Comparison of Methods for Estimating Age, Growth, and Related Population Characteristics of White Crappies

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Abstract. - Estimates of age and growth of the white crappie Pomoxis annularis in Mississippi were based on 2,162 sets of scales and otoliths and on 4,196 length samples. The maximum ages identified were 8 years from otoliths, 7 from scales, and 6 from length-frequency analysis with the computer program MIX. Ages assigned to scales and otoliths by two readers agreed 79 and 91% of the time, respectively. Ages assigned to scales and otoliths taken from the same fish agreed only 74% of the time. Ages determined from scale and otolith samples obtained from known-age white crappies disagreed because the scales had developed a false annulus. At age 1, but not at older ages, estimates of growth derived from otoliths were significantly ($P \le 0.05$) higher than those derived from scales. Growth estimated from length-frequency modes was generally slower than that estimated from scales or otoliths, but it was significantly slower only at age 1. Unless length samples are obtained during the period of annulus formation, length modes probably will incorrectly estimate length at age. Despite discrepancies among age and growth estimates provided by the three methods, population statistics derived from estimates the methods provided were similar. We suggest that otoliths be used to estimate age and growth of white crappies. Alternatively, if the application allows for reduced accuracy, or if releasing fish alive is a major concern, the scale and length-frequency methods can provide age and growth data that yield population statistics sufficiently similar to those produced by otoliths to be useful in assessing fisheries.

Populations of white crappies Pomoxis annularis support important sport fisheries in reservoirs and natural lakes. To monitor and manage these fisheries, scientists typically estimate various fishpopulation statistics, including age distribution and growth. Age and growth data often are compared to detect changes and diagnose environmental or ecological conditions influencing growth; to estimate age structure, year-class strength, and mortality; and to calculate indices such as longevity and years required to reach sexual maturity or other key sizes. Although quantification of age distribution and growth rate is fundamental to fishery management, the collection and analysis of age and growth data are time-consuming and sometimes impractical. Consequently, researchers have devoted considerable effort toward improving and developing aging techniques and growth analyses.

Various methods have been developed to age fish (Jearld 1983). Length-frequency analysis, one of the oldest methods, involves assigning ages to length modes in the length-frequency distribution; these length modes represent successively older

fish and result from length variations within and among year-classes. Usually the length-frequency method is adequate only for aging fish of recent year-classes; older year-classes are more difficult to identify because of increased variance in length that leads to increased overlap in length modes, and because of asymptotic growth that results in shortened distances between the modes of older age-groups. The scale method, widely used to age freshwater fish (Carlander 1987), involves assigning ages on the basis of markings developed during periods of slow growth. However, evidence that this method is unreliable has been accumulating (Beamish and McFarlane 1987) and has forced freshwater fishery scientists to use other calcified structures, especially otoliths. Otoliths, like scales, record growth zones associated with annual cycles but are more reliable for aging centrarchid species, including white crappies and black crappies P. nigromaculatus (Schramm and Doerzbacher 1985; Boxrucker 1986; Crumpton et al. 1988). Boxrucker (1986) used scales and otoliths of white crappies to compare within-structure rate of reader agreement, but between-structure rate of age agreement and between-structure length-at-age agreement have not been investigated.

We conducted this study to find a practical, efficient method of aging white crappies in Mississippi, one that would be suitable for obtaining age-

¹ The Unit is sponsored jointly by Mississippi State University, the Mississippi Department of Wildlife, Fisheries and Parks, the U.S. Fish and Wildlife Service, and the Wildlife Management Institute.

distribution and growth estimates for use in fishery management. We believed that the length-frequency method deserved to be considered because it is based on length data regularly collected in fishery surveys; also, recent advances in statistical methods and microcomputers have reduced the subjectivity in recognition of length modes. Scales were considered because they have long been a standard for estimating age and growth of freshwater fish (Carlander 1987). Otoliths were evaluated because recent reports have suggested that they provide more accurate estimates than scales (Beamish and McFarlane 1987; Heidinger and Clodfelter 1987).

Fish Collections and Aging

White crappies were collected with electrofishing and trap-netting gear in three large reservoirs (Columbus, Grenada, and Ross Barnett) and one oxbow lake (Moon) in northern Mississippi from fall 1987 to spring 1989. Total length of each fish was recorded to the nearest millimeter. During fall sampling, we removed scales and sagittal otoliths from subsamples consisting of at least 10 fish in each 1-cm length-class (total length) when available. Scales were collected near the distal end of the appressed pectoral fin below the lateral line.

We mounted scales between two glass slides and examined them at 40× magnification using an Eberbach projector. Distances along the right anterolateral axis of the scale were measured with a digitizing bar. To age otoliths, we followed Maceina and Betsill (1987), who compared age determination for sectioned and whole-view otoliths and established that the examination of whole otoliths was reliable for determining age of white crappies. We placed otoliths in a black dish with water, examined them whole under reflected light through a dissecting scope (10-40 \times), and with an ocular micrometer measured distances along a straight line running from the kernel to the anterior tip. Initially, we soaked otoliths in glycerin for 1-2 weeks to try to improve reading, but this practice was discontinued when comparisons of soaked and unsoaked otoliths showed that soaking yielded no marked improvement. Annuli on scales and otoliths were identified by the criteria suggested by Jearld (1983) and measured to their outside edge. Two persons examined each structure independently; if agreement could not be reached on the age of a fish, it was omitted from further analysis.

We back-calculated lengths at age with the Fraser-Lee method (Bagenal and Tesch 1978) using log-transformed measurements (Maceina and Betsill 1987). The intercept (a) of the regression of total length on bony structure radius was 41 mm for scales and 39 mm for otoliths. Because these values were similar to the 35-mm standard a value suggested for white crappies by Carlander (1982), and the small deviation did not produce notable differences in back-calculated lengths, we used the standard a value in all back-calculations.

We counted the number of rings in scales and otoliths of known-age white crappies to assess accuracy of these structures in aging fish. A sample of age-0 fish spawned in the laboratory and stocked in a culture pond at the University of Mississippi was transferred to a culture pond at Mississippi State University in August 1987. Fish from this pond were seined during late June and early July in 1988, 1989, and 1990 to obtain scale and otolith samples.

Aging from spring length-frequency distributions was conducted with the software package MIX (Ichthus Data Systems, Hamilton, Ontario). This microcomputer program separates overlapping length modes by using maximum-likelihood estimation to find a set of distributions that gives the best fit to the length-frequency histogram (Macdonald 1987). The program works interactively and generates several statistics including mean length and number of fish in each mode.

Data Analyses

Ages assigned to scales and otoliths were analyzed to determine within-structure rate of reader agreement and between-structure rate of age agreement. Estimates of mean length at age derived from back-calculations based on scales and otoliths, and from analysis of length-frequency modes, were compared according to lake, sampling year, gear, and age-group. Ages represented by less than three scale or otolith samples per collection were not included in length comparisons. Inasmuch as white crappies form annuli in late spring to early summer (Maceina and Betsill 1987), we compared lengths at age back-calculated from scales and otoliths collected in fall with the modal lengths of fish collected in the previous spring. Because field sampling was conducted from fall 1987 through spring 1989, the fall collections of 1987 and 1988 were available for comparing bony structures, but only the 1988 collections could be used for comparing ages determined from scales and otoliths with those determined from modal lengths.

Disagreements between growth estimates made from scale and otolith samples could presumably be caused by errors in age assignments, errors in

TABLE 1.—Within-structure rate of agreement in ages assigned independently by two readers to scale and oto-lith samples of white crappies collected from four Mississippi lakes, 1988.

	Scale		Otolith		
Assigned age	Percent agree- ment	N	Percent agree- ment	N	
≤l	98	499	96	645	
≤2	89	785	92	925	
≤3	85	1,085	93	1,217	
≤4	81	1,207	92	1,315	
≤5	80	1,244	92	1,342	
≤6	79	1,252	91	1,356	
≤7	79	1,257	91	1,357	
≤8	79	1,257	91	1,358	

measuring distances between annuli, and deviations of the back-calculation model from the population's actual relation between fish length and scale or otolith radius. To eliminate error due to incorrect age assignment, we reanalyzed our data using only samples for which age estimated from scales and otoliths agreed.

We used age estimates obtained with the three methods to compute selected population statistics used by fishery managers. This analysis was limited to fish collected with trap nets in Columbus Lake in 1988 because a large sample was available for assembling age- and length-frequency distributions. Statistics computed included longevity, asymptotic length (L_{∞}) , growth coefficient (K), years required to reach sexual maturity (175 mm; Goodson 1966) and the smallest size that most anglers like to harvest (200 mm; Miranda and Frese 1991), and annual mortality. The L_{∞} and K were estimated with von Bertalanffy's equation (Ricker 1975). This equation was then used to calculate age at sexual maturity and at harvestable size. A catch curve was constructed on the basis of total number of fish collected in each age-group. For the scale and otolith methods, we estimated the total number of fish collected in each age-group by expanding the subsample of fish aged to the entire sample of fish collected using an age-length key (Ricker 1975). For the length-frequency method, the total number of fish collected in each agegroup was given by MIX. Annual mortality (A) was computed on the basis of the descending portion of the catch curve. The log10 of fish abundance was regressed on age, the resulting slope was multiplied by 2.3026 to obtain instantaneous mortality Z, and A was computed as $1 - e^{-Z}$ (Ricker 1975). We then qualitatively compared popula-

TABLE 2.—Between-structure rate of agreement in ages assigned to scale and otolith samples taken from white crappies collected from four Mississippi lakes, 1987 and 1988.

Assigned age	Percent agreement	N
<u>≤</u> 1	96	891
≤2	85	1,463
≤3	78	1,982
≤4	76	2,121
≤5	75	2,141
≤6	74	2,158
≤ 7	74	2,160
≤8	74	2,162

tion statistics derived with the three aging methods to judge whether they might lead to different management decisions.

Results

We used 2,162 scale and otolith sets and 4,196 length samples to age white crappies. Maximum ages identified by the otolith, scale, and length-frequency methods were 8, 7, and 6 years, respectively. The longevity estimate provided by the length-frequency method is a minimum estimate. Operation of MIX with the typically few large fish collected requires combining large fish into one age-group; consequently, the oldest age-group must be interpreted as possibly including fish of that age and older.

Agreement of ages assigned by the two readers was greater when otoliths were used (91%) than when scales were used (79%), corroborating Boxrucker's (1986) findings. Rates of reader agreement in assessing ages from scales and otoliths were similar when fish were age 2 or less; when older fish were included, agreement in ages predicted from scales became progressively lower, whereas those predicted from otoliths remained above 91% (Table 1). Readers agreed on ages within ± 1 year for 98% of the scale samples and for nearly 100% of the otolith samples.

Ages assigned from otoliths agreed with those assigned from scales in 74% of the comparisons, a slightly higher agreement than the 65% reported for black crappies in Florida by Schramm and Doerzbacher (1985). Agreement was highest for fish age 1 and younger (Table 2). Ages provided by the two structures agreed within ± 1 year in 99% of the samples. All of the ages determined from scale and otolith samples obtained from known-age white crappies (40 in 1988, 20 in 1989, and 1 in 1990) disagreed. Each year, true ages were

TABLE 3.—Comparison of length-at-age estimates for white crappies determined from scales, otoliths, and length-frequencies. Ages with less than three scale or otolith samples per collection were omitted. Values indicate the ratio of length predicted by two methods, and they represent the mean of N ratios obtained with two gears from four Mississippi lakes during 2 years. Asterisks identify ratios significantly different from 1.00 (paired-sample t-tests; $P \le 0.05$).

C		Otolith: scale		Otolith: length frequency			Scale: length frequency		
Age	Ratio	SE	N	Ratio	SE	N	Ratio	SE	N
1	1.10*	0.023	16	1.28*	0.034	5	1.13*	0.024	
2	1.00	0.022	15	1.13	0.063	5	1.09	0.062	5
3	0.95	0.027	14	1.10	0.104	4	1.08	0.167	5
4	0.86	0.048	7	1.07	0.089	3	1.15	0.089	3
5	0.94	0.036	5	1.12	0.068	3	1.13	0.084	3

overestimated by 1 year from scales but were estimated correctly from otoliths.

Length-frequency analysis with MIX was conducted on 11 of 16 samples. Four of the samples that could not be analyzed had only one or no discernible mode, and the other sample was too small to allow the operation of MIX. With the remaining distributions, MIX converged to a solution after 1-10 h of interactive use. The sample size needed for length-mode separation is proportional to the number of modes and degree of overlap. The number of length modes is affected by longevity, and the overlap of modes is affected by rate of growth. Using the number of length modes (usually ≤ 5) and the growth rate characteristic of our data, we found that a sample of more than 70-80 fish was required to enable MIX to converge to a solution.

Back-calculated total lengths based on otolith samples collected in the four lakes averaged 114, 171, 223, 245, 281, 291, 333, and 365 mm for ages 1–8. Overall, back-calculated lengths based on otolith samples were significantly greater ($P \le 0.05$) than those based on scales at age 1 but were not significantly different at older ages (Table 3). Although back-calculated lengths based on scale or otolith samples were generally larger than those based on length-frequency modes, they were significantly larger only at age 1.

Lengths back-calculated from scales and otoliths disagreed even after structures taken only from the same fish and assigned the same age were used in the calculations (Table 4). Back-calculated lengths from these structures disagreed by 10% at age 1 but by 5% or less at older ages. Apparently, errors associated with measuring distances between the nucleus and the annuli, and limitations in the back-calculation model, prevented back-calculation to the same lengths even when aging structures came from the same fish. Error may be introduced by

the back-calculation technique when the assumed relation between fish and structure size deviates from the true relation, or when the assumed correction factor a deviates greatly from the true population value.

Population statistics estimated by the scale, otolith, and length-frequency methods were generally similar (Table 5, Figure 1). No one method consistently produced higher or lower estimates of the statistics considered. Qualitatively, we concluded that fishery statistics computed from age and growth data provided by the three aging methods in Columbus Lake would normally not lead to population interpretations discordant enough to suggest different management strategies.

Discussion

Ages of white crappies based on otoliths seemed to be more accurate and statistically more precise than those based on scales. Scales, but not otoliths, formed a false annulus when fish held under

TABLE 4.—Comparison of length-at-age estimates for white crappies determined by the scale and otolith methods of aging fish. Ages with less than three scale or otolith samples per collection were omitted. Values indicate the ratio of length predicted by the two methods, and they represent the mean of N ratios obtained with two gears from four Mississippi lakes during 2 years. Calculations include only samples for which ages assigned by the two methods agreed. Asterisk identifies the only ratio significantly different from 1.00 (paired-sample t-test; $P \le 0.05$).

		Otolith: scale	
Age	Ratio	SE	N
1	1.10*	0.012	16
2	1.00	0.013	13
3	0.96	0.016	12
4	0.98	0.005	4
5	0.95		1

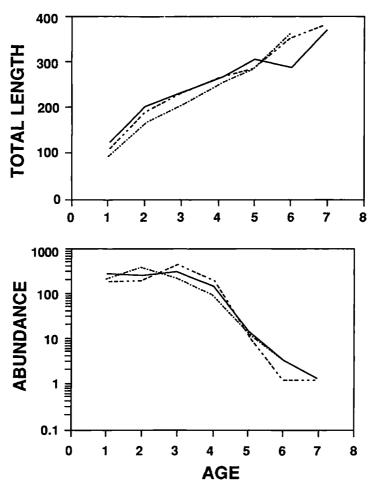


FIGURE 1.—Relation between age and length, and between age and abundance, of white crappies collected with trap nets in Columbus Lake, Mississippi, 1988. Curves were derived from aging with scales (dashed line), otoliths (solid line), and length-frequency modes (dotted line).

crowded conditions were moved into a lesscrowded environment. The stress of hauling and resumption of growth in a more favorable environment probably induced formation of the false annulus. Because otoliths were less likely to form false annuli, we suggest that they are more accurate than scales for aging white crappies. Higher statistical precision is suggested by the greater agreement in ages assigned by independent readers. Moreover, for older fish, annuli were easier to recognize on otoliths than on scales, which probably led to more-precise age assignments. Because aging of white crappie otoliths was done without sectioning, whereas scales had to be mounted between two glass slides, preparation time was less for otoliths. Additionally, because annuli were

more easily recognized in otoliths, otoliths could be read faster than scales.

Measurement error was responsible for most of the differences in length-at-age estimates derived from scales and otoliths. Although incorrect aging would affect back-calculated lengths of individual fish, these errors would be largely nullified by overaging and underaging when mean back-calculated lengths were computed; thus, they would not greatly affect means—particularly for younger agegroups, which often are represented by larger samples. Measurement error can result from difficulty in locating the exact center of the scale's focus or the otolith's kernel and in identifying the margin of annuli or the location where faster growth resumed. Such error is most noticeable at younger

ages because the measurements involved are small and the error is more influential. Differences between lengths back-calculated from scale and otolith samples, whether the calculation included all samples or only those for which ages assigned by the two methods agreed, were almost identical at ages 1-3. These differences could be attributed largely to back-calculation error. At older ages, the scale and otolith methods disagreed more often, and length differences were larger when all fish were included than when only fish were included for which ages assigned by the two methods agreed. These differences could be attributed to back-calculation error as well as to errors in age assignment. Numerous studies, including ours, have demonstrated that scales tend to underestimate the age of older fish (Beamish and McFarlane 1987; Heidinger and Clodfelter 1987). As growth of fish becomes asymptotic, the scale evidently becomes an inaccurate indicator of age. If fish are underaged by scales, growth will be overestimated, as occurred in our study at ages of 3 and older.

The mean lengths of age-groups estimated by length-frequency analysis tended to be smaller than those back-calculated from scale and otolith samples, possibly because fish for length-frequency analysis were collected during March-May, when annulus formation may be incomplete (Maceina and Betsill 1987). Unless length samples are obtained during the period of annulus formation, length modes probably estimate lengths at age incorrectly, biasing the population statistics derived from them. However, we expect that population statistics that require only age data, such as catch curves, are less likely to be influenced by differences in time of collection.

Otoliths were more suitable than scales for aging white crappies because they required no preparation time and were less likely to have false annuli; moreover, their annuli were easier to identify, as suggested by greater agreement between readers. The length-frequency method was also less desirable than the otolith method because separation of highly overlapping modes was difficult, agegroups in the right tail of the length distribution could not be identified, and estimated length-atage values were sensitive to month of collection. Additionally, aging with MIX was an enervating task because no matter how much time was invested, there was no guarantee that the program would eventually converge to a statistically valid solution.

Despite discrepancies among the back-calculated lengths provided by the three methods, most

TABLE 5.—Estimates of selected population characteristics based on age and growth data derived by the scale, otolith, and length-frequency methods. Estimates are for white crappies collected in trap nets in Columbus Lake, Mississippi, 1988.

	Aging method			
Characteristic	Scale	Otolith	Length- frequency	
Sample size	231	231	924	
Longevity (years)	7	7	6	
Growth coefficient (K)2	0.453	0.313	0.398	
L_{∞} (mm) ^a	319	364	334	
Years to sexual				
maturity (175 mm)	1.8	1.7	2.0	
Years to harvestable				
size (200 mm)	2.2	2.2	2.4	
Annual mortality (%)	81	77	72	

^a K and L_{∞} denote the coefficient and asymptopic length in the von Bertalanffy growth equation.

population statistics derived from the data the methods provided did not differ greatly. We suggest that otoliths be used to age white crappies. Alternatively, if the application tolerates reduced accuracy, or if releasing fish alive is a major concern, the scale and length-frequency methods can provide age and growth data that produce population statistics sufficiently similar to those produced by otoliths to be useful in assessing fisheries.

Acknowledgments

This research was funded by the Mississippi Department of Wildlife, Fisheries and Parks through Federal Aid in Sport Fish Restoration Act, project F-87, and by the Mississippi Agriculture and Forestry Experiment Station. We thank Mississippi Cooperative Fish and Wildlife Research Unit students J. Holder, M. Schorr, G. Williams, and Y. Zhao and Mississippi Department of Wildlife, Fisheries and Parks biologists H. Folmar, W. Hubbard, G. Lucas, and K. Meals for their assistance in field collections. M. Brunson, P. Eschmeyer, D. Jackson, S. Miller, and R. Reagan provided helpful reviews.

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