Abstract.– Ages were estimated for sheepshead *Archosargus probatocephalus* (Pisces:Sparidae) from Louisiana waters using transverse sections of sagittae (otoliths). Opaque annuli were validated to have formed in sagittae once per year during April and May in 1987 and 1988. Age range was 1–20 years for fish measuring 22–56 cm fork length and weighing 0.4–3.6 kg. Von Bertalanffy growth models were different for males and females; females exhibited a faster growth rate and achieved larger maximum sizes. There was great variability in age at a given length or weight, which precludes the use of morphometrics as age indices. Otolith weight provided a more precise estimate of age than fish length or weight. The consideration of fish length or weight in addition to otolith weight significantly improved the predictive capability of multiple regression models.

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Age and Growth-Rate Estimation of Sheepshead *Archosargus probatocephalus* in Louisiana Waters Using Otoliths

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The sheepshead *Archosargus probatocephalus* is an estuarine/marine sparid common in coastal waters of the northern Gulf of Mexico. This species supports significant commercial and recreational fisheries off Louisiana. Louisiana commercial landings of sheepshead have increased substantially in recent years, from 59 to 1111 metric tons between 1981 and 1989 (NMFS 1982, 1990), resulting in concern for the species and consideration of development of a management plan. However, little has been reported on sheepshead biology and population dynamics. Of particular concern is the lack of information on age and growth. The only information reported are average growth rates for juveniles in North Carolina (Hildebrand and Cable 1938) and Florida (Springer and Woodburn 1960). The development of valid management plans based on the current available information would be difficult.

Otolith analyses have been proven valid for age estimation of several fish species occurring in the temperate waters of the northern Gulf of Mexico (Johnson et al. 1983, Barger 1985, Beckman et al. 1989, Beckman et al. 1990a). Sectioning of otoliths is often required in order to accurately enumerate annuli for age estimation, especially for long-lived species with large robust otoliths. Sample preparation and ageing are often labor intensive. As an alternative, Boehlert (1985) suggested that otolith size may provide objective, repeatable age estimates and save time and cost in sample processing. Several studies have documented otolith size as greater for older fish than for younger fish of the same size (Templeman and Squires 1956, Wilson and Dean 1983, Boehlert 1985, Reznick et al. 1989, Secor and Dean 1989), and suggested that otolith weight be used to estimate age.

The purposes of this study were to validate age estimates of sheepshead in Louisiana waters using otolith (sagitta) transverse sections, to derive fish growth models, and to determine the potential of using otolith weight for age estimation of this species.

Methods

We sampled sheepshead ($n = 784$) from February 1987 to August 1988. Samples were taken by commercial gillnet (15–18 cm [6–7 inch] stretch mesh) ($n = 461$), trawl ($n = 163$), and haul seine ($n = 43$); recreational hook-and-line ($n = 38$) and spearfishing ($n = 27$); and unknown gear types ($n = 52$). Gillnet and haul seine samples were predominantly from inshore waters in the Mississippi Delta–Lake

Pontchartrain region. Trawl samples were from waters offshore of the Mississippi Delta region. Hook-and-line and spearfish samples were predominantly captured around offshore oil and gas structures during fishing tournaments.

Fork length (FL, mm), total weight (W, g), and sex were recorded and sagittae (otoliths) were removed, stored dry, and weighed (unless damaged in removal). Otoliths were prepared and examined for age determination as described by Beckman et al. (1989). Sagittae were embedded in an epoxy resin medium (Spurr 1969), sectioned in the transverse plane using a Buehler Isomet low-speed saw, mounted on glass slides, and viewed at 15–40× using a stereomicroscope. Terminology is used as defined by Wilson et al. (1987).

Three readers independently counted annuli in each otolith section and estimated the degree of completion of the marginal annulus, as follows: When any portion of an annulus was present at the growing edge, the margin was referred to as "opaque." Translucent edges were assigned to one of three categories: + indicated a translucent zone judged to be 0 to 1/3 complete; ++, 1/3 to 2/3 complete; and +++, 2/3 to totally complete. The completeness of translucent zones was judged based on the estimated width of the adjacent translucent zone and the widths of comparable zones in other otoliths.

We assigned ages based on annulus counts, assuming a 1 January date of birth for convenience and based on spawning periodicity (Wilson et al. 1988).

We validated age estimates by marginal increment analysis, which documents the time of annulus formation at the otolith's edge. Reproducibility of age estimates was determined using the coefficient of variation, index of precision (Chang 1982), and average percent error (Beamish and Fournier 1981). The ages used in analyses were those upon which at least two of the readers agreed. If all readers disagreed on age estimates, the fish was excluded from analyses.

Fork length–weight regressions were fit to the data using the model: $Weight = aFL^b$. Regressions for males and females were compared using analysis of covariance (Ott 1988).

Growth curves were fit by nonlinear regression on raw data (Statistical Analysis Systems 1985). The growth equation for length (von Bertalanffy 1938, 1957) was of the form: $L_t = L_\infty[1 - e^{-K(t-t_0)}]$, and for weight $W_t = W_\infty[1 - e^{-K(t-t_0)}]^b$, where L_t and W_t are the estimated length and weight, L_∞ and W_∞ are the asymptotic length and weight, K is the growth coefficient, t is the age (years), t_0 is the hypothetical age when length or weight would be zero, and b is the exponent from the length-weight regression.

Plots of residuals from regression models were used to check the assumption of normality (Sokal and Rohlf 1981). To test for differences in growth for males and females, a full model, in which sexes were modeled separately, was compared with a reduced model, in which sexes were grouped. An F-test (Ott 1988) was used to test for differences in the models.

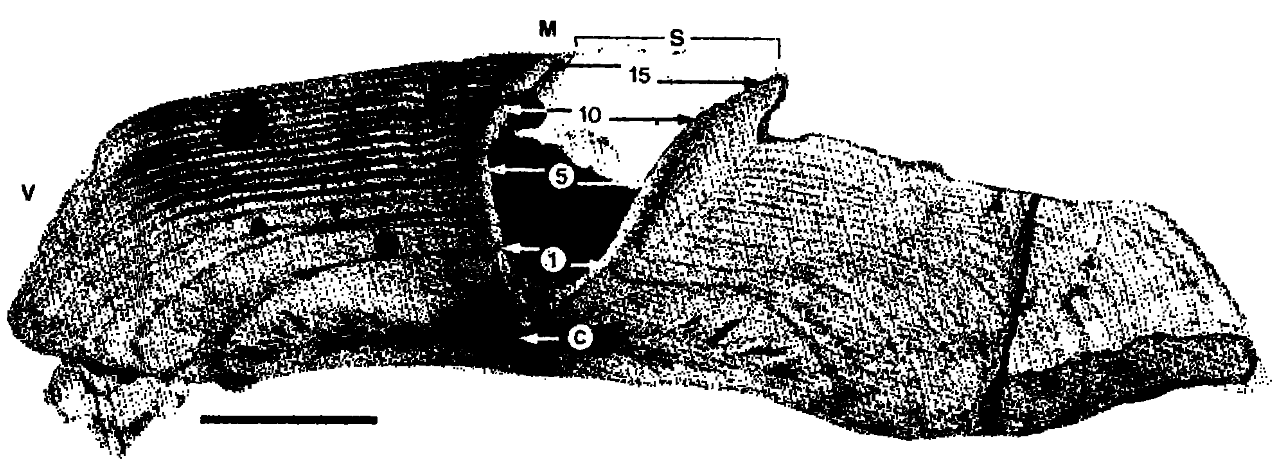

Figure 1
Photomicrograph of a transverse section of a sheepshead otolith (sagitta) under transmitted light. Numbers identify annuli. There are 15 annuli, the margin is translucent, and the fish was captured in February 1988. C = core; S = sulcus; M = medial; V = ventral; Bar = 1 mm.

Multiple linear-regression models were used to estimate age based on otolith weight and fish size. Regressions were fit in a stepwise manner (Statistical Analysis Systems 1985). Independent variables included in models were otolith weight (OW), fork length (FL), total weight (W), condition factor ($CF = W/FL^b$), square and cubic terms for length and weight, and interaction terms (OW–FL, OW–W, OW–CF). All variables were log-transformed to meet the assumptions of normality and homogeneous variances. Regressions for males and females were compared using analysis of covariance.

Results and discussion

In sheepshead, the sagitta is the largest otolith and is oval-shaped with a pointed rostrum. It is laterally compressed with a deeply indented sulcus on its medial surface. It was not possible to discern all annuli for age estimation in whole sagittae. Thin transverse sections exposed narrow opaque and broad translucent zones which alternated from the core out to the growing edge (Fig. 1). Although it was not the axis of most rapid growth, the only axis where annuli were consistently deposited was on the medial surface, ventral to the sulcus (Fig. 1). Counts of annuli (opaque zones) and marginal increment analyses were made in this region using transmitted light. Annulus deposition was either inconsistent or discontinuous in other regions of the sagittae, since annuli were indiscernible there.

One annulus formed per year on the medial surface of sheepshead sagittae. Annulus formation occurred primarily during April and May in 1987 and 1988 (Fig. 2). A translucent zone was formed continuously during non-annulus-forming months, as indicated by the progression of peaks for each marginal index. A substantial translucent zone had formed in most otoliths by July and was estimated as greater than 2/3 complete by December, although most otoliths did not begin annulus formation until the following April.

Only three otoliths (0.4%) were excluded from analyses due to lack of agreement on age estimates among the three readers. At least two readers agreed on ages for all other fish, and these age estimates were used in analyses. All three readers agreed on 75% (566 of 758) of age estimates. Ageing precision was high, based on a mean coefficient of variation (V) of 0.0304, a mean index of precision (D) of 0.0175, and an average percent error (APE) of 0.0234.

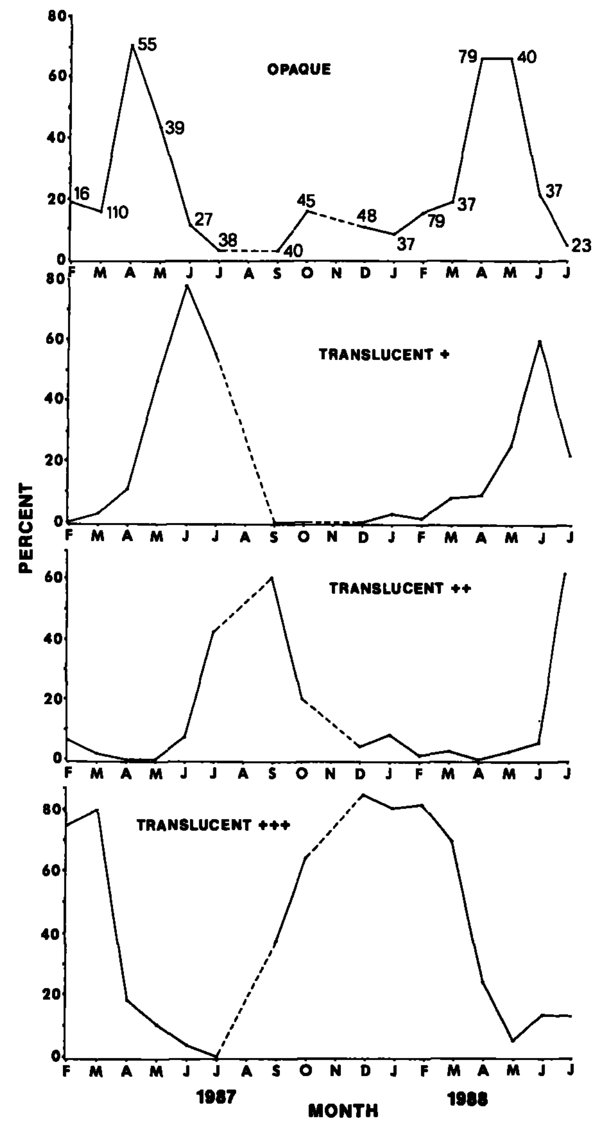

Figure 2
Plot of percent frequency of margin conditions in otoliths (sagittae) of sheepshead vs. month of capture. "Opaque" margins refer to an annulus at the growing edge. "Translucent" margin conditions indicate the estimated degree of completion of the translucent zone at the growing edge: (+) 0 to 1/3 complete; (++) 1/3 to 2/3 complete; (+++) 2/3 to totally complete. Numbers next to the points for opaque margins indicate the sample size for each month.

Annulus deposition in sheepshead otoliths coincided with its reported peak spawning period (March–April; Wilson et al. 1988). However, annulus formation is apparently not a direct result of spawning since it occurred during the same period in mature and immature fish. Reported age at first reproduction is 2–4 years (Wilson et al. 1988). Annuli were deposited in sheepshead otoliths over a similar, but shorter, time period (April–May) as reported for red drum *Sciaenops ocellatus* (January–May; Beckman et al. 1989), black

Table 1

Summary of age and growth analyses of sparids. K and L_∞ are parameters from von Bertalanffy growth models. Age and length are the maximums reported by the source. Lengths marked (*) are total lengths, others are fork lengths. M and F refer to parameters for males and females, when reported.

Species	Source	Location		K	L_∞	Age (max.)	Length (max.)
Archosargus probatocephalus	This study	N. Gulf of Mexico	(M)	0.42	419	20	500
			(F)	0.37	446	20	500
Stenotomus caprinus	Geoghegan and Chittenden (1982)	N. Gulf of Mexico		—	—	3	193
Calamus leucosteus	Waltz et al. (1982)	U.S. Atlantic		0.17	331	12	410
Pagrus pagrus	Manooch and Huntsman (1977)	U.S. Atlantic		0.10	763	15	*690
Stenotomus chrysops	Finkelstein (1969)	U.S. Atlantic	(M)	0.27	343	15	370
			(F)	0.23	374		
Cheimerius nufar	Coetzee and Baird (1981)	South Africa		0.07	954	22	*705
Cymatoceps nasutus	Buxton and Clarke (1989)	South Africa		0.05	1090	45	1099
Pachymetopon aeneum	Buxton and Clarke (1986)	South Africa		0.13	467	12	400
Pachymetopon blochii	Pulfrich and Griffiths (1988)	South Africa		0.16	411	12	350
Pterogymnus laniarius	Hecht and Baird (1977)	South Africa		0.19	481	11	*422
Pagellus bellottii	Koranteng and Pitcher (1987)	Ghana	(M)	0.38	257	6	250
			(F)	0.23	286		
Pagrus major	Sakamoto (1984)	Japan		0.21	670	10	590
Chrysophrys auratus	Horn (1986)	New Zealand		—	—	60	650

drum *Pogonias cromis* (January–April; Beckman et al. 1990a), and Atlantic croaker *Micropogonias undulatus* (February–April; Barger 1985) in the northern Gulf of Mexico. It is likely that annulus formation in sagittae of these species is in response to environmental factors and is not related to reproductive seasonality, since all three species exhibit different spawning seasons: red drum, August–October (Wilson et al. 1989); black drum, December–April (Beckman et al. 1990b); Atlantic croaker, September–March (White and Chittenden 1987).

Sheepshead are relatively long-lived, with a maximum life span of at least 20 years based on our estimates. Greater ages are likely since the Louisiana gamefish record is 9.6 kg (Louisiana Outdoor Writers Assoc. 1987), and the maximum sized fish in this study was 3.9 kg. The maximum age we observed for sheepshead is greater than reported for other Gulf/U.S. Atlantic sparids (Table 1). However, great longevity is apparently not unusual for this family, as greater maximum ages have been reported for sparids elsewhere (Table 1).

Length–weight regressions for males and females were not significantly different ($P = 0.991$ for intercepts, $P = 0.647$ for slopes). However, since the exponents are used in growth models, regressions are presented for both sexes. Regressions were,

for males:

$$\text{Weight} = 4.48 \times 10^{-5}\ \text{FL}^{2.88} \quad r^2 = 0.943$$

for females:

$$\text{Weight} = 5.30 \times 10^{-5}\ \text{FL}^{2.85} \quad r^2 = 0.926$$

sexes combined:

$$\text{Weight} = 5.46 \times 10^{-5}\ \text{FL}^{2.86} \quad r^2 = 0.923.$$

The separation of sexes in growth models resulted in a significantly better fit by length and weight when compared with models in which sexes were combined ($P<0.001$). Therefore, separate von Bertalanffy growth curves for males and females were used to model growth in length (Fig. 3) and weight (Fig. 4). Residuals appeared normally distributed about the regression lines. Growth models fit were, by length,

males:

$$L_t = 419(1 - e^{-0.417(t+0.901)}) \quad r^2 = 0.589$$

females:

$$L_t = 447(1 - e^{-0.367(t+1.025)}) \quad r^2 = 0.532,$$

and by weight,

males:

$$W_t = 1900(1 - e^{-0.280(t+2.657)})^{2.88} \quad r^2 = 0.549$$

females:

$$W_t = 2557(1 - e^{-0.219(t+3.061)})^{2.85} \quad r^2 = 0.474,$$

The growth curves suggest rapid growth for sheepshead to an age of 6–8 years, after which an asymptote is approached. The values of K, the von Bertalanffy growth coefficient, for sheepshead are relatively high when compared with other sparids (Table 1) and to nonsparid perciform fish of similar size (see Pauly 1980). This indicates that sheepshead exhibit relatively rapid growth to an asymptotic size. This could be a result of living in the highly productive waters adjacent to the Mississippi Delta.

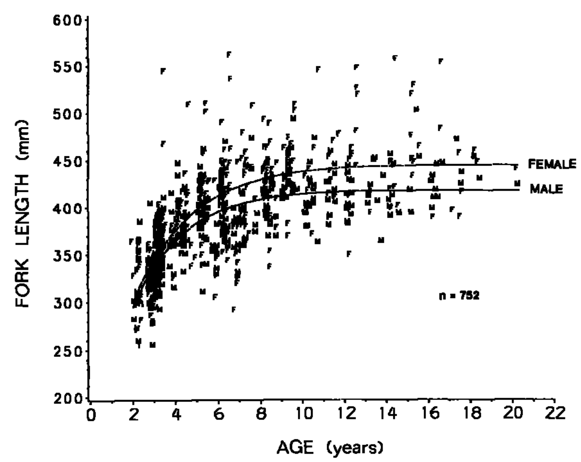

Figure 3
Von Bertalanffy growth models by length for male and female sheepshead. M = male; F = female.

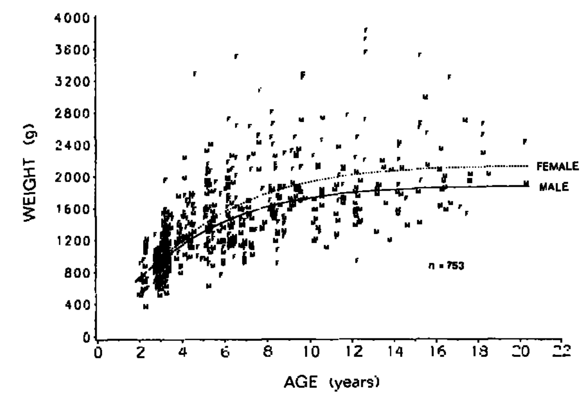

Figure 4
Von Bertalanffy growth models by weight for male and female sheepshead. M = male; F = female.

Due to the large variability in age at a given body size, size does not accurately estimate age for sheepshead, especially beyond 2–3 years of age. For example, a given sheepshead greater than 400 mm or 1.5 kg could be of any age from 3 to 20 years.

Otoliths ranged in weight from 28.3 mg (for a 229-mm, 312-g, 2-year-old fish) to 323.5 mg (for a 450-mm, 2410-g, 18-year-old fish). Age-otolith weight (OW) regressions (Fig. 5) were significantly different for males and females ($P<0.0001$ for slopes, $P=0.0006$ for intercepts); therefore multiple-regression models were fit separately by sex. Dependent variables included in multiple regression models at the 0.10 level of significance were otolith weight and total weight for males, and otolith weight and fork length for females. The addition of any other variables did not significantly improve the fit of the models. The model statistics are presented in Table 2.

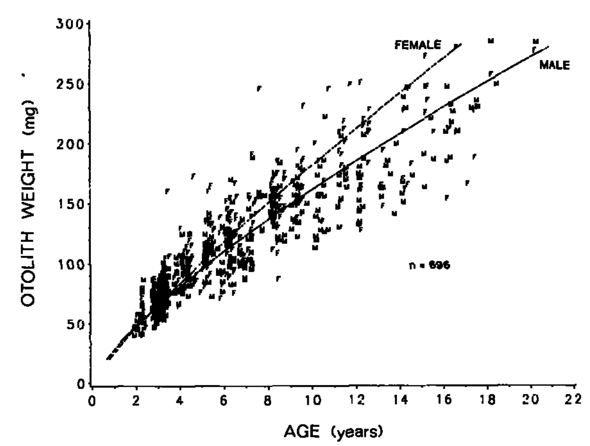

Figure 5
Log-linear growth models by otolith weight for male and female sheepshead. M = male; F = female.

Since otolith weight accounted for more of the variability in age (83–85% vs. <60% for fish length or weight), it was the best estimator of age of all morphometric variables considered. However, there was still considerable variability in otolith weight within each age class. Although some of the remaining variability (1–2%) was accounted for by considering fish length or weight in addition to otolith weight, the unexplained variability was great enough that these models could not be used for precise estimation of sheepshead age, such as is needed to determine population year-class structure. However, they could be used to approximate age distribution patterns in the population. In order to obtain precise age estimates of individual fish, otolith annulus counts are necessary.

The linear relationship between otolith weight and age indicates that otolith growth is continuous for sheepshead, whereas fish size (length and weight) asymptotes at intermediate ages and, therefore, is not continuous. This suggests that fast-growing (younger) sheepshead have lighter otoliths than equal-sized slow-growing (older) sheepshead, i.e., otolith growth continues with age, independent of fish growth. This may be a general characteristic of fish growth, as similar observations have been made for other fish species (Templeman and Squires 1956, Beamish 1979, Wilson

Table 2

Regression coefficients and statistics on multiple-regression models of age for sheepshead. Models were fit in a stepwise manner using independent variables of otolith weight, fish standard length, fish total weight, condition factor, and associated interaction terms. Variables were log-transformed for analyses.

Variable	Coefficient	SE	P	Partial r^2
Males (n = 330)				
(1-variable model)				
Intercept = −4.420				
Otolith weight	1.321	0.0305	<0.0001	0.850
(2-variable model)				
Intercept = −3.207				
Otolith weight	1.569	0.0594	<0.0001	0.850
Total weight	−0.331	0.0686	<0.0001	0.010
Females (n = 366)				
(1-variable model)				
Intercept = −3.824				
Otolith weight	1.176	0.0276	<0.0001	0.832
(2-variable model)				
Intercept = 1.258				
Otolith weight	1.484	0.0502	<0.0001	0.832
Fork length	−1.094	0.1531	<0.0001	0.021

and Dean 1983, Radtke et al. 1985, Reznick et al. 1989, Secor et al. 1989). Since fish length or weight accounts for significant variability in age after considering otolith weight, large fish have larger otoliths than equal-aged small fish, i.e., otolith growth is affected by fish growth. These observations support the proposition by Secor and Dean (1989) that not only do otoliths grow in a continuous manner, independent of somatic growth, but also that otolith growth is coupled in some manner to somatic growth.

These growth patterns should be considered when using otoliths for back-calculation of fish size at age. Since continued otolith growth uncoupled from somatic growth would result in slower-growing fish having larger otoliths at a given fish size, the fish-otolith size relationship would be different for fast-growing and slow-growing fish. This bias would be more pronounced at older ages, since otolith growth could continue even if somatic growth has stopped.

Due to gear selectivity and sorting of some samples by fishermen, the age distribution of our samples was not considered to be representative of the Louisiana sheepshead population. Future research should include fishery-independent sampling to accurately characterize the age structure of the sheepshead population, determine variability in recruitment, estimate mortality rates, and identify sources of variability in growth. Additional samples of older fish are required to complete validation of age estimates for the oldest individuals.

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