BIOLOGY OF THE WHITEBONE PORGY, *CALAMUS LEUCOSTEUS*, IN THE SOUTH ATLANTIC BIGHT[1]

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ABSTRACT

Whitebone porgy, *Calamus leucosteus*, were taken in trawl surveys over reef and nonreef habitats in the South Atlantic Bight in depths of 11 to 88 m. Larger individuals were taken in greater depths. Twelve age groups can be identified with sectioned otoliths and nine using scales. Annulus formation for otoliths and scales occurs between June and July. Von Bertalanffy growth equations of $L_t = 331\left[1 - e^{-0.1731\,(t+2.6390)}\right]$ from otoliths and $L_t = 362\left[1 - e^{-0.2611\,(t+0.3973)}\right]$ from scales suggest that attainment of maximum size for this species is similar to reports for other reef species. The fork length-weight relationship for *C. leucosteus* can be described by $W = 0.00004\ \mathrm{FL}^{2.907}$. The whitebone porgy is a protogynous hermaphrodite; younger, smaller fish are predominately females, and older, large fish are mostly males. Sexual transition most commonly occurs between ages II-IV and fork lengths 18-25 cm. Peak spawning occurs in May with total fecundity ranging from 30,400 to 1,587,400 eggs. The fecundity-weight relationship can be described by $F = 10.29438\ W^{1.6562}$. Regional landings data are not available for *C. leucosteus*; however, it was the third and fourth most abundant species by weight from trawler landings in South Carolina during 1979 and 1980.

The whitebone porgy, *Calamus leucosteus*, occurs from the Carolinas south to the Florida keys and throughout the Gulf of Mexico (Fischer 1978). Although more abundant and more frequently encountered in or near sponge-coral habitats at depths from 10 to 100 m (Fischer 1978; Powles and Barans 1980), individuals are sometimes taken from predominantly sandy bottoms (Wenner et al. 1979). This species is of commercial importance to trawl fishermen, but little information is available on its life history. The purpose of this paper is to present data on age, growth, reproductive biology, distribution, and relative abundance of *C. leucosteus* in the South Atlantic Bight.

MATERIALS AND METHODS

Distribution and relative abundance were determined from seasonal (fall 1973 to winter 1977) stratified random otter trawl surveys (Grosslein 1969) from Cape Fear, N.C., to Cape Canaveral, Fla. Sampling was conducted from the RV *Dolphin* with a 3/4 scale version of a Yankee No. 36 otter trawl (Wilk and Silverman 1976) towed for 0.5 h at 6.5 km/h.

Most specimens (~98%) used for analysis of age, growth, and reproductive biology were collected with otter trawls (3/4 Yankee No. 36, 40/54 fly net, University of Rhode Island high rise trawl (Hillier 1974)) from 1975 to 1980. The remainder were caught with baited fish traps and handlines. Fish were weighed (nearest gram) and measured (nearest mm total length [TL], fork length [FL], and standard length [SL]). Sagittae and scales from beneath and/or just behind the posterior edge of the pectoral fin below the lateral line were removed and stored dry. Impressions of several scales from each fish were made on clear acetate sheets with a model C Carver Laboratory Press[3] (1,547-1,687 kg/cm^2, 65.5°C, 5-10 min). Readability was reduced in large otoliths due to clouding of the central area and crowding of the rings along the outer margin; opaqueness also increased in all otoliths with storage time. These problems were corrected by preparing dorsal-ventral cross sections (~0.4 mm thick) on a plane perpendicular to the anterior-posterior axis through the center of the nucleus with a Buehler Isomet low speed saw.

Aging structures were analyzed using transmitted light on a microprojector at 40×. Scale measurements were made on a line through the center of the scale from the focus to the outer edge, whereas otolith measurements were taken from the center of the nucleus to the outer

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margin along the ventral edge of the sulcus acousticus. Two independent readings were made on each.

Most analyses were performed using the Statistical Analysis System (Helwig and Council 1979). A FORTRAN program based on Poole (1961) gave back-calculated length at age. The von Bertalanffy growth equation (Bertalanffy 1938) was fitted to mean back-calculated fork length at age using parameters derived from Walford lines obtained by least square linear regressions (Everhart et al. 1975). All regression equations other than the regressions of radial measurement on fork length are the functional regressions of Ricker (1973, 1975).

Sex and reproductive condition of most fish were determined by histological examination of the gonads, which were fixed in formal-alcohol solution (Humason 1972). Tissues were prepared for embedding by passage through an Autotechnicon Duo Model 2A Automatic Tissue Processor. Gonads were embedded in paraffin, sectioned at ~7μ with a rotary microtome, stained with Harris' hematoxylin and counterstained with eosin Y. The first 200 slides were read by two individuals, then, following agreement on interpretation, the remaining sections were viewed by a single observer. Sex and maturity codes were formed by modifying Moe (1969) and Mercer (1978) and applying the four part index of Hilge (1977). The sex codes include hermaphrodite recognition and, when used with the maturity stages, give an accurate and objective estimate of reproductive status. Sexes were identified as undifferentiated, male, female, simultaneous hermaphrodites, male-predominating hermaphrodite, and female-predominating hermaphrodite. Maturity was classed as follows:

Class	*Testicular state*	*Ovarian state*
Immature	little or no spermatocyte development	small, basophilic oocytes
Ripening	from gonads with a few primary and secondary spermatocytes through those where lumen filled with spermatozoa	from relatively acidophilic oocytes through large yolky oocytes
Ripe (running)	predominance of spermatozoa, little active spermatogenesis	predominance of yolk filled oocytes, few hydrated eggs present
Spent	no spermatogenic activity, some residual sperm present in tubules	nonspawned mature eggs becoming atretic
Resting	some mitotic regeneration of spermatogonia	predominately with small basophilic oocytes, few traces of atretic activity
Transitional	resting testicular tissue with ovarian tissue in active development	resting ovarian tissue with testicular tissue in active development.

Terminology used in histological descriptions of gonadal development follows Hyder (1969) and Combs (1969).

Fecundity estimates were obtained from developing ovaries which were weighed (nearest gram) and placed in Gilson's solution (Humason 1972). Following digestion of the connective tissue and external tunic, the eggs were washed and stored in 50% isopropyl alcohol. Eggs were diluted to 1 l, and three to four 1 ml subsamples were removed from a well-mixed suspension, placed in gridded petri dishes, and counted at 12×. The mean of the individual counts expanded to the 1 l volume was used to estimate total fecundity. Histological examination revealed that eggs of diameter <0.15 mm were retained in spent ovaries without signs of atresia, while larger unshed oocytes atrophied. Eggs >0.15 mm were considered potential gametes for the impending spawn and were the only ones included in the fecundity estimates.

RESULTS

Distribution and Abundance

Calamus leucosteus occurred in 94 of 575 stratified random otter trawl tows in depths <110 m during research survey cruises from 1973 to 1977. This species was taken in depths of 11 to 88 m from lat. 28°50′N to 34°36′N (Fig. 1). Although whitebone porgies were caught over the sandy bottom of the open shelf habitat, they were more frequently taken in trawl tows that contained sponges and corals, indicative of isolated patch reefs. *Calamus leucosteus* was found in 58% of the 67 trawl tows containing live bottom organisms and 11% of the open shelf tows during the surveys from 1973 to 1977. During the spring of 1978, otter trawl sampling in shallow water (18-42 m) sponge-coral habitat from Florida to North Carolina collected *C. leucosteus* in 43 of 57 tows. Thus, *C. leucosteus* may be found in reef and nonreef habitats in the South Atlantic Bight.

Seasonal catch/tow values indicated that *C. leucosteus* moved into warmer offshore waters

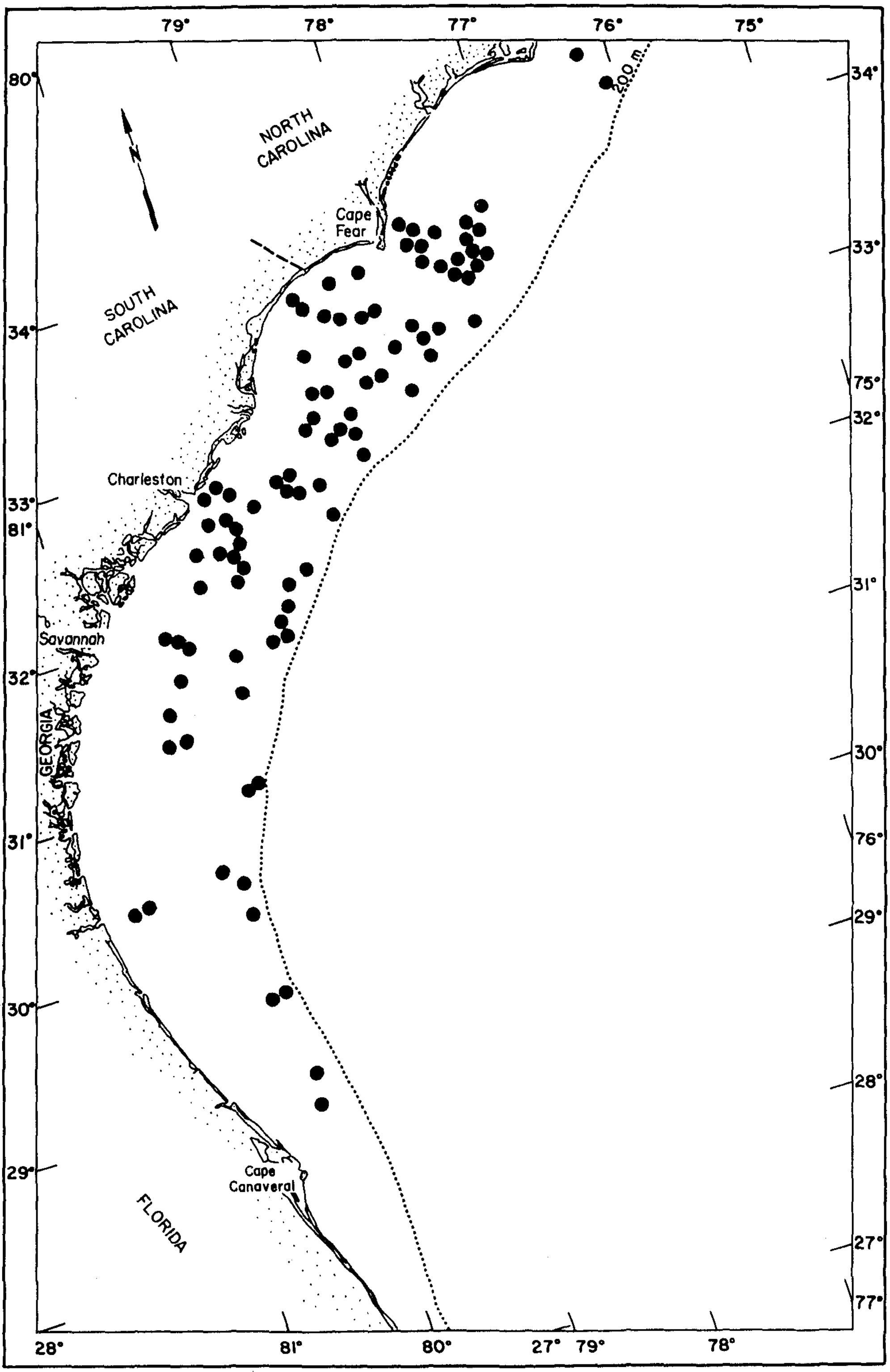

FIGURE 1.—Locations where whitebone porgy, *Calamus leucosteus*, were taken during stratified random trawl surveys from 1973 to 1977.

during winter months, when inshore waters of the South Atlantic Bight have their annual minimum values (Table 1). They were absent in 55 trawl tows made during winter in the 9-18 m depth zone and showed variable frequencies of occurrence in other seasons in comparable depths.

A trend for an increase in modal length with increasing trawl depth was apparent (Fig. 2). All specimens <24 cm FL were encountered in depths <56 m.

TABLE 1.—Catch/tow values from whitebone porgies, *Calamus leucosteus*, from stratified random research surveys from 1973 to 1977. n_1 = number of trawl tows which contained *C. leucosteus*; n = total trawls in depth zone.

Season	Catch/tow	Depth zone (m) 9-18	19-27	28-55	56-110
Winter	$\bar{x}$ catch/tow number	0	4.0	2.0	0.7
	$\bar{x}$ catch/tow weight (kg)	0	1.23	1.07	0.43
	n_1/n	0/55	13/50	9/66	4/42
Spring	$\bar{x}$ catch/tow number	0.3	1.4	0.3	1.3
	$\bar{x}$ catch/tow weight (kg)	0.03	0.55	0.10	1.03
	n_1/n	2/22	5/20	4/28	4/18
Summer	$\bar{x}$ catch/tow number	4.3	2.6	3.1	0.6
	$\bar{x}$ catch/tow weight (kg)	1.12	1.02	1.65	0.43
	n_1/n	9/48	10/50	16/66	5/41
Fall	$\bar{x}$ catch/tow number	2.7	2.6	0.8	0.6
	$\bar{x}$ catch/tow weight (kg)	0.82	1.08	0.24	0.52
	n_1/n	4/18	4/18	3/19	2/14

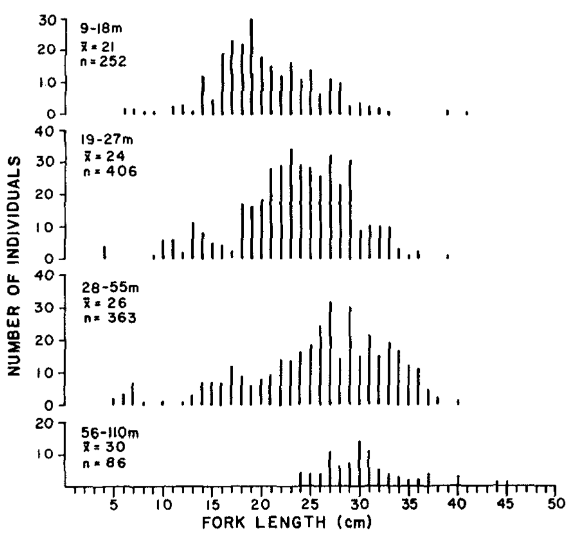

FIGURE 2.—Length-frequency distribution of *Calamus leucosteus* by depth zone for 3/4 Yankee trawl caught specimens (1973-77).

Age and Growth

Life history information was obtained from 1,732 fish collected from 1975 to 1980. Age determinations were attempted for 1,664 pairs of otoliths and 1,679 scale samples, and of these, 80% of the otoliths and 45% of the scales showed discernible rings. There was a 62.8% 1:1 agreement in ages obtained from both scales and otoliths from 760 individuals.

Mean marginal increments by month for scales and otoliths were examined to determine the time of annulus formation (Fig. 3). Samples were combined by month regardless of the year of capture. Mean marginal increments should approach zero at the time of annulus formation; this occurs in June on scales and in July on otoliths.

Fork lengths increased with increasing age as shown by scales and otoliths (Table 2); however, this progression was obscured in older age groups by smaller sample sizes. In general, average fork lengths derived from scale age and otolith age were similar for the first few years, then fish aged by otoliths tended to be smaller then those aged by scales. Fish given identical ages using both scales and otoliths showed average fork lengths at age similar to those derived by scales alone.

The relationships of fork length to otolith and scale radius were best described by the equations

$$\log FL = 1.041 + 0.844 \log OR$$
$$n = 1{,}320 \quad r^2 = 0.70$$

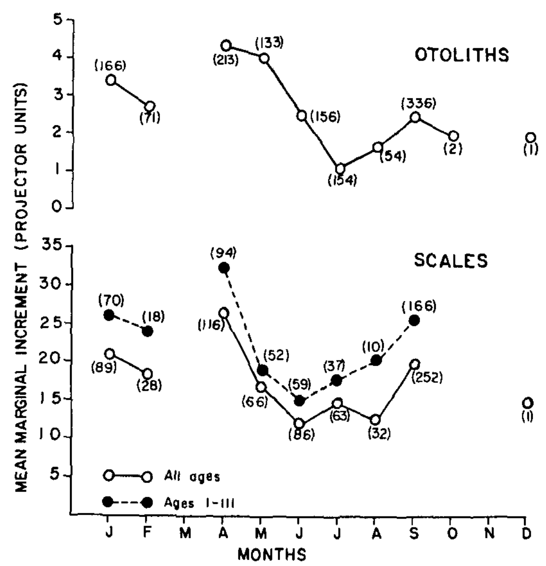

FIGURE 3.—Mean marginal increments for otoliths and scales by month for *Calamus leucosteus*. Number in parentheses = sample size.

TABLE 2.—Mean observed fork length, number and standard deviation (SD) by age for otoliths, scales, and individuals given identical ages by scales and otoliths of *Calamus leucosteus*.

	Otoliths			Scales			Otolith-scales		
Age	No.	$\overline{FL}$	SD	No.	$\overline{FL}$	SD	No.	$\overline{FL}$	SD
0	34	111	22.4	24	98	18.2	16	96	17.9
I	174	153	25.6	122	143	23.4	98	144	22.6
II	319	201	23.5	238	191	22.1	183	194	20.5
III	172	225	23.2	145	225	22.0	93	225	20.1
IV	138	248	22.5	73	256	28.9	41	247	20.0
V	155	263	26.3	77	284	30.8	29	280	27.7
VI	109	280	27.2	54	314	29.0	10	314	19.9
VII	73	284	31.6	18	312	33.5	6	295	44.0
VIII	57	279	32.0	6	345	29.3	—	—	—
IX	34	289	26.1	2	313	66.4	—	—	—
X	25	290	31.5	—	—	—	—	—	—
XI	26	301	33.0	—	—	—	—	—	—
XII	8	309	26.9	—	—	—	—	—	—

$$FL = -36.713 + 1.176\,SR \qquad n = 757 \quad r^2 = 0.82$$

where FL = fork length (mm), OR = otolith radius (projector units), and SR = scale radius (projector units). The intercepts of these predictive equations were used as correction factors in deriving average back-calculated fork length at age (Table 3). Average back-calculated fork lengths for fish aged with otoliths up to age XII are 136, 179, 207, 227, 242, 252, 259, 264, 273, 280, 291, and 301 mm. For fish aged with scales up to age IX average back-calculated fork lengths were 102, 170, 215, 249, 275, 298, 303, 323, and 306 mm. Average observed fork lengths were greater than average calculated lengths in all cases for otolith and scale ages. Calculated lengths for fish aged with otoliths show a closer agreement with observed lengths than do calculated lengths derived using scales.

Mean back-calculated fork lengths (otolith ages: I-XII; scale ages: I-VIII) were used to obtain von Bertalanffy growth equations. Trial values of $L_\infty = 304$ for otoliths and $L_\infty = 349$ for scales appeared low. We were able to determine the best value of L_∞ by using several trial values of L_∞ and regressing $\ln(L_\infty - L)$ against t, where L = mean back-calculated fork length and t = age (Ricker 1975). The straightness of this line is sensitive to changes in L_∞ and the L_∞ that produced the straightest line was $L_\infty = 331$ for otoliths and $L_\infty = 362$ for scales. Values of $K = 0.1731$, $t_0 = -2.6390$ for otolith ages and $K = 0.2611$, $t_0 = -0.3973$ for scale ages were obtained. The theoretical growth equations derived from these values were

$$\text{otoliths } L_t = 331 \left[1 - e^{-0.1731(t+2.6390)}\right]$$

$$\text{scales } L_t = 362 \left[1 - e^{-0.2611(t+0.3973)}\right].$$

TABLE 3.—Back-calculated fork length at age for *Calamus leucosteus* aged by scales and otoliths.

	Otoliths				Scales			
Age	No.	$\overline{FL}$	SD	Range	No.	$\overline{FL}$	SD	Range
I	1,286	136	17.3	54-231	733	102	20.0	31-183
II	1,112	179	19.3	101-269	611	170	22.9	92-238
III	793	207	21.5	110-273	373	215	26.3	116-297
IV	621	227	23.7	152-303	228	249	28.9	164-334
V	483	242	26.5	165-325	155	275	30.2	189-345
VI	329	252	28.4	180-339	79	298	30.1	200-363
VII	222	259	29.0	186-347	25	303	33.0	238-352
VIII	150	264	28.3	193-360	7	323	42.0	244-366
IX	93	273	28.4	199-354	2	306	63.9	261-351
X	59	280	29.7	209-350	—	—	—	—
XI	34	291	31.3	245-370	—	—	—	—
XII	8	301	24.9	272-340	—	—	—	—

Theoretical, back-calculated, and observed fork lengths at age for scales and otoliths are compared in Figure 4.

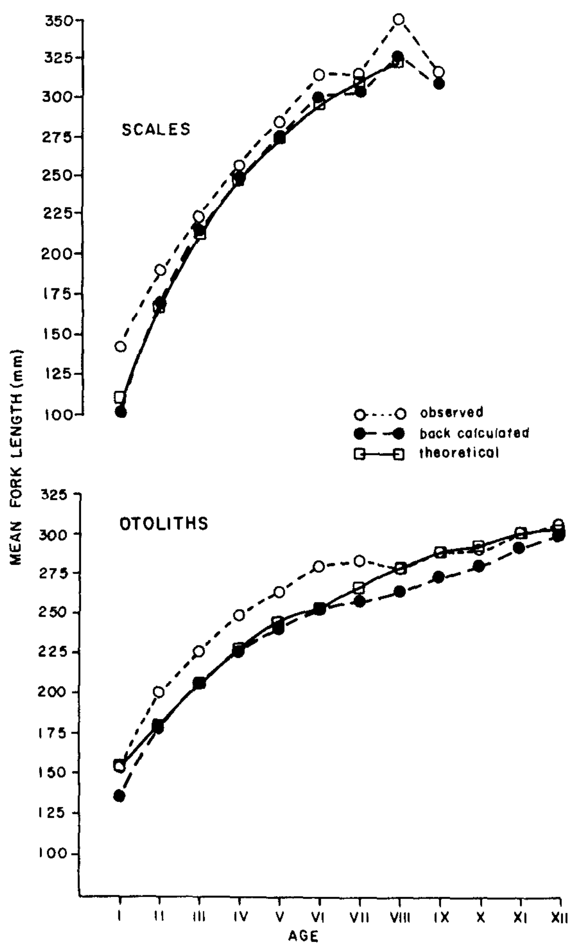

FIGURE 4.—Observed, back-calculated, and theoretical fork lengths of *Calamus leucosteus* aged by scales and otoliths.

Functional length-length and length-weight relationships for *C. leucosteus* are (length in millimeters; weight in grams)

$$FL = 1.13(SL) + 3.9 \quad n = 1464 \quad r^2 = 0.97$$
$$FL = 0.86(TL) - 2.0 \quad n = 1428 \quad r^2 = 0.98$$

$$\log Wt = 2.907(\log FL) - 4.367 \quad n = 1{,}719 \quad r^2 = 0.97$$
$$\log Wt = 2.858(\log SL) - 4.078 \quad n = 1{,}454 \quad r^2 = 0.98$$
$$\log Wt = 2.903(\log TL) - 4.553 \quad n = 1{,}416 \quad r^2 = 0.97.$$

Reproduction

Male and female gonads of *Calamus leucosteus* are paired glands suspended in the posterior body cavity by mesorchia. They join posteriorly into a common duct before the external genital opening. Gonads must be examined histologically for determination of both sex and maturity. Many of the 1,274 fish examined showed protogyny.

Immature female gonads possessed only small (<100 μ), densely basophilic oocytes (Fig. 5A) whereas developing ovaries showed a predominance of larger (~100-500 μ) acidophilic oocytes (Fig. 5B). Paraffin infiltration was poor in large (~500-700 μ), hydrated oocytes and resulted in unsatisfactory sections of ripe ovaries. Atretic oocytes (Fig. 5C) were common in spent gonads whereas resting tissue was identified by traces of atresia and the predominance of small basophilic oocytes. Transitional gonads had most of their bulk as nonactive ovarian tissue, while the testicular tissue was developing (Fig. 5D).

The small, immature testes showed little spermatogenic activity and were largely composed of primary and secondary spermatogonia. Early spermatogenesis and all phases of sperm formation through packing of lumina with spermatozoa (Fig. 6A) were characteristic of developing testes. Ripe testes showed little spermatogenesis with all lumina filled with sperm. Spent testes had convoluted tubules with evidence of residual sperm resorption. The resorptive process was largely completed in resting testes, and mitotic proliferation of spermatogonia had started.

Residual oocytes were present in 58% of the males. These were treated as functional males and all maturity stages (except immature) given to normal males were applied to these primarily male hermaphrodites (Fig. 6B). Traces of nonactive testicular tissue were found in 16.2% of the females (Fig. 6C), and these were treated as functional females. Juvenile hermaphrodites and a few other specimens in which both types of gonadal tissue were not only present, but equally developed, were considered simultaneous hermaphrodites (Fig. 6D). This phenomenon occurred in 3.4% of all gonads and was excluded from further analysis.

Females (Fig. 7) accounted for about 80% of the smaller, younger fishes, while males comprised approximately 70% of the largest size groups and about 80% of the oldest fish. Fish undergoing transition were found in ages I through VII (Fig. 7) and clustered around inflection points of both graphs (lengths: 18-25 cm FL; ages: II-IV). These figures imply that about 20% of young males remain males throughout life and that approximately 20% of the females remain females. Histological evidence demonstrates no case of males transforming to females and indicates females occur in all size and age groups sampled. Thus, approximately 60% of *C. leucosteus* undergo sex reversal.

This species spawns from April to August with peak spawning probably in May (Table 4). Of the fish examined, 100% were developing in March;

TABLE 4.—Percentages of *Calamus leucosteus* in different gonadal states by month of capture.

Month	n	Immature	Developing	Ripe	Spent	Resting	Transitional
January	117	2.0	42.4	—	1.0	55.6	—
February	84	—	31.0	—	25.2	41.0	3.6
March	16	—	100.0	—	—	—	—
April	238	11.9	79.1	8.1	1.0	1.0	0.5
May	157	6.4	41.5	32.3	16.0	4.5	—
June	162	17.3	42.1	2.6	14.2	19.8	3.7
July	173	15.6	18.7	3.6	9.9	50.3	—
August	60	1.7	31.7	3.4	1.7	46.7	11.7
September	214	12.7	27.6	—	1.9	44.0	13.6
October	2	—	—	—	—	100.0	—
November	—	—	—	—	—	—	—
December	1	—	—	—	—	100.0	—

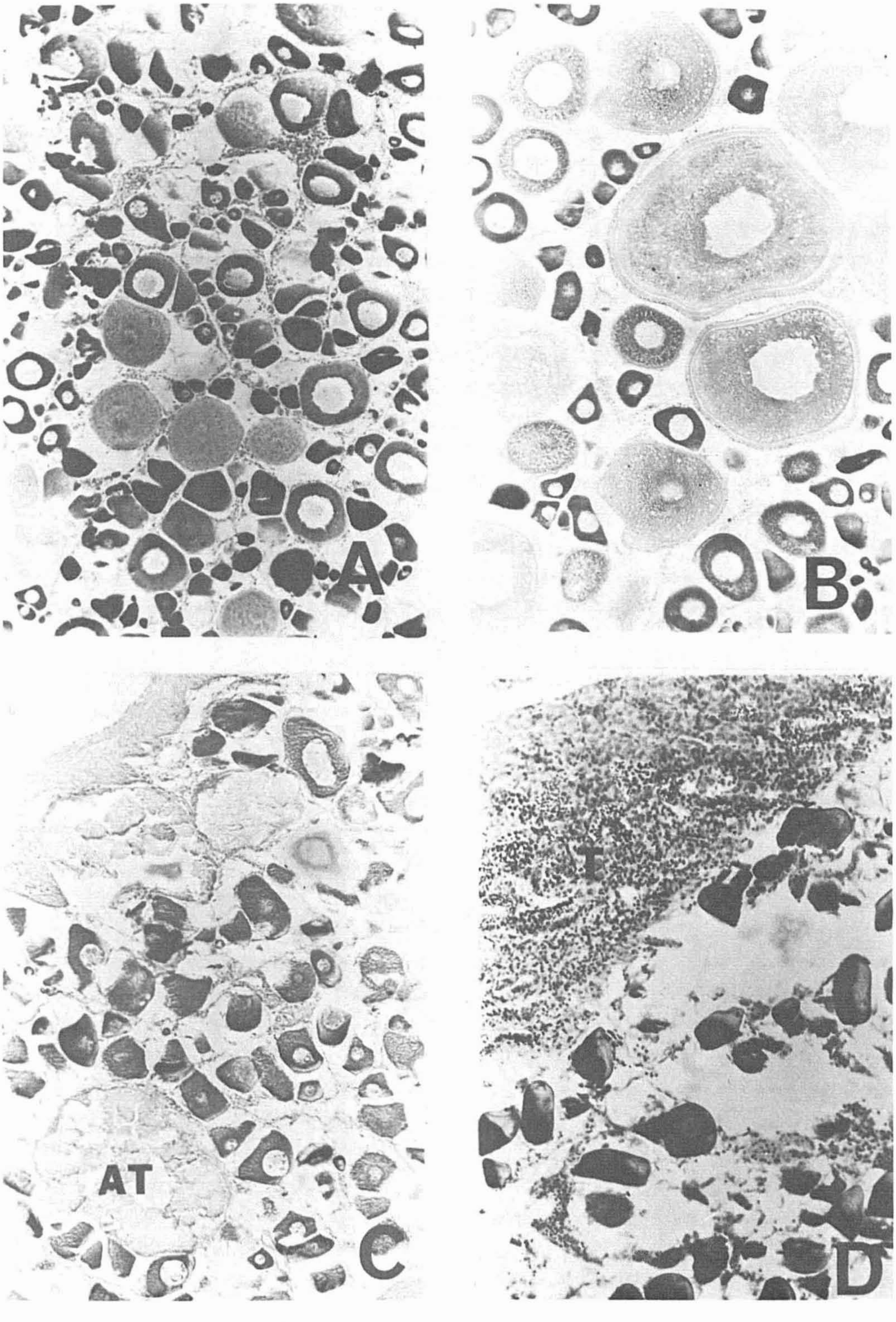

FIGURE 5.—Histological sections of *Calamus leucosteus* gonads. A, immature female; B, developing female; C, spent female; D, transitional gonad. AT = atretic oocyte, T = testicular tissue.

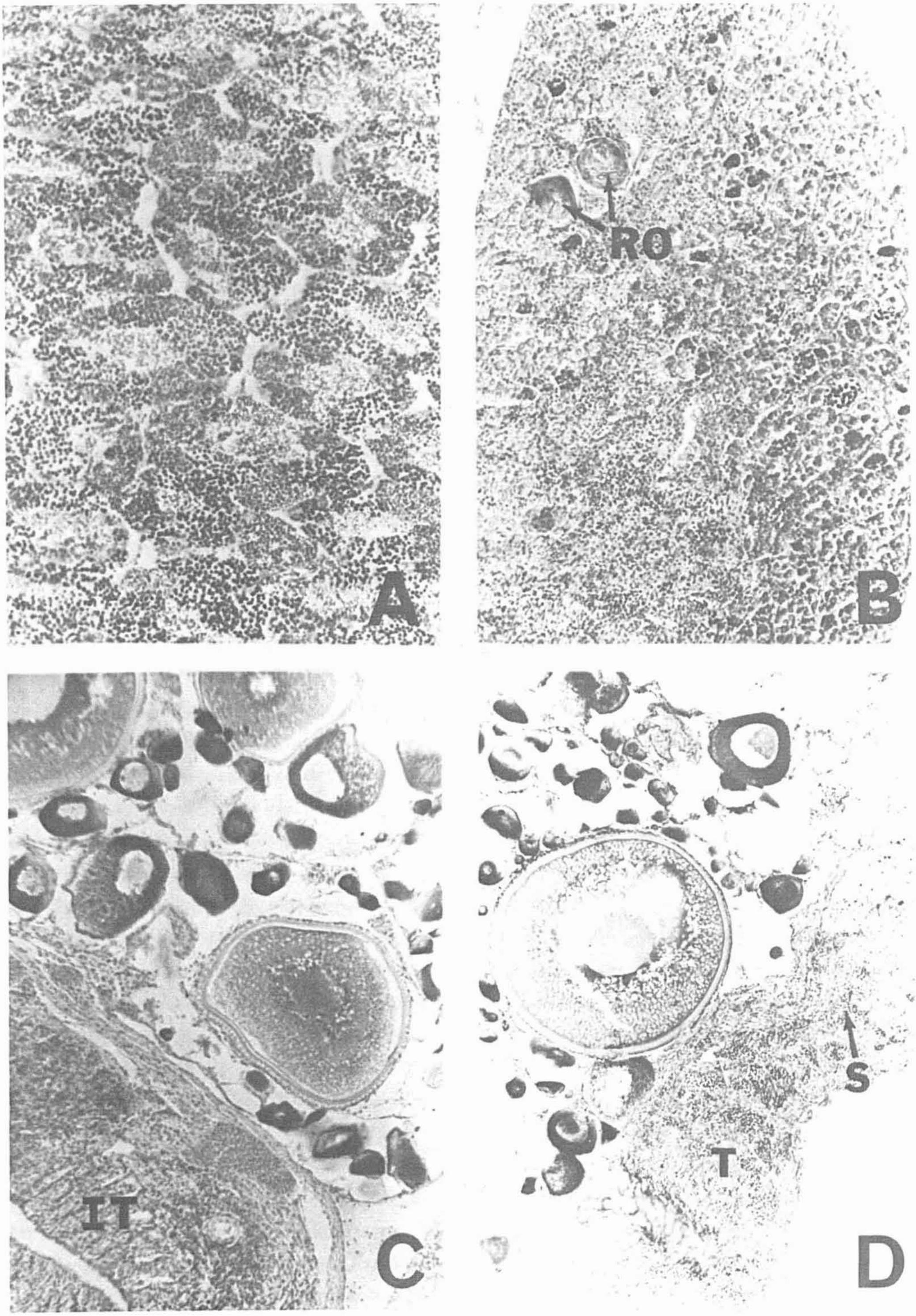

FIGURE 6.—Histological sections of *Calamus leucosteus* gonads. A, developing male; B, developing male with residual oocytes in testes; C, developing female with inactive testicular tissue present; D, simultaneous development in both ovarian and testicular tissue. IT = inactive testicular tissue, RO = residual oocyte, S = spermatozoa, T = testicular tissue.

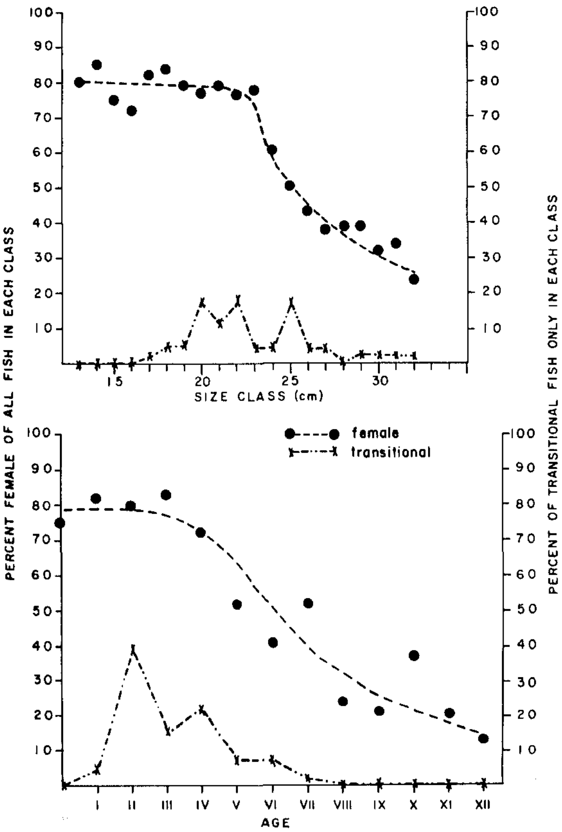

FIGURE 7.—Percent of all *Calamus leucosteus* that were females or functional females and the percent occurrence of transitional fish only by size and age.

this decreased to 79% in April, whereas the highest percentage of ripe fish were observed in May (32%). No ripe fish were encountered before April or after August. Fish undergoing transition were more frequently encountered after spawning (Table 4). The highest percentages of transitional fish were observed in August (11.7%) and September (13.6%). Both sexes may mature at age 1 and females as small as 179 mm FL have been observed with hydrated eggs.

Fecundity ranged from 30,400 to 1,587,400 eggs and generally increased with age (Table 5). It was significantly related to length and weight. The functional regressions for fecundity verses length and weight are

$$\log \text{fecundity} = 4.463(\log FL) - 5.347 \quad n = 63 \;\; r^2 = 0.64$$

$$\log \text{fecundity} = 4.475(\log SL) - 5.093 \quad n = 63 \;\; r^2 = 0.66$$

TABLE 5.—Otolith age-mean fecundity values for *Calamus leucosteus*. The Bliss (1967) approximation was used in transforming the mean from logarithmic to arithmetic units.

Age	Number of individuals	Mean fecundity	Range
I	3	85,192	59,000-129,400
II	11	124,911	30,400-334,700
III	16	215,601	63,700-366,700
IV	5	236,892	119,400-431,400
V	9	285,824	145,000-532,400
VI	4	236,674	60,400-374,700
VII	6	266,348	174,000-617,700
VIII	—	—	—
IX	—	—	—
X	1	869,400	—
XI	1	1,587,400	—

$$\log \text{fecundity} = 4.501(\log TL) - 5.742 \quad n = 62 \;\; r^2 = 0.64$$

$$\log \text{fecundity} = 1.656(\log W) + 1.013 \quad n = 63 \;\; r^2 = 0.66$$

where *FL*, *SL*, and *TL* are in mm and *W* in g.

South Carolina Commercial Landings

Regional catch and landing data for *C. leucosteus* are available only as the combined values of *C. leucosteus* and *Stenotomus* sp. from the offshore trawl fishery (Table 6). Whitebone porgy represent approximately 98% of these values (Ulrich[4]). The mean size of random subsamples of the trawl catch (1979: $\overline{FL} = 27$ cm; 1980: $\overline{FL} = 26$ cm) was very similar for both years (Fig. 8).

[4]G. Ulrich, Finfish Management Section, Division of Marine Resources, South Carolina Wildlife and Marine Resources Department, P.O. Box 12559, Charleston, SC 29412, pers. commun. 19 May 1980.

TABLE 6.—Reported landings of *Calamus leucosteus* and *Stenotomus* sp. from the South Carolina offshore trawl fishery 1979 and 1980. Values for November and December 1980 are low because of incomplete landings data from one Charleston, S.C. dock.

	1979		1980	
Month	Weight (kg)	Percent of total catch	Weight (kg)	Percent of total catch
January	1,525	20	4,794	11
February	3,452	18	4,178	9
March	2,722	12	5,081	7
April	2,779	12	3,346	9
May	264	3	560	6
June	132	11	n.a.[1]	—
July	n.a.	—	n.a.	—
August	n.a.	—	n.a.	—
September	n.a.	—	n.a.	—
October	n.a.	—	n.a.	—
November	n.a.	—	2,180	16
December	n.a.	—	1,536	12
Total	10,873	13.4	21,675	9.2

[1]n.a. = not available.

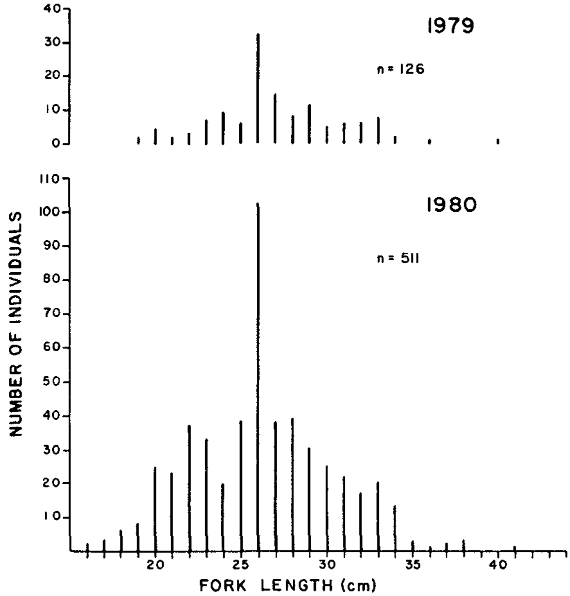

FIGURE 8.—Length-frequency subsamples from trawl caught *Calamus leucosteus* landed in South Carolina offshore trawl fishery, 1979 and 1980.

DISCUSSION

The time of annulus formation is similar in otoliths and scales, it occurs when water temperatures are warm, photoperiod is long, and, in mature fish, just after spawining. The annulus is formed later in the year (June-July) than in some other reef species: vermilion snapper, *Rhomboplites aurorubens*, March-May (Grimes 1978); black sea bass, *Centropristis striata*, March-June (Mercer 1978); red porgy, *Pagrus pagrus*, March-April (Manooch and Huntsman 1977).

Twelve age groups could be identified using otoliths, whereas only nine were determined from scales because of the inability to read those of older fish. In addition, some older fish aged with otoliths had one or more rings than scales. As a result, larger fish aged by scales appear younger than those aged by otoliths, and this is reflected in back-calculated and theoretical lengths at age. The relationship of fork length to otolith radius appears to be curvilinear. The measurement of otolith radius used in this study is actually a measurement of otolith thickness. Beamish (1979) noted in the Pacific hake, *Merluccius productus*, that growth of all parts of the otolith was not identical throughout the life of the fish. He found that growth of older otoliths continues, but that increases in thickness, especially in the ventral interior portion, becomes proportionally more important than increases in otolith length or height. *Calamus leucosteus* appears to be best aged, using this measurement from sectioned otoliths.

Estimates of $L_\infty = 331$ mm FL for otoliths and 362 mm FL for scales appear low since a maximum size of 18 in TL (391 mm FL) was reported by Jordan and Gilbert (1884) and we observed a 407 mm FL fish. The calculation of L_∞ depends on the number of age groups present and the distribution of individuals within each group. Higher values of L_∞ should have been expected if a larger number of bigger older fish could have been aged and included in the calculations. Comparison of growth coefficients (scales: $K = 0.2611$; otoliths: $K = 0.1731$) indicates that *C. leucosteus* attains maximum size at a rate similar to *Centropristis striata*, $K = 0.219$ (Mercer 1978), *Pagrus pagrus*, $K = 0.096$ (Manooch and Huntsman 1977), *Rhomboplites aurorubens*, $K = 0.198$ (Grimes 1978), and red grouper, *Epinephelus morio*, $K = 0.179$ (Moe 1969).

Calamus leucosteus spawns from April through August, with peak spawning in May. Both sexes may mature at age 1 and fecundity estimates range from 30,400 to 1,587,400 eggs. *Pagrus pagrus*, another commercially important sparid occupying the same range, spawns from January through April, matures at age 2, and has fecundity estimates ranging from 48,660 to 488,600 eggs (Manooch 1976).

Calamus leucosteus, as well as several western Atlantic sparids (Reinboth 1970; Manooch 1976; Roumillat pers. obs.), demonstrates protogynous hermaphroditism, which can only be determined by histological observations. Sexual transition in *C. leucosteus* involves the rapid proliferation of testicular tissue in the posteroventral tunica of the ovary which is the typical sparid protogynous pattern (Smith 1975). The testes does not infiltrate the ovarian lamellae as in groupers (Smith 1965), but envelops the regressing female tissue. Male and female tissues are separated during transition by connective tissue, but the sperm ducts pass within the ovarian wall. Other western Atlantic families that demonstrate protogynous hermaphroditism in addition to the Sparidae are the Serranidae (Smith 1965, 1975), the Labridae (Warner and Robertson 1978), and Scaridae (Robertson and Warner 1978). The labrids and scarids have complex socially influenced reproductive strategies that have not yet been documented for sparids or serranids.

The South Carolina offshore trawl fishery is highly seasonal. Landings are greatest during the winter months after the closing of the shrimp season. *Calamus leucosteus* is the third or fourth most abundant species by weight in trawler landings. These are primarily age IV-VI fish. Red porgy and vermilion snapper are the most abundant trawl-caught commercial fish.

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