

AGE AND GROWTH OF SHEEPSHEAD, *ARCHOSARGUS PROBATOCEPHALUS* (PISCES: SPARIDAE), FROM THE NORTHWEST COAST OF FLORIDA

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ABSTRACT

Age and growth is described for sheepshead (*Archosargus probatocephalus*) from the northwest coast of Florida. Fish ($n = 511$) were collected from Cedar Key to Keaton Beach, Florida, from March 1997 to November 1998. The majority of fish were subspecies *A. p. probatocephalus* (84%), 11% were *A. p. oviceps*, and 5% could not be designated. Fish were aged using sectioned sagittal otoliths. Maximum ages were 12 and 14 yrs for females and males, respectively. Marginal-increment analysis and chemical marking validated the formation of only one annulus per year. Annulus deposition occurred during March and April, and was complete by May. Patterns of growth in both length-at-age and weight-at-age were not different either between the sexes or between subspecies. Sheepshead were smaller at any given age compared to fish from South Carolina, but were generally larger than sheepshead used in coast-wide estimates for Florida. Fish from Louisiana were of similar overall size compared to sheepshead from both the northwest coast of Florida and coast-wide Florida. The use of regionally-explicit models of growth may be appropriate for sheepshead because of growth differences among populations in the southeastern United States. These differences in growth may result from several factors, including differences in mortality rates, environmental conditions, or genetic variation.

Sheepshead (*Archosargus probatocephalus*) (Family Sparidae) occur in coastal waters from Nova Scotia to Brazil (Caldwell, 1965) and are common in nearshore waters of the southeastern United States (Jennings, 1985). Combined landings of sheepshead by recreational and commercial fishers in Florida peaked at 2540 t (5.6 million pounds) in 1992. From 1986–1996, ~60% of Florida's total catch was from the Gulf coast, with the remainder from the Atlantic coast. An average of 83% of the annual combined harvest from the Gulf coast of Florida was landed in the recreational fishery, compared with 17% from the commercial fishery. Since 1992 the catch has decreased by 50% statewide (Murphy et al., 1997), resulting primarily from the enactment of new fishing regulations including a statewide ban on the use of large gill nets in 1995. Concomitant with this was the introduction of minimum size and bag limits intended to lower fishing mortality (Murphy et al., 1997).

One essential component of the population dynamics of sheepshead needed for effective management is comprehensive age and growth studies. Limited age and growth data are available for sheepshead from Georgia (Music and Pafford, 1984) and near Cape Fear off North Carolina (Schwartz, 1990), based on aging sheepshead using scales. These studies are problematic, however, because scales of older sheepshead (>4 yrs) are difficult to read and may underestimate their age by one or more years (Schwartz, 1990; Dutka-Gianelli, 1999). As a result, studies based on scale analysis may not be directly comparable to more recent studies based on determining ages using otoliths. Ages have been obtained using sectioned otoliths for sheepshead from Lake Pontchartrain and the Mississippi delta area of Louisiana in the northern Gulf of Mexico (Beckman et al., 1991)

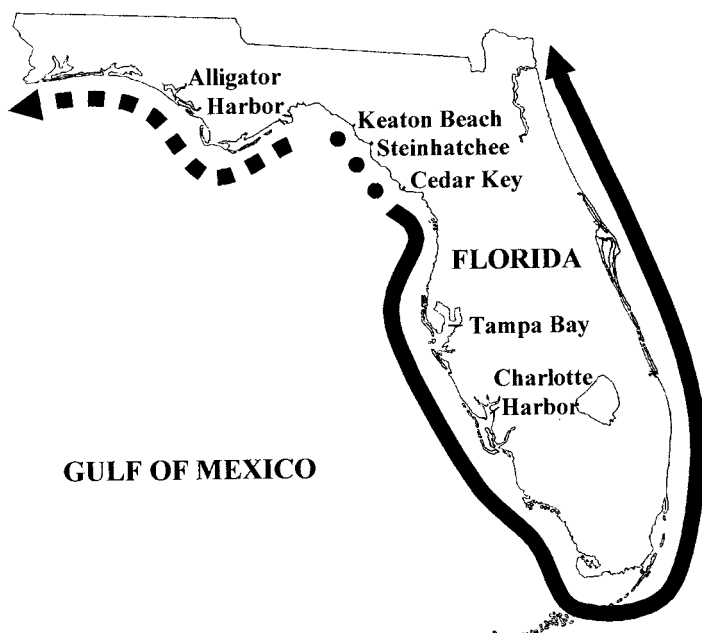


Figure 1. Distribution and sampling of sheepshead (*Archosargus probatocephalus*) subspecies in Florida: *A. p. probatocephalus* (solid line) and *A. p. oviceps* (dashed line) (after Caldwell 1965); and sampling area (dotted line).

and in coastal waters of South Carolina (Wenner, 1996). Murphy et al. (1997) in a summary of unpublished data from the Florida Department of Environmental Protection-Florida Marine Research Institute (FDEP-FMRI) obtained coast-specific age and growth estimates of sheepshead in Florida for a stock assessment. A more detailed analysis of the specific age and growth of sheepshead from Tampa Bay, Florida, is in progress [Tim McDonald, pers. comm., FDEP-FMRI, 100 Eighth Avenue SE, St. Petersburg, Florida 33701-5095]. To date, no detailed relationships of age and growth have been published for sheepshead from the northwest coast of Florida. In addition, the use of sectioned otoliths to age sheepshead has been validated using marginal-increment analysis for fish from Louisiana (Beckman et al., 1991) and South Carolina (Wenner, 1996, for fish <4 yrs old), but not from Florida. Chemical marking techniques (Tanaka et al., 1981; Beamish and McFarlane, 1987; Thomas et al., 1995) have yet to be applied to sheepshead.

The biological characteristics upon which management policies for sheepshead are based may be further complicated by the co-occurrence of both of the recognized North American subspecies of sheepshead on the west coast of Florida. These two subspecies appear to have disjunct geographical ranges in the Gulf of Mexico (Fig. 1), with *A. p. oviceps* ranging from Alligator Harbor (29°54'N, 84°23'W), Florida, to Campeche Bank, Mexico, and *A. p. probatocephalus* ranging from Cedar Key, Florida (29°08'N, 83°02'W) to Nova Scotia (Caldwell, 1965). Subspecific designation is based on coloration (size and number of black body bars), the number of gill rakers on the lower limb of the first gill arch, the number of lateral line scales, and the number of spines and rays in the dorsal fin (Caldwell, 1965) (Table 1). The subspecific status of sheepshead on the west coast of Florida between Cedar Key and Alligator Harbor is unknown even though there are well

developed recreational and commercial fisheries in that area (Murphy et al., 1997). The presence of subspecific differences in age and growth relationships of sheepshead on the west coast of Florida could affect whether sheepshead require management plans on a coast-wide or subspecific (and therefore regional) basis.

The objectives of this study were: (1) to identify the subspecies of sheepshead present on the northwest coast of Florida; (2) to validate ages derived from otoliths for these sheepshead using marginal-increment analysis and chemical marking; (3) to model their age and growth; and (4) to compare the age and growth of sheepshead from the northwest coast of Florida with fish from Louisiana (Beckman et al., 1991), South Carolina (Wenner, 1996), and from Florida, based on generalized, coast-wide estimates of growth for sheepshead (Murphy et al., 1997).

MATERIALS AND METHODS

FISH COLLECTION AND SAMPLING

Sheepshead were collected along the Gulf of Mexico coast of Florida from areas around Cedar Key (29°8'N, 83°W) (n = 101 fish) and from Steinhatchee to Keaton Beach (29°50'N, 83°35'W) (n = 410 fish) (Fig. 1), in water less than 10 m (35 ft) depth. Collections were made monthly from March 1997 to November 1998. Fish were sampled from research collections (n = 151) and from the commercial fishery (n = 360). Sheepshead were caught by hook-and-line (n = 209) using natural bait (e.g., shrimp, squid, octopus, and crab), spearfishing (n = 66), gillnetting (n = 8), castnetting (n = 37), beach seining (n = 11), and trapping (n = 37) around offshore structures, oysters bars, river mouths, and artificial reefs. Gear type for 143 fish sampled from commercial catches was unknown.

Fish were measured for fork length (FL) to the nearest 1 mm and weighed to the nearest 0.1 g. Each fish was identified to subspecies based on meristic characters (Table 1). Fish were sexed based on internal examination of the gonads, and sagittal otoliths were removed for aging.

AGE DETERMINATION

The left sagittal otolith was prepared for aging using thin-sections (Chilton and Beamish, 1982). The whole otolith was secured to a glass slide using a hot glue gun and ~2–3 sections of ~0.5 mm thick were taken through the core using a Buehler® Isomet 1000 low-speed saw. Sections were then permanently mounted on glass slides using Histomount® (National Diagnostics) and examined for annuli using a compound microscope. Otoliths of each fish were read twice independently by the primary reader (JDG) with a 2–4 wk interval between counts. A subset of otoliths (n = 75) was read by a second reader (DJM). When readers disagreed the otolith was aged independently again by both after a 2–4 wk interval. Only age estimates that agreed in a minimum of three out of four

Table 1. Summary of the variation in meristic characters in the two North American subspecies of sheepshead (*Archosargus probatocephalus*) (based on tables 1–4 in Caldwell, 1965). Ranges are given in parentheses.

Subspecies	Number of body bars (left/right side)	Mean number of scales on lateral line	Mean number of gill rakers ^a	Number of dorsal fin spines/rays
<i>A. p. oviceps</i>	5/5 (6/6, 5/6, 4/4, 4/5, 6/7)	46.7 (43–53)	8.8 (7–9)	XI–XII/11–12 (XI–XII/10–13)
<i>A. p. probatocephalus</i>	6/6 (5/5, 5/6, 6/7)	45.3 (41–50)	8.4 (7–9)	XII/11–12 (X–XII/10–13)

^a counted on the lower limb of the first gill arch

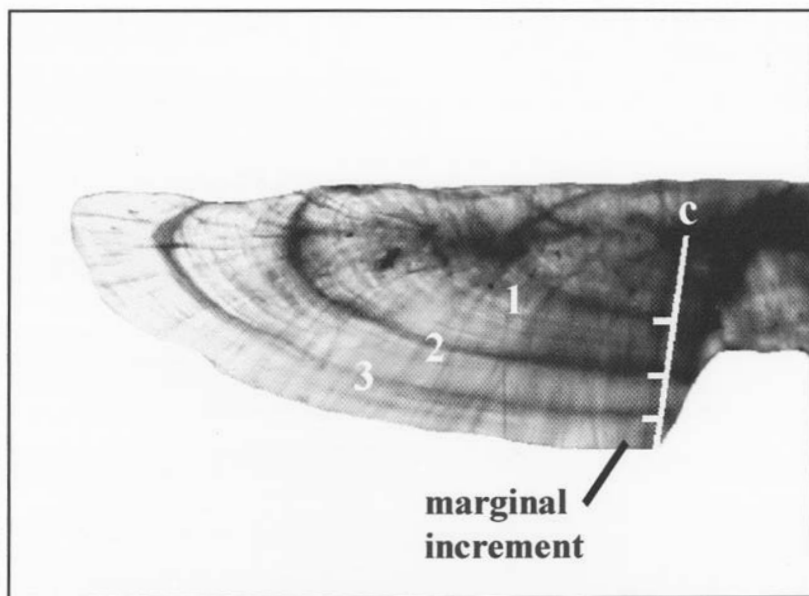


Figure 2. Thin-sectioned otolith from a 3-yr old sheephead showing the core (C) of the otolith, the measuring axis, and the marginal-increment or growth on the edge of the otolith.

examinations were included in the analysis. Aging precision (i.e., reproducibility of age estimates) between and within readers was estimated using percent agreement (Kimura and Lyons, 1991), and the coefficient of variation and index of precision (Chang, 1982).

AGING VALIDATION

Ages determined from the examination of otolith sections from sheephead were validated by marginal-increment analysis and chemical marking.

Marginal-Increment Analysis.—The periodicity in annulus deposition was determined using the index of completion $C = (W_n / W_{n-1}) \cdot 100$ (Tanaka et al., 1981); where W_n is the size of the marginal-increment; and W_{n-1} is the size of the previously completed increment. Measurements were made with a digital image analysis system (Image-1®, Universal Imaging Corp.). Otoliths were measured along an axis on the proximal (internal) medial surface, ventral to the sulcus, where the annuli were most distinct (Fig. 2). A plot of the monthly mean index of completion and standard error over a 12-mo period was examined for the number and timing of minima present.

Chemical Marking.—Sheepshead ($n = 18$) were collected from the northwest coast of Florida, near the mouth of Suwannee and Wacassasa Rivers, in late March/early April 1998. Fish were transported live to the Whitney Marine Laboratory, University of Florida, St. Augustine, where they were maintained in outdoor, flow-through seawater tanks (~6 m diameter and ~1.5 m deep) under ambient light. Sheepshead were fed 1–2% body weight d^{-1} on a variety of foods, including fresh and frozen shrimp, squid, and SilverCup® fish pellets. Following a recovery period in captivity of a few days, each fish was anesthetized with tricaine methanesulfonate (MS-222) and measured for length and weight. A passive integrated transponder (PIT) tag was inserted into the left epaxial musculature to allow individual fish identification (Jenkins and Smith, 1990; Prentice et al., 1990). Nine fish were interperitoneally injected with oxytetracycline (OTC) dissolved in sterile saline at a concentration of 50 mg kg^{-1} body weight (Beamish et al., 1983; Thomas et al., 1995). Another nine fish were injected with calcein (CAL) dissolved in sterile saline at a concentration of 25 mg kg^{-1} body weight (Thomas et al., 1995). After recovering from the anesthetic, all fish were returned to

the large outdoor tanks. Two weeks after the injections of OTC or CAL, two sheephead were sacrificed to verify that the chemical marking agent had been incorporated into their otoliths. For the next 12 mo, tanks were drained and cleaned periodically, and PIT tag retention was checked. At the end of 12 mo, all surviving fish were sacrificed and their otoliths were removed and prepared for aging. Otoliths of OTC- and CAL- injected fish were stored in the dark to prevent fading of the fluorescent mark (Beamish et al., 1983). Once sectioned, otoliths were exposed to both transmitted visible light to enumerate and locate all annuli, and then to epi-fluorescence illumination to view the fluorescent mark of the OTC or CAL. Digital images from the visible and epi-fluorescent illumination were then superimposed using Adobe® Photoshop® 4.2 to indicate the position and number of the annuli in relation to the OTC/CAL mark. The number of annuli formed after the OTC/CAL mark indicated the number of annuli formed in a 12-mo period.

GROWTH OF SHEEPSHEAD

Total weight (W , in g) as a function of fork length (FL , in mm) was described by $\log_{10} W = \log a + b \log_{10} FL$; where a is the y-axis intercept of the regression and b is the slope of the regression (Anderson and Neumann, 1996). Difference in the weight-length relationship between males and females was tested using analysis of covariance (Zar, 1996).

For the growth analyses, age of sheephead was calculated as absolute age based on an April 1st birth date, which coincided with spawning of sheephead in the area (Jennings, 1985), as well as annulus formation (March/April/May). Age was therefore assigned as a decimal fraction of the month of capture of the fish past April 1st. The von Bertalanffy growth equation

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

was fit to fork length and age data of male and female sheephead using a Marquardt-Levenberg algorithm (Axum 5.0, Mathsoft); where L_t = predicted length at time t (age), L_{∞} = asymptotic length, k = growth coefficient, and t_0 = theoretical time (age) when length would be 0 (von Bertalanffy, 1938; Ricker, 1975). Von Bertalanffy growth model parameters were estimated for observed total body weight as a function of absolute age by substituting weights in place of lengths in the von Bertalanffy growth equation and incorporating b (derived by the weight-length regression)

$$W_t = W_{\infty} \left[1 - e^{-k(t-t_0)} \right]^b \quad (\text{Beckman et al., 1991; Beverton and Holt, 1957}).$$

Differences in growth between male and female sheephead, and between subspecies, were determined using a variance ratio test (Zar, 1996) comparing the mean square error of each full regression model (based on modeling the sexes separately) to the mean square error of a reduced regression model with the sexes pooled (Davis and West, 1992; Murphy and Taylor, 1994). Sexes were pooled for growth analyses if there was no significant difference in the growth between males and females. All tests of significance were at $\alpha \leq 0.05$.

RESULTS

SAMPLING

Of the 511 sheephead from the northwestern Gulf of Mexico, 238 were male, 265 were female, and eight were of unknown sex. Legal-sized sheephead (>12 in or >305 mm FL) caught in the commercial fishery or research fishing ranged between 305 and 522 mm FL (Fig. 3), with the majority (>60%) between 305–410 mm FL. Sub-legal sized

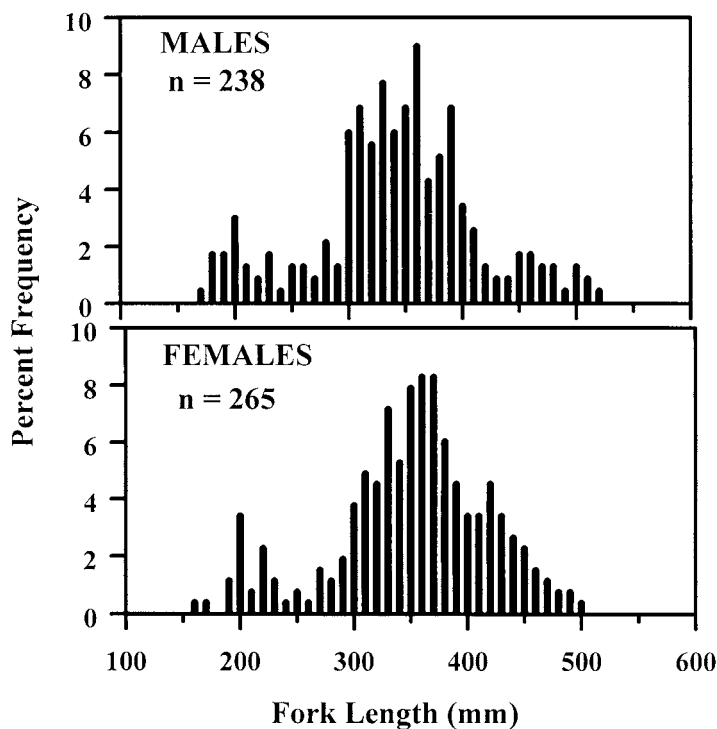


Figure 3. Length-frequency distributions of male and female sheephead from the northwest coast of Florida. Fork lengths are in 10-mm intervals.

sheepshead obtained through research hook-and-line fishing ranged from 165–300 mm FL (Fig. 3).

Meristic characters (Table 1) indicated that 84% ($n = 428$ of 511 total) of the fish were *A. p. probatocephalus* and 11% ($n = 56$) were *A. p. oviceps*. Of the total, 5% ($n = 27$) were not classified because of overlapping meristic characters (e.g., asymmetry in the number of body bars with five on one side and six on the other side of the same fish).

AGE DETERMINATION

Annuli observed in sectioned sagittae of sheepshead were most distinct to count and measure along the ventral axis of the sulcus (Fig. 2). Twelve otoliths were excluded from aging analysis because of disagreement in four independent readings. For the primary reader, the percent agreement was 98.8%, the coefficient of variation (CV) was 0.26%, and the index of precision (D) was 0.21%. Between the primary and secondary readers, the percent agreement was 97.3%, CV was 0.17%, and D was 0.12%. The majority of sheepshead were 3 to 6 yrs of age, with maximum ages of 12 and 15 yrs for females and males, respectively.

AGE VALIDATION

Marginal-Increment Analysis.—Based on measurements of sectioned otoliths, the mean monthly index of completion showed that the majority of the fish deposited their annulus

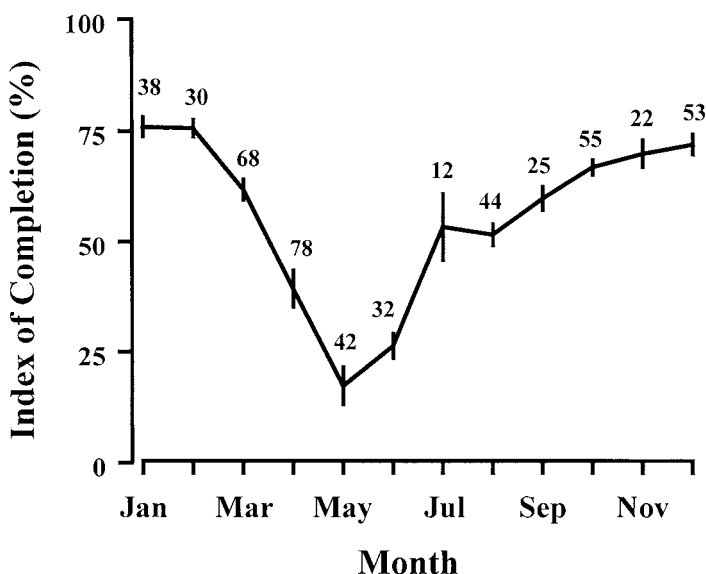


Figure 4. Mean index of completion of thin-sectioned otoliths of sheepshead over a 12-mo period. Vertical bars are standard errors.

during March, April and May, with a minimum in May (Fig. 4). The uni-modal plot also indicated that only one annulus was formed in a 12-mo period in otoliths of sheepshead from the northwest coast of Florida.

Chemical Marking.—All seven OTC-injected sheepshead survived 1 yr in captivity but eight of the nine CAL-injected fish died within 24-hr after injection. Fish were between 200 and 305 mm FL and either 2 or 3 yrs old when initially injected. After 1 yr in captivity, fish were sacrificed and their otoliths extracted. Otolith sections showed that only one annulus had formed in the year between the time of the injection (the fluorescent mark) and the excision of the sagittae. This indicated that only one annulus had formed in a 12-mo period.

GROWTH OF SHEEPSHEAD

Length-Weight.—The relationship of total weight to fork length for male and female sheepshead was not significantly different between the sexes (ANCOVA: slopes $F = 0.37$, $P = 0.54$; elevations $F = 0.45$, $P = 0.50$). Sexes were therefore pooled and a regression of their total body weight (W) in relation to their fork length (FL) was significant ($F = 29899$, $P < 0.001$) and described by $W = 4.4 \times 10^{-5} FL^{2.89}$ ($r^2 = 0.98$, $n = 511$).

Length and Weight in Relation to Age.—Examination of the growth curves for the two subspecies of sheepshead (*A. p. probatocephalus* versus *A. p. oviceps*) found no significant difference in von Bertalanffy growth curves for length (Variance Ratio Test: $F_{\text{calc}} = 1.05$, $P > 0.5$). Therefore, for final analysis both subspecies were pooled, as well as those individuals that were not designated as *A. p. probatocephalus* or *A. p. oviceps*. Since von Bertalanffy growth curves for female and male sheepshead were also not significantly different (Table 2), the sexes were pooled. The resulting equation for the relationship of length at age for all fish was:

$$L_t = 490.4 \left[1 - e^{-0.26(t+0.42)} \right] \quad (r^2 = 0.74, n = 499) \text{ (Fig. 5).}$$

The rapid growth for the first 4–5 yrs was followed by a reduced rate which reached an asymptote at ~490 mm.

Von Bertalanffy growth curves derived from observed weight at age for female and male sheephead were not significantly different (Table 2). Parameter estimates of the von Bertalanffy equation fit to the pooled data were

$$W_t = 2731.2 \left[1 - e^{-0.25(t+0.53)} \right]^{2.89} \quad (r^2 = 0.65, n = 499) \text{ (Fig. 6).}$$

As with length, sheephead gained weight rapidly in their first 4–5 yrs, after which their rate of weight gain decreased.

Table 2. Von Bertalanffy parameters fitted to observed fork length (mm) and total weight (g) as a function of absolute age for sheephead from the northwest coast of Florida. Variance ratio tests were used to compare the separate-sex models to the model for sexes combined. Combined models include immature sheephead.

Variable	Sex	L_∞ or W_∞	k	t_0 (yr)	df	MSE	F_{calc}	P
Fork Length	Male	509.2	0.23	−0.52	230	1,189.8	1.08	>0.2
	Female	475.7	0.28	−0.46	255	1,425.7	1.11	>0.2
	Combined	490.4	0.26	−0.42	496	1,321.7		
Weight	Male	2,934.9	0.23	−0.53	230	106,873.0	1.12	>0.5
	Female	2,523.9	0.28	−0.52	255	134,439.0	1.13	>0.5
	Combined	2,731.2	0.25	−0.53	496	120,294.0		

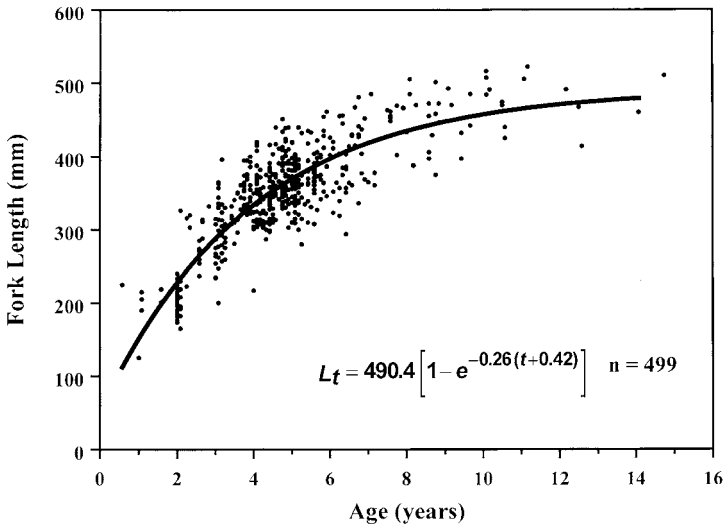


Figure 5. Fork length as a function of age for sheephead from the northwest coast of Florida. Solid line is the von Bertalanffy growth curve for both sexes combined.

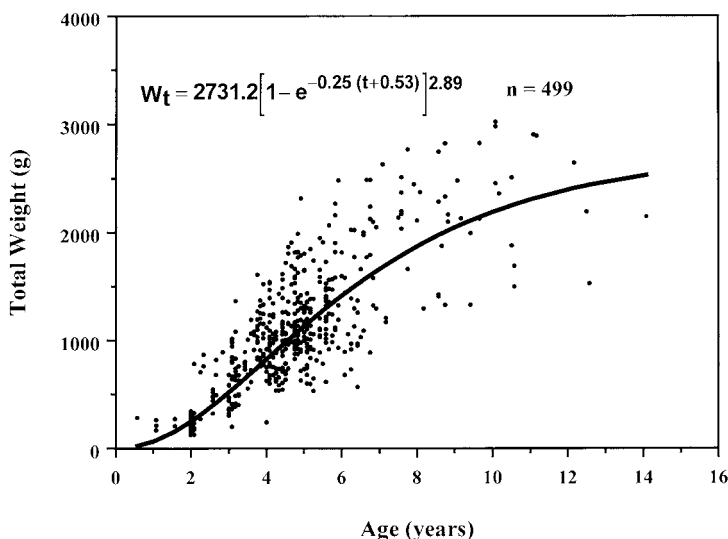


Figure 6. Total weight as a function of age for sheepshead from the northwest coast of Florida. Solid line is the von Bertalanffy growth curve for both sexes combined.

DISCUSSION

AGE DETERMINATION AND VALIDATION. —Annuli observed in thin-sectioned otoliths of sheepshead were distinct for fish in all age classes and aging precision was high (98.8%). The validation of the sectioned-otolith method for age determination by marginal-increment analysis (Fig. 4) and chemical marking also supported this technique as an accurate aging method for sheepshead from the northwest coast of Florida. Fish injected with oxytetracycline had higher survival than sheepshead injected with calcein. This has also been observed in immersion marking of red drum (*Sciaenops ocellatus*) at higher concentrations of calcein (Thomas et al., 1995) and in various other marking studies (C. Wilson, pers. comm., Louisiana State University, Baton Rouge, Louisiana 70803-7503).

The period of opaque zone formation (annulus) in the otolith (March–May) coincided with the time of annulus deposition for sheepshead in the northern Gulf of Mexico (April–May) (Beckman et al., 1991). Beckman et al. (1991) and Wenner (1996) also used thin-sections of otoliths to age sheepshead from Louisiana and South Carolina, respectively (Table 3). Based on otoliths, the maximum age reported for sheepshead in South Carolina (26 yrs; Wenner, 1996) was greater than ages reported for sheepshead in Louisiana (20 yrs; Beckman et al., 1991), and Florida (14 yrs; Murphy et al., 1997; and this study).

Music and Pafford (1984) aged sheepshead from Georgia using scales up to the age of 14 yrs but only validated their method using marginal-increment analysis for fish less than 5 yrs old. Schwartz (1990) aged sheepshead up to 8 yrs old from North Carolina using scales but did not validate his technique. Wenner (1996), however, found sheepshead scales to be unreadable after 2 yrs of age. Similarly, Dutka-Gianelli (1999) in a comparison of age estimates obtained from scales and sectioned otoliths of sheepshead also concluded that scales underestimated the age of fish >3 yrs. All of the studies using scales to age sheepshead were therefore not used in any further comparisons.

Table 3. Von Bertalanffy growth curve parameters, maximum fork length, maximum age, aging method, and validation studies reported for sheephead. (MI = Marginal-increment analyses and CL = chemical labeling using oxytetracycline and calcein).

Source	Location	Sex	L_{∞}	k	Maximum Length (mm)	Maximum Age (yrs)	Aging Method	Validation/Technique
This study	Northwest Florida	combined	490	0.26	522	14	otoliths	yes/MI, CL
Murphy et al. (1997)	Florida: Gulf coast	combined	449	0.20	-	11-14	otoliths	-
	Florida: Atlantic coast	combined	405	0.33	-	11-14	otoliths	-
Wenner (1996)	South Carolina	combined	505	0.29	560 ^a	26	otoliths	yes/MI (fish <4 yrs)
Beckman et al. (1991)	Louisiana	males	419	0.37	505	20	otoliths	yes/MI
		females	446	0.42	563	20		
Schwartz (1990)	North Carolina	combined	-	-	662 ^b	8	scales	no
Music and Pafford (1984)	Georgia	males	-	-	515	-	scales	yes/MI
		females	-	-	541	-		(fish <5 yrs)

^aWenner (1996) data initially reported as total length. Data converted to fork length by TL-FL relationship given in his report.

^bSchwartz (1990) data initially reported as total length. Data converted to fork length by TL-FL relationship given in Dutka-Gianelli (1999) (not available in Schwartz's report).

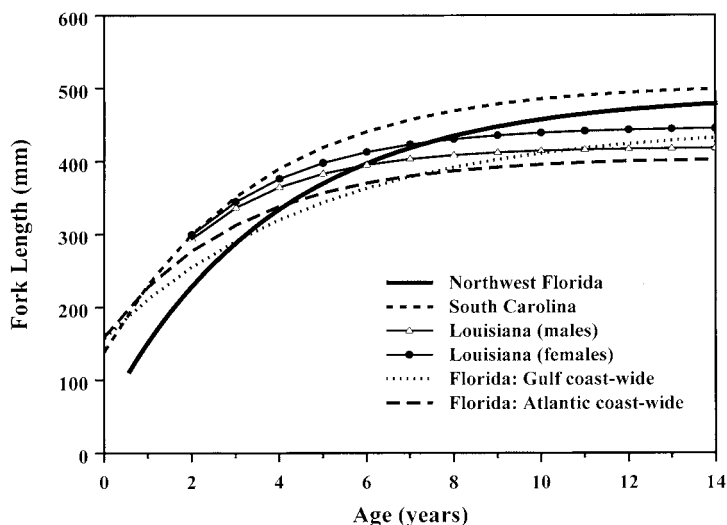


Figure 7. Von Bertalanffy growth curves for fork length as a function of age for sheephead from the northwest coast of Florida, Louisiana, South Carolina, and coast-wide Atlantic and Gulf coasts of Florida. Curves are truncated at 14 yrs; refer to Table 3 for maximum ages.

GROWTH OF SHEEPSHEAD.—Sheepshead grew quickly in length until ~ age 4. This was followed by a reduced growth rate (Figs. 5, 6) that coincided with sexual maturity (~2–3 yrs of age for males and ~3–4 yrs of age for females; Render and Wilson, 1992). There was high variability in length-at-age of sheepshead, and length was not a good predictor of fish age (i.e., fish of 400 mm FL could be 3 to 9 yrs of age) (Fig. 5). Sheepshead also increased in weight rapidly until 4–6 yrs of age before growth was reduced. Weight-at-age was more variable and a 2 kg fish could be from 4–14 yrs old (Fig. 6).

Comparing sheepshead growth among different geographical areas is difficult because of differences in sampling gears and distributions, sample sizes, and aging methods used in the von Bertalanffy models among the various studies. Statistically valid comparisons await collaborative access to multiple data sources so that, at a minimum, weighted von Bertalanffy growth curves can be generated. It is nevertheless instructive to qualitatively compare the growth of sheepshead from various areas to determine if the variability in growth potential is large or narrow. Comparatively, sheepshead from South Carolina (Wenner, 1996) appeared to be relatively large, whereas fish used in the coast-wide estimates for Florida (Murphy et al., 1997) appeared to be relatively small, compared to our sheepshead from the northwest coast of Florida (Fig. 7, Table 3). Fish from Louisiana were also smaller than fish from South Carolina, but their overall size range was similar to our fish from northwest Florida and for fish from coast-wide Florida (Murphy et al., 1997). It was therefore evident that sheepshead from different states and different regions within a state had the potential for differences in growth characteristics.

The variability in growth of sheepshead from various locations may result from several factors, including differences in mortality rates (i.e., natural mortality or fishing pressure), environmental conditions, or genetic variation. For example, selective pressures of commercial and recreational fisheries on sheepshead may affect their age and growth characteristics by selectively removing the fast-growing, larger fish (Ricker, 1975). Al-

though sex-specific differences in growth were not significant in sheepshead from our study area, female sheepshead were observed to be larger than males in Louisiana (Beckman et al., 1991), and the same pattern appears to hold for sheepshead from Tampa Bay (pers. comm., Tim McDonald, FDEP-FMRI, St. Petersburg, Florida). The lack of sexually dimorphic growth in our study may be related to differences in sex-specific selective pressures or fishing mortality rates among the areas during the offshore aggregation and spawning season, when sheepshead landings are the greatest on the Gulf coast of Florida (November–April) (Murphy et al., 1997).

In addition, in the estimate of sheepshead growth for the Gulf coast of Florida (Murphy et al., 1997), ~80% of the specimens were from the inshore waters of either Tampa Bay or Charlotte Harbor (pers. comm., Tim McDonald, FDEP-FMRI, St. Petersburg, Florida). The sheepshead for our estimates were collected >200 km north of both Charlotte Harbor and Tampa Bay (Fig. 1). This Gulf coast area has a lower human population density and, presumably, has been subject to less long-term fishing mortality. Although area-specific fishing mortalities are currently unavailable in Florida, commercial landings of sheepshead indicate greater landings in Tampa Bay and Charlotte Harbor than in our study area (e.g., in 1996 landings were approximately 10 times greater in these southern areas; Murphy et al., 1997). Trends in recreational landings by area, however, were all high in coastal areas and were therefore not specifically differentiated by county by Murphy et al. (1997).

There were further indications that various studies on growth of sheepshead have had inherent biases in their collections due to gear selectivity. For example, most of the sheepshead >300 mm total length in Wenner's (1996) study were sampled from fishing tournaments and this may account for the relatively larger-sized and older fish (up to 26 yrs) in his study. Beckman et al. (1991) obtained ~80% of their sheepshead from commercial gillnets (59%) or trawls (21%). They stated that the age distribution of their sample was not representative of the sheepshead population in Louisiana because of "gear selectivity and sorting of some of the samples by fishermen." They advocated inclusion of more fishery-independent samples. Our sheepshead (70% of fish) were collected from the commercial fishery, which used a variety of gears (mostly hook-and-line, spearfishing, trapping, and castnetting). These gears were the same as those used in our fishery-independent sampling and the diversity of gears with different selective properties probably minimized any bias.

Differences in growth among sheepshead could also be attributed to changes in geographical distribution and environmental conditions, such as differences in temperature regimes and food availability. Our sheepshead came from relatively open coastal areas that included both inshore and offshore habitats, rather than the mainly inshore bay areas of Tampa Bay and Charlotte Harbor used in the Gulf coast-wide estimate (pers. comm., Tim McDonald, FDEP-FMRI, St. Petersburg, Florida; Murphy et al., 1997). Differences in growth of sheepshead in Florida may therefore also be related to specific coastal habitats. Beckman et al. (1991) suggested that the more rapid growth observed for sheepshead from the Louisiana coast may be in response to the highly productive waters near the Mississippi Delta. According to Caldwell (1965), the distribution of *A. p. oviceps* (northern Gulf of Mexico) was correlated with mud and soft bottom habitat, whereas *A. p. probatocephalus* (southeastern Gulf of Mexico and Atlantic) was associated with hard bottom. It is therefore possible that differences in growth among sheepshead in different geographical locations may also be related to the habitat or associated habitat-related features, such as prey type and availability.

Finally, variability in growth may be a result of genetic variability. Based on the geographical location of the study in relation to the known ranges of the subspecies of sheephead (Table 3), Beckman et al. (1991) aged *A. p. oviceps* while all others aged *A. p. probatocephalus*. Based on meristics, including barring patterns, both subspecies were collected in our study. However, there was no significant difference in the growth between sheephead designated as *A. p. probatocephalus* (84% of the total fish sampled) and as *A. p. oviceps* (11% of the total fish sampled). Although these results are preliminary because of relatively small representation of *A. p. oviceps* in the sample, similarity in growth between the subspecies collected from the same geographical location would indicate that their growth is not affected by a genetic component (with the subspecific status based on meristics). Further studies are underway to examine if subspecific status of sheephead using meristics and morphometrics agree with subspecific status determined through mitochondrial DNA analysis.

Additional research on the growth and genetics of the subspecies of sheephead is necessary to differentiate environmental versus genetic influences on the structure of the sheephead stock(s). Variability in growth of sheephead from different locations indicates that regional management may be a more appropriate approach until stock composition of sheephead populations are known.

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