

# CONTRIBUTIONS TO THE LIFE HISTORY OF BLACK SEA BASS, *CENTROPRISTIS STRIATA*, OFF THE SOUTHEASTERN UNITED STATES<sup>1</sup>

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## ABSTRACT

Ages of black sea bass, *Centropristis striata*, from the South Atlantic Bight were determined from otoliths. Analysis of marginal increments showed that annulus formation occurred in April and May. The von Bertalanffy growth equation derived from back-calculated mean standard lengths at age was  $l_t = 341(1 - e^{-0.2309(t+0.3010)})$ , where  $t$  is age in years and  $l_t$  = standard length at age. The oldest fish was age 10.

*Centropristis striata* is a protogynous hermaphrodite that undergoes sex succession at ages 1 through 8. The process of sex succession is described from histological examination of the gonads. The major spawning period is from March to May, and a minor spawn occurs in September-October. Mature males and females were encountered at age 1. Fecundity estimates ranged from 17,000 in a 108 mm SL female to 1,050,000 in a 438 mm SL fish, and were significantly related to length, weight, and age.

The instantaneous rate of total mortality of *C. striata* from catch curve analysis, ranged from 0.721 in 1978 to 1.320 in 1981 for commercial fish traps and 0.726 in 1979 to 1.430 in 1981 for hook-and-line gear. Petersen mark-recapture techniques were used to determine the population size of *C. striata* on two shallow-water patch reefs. Conversions of these estimates to densities gave 14-125 individuals per hectare.

The black sea bass, *Centropristis striata* (Linnaeus), is an important recreational and commercial seranid (Huntsman 1976; Musick and Mercer 1977; Low 1981) that occurs along the east coast of the United States from Massachusetts to Florida, with occasional individuals as far south as the Florida Keys (Fischer 1978). Within this range, *C. striata* is thought to form two populations separated at Cape Hatteras (Mercer 1978). The northern population migrates seasonally from shallow waters along the Middle Atlantic and southern New England coasts during summer to deeper water in the southern part of the Middle Atlantic Bight during the winter (Musick and Mercer 1977). Black sea bass in the Middle Atlantic Bight are harvested commercially with traps in shallow water during summer and with otter trawl gear when aggregated in deeper water in winter (Frame and Pearce 1973). Commercial catches are almost exclusively from traps in that part of the South Atlantic Bight from Cape Fear, NC to Cape Canaveral, FL where fishing is largely confined to patch reefs (live bottom habitat of Struhsaker 1969 or inshore sponge-coral

habitat of Powles and Barans 1980) at depths from 20 to 46 m. South Carolina commercial landings were as high as 350.7 metric tons (t) in 1970, but show large annual fluctuations (Fig. 1).

Both the northern and southern populations have been aged by analyzing otoliths (Mercer 1978), with nine age groups identified north of Cape Hatteras and eight along the southeastern U.S. coast. However, sampling techniques could have biased the findings on southern *C. striata* since fishes came from commercial catches which are frequently culled at sea (Mercer 1978).

Black sea bass are protogynous hermaphrodites (Lavenda 1949), wherein most individuals function first as a female and later as a male. Most females mature by age 2; older age classes are composed predominately of male fish although sexually active males are in all age groups. Sexual succession occurs at ages 1 through 5 (Mercer 1978). The northern population spawns from June to October with peak reproduction in July and August off Virginia (Mercer 1978).

There is insufficient published information to describe the life history of this valuable commercial and recreational species in the South Atlantic Bight in detail. This report describes aspects of the life history of *C. striata* from the South Atlantic Bight, including age and growth, sex ratios, size and age

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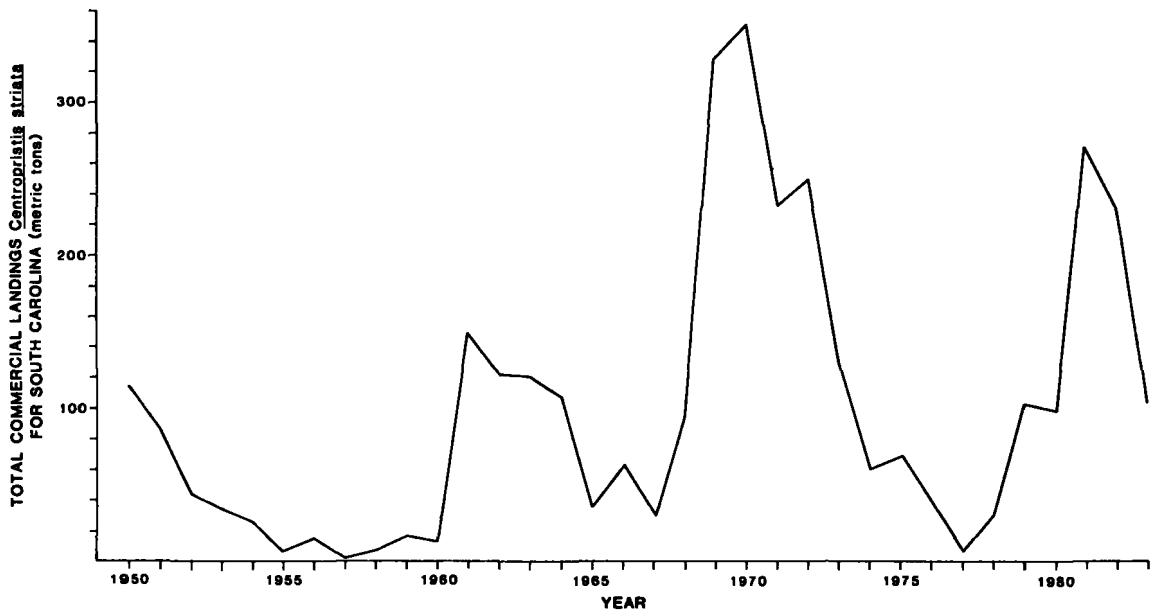


FIGURE 1.—Annual commercial landings of *Centropristis striata* in South Carolina.

at maturity and sexual succession, and fecundity. Additional information includes Petersen mark-recapture estimates of standing crop on reefs, and trends in the size and age composition with increased exploitation.

## MATERIALS AND METHODS

### Age and Growth

Most specimens were taken from the inshore sponge-coral habitat between lat. 31.5° and 33.5°N by commercial black sea bass traps (Rivers 1966), Antillean-S traps (Powles and Barans 1980), handlines, and trawl surveys from June 1978 through September 1981. Supplemental specimens were obtained from South Carolina commercial landings and other research programs to determine seasonal gonadal condition and time of annulus formation.

*Centropristis striata* were weighed to the nearest g and total (TL) and standard (SL) lengths were recorded to the nearest mm. Sagittae were removed and stored dry in envelopes for subsequent age determination. Unless damaged, the left sagitta was placed concave side up in a dish of water over a dark field and viewed at 12× magnification using a binocular microscope. When viewed with reflected light, sagittae displayed a central opaque field surrounded by alternating translucent and opaque bands. The

central field varied in size and shape from a small opaque nucleus to a large opaque zone consisting of one or more broken rings (Fig. 2A, B). Since apparent daily growth rings have been observed on both the sagitta and lapillus of *C. striata* (Johnson<sup>3</sup>), this zone was interpreted by counting rings from the primordium to the edge of the central field. Otoliths were finely ground on both sides until the central area of apparent daily rings could be observed (Fig. 3A, B). They were then viewed with transmitted light on a compound microscope at 500× and/or 1,000× magnification.

The intercept of the otolith radius-SL relationship was used to derive mean back-calculated size at age by the Fraser-Lee method (Poole 1961; Carlander 1982). The von Bertalanffy growth equation (Bertalanffy 1938) was fitted to mean back-calculated SL at age using the SAS NLIN procedure (Helwig and Council 1979) employing Marquardt's algorithm and the SAS NLIN weight statement; mean back-calculated lengths were weighted by the reciprocal of the standard error of the mean squared. Both standard least squares linear regression (Sokal and Rohlf 1981) and geometric mean (GM) functional regression analyses were used to describe the relationship of length to length and length to weight.

<sup>3</sup>G. David Johnson, Fish Division, U.S. National Museum, Washington, D.C. 20560, pers. commun. April 1982.

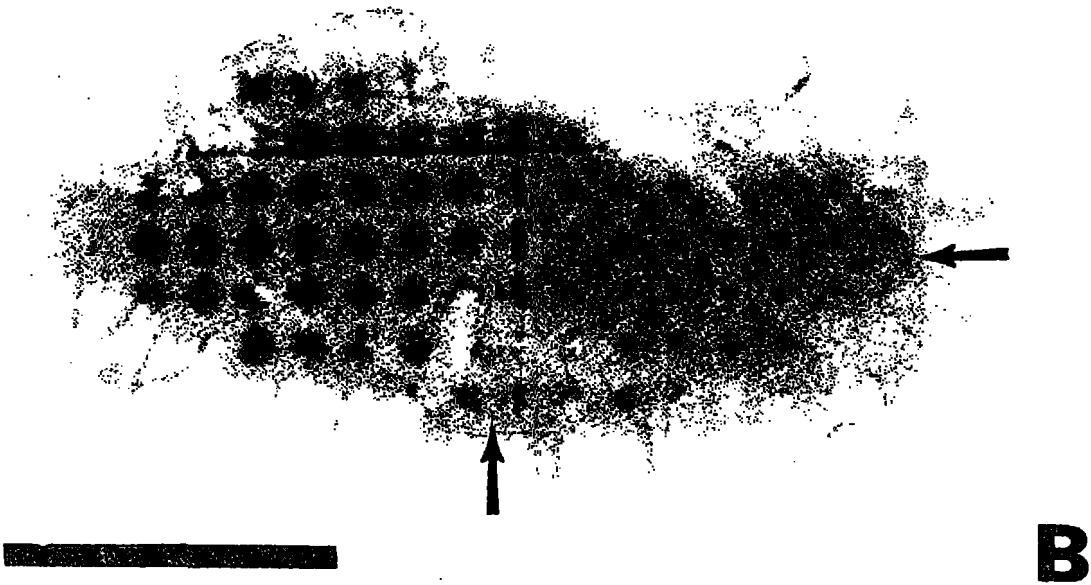
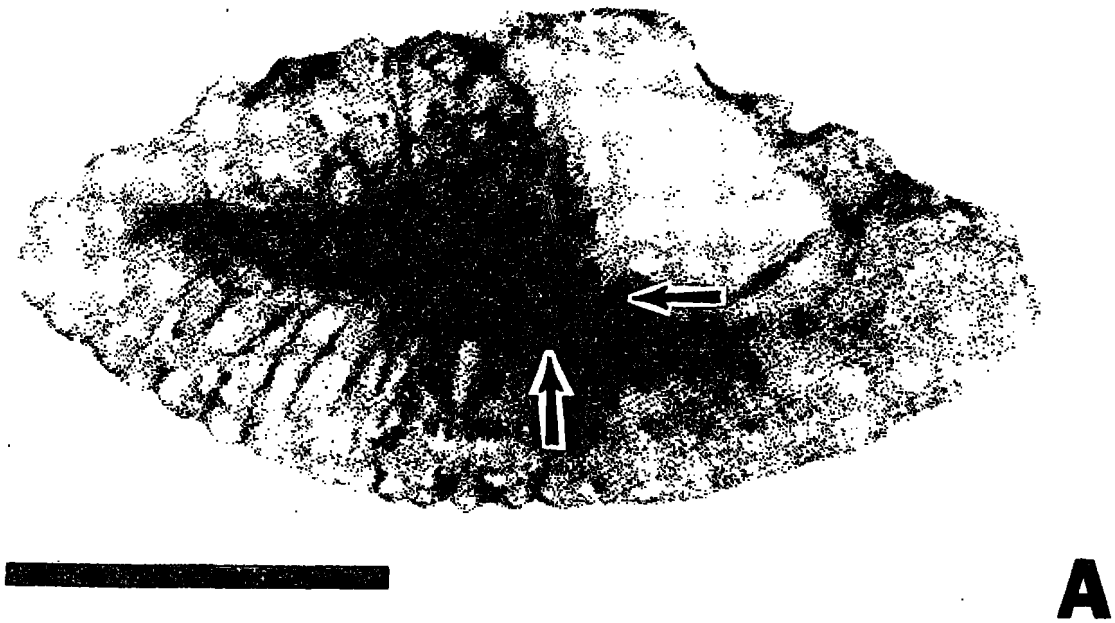


FIGURE 2.—Photomicrograph (16 $\times$ ) of the left sagittae from young-of-the-year *Centropristis striata*. A) Otolith with a small central nucleus (between arrows). B) Otolith with a large central zone consisting of a few broken rings (between arrows). Bars equal 1 mm.

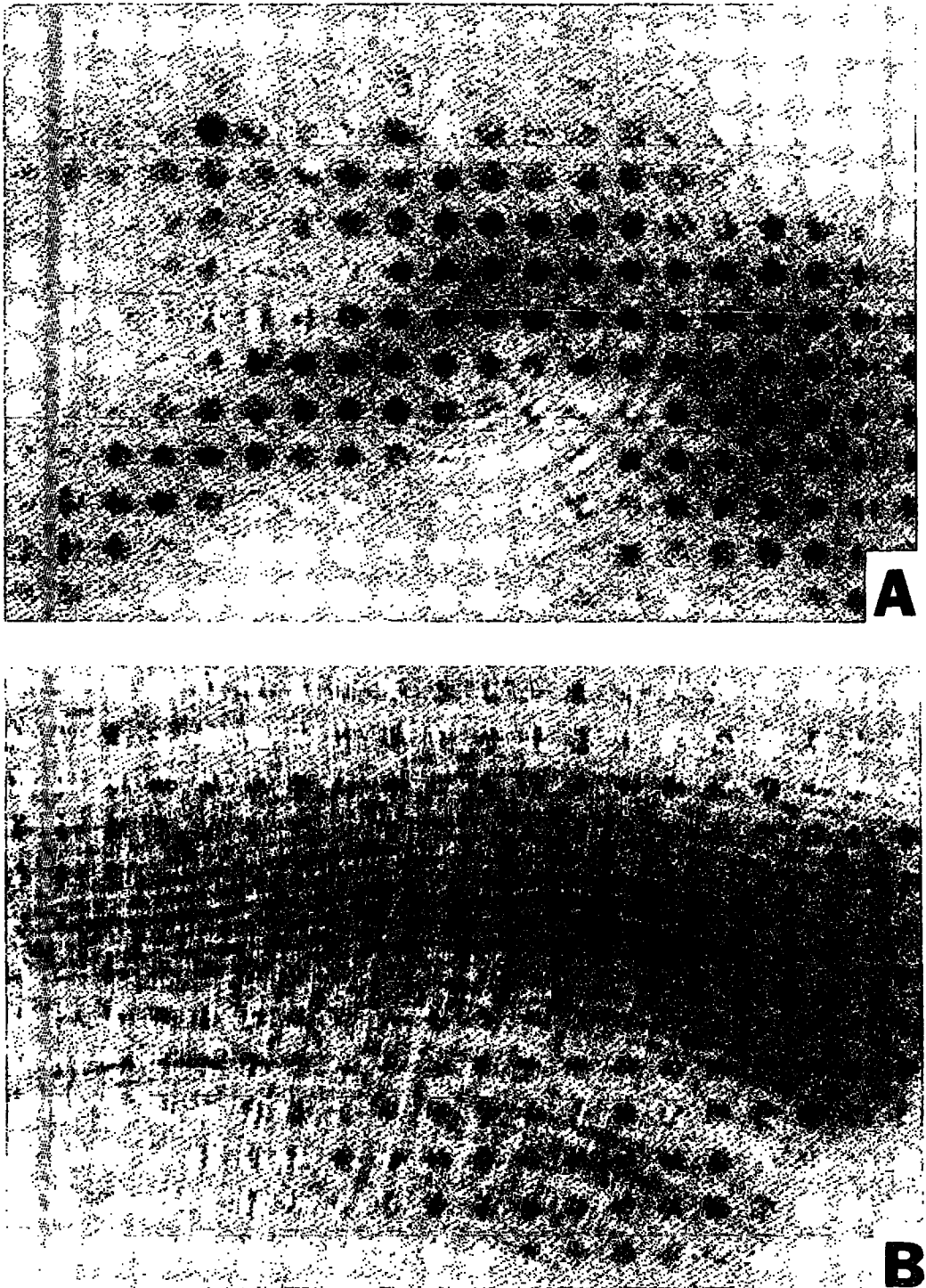


FIGURE 3.—Photomicrograph of sagittae from young-of-the-year *Centropristis striata*. A) Central primordium of the opaque nucleus showing growth rings for fish #1, Table 2; 400 $\times$  magnification. B) Area of otolith near the edge of the central zone showing growth rings of fish #8, Table 2; 250 $\times$  magnification.

## Reproduction

Reproductive organs from 6,685 *C. striata* were resected at sea and fixed in formol-alcohol solution (Humason 1972) or 10% seawater Formalin<sup>4</sup>. After 2-6 wk fixation, the tissues were transferred to 50% isopropanol, processed through an Auto-Technica 2A Tissue Processor, vacuum infiltrated, and blocked in paraffin. Sections (7  $\mu$ m) were cut from each gonad by a rotary microtome, stained with Harris hematoxylin, and counter-stained with eosin-y. Histological sections from 300 fishes were read by two observers to develop agreement on sex and maturity stages; the remaining sections were then examined by a single observer. Sex and maturity stages (Table 1) which provided an accurate and objective estimate of reproductive status were modified from Smith (1965), Hilge (1977), and Mercer (1978) to determine size and age at first maturity, spawning season, and sex composition. The stage of gametogenesis and terminology used in gonadal descriptions follow Smith (1965), Combs (1969), Hyder (1969), Moe (1969), Mercer (1978), and Wallace and Selman (1981).

We included as males not only individuals whose gonads consisted entirely of testicular tissue but also those with functional testicular tissue (as judged by active spermatogenesis) as well as traces of inactive ovarian tissue. Females were defined as either having entirely ovarian gonads or inactive testicular

<sup>4</sup>Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Histological criteria used in determining gonadal condition of black sea bass, *Centropristis striata*.

Gonad class	Testicular state	Ovarian state
Immature	Little or no spermatocyte development.	Small (<100 $\mu$ m) basophilic oocytes.
Developing	A few primary and secondary spermatocytes through lumina filled with spermatozoa.	Predominance of oocytes with yolk vesicle formation through late vitellogenesis.
Ripe (running)	Predominance of spermatozoa, little active spermatogenesis.	Late vitellogenesis and presence of hydrated oocytes.
Spent	No spermatogenic activity, some residual sperm present in tubules.	Unspawned, mature oocytes undergoing atresia.
Resting	Some mitotic regeneration of spermatogonia and interstitial tissues.	Predominance of small basophilic oocytes with residual traces of atresia.
Transitional	—	Inactive or regressing ovarian tissue with concurrent testicular proliferation.

tissue in a functional ovary. Transitional gonads included only those with obviously proliferating testicular tissue within a nonactive, regressing ovary. Simultaneous gonads were those combining equally developed male and female tissue. Immature bisexual gonads were designated as simultaneous juveniles to avoid any implication as to their function at maturity.

We successfully sexed 80-90% of the fish sampled by histological examination every month but April. More than 75% of those sampled in April were sexed by gross examination of the gonads, and although our determinations of the functional sexes of these gonads were probably correct, the relative occurrence of transitional and simultaneous gonads in April samples remains unclear. These data were thus used only to complete the seasonal frequencies of functional sexes.

Gonads from 115 maturing females collected during April 1979 were removed at sea, split open with a longitudinal incision, and placed in Gilson's solution (Bagenal 1967). Separated oocytes were washed and stored in 70% isopropyl alcohol after digestion of the ovarian tunic and connective tissue and then were decanted into a separatory funnel and diluted to 1 L for enumeration. Three to five 1 mL subsamples were removed from the suspension, which was well mixed by continuous aeration through the bottom of the funnel. Each subsample was transferred to a petri dish and counted at a magnification of 10 $\times$ . Only ova >0.15 mm in diameter were counted since histological examination of the gonads of maturing and spent females showed only oocytes >0.15 mm developed during the spawning season. Total fecundity was estimated by expanding the mean of the subsamples to the total sample volume. Total fecundity was related to length and weight by standard least squares linear regression (Sokol and Rohlf 1981) and GM functional regression (Ricker 1973).

## Mortality Estimates

Plots of log<sub>e</sub> frequency on age indicated that black sea bass are fully recruited to commercial traps and hook-and-line gear at age 4, so mortality analysis applies to age 4 and older. The instantaneous rate of total mortality (*Z*) was estimated by standard least squares regression (Sokol and Rohlf 1981) from the slope of the right descending limb of the catch curve (Ricker 1975). Values of *Z* were also obtained by converting (appendix I in Ricker 1975) rates of survival (*S*) derived by Heinke, and Chapman and Robson estimates (Everhart and

Youngs 1981). Not all fish collected were aged, so fish of known age were grouped into 1 cm length intervals by gear type for each survey to calculate percentages of each age in each size interval. These percentages were applied to the number of *C. striata* in each length interval to estimate age composition for the unaged fish (Ricker 1975).

### Population Estimates at Specific Reef Sites

Petersen mark-recapture experiments were conducted at site 1 (lat. 32°30.3'N, long. 79°41.9'W; depth = 20 m; area  $\cong$  160 ha) during the summer of 1981 to estimate the population size of *C. striata* on this reef. In the summers of 1982 and 1983, we studied a second reef also (site 2: lat. 32°28.3'N, long. 78°14.5'W; depth = 23 m; area  $\cong$  120 ha). These reef areas were defined by the presence of attached algae and invertebrate growth (porifera, corals, echinoderms, bryozoans, anthozoans, and ascidians) as observed with a HYDRO products TC-125-5DA low-light-level underwater television camera during transects across the sites (for more details, see Wenner 1983). Study areas were mapped with an EPSCO C-Plot II LORAN-C plotter interphased with a SITEX 707 LORAN-C receiver.

Black sea bass were captured and recaptured at each site with commercial traps (Rivers 1966) and Florida snapper traps (0.9 m wide  $\times$  1.2 m long  $\times$  0.6 m high) fished for 45-90 min with cut clupeid bait (*Brevoortia tyrannus* and *Alosa aestivalis*). Black sea bass >20 cm TL, the approximate size of full retention in the traps, were measured to the nearest mm TL and tagged with 13 mm diameter plastic disc tags attached under the first dorsal fin with a nickel pin trimmed to the proper length and held in place with a 13 mm diameter plastic backing disc. Expansion of the swim bladder, due to reduced hydrostatic pressure, caused captured fish to float, so gas was released from the swim bladder with a 20-gauge hypodermic needle to enable fish to return to the bottom. For each experiment, 50-75 tagged fish, handled in the same fashion as those released, were held on the bottom in wire cages for about 24 h to determine tag-related mortality. Tagged fish were released over the reef, and sampling for recaptures started 24 h after tagging began. Experiments were completed in 48 h except at site 2 during the summer of 1982 when tagging was interrupted for 48 h by weather.

Preliminary estimates of population size are needed to determine sample sizes required for precise Petersen estimates (Everhart and Youngs

1981). Powles and Barans (1980) estimated the mean density of *C. striata* on reefs was 51 fish/ha from underwater television transects; expansion to the areas of our study sites gave preliminary estimates of 8,160 *C. striata* on site 1 and 6,120 on site 2. At site 1 we needed to tag 1,000 fish and examine 550 for tags to have an error no greater than 25% for 19 times out of 20 ( $1 - \alpha = 0.95$  and  $P = 0.25$ ). At site 2, we needed to tag 1,000 fish and examine 500. We used the adjusted Petersen estimate (Ricker 1975, p. 78):

$$N^* = \frac{(M + 1)(C + 1)}{(R + 1)}$$

where  $N^*$  = estimated population size  
 $M$  = number of fish tagged  
 $C$  = sample taken for census  
 $R$  = number of tags returned in the sample taken for census.

The biomass of *C. striata* for each year and site was estimated as

$$\text{Biomass} = \sum_1^a \left( \frac{n^1}{n} \times PE \times g \right)$$

where  $n^1$  = number of tagged fish in each 1 cm TL interval  
 $n$  = total number of tagged fish  
 $PE$  = population size from the Petersen estimate  
 $g$  = weight in grams for the midpoint of each 1 cm TL size interval derived from the total length-weight relationship  
 $a$  = number of 1 cm TL intervals of tagged fish.

In addition, the upper and lower confidence limits were substituted for  $PE$  in the above expression for estimates of the biomass at those population sizes.

## RESULTS

### Age and Growth

We believe that the central opaque zone of the sagitta may represent the first 1-4 mo of life in *C. striata*. This zone varied in length from 1.16 to 3.60 mm in the anteroposterior plane and from 0.56 to 1.54 mm in the dorsoventral plane (Fig. 4). We were not always able to make counts along a continuous

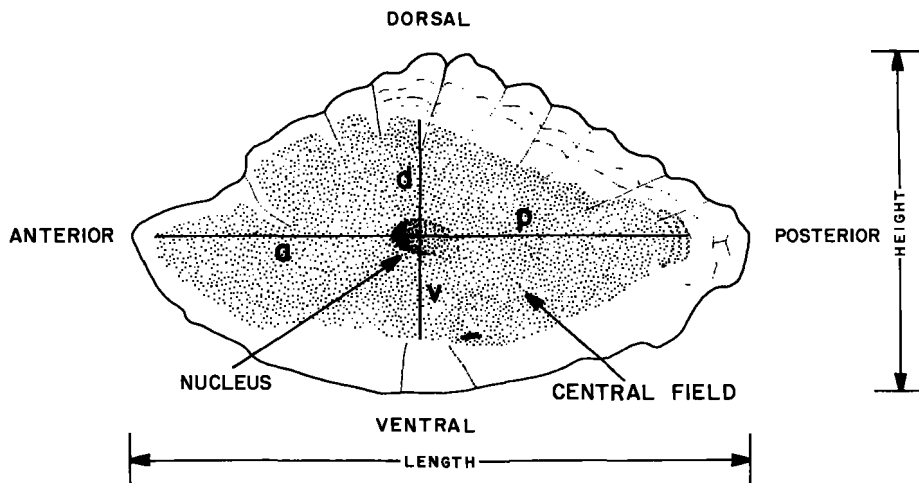


FIGURE 4.—Schematic representation of the left sagitta in young of the year *Centropristis striata* showing the orientation and direction of growth ring-counts in the central opaque zone. a = anterior, d = dorsal, p = posterior, v = ventral.

line because grinding did not expose all rings equally in the central zone. Also, in some instances, counting was halted at a distinct mark, such as a ring more distinctive than others, and we followed this mark around the sagitta to a site where rings were again visible and resumed counting. The number of rings in the central zone varied because of the otolith asymmetry and with the direction of the count (Table 2). For example, we obtained the following counts from the central primordium in one specimen (number 9 of Table 2): 90 rings to the dorsal edge of the central field (d of Fig. 4); 95 rings to the ventral edge (v of Fig. 4); 129 rings to the posterior edge (p of Fig. 4).

Since marginal increments on the otoliths should approach zero during the time of annulus formation, we calculated their monthly means to determine if one opaque band was laid down during each year

on the sagittae of *C. striata*. Generally, a single annulus was formed during April and May in all age groups (Fig. 5). We found that the ring was deposited unevenly around the sagitta, with the dorsal margin of the annulus being the last to be completed.

We identified 10 age groups in the South Atlantic Bight population of *C. striata*, which exceeded the previous reports of 7 (Cupka et al. 1973<sup>6</sup>) and 8 (Mercer 1978) groups. Observed mean lengths and weights increased with age; however, small sample sizes in ages 8 through 10 masked this trend (Table 3). Regressions of weight on length (TL and SL) and length on length are in Table 4.

<sup>6</sup>Cupka, D. M., R. K. Dias, and J. Tucker. 1973. Biology of black sea bass, *Centropristis striata* from South Carolina waters. Unpubl. manuscript. South Carolina Wildlife and Marine Resources Department, P.O. Box 12559, Charleston, SC 29412.

TABLE 2.—Data from *Centropristis striata* examined for daily growth rings. Refer to Figure 2 for otolith morphology and terms (d, v, p, and a) used in the counts. Numbers in parentheses are ranges of several counts; dashes indicate no counts made.

No.	Fish			Otolith		Central field					
	TL (mm)	SL (mm)	WT (g)	Height (mm)	Length (mm)	Height (mm)	Length (mm)	Daily ring counts			
								d	v	p	a
1	66	54	4	1.56	broken	0.92	1.76	—	—	(84-89)	—
2	60	48	2	1.52	3.08	0.56	1.16	28	(25-26)	(50-51)	—
3	95	74	11	2.24	4.44	1.54	3.25	—	(109-120)	—	—
4	125	98	30	2.92	4.88	1.54	3.60	—	135	—	—
5	78	61	4	1.82	broken	0.98	broken	105	—	—	—
6	76	58	5	1.84	3.44	1.08	2.68	106	—	121	—
7	78	60	4	1.78	3.40	1.12	2.88	(98-106)	—	—	—
8	81	63	5	1.92	3.80	1.52	3.40	51	—	—	81
9	—	64	6	1.84	3.52	1.16	3.08	90	95	—	129

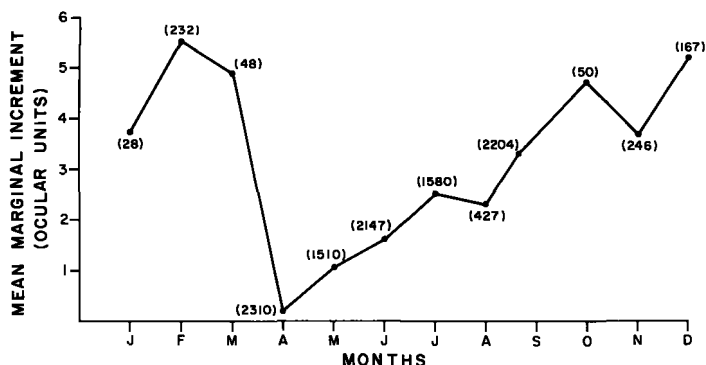


FIGURE 5.—Mean marginal increment by month for otoliths of *Centropristis striata*. Number in parentheses represent monthly number of otoliths examined.

TABLE 3.—Means ( $\bar{x}$ ), standard deviations and sample sizes for observed lengths (mm) and weights (g) by age for *Centropristis striata*.

Age	Total length			Standard length			Weight		
	n	( $\bar{x}$ )	SD	n	( $\bar{x}$ )	SD	n	( $\bar{x}$ )	SD
0	185	94	25	186	73	20	186	17	16
1	818	163	27	830	127	21	822	70	38
2	2,712	215	28	2,714	167	21	2,688	152	65
3	4,271	249	34	4,263	192	24	4,246	228	102
4	2,376	291	40	2,371	222	28	2,350	348	142
5	951	337	46	950	256	32	904	520	206
6	497	375	48	497	284	35	460	711	266
7	138	395	50	139	299	38	121	623	280
8	48	394	50	48	301	38	43	838	289
9	10	406	58	10	305	46	7	816	383
10	4	404	45	4	303	35	3	685	85

TABLE 4.—Least square linear and geometric mean functional regression equations of weight (WT) on total length (TL) and standard length (SL), and length-length for *Centropristis striata*. Weight units are grams and lengths are millimeters. All least squares regressions were significant at  $\alpha = 0.01$ .

Least squares equation	n	r <sup>2</sup>	GM functional equation
$\log_{10} WT = -4.375 + 2.800 \log_{10} TL$	12,281	0.97	$\log_{10} WT = -4.478 + 2.844 \log_{10} TL$
$\log_{10} WT = -4.328 + 2.978 \log_{10} SL$	12,284	0.98	$\log_{10} WT = -4.398 + 2.949 \log_{10} SL$
$TL = -9 + 1.4 SL$	12,473	0.97	$TL = -12 + 1.4 SL$
$SL = 12 + 0.7 TL$	12,473	0.97	$SL = 9 + 0.7 TL$

Least squares regressions of SL (mm) on otolith radius (OR in ocular units) are

$$\log_{10} SL = 0.668 + 1.056 \log_{10} OR;$$

$$n = 12,011; r^2 = 0.89.$$

The intercept of the SL-OR relationship was used to obtain the mean back-calculated SL's at age which were lower than observed SL's in all cases (Table 5). Weighted least square estimates of von Bertalanffy parameters, asymptotic 95% confidence

TABLE 5.—Observed and back-calculated mean standard length in mm and von Bertalanffy standard length at age for *Centropristis striata*.

Age	n	Observed SL	Back-calculated SL	von Bertalanffy SL
1	830	127	88	88
2	2,714	167	142	141
3	4,263	192	180	182
4	2,371	222	212	215
5	950	256	244	241
6	496	284	271	261
7	139	299	283	278
8	48	301	289	291
9	10	305	296	301
10	4	303	303	309



limits and asymptotic standard errors were also derived from these data (Table 6). Estimates of an average asymptotic size ( $L_{\infty}$ ) depended not only on the number of age groups present and the distribution of individuals within each group, but also on the curvature of the age-size relationship. An average asymptotic size of 341 mm SL appeared conservative. The largest fish aged was 390 mm SL and only 0.6% of all *C. striata* sampled were larger than 341 mm SL. The largest specimen caught off the South Carolina coast was estimated to be about 490 mm SL (S.C. Wildlife and Marine Resources Department<sup>6</sup>). Comparisons of von Bertalanffy back-calculated and observed SL at age are in Table 5.

TABLE 6.—Estimated von Bertalanffy parameters describing the growth of *Centropristis striata*. The weighted residual sums of squares = 238.46. SE = standard error; C.L. = confidence limits.

Parameter	Estimate	Asymptotic SE	Asymptotic 95% C.L.	
			lower	upper
$L_{\infty}$	341	17.818	298	383
$k^{\infty}$	0.2309	0.0221	0.1787	0.2831
$t_0$	-0.3010	0.0560	-0.4335	-0.1685

## Reproduction

The generalized ovarian structure of *C. striata* is similar to that of *Epinephelus fulva* (Smith 1965), *E. morio* (Moe 1969), and *Hemanthias vivanus* (Hastings 1981). The bilobed organ is suspended by mesenteries from the swim bladder in the posterior region of the body cavity. The lobes fuse posteriorly, and their lumina form a common oviduct. Blood vessels and nerves enter the ovary at the anterior point of each lobe's suspension and continue posteriorly medial to the supportive mesenteries along the dorsomedial surface of each lobe. The lumina are lined with folded germinal epithelium (ovarian lamellae), within which oocytes develop and mature. The lamellae are first seen protruding from the dorsal region of the lumen at the boundary of the ovary and the lamellar oviduct. They continue along both sides of the lumen in the area of gonadal confluence until only the ventralmost region of the ovary is lamellar. This lamellar area is confluent with the oviduct and extends anteriorly to half of the lengths of each ovarian lobe (Fig. 6A). The lamellar regions of female gonads were bordered throughout their extent by testicular precursor cells (Figs. 6A, B; 7A).

<sup>6</sup>Office of Conservation, Management, Marketing and Recreational Fisheries, S.C. Wildlife and Marine Resources Department, 1982. South Carolina Saltwater Sport Fishing Tournaments and State Record Fish. S.C. Wildlife and Marine Resources Department, P.O. Box 12559, Charleston, SC 29412.

Although these bands of cells were found in varying stages of development in all ovarian tissues, the most active proliferation of identifiable spermatogenic tissue (as manifested by transitional gonads; Table 7) occurred after the spring and fall spawning seasons (described later). Both increased ovarian inactivity and degeneration coincided with the proliferation of testicular tissue during sexual succession (simultaneous hermaphroditic development is treated below). No instance of active ovarian development concurrent with testicular degeneration was observed.

Sexual transition commenced in the posterior region of the ovary with the expansion of testicular lobes into the ovarian lumen. This proliferation proceeds anteriorly, with sperm sinus forming in the ovarian tunic adjacent to the testes. Testicular growth appears to be the result of mitotic spermatogenic processes, including spermatozoa formation, are not uncommon (Fig. 7B). The sperm sinuses, as well as the vas deferens (which form within the oviductal wall) apparently result from ruptures in their respective surrounding tissues, as suggested by Hastings (1981), because there was no cell lining associated with these structures (Fig. 7B).

Simultaneously developed hermaphroditic gonads were found in all maturity stages. However, only 3% of the fishes exhibited this phenomenon, and we were unable to determine if the vas deferens had an external opening; therefore, we lack definitive proof that these fish were functional simultaneous hermaphrodites.

Histological sections of immature ovaries contained only oogonia and small basophilic, previtellogenic oocytes about 8-100  $\mu\text{m}$  in diameter. Maturing ovaries had oocytes 100-500  $\mu\text{m}$  in diameter, in

TABLE 7.—Monthly sex composition data for *Centropristis striata* along with  $\chi^2$  values for tests of a 1:1 sex ratio. \*\* =  $P < 0.01$ , 1 df; \* =  $P < 0.05$ , 1 df.

Month	Males	Females	Transitional	Transitional (%)	♂:♀	$\chi^2$
January	13	13	1	3.7	1:1	—
February	111	107	8	3.6	1:0.96	0.07
March	15	7	0	0	1:0.47	2.91
April	928	1,685	122	4.5	1:1.82	219.30**
May	404	497	145	13.9	1:1.23	9.60**
June	509	1,039	383	19.8	1:2.04	181.46**
July	132	368	84	14.4	1:2.79	111.39**
August	112	246	42	10.5	1:2.20	50.16**
September	668	1,109	262	12.8	1:1.66	109.44**
October	35	17	1	1.9	1:2.05	5.12*
November	64	150	27	11.2	1:2.34	34.56**
December	34	19	13	19.7	1:0.56	4.45

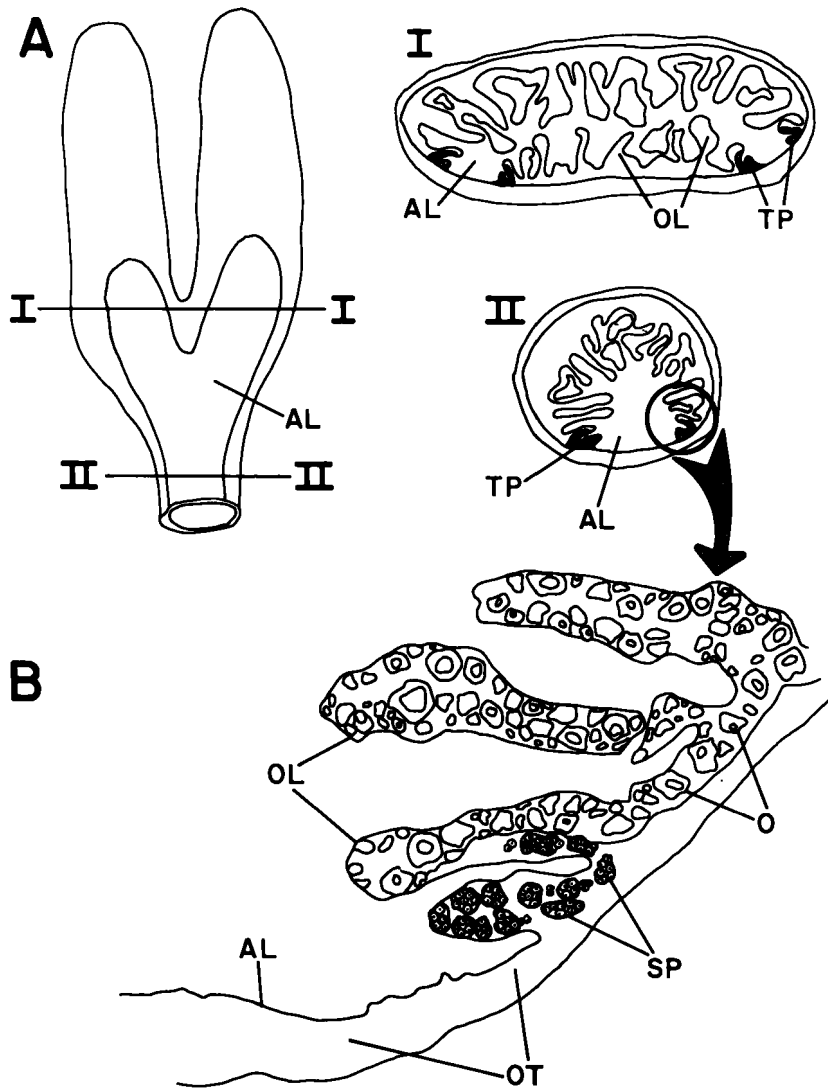
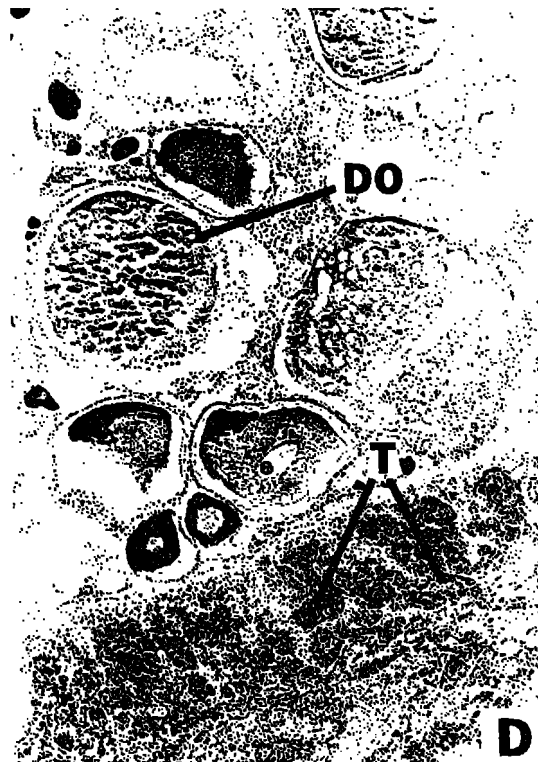
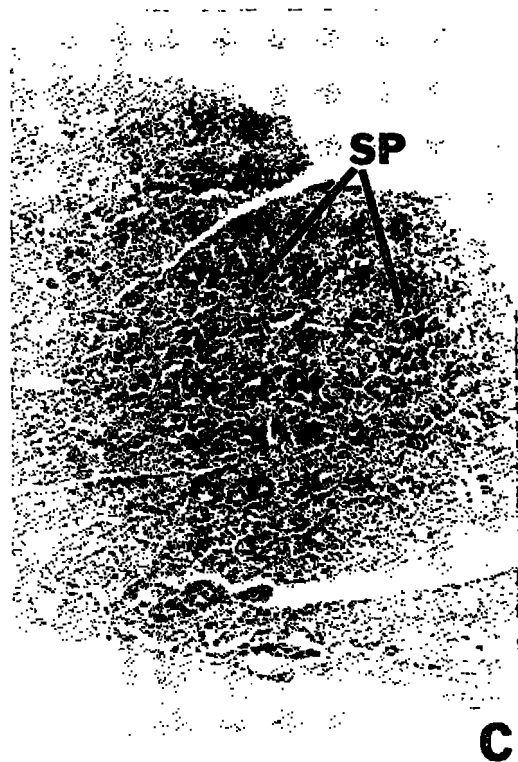
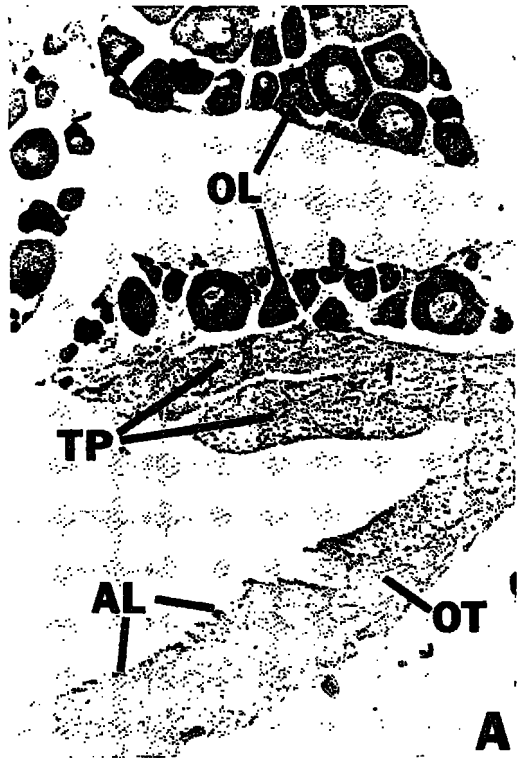


FIGURE 6.—Schematic representation of a functionally female ovary from *Centropristis striata*. A) Ventral view of ovary showing the alamellar region. Cross sections of the ovary were made in planes I-I and II-II, and show the positioning of the primordial testicular tissue at the boundary of the alamellar regions. B) An enlargement of the area indicated, showing the cellular relationships of the alamellar area, testicular primordia and ovarian lamellae. AL = alamellar region, O = oocytes, OL = ovarian lamellae, OT = ovarian tunic, SP = chords of spermatogonia, TP = testicular primordia.

FIGURE 7.—Photomicrographs of histological sections of gonads from *Centropristis striata*. A) Cross section taken from the posterior region of a functional ovary showing the alamellar region and testicular primordia, 250 $\times$  magnification. B) Cross section taken from the posterior region of a gonad undergoing transition, 250 $\times$  magnification. C) Cross section of immature testicular tissue from a 133 mm SL fish, 100 $\times$  magnification. D) Cross section of a simultaneous gonad showing active testicular and ovarian development, 100 $\times$  magnification. AL = alamellar region, DO = developing oocyte, OL = ovarian lamellae, OT = ovarian tunic, S = spermatozoa, SP = spermatogonia, T = testicular tissue.



stages from yolk vesicle formation (Wallace and Selman 1981) through late vitellogenesis. Oocytes (500-740  $\mu\text{m}$  in diameter) in ripe ovaries showed coalescence of yolk globules and hydration. Gonads from spent and resting females contained decreasing amounts of unspawned, atretic oocytes and empty, ruptured follicles.

Gonads from immature males were characterized by primary and secondary spermatogonia (Fig. 7C), and isolated, more fully developed seminiferous crypts in some instances. In developing testes we saw several stages that included gonadal tissue composed mostly of primary and secondary spermatocytes, as well as sperm sinuses filled with mature spermatozoa. Ripe testes had sperm sinuses and ducts packed with spermatozoa; the remainder of the gonad showed only a little spermatogenesis. Spent testes showed both the lack of spermatogenic activity and the presence of large amounts of unshed sperm, whereas gonads in resting males showed mitotic proliferation of next season's spermatogonia and interstitial tissues.

Females comprised 52% of the sexed *C. striata* and were mature in ages 1 through 8. We found mature gonads in none of the females at age 0, 48.4% at age 1, 90.3% at age 2, 99.1% at age 3, and 100% at all older ages. Immature females were 50-180 mm SL, and the smallest mature specimen was 110 mm SL. Males made up 30.6% of the fishes sexed, and 1.3% of these males were immature and were in ages 0-1 with lengths of 50-180 mm SL. The smallest mature male was 100 mm SL.

Gonads of 14% of the *C. striata* examined histologically showed these fishes undergoing sex succession. These were found primarily after the major spawn (January-April), and during a brief period after the lesser spawn during September-October (Table 7). The smallest individuals exhibiting sex succession were in the 120-139 mm SL interval (Table 8); however, the greatest frequency of transitional gonads (77%) occurred in fishes 160-259 mm SL. Males made up 15.4% of the age 0 *C. striata* and 10.5% of fishes <120 mm SL (Tables 8, 9; Fig. 8). The relative abundance of males increased with both size and age, and fish containing transitional gonads increased in abundance during the period of the most rapid decline in the relative number of females (Fig. 8).

Both male and female tissue developed simultaneously in the same gonad in 3% of the *C. striata* examined histologically (Fig. 7D). This occurred in immature, developing, spent, and resting fishes. Both testicular and ovarian tissues showed equivalent maturity stages within the same gonad; that

is, male and female germinal tissue developed concurrently.

The overall sex ratio for *C. striata* in the South Atlantic Bight was 1♂:1.71♀. We found significantly more females than males from April through November, and inconsistency in the ratio between December and March probably reflected both inadequate and biased samples from these months. Ratios were significantly different at all sizes from an hypothesized 1:1 (Table 8) except at 200-219 mm SL. The abundance of males begins to increase in that size group and also in age class 4 (Table 9) as the abundance of females declines, reflecting the increased frequency of the sex succession process.

*Centropristis striata* has a major spawn from January through April when 80-100% of the ovaries were developing or ripe (Fig. 9). Although a second period of ovarian activity was found in September, it was interpreted as being of a lesser nature since only 30% of the females were developing or ripe.

TABLE 8.—Sex composition and  $\chi^2$  values for tests of a 1:1 sex ratio of *Centropristis striata* by 20 mm SL intervals. \*\* =  $P < 0.01$ , 1 df; \* =  $P < 0.05$ , 1 df.

SL	Males	Females	Transitional	Transitional (%)	♂:♀	$\chi^2$
-119	16	136	0	0	1:8.50	94.74**
120-139	28	206	4	1.7	1:7.36	135.40**
140-159	74	525	46	7.1	1:7.10	339.57**
160-179	170	1,145	200	13.2	1:6.74	722.91**
180-199	301	796	289	20.8	1:2.64	223.36**
200-219	347	423	112	15.3	1:1.22	7.50*
220-239	335	185	94	14.8	1:0.55	43.27**
240-259	278	106	67	13.0	1:0.38	77.04**
260-279	179	41	33	4.2	1:0.23	86.56**
280-299	154	26	8	2.5	1:0.17	91.02**
300-319	111	5	3	3.3	1:0.04	96.86**
320-339	57	1	2	3.5	1:0.02	54.07**
>339	55	0	2	3.6		
Total	2,105	3,595			1:1.70	

TABLE 9.—Sex composition and  $\chi^2$  values for tests of a 1:1 sex ratio of *Centropristis striata* by age. \*\* =  $P < 0.01$ , 1 df.

Age	Males	Females	Transitional	Transitional (%)	♂:♀	$\chi^2$
0	10	55	0	0	1:5.50	31.2**
1	42	315	20	5.3	1:7.50	208.8**
2	251	1,066	185	12.3	1:4.20	504.3**
3	561	1,449	447	18.2	1:2.60	392.3**
4	635	479	223	16.7	1:0.75	21.8**
5	274	84	59	5.0	1:0.31	100.8**
6	189	17	8	3.7	1:0.09	143.6**
7	54	2	2	3.4	1:0.04	48.3**
8	13	0	0	0		
9	2	0	0	0		
10	2	0	0	0		

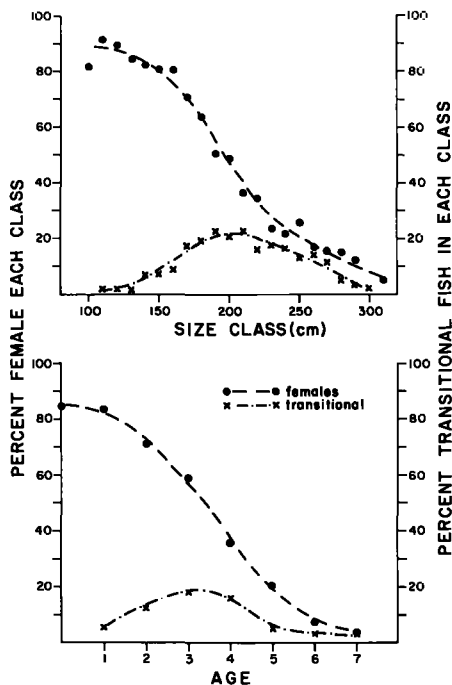


FIGURE 8.—Percent female and transitional *Centropristis striata* by size and age.

Fall spawning probably extended into October because many fishes obtained in November had recently spent ovaries.

Fecundity was significantly related to SL, TL, weight, and age with the former three equations having by far the highest  $r^2$  values (Table 10). The

TABLE 10.—Least squares linear and geometric mean functional regression equations of fecundity (fec) on total length (TL), standard length (SL), weight (WT), and age for *Centropristis striata*. Weight units are grams and lengths are millimeters. All least squares regressions were significant at  $\alpha = 0.01$ .

Least squares equation	n	r <sup>2</sup>	GM functional equation
$\log_{10} \text{ fec} = -0.605 + 2.335 (\log_{10} \text{ TL})$	115	0.62	$\log_{10} \text{ fec} = -2.098 + 2.959 (\log_{10} \text{ TL})$
$\log_{10} \text{ fec} = -0.309 + 2.318 (\log_{10} \text{ SL})$	115	0.65	$\log_{10} \text{ fec} = -1.589 + 2.879 (\log_{10} \text{ SL})$
$\log_{10} \text{ fec} = 3.057 + 0.822 (\log_{10} \text{ WT})$	115	0.65	$\log_{10} \text{ fec} = 2.587 + 1.022 (\log_{10} \text{ WT})$
$\log_{10} \text{ fec} = 4.529 + 0.913 (\log_{10} \text{ Age})$	110	0.33	$\log_{10} \text{ fec} = 4.196 + 1.580 (\log_{10} \text{ Age})$

TABLE 11.—Observed mean fecundity at age and its standard error ( $S_{\bar{x}}$ ) for *Centropristis striata*, in the South Atlantic Bight.

Age	Mean fecundity	$S_{\bar{x}}$	n
2	61,846	8,089	13
3	94,801	4,406	55
4	115,411	8,900	27
5	160,000	50,720	7
6	226,040	46,706	5
7	287,350	80,650	2
8	137,400	—	1

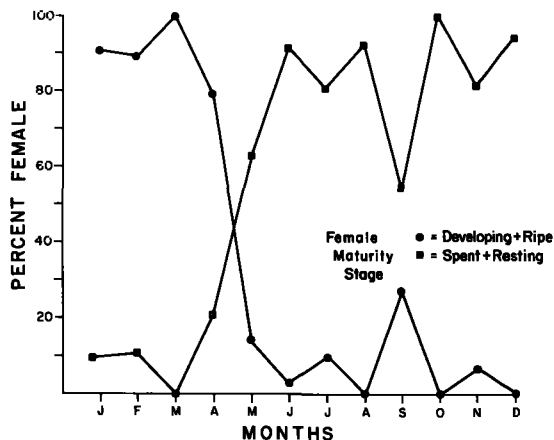


FIGURE 9.—Maturity stages of female *Centropristis striata* by month to illustrate bimodal spawning.

least squares linear regression model of fecundity on age explained only 33% of the variation in fecundity. Observed mean fecundity and its standard error increased with age (Table 11). The lowest observed fecundity (17,000) was in a 2-yr-old fish (SL = 108 mm; TL = 140 mm; weight = 45 g) and the largest (1,050,000) was in a 438 mm SL fish (TL = 454; weight = 1,371 g) of undetermined age.

### Mortality

Instantaneous rates of total mortality, as derived from catch curves, for *C. striata* ranged from 0.721

to 1.430, and actual mortality rates were from 0.513 to 0.761. Values increased from 1978 to 1981. For example, values of A rose from 51.3 to 73.3% for trap-caught fish and from 51.6 to 76.1% for hook-and-line caught fish older than age 4 (Table 12). Mortality values of trap-caught and hook-and-line caught *C. striata* were similar within years for each estimation procedure. Mortality values, moreover were similar between estimation procedures. We found a significant correlation between the instantaneous

TABLE 12.—Instantaneous (Z) and actual (A) rates of total mortality for *Centropristis striata* in the South Atlantic Bight. Gear types: T = trap; H&L = hook and line.

Year	Gear	Catch curve		Heinke		Chapman-Robson		Means	
		Z	A	Z	A	Z	A	Z	A
1978	T	0.721	0.513	0.841	0.568	0.991	0.628	0.851	0.569
1979	T	0.906	0.595	0.819	0.559	0.872	0.582	0.866	0.579
1979	H&L	0.726	0.516	0.759	0.532	0.650	0.478	0.712	0.509
1980	T	1.030	0.643	1.020	0.639	1.181	0.693	1.077	0.658
1980	H&L	0.905	0.595	0.944	0.611	1.016	0.638	0.955	0.615
1981	T	1.320	0.733	1.347	0.740	1.328	0.735	1.332	0.736
1981	H&L	1.430	0.761	1.347	0.740	1.492	0.775	1.423	0.759
1982	T	1.279	0.722	1.382	0.749	1.443	0.764	1.368	0.745
1982	H&L	1.246	0.712	1.277	0.721	1.309	0.730	1.277	0.721

rate of total mortality from trap data and the South Carolina commercial landings from 1978 to 1982 (Fig. 10).

### Population Estimates at Specific Sites

Mortality of *C. striata* attributable to tagging occurred only once, during the 1983 experiment of site 2 when 6% of the fishes (3 of 50) died during the holding period. Therefore, we reduced the number of tagged fish-at-large (M) by 6% to account for this tagging related mortality.

Between 1981 and 1983, a decline in the order of magnitude from 20,070 to 2,236 individuals (88.9%) occurred in the estimated abundance of *C. striata* at site 1. On this reef, the abundance declined 60.6% from 1981 to 1982 and another 75.5% from 1982 to

1983 (Table 13). Abundance at site 2 declined 52.9% between 1982 and 1983. Biomass of *C. striata* declined by an order of magnitude on site 1 from 4,836 kg in 1981 to 491 kg in 1983 (Table 13). This was an overall decrease of 89.9%. Site 2 had a 62% decline in biomass from 2,150 kg in 1982 to 810 kg in 1983. Our estimates are for fish >20 cm TL, the only ones vulnerable to the traps. Therefore, density and biomass estimates are minimum values.

In addition to the declines in population size and biomass of *C. striata*, there were decreases in mean size and age. Mean TL was 3 cm less in 1983 than in 1981 at site 1, whereas *C. striata* were on average 2 cm smaller in 1983 than 1982 at site 2. Not only were the means reduced, but also the frequency distribution became more skewed towards the smaller size intervals and the contributions of larger

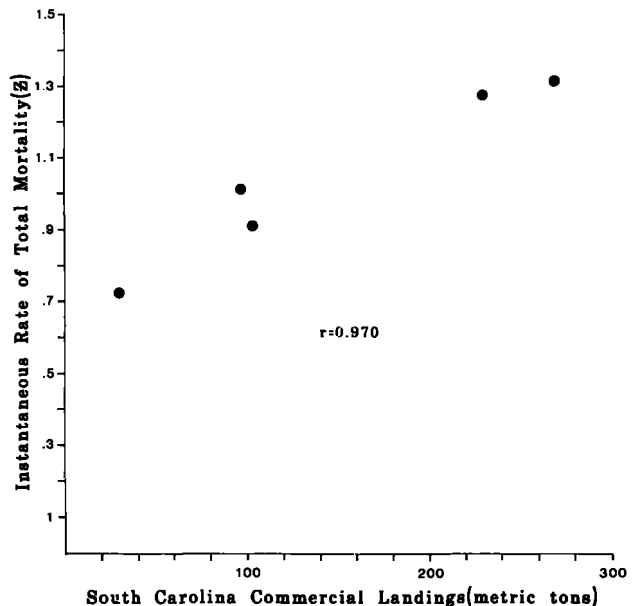


FIGURE 10.—Plot of the instantaneous rate of total mortality (Z) as determined from resource survey data (1978-81) and the South Carolina commercial landings of *Centropristis striata* for that year.

TABLE 13.—Summary of Petersen mark-recapture population estimates, biomass, and density (number and kg/ha) estimates for black sea bass, *Centropristis striata*, on two sponge-coral habitat sites. 95% confidence limits (C.L.) of  $p (= R/C)$  were determined by the methods of Cochran (1977).

	Site 1			Site 2	
	1981	1982	1983	1982	1983
C	634	529	438	446	679
M	1,042	1,169	1,084	901	854
R	32	67	212	50	155
95% C.L. of R	21.9-44.2	53.4-83.1	193.2-230.8	33.9-57.5	135.1-175.2
p	0.50	0.127	0.484	0.112	0.228
95% C.L. of p	0.035-0.070	0.101-0.157	0.441-0.527	0.076-0.129	0.199-0.258
$N^*$ <sup>1</sup>	20,070	9,119	2,236	7,906	3,727
95% C.L. of $N^*$	14,653-28,921	7,347-11,399	2,055-2,453	6,892-11,553	3,300-4,272
$\mu$	0.032	0.058	0.196	0.056	0.182
95% C.L. of $\mu$	0.022-0.043	0.046-0.072	0.179-0.213	0.039-0.065	0.159-0.206
Biomass (kg)	4,836	2,077	491	2,150	810
95% of biomass (kg)	3,530-6,959	1,673-2,595	451-539	1,874-3,142	717-928
Number/ha	125	57	14	66	31
95% C.L. of number/ha	92-181	46-71	13-15	57-96	28-36
kg/ha	30.2	13.0	3.1	17.9	6.7
95% C.L. of kg/ha	22.1-43.5	10.5-16.2	2.8-3.4	15.6-26.2	6.0-7.7

<sup>1</sup>Adjusted Petersen estimate (Ricker 1975).

fishes to the populations was greatly reduced (Fig. 11). Mean age declined 0.5 years at site 1, and the age composition shifted towards younger age classes

(Fig. 12). Fishes age 4 and older went from 42% of the population in 1981 to 25% in 1982 and 9% in 1983.

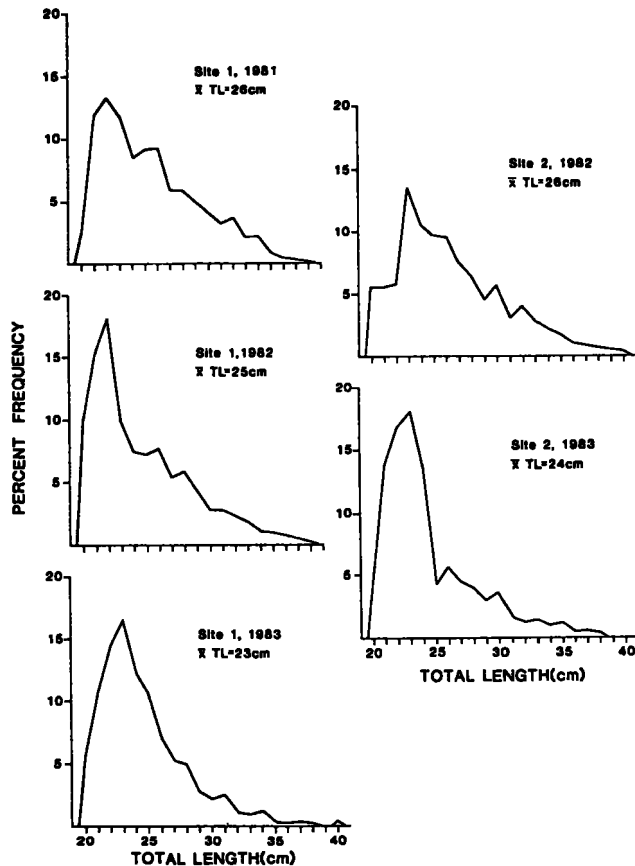


FIGURE 11.—Size-frequency distribution of *Centropristis striata* from five discrete mark-recapture tagging studies.

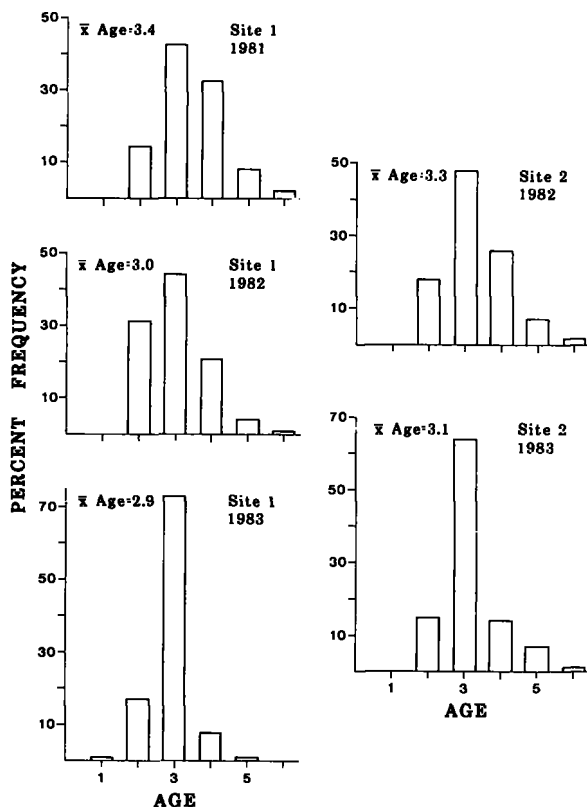


FIGURE 12.—Age composition of *Centropristis striata* at the two experimental mark-recapture sites.

## DISCUSSION

### Age and Growth

The cause of the variation in size and shape of the sagitta's central field in *C. striata* is unknown, however, differing size of the nuclei of Atlantic herring, *Clupea harengus*, can be related to spawning season (Postuma 1974). Further studies are needed to determine if these differences can be related to spawning time of *C. striata* in the South Atlantic Bight.

Inadequate validation in many studies that estimate age have been noted by Beamish and McFarlane (1983), and they have reemphasized the need for verification of aging technique. Our attempts at validation have shown that one annulus is formed each year during April-May. Also, our counts of presumed daily growth rings have provided circumstantial support for the formation of the first annulus. A similar approach was used by Radtke et al. (1985) in their study of the oyster toadfish, *Opsanus tau*.

Our mean back-calculated lengths agree well with Mercer's (1978) data for *C. striata* from the South

Atlantic Bight up to age 5; however, ours are much smaller than Cupka et al. (fn. 5). Our lengths at age are consistently smaller than *C. striata* from the Middle Atlantic Bight (Mercer 1978). Mercer (1978) attributed size at age differences between the two areas to gear selectivity, yet our results suggest that *C. striata* from the South Atlantic Bight are smaller than those of the Middle Atlantic Bight. The larger size at age found by Cupka et al. (fn. 5) may reflect the population of *C. striata* in the South Atlantic Bight prior to heavy exploitation that began in 1969.

Since estimates of  $L_{\infty}$ ,  $K$ , and  $t_0$  are affected by several nonbiological, methodical factors, direct comparisons of these growth parameters between different studies are of limited value. However, when viewed in relative terms, they can indicate general differences or similarities between studies, species, or areas. Our estimate of  $L_{\infty}$  (341 mm SL) was much closer to Mercer's (1978) value ( $L_{\infty} = 352$  mm SL) than that of Cupka et al. (fn. 5) (625 mm SL). Our growth coefficient ( $K$ ) was higher, indicating that *C. striata* achieves maximum attainable size more rapidly than previously reported. These differences could have been caused by sampling methodologies and/or conditions of the popula-



tion of South Atlantic Bight *C. striata* at the time the studies were conducted.

### Reproduction

Smith (1965) established a phylogeny of serranid fishes based on three types of hermaphroditism. Most primitive is the *Serranus*-type gonad found in *Serranus* and *Hypoplectrus*, genera which are simultaneously hermaphroditic with male and female germinal tissues well separated by connective tissues. The middle type of this trio is the protogynously hermaphroditic *Rypticus-Anthias*-type gonad where testicular takeover commences with proliferation of preexisting spermatogonia located in crypts along the alamellar regions of the ovary and gametogenic tissues remain separated by connective tissue throughout sexual transition. Most advanced is the protogynous hermaphroditic *Epinephelus*-type gonad where testicular tissue cannot be found before sexual transition commences. During this process, crypts of spermatogonia differentiate and proliferate within the ovarian lamellae where they are intermixed with oogonia and oocytes.

Citing Lavenda (1949), Smith (1965) classified *C. striata* within the *Epinephelus*-type, an error corrected by Mercer's (1978) demonstration that morphological events during sexual transition in *C. striata* most resemble those of the *Rypticus-Anthias*-type gonad. Sexual succession in *C. striata* results from hypertrophy of bands of testicular primordia that lie along borders of the alamellar region of the ovary, not the proliferation of crypts of tissue that Mercer (1978; see also Smith 1965) reported. The arrangement of the primordial testicular ridges in *C. striata* is the same as in the protogynous *Hemanthias vivanus* (Hastings 1981).

The testicular primordia in *C. striata* is located in a similar region of the gonad as is the testicular portion of the simultaneously functioning gonad of *Serranus tigrinus* (Smith 1965). Though not stated by Smith (1965), the testes of *S. tigrinus* might border the alamellar region of the ovarian section as does the testicular primordial cells in *C. striata*, a gonadal similarity also noted between *H. vivanus* and *S. tigrinus* (Hastings 1981). No phylogenetic inferences should be drawn from these data, because gonadal development varies even among the closely related simultaneous hermaphrodites of the genera *Serranus* and *Diplectrum*. *Centropristis striata*, *H. vivanus*, and probably *R. maculatus* (see Smith 1965) have similar gonadal morphologies and strategies of sex succession, but these species are usually not considered closely related. Gonadal mor-

phologies may one day be important in determining serranid phylogenetic relationships; but more observations of all serranids are necessary.

The simultaneously functioning gonad of *C. striata* has morphology similar to that of *Serranus* (Smith 1965) in which discrete areas of testicular tissue empty into peripherally located sinuses, and oocytes discharge centrally. Sperm sinuses within the wall of the simultaneous gonads are well developed in *C. striata*, but it is not known if they are functional, i.e., permit sperm to exit the body along with the oocytes.

We found sizes and ages of *C. striata* undergoing sex succession which were similar to those Mercer (1978) reported in the South Atlantic Bight; however, we found a much higher incidence of transitional fish. Since Mercer (1978) found only 4% of *C. striata* from this area were undergoing sex succession, she offered two mechanisms for her abundance (38%) of mature males: 1) development of mature males from both immature males and juvenile hermaphrodites was very important, or 2) the rate of sexual transition was very rapid in this species.

We feel that both of Mercer's arguments were at best incomplete because of her small sample sizes from the South Atlantic Bight. Since we found few immature males and juvenile hermaphrodites in our samples, the probability is low that mature males develop solely from these. Also, we acknowledge the presence of serranids which show rapid sex succession (Fishelson 1970; Fricke and Fricke 1977) and believe the low frequency of individuals undergoing sex succession seen in most Epinepheline groupers probably reflects a similarly short-lived process. However, the presence of *C. striata* undergoing sex succession throughout the year, and their occurrence at sizes where the frequency of females declines, leads us to conclude that the primary source of mature males is through sex succession from active females.

We found secondary testes (sensu Harrington 1971) in all male *C. striata* including immature specimens. This morphology is not unique to *C. striata*. Hastings (1981) observed no primary male *H. vivanus* and suggested they all passed through an initial female phase. This same secondary gonadal morphology occurs in the secondarily gonochoristic serranid *Paralabrax clathratus* (Smith and Young 1966), and Reinboth (1970) indicated all male serranids are derived from females.

Overall, sex ratios of *C. striata* were significantly different from an hypothesized 1♂:1♀ in favor of females. Females significantly outnumbered males

up to an intermediate size and age, at which time the significantly different ratios favored males. Fishelson (1975) stated that sex ratios should approximate 1♂:1♀ at some stage if all protogynous females undergo sex succession. Given the alternating ratios of sexual abundance with size and age, and considering that no female older than age 7 and few larger than 330 mm SL were found in our samples, leads us to conclude that all *C. striata* have the potential to undergo sex succession.

### Population Estimates

The underlying assumptions of the Petersen method for population estimates were met in this study. We found tag-related mortality in only one experiment and adjusted the number of fish marked for it. We feel all tags were accounted for and tag loss was minimal, because tags were firmly anchored to the fish and were bright orange. Tagged fish were not randomly distributed over the study site, but they were released during vessel drifts governed by wind and surface currents and may be effectively random. We assumed minimal immigration and emigration because our experiments covered a brief time period.

Powles and Barans (1980) estimated density of *C. striata* in the sponge-coral habitat of the South Atlantic Bight. The estimates of 51 fish/ha and 7.6 kg/ha derived from the data of Powles and Barans (1980) were 37-66% and 23-44% of our mark-recapture values. Powles and Barans (1980) indicated that possible sources of error in their study were distance determinations from loran-A, which are much less precise than distances derived from loran-C readings, and variable visibility.

### ACKNOWLEDGMENTS

This work was funded by the National Marine Fisheries Service under contract NA-84-WCC-06101 to the South Carolina Wildlife and Marine Resources Department. We appreciate the Assistance of A. J. Kemmerer and W. Nelson of NMFS.

We thank Captain John Causby and First Mate Julian Mikell of the RV *Oregon* for the exceptional navigational and vessel handling skills enabling us to sample open ocean patch reefs not much larger than a few football fields with a 90-ft vessel. The difficulties involved can be appreciated only by one who has been there. It would not have been possible to process the numerous histological samples without the help of D. Stubbs. We are grateful to the many individuals who participated in the field

effort, several of whom suffered punctures by fish spines and lacerations by sea bass preopercles during the tagging study. A. G. Gash provided assistance with the computer analysis, K. Swanson drew the figures and N. Beaumont and M. Lentz typed the manuscript. Helpful critical reviews of the manuscript were made by C. A. Barans, E. L. Wenner, R. Warner, P. Hastings, G. Huntsman, P. Eldridge, and two anonymous reviewers.

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