Age and Growth of a Native, Lightly Exploited Population of *Coregonus clupeaformis* (Lake Whitefish) in a Small Natural Lake in Maine

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Abstract - We assessed annual growth of *Coregonus clupeaformis* (Lake Whitefish) from a natural, lightly exploited population in a small lake in northern Maine using observed and back-calculated length-at-age data. We sampled Lake Whitefish from Clear Lake, ME, with gill nets and extracted otoliths from 57 fish. We incorporated age-at-length data into a von Bertalanffy growth function, which we employed to model growth trajectories from individual fish. We used these estimates to evaluate length-at-age variability within this population. Ages for Lake Whitefish varied from 8 y to 30 y. Among all fish, we characterized incremental growth by an average-growth coefficient of $K = 0.156$ and an estimated L_∞ of 484 mm. The oldest individuals demonstrated the slowest incremental growth ($K = 0.106$) when compared to younger cohorts ($K = 0.218$). We observed an inverse relationship between L_∞ and K and the estimated age-at-capture ($R^2 = 0.178$ and 0.723, respectively), which suggests relatively slow growth and a smaller maximum size for the longest living members of the population. Our estimated parameters serve as a reference to inform management of populations of Lake Whitefish.

Introduction

Fish growth rates and trajectories are important correlates of survival, size, age at maturity, and longevity, and may indicate surplus energy allocated towards somatic growth or reproduction (Beverton and Holt 1959, Charnov 1993, Ware 1980). Furthermore, age and growth data are critical components used to inform management and conservation planning for monitoring populations and shaping harvest strategies for commercial or recreational fisheries (Hilborn and Walters 1992, Isely and Grabowski 2007). Many of the world's fisheries are overexploited (FAO 2016), but describing a species' growth parameters in the absence of strong fishery pressure allows for greater predictive power to estimate changes in population dynamics from management strategies, recruitment success, and effects from environmental factors.

In North America, *Coregonus clupeaformis* (Lake Whitefish) is distributed from northern Maine to the Great Lakes' region, northwest into interior Canada and Alaska, and eastward into Labrador (Evans et al. 1988). Lake Whitefish support

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commercial, recreational, and subsistence fisheries, and are a valuable economic resource in the Great Lakes (Fleischer 1992, Spangler 1970) and throughout much of Canada (Scott and Crossman 1973). Overexploitation (Mohr and Ebener 2005, Rennie et al. 2009), the introduction of nonnative species (DeBruyne et al. 2008, Herbst et al. 2013, Hoyle 2005), and habitat destruction (Bronte et al. 2003) have caused declines in many populations, although some recent evidence hints at local recovery (e.g., in the Chaumont Bay area of Lake Ontario; McKenna and Johnson 2009). A thorough understanding of growth and age structure of Lake Whitefish is necessary to guide conservation and management of the fishery.

In contrast to populations in the Great Lakes' region, Lake Whitefish in Maine are found in small natural lakes and are not subject to commercial harvest. These populations experience minimal impact from recreational fisheries, although historically, their exploitation for subsistence has waxed and waned with human settlement and establishment of logging camps (Basley 2001, Wood 2016). Despite presumably low levels of fishing mortality, populations of Lake Whitefish in Maine have still suffered declines and extirpation, perhaps due to habitat degradation and interactions with invasive *Osmerus mordax* (Mitchill) (Rainbow Smelt) and landlocked *Salmo salar* L. (Atlantic Salmon) (Basley 2001, Gorsky and Zydlewski 2013). The characterization of unexploited populations of Lake Whitefish in these small lakes, however, may reveal novel dynamics that provide fisheries managers with benchmark data to inform existing management strategies (Hilborn and Walters 1992). We determined the age and size structure of a natural, lightly exploited population of Lake Whitefish in a small lake in Maine.

Field-Site Description

We studied a population of Lake Whitefish in Clear Lake (253 ha) located in the unorganized township T10 R11 WELS, Piscataquis County, ME (46°31'16.02''N, 69°7'33.97''W; Fig. 1). Clear Lake is an oligotrophic lake with a mean depth of 8.8 m and a maximum depth of 26.2 m (Lake Stewards of Maine 2011). The fish assemblage of Clear Lake consists of 13 game and nongame species (Table 1). The assemblage is characteristic of other natural lakes in the region, though Rainbow Smelt are a recent nonnative addition.

Methods

We sampled fish during the summer of 2011with 3 identical 122-m experimental gill nets (3.8–8.9-cm mesh size). We euthanized all fish with buffered tricaine methanesulfonate (Institutional Animal Care and Use Committee protocol number A2011-06-02). For all captured Lake Whitefish, we measured total length to the nearest mm and mass to the nearest 0.1 g, determined sex, and removed sagittal otoliths. We included a total of 57 otoliths for age and growth analysis.

Otolith removal and preparation

We employed sagittal otoliths to examine fish age (Herbst and Marsden 2011). We wiped clean, air dried, and stored all otoliths, after using foceps to remove them from the fish. To facilitate sectioning, we embedded the otoliths in Epothin epoxy resin (Electron Microscopy Sciences, Hatfield, PA) and sectioned them with an IsoMet low-speed saw (Buehler, Lake Bluff, IL). We cut 1-mm–thick sections transversely through the otolith core, positioned sections on glass microscope

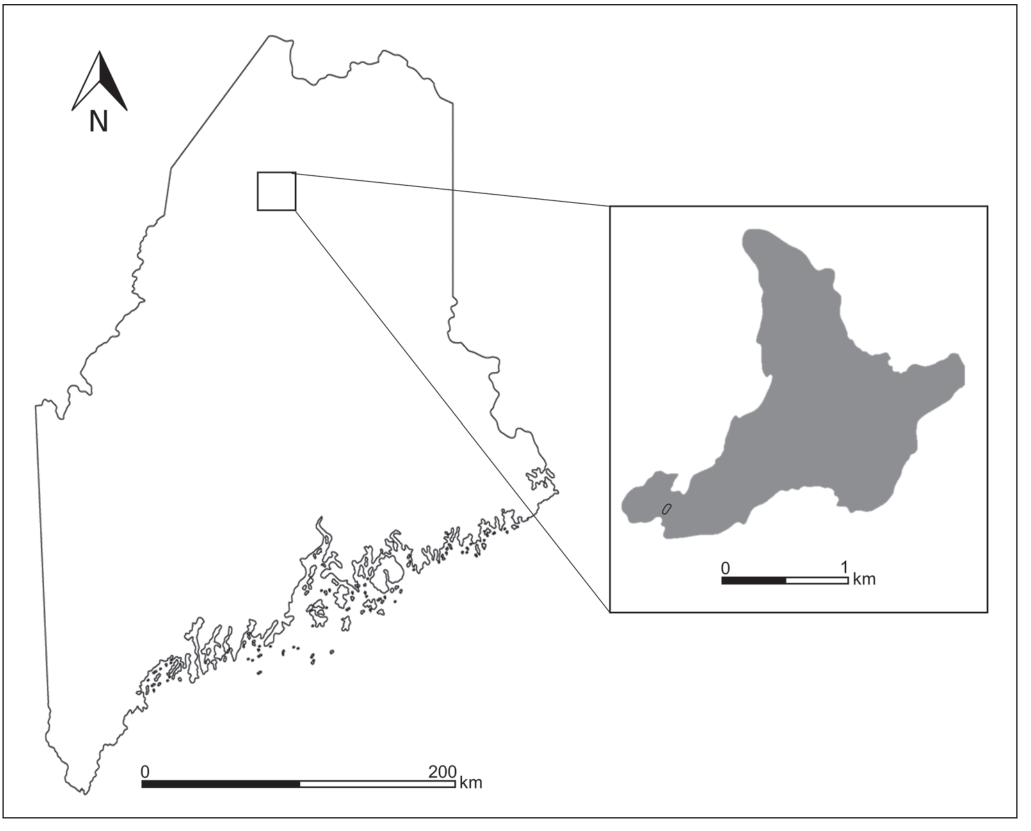

Figure 1. Map of Maine. Inset indicates location of Clear Lake.

Table 1. Fish species present in Clear Lake, ME.

Common name	Scientific name
Blacknose Dace	*Rhinichthys atratulus* (Hermann)
Brook Trout	*Salvelinus fontinalis* (Mitchill)
Brown Bullhead	*Ameiurus nebulosus* (Lesueur)
Burbot	*Lota lota* (L.)
Creek Chub	*Semotilus atromaculatus* (Mitchill)
Lake Chub	*Couesius plumbeus* (Agassiz)
Lake Trout	*Salvelinus namaycush* (Walbaum in Artedi)
Lake Whitefish	*Coregonus clupeaformis* (Mitchill)
Northern Red Belly Dace	*Phoxinus eos* (Cope)
Rainbow Smelt	*Osmerus mordax* (Mitchill)
Slimy Sculpin	*Cottus cognatus* Richardson
Three Spine Stickleback	*Gasterosteus aculeatus* L.
White Sucker	*Catostomus commersonii* (Lacepède)

slides with Crystalbond adhesive (SPI Supplies, West Chester, PA), and sanded and polished them lightly to improve visual clarity.

Otolith analysis

We imaged otoliths with a Nikon Digital Sight DS-5M digital camera (Nikon Inc., Melville, NY) interfaced with a dissecting microscope (Nikon SMZ800). Images were captured using incident (fluorescent) lighting and analyzed with Alicona–TEX–Basic imaging software (version 1.4.2; Alicona Corporation, Bartlett, IL). We used as a training data-set otoliths from known-age hatchery-stocked Lake Whitefish from St. Froid Lake, ME, and followed the methods reported by Mills and Chalanchuk (2004). Staff from the Michigan Department of Natural Resources, Charlevoix Research Station (Charlevoix, MI) externally validated a subset of aged otoliths from Clear Lake.

We employed Image J software (version 1.8.0; Research Services Branch, National Institute of Health, Bethesda, MD; Abramoff et al. 2004) to obtain measurements of annular increments. We created growth transects at a ~45-degree angle towards the dorsal surface of the otolith. Each pair of light (hyaline) and dark (opaque) growth zones visible with transmitted light constituted 1 y of fish growth. We measured the distance between opaque zones (annulus to annulus) as an indicator of annual growth in body length. We followed Fraser–Lee methods (including a standard intercept-correction factor) to back-calculate lengths-at-age for individual fish, and provide individual growth trajectories throughout the lifetime of the fish (Isely and Grabowski 2007).

Growth model

We performed retrospective increment-analysis on otoliths to reconstruct growth histories of individual Lake Whitefish and used the von Bertalanffy growth function (VBGF; von Bertalanffy 1938) to describe patterns in lifetime growth:

$$L_t = L_\infty(1 - e^{-K[t - t_0]}),$$

where L_t is the mean length of fish at time t (years), L_∞ is the theoretical maximum mean asymptotic length at age, K is the Brody growth coefficient that describes the decline in the growth rate as an individual approaches L_∞, and t_0 is the theoretical age at which body length is zero (Isley and Grabowski 2007). We incorporated back-calculated lengths at age of individual fish into a VBGF. We used nonlinear least squares to estimate parameters for individual fish. We initialized starting values of the parameters of the model by designating L_∞ as the maximum total length in the observed data, $K = 0.2$, and $t_0 = 0$. We averaged parameter values across all fish to arrive at a model describing the average growth pattern.

To better account for the variation in growth trajectories and compare VBGF parameters among old and young individuals and also to reduce the effect of individual variability described above, we grouped fish into 3 arbitrary age categories (8–10 y, 11–15 y, and >15 y) to depict young, middle-aged, and older fish. We also based categories on sufficient sample size for each age category to obtain a precise mean value sufficient for comparison. We conducted a 1-way analysis of variance

(ANOVA) to assess differences in mean growth parameters L_∞ and K among the 3 age categories. We also analyzed the relationship between those 2 growth parameters and the estimated age at capture of all fish with least squares linear regression. We conducted all parameter estimations and statistical tests in the statistical package RStudio (version 1.1.447, RStudio, Boston, MA). For all tests, we set $P < 0.05$ as the threshold for statistical significance. We conducted a Tukey post hoc test with adjusted family-wise error rates to further examine ANOVA tests with a significant age-category effect.

Results

Fish capture

Lake Whitefish varied in age from 8 y to 30 y and in total length at capture from 370 mm to 514 mm (Fig. 2, Table 2). All ages <8 y and several intermediate age classes were not represented in the sample. Few (6) old-age fish (>20 y old) were captured, and this age class comprised a small component of the wild population we studied. Back-calculation methods provided 822 lengths-at-ages for analysis (Fig. 2).

Individual growth trajectory

Our inspection of growth trajectories of individual fish within each sample revealed substantial variation among curvature (K) and/or asymptotic length (L_∞)

			Calculated size at age (mm)																													
n	Capture size at age (mm)	Age	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*12*	*13*	*14*	*15*	*16*	*17*	*18*	*19*	*20*	*21*	*22*	*23*	*24*	*25*	*26*	*27*	*28*	*29*	*30*
0		*1*	--																													
0		*2*	--	--																												
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0		*5*	--	--	--	--	--																									
0		*6*	--	--	--	--	--	--																								
0		*7*	--	--	--	--	--	--	--																							
3		*8*	169	240	287	332	363	388	416	**435**																						
15		*9*	160	223	263	298	324	347	369	386	**393**																					
2		*10*	152	215	257	291	313	338	361	379	394	**403**																				
0		*11*	--	--	--	--	--	--	--	--	--	--	--																			
1		*12*	156	208	256	313	343	363	383	399	415	434	449	**462**																		
1		*13*	146	218	250	279	301	323	343	368	382	398	410	422	**430**																	
1		*14*	170	221	264	295	316	333	352	369	383	398	409	420	434	**444**																
12		*15*	162	217	259	290	314	335	354	373	389	402	415	427	439	449	**455**															
11		*16*	159	206	240	271	297	318	336	353	369	382	395	406	418	430	441	**447**														
2		*17*	159	211	244	276	299	318	338	356	372	386	399	411	422	430	438	445	**450**													
1		*18*	156	217	260	293	315	333	350	366	379	395	403	411	418	426	434	442	448	**452**												
1		*19*	155	197	230	254	273	289	303	317	332	345	354	367	377	388	396	410	419	427	**433**											
0		*20*	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--										
1		*21*	119	144	180	221	256	278	294	306	318	329	342	354	366	375	395	416	432	441	449	457	**462**									
1		*22*	157	209	242	263	288	305	323	337	353	365	380	393	402	415	424	433	441	447	452	457	462	**465**								
0		*23*	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--							
1		*24*	133	166	189	213	227	241	257	271	280	289	310	320	329	336	344	359	364	373	379	386	394	402	411	**417**						
1		*25*	119	163	191	221	240	259	273	287	299	313	325	336	346	358	368	378	388	399	409	417	429	441	450	457	**464**					
1		*26*	127	171	191	208	229	252	264	278	286	298	311	320	330	341	352	359	366	376	383	391	398	405	413	423	430	**435**				
0		*27*	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--			
0		*28*	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--		
0		*29*	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	
2		*30*	114	156	182	201	220	241	256	268	279	289	301	312	321	330	339	349	358	366	375	383	391	399	407	412	417	422	426	430	434	**437**

Figure 2. Number sampled (*n*), estimated capture age, and back-calculated size-at-age of Lake Whitefish from Clear Lake, ME. Bolded values indicate the mean measured captured length (mm) of fish (*n*) sampled for estimated capture age.

values among young and old fish (Fig. 3A). We observed that back-calculated lengths-at-age varied nearly 100 mm in age-1 total length. Variability in length-at-age increased with increasing age. Back-calculated lengths-at-age demonstrated that older fish were also the slowest growing individuals, exhibiting smaller lengths-at-age in comparison to younger cohorts. This finding may result in an underestimate of mean *K* and/or an overestimate of mean length-at-age (L_t), which are otherwise useful in describing the average growth pattern of a population.

Table 2. Mean total length and mass, numbers of males and females, and mean (± SD) L_∞ and *K* growth parameters of 3 age groups among Lake Whitefish sampled in Clear Lake, ME. Superscripted letters identify significantly different L_∞ and *K* parameters among age groups from a Tukey post-hoc test.

Age group	Average total length (mm)	Average mass (g)	# of males	# of females	$L\infty$ ± SD (mm)	*K* ± SD
8–10	400.2	678.8	11	9	457 ± 36^A	0.218 ± 0.038^A
11–15	453.0	1048.5	5	10	496 ± 36^B	0.146 ± 0.019^B
>15	446.5	988.7	14	8	501 ± 27^B	0.106 ± 0.032^C
All individuals	433.6	905.5	30	27	484 ± 38	0.156 ± 0.058

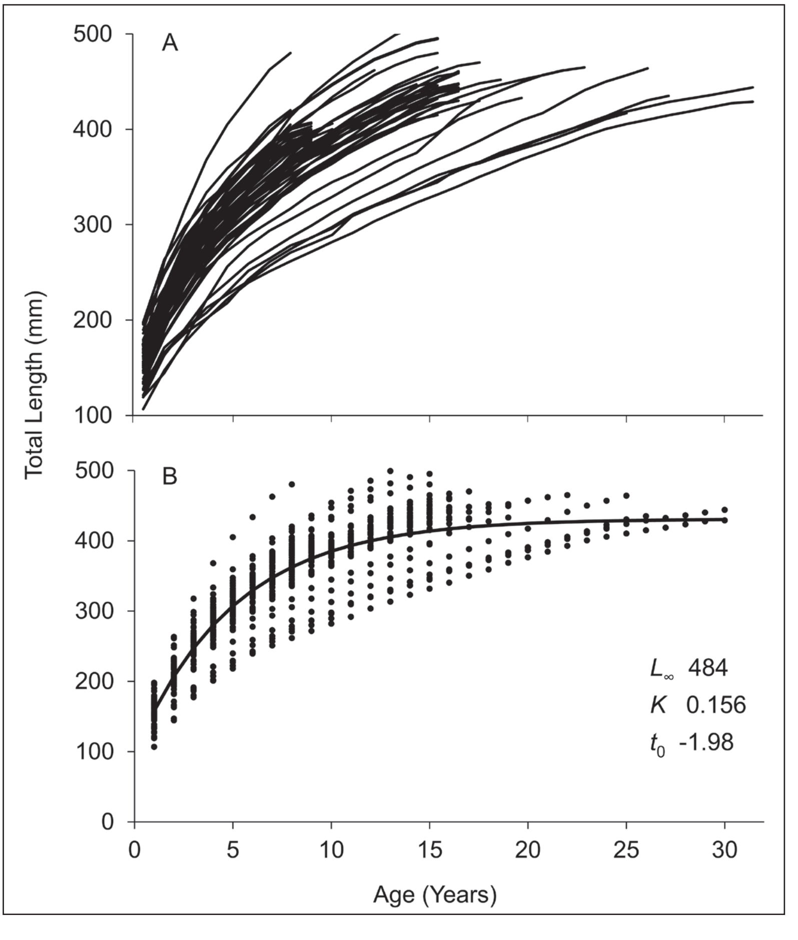

Figure 3. Sampled Lake Whitefish from Clear Lake, ME, depicting (A) length-at-age growth trajectories using Fraser–Lee back calculation and (B) back-calculated lengths-at-age and von Bertalanffy growth curve describing the average growth (all sampled fish) with associated parameters.

Growth model

The predicted total length (mm) was described by the VBGF as

$L_t = 484(1 - e^{-0.156[t - 1.98]})$.

When we plotted back-calculated lengths-at-age along with the VBGF curves, the influence of older and slower-growing fish was evident (Fig. 3B).

Mean L_∞ and K parameters differed across the 3 age categories ($P < 0.05$; Table 2). Tukey post hoc comparisons of the 3 categories indicated that the 8–10 y-old group (L_∞ = 457 ± 36 mm) had a lower asymptotic length when compared to the 11–15-y-old group (L_∞ = 496 ± 36 mm) and the >15-y-old group (L_∞ = 501 ± 29 mm). Tukey post hoc comparisons indicated that all age groups differed from one another in growth coefficients (Table 2). We also observed a strong negative relationship between K and estimated age-at-capture ($n = 57$, $R^2 = 0.723$, $P < 0.05$; Fig. 4). Conversely, we observed a modest positive relationship between L_∞ and estimated age-at-capture ($n = 57$, $R^2 = 0.178$, $P < 0.05$; Fig. 4).

Discussion

Few studies have examined unexploited or lightly exploited populations of Lake Whitefish in their native range (see Healey 1975, Johnson 1976, Mills et al. 2004 as examples). We examined the age and growth of Lake Whitefish in a small oligotrophic lake in northern Maine by estimating growth parameters for a population experiencing relatively little exploitation and perturbation. Our results can inform management agencies regarding the growth dynamics of Lake Whitefish to aid in

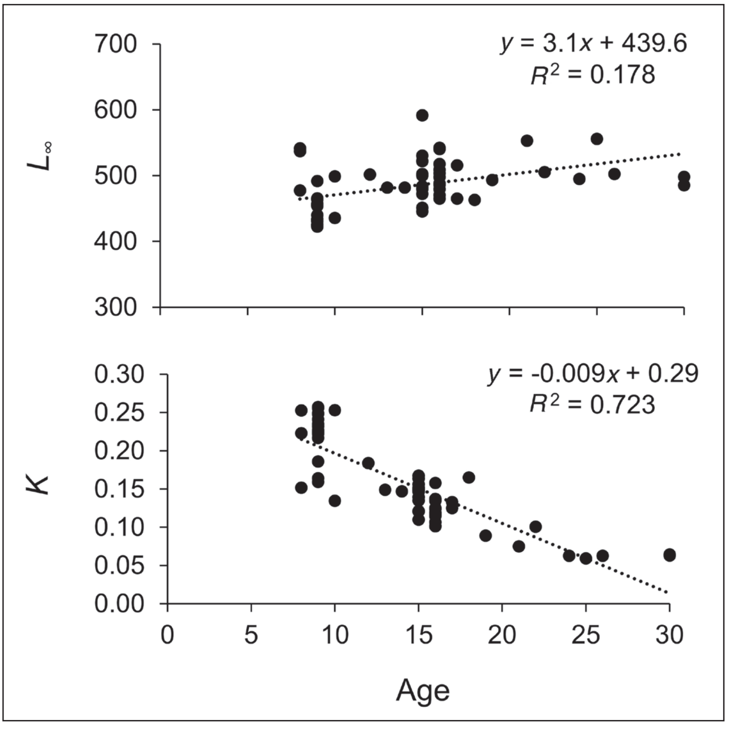

Figure 4. Linear regressions with associated equations and R^2 comparing L_∞ and K von Bertalanffy growth parameters with the estimated age-at-capture for all sampled Lake Whitefish in Clear Lake, ME. $P < 0.05$ for both regression analyses, which indicated a nonzero correlation.

developing fisheries-management plans by serving as a reference for commercially exploited stocks.

Our VBGM demonstrated a general pattern seen in many fish populations, whereby rapid growth in early life stages resulted in earlier maturity, faster decline in growth rate (high K), and decreased life span compared to slower-growing individuals (Alm 1959, Beverton and Holt 1959, Hutchings 1993). Our estimates of average L_∞ and K values (484 mm and 0.156 respectively) were consistent with reported values for a nonnative unexploited population of Lake Whitefish (L_∞ = ~500 mm; K = 0.14–0.15; Hosack and Hansen 2014) and observed growth patterns for native unexploited populations (Healey 1975, Mills et al. 2004) as well as exploited populations or stocks that are commercially fished (L_∞ = ~500–800 mm, K = 0.12–0.84; Bronte et al. 2003, Chu and Koops 2007, Cook et al. 2005, Zhu et al. 2016). In theory, estimates of K among exploited populations may be higher than for unexploited populations because larger, older fish are generally harvested first.

We observed a maximum age of 30 y, which is consistent with other observations of longevity in this species (Barnes and Power 1984, Herbst et al. 2011, Mills et al. 2004). In contrast, studies of commercially exploited populations in the Great Lakes generally estimated lower maximum ages varying from 5 y to 10 y (Cook et al. 2005, DeBruyne et al. 2008, Healey 1978); however, older fish (17–20 y old) are occasionally harvested (Bronte et al. 2003, Schorfhaar and Schneeberger 1997). Harvest has the potential to shape the size structure and sustainability of a fishery (Post et al. 2002). Lake Whitefish from Clear Lake may mature later, live longer, and defer growth at older ages, compared to exploited populations that may grow quickly and reach sexual maturity earlier at a smaller size (sensu Healey 1975).

We observed substantial variation in length-at-age among individual fish, demonstrated by a wide age-distribution and growth trajectories of individuals that diverged with increasing time at large (Table 2, Fig. 3A). Based on our VBGF trajectories, size estimates for early age classes (i.e., 1–5 y) derived from older fish at capture were markedly smaller (and had a lower growth coefficient; K) than those derived from fish captured at a younger age. Although this finding suggests differences in the growth trajectories of fish based on longevity, it is important to consider the possibility of this difference being an artifact of our sampling. Similar observations a have been attributed to Lee's phenomenon, a pattern in which back-calculated lengths are smaller than actual lengths, caused by increased error in older fish age (Duncan 1980, Schirripa 2002). Thus, our estimated growth trajectories for older fish may need to be interpreted with caution. Cautions withstanding, our regression analyses revealed a marked decrease in K with age-at-capture and an increase in L_∞. Such observations were congruent with the hypothesis that longer-lived individuals grew slower and may have an increase in maximum size (Alm 1959, Beverton and Holt 1959, Hutchings 1993).

Invasive species may compete with native species. Research from Lake Erie suggests Rainbow Smelt reduced abundance and growth of Lake Whitefish through predation and competition for resources (Oldenburg et al. 2007). In Europe, species of native *Coregonus lavaretus* (L.) (European Whitefish) have depressed growth and reduced abundance due to the introduction of other congener species such as

Rutilus rutilus (L.) (Roach; Raitaniemi et al. 1999) and *Coregonus albula* (L.) (Vendace; Bhat et al. 2014). Clear Lake has an established population of Rainbow Smelt; however, the effects that population may have on recruitment and growth of Lake Whitefish is unknown. Other work has demonstrated positive relationships among prey density, growth, and survival of larval and adult Lake Whitefish (Brown and Taylor 1992, Lumb et al. 2007), which may be reduced in the presence of competing invasive species.

Size and age structure are critical components used to make informed decisions regarding fisheries management (Pope et al. 2010). Our study described the age and growth of a lightly exploited population of Lake Whitefish in a small Maine lake. Our work complements existing studies that examined lightly exploited or unexploited populations (e.g., Healey 1975, Hosack and Hansen 2014, Johnson 1976, Mills et al. 2004). In addition, our work directly allows comparisons to populations that are exploited commercially (e.g., the Great Lakes; DeBruyne et al. 2008, Rennie et al. 2009, Wang et al. 2008), or in the process of recovery (Herbst et al. 2011). Quantifying age and growth parameters for Lake Whitefish can aid with the development of informed strategies for the conservation and management of populations and stocks.

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