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ARTICLE

Size and Age Structure of Anadromous and Landlocked Populations of Rainbow Smelt

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Abstract

Rainbow Smelt *Osmerus mordax* are widely distributed in both anadromous and landlocked populations throughout northeastern North America; abundance, size at age, and maximum size vary widely among populations and life histories. In the present study, size at age, von Bertalanffy growth parameters, population age distributions, and precision and bias in age assessment based on scales and sectioned otoliths were compared between ecotypes and among populations of Rainbow Smelt. To compare the ecotypes, we collected spawning adults from four anadromous and three landlocked populations in Maine during spring 2014. A significant bias was identified in only one of four scale comparisons but in four of seven otolith comparisons; however, a comparable level of precision was indicated. Anadromous populations had larger and more variable size at age and von Bertalanffy growth parameters than landlocked fish. Populations were composed of ages 1–4; six populations were dominated by age-2 or age-3 individuals, and one population was dominated by age-1 fish. These data suggest the presence of considerable plasticity among populations. A latitudinal gradient was observed in the anadromous Rainbow Smelt, which may show signs of population stress at the southern extent of their distribution.

Rainbow Smelt *Osmerus mordax* are widely distributed throughout northeastern North America and are targeted by commercial and recreational fisheries. Rainbow Smelt are a major food source for other piscivores (Havey 1973; Sayers et al. 1989). They have a short life cycle and high fecundity, often resulting in highly variable abundance (Gorman 2007; Stritzel Thomson et al. 2011). Populations of Rainbow Smelt exhibit flexibility in life history strategies, either as anadromous fish along the coast or as landlocked fish in cold lakes (Nellbring 1989). Anadromous populations of Rainbow Smelt were once found along the coast from Labrador, Canada, to

New Jersey, USA, but they have experienced a northward range contraction of 500 km in the last 200 years and currently are only abundant from Maine northward (Scott and Crossman 1973). This is likely attributable to a suite of anthropogenic perturbations, including pollution, loss of spawning habitat, and fishing pressure, as this region is one of the most heavily developed areas of North America (McKenzie 1947; Brown and Taylor 1995; Fuda et al. 2007).

Within Maine, landlocked Rainbow Smelt occur naturally in a few lakes along coastal areas that were accessible at the end of the last ice age (~13,000 years ago). In contrast to the

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anadromous populations, landlocked populations have proliferated in recent times (Nellbring 1989; Franzin et al. 1994; Hrabik and Magnuson 1999). They have spread throughout the Great Lakes and in many smaller waters within the Hudson Bay and Mississippi River watersheds as the result of intentional and unintentional introductions (Kendall 1918; Evans and Loftus 1987; Mercado-Silva et al. 2006). Introduced fish are often the progeny of anadromous adults; no distinction has been made regarding the success of stocking from anadromous versus landlocked sources (Bridges and Hambly 1971). The Rainbow Smelt's range expansion to new lakes has been associated with significant ecological and economic impacts (Havey 1973; Hrabik et al. 1998). Rainbow Smelt can out-compete some native species, such as the Yellow Perch *Perca flavescens* and Cisco *Coregonus artedii*, while simultaneously providing forage for other native and introduced species, such as Atlantic Salmon *Salmo salar* and Pacific salmon *Oncorhynchus* spp. (Hoover 1936; Havey 1973; Hrabik et al. 1998).

Both anadromous and landlocked Rainbow Smelt exhibit sexual dimorphism, with females being longer lived and having larger sizes at age than males (McKenzie 1958; Bailey 1964). In many populations, the males mature 1 year earlier than the females (McKenzie 1958, 1964; Nellbring 1989). Age of maturation can vary among populations of Rainbow Smelt, as some populations are dominated by age-1 spawners, while other spawning runs comprise individuals of ages 2–4 (McKenzie 1958; Murawski and Cole 1978). The Rainbow Smelt is an iteroparous species, and individuals as old as age 8 have been identified (Bailey 1964; Kirn and Labar 1996). These differences in age at reproduction and longevity are tied to the wide range of body sizes that occur both within and among populations, with important implications for the number of eggs produced because of the exponential relationship between size and fecundity (Beckman 1942; McKenzie 1958, 1964; Rupp and Redmond 1966; Kirn and Labar 1996; Feiner et al. 2015). There exists a large difference in growth potential between the highly productive marine environment that is exploited by the anadromous fish and the oligotrophic lakes in which landlocked populations reside (Rupp 1959; Murawski and Cole 1978).

The differences in size, age, and longevity of Rainbow Smelt from different populations can be important considerations when managing these fish as a prey base or for commercial exploitation. There is a need for an informed choice on which anatomical structure (e.g., scales or otoliths) is the best for use in specific age and growth studies, as accuracy and precision can vary between structures and among populations (Brooks et al. 1994; Sepulveda 1994; Volk et al. 1994; Campana 1999; Walsh et al. 2008). Measurements of age and growth should be precise, accurate, and easily obtained to allow researchers and managers to make the best possible decisions (Secor et al. 1991; McBride 2015). We estimated age from scales and sectioned otoliths to find the more precise

and accurate method for aging Rainbow Smelt. In addition, we compared Rainbow Smelt growth, maximum size, and age structure between and among anadromous populations, which are experiencing heavy declines in the southern portion of their range, and landlocked populations in Maine, which are heavily exploited for forage and commercial purposes.

METHODS

Anadromous fish collections.—Anadromous Rainbow Smelt were captured from four coastal streams with naturally occurring spawning populations: Mast Landing, Deer Meadow Brook, Tannery Brook, and Schoppee Brook (Table 1). The study streams are separated from each other by 70–100 km and span the coast of Maine. We considered the fish in each stream to be a separate spawning population, although the only barrier to movement between locations was distance. The fish were collected with fyke nets (7-mm mesh, 1- × 1-m mouth; two 1- × 1-m wings) deployed in the intertidal zone near the mouth of each brook. The nets were set mid-channel with the net opening facing downstream. Nets were checked during morning low tide to record the catch during the previous high tide on three consecutive days per week for the duration of the 2014 spawning season and were closed for the remainder of the week (Table 1). These fyke nets are operated annually as an established long-term monitoring project for Rainbow Smelt (C. Enterline, unpublished data). Fish TL was recorded from the first 100 males and first 100 females each day, and a count was made of all remaining individuals. A subsample of up to 15 fish per sex was sacrificed and frozen from each of three size bins (<15, 15–20, and >20 cm TL) based on presumed ages from previous work (Enterline, unpublished data), allowing for up to 90 Rainbow Smelt collected per population and stratified throughout the run (Table 1).

Landlocked fish collections.—We collected landlocked Rainbow Smelt from three lakes: Wyman, Rangeley, and Richardson. All three lakes are large oligotrophic systems in western Maine (Table 2). Rangeley and Richardson lakes are both part of the Androscoggin River watershed but are separated by enough distance (23 km and another lake) that the two populations are assumed to be isolated from one another. Rainbow Smelt became established in these lakes in around 1900 from an undocumented source (Cooper 1940). Wyman Lake is a reservoir that was created in the Kennebec River watershed during the 1930s and is isolated from the other two lakes. Rainbow Smelt were likely naturally established in Wyman Lake in approximately the 1950s from other upstream landlocked populations (R. VanRiper, Maine Department of Inland Fisheries and Wildlife [MDIFW], unpublished data). Fish collection at each lake took place in a single tributary just upstream from the lake. Fish were dipnetted on one to three consecutive nights near the peak of the spawning run during spring 2014 and were transported to a hatchery as broodstock (Table 2). After spawning at the

TABLE 1. Counts of anadromous Rainbow Smelt sampled from four coastal streams in Maine, including the dates and number of fish sampled. The fish used for the age and growth analysis are categorized by sex (M = male; F = female; U = immature/unknown) and size bin (mm TL).

Population and letter code	Coordinates	Sample dates	Sex	Number aged by size			Total number measured
				<150 mm	150–200 mm	>200 mm	
Mast Landing (A)	43.858°N, 70.085°W	Apr 15–May 20	M	20	3	5	65
			F	15	1	2	31
			U	2	0	0	4
Deer Meadow (B)	44.033°N, 69.587°W	Apr 14–May 29	M	12	18	11	393
			F	7	17	7	50
			U	5	0	0	5
Tannery Brook (C)	44.571°N, 68.789°W	Apr 15–Jun 19	M	18	16	2	500
			F	18	17	6	223
			U	2	0	0	2
Schoppee Brook (D)	44.663°N, 67.553°W	Apr 29–Jun 26	M	15	21	11	1,009
			F	2	16	20	532
			U	0	0	0	172

hatchery, all Rainbow Smelt were frozen in batches of 10–20 individuals, which were sampled by utilizing all individuals in a bag until a total of 200 fish/site was reached.

Length correction.—After the Rainbow Smelt were defrosted, fish were sexed and measured for TL and SL. Total length of fish decreased by approximately 5% after freezing ($n = 58$, $r^2 = 0.996$, $P < 0.01$). The pre-freezing TL was used for the computations described throughout the remainder of this paper. If the pre-freezing TL was missing, it was estimated from the postfreezing SL by using a simple linear regression ($n = 792$, $r^2 = 0.994$, $P < 0.01$).

Otolith removal, preparation, and reading.—Sagittal otoliths were removed by cutting through the gill isthmus and then breaking through the prootic bone to remove the sagittae (Secor et al. 1991). Otoliths were cleaned with a 10% sodium hypochlorite (bleach) solution to remove soft tissue, were placed in deionized water to remove the bleach,

and then were allowed to dry (Secor et al. 1991). Otoliths were mounted in a two-part epoxy for sectioning (Epo-Fix; Electron Microscopy Sciences). An approximately 0.3-mm-thick transverse section encompassing or close to the primordium was taken from each otolith by using a low-speed saw (IsoMet; Buehler). The sections were mounted on microscope slides with thermoplastic glue (Crystalbond; Structure Probe); they were imaged with a digital camera (Spot Insight 2; Spot Imaging Solutions) attached to a stereo microscope (EMZ-13TR; Meiji Techno) and were viewed under transmitted light at 30× magnification. Immersion oil was used to improve the contrast of the otolith and to obviate sanding. When possible, the left otolith was used for all fish ($n = 726$), but if that otolith was damaged or unreadable, then the right one was used ($n = 118$). If neither otolith was readable, the fish was excluded from the growth analysis ($n = 3$). The otoliths displayed two distinct regions of growth

TABLE 2. Counts of Rainbow Smelt from landlocked populations that were sampled from tributaries to three lakes in Maine during spring 2014. Included are lake area, maximum (max) lake depth, sampling dates, the number of fish that were aged (M = male; F = female; U = immature/unknown), and the number of fish that were measured for TL (mm).

Population and letter code	Coordinates	Area (ha)	Max depth (m)	Sample dates	Sex	Number aged	Total number measured
Wyman (E)	45.088°N, 69.936°W	736	42.7	Apr 27–29	M	95	95
					F	78	78
					U	0	0
Rangeley (F)	44.946°N, 70.683°W	2,550	45.4	May 6	M	89	103
					F	75	75
					U	0	197
Richardson (G)	44.857°N, 70.869°W	3,137	33	May 5	M	106	134
					F	81	82
					U	0	272

when viewed under transmitted light: a wide, opaque continuous zone that corresponded to summer growth; and a narrow, translucent, discontinuous zone representing winter growth (Figure 1). Each pair of continuous and discontinuous zones represented one complete year of growth. We measured each annual growth increment to the outer edge of the discontinuous zone, which was assumed to correspond with the onset of spring growth. The fish were captured early in the spring and did not show a partial growing season, so the margin was assumed to be a completed annulus. Each otolith was aged by two readers, and measurements of annual growth were made with ImageJ version 1.48 (National Institutes of Health, Research Services Branch). The annual growth increments were measured along a straight line from the centrum to the dorsal margin of the otolith and were

calibrated by using a stage micrometer (Figure 1). The number of increments that were measured corresponded to the consensus age of the fish as described later.

Scale reading for anadromous fish.—In addition to reading otoliths from anadromous fish, scales were also read. Scales were cleaned in a sonicator (Model 32V118; Lab Safety Supply) while immersed in a 5% pancreatin solution (Now Foods, Bloomingdale, Illinois) as described by Whaley (1991). Scales were mounted on glass slides with a cover slip and were read under a microscope with transmitted light (Figure 1). Scale age analysis followed the methods of McKenzie (1958), with “shiny lines” and incomplete circuli used as the primary indicators of annuli.

Assignment and analysis of ages.—All scales and otoliths were examined independently by the same two readers. The

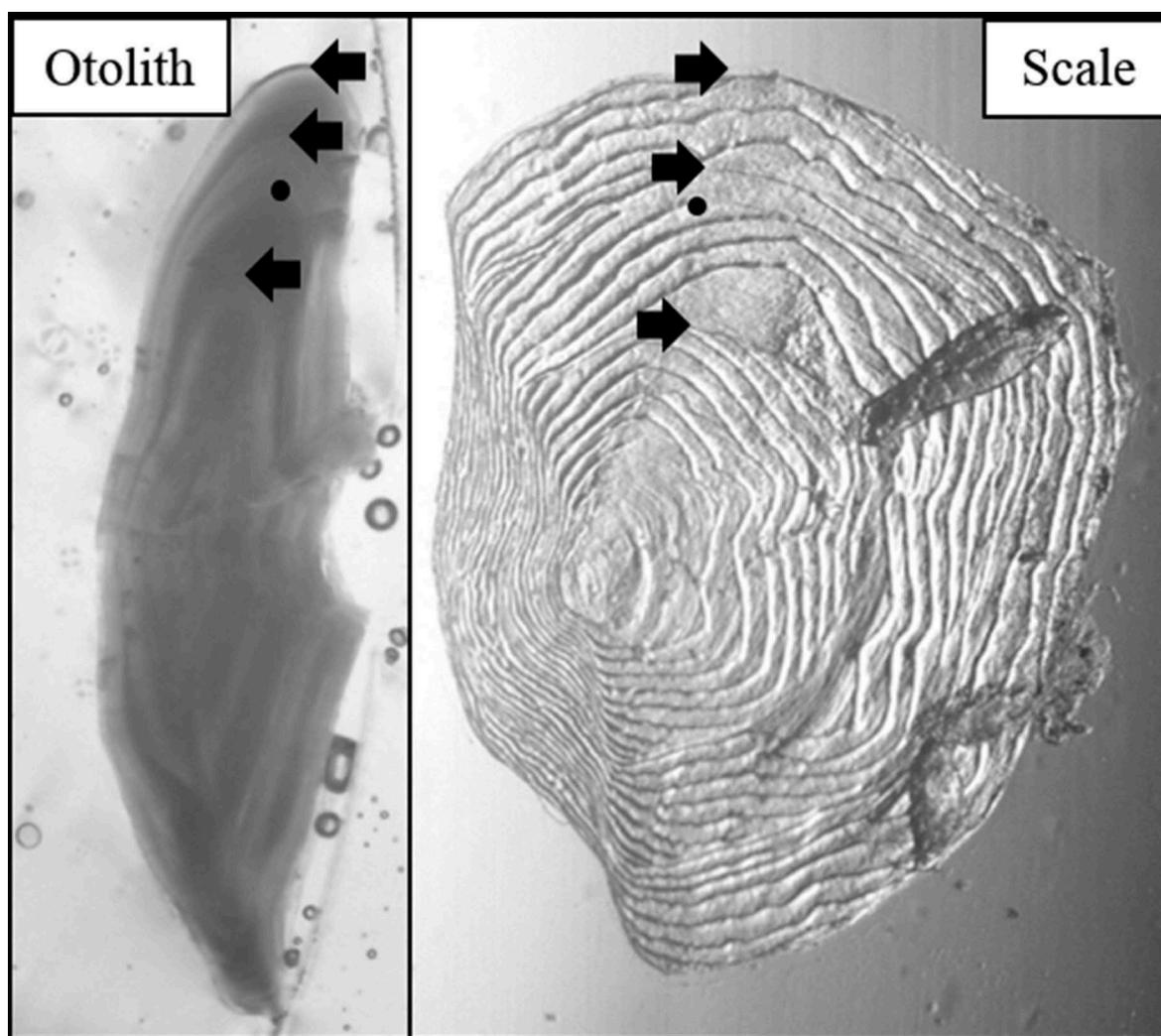


FIGURE 1. Example transverse otolith section (left) and scale (right) from a selected age-3 Rainbow Smelt sampled from Deer Meadow Brook, Maine. The three arrows in each picture correspond to the annuli, and the black dots correspond to false annuli. The otolith is oriented with the dorsal margin up and the sulcus to the right of the image. The scale is oriented with the anterior end to the right of the image. Images have been resized to fit and are not at the same magnification.

readers were novices in analyzing Rainbow Smelt otoliths, but each had at least 2 years of experience in reading otoliths of other species. Reader 1 had over 5 years of experience in reading scales from Rainbow Smelt, whereas reader 2 had over 5 years of experience in reading scales from species other than Rainbow Smelt. The following decision tree was used to assign consensus ages to each structure (scales: $n = 271$; otoliths: $n = 846$) separately as well as a consensus age to each fish ($n = 854$), which was used in lieu of a known age: if all four assigned ages matched (both readers agreed on both scales and otoliths; $n = 147$) or if three of four ages matched and the remaining age differed by no more than 1 year ($n = 65$), then the fish was given a consensus age matching the majority of the assigned ages. If only one structure was present and the two readers agreed on the age, then that age was used as the consensus age for the fish (otoliths: $n = 501$; scales: $n = 7$). If only one structure was present and the readers did not agree ($n = 83$), the consensus age was reached by discussion between the readers. If both scales and otoliths were aged and two or more of the assigned ages differed ($n = 51$), the consensus age was reached by discussion between the readers. To reach an informed decision, these discussions involved comparing the individual's population, length, and sex against the characteristics of other fish that had high agreement between readers and structures.

Comparison of scale ages against otolith ages utilized only those fish for which both readers assigned the same age to each structure during the initial read ($n = 168$). Comparisons between the two readers and against the consensus age of the fish (in lieu of true age) used the ages of all fish, including those for which readers reached agreement with initial aging ($n = 720$) and by discussion ($n = 134$). These comparisons of precision and bias were conducted using FSA version 0.8.4 (D. Ogle, Northland College, personal communication; available at www.fishr.wordpress.com/fsa/) within R version 3.2.0 (R Core Team; available at www.r-project.org). Precision and bias between readers for a given structure and between scales and otoliths were examined by using the average coefficient of variation (ACV) for precision and a Bowker's test of symmetry for bias (Bowker 1948; Chang 1982). The critical value for a statistical difference was set at $P \leq 0.05$ for bias; ACVs less than 5.0% indicated precision (McBride 2015).

Size at age and von Bertalanffy growth.—We estimated individual size at age for both anadromous and landlocked Rainbow Smelt via the Fraser–Lee back-calculation method, and the results were rounded to the nearest millimeter (Lee 1920). Growth trajectories for size at age (L_t) were estimated for each population by using a von Bertalanffy growth function (von Bertalanffy 1938) expressed as

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

Three parameters—asymptotic length (L_∞), theoretical age at zero length (t_0), and growth coefficient (K)—were estimated for males and females of each population and were compared by using a log likelihood ratio test for differences. These parameter estimates were obtained by using the “growth” function within Fishmethods version 1.7-0 for R software (G. Nelson, Massachusetts Division of Marine Fisheries, personal communication; available at www.cran.r-project.org/web/packages/fishmethods).

Bayesian mixture models of age-class contribution to spawning.—The aged Rainbow Smelt were just a subsample of individuals that were captured and measured from each of the anadromous and landlocked populations. The distribution of sizes for all measured fish was different from the size distribution for the aged subsample. We used a Bayesian mixture model to estimate the proportions by age of all captured fish. The TL distribution of the population was modeled as a weighted mixture of the observed age-classes as

$$f(y) = \sum_1^i \pi_i f_i(y),$$

where π_i is the age-class proportion and $f_i(y)$ is the TL probability density function for each age-class observed. The mixture model was implemented in a Bayesian framework using MixDist version 0.5-4 for R software (P. Macdonald and J. Du, McMaster University, personal communication; available at www.cran.r-project.org/web/packages/mixdist). Model parameters were the mean (μ_i) and SD (σ_i) for each age-class i and the proportion of the measured fish belonging to each age-class (π_i). Two populations had a single age-1 individual, so the mean SD for age 1 from the other populations was used as a prior. Uncertainty for each parameter was characterized by an estimated 95% credible interval. Parameters were estimated with an expectation maximization algorithm.

RESULTS

Precision and Bias between Readers and between Structures

First, we combined all populations and tested for a bias between scales and otoliths by using only those fish with initial reads that were in agreement between the two readers. We found a statistical bias ($n = 168$, ACV = 2.9%, $P = 0.03$) wherein the readers tended to underestimate the age from scales in comparison with estimates from otoliths for age-3 and older fish (Figure 2). We then tested for a bias between readers by using the ages assigned during initial reads to scales ($n = 263$, ACV = 2.3%, $P = 0.04$) and otoliths ($n = 834$, ACV = 5.0%, $P < 0.01$). A similar bias between readers was seen for both otoliths and scales but was stronger for otoliths, suggesting that agreement between readers was greater for scales than for otoliths (Figure 3).

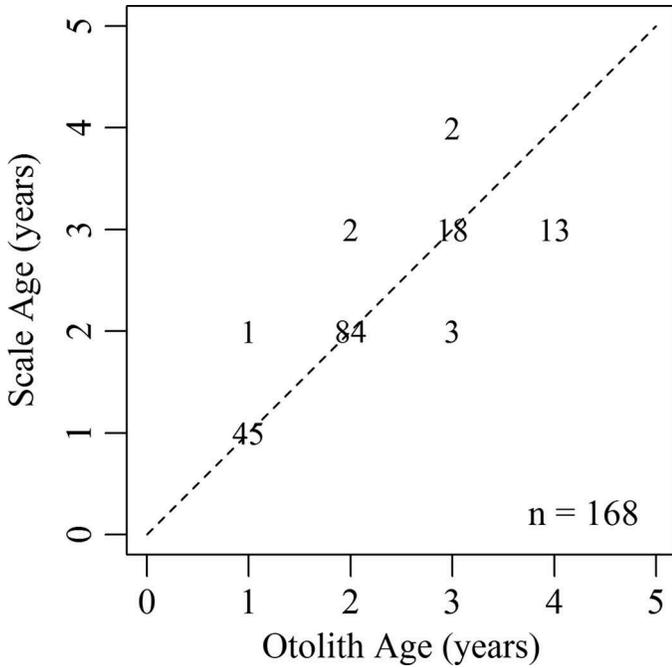


FIGURE 2. Age bias plot for scale ages and sectioned otolith ages estimated for anadromous Rainbow Smelt. Only data from fish for which the initial ages matched between the two readers are presented. The dashed line represents the 1:1 line for agreement between ages. Numbers represent the number of observations for each age combination.

After identifying an overall bias between readers, we assessed the bias in ages between readers for each population by using a Bowker’s test. Despite the smaller sample size, a bias between readers was detected ($P < 0.05$) in one of four comparisons for scales, three of four comparisons for otoliths of anadromous fish, and one of three comparisons for otoliths of landlocked fish (Table 3). Precision was measured by comparing the initial reader ages to the consensus age for the fish, as determined from (1) examining scales and otoliths from each fish when both structures were available or (2) by discussion if only one structure was available and the initial readings did not agree. Precision was generally high (0.0–7.5% ACV), with only 4 of 22 comparisons having an ACV greater than 5% between the initial reader age and the consensus age (Table 3; McBride 2015). All comparisons with low precision were from anadromous fish—one from scales and the other three from otoliths. Precision was highest on average for otoliths from landlocked fish, followed by scales from anadromous fish and finally by otoliths from anadromous fish.

Back-Calculated Growth

Size at age was back-calculated by using the intercept-corrected proportional method. The slope was estimated as 0.0073 mm and the intercept was estimated as 0.241 mm based on the ratio of otolith radius to total body size from

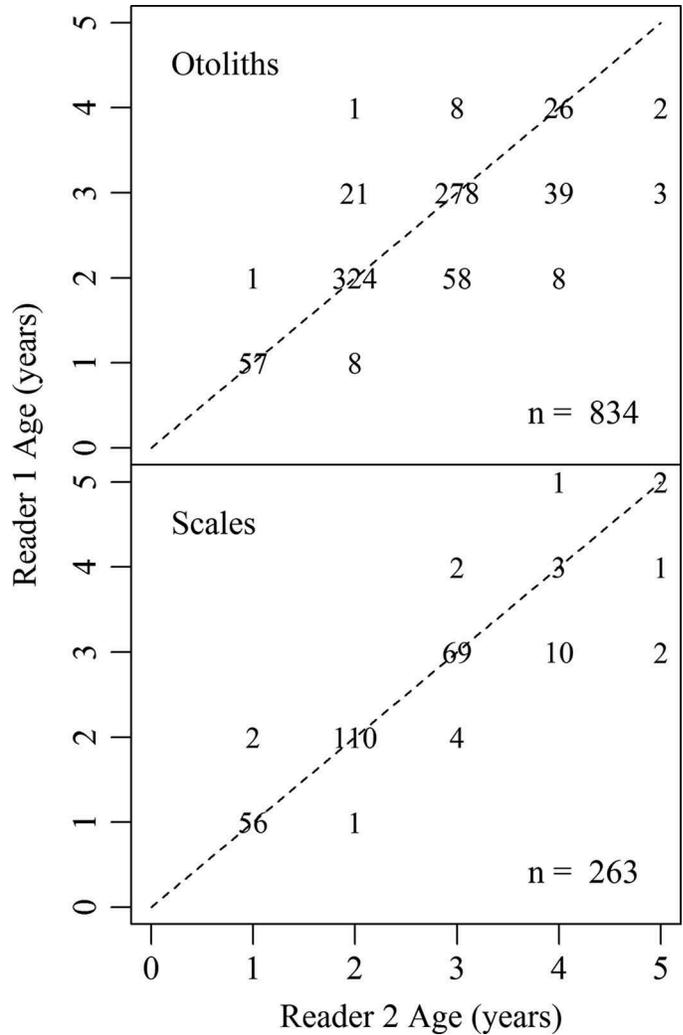


FIGURE 3. Age bias plots for initial scale and otolith age estimates produced by two readers examining samples from seven populations of Rainbow Smelt (anadromous and landlocked) in Maine. The dashed line represents the 1:1 line for agreement between ages. Numbers represent the number of observations for each age combination. Reader biases showed a similar pattern for individual populations.

846 Rainbow Smelt ($r^2 = 0.843$, $P < 0.001$). Variation in size at age was observed both among populations and between ecotypes, with a greater and more variable size at age in anadromous fish than in individuals from landlocked populations. For each population, the mean back-calculated sizes at age agreed closely with observed sizes for ages 2–4. Observed and calculated sizes at age 1 exhibited a larger departure, with a mean of 15.6 mm. Three of the anadromous populations had very similar growth trajectories, whereas the most southerly anadromous population had a much more asymptotic growth trajectory and a similar size at age 4 (Table 4). In contrast, the three landlocked populations showed variation in size at age 1, and the relative magnitude of the differences was maintained throughout all age-classes observed (Table 4).

TABLE 3. Tests of symmetry and bias in age estimates from two readers examining scales and otoliths from Rainbow Smelt belonging to anadromous and landlocked populations in Maine (population codes are defined in Tables 1 and 2). Bowker's test of symmetry examined for bias between readers. The average coefficient of variation (ACV) between each reader and the consensus age for the fish is also presented. Asterisks denote the significance level ($*P < 0.05$; $**P < 0.01$).

Structure	Population code	Bowker's test (P)	ACV (%)		Sample size
			Reader 1	Reader 2	
Anadromous populations					
Scales	A	0.317	1.9	3.7	51
	B	0.416	5.0	3.4	69
	C	0.135	0.3	1.4	67
	D	0.030*	5.9	4.4	76
	Average		3.3	3.2	66
Otoliths	A	0.513	1.9	0.0	48
	B	0.025*	5.7	7.5	76
	C	0.006**	3.0	4.7	79
	D	<0.001**	4.6	6.1	85
	Average		3.8	4.6	72
Landlocked populations					
Otoliths	E	<0.001**	3.7	2.3	164
	F	0.083	1.5	2.6	198
	G	0.102	0.8	0.1	184
	Average		2.0	1.7	182

Von Bertalanffy Growth Modeling

Back-calculated sizes at age produced growth trajectories that were used to fit von Bertalanffy growth models for males and females from each population, and the models were tested for statistically significant differences ($P < 0.05$) using stepwise model selection. The growth models differed significantly

between males and females in two of the four anadromous populations (Mast Landing: $P = 0.03$; Tannery Brook: $P = 0.04$) but none of the three landlocked populations (Table 5). Although a statistical difference was found in only two of seven comparisons, the estimated L_{∞} was larger for females than for males in all seven populations. The parameter estimates for the four anadromous populations were very similar to one another; parameters for two of the landlocked runs (Rangeley and Richardson lakes) were similar, whereas parameters for the third landlocked run (Wyman Lake) were intermediate to those of the anadromous and the landlocked populations (Table 5).

Run Proportion by Age

The Rainbow Smelt that were used in age analysis constituted a small subsample of the fish collected from each population. Using the body sizes and assigned ages from that subsample, we employed a mixture model to estimate the proportional contribution of each age-class to their respective populations. This was done for all populations except the Wyman Lake population, for which no additional fish were measured, so the proportional contribution of each age-class was assumed to reflect the contributions occurring in the population. The model was constrained by forcing the mean size at age to fit a von Bertalanffy growth curve. Most populations predominantly comprised individuals of age 2 or age 3, which constituted 78–98% of the observed fish in each run for six of the seven populations. The outlier was an anadromous population (Mast Landing) that was dominated by age-1 fish (89%), whereas this age-class only contributed 0–10% of the other six populations. Age-4 and older fish made up a small part of the run (Figure 4).

DISCUSSION

There was a notable difference in the clarity and readability of otoliths from different Rainbow Smelt populations despite

TABLE 4. Mean observed (Obs.) and calculated (Calc.) sizes (TL, mm) from von Bertalanffy modeling for age-1–4 Rainbow Smelt belonging to anadromous and landlocked populations in Maine (population codes are defined in Tables 1 and 2). Dashes indicate that no fish of the specified age were observed. Asterisks denote significant differences between observed and calculated sizes at age ($*P < 0.05$; $**P < 0.01$).

Population code	Age 1		Age 2		Age 3		Age 4	
	Obs.	Calc.	Obs.	Calc.	Obs.	Calc.	Obs.	Calc.
Anadromous populations								
A	135	134	198	185	216	200	216	216
B	111	94**	158	153	190	187	208	208
C	100	75	145	146	185	185	208	208
D	105	96	168	161	200	192	215	215
Landlocked populations								
E	111	85*	137	129**	153	153	180	180
F	–	66	121	118**	127	126	130	130
G	–	52	100	92**	106	106	114	114

TABLE 5. Estimated von Bertalanffy growth parameters for Rainbow Smelt belonging to anadromous and landlocked populations in Maine (population codes are defined in Tables 1 and 2). Estimates (\pm SE) of asymptotic length (L_{∞}), growth coefficient (K), and theoretical age at zero length (t_0) are presented. Models were run for females (F), males (M), and all fish combined (A). Asterisks denote significant differences between sexes within a given population ($*P < 0.05$).

Population code	Sex	L_{∞}	K	t_0	Sample size
Anadromous populations					
A	A	216 \pm 24	0.9 \pm 0.6	0.0 \pm 0.5	54
	F	301 \pm 183*	0.3 \pm 0.4*	-1.3 \pm 1.6*	22
	M	199 \pm 158*	1.7 \pm 1.2*	0.3 \pm 0.4*	30
B	A	237 \pm 25	0.5 \pm 0.1	0.1 \pm 0.1	78
	F	238 \pm 32	0.5 \pm 0.2	0.0 \pm 0.2	31
	M	237 \pm 37	0.5 \pm 0.2	0.1 \pm 0.2	42
C	A	231 \pm 24	0.6 \pm 0.1	0.4 \pm 0.1	79
	F	250 \pm 36*	0.5 \pm 0.2	0.3 \pm 0.1	41
	M	199 \pm 23*	0.8 \pm 0.3	0.4 \pm 0.1	36
D	A	232 \pm 14	0.6 \pm 0.1	0.2 \pm 0.1	85
	F	240 \pm 20	0.6 \pm 0.1	0.1 \pm 0.1	38
	M	215 \pm 17	0.8 \pm 0.2	0.3 \pm 0.1	47
Landlocked populations					
E	A	186 \pm 8	0.6 \pm 0.1	-0.1 \pm 0.1	173
	F	200 \pm 17	0.5 \pm 0.1	-0.2 \pm 0.1	78
	M	177 \pm 8	0.6 \pm 0.1	0.0 \pm 0.1	95
F	A	128 \pm 3	1.8 \pm 0.3	0.6 \pm 0.1	198
	F	130 \pm 6	1.6 \pm 0.4	0.6 \pm 0.1	74
	M	126 \pm 4	2.0 \pm 0.5	0.6 \pm 0.1	89
G	A	116 \pm 3	1.0 \pm 0.1	0.4 \pm 0.0	186
	F	117 \pm 5	0.9 \pm 0.1	0.4 \pm 0.1	81
	M	115 \pm 4	1.0 \pm 0.1	0.4 \pm 0.1	105

the same handling procedures. Two of the landlocked populations had otoliths that bore a sharp transition between winter and summer growth, thereby facilitating the high degree of precision for those populations. The remaining populations displayed a gradual transition and a higher incidence of presumed false annuli, with similar low estimates of precision. Differences in seasonal transitions may be due to differences in winter feeding or seasonal temperature regimes in the water bodies, which are likely widely variable between populations (Lantry and Stewart 1993; Brooks et al. 1994; Campana and Thorrold 2001). These findings demonstrate that the precision and ease of estimating age have the potential to vary widely throughout the Rainbow Smelt's range. Because we lacked true ages for fish in our study, we used consensus ages as a proxy. If there had been a systematic bias in one of the structures, the difference in age between structures would have highlighted it (McBride 2015). Systematic biases in both structures would have canceled each other out, making the bias in each undetectable. Although the true ages of the fish were unknown, we propose that a structure with higher agreement between readers is preferable to one with lower agreement (Chang 1982; McBride 2015).

Our direct comparison of ages based on scales and otoliths obtained from the same fish identified the scale ages to have higher precision and less bias. The ability to mount and read a larger number of scales (~10 per fish were used) from each individual helped in the detection of check marks and false annuli as opposed to the single otolith used. Unfortunately, we did not collect scales from landlocked Rainbow Smelt to increase the number of populations for which this comparison was made. The high between-reader precision of otolith ages from landlocked fish suggests that a more clearly defined pattern of seasonal growth is present on the scales of these fish, but this remains to be proven. In a similar study, Walsh et al. (2008) found whole otoliths to be less precise than fin rays for age determination in Rainbow Smelt. In our study, sectioned otoliths were identified as being less precise than scales. Thus, in both studies, alternative structures were more precise than otoliths. Collection of scales is a less-invasive procedure than fin ray removal or otolith extraction, the latter of which requires sacrificing the fish (Campana and Thorrold 2001). Although Rainbow Smelt can at times be found in enormous abundance, unnecessary mortality is still a management concern, especially in regions where populations are

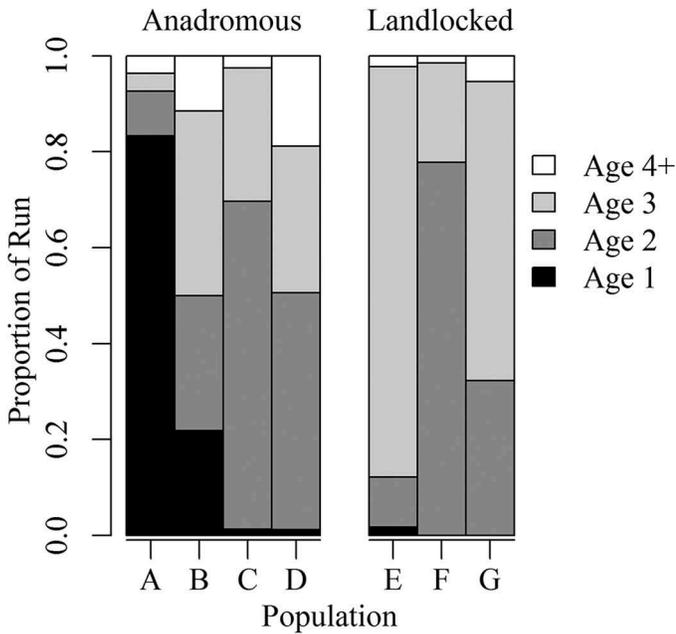


FIGURE 4. Proportional contribution of each age-class to anadromous and landlocked populations of Rainbow Smelt in Maine (population letter codes are defined in Tables 1 and 2). Proportions were estimated by applying a Bayesian mixture model based on individuals of known sizes and ages to the length distribution of unaged fish. Wyman Lake (population E) did not have any fish of unknown age, so the observed proportions are presented.

struggling, such as along southern coastal Maine (Nellbring 1989; Brown and Taylor 1995; Gorman 2007). Scales may be advantageous for direct aging, but otoliths are superior for growth analysis in many species due to the potential resorption of scales in older individuals, which can bias results (Hernandez et al. 2014).

The anadromous Rainbow Smelt populations had larger back-calculated sizes at age and greater L_{∞} values than the landlocked populations. This is consistent with the hypothesis that anadromous fish living in the more productive coastal environment have greater growth potential (Rupp 1959; Murawski and Cole 1978). The difference was great enough that not only did our fastest growing fish have larger maximum sizes, they were larger at age 1 than our slowest growing fish were at age 4. The nonlinear relationship between fish size and fecundity means that maximum size has important implications for both egg production and recruitment (McKenzie 1964; Feiner et al. 2015). Additionally, body size plays an important role in prey selection and predation risk, as individuals can become too large to be effectively preyed upon by desired sport fish and can grow large enough to be predators of other desired species (McCullough and Stanley 1981; Lantry and Stewart 1993; Kirn and Labar 1996).

The back-calculated size at age for the four anadromous Rainbow Smelt populations were similar to those reported in other studies (McKenzie 1958; Murawski and Cole 1978).

McKenzie (1958) reported a smaller average size at age for Rainbow Smelt belonging to a more northerly population (Miramichi River estuary, New Brunswick, Canada). In the Parker River estuary, Massachusetts (i.e., south of our study area), Rainbow Smelt size at age was similar to but slightly larger than that of our fastest growing population (Murawski and Cole 1978). These findings are consistent with a thermal or latitudinal gradient in Rainbow Smelt growth along the Atlantic coast from Massachusetts to New Brunswick (Morgan and Colbourne 1999).

Our back-calculated sizes at age for landlocked populations were generally smaller than those reported in the literature. Bailey (1964), Frie and Spangler (1985), Kirn and Labar (1996), and Rupp and Redmond (1966) all reported Rainbow Smelt sizes at age that were at or above the upper limit of the growth rates exhibited by landlocked populations in the present study. The two slower growing populations sampled in our study reflect the Rainbow Smelt sizes observed in many water bodies within Maine (S. Davis, MDIFW, personal communication). This discrepancy in growth rates may be due to the greater productivity of the larger, deeper water bodies examined in the previous studies (Bailey 1964; Frie and Spangler 1985; Kirn and Labar 1996) relative to our study lakes. The sizes and growth rates of Rainbow Smelt in smaller water bodies are not as frequently described, even though the number of small water bodies inhabited by this species is much greater and is likely to increase (Franzin et al. 1994; Hrabik and Magnuson 1999; Mercado-Silva et al. 2006). The differing sizes and growth rates in smaller water bodies have implications for evaluating Rainbow Smelt population persistence and invasion potential in such waters (Rupp and Redmond 1966).

Interestingly, the populations that contained the fastest growing Rainbow Smelt (Mast Landing) and the slowest growing individuals (Rangeley and Richardson lakes) had very high K -values ranging from 0.9 to 1.8. These individuals did much of their growing in the first year of life and demonstrated little sustained growth thereafter. The three anadromous populations and one remaining landlocked population displayed lower K -values of 0.5–0.6, indicating lower growth early in life but sustained growth through older age-classes. This suggests that populations are responding to the tradeoffs between somatic growth, reproduction, and survival in different ways. The populations with high K -values were dominated by age-1 and age-2 fish, whereas the populations with low K predominantly contained age-3 fish at the remaining sites. Although the different number of fish sampled from each age-class may have biased the parameter estimates, the age distributions of the anadromous populations were consistent with eight previous years of sampling, which elucidated differential survival to older age-classes between populations (Enterline, unpublished data). Mixture modeling showed that Rainbow Smelt of ages 2 and 3, which comprised 82–99% of individual runs, dominated both the anadromous and the

landlocked spawning populations. This pattern was also observed by Bailey (1964), Gorman (2007), and Murawski and Cole (1978), among others. Age-4 and older Rainbow Smelt comprise less than 18% of any population, with no clear trend between anadromous and landlocked populations. The larger overall body size of anadromous populations relative to the landlocked populations for both high and low *K*-values constitutes strong evidence that the anadromous populations experienced conditions that were more bioenergetically profitable and supported continued growth (Lantry and Stewart 1993).

Recruitment to spawning is linked to individual growth opportunity (Morgan and Colbourne 1999). Three of the four anadromous populations and one of the landlocked populations showed a difference of 9–33% between the observed and back-calculated sizes at age 1; this is commonly seen in back-calculated growth and is known as Lee's phenomenon (Lee 1920). The difference between observed and calculated sizes indicates that the age-1 fish are not fully recruited to the spawning run. Strong evidence of this was apparent from our two landlocked populations in which no mature age-1 fish were observed, lending credence to incomplete recruitment at age (Lee 1920; McKenzie 1958; Murawski and Cole 1978; Campana 1990).

As mentioned earlier, one Rainbow Smelt population (Mast Landing) was unusual in that it was dominated by age-1 fish (89%). This run occurs near the southern extent of the range of anadromous Rainbow Smelt and may reflect a transition in life history strategy to cope with warmer waters, a longer growing season, and other factors that have caused the collapse of more southerly populations (Murawski and Cole 1978; Morgan and Colbourne 1999; Fuda et al. 2007). The exceptional growth of these fish may be driving the earlier maturation compared to the other populations. The low survival to older age-classes in this population is likely linked to earlier maturation, but it is difficult to determine which effect is driving the other (Trippel 1995; Morgan and Colbourne 1999).

The Rainbow Smelt populations we studied demonstrated considerable variation in the tradeoffs between growth and reproduction. The present results indicate that anadromous fish are growing faster than their landlocked counterparts. Differences in body size are broadly driven by growth rate but may be offset by differences in survival to older age-classes, which can obscure trends in the average size of spawning fish. Landlocked Rainbow Smelt from smaller water bodies are not growing as fast as their counterparts in the Great Lakes and other very large water bodies. Our study also demonstrates that for Rainbow Smelt, scales are more easily read and have higher precision than otoliths as aging structures and can be obtained nonlethally.

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