Environ Biol Fish
DOI 10.1007/s10641-015-0403-7

Validation of a relationship between statolith size and age of larval Great Lakes sea lamprey (*Petromyzon marinus*)

Danielle D. Potts · Heather A. Dawson · Michael L. Jones

Received: 15 October 2014 / Accepted: 13 February 2015

Abstract Sea lampreys (*Petromyzon marinus*) are parasitic pests in the Great Lakes that have negatively affected game fish populations. Accurate aging of pest species such as sea lampreys can provide estimates of growth and mortality rates, which can direct control efforts. Because growth of larval sea lampreys is both slow and variable, determining age based solely on visual assessments of length-frequency distributions is subject to considerable uncertainty. Otoliths have been used to estimate age in teleosts through annuli counts and otolith size metrics. Lampreys do not have otoliths, having instead an analogous structure called a statolith. Determining age based on statolith annuli counts has been found to be imprecise and inaccurate. Therefore, we evaluated whether statolith size was correlated with ammocoete age using known-age populations of ammocoetes from two Great Lakes streams with contrasting physical conditions that affect larval sea lamprey growth. A morphometric system was used to measure length, width, and height of statoliths from these known-age populations. Statolith width was found to be the measurement that best distinguished the age-classes within the populations. A likelihood-based statistical model was used to assess ammocoete population age composition. Even though statolith width was clearly associated with age, combining statolith width data and length-frequency did not improve estimates of proportions at age relative to those estimated using only length-frequency information.

Keywords Sea lamprey · Statolith · Aging · Length-frequency analysis

D. D. Potts · H. A. Dawson (✉)
Biology Department, University of Michigan-Flint, 303 E. Kearsley St., Flint, MI 48502, USA
e-mail: hdawson@umflint.edu

M. L. Jones
Quantitative Fisheries Center, Department of Fisheries and Wildlife, Michigan State University, 13 Natural Resources Bldg., East Lansing, MI 48824, USA

Introduction

Growth and mortality rates of fish populations can be assessed by monitoring size and age composition. Because fish have indeterminate growth patterns that are heavily influenced by the environment (Campana 2001), use of environmentally plastic traits such as body size to infer age will bias estimates of population productivity without accurate methods for age determination (Campana and Thorrold 2001). In teleost fish, age determination of individuals and populations has been achieved through the interpretation of calcified structures, primarily scales and otoliths. The chronological properties of otoliths are unparalleled in the animal world, allowing accurate estimates of age and growth at both the daily and the yearly scale through the interpretation of circuli and annuli (Campana 2001). Additionally, otolith size tends to be somewhat more correlated with fish age than is fish length (Boehlert 1985). Thus, a number of studies have statistically related various measurements of otolith size (e.g., otolith weight, length, area) to annulus-based age, and then

Published online: 05 March 2015

used the resulting relationships to estimate the age composition of the remaining, unaged fish (Boehlert 1985; Pawson 1990; Worthington et al. 1995a). However, managers of non-teleost fish must rely on less refined, and often less accurate methods of aging, such as the interpretation or measurements of other bony structures such as vertebrae, or measurements of body size over time. In this paper, we evaluate the use of measurements of the statolith, an analogous structure to the otolith, to determine age of an important pest species, the Great Lakes sea lamprey (*Petromyzon marinus*).

Accurate aging can provide estimates of growth and mortality rates, which inform decisions about sustainable harvest rates for fish populations. Analogously, these estimates can inform pest control efforts where the goal is to remove individuals at rates greater than individuals can be replaced (Dawson and Jones 2009). Natural variation in recruitment, growth rates, and survival of sea lamprey larvae (ammocoetes) make it impossible to predict with certainty the optimal time to undertake control efforts at a specific location to minimize the downstream migration of parasitic juveniles (Anderson 2006). Being able to more accurately assess ammocoete population age composition would help inform estimates of ammocoete growth and mortality rates, increasing the accuracy of stream-level population forecasts, and thus increasing confidence in control decisions.

The use of age composition data for ammocoetes to aid in sea lamprey control efforts has been discouraged by the unreliability of age-assessment methods. Determining larval sea lamprey age based on visual assessments of length-frequency distributions is very difficult for ages greater than one (Jones et al. 2003; Dawson et al. 2009). Growth rates of sea lamprey ammocoetes are affected by factors such as water temperature, stream productivity, and ammocoete density (Holmes 1990; Rodríguez-Muñoz et al. 2001). Therefore, growth rates are likely to vary among populations, spatially among sections of the same stream, and even over time within stream populations; this variation is large relative to average growth rates, which contributes to considerable size overlap between age-classes (Hansen et al. 2003). Determining age based on counts of annuli on ammocoete statoliths, the analogous structure to teleost otoliths, has also been found to be imprecise and inaccurate (Dawson et al. 2009). Interpreting annuli formation on statoliths is also more difficult than observing annuli on otoliths in teleost fishes for two reasons. Firstly, statoliths are much harder to grind or section for analysis because they are primarily composed of a softer substance (calcium phosphate) than otoliths (calcium carbonate), so annuli must be observed on the intact three-dimensional statolith. Secondly, statoliths are usually much smaller than otoliths (Arkhipkin and Shcherbich 2012). Common sizes of otoliths of adult fish vary from several mm to several cm in length, whereas statoliths rarely exceed 2 mm, being 1–1.5 mm even in the giant squid (*Architeuthis dux*), which can attain 100 kg body weight (Roeleveld and Lipinski 1991). However, Beamish and Medland (1988) stated that statolith growth patterns appear to be tightly correlated to sea lamprey ammocoete body size and growth rates. Thus, just as otolith size has been used to infer fish age in teleosts (Francis and Campana 2004), and has been used as a predictor in previous studies (Boehlert 1985; Pawson 1990; Worthington et al. 1995a), statolith size could potentially be used to infer ammocoete age.

Validating whether statolith size is correlated with ammocoete age requires knowledge of the absolute age of the fish. However, in fish aging studies rarely is the absolute age of the fish known without error. Campana (2001) state that of 372 papers reporting age validation since 1983, only 15 % actually validated the absolute age of wild fish. In this paper, we evaluate whether statolith size is correlated with ammocoete age using the most rigorous of age validation methods; release of known-age fish into the wild with the absolute age of recaptured fish being known without error (Campana 2001). Because using an objective, likelihood-based method in the development of a standard protocol for ammocoete age-assessment would be an important advance in sea lamprey management, we also evaluated a statistical method for ammocoete age assessment. This statistical method estimated age composition from length-frequencies and partial ages (using statolith size to infer age) using maximum likelihood.

Methods

Known age population of ammocoetes

Statoliths were obtained from known-age ammocoete populations established in a previous study by Dawson et al. (2009). Spawners were released above barriers in the Big Garlic River, a cold, low-alkalinity (mean alkalinity = 52 mg/L $CaCO_3$) tributary of Lake Superior, and in

Ogemaw Creek, a warmer, high-alkalinity (mean alkalinity = 175 mg/L $CaCO_3$) tributary of Lake Huron (Fig. 1), in 2002 and 2003 respectively (adult sea lampreys spawn only once before they die). The rivers were then sampled for ammocoetes every summer through 2007, producing ages of 1, 2, 3, 4, and 5 for Big Garlic River and 1, 2, 3, and 4 for Ogemaw Creek. A total of 530 ammocoetes were collected and body lengths measured among the five age classes of the Big Garlic River. The number of ammocoetes measured for each age class ranged from 65 to 175 individuals (mean – 106). From Ogemaw Creek, a total of 434 ammocoetes were collected and body lengths measured among the four age classes. The number of ammocoetes measured for each age class ranged from 73 to 170 individuals (mean – 108). Statoliths were removed from a subsample of at least 25 ammocoetes from each age class in each river and transferred into individual wells filled with immersion oil for 9–18 days to improve visibility. We also obtained ammocoetes of unknown age from another river for statolith extraction to minimize reader bias when measurements were taken (i.e., knowledge of age-classes of the known-age populations). Dawson et al. (2009) then assigned unique random numbers to each statolith and aged them in immersion oil, or aged them after sealing them in Crystal Bond™ adhesive and placing them on microscope slides. Statoliths that were sealed and placed on microscope slides (and thus preserved) were measured in this study. Those statoliths aged in immersion oil were not preserved, and so could not be measured in this study; they included age class 3 from Ogemaw Creek and age class 4 from Big Garlic River. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

Statolith measurements

To collect measurements of the statoliths, a digital microscope and computer were used to measure the length, width, and height of each prepared statolith. Crystal Bond™ adhesive was heated until softened and the statolith manually manipulated into the position necessary for measurement with assistance of a compound microscope. The slide was then transferred to the digital microscope fitted with a Q-Imaging Micropublisher camera (W. Nuhsbaum 2014) to capture the image. Measurements of the statolith image were taken at 100x magnification using Q-Imaging Professional Version 7.0 software (W. Nuhsbaum 2014). Statolith length and width were measured from the dorsal side while the statolith was positioned flat on its bottom with both edges equally in focus (Fig. 2a). The length was measured from the top of the apex straight down, and the width was measured perpendicular to the length measurement, at the widest point (Fig. 2a). The height measurement was collected by then placing the statolith on its side and measuring from the highest point to the bottom edge of the statolith (Fig. 2b).

Principal components analysis was performed on the three statolith metrics for each stream to reduce the data by forming linear combinations of the original observed variables, thereby grouping together these correlated variables (SPSS® version 22; IBM Corp 2013). The number of components that best represented the data was chosen based on the scree plots and eigenvalues. Factor scores were calculated for the principal component for each statolith. A one-way ANOVA was used to test for differences in factor scores between each of the age classes for both the Big Garlic River and Ogemaw Creek (SPSS® version 22; IIBM Corp 2013). To determine whether one statolith metric performed as well as the principal component (a linear combination of all three original observed variables), another one-way ANOVA was used to test for differences in raw statolith measurements (length, width, and height) between each of the age classes for both the Big Garlic River and Ogemaw Creek (SPSS® version 22; IBM Corp 2013).

Estimating proportion at age

In this study we used an objective, likelihood-based statistical model used previously by Dawson et al. (2009) to evaluate a statistical method for ammocoete age assessment. We combined the data across years for each stream to mimic a mixed-age population, but for which we know the actual proportions at age. We implemented the model in AD Model Builder (Fournier et al. 2012) and combined length-frequency data with statolith size data to estimate proportions at age, which we could then compare to the known values. We only use the statolith metric (the principal component which is a linear combination of all three metrics, or only width, only length, or only height) in the model that most distinctly separated the age classes for both Big Garlic River and Ogemaw Creek. We used the results of the ANOVA and post-hoc comparisons to select the metric that was best at separating the age-classes of the populations. The model was adapted from Schnute and

Fig. 1 Locations of the streams used to create known age populations of sea lamprey to establish a relationship between age and statolith size

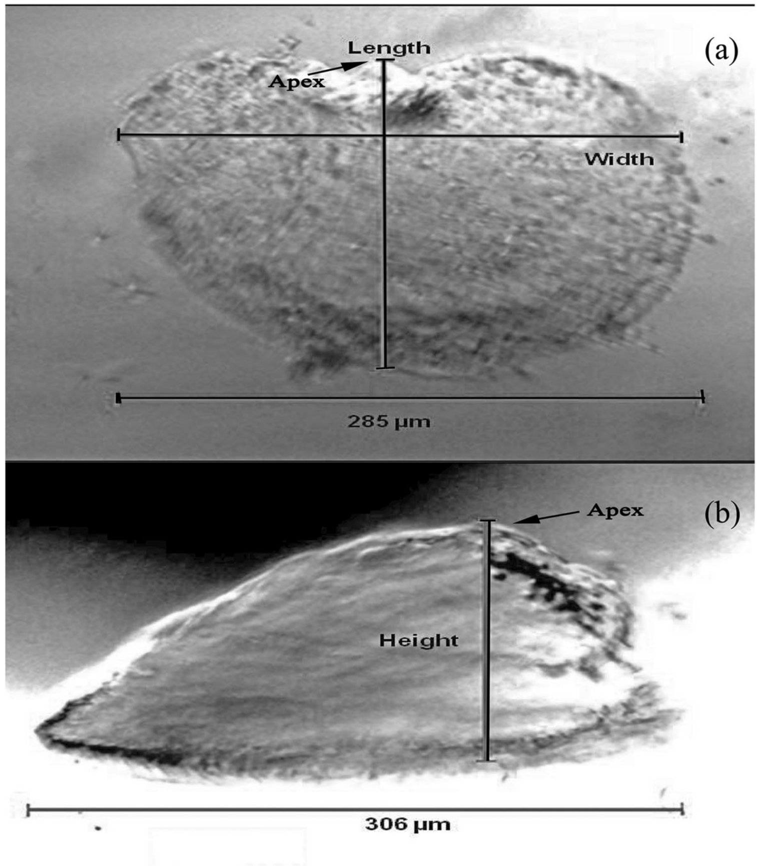

Fig. 2 Digital images of statoliths from ammocoetes; (**a**) statolith length and width measured from the dorsal view and (**b**) statolith height measured from the lateral view

Fournier (1980) and Fournier (1983); it assumes that both ammocoetes and their statoliths grow according to a von-Bertalanffy growth curve, and that ammocoete lengths and statolith measurements vary among individuals in an age class according to a normal distribution (Dawson et al. 2009). Accordingly, standard deviations around ammocoete length and the chosen statolith metric were assumed to increase as a linear function of age by the following formula:

$$\sigma = \lambda^1 + \lambda^2 a, \qquad (1)$$

where λ^1 and λ^2 are the y-intercept and slope estimated by performing a linear regression of the standard deviation of ammocoete length vs. age or the standard deviation of the chosen statolith metric vs. age (Table 1), and *a* is age. We estimated the most likely proportions at age given ammocoete length and the standard deviation around length using multinomial log-likelihood. To include statolith data, we estimated the most likely proportions at age given the chosen statolith metric and the standard deviation around that metric by adding a second multinomial log-likelihood to the objective function. The two likelihoods were equally weighted and added together to estimate proportions at age using ammocoete length and the chosen statolith metric by minimizing the negative log-likelihood using a convergence criterion of 10^{-4} for the maximum gradient component. Proportions at age 3 for Ogemaw Creek and age 4 for Big Garlic River were estimated using only ammocoete length, as statolith measurements were not available for these two river-by-age class combinations.

Accuracy of the model estimates were tested by computing the proportion at age of the two known-age populations when ammocoete samples from several years were combined into a single length-frequency data set (Dawson et al. 2009). We used the statistical model to estimate the proportion at age using the ammocoete length-frequency information alone and then combined with the chosen statolith metric data. The estimates were

Table 1 Estimated standard deviations (σ) for ammocoete length (mm) and statolith width (μm) as well as λ^1 and λ^2 used in the model (to calculate σ as in Eq. (1)) for both Big Garlic River and Ogemaw Creek

Age	Obs. ammocoete length σ (mm)	Obs. statolith width σ (μm)	Model λ^1 and λ^2 for ammocoete length (mm)	Model λ^1 and λ^2 for statolith width (μm)
Big Garlic River				
1	4.04	58.35	3.6, 1.9	41, 0
2	9.86	36.60	3.6, 1.9	41, 0
3	8.58	29.88	3.6, 1.9	41, 0
4	10.88	–	3.6, 1.9	–
5	12.97	37.62	3.6, 1.9	41, 0
Ogemaw Creek				
1	7	48.85	3.5, 3.5	43, 0
2	9.94	35.18	3.5, 3.5	43, 0
3	15.37	–	3.5, 3.5	–
4	17.02	43.35	3.5, 3.5	43, 0

compared to the known proportions at age of the two populations.

Results

Statolith measurements

A total of 330 statoliths were examined. There were 58 statoliths from which no measurements were collected due to an unreadable or damaged structure, and not all measurements were obtainable from the remaining statoliths due to difficulty in attaining the proper positioning for some of the statoliths (Table 2). At least one of the three measurements was collected from the remaining statoliths, 117 from the Big Garlic River and 103 from Ogemaw Creek. We also collected measurements from 52 statoliths of unknown age (collected from another river) to minimize reader bias (i.e., knowledge of age-classes of the known-age populations). Statolith height was only measureable for 78.6 % of the statoliths due to difficulty of positioning the statolith for this measurement. Statolith height was more difficult to measure in smaller statoliths, with only 3.7–9.5 % of the statoliths for which height was not measured occurring in the oldest age class from each river.

Table 2 Average length, width, and height of statoliths for each age class in Big Garlic River and Ogemaw Creek, with the number of statoliths measured indicated in parentheses

Age class	Length (μm)	Width (μm)	Height (μm)
Big Garlic River			
1	170.4 (19)	150.5 (19)	95.2 (10)
2	173.9 (29)	161.5 (31)	95.2 (23)
3	195.6 (32)	171.7 (34)	90.2 (26)
5	216.4 (32)	220.4 (33)	107.7 (33)
Ogemaw Creek			
1	162.8 (22)	151.2 (22)	87.7 (14)
2	217.0 (37)	213.5 (38)	112.9 (28)
4	247.4 (43)	277.8 (43)	125.7 (41)

For the Big Garlic River population, only one principal component resulted when combining the three statolith metrics, with all metrics positively loading and accounting for 81.9 % of the variance (Table 3). In this river, the principal component, statolith width, length, and height measurements all differed significantly between age classes (Table 4). Tukey post-hoc comparisons for both the principal component and statolith width indicated that each of the age classes, 1, 2, and 3, differed significantly from age class 5, $p<0.01$. Tukey post-hoc comparisons for statolith length indicated significant differences between age classes 1 and 5, $p=0.001$, and 2 and 5, $p<0.0001$. The significant difference between age classes for statolith height was between age classes 3 and 5, $p=0.009$ because statolith height did not increase with age in sea lamprey from this river (average statolith height was smallest for age class 3). Apparently, material is not consistently deposited in a manner that increases the height of a statolith over time. Overall, inferring ammocoete age using only statolith width was found to be just as accurate as using the principle component for the Big Garlic River.

Table 3 Component loadings, eigenvalues, and percent of variance explained by the principal component of the statolith measurements from the Big Garlic River and Ogemaw Creek populations

Measurement	Principal component
Big Garlic River	
Statolith width	0.93
Statolith length	0.92
Statolith height	0.86
Eigenvalue	2.46
Percent variance explained	81.9
Ogemaw Creek	
Statolith width	0.92
Statolith length	0.93
Statolith height	0.85
Eigenvalue	2.43
Percent variance explained	81.0

For the Ogemaw Creek population, only one principal component resulted when combining the three statolith metrics, with all metrics positively loading and accounting for 81.0 % of the variance (Table 3). In this river, the principal component, statolith width, length, and height measurements all differed significantly between age classes (Table 4). Tukey post-hoc comparisons for the principal component, statolith width, length, and height indicated that each of the age classes, 1 and 2, and 4 differed significantly from each other, $p<0.05$. Statolith height did increase with age in sea lamprey

Table 4 One-way ANOVA results for the differences in factor scores of the principal component, statolith width, length, and height between age classes in Big Garlic River and Ogemaw Creek (degrees of freedom between groups and within groups, *F*-statistic, and *p* value are reported)

Variable	df	*F*	*p*
Big Garlic River			
Principal component	3,84	9.34	<0.0001
Statolith width	3, 113	17.8	<0.0001
Statolith length	3, 108	8.04	<0.0001
Statolith height	3, 88	3.89	0.012
Ogemaw Creek			
Principal component	2, 79	53.3	<0.0001
Statolith width	2, 100	69.8	<0.0001
Statolith length	2, 99	42.4	<0.0001
Statolith height	2, 80	19.4	<0.0001

from this river. Overall, inferring ammocoete age using only statolith width was found to be just as accurate as using the principle component for Ogemaw Creek.

An increase in average length of the ammocoetes as they aged was observed in both Big Garlic River and Ogemaw Creek populations, although growth slowed with age in both populations (Fig. 3). An increase in statolith width with age was also observed in both known-age populations (Fig. 4). Length-frequency distribution graphs of statolith widths for all ages combined and with each age class individually for Big Garlic River (Fig. 5) and Ogemaw Creek (Fig. 6) show distribution of statolith width measurements among the known age samples. There is a high degree of overlap among age classes especially for the slow growing population in the Big Garlic River.

Estimating proportion at age

The model's estimates of proportion at age when using both ammocoete length and statolith width (to infer age) data did not increase age assignment accuracy over estimates using only ammocoete length. In fact, proportion at age estimates changed very little with the addition of statolith width data (Table 5). Regardless of whether only ammocoeote length data or both ammocoete length and statolith width data was included, the true proportion at age deviated from the estimated proportion at age by approximately 7 % (±5.65 %) and 8.7 % (±6.6 %) for Big Garlic River and Ogemaw Creek, respectively (Table 5).

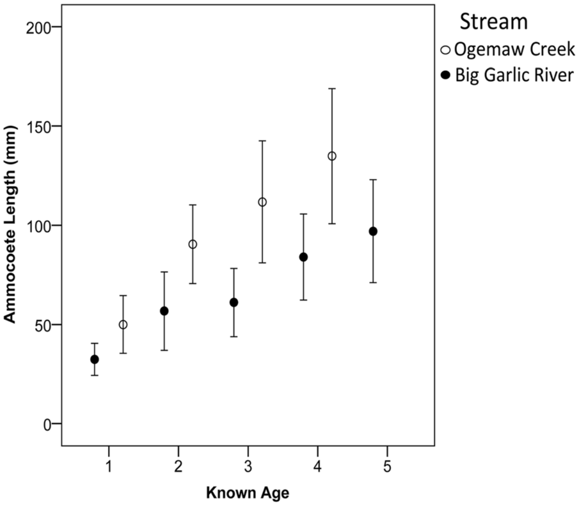

Fig. 3 Ammocoete length at age for both Big Garlic River and Ogemaw Creek (*error bars* indicate standard deviation)

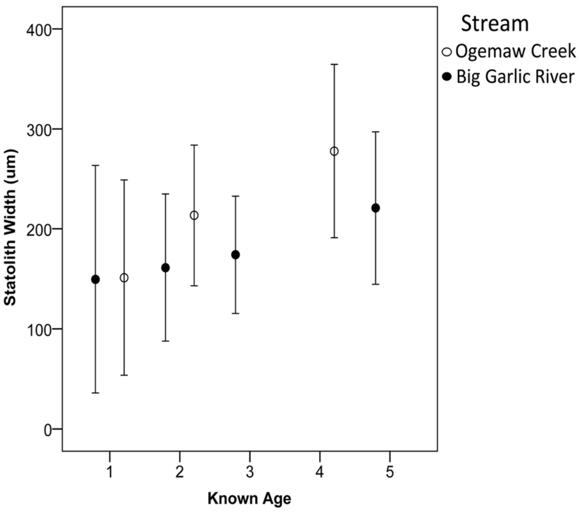

Fig. 4 Ammocoete statolith width at age for both Big Garlic River and Ogemaw Creek (*errors bars* indicate standard deviation)

Discussion

At present, length-frequency analysis and statolith interpretation are the only known potential methods for assessing age of sea lampreys. High variability among fish of the same age in statolith measurements tested in this study results in these measures adding little information to that which can be obtained from body lengths for the determination of age. Thus, model estimates of proportion at age were not improved when some statolith width data was included with length-frequency data. We will have to continue to rely upon aging sea lamprey using length-frequency distributions, which require large sample sizes and cannot discriminate well between older age-classes due to overlapping length distributions (Barker et al. 1997). However, length-frequency data can be used to estimate recruitment (age 1 proportion; Dawson and Jones 2009), which is an important management parameter.

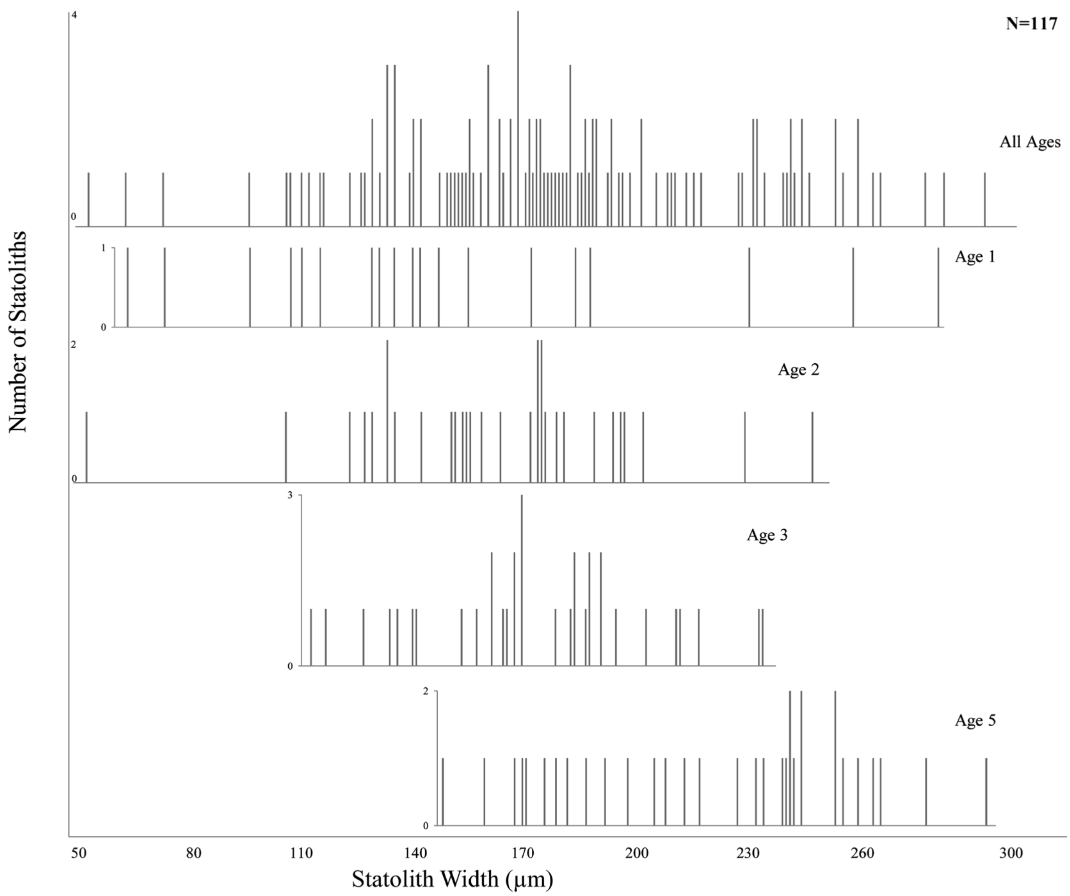

Fig. 5 Frequency distributions of statolith widths for all ages combined and for age 1, 2, 3, and 5 individually for a known age population of sea lamprey ammocoetes from Big Garlic River. N equals the total number of statoliths measured

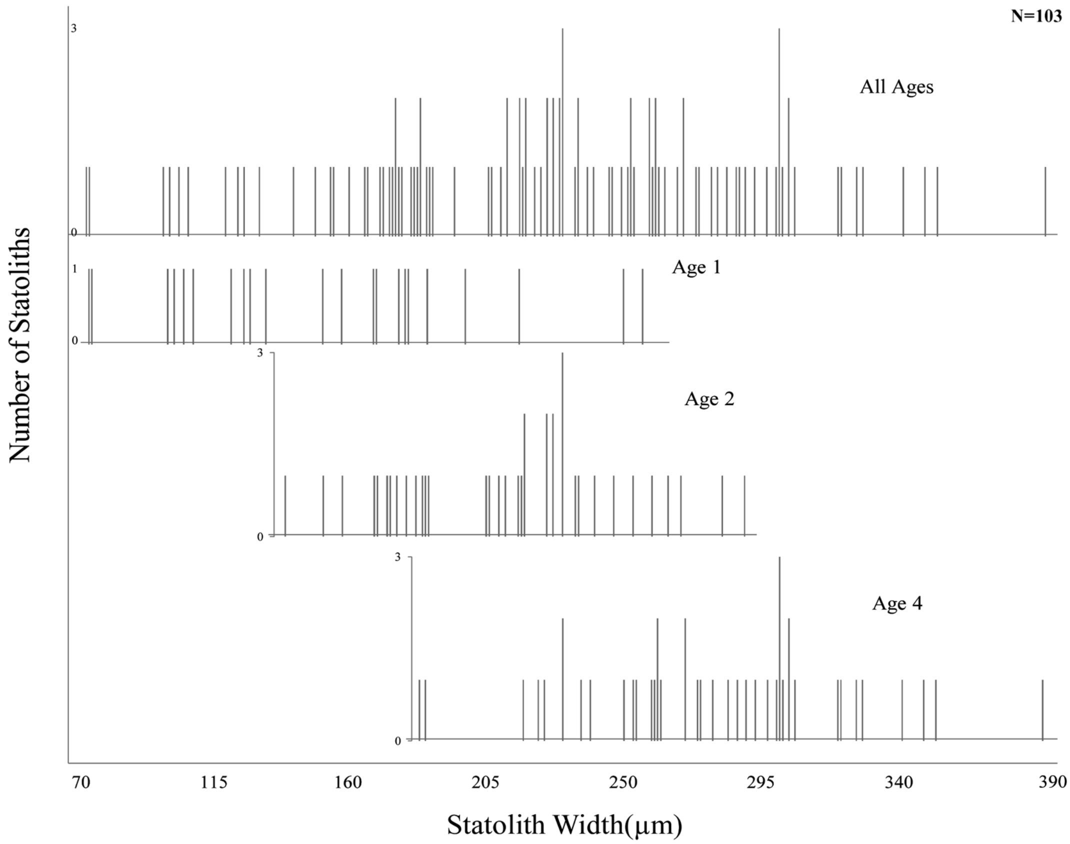

Fig. 6 Frequency distributions of statolith widths for all ages combined and for age 1, 2, and 4 individually for a known age population of sea lamprey ammocoetes from Ogemaw Creek. N equals the total number of statoliths measured

Table 5 True proportions at age and those estimated by the model using ammocoete length data alone and ammocoete length and statolith width data combined for known-age sea lamprey populations in Big Garlic River and Ogemaw Creek

Age-class	True proportion	Estimated using ammocoete length data only	Estimated using ammocoete length and statolith width data
Big Garlic River			
1	0.123	0.140	0.140
2	0.330	0.476	0.475
3	0.240	0.167	0.164
4	0.153	0.166	–
5	0.155	0.051	0.057
Ogemaw Creek			
1	0.212	0.206	0.1206
2	0.228	0.303	0.305
3	0.168	0.001	–
4	0.392	0.490	0.489

Measuring statoliths is much cheaper (in regards to processing time) than annulus counting and using statolith measurements instead of annuli counts to age ammocoetes eliminates the reader bias that was as high as 30 % in studies conducted by Meeuwig and Bayer (2005) and Dawson et al. (2009). Excluding extraction time and prep time, measuring statolith length or width took approximately 5 min, while counting annuli using two readers doing two counts takes four times longer (Dawson et al. 2009). Cost-benefit analyses evaluating the relative merits of using otolith measurements vs. otolith annuli counts in teleosts found that there is the potential for great cost savings if otolith measurements can be used to infer age (Worthington et al. 1995b; Francis and Campana 2004). However, while the chronological properties of otoliths are unparalleled in the animal world (Campana 2001), the use of statoliths as a reliable aging tool has not been established. Most statolith measurements (with the exception of height) did increase with age as expected. Variation around sea lamprey length increased with age reflecting typical fish growth, but variation around statolith width in sea lampreys from both streams was largest for the first age-class. This trend is not seen in otoliths, implying differences in the deposition of material on statoliths vs. otoliths as a fish ages.

If a statolith measurement could be found that better separated age classes in sea lamprey populations we could improve age estimates. In teleosts, the otolith measurement that is most highly correlated with age is otolith weight (Boehlert 1985; Fossen et al. 2003), and otolith size can better be used to infer fish age than can fish length. Otolith weight continues to increase with age, while other measurements slow down with age, because of continued deposition of material on the medial surface of the otolith (Blacker 1974; Boehlert 1985; Anderson et al. 1992). The correlation between statolith weight and age has yet to be examined in lamprey. We could not measure statolith weight in this study because the statoliths were preserved in a transparent adhesive that could not be completely removed from each statolith. If material was consistently deposited on statoliths as a lamprey aged, statolith weight may be useful in improving sea lamprey age assessments. Statolith weight correlates well with mantle length in the oceanic squid (*Sthenoteuthis oualaniensis*; Zakaria 1999), but chemical composition and structure of mollusk statoliths are different than those of lamprey. Meeuwig and Bayer (2005) found statolith width to be most closely correlated, assuming a quadratic relationship, with length in larval Pacific (*Entosphenus tridentatus*) and western brook lampreys (*Lampetra rischardsoni*), but statolith weight was not measured in their study.

Any evaluation of statoliths as a management tool should consider that different factors have been found to disrupt calcium deposition and resorption in calcified structures in fishes, which has implications for using these structures for aging purposes. Stress has been found to disrupt calcium uptake, which ultimately influences calcium deposition in otoliths (Campana 1983). Water temperature was found to be an important factor in regulating otolith growth in teleost fish, with species living in cold waters having calcified structures that were smaller and thinner than the calcified structures of species living in warmer waters (Lombarte and Lleonart 1993). We observed this effect on statoliths in our study with sea lamprey from the cold, low alkalinity stream having smaller and thinner statoliths than sea lamprey from the warm, high alkalinity stream. Larval lamprey statoliths have been found to exhibit irregularities in annuli formation and size, or even be absent from ammocetes in streams with alkalinities below 30 mg/L CaCO3, which is most likely due to resorption of calcium from the statolith in animals inhabiting low alkalinity (Medland and Beamish 1991; Barker et al. 1997) environments. This emphasizes the importance of using length-frequency distributions in combination with calcified structures to verify assigned ages for sea lampreys.

Acknowledgments We are grateful to the University of Michigan-Flint for funding and actively supporting this research through a Research and Creative Activity Award to the corresponding author. Thank you also to Iyob Tsehaye at Michigan State University for his help and knowledge with AD Model Builder. Comments from anonymous reviewers helped improve the manuscript. This is contribution number 2015-03 of the Quantitative Fisheries Center at Michigan State University.

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