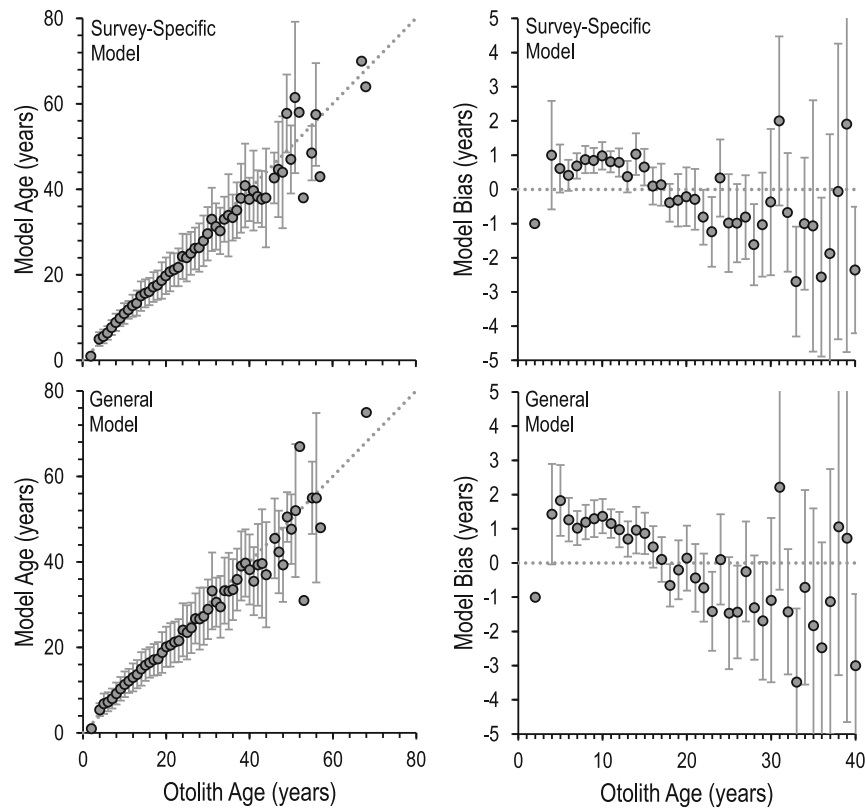
FIGURE 3. Age-bias plots of age (upper and lower left panels; means = circles, error bars = 1 standard deviation) and age-specific bias (upper and lower right panels; means = circles, error bars = 95% confidence limits) estimated from otolith age–weight relationships from survey-specific relationships (upper two panels) and general relationships derived from all fish combined from other surveys (lower two panels) plotted against otolith age for Lake Trout sampled across North America. In the left panels, the gray dashed line depicts the 1:1 line against which each was compared for intercept = 0.0 and slope = 1.0 (upper left panel, intercept t_{53} = 0.12, P = 0.90; slope t_{53} = 1.25, P = 0.22, r^2 = 0.95, SE = 3.8 years; lower left panel, intercept t_{53} = 0.22, P = 0.83; slope t_{53} = 0.82, P = 0.42, r^2 = 0.92, SE = 4.6 years). In the right panels, the gray dashed line depicts no age estimation bias.

(Figure 4). Relative bias of A_{50} estimates was only 3% based on survey-specific age estimates (mean absolute bias = 0.1 years; SD = 1.1; range = −1.7 to +3.5 years). In contrast, A_{50} estimates from general otolith age–weight models were relatively precise (mean CV = 0.149), but bias was significant for 5 of 15 lakes or areas (Great Bear, McTavish Arm, Superior, Superior Shoal, and Big Reef; Figure 4). Relative bias of A_{50} estimates was only slightly higher for general-model age estimates (5%) than for survey-specific age estimates (mean absolute bias = 0.5 years; SD = 1.6; range = −2.5 to +3.3 years).

Annual survival S estimates based on indirect estimates of age were even more precise than A_{50} estimates, and therefore small bias was significant for about half of the estimates (Figure 4). Survival (S) estimates from survey-specific otolith age–weight models were precise (mean CV = 0.012), and bias was significant for only 3 of 15 lakes or areas within lakes (Superior, Isle Royale, and Grand Marais; Figure 4). Relative bias of S estimates averaged only 1.5% from survey-specific age-frequency estimates (mean

absolute bias = −0.012; SD = 0.019; range = −0.077 to +6.7 × 10⁻⁶). Similarly, S estimates from general otolith age–weight models were similarly precise (mean CV = 0.010), but bias was significant for 9 of 15 lakes or areas within lakes (Great Bear, Dease Arm, Great Slave, Skilak, Mistassini, Superior, Superior Shoal, Big Reef, and Rush; Figure 4). Relative bias of S estimates averaged 0.3% from general-model age–frequency estimates (mean absolute bias = −0.002; SD = 0.023; range = −0.048 to +0.024).

DISCUSSION

In contrast to other studies of relationships between fish age and otolith weight, we found that only location, not fish length, maturity, sex, or morph, was a useful added predictor of fish age. Our finding was least surprising for location because the spatial scale of our samples was similar to that of Common Coral Trout on the Great Barrier Reef, Australia, where location was important (Lou et al. 2005). In contrast, our finding was unexpected for fish
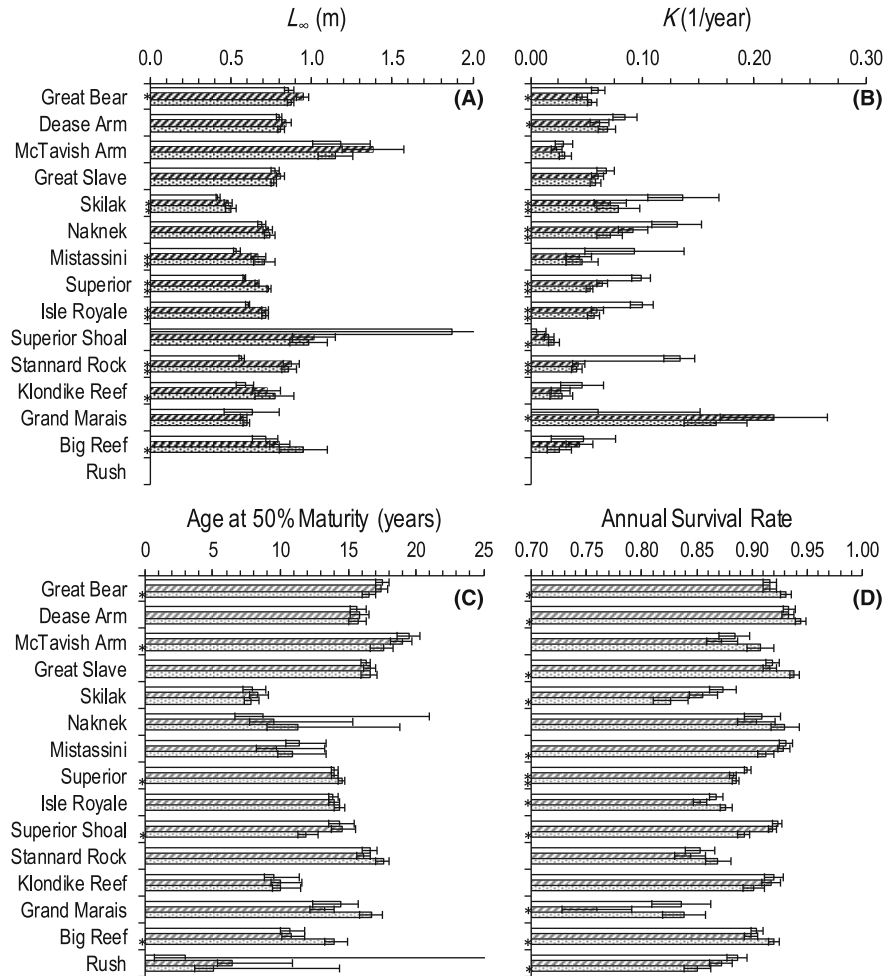
FIGURE 4. Age-dependent life history parameters, including asymptotic length (upper left panel; L_∞ = mm), instantaneous growth coefficient (upper right panel; K = 1/years), age at 50% maturity (lower left panel; A_{50} = years), and survival rate (lower right panel; S = proportion) estimated from otolith age (open bars), survey-specific otolith age–weight models (diagonal hatched bars), and general otolith age–weight models (stippled bars) for Lake Trout populations in North American lakes during 2001–2018. Survival was estimated across mature age-classes A_{50} (estimated from otolith ages). Estimates from otolith age–weight models that differed significantly ($P \le 0.05$) from otolith ages are denoted by an asterisk at the base of each bar. Growth parameters were not estimable for Rush Lake.

length, a variable that has often been found to be a useful predictor of fish age (e.g., Boehlert 1985; Pawson 1990; Araya et al. 2001; Lepak et al. 2012). Similarly, our findings were not unexpected for sex or age at maturity because male and female Lake Trout do not differ in somatic growth (Martin and Olver 1980; Gunn 1995; Esteve 2005; Esteve et al. 2008; Muir et al. 2014) or age at maturity (Hansen et al. 2021), unlike other species for which sex and maturity were useful predictors of age (e.g., Lepak et al. 2012). In addition, maturity may not be useful for predicating Lake Trout age because age at maturity varied over too narrow of a range relative to the total age range to be estimated (Hansen et al. 2021), compared with other short-lived species like kokanee *Oncorhynchus nerka* for which maturity was a useful predictor of only four

age-groups (Lepak et al. 2012). Last, our finding that morph was not a useful predictor of fish age was somewhat unexpected because Lake Trout morphs differ in somatic growth (e.g., Great Bear Lake, Chavarie et al. 2016; Great Slave Lake, Hansen et al. 2016a; Lake Mistassini, Hansen et al. 2012; and Lake Superior, Hansen et al. 2016b), albeit perhaps not enough to improve accuracy of age estimates from otolith weight–age relationships.

Age estimates from otolith weights of Lake Trout were not accurate enough to be reliable for individual fish, as was found for many other fish populations (reviewed by Francis and Campana 2004). Small bias may be tolerable if age estimates are precise (Francis and Campana 2004), but model-based estimates of Lake Trout age were not, a pattern that was consistent across all age-classes. In

contrast, age assignment accuracy of Lake Trout in Lake Michigan from otolith weight and fish length decreased by more than 50% when fish were older (e.g., ~20 years) compared with younger (~3 years) (Hanson and Stafford 2017). However, age increased with otolith weight at a slower rate (and otolith weight increased at a faster rate with age) in Lake Michigan (mean = 0.47 years/mg, inverse of 2.11 mg/year in Table 2 of Hanson and Stafford 2017) than all but one of the populations sampled in our study (range = 0.30–2.07 years/mg or 0.48–3.30 mg/year), which may explain the difference between these two studies of Lake Trout otolith weight–age relationships. Such variation in growth among populations causes otolith age–weight relationships to vary spatially (Lou et al. 2005) and temporally (Pawson 1990), which explains why otolith age–weight relationships in our study differed among years, locations, and lakes for Lake Trout. Regardless of such spatial or temporal variation, the key to estimating age of individual fish from otolith weight is that age groups do not overlap, or overlap very little, in length, which is generally true for young ages of long-lived species or for short-lived species (Pawson 1990; Fletcher 1991, 1995; Worthington et al. 1995a; Cardinale et al. 2000; Labropoulou and Papaconstantinou 2000; Araya et al. 2001; Francis and Campana 2004). Alternatively, the mean age of long-lived species can be estimated accurately if other variables, such as fish length or other otolith dimensions (not available for this study), are incorporated into predictive models (e.g., Boehlert 1985; Lepak et al. 2012; Hanson and Stafford 2017).

Growth parameters L_∞ and K estimated from indirect otolith weight-based ages often differed significantly from those estimated from direct otolith age estimates for samples of Lake Trout populations, unlike similar analyses of length–age parameters L_∞ and K in other studies (Pilchard, Fletcher 1995; Common Coral Trout, Lou et al. 2005). Greater accuracy and precision of estimated growth parameters in those studies was likely because they were derived from a younger age range of studied fish species (ages 2–8, Fletcher 1995; ages 3–7, Lou et al. 2005) than for Lake Trout (ages 2–68). In contrast to cases where length at relatively young ages is used, growth parameters L_∞ and K are likely estimated with large error for longer-lived species because of the strong influence of large, old individuals that are inherently rare in samples. Such large, old individuals substantially influence growth curvature K and asymptote L_∞ but are nonetheless crucial to accurately estimating both parameters in long-lived populations (Ricker 1975). To overcome the influence of old, usually large fish on estimated growth parameters, growth histories would need to be back-calculated for analysis in nonlinear mixed-effects models (Vigliola and Meekan 2009) as was previously done for many of the samples included in this analysis

(Hansen et al. 2012, 2016a, 2016b, 2021; Chavarie et al. 2017, 2018, 2019, 2021).

Unlike growth parameters L_∞ and K, age-at-maturity A_{50} for Lake Trout populations was estimated with relatively high precision and low bias, and to our knowledge, ours was the first attempt to estimate age at maturity from otolith weight. Age at maturity is inversely related to total mortality for Lake Trout (Hansen et al. 2021), so it is an important life history parameter for monitoring population response to fishery exploitation (Regier and Loftus 1972; Trippel 1995). Age at 50% maturity in Lake Trout occurs at a relatively young age (median $A_{50}/A_{max} = 0.313$; 95% CI = 0.151–0.614; Hansen et al. 2021), which allows more accurate and precise estimation from otolith weight than was true of L_∞ and K due to a reliance on younger ages as has been true of studies of otolith weight–age relationships for most other species (e.g., Pawson 1990; Fletcher 1991, 1995; Worthington et al. 1995a; Cardinale et al. 2000; Labropoulou and Papaconstantinou 2000; Francis and Campana 2004). Based on our findings for precision and accuracy of A_{50} based on indirect age estimates for a long-lived species, the Lake Trout, we anticipate that A_{50} can be estimated accurately and precisely for most other fish species.

Like A_{50}, survival S of Lake Trout was estimated with high precision and low bias, although very high precision enabled detection of significant but very small bias as observed frequently in other fish species (e.g., Fletcher 1991, 1995; Worthington et al. 1995a; Cardinale et al. 2000; Pilling et al. 2003; Francis and Campana 2004; Lou et al. 2005). Survival is estimated from the age-frequency distribution, which is the most commonly estimated population metric for fish stocks worldwide, especially those that are monitored annually as part of stock assessment programs (Francis and Campana 2004). Low absolute bias of S is likely enabled because it is less influenced by accuracy of individual age estimates from otolith weight or other measures such as length (Francis and Campana 2004). Nonetheless, S is still influenced by indirect age estimates of old, usually large individuals in samples, like L_∞ and K, which led to a high frequency of occurrence of significant bias of S despite a relatively low absolute magnitude of bias for individual samples.

Management Implications

We conclude that our general model for estimating Lake Trout age from otolith weight may be useful for maturity and survival analyses that are less susceptible to estimation error of individual (often old) fish than for growth analysis that can be susceptible to estimation error of individual (often old) fish. Our findings confirm the importance of focusing on the ultimate use of indirect estimates of age, rather than on accuracy and precision of individual age estimates when using proxies such as otolith

weight (Francis and Campana 2004). We found that indirect estimates of Lake Trout age from otolith weight were not accurate for individual fish and perhaps not accurate enough for estimating growth parameters L_∞ and K but were accurate for estimating population-level survival S and age at 50% maturity A_{50}. Usefulness of life history parameters from indirect age estimates depends on the specific application. For example, age at maturity (A_{50}) estimated indirectly from otolith weight is likely accurate enough for use in setting a minimum length limit to protect fish through their first spawning (e.g., Isermann and Paukert 2010). Similarly, total annual survival or mortality estimated from indirect estimates of age are likely accurate enough to use for monitoring a mortality target or limit reference point (e.g., Hansen 1996; Hansen et al. 1997). In contrast, growth parameters (L_∞ and K) estimated indirectly from an otolith weight–age relationship may not be accurate enough to use in a yield–recruit model for developing harvest management quotas (e.g., Lai and Gunderson 1987).

The ability to accurately estimate age-based life history traits of Lake Trout from otolith weight would be beneficial because: (1) life history information is needed for managing sustainable fisheries for Lake Trout (Shuter et al. 1998; Lester et al. 2021), (2) Lake Trout is a species that is vulnerable to collapse because of its low net reproductive rate and long generation time (Winemiller and Rose 1992), and (3) fishery managers must manage thousands of Lake Trout populations with limited resources to monitor the status and trends of fisheries within their jurisdiction (Post et al. 2002). Monitoring the status and trends of Lake Trout populations is challenging, if not impossible, in nearly 5,000 lakes ranging widely in surface area (3.4 to 8,210,000 ha) and distributed across more than 32 degrees of latitude and 98 degrees of longitude in North America (Muir et al. 2021). Agencies charged with monitoring and managing such species and associated fisheries would benefit from anything that reduces time spent on otolith preparation for age and growth analysis (e.g., Muir et al. 2008; Sakaris and Bonvechio 2020). The processing time needed to estimate an age from otolith weight is 5–10 times shorter than when using annuli, thereby enabling 5–10 times more fish ages to be estimated from otolith weight (Worthington et al. 1995b) or allowing agencies to allocate effort away from age estimation toward other activities (Muir et al. 2008). Unfortunately, we found that indirect estimates of Lake Trout age based on otolith weight were only accurate and precise enough for estimating age at maturity A_{50} and survival S but perhaps not for estimating growth parameters L_∞ and K (unless the level of estimation bias of growth parameters is acceptable). Therefore, our findings will be limited in usefulness to agency programs that rely on biological reference points, such as age at maturity A_{50} and survival S, for monitoring the status of Lake Trout populations.

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