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[Article]

Morphology and Aging Precision of Statoliths from Larvae of Columbia River Basin Lampreys

MICHAEL H. MEEUWIG*[1] AND JENNIFER M. BAYER

U.S. Geological Survey, Western Fisheries Research Center, Columbia River Research Laboratory, 5501A Cook-Underwood Road, Cook, Washington 98605, USA

Abstract.—The general morphology and precision associated with age determination of statoliths from larval Pacific lampreys *Lampetra tridentata* and western brook lampreys *L. richardsoni* found within the Columbia River basin were examined. Significant positive correlations were observed between the size of left and right statoliths from individuals. Principal components analysis indicated an allometric relationship between lamprey length and statolith size as well as a potential species grouping based on these measurements. Discriminant analysis was able to correctly classify more than 94% of Pacific lampreys and 92% of western brook lampreys based on lamprey length and statolith size, and Pacific lamprey statoliths tended to be larger than western brook lamprey statoliths for lampreys of a given size. Reader bias in age estimates of statoliths was greater for older lampreys. Multiple independent age readings of both statoliths from individual lampreys indicated that the overall average percent error was 16.7% for Pacific lampreys and 33.0% for western brook lampreys. Within-individual average percent error ranged from 5.1% to 20.1% among species and readers. Within-reader average percent error ranged from 6.4% to 17.8% among species and readers. The average percent error observed in this study was greater than that observed in studies of other species of lampreys; however, statoliths that were ambiguous or difficult to read were not excluded from this study. In general, the modal separation of age-groups observed in length-frequency distributions for lampreys is poor, as seen in this study; therefore, statolith-based ages may verify or provide better estimates of population age structure. These data demonstrate that estimates of precision are necessary before management actions founded on statolith-based age structure determination are implemented.

An understanding of a population's demography is essential for species monitoring and management. Because survival and reproductive status can be age dependent (Gotelli 1995), the age structure of a population is among the most important demographic parameters used to describe populations. For animals that exhibit rapid seasonal growth, an individual's size may be used to establish its age within a population. A common and useful technique in fisheries management has been to examine length-frequency distributions of populations to infer age structure, given that fish from the same year-class tend to be distributed around a common modal size (Jearld 1983). Although the length-frequency distribution of a population may be relatively easy to produce, as fish increase in age, size growth rates often decrease, resulting in less distinct modal separation for older age classes (Potter 1980). Also, large sample sizes are often necessary for age structure to be determined from length-frequency distributions (Beamish and Medland 1988). More accurate estimates of individual age and population age structure may be obtained through aging calcified structures. For many fish, age may be determined through examination of annular and subannular growth patterns of calcified structures, such as otoliths, scales, fin spines and rays, and bones (Jearld 1983).

Unlike gnathostomous fish, lampreys lack the calcified structures generally used to estimate age; however, the lamprey statolith is a potentially useful structure for age determination in individuals (Volk 1986). Located within each otic capsule (Bardack and Zangerl 1971), also known as the auditory capsule (Lowenstein et al. 1968), the labyrinth of lampreys is composed of two semicircular canals. In his examination of the European river lamprey *Lampetra fluviatilis*, Carlström (1963) observed that within each labyrinth are numerous statoconia and a few microstatoliths (generally referred to as statoliths). The lamprey statolith is composed of mostly calcium phosphate,

* Corresponding author: mmeeuwig@montana.edu
[1] Present address: Montana Cooperative Fishery Research Unit, Montana State University–Ecology, Post Office Box 173460, Bozeman, Montana 59717-3460, USA.

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with some carbonate, and is believed to be functionally analogous to the teleost otolith (Carlström 1963; Jebbink and Beamish 1995). Examinations of statoliths have revealed internal patterns of alternating broad opaque bands and narrow translucent bands (terminology follows Jearld 1983; Jebbink and Beamish 1995). Volk (1986) observed a direct relationship between the number of narrow bands and the known age of larval sea lampreys *Petromyzon marinus*, and Medland and Beamish (1987) used the fluorochrome oxytetracycline to validate the annular deposition of the narrow bands within statoliths of mountain brook lampreys *Ichthyomyzon greeleyi*. On the basis of their findings, Medland and Beamish (1987) suggest that the broad opaque bands are the result of rapid growth during the spring and summer, whereas the narrow translucent bands observed in statoliths, which represent the annuli (Jearld 1983), are produced in the winter during periods of slow growth. Although many studies have indicated the value of using statoliths to determine the age of lampreys, this approach is not problem-free. Temperature, water alkalinity, and geographic distribution of populations have been shown to affect the growth, annuli formation, and presence of statoliths (Medland and Beamish 1991; Barker et al. 1997). Because these characteristics are geographically variable, some have suggested that the efficacy of using statoliths to determine lamprey age should be examined on a regional basis.

Within the Columbia River basin, both Pacific lampreys *L. tridentata* and western brook lampreys *L. richardsoni* are known to occur. Historically, Pacific lampreys were of great cultural significance, being used by Native American tribes for sustenance, ceremonial, and medicinal purposes (Close et al. 2002). Lampreys also fill an important biological niche by providing a food source for a variety of animals and may provide a buffer to marine mammal predation on salmonids and other fishes (Semakula and Larkin 1968; Jameson and Kenyon 1977; Beamish 1980; Close et al. 2002). Lampreys may also provide a seasonally abundant source of nutrient input to stream systems as a result of postspawning mortality (Close et al. 2002), similar to semelparous salmonids (Chaloner et al. 2002; Thomas et al. 2003). Although the distribution and abundance of these species within the basin are unknown, anecdotal information and dam passage data indicate that Pacific lamprey populations are in decline (Close et al. 2002). This trend has prompted interest in management and restoration of Pacific lamprey populations as well as interest in the status of other lamprey species.

In this study we describe the general morphology of statoliths from larval Pacific and western brook lampreys from the Columbia River basin and provide information on the precision of age estimates based on statolith banding patterns. An understanding of these topics is necessary before implementation of statolith-based aging for management. Specifically, we examined the morphology of statoliths in comparison with lamprey size and species, trends in bias among age estimates, and the overall precision associated with statolith-based aging. We also evaluated the agreement between statoliths from within an individual (variation of statolith banding patterns inherent in individual lampreys) and the precision associated with multiple age readings by the same reader (variation due to human error).

Methods

In September 2001, larval Pacific lampreys were collected from the Middle Fork John Day River (44°47′40N, 118°57′17″W) and larval western brook lampreys were collected from the South Fork Walla Walla River (45°51′31″N, 118°13′21″W). These collection sites, both in Oregon, are believed to be monospecific with regard to lamprey species, and all lampreys collected were identified to species based on caudal fin pigmentation (Richards et al. 1982). For each species, larvae were collected from one 7.5-m^2 site with an AbP-2 backpack electrofishing unit (Engineering Technical Services, Madison, Wisconsin). Within each site, a two-pass depletion was performed with a shocking rate of approximately 90 s/m^2. All lampreys captured were anesthetized in tricaine methanesulfonate (MS-222; 250 mg/L) buffered with an equal concentration of sodium bicarbonate and measured for total length (± 1 mm). A total of 511 Pacific lampreys (total length, 40–117 mm) and 395 western brook lampreys (total length, 12–132 mm) were captured. For each species, collected lampreys were divided into length-groups at 10-mm increments and a subsample of as many as 10 live individuals from each length-group was transported to the Columbia River Research Laboratory, Cook, Washington. Lampreys were subsampled in this manner to provide representation of all length categories observed (Ketchen 1949).

At the laboratory, larvae were transferred to aquaria containing suitable burrowing substrate. Aquaria were provided with a continuous inflow of filtered and aerated river water (from the Little White Salmon River, Washington), and exposed to a simulated natural photoperiod provided by incandescent lights with 0.5 h of increasing and decreasing illumination at the beginning and ending of the light phase, respectively. Water temperatures were adjusted to mimic daily mean water temperatures of the Columbia River at Bonneville Dam (University of Washington 2001).

Within 14 d of collection, lampreys were immersed in an overdose of MS-222 (500 mg/L) and measured for total length ($\pm$1 mm), after which statoliths were removed and stored in immersion oil for at least 14 d, as in Volk (1986). Statoliths stored longer than 14 d showed no signs of degradation. When more than one statolith was present in an otic capsule, we removed the largest for examination. Statoliths were removed from a total of 68 Pacific and 109 western brook lampreys. Loss or breakage resulted in successful removal only one statolith from 15 Pacific and 15 western brook lampreys.

Dorsal and lateral views of each statolith were digitized by using a Spot Insight digital camera (Diagnostic Instruments, Inc., Sterling Heights, Michigan) mounted to a stereomicroscope (Wild M3Z; Leica AG, Heerbrugg, Switzerland). Statoliths were measured along three axes (Figure 1; as in Volk 1986) by using image analysis software (Image Pro Plus; Media Cybernetics, Silver Spring, Maryland). Axes were defined in relation to the apex of the statolith, which is present towards the anterior edge of the statolith in dorsal view. Axis C was measured as the distance from the base of the statolith to the apex in lateral view. Axis B was measured as the greatest distance from the posterior edge to the anterior edge in dorsal view. Axis A was measured as the greatest distance of a line perpendicular to axis B. Some statoliths had fewer than three measurements because of damage caused during removal and manipulation. Using a stereomicroscope at 80$\times$, three readers counted the number of annuli on each statolith independently.

To examine the precision associated with aging a randomly selected sample, statoliths that were difficult to read were not excluded from this study. Statoliths were stored and coded in such a way that lamprey length and previously assigned age could not be determined at the time of examination. On the basis of age validation studies of lampreys from temperate regions (Medland and Beamish 1987; Beamish and Medland 1988) and examinations of statolith banding patterns in relation to length-frequency distributions (Volk 1986; van de Wetering 1999), we assumed that lamprey age corresponded to the number of annuli present. Random subsets of 30% of the Pacific lamprey statoliths and 27% of the western brook lamprey statoliths were examined and aged twice by each reader to allow for calculations of within-reader precision.

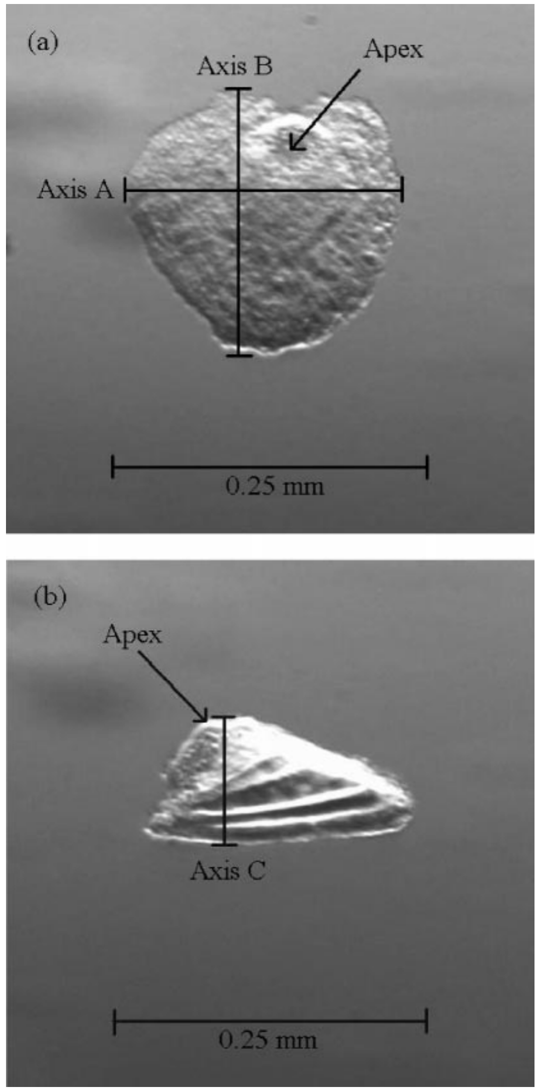

FIGURE 1.—Digital images of a statolith from a 108–mm-long western brook lamprey assigned an age of 4 years; **(a)** axis A (0.22 mm) and axis B (0.21 mm) were measured from the dorsal view **(b)** axis C (0.11 mm) from the lateral view.

All analyses were performed with SAS software (SAS Institute 1989) with statistical significance set at $\alpha = 0.05$. For each axis of measurement, we

TABLE 1.—The number of Pacific and western brook lampreys for which both statoliths were measured (N), along with the correlation coefficients (r) and P-values for correlations between the sizes of the left and right statoliths from individuals measured along three axes (see Figure 1).

Axis of measurement	N	r	P
Pacific lampreys			
Axis A	49	0.88	<0.0001
Axis B	52	0.77	<0.0001
Axis C	53	0.63	<0.0001
Western brook lampreys			
Axis A	83	0.93	<0.0001
Axis B	92	0.91	<0.0001
Axis C	94	0.82	<0.0001

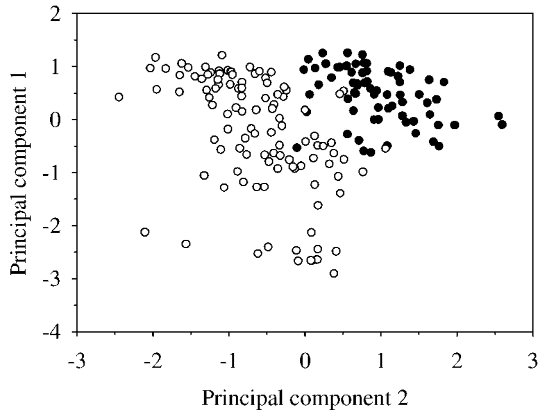

FIGURE 2.—Component plot of principal component 2 versus principle component 1 of $\log_e$ transformed lamprey length and statolith measurements. Closed circles represent Pacific lampreys and open circles western brook lampreys.

calculated within-species correlations between left and right statoliths from within individuals to determine the degree of covariation, using a Pearson product-moment correlation (PROC CORR; Sokal and Rohlf 1995; Cody and Smith 1997). Because significant correlations were observed between left and right statoliths (Table 1), we performed regression analysis and multivariate analyses (principal components analysis and discriminant analysis) of statolith measurements by using the mean value when two statoliths were available for an individual and the single value when only one statolith was available. Regression analysis (PROC REG; SAS Institute 1989) was used to describe statolith size as a function of lamprey length. Separate analyses were performed for each measurement axis and species.

Principal components analysis of the covariance matrix was used to examine the relationships between the lengths of the three axes of the statoliths and the total length of the lamprey (PROC PRINCOMP; SAS Institute 1989). Scree plots and eigenvalues were examined and principal components were retained until 95% of the variance in the data was explained (Tabachnick and Fidell 2001). Morphometric data were $\log_e$ transformed before multivariate analyses (Bookstein et al. 1985). Because a noticeable species grouping was observed in the principal component plot (Figure 2), we performed standard (direct) discriminant analysis (PROC DISCRIM; SAS Institute 1989; Tabachnick and Fidell 2001) to examine the ability of these four measurements to predict group membership (i.e., species). A training data set, established by randomly selecting half of the individuals from each species, was used to develop the discriminant function. The ability of this discriminant function to predict group membership of individual lampreys other than those present in the training data set was tested with the remaining individuals (test data set).

The precision, or reproducibility, of statolith aging techniques for use with Columbia River basin lampreys was examined visually by age bias plots (Campana et al. 1995) and by comparing estimates of average percent error (APE). Age bias plots were constructed to examine the variability in ages assigned by one reader for all statoliths assigned a given age by a second reader. Calculations of APE followed the equation

$$100 \times \frac{1}{N}\sum_{j=1}^{N}\left(\frac{1}{R}\sum_{i=1}^{R}\frac{|X_{ij} - X_j|}{X_{ij}}\right),$$

where N is the number of lampreys aged, R is the number of times each lamprey was aged, X_{ij} is the ith age determination of the jth lamprey, and X_j is the average age calculated for the jth lamprey (Beamish and Fournier 1981). Overall APE was calculated where the mean age was based on the results of multiple readers (three) who examined both statoliths per individual lamprey, unless only one statolith was successfully extracted (Campana and Jones 1992). Equation (1) was modified to examine variation in statolith banding patterns between the left and right statolith from the same lamprey (within-individual APE), and to examine variation in age determination attributable to human error (within-reader APE). For within-individual APE, each statolith within an individual was aged once; therefore, R equaled 2 and X_j

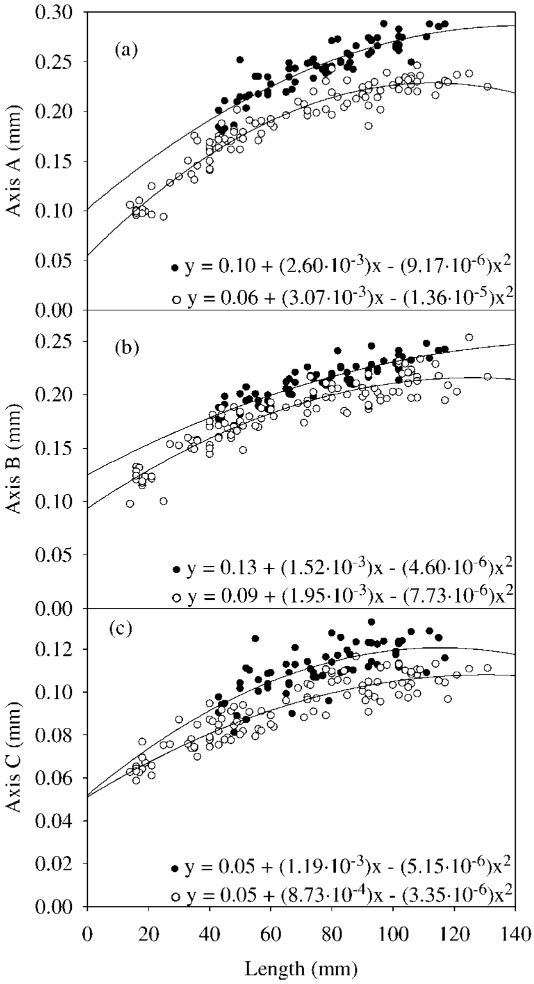

FIGURE 3.—Scatter plots of lamprey length versus **(a)** statolith axis A, **(b)** statolith axis B, and **(c)** statolith axis C. Closed circles represent Pacific lampreys and open circles represent western brook lampreys. Trend lines were derived from the reported quadratic regression models.

equaled the mean age of the statoliths from within an individual. For within-reader APE, each statolith was aged twice; therefore, N equaled the number of statoliths aged, R equaled 2, X_{ij} was the ith age determination of the jth statolith, and X_j was the average age calculated for the jth statolith.

Based on the overall mean age (X_j from three readers examining both statoliths per individuals rounded to the nearest whole number), descriptive statistics for total length were calculated for each age-group within species. Plots of length-frequency distributions of all lampreys sampled at field sites (Pacific lamprey: N = 511; western brook lamprey: N = 395) were compared with length versus age distributions.

TABLE 2.—Sample sizes (N) and summary of results from regression analyses describing individual statolith measurement axes (see Figure 1) as a function of length for Pacific and western brook lampreys. Coefficients of determination (r^2) and P-values were produced by fitting quadratic regression models.

Axis of measurement	N	r^2	P
Pacific lampreys			
Axis A	68	0.82	<0.0001
Axis B	68	0.78	<0.0001
Axis C	68	0.55	<0.0001
Western brook lampreys			
Axis A	108	0.93	<0.0001
Axis B	109	0.86	<0.0001
Axis C	109	0.84	<0.0001

Results

Significant positive correlations were observed for all axes of measurement, indicating that the growth patterns of the left and right statoliths from within individuals were directly related. For both species, correlation coefficients were greatest for axis A measurements, intermediate for axis B measurements, and least for axis C measurements (Table 1). Examination of scatter plots (Figure 3) and parameter estimates indicated a quadratic relationship between statolith size and lamprey length; therefore, we used quadratic regression models to describe statolith size as a function of lamprey length. Lamprey length had a significant quadratic relationship with all statolith measurement axes for both species and accounted for a larger proportion of the variance in the statolith measurements (Table 2). In general, Pacific lamprey statoliths appear to be larger along each axis of measurement than western brook lamprey statoliths for individuals of a given length (Figure 3).

The first two principal components accounted for 98.5% of the variation in the data (Table 3). All variables loaded positively on principal component 1; however, total length dominated principal component 1 and the statolith measurements grouped together, suggesting allometric growth (Bookstein et al. 1985). The three statolith measurements grouped together and loaded positively on principal component 2, whereas total length loaded negatively on principal component 2 (Table 3). Visual inspection of the component plot of principal component 1 and principal component 2 suggests that species grouping may be predicted

TABLE 3.—Component loadings, eigenvalues, and percent of variance explained by the first two principal components and loadings for the discriminant function of $\log_e$ transformed lamprey length and statolith measurements.

Measurement[a]	Principal component 1	Principal component 2	Discriminant function
Total length	0.82	−0.56	0.16
Axis A	0.41	0.60	0.43
Axis B	0.28	0.30	0.31
Axis C	0.27	0.49	0.43
Eigenvalue	0.39	0.01	
Percent variance explained	94.8	3.6	

[a] See Figure 1 for axis identifications.

based on the variables measured (Figure 2); therefore, we performed a discriminant analysis to determine the accuracy with which group membership could be predicted on the basis of lamprey length and statolith size. The discriminant analysis of total length and the three statolith measurements correctly grouped 94.1% of the Pacific lampreys and 92.6% of the western brook lampreys in the training data set. The discriminant function correlated highly with the three statolith measurements, whereas the correlation between the discriminant function and lamprey length was relatively low (Table 3). Application of the discriminant function derived from the training data set to the test data set resulted in correct classification of 97.1% of the Pacific lampreys and 98.2% of the western brook lampreys, suggesting that the discriminant function from the training data set can be applied to other individuals.

Bias was observed among age readers for both Pacific and western brook lampreys (Figure 4). For most comparisons, systematic bias was observed with increasing divergence at older ages. Therefore, statoliths with fewer annuli appear to be aged with less bias than statoliths with more annuli. The comparisons between the age of Pacific lampreys estimated by reader 2 and ages assigned by reader 3 indicated nonlinear bias (Figure 4c). The nonlinear trend was largely driven by the observation of six annuli on one statolith by both readers. Except for this observation, reader 3 tended to overestimate the number annuli for young lampreys and underestimate the number of annuli for older lampreys with respect to ages estimated by reader 2. Overall APE was 16.7% for Pacific lampreys and 33.0% for western brook lampreys. Within-individual APE ranged from 5.1% to 20.1% among species and readers (Table 4). Within-reader APE ranged from 6.4% to 17.8% among species and readers (Table 4).

Statolith-based aging indicated that five age-groups of Pacific lampreys (ages 1 through 5) and five age-groups of western brook lampreys (ages 0 through 4) were present in the samples. Descriptive statistics for the size range (total length) of lampreys found in each age-group by species are presented in Table 5. Visual inspection of the length-frequency distribution of all Pacific lampreys captured indicated virtually no modal separation among age-groups (Figure 5a); however, some modal separation observed in the length-frequency distribution of all western brook lampreys captured (Figure 6a) may be useful for determining or corroborating population age structure. For both species, substantial overlap in lamprey size (total length) among age-groups was observed for age-groups based on statolith-derived ages (Figures 5b, 6b).

Discussion

Significant positive correlations between left and right statoliths from within individuals were observed along the three axes of measurement examined in this study. These correlations suggest that growth patterns of the left and right statoliths are directly related; however, the correlation coefficient for axis C, the axis most closely associated with interannuli distance, was less than that for the other two axes of measurement. The smaller correlation coefficient with respect to this axis may correspond to differences in interannuli distances between statoliths within individuals, and more closely spaced annuli may be more difficult to resolve (Volk 1986). This is supported by the relatively high within-individual APE observed in this study (Table 4). Also, the curvilinear trend in statolith growth as a function of lamprey length indicates that statolith size increases at a decreasing rate, which may result in a negative relationship between interannuli distance and lamprey age. The proximity of annuli may have resulted in the systematic bias observed in this study because some readers may be more likely to over- or underestimate age as interannuli distance decreases (Figure 4). Therefore, reading only one statolith may remove variation intrinsic to individuals and result in inaccurate or biased age estimates.

The discriminant function developed in this study was very effective and correctly classified more than 92% of the lampreys in the training data set and more than 97% of the lampreys in the test data sets. Correlations between the three statolith

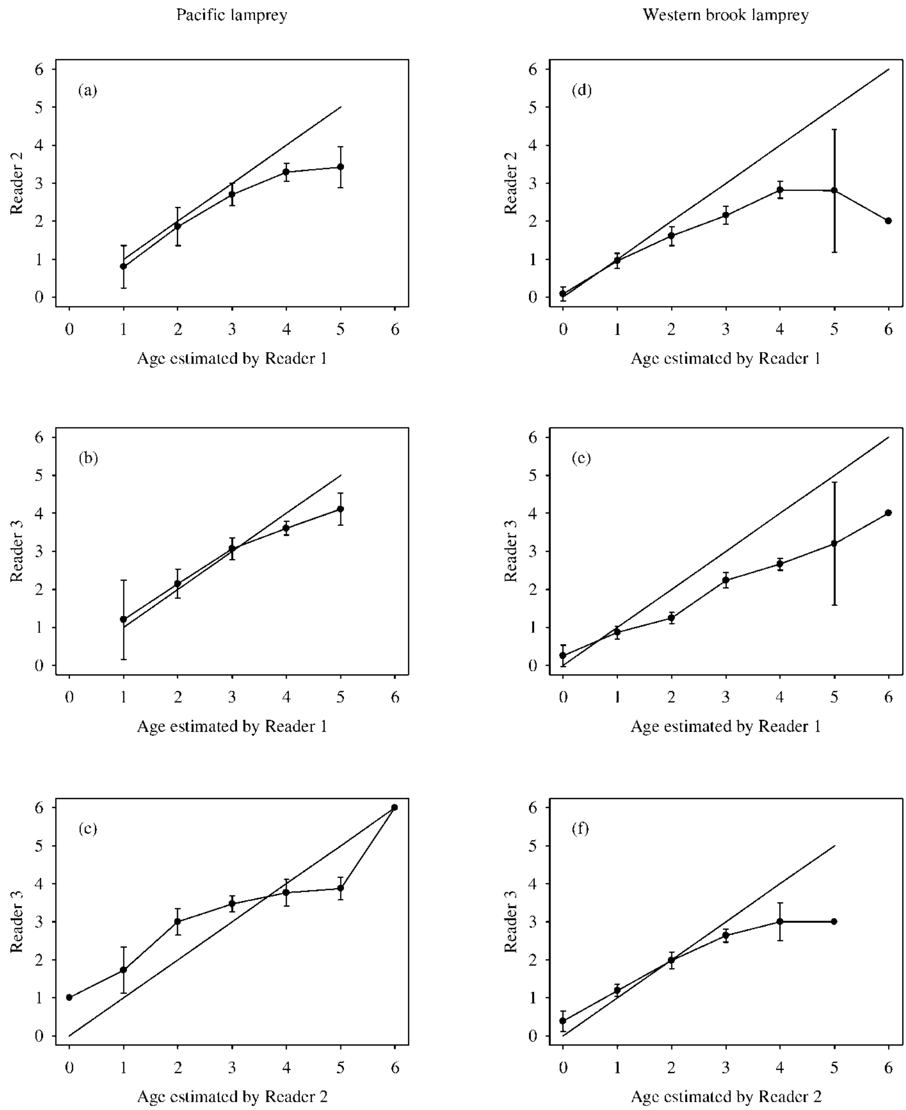

FIGURE 4.—Age bias plots constructed from **(a−c)** 121 Pacific lamprey statoliths and **(d−f)** 203 western brook lamprey statoliths aged by three readers. Error bars represent the 95% confidence intervals about the mean age assigned by one reader for all statoliths assigned a given age by a second reader. Deviation from the 1:1 (45°) equivalence line indicates bias between readers.

measurements and the discriminant function (Table 3), as well as visual examination of relationships between lamprey size and statolith measurements (Figure 3), suggest that species discrimination was determined by statolith size (i.e., for a given lamprey size, Pacific lampreys have larger statoliths than western brook lampreys). Larval lampreys are often phenotypically similar, and traditional methods of species separation such as pigmentation patterns (Richards et al. 1982) may not be viable because of potential geographic variability (Moyle and Cech 1996); therefore, morphometric methods of species separation may be a possible alternative. Collecting morphometric data on body shape may not be practical in field situations, given the fine scale at which measurements must be taken; however, measurements could be made on statoliths from lampreys killed for examinations of population age structure. If these measurements can successfully classify species, they may verify field identification. Although the data used in this study were composed of a

TABLE 4.—Average percent error (APE), standard error (SE), and sample size (*N*) for within-individual and within-reader APEs for statolith ages determined by three readers for two lamprey species.

Reader	Within individual APE	Within individual SE	Within individual *N*	Within reader APE	Within reader SE	Within reader *N*
Pacific lampreys						
1	5.1	0.94	53	8.4	1.71	36
2	13.9	2.43	53	17.8	3.33	36
3	7.0	2.15	53	11.8	1.90	36
Western brook lampreys						
1	16.2	2.64	94	10.5	2.05	55
2	20.1	2.67	94	13.3	2.15	55
3	5.5	1.42	94	6.4	1.36	55

TABLE 5.—Descriptive statistics for total length of Pacific and western brook lampreys grouped by statolith-based age estimates.

Age (years)	*N*	Total length (mm) Mean	SE	Minimum	Maximum
Pacific lampreys					
1	4	46	1.38	43	49
2	7	51	2.65	43	59
3	24	79	4.36	50	117
4	32	85	2.51	60	112
5	1	102		102	102
Western brook lampreys					
0	10	18	0.72	14	21
1	30	39	2.22	16	73
2	24	63	4.21	36	103
3	37	93	2.67	55	125
4	8	108	5.29	85	131

limited sample from two populations of lampreys, they provide support for further examination of this technique for species identification.

The accuracy and precision of any aging technique should be considered before it is applied for management purposes. In temperate regions, characterized by seasonally variable periods of growth, banding patterns of statoliths are accurate estimators of age in lamprey larvae (Medland and Beamish 1987; Beamish and Medland 1988). However, reports of false annuli and ambiguous or unreadable statoliths (Volk 1986; Barker et al. 1997) suggest the potential for subjectivity and decreased precision associated with statolith-based ages. The overall APE observed in this study was 16.7% for Pacific lampreys and 33.0% for western brook lampreys. Within-reader APE, ranging from 6.4% to 17.8% among readers and species, also indicated substantial error associated with the reproducibility of statolith-based age estimates for Columbia River basin lampreys. Average percent error values observed in this study were greater than those reported by Medland and Beamish (1987) for the mountain brook lamprey (2.4%) and Beamish and Medland (1988) for the sea lamprey (2.8% to 5.2%) and the American brook lamprey *L. appendix* (1.4% to 2.7%). Also, Volk (1986) reported a low incidence of error in repeated sampling of the same statolith from sea lampreys. However, the exclusion of statoliths for which age could not be assigned (Beamish and Medland 1988) or that were considered ambiguous or unreadable (Volk 1986) might have affected aging precision in those studies.

The greater APE observed in this study may reflect the different environmental conditions within the sample sites or region. Environmental conditions have been shown to have a strong influence on the growth and, in extreme cases, the presence of statoliths. Among 16 collection sites in the Laurentian Great Lakes, from 0% to 27% of the sea lamprey statoliths examined by Volk (1986) were considered ambiguous or unreadable. Medland and Beamish (1991) induced changes in statolith growth and annuli formation through al-

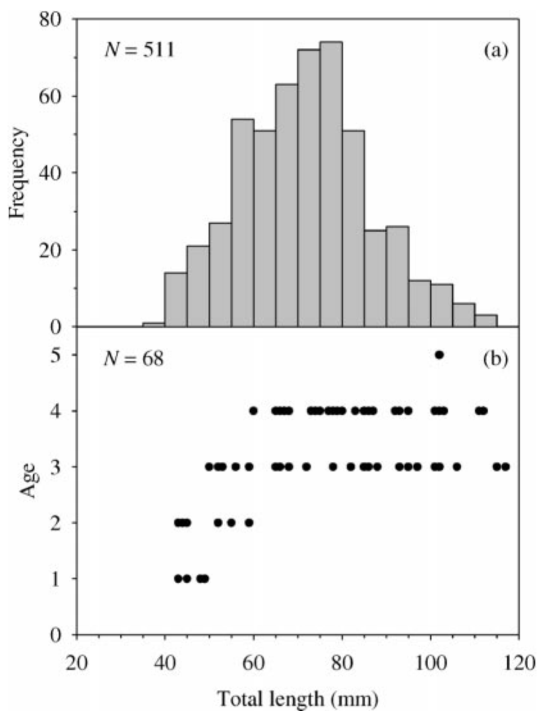

FIGURE 5.—Panel **(a)** shows a length frequency distribution and panel **(b)** a length-versus-age distribution for Pacific lampreys collected from the Middle Fork John Day River.

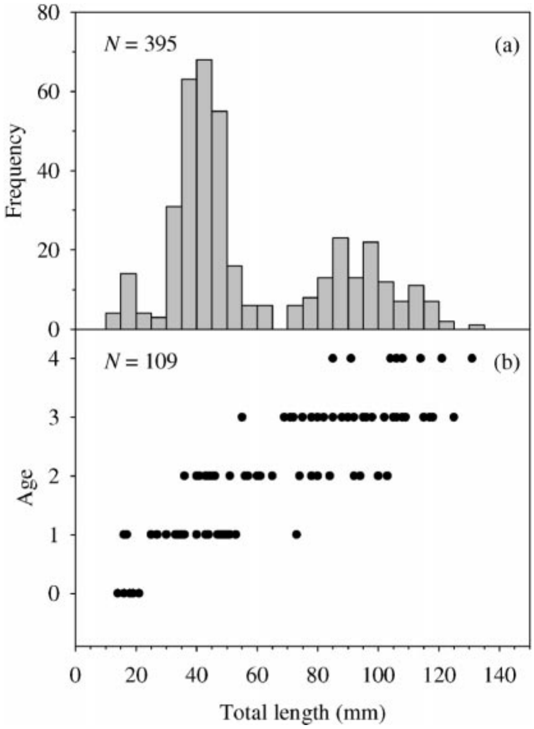

FIGURE 6.—Panel **(a)** shows a length frequency distribution and panel **(b)** a length-versus-age distribution for western brook lampreys collected from the South Fork Walla Walla River.

tered thermal regimes. Barker et al. (1997) observed variation in the size and presence of statoliths among populations of sea lampreys from streams of various alkalinity values and also inconsistencies between ages assigned from statoliths and length-frequency analysis. In this study, statoliths were present in all lampreys sampled and results from quadratic regression models indicated a strong positive relationship between lamprey length and statolith size for the individuals sampled (Table 2). Therefore, unlike Barker et al. (1997), we did not observe inconsistencies in size or presence of statoliths. Aging precision has also been shown to vary among fish species and populations (Campana 2001); therefore, the aging precision observed in this study may be the result of the particular species examined. In a study of Pacific lampreys from the Fraser River, British Columbia, Beamish and Levings (1991) observed anomalous age readings, based on comparisons of statolith-based aging and lamprey length, for 15% of the statoliths examined—even after reexamination of statoliths that were not aged identically by two readers. Also, van de Wetering (1999) reported differences between statolith-based and length-frequency–based age structures for a population of Pacific lampreys from Tenmile Creek, Oregon.

Visual examinations of the length-frequency distributions from our sample sites illustrate the difficulty in using this technique for determination of lamprey population age structure. Although many fishes exhibit rapid seasonal growth throughout their life, and especially during their early development, larval lampreys often exhibit small incremental growth and even arrested growth for as long as a year before metamorphosis into the juvenile form (see Hardisty and Potter 1971). This aspect of lamprey biology makes it difficult to estimate age based on length-frequency analysis of populations. We observed some modal separation in the length-frequency distribution for western brook lampreys (Figure 6), but essentially no modal separation among age-groups was present for the Pacific lampreys sampled (Figure 5). Age-groups based on statolith banding patterns displayed substantial overlap in lamprey length, especially for older lampreys (Table 5); however, this amount of overlap is not uncommon for lamprey species (see Medland and Beamish 1987; Beamish and Levings 1991). Complete overlap of lamprey size for older age-groups may be indicative of substantial individual growth variation (Volk 1986), or it may represent lampreys that were sampled before metamorphosis (Potter 1980).

With increasing interest in the status of lamprey species within the Columbia River basin, management of lamprey populations may become more prevalent, and an understanding of population age structure will greatly aid in the management process. Because of the slow growth rates of larval lampreys and overlap of body lengths among age-groups, the age structures of lamprey populations are often difficult to estimate based solely on length-frequency distributions. Therefore, statolith-based aging is a potentially useful tool for age determination and may provide corroboration for, or even better age estimates than, length-frequency distributions, even though APE was comparatively high for the lamprey species examined in this study. Additionally, prior knowledge of the potential bias and error associated with this technique may provide direction for experimental design and sampling methods as well as information necessary for proper statistical treatment of the resulting age structure data obtained.

This study also revealed the potential for a novel method of morphological discrimination of Columbia River basin lamprey species. Although statolith morphology was extremely effective in predicting species grouping in this study, further examination of this technique, as well as other techniques for discrimination of larval lampreys, should be conducted across a broader geographic distribution.

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