AGE, GROWTH, REPRODUCTION, AND THE FEEDING ECOLOGY OF BLACK SEA BASS, CENTROPRISTIS STRIATA (PISCES: SERRANIDAE), IN THE EASTERN GULF OF MEXICO

Peter B. Hood, Mark F. Godcharles and Rena S. Barco

ABSTRACT

Aspects of life history and feeding ecology are described for black sea bass, Centropristis striata, collected from the eastern Gulf of Mexico primarily between December 1966 and December 1967. Marginal increment analysis suggests that bands on sagittae are deposited once a year during the late spring to early summer. Mean empirical standard lengths ranged from 106 mm at age 0 to 278 mm at age VII. Estimates of parameters for a von Bertalanffy growth equation were calculated for males ($L_{\infty} = 265$ mm, k = 0.29, $t_o = -1.28$), for females $(L_{\infty} = 218 \text{ mm}, k = 0.36, t_0 = -1.31)$, and for all aged fish $(L_{\infty} = 311 \text{ mm}, k = 0.16, t_0 =$ -2.00). Mean length at age was greater for males than for females. Black sea bass are protogynous hermaphrodites, with females outnumbering males by 1.5:1 in our samples. Females became mature between ages I and III (120-190 mm SL). No females were older than age VI. Most transitional fish were between ages II and IV (160-230 mm SL), Males were present at all ages, and mature males were 90-330 mm SL. Histological analysis of gonads suggested that spawning occurs from December to April. Forty-two prey species and 44 additional diet items identified to higher taxonomic categories were found in stomach contents, Amphipods, stomatopods, shrimps, crabs, and fishes were numerically the most common prey species. Caridean shrimp, penaeid shrimp, and xanthid crabs were the dominant prey items for inshore black sea bass, whereas majid crabs, stomatopods, and fishes dominated the diet of offshore fish.

Black sea bass, Centropristis striata, range from the northeastern Gulf of Mexico, around the Florida Keys, and north to the Gulf of Maine (Bigelow and Schroeder, 1953; Briggs, 1958; Topp, 1963; Lindall et al., 1973). Based on gill-raker and pectoral-fin-ray counts, Ginsburg (1952) separated Gulf of Mexico and northwest Atlantic populations into two species—C. melanus and C. striata, respectively. He postulated that the two populations were genetically isolated by the subtropical waters of the northern Florida Keys. Miller (1959) analyzed morphometric and meristic data from a greater number of specimens and concluded that the divergence between populations warranted only subspecific designations: C. striata striata and C. s. melana. Miller's subspecific designations were corroborated in subsequent studies by Bortone (1977), who examined osteological characters; Chapman (1977), who examined allozyme and plasma protein variation; and Bowen and Avise (1990), who examined mtDNA variation.

Off the west coast of Florida, adult black sea bass are commonly found between Tampa and Apalachee bays at depths of 7.3–18.3 m (Godcharles, 1970). Adults aggregate around limestone and coral outcroppings or other low-relief forms and are rarely found off deeper ledges inhabited by larger serranids (Topp, 1963; Godcharles, 1970; Smith, 1976; Bortone, 1977). Juveniles and subadults are generally found in the lower reaches of Florida west coast estuaries; however, their seasonal disappearance from inshore collections suggests an offshore movement during the fall when waters cool (Reid, 1954; Joseph and Yerger, 1956; Springer and Woodburn, 1960; Hastings, 1972; Mountain, 1972). Seasonal inshore/offshore movements of adult black sea bass have been reported for Atlantic populations (Lavenda, 1949; Kendall, 1977; Musick and Mercer, 1977); however,

tagging studies in the northeastern Gulf have indicated that adult black sea bass are nonmigratory over the short term and become residential once established on a reef (Topp, 1963; Beaumariage, 1964; Beaumariage and Wittich, 1966; Moe, 1966).

Lavenda (1949) first suggested that black sea bass are protogynous hermaphrodites based on differences between length-frequencies of males and females. Subsequently, evidence of the sexual transformation of the gonads was presented by Mercer (1978), Link (1980), and Wenner et al. (1986). In Atlantic populations, females mature between ages I and III, and sexual transformation occurs primarily between ages II and V (Mercer, 1978; Waltz et al., 1979; Link, 1980; Wenner et al., 1986).

Trap and handline fisheries for black sea bass have historically supported a productive fishery along the Atlantic coast (Rivers, 1966; Frame and Pearce, 1973; Cupka et al., 1973; Kendall, 1977; Musick and Mercer, 1977; Low, 1982). Researchers in the northeastern Gulf of Mexico during the 1960s collected large numbers of black sea bass from low reefs along the Florida west coast (Moe, 1963; Topp, 1963; Tyler, 1964; Moe, 1966; Joyce, 1968; Joyce and Williams, 1969). These findings prompted further investigations of their fisheries potential (Godcharles, 1970) and life history. In this paper we report on the age, growth, reproduction, and feeding ecology of black sea bass from the eastern Gulf of Mexico.

MATERIALS AND METHODS

Black sea bass were collected along the west-central Florida coast from estuaries and offshore to depths of 19.3 m from St. Martins Reef off New Port Richey (28°38'N, 82°47'W) south to Egmont Key off Tampa Bay (27°38'N, 82°46'W). Handlines and traps were the primary collecting gear (Joyce and Williams, 1969; Godcharles, 1970). Most black sea bass (68%) were collected from December 1966 to December 1967 during 13 monthly trapping cruises (Joyce and Williams, 1969). Ancillary collections were made to supplement monthly samples and to increase the sample of small fish; these collections came from a commercial fish house, party boats, miscellaneous hook-and-line collections by Florida Marine Research Institute personnel, and trynet and trammel net catches by the University of South Florida (USF) Anclote Environmental Project (Humm et al., 1971; Baird et al., 1972, 1973, 1975; Rolfes et al., 1974).

Total length (TL) and standard length (SL) of black sea bass were measured to the nearest millimeter, and whole weight (WT) was measured to the nearest ounce and converted to grams. Unless stated otherwise, all lengths presented are standard lengths. Sagittae were removed and stored in glycerol. Gonads were fixed in Bouin's or Davidson's solution for approximately 24 h, rinsed in water, and then transferred to 95% ethanol. When possible, stomachs were also removed, fixed in 10% formalin, and then transferred to 70% ethanol.

Thin sections of sagittae were used for age determination. The left otolith was sectioned at 0.5-mm intervals along a transverse dorsoventral plane through the core using an Isomet diamond saw. Mounted sections were placed on a black field, illuminated with reflected light, and examined with a binocular dissecting microscope at 20× magnification. The magnified image was transmitted via video camera to a video monitor and was analyzed using an Optical Pattern Recognition System (OPRS) data-acquisition software package (Biosonics, 1987). This system allowed direct computer entry of the number of opaque bands and the corresponding distance measurements from the otolith core to the dorsal edge of the otolith (otolith radius) and to the distal edge of each opaque band.

To determine the accuracy of band counts, otolith sections from 62 specimens were read independently by two investigators. Because agreement between readers was high (97%), only one reader examined the remaining sections. Each otolith section was used for age and growth analysis only if two of three separate readings were the same and if the greatest difference between dissimilar counts was only one. We used marginal increment analysis and the relationship between fish length and otolith radius to validate our aging technique. The relative size of a marginal increment was calculated as a percentage by dividing the width of the marginal increment by the distance between the last two bands and multiplying that by 100, and monthly means were plotted and compared. Relationships of fish length to otolith radius were determined using least-squares regression analysis (SAS Institute, Inc., 1985) and were compared by analysis of covariance (ANCOVA; Sokal and Rohlf, 1981). Fish length at the time of the last opaque band formation was back-calculated using a regression of ln SL on ln otolith radius (Ricker, 1973; Bagenal and Tesch, 1981). Estimated lengths and corresponding

ages were used to estimate the parameters of a von Bertalanffy growth equation $[L_t = L_{\infty} \mid 1 - \exp(-K(t - t_0)) \mid]$ using the Marquardt algorithm for calculating a nonlinear regression (SAS Institute, Inc., 1985). We pooled data from both sexes to describe the generalized growth of this species. The mean empirical lengths at age of males and females were compared using analysis of variance (SAS Institute, Inc., 1985). Relationships between TL and SL and between \log_{10} -transformed whole weights and lengths were determined by least-squares regression analysis (SAS Institute, Inc., 1985).

Reproductive analyses were based on histological examination of gonadal tissue. The posterior portion of each preserved gonad was embedded in paraffin, thin-sectioned at 5.0 μ m, stained with Harris' haematoxylin, counterstained with eosin (Humason, 1972), and examined under a compound microscope. Sex and gonad developmental state were determined using classes developed by Moe (1969) for red grouper (*Epinephelus morio*). The presence or absence of buds of precursor testicular tissue was noted for all examined ovaries (Wenner et al., 1986). Female reproductive state for black sea bass captured between December 1966 and December 1967 was further quantified by calculating a mean maximum oocyte diameter for each mature female (Hood et al., 1988). Diameters of the ten largest, round oocytes in a section were measured using a binocular dissecting microscope at $50 \times$ magnification and the OPRS software package (Biosonics, 1987). The diameter of oocytes in the later stages of development (possibly hydrating) could not be accurately measured because they were misshapen by the histological processing. Therefore, the presence or absence of these oocytes was noted, and diameters were recorded for the largest oocytes that still retained their circular shape. Sex ratios were compared by age and 10-mm length classes with Chi-square analysis (Sokal and Rohlf, 1981).

Stomach contents were used to qualitatively examine inshore and offshore diets of black sea bass. Inshore fish were collected in the estuarine regions of Anclote Anchorage and Lower Tampa Bay. Offshore fish came from the 13 monthly trapping cruises. Prey items were identified to the lowest possible taxon.

RESULTS

Age and Growth.—We examined 1,095 black sea bass 39 to 330 mm SL, but not all the specimens could be used for every analysis. The majority (68%) were captured during 13 monthly cruises and ranged from 118 to 284 mm.

Black sea bass otoliths were examined from 683 fish, which were 76 to 278 mm in length. Forty-two (6.1%) of the sections were illegible, possibly due to long-term storage in glycerin. The number of bands could be counted, but no measurements could be recorded for 39 (5.7%) otolith sections because they were broken, had an odd shape, or were not sectioned through the core. The number of opaque bands counted from legible otoliths ranged from 0 to 7.

Opaque bands were deposited during late spring to early summer. The relative sizes of the marginal increments decreased from a maximum of 71.2% in February to a minimum of 22.2% in June, then increased each month through January (Fig. 1). This trend indicates that bands were laid down once a year between March and June.

The validity of using sectioned otoliths for growth analysis was further supported by the positive correlation between fish length and otolith radius. This relationship, however, was significantly different between males and females (ANCOVA; slopes: F = 4.59, P < 0.05 and intercepts: F = 52.17, P < 0.01). For females, the relationship was

$$ln(SL) = 0.707 ln(otolith radius) + 5.219;$$
 $r^2 = 0.72;$

and for males it was

$$ln(SL) = 0.674 ln(otolith radius) + 5.296;$$
 $r^2 = 0.61.$

Mean empirical lengths for all aged fish increased with age, ranging from 111 mm at age 0 to 274 mm at age VII (Table 1). Growth rate between ages 0 and I was relatively rapid, 37 mm·yr⁻¹; however, it slowed with age from an average of 23 mm between ages I and II to 6 mm between ages V and VI. An exception to this trend was observed between ages VI and VII, when the increase was 42 mm; however, this is based on only three fish, and all were males. The von

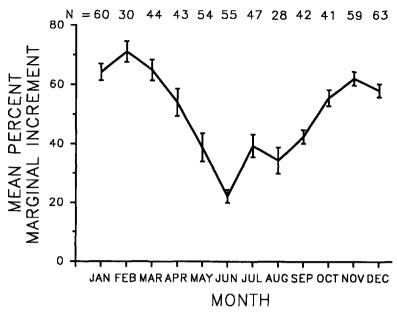


Figure 1. Monthly mean percentages of the relative sizes of marginal increments for sagittae sections from age I to age VI black sea bass. Vertical bars indicate one standard error with number above each bar.

Bertalanffy growth model accurately estimated growth for all aged fish (Table 2) because predicted values from this curve were similar to mean empirical and mean back-calculated lengths (Table 1).

Males were larger than females in each age class (0-VI) except for age I (Table 1). Empirically, the mean size of males was significantly larger (ANOVA; P < 0.05) than females for age classes II to V, when sample size was sufficient for statistical comparisons (Table 1). Von Bertalanffy growth equations predicted larger sizes for males than females in all age classes (Tables 1, 2).

The relationships between total and standard lengths, and total and standard lengths and whole weight were highly correlated (N = 1,088):

$$TL = 1.4 \text{ SL} - 13.6;$$
 $r^2 = 0.98;$ $SL = 0.7 \text{ TL} + 12.5;$ $r^2 = 0.98;$ $Log_{10} \text{ WT} = 3.1 \text{ Log}_{10} \text{ SL} - 4.7;$ $r^2 = 0.97;$ $Log_{10} \text{ WT} = 2.9 \text{ Log}_{10} \text{ TL} - 4.6;$ $r^2 = 0.97.$

Reproduction.—Mature females could be distinguished from immature females by the presence of vitellogenic oocytes and/or atretic bodies. Most females matured between ages I and III (130–170 mm; Fig. 2). Immature females ranged from 46 to 193 mm. The smallest mature female observed was 118 mm (Fig. 3A). Testicular precursor cells were observed in 6 of 106 immature ovaries and 86 of 375 mature ovaries, and all of these fish were >120 mm. These fish were not classified as transitional because little proliferation of the testicular tissue had occurred, and no ovarian tissue degeneration was observed.

Transition from ovarian to testicular tissue began in the posterior portion of the gonad. Testicular tissue proliferated anteriorly, whereas ovarian tissue degen-

Table 1. Number of black sea bass sampled, mean standard length (MSL), the difference between lengths, standard error (SE), minimum (Min SL) and maximum (Max SL) lengths, predicted length* (PSL), and mean back-calculated length (MBCL) at age for A) all fish aged (N = 640), B) females (N = 298), C) transitionals (N = 36), and D) males (N = 196).

Age	N	MSL	Difference	SE	Min SL	Max SL	PSL	MBCL
			A) A	aged f	ish			
0	33	111	37	5	76	145		
I	85	148	23	5 3 2 2 2 2 3 5	89	208	124	122
II	127	171	23	2	125	246	153	155
III	157	193		2	156	268	177	176
IV	162	211	18 13	2	167	260	198	198
V	56	224		3	172	275	216	217
VI	17	232	6 42	5	186	264	230	225
VII	3	274	42	3	268	278	243	270
			B)	Female	s			
0	21	103	44	3	76	135		
I	56	147	21	3 3 2 2 2 2 3	89	203	123	123
II	72	168†	19	2	125	209	152	152
III	82	187†	19	2	157	226	172	172
IV	54	197†	-3	2	167	250	186	187
V	11	194 †		3	172	212	196	189
VI	2	213	20	27	186	240	203	210
			C) T	ransition	nals			
I	3	180		6	174	191		
II	10	177	-3	3	160	191		
III	9	194	17	3	185	204		
IV	12	203	9	4	189	230		
v	2	205	2	9	196	213		
			Γ) Males				
0	3	113		17	87	145		
Ĭ	11	146	33	5	132	190	128	123
ΙΪ	16	195	49	6	158	246	163	174
Ш	41	206	11	4	156	268	188	186
IV	72	221	15	2	180	260	208	207
v	38	232	11	3	200	275	222	223
νÏ	12	233	1	5	200	264	233	227
VII	3	274	41	2 3 5 3	268	278	241	270
7 11	<i></i>				200	270	271	2,0

erated. Transitional black sea bass ranged from 160 to 230 mm and ages I to V, with 86% ages II to IV (Table 1; Fig. 3). Presumably, transitionals exist at smaller sizes because both immature and mature males < 160 mm were observed.

Spermatogonia developed within crypts located in the lamellae of testicular tissue. As spermatogenesis progressed, the surrounding connective tissue broke down, and sperm began to fill the sperm sinuses and ducts. Brown bodies (sensu

Table 2. Estimated von Bertalanffy growth parameters (asymptotic standard error) and number of fish used (N) for black sea bass. Parameters estimated for all aged fish, females, and males.

	I _×	К	t _o	N
All aged fish	311 (30)	0.16 (0.04)	-2.00 (0.34)	560
Female	218 (14)	0.36 (0.09)	-1.31(0.38)	257
Male	265 (17)	0.29 (0.07)	-1.28 (0.43)	175

Predicted lengths calculated from von Bertalanffy growth curves presented in Table 2.
 Mean length significantly different from males the same age (ANOVA; SAS Institute, Inc., 1985).

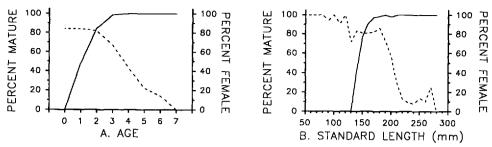


Figure 2. The percentage of black sea bass females that were mature (solid line) and the percentage of the sample that were female (dashed line) by A) age (left) and B) 10-mm length classes (right).

Grier, 1987) were observed in spent and inactive testes. Males were found at all ages (Table 1), and mature males ranged from 90 to 330 mm (Fig. 3B). We did not determine the age of the 330-mm male.

The overall sex ratio of the fish sexed histologically was significantly different from 1:1 (Chi-square test; $\chi^2_{df=1}=4.00$, P<0.05); 57% (480) were females, 38% (322) were males, and 5% (45) were in transition from female to male. The percentage of females was inversely related to both size and age. Females ages I–III and <200 mm significantly outnumbered males ($\chi^2_{df=1} \ge 13.11$, P<0.05 and Fig. 3A for age; $\chi^2_{df=1} \ge 21.59$, P<0.05 and Fig. 2B for length). The sex ratio did not differ from 1:1 at age IV, but above age IV and lengths >210 mm, males predominated ($\chi^2_{df=1} \ge 7.44$, P<0.05 for age and $\chi^2_{df=1} \ge 8.85$, P<0.05 for length).

Black sea bass spawn from December to April. Mature active ovaries were observed as early as September (Fig. 4A); however, no evidence of spawning (i.e., hydrating oocytes) was observed until December and January (Fig. 5). Also during September to April, mean maximum oocyte diameters were greater than 300 μ m (Fig. 6). Ripening mature testes were observed from September to May; the highest percentage of ripe testes occurred in March and April (Fig. 4B). Spent females were observed in April (Fig. 4A) and the percentage of spent males increased from April to May, indicating an end or a decline in spawning activity (Fig. 4). Mature inactive ovaries were present from May to September and inactive testes from April to September (Fig. 4). Mean maximum oocyte diameters found in ovaries from specimens collected between May and September remained between 50 and

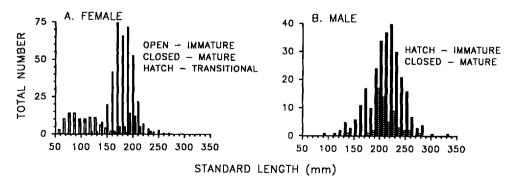


Figure 3. Length-frequency distributions of black sea bass maturity stages for A) females and transitionals (N = 425) and B) males (N = 319). Open bars represent immature fish, closed bars mature fish, and hatched bars transitional fish.

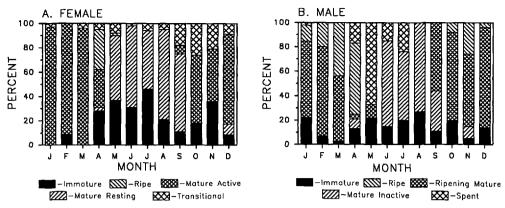


Figure 4. Monthly percentages of reproductive classes for all years combined for A) female and B) male black sea bass.

110 μ m, reflecting the presence of pre-vitellogenic oocytes (Fig. 6). Sex change was most common just prior to the spawning season; the percentage of transitional black sea bass was highest from September to November (18% to 26%; Fig. 4A).

Feeding Ecology. — Numerically, the diet was composed primarily of stomatopods, amphipods, shrimps, crabs, and fishes (Table 3). Forty-two prey items were identified to the species level and 44 to higher taxon categories from the 152 stomachs examined. Echinoderms, ascidians, bivalves, gastropods, cephalopods, nematodes, and polychaetes constituted only a minor portion of the diet. Diets of black sea bass from inshore, estuarine locations were numerically dominated by caridean and penaeid shrimps, amphipods, and xanthid crabs (N = 71). In 81 stomachs of fish from offshore habitats, majid crabs, stomatopods, and fishes were the most

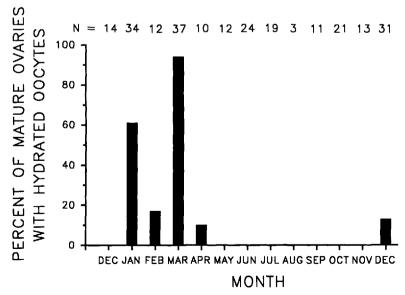


Figure 5. Monthly percentages of mature ovaries containing hydrated oocytes from black sea bass collected from December 1966 to December 1967 off the west central Florida coast.

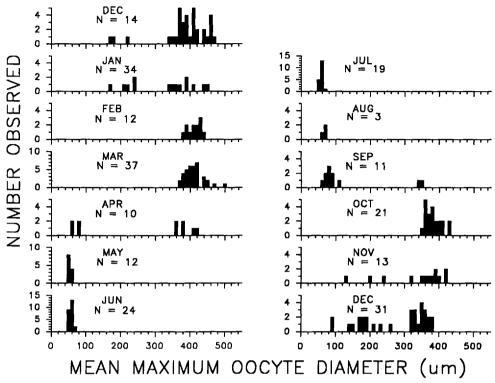


Figure 6. Monthly frequency distributions of mean maximum oocyte diameters of mature ovaries (μm) from black sea bass collected off the west central Florida coast from December 1966 to December 1967.

common prey items. The number of prey items in stomachs of inshore (presumably younger) fish was high and may be related to the need to consume a high number of small prey (e.g., amphipods and isopods) to meet energy needs. Although seagrasses were found in the stomachs of 15 inshore fish, we did not list them as prey items because we believed that they were incidentally ingested during normal feeding activity.

DISCUSSION

Age and Growth.—Our study verifies that sagittae can be used to age eastern Gulf of Mexico black sea bass. Cupka et al. (1973), Mercer (1978), and Link (1980) determined that sagittae were far more effective than scales, opercular bones, or vertebrae for aging black sea bass. Collins et al. (1990) recovered four tagged, tetracycline-marked black sea bass off South Carolina and found that opaque bands were formed once a year. We found that bands were formed between March and June, which is similar to the March–July times of formation reported for Atlantic populations (Cupka et al., 1973; Briggs, 1978; Mercer, 1978; Waltz et al., 1979; Link, 1980; Wenner et al., 1986). Annulus formation may be related to spawning period (Cupka et al., 1973; Mercer, 1978; Waltz et al., 1979; Link, 1980).

Eastern Gulf of Mexico black sea bass apparently do not reach the size and age of Atlantic coast populations. We found that Gulf black sea bass attained a maximum age of 7 yr and a maximum length of 330 mm. Reports of maximum ages

Table 3. Prey items in black sea bass stomachs from inshore, lower estuarine, and offshore eastern Gulf of Mexico locations. Number of prey items is followed parenthetically by number of stomachs.

Item	Inshore	Offshore	Item	Inshore	Offshore
Gastropoda			Portunus ordwayi	3(2)	
Calyptraeidae Crepidula			Portunus sp.	1(1)	
fornicata		1(1)	Xanthidae	16(11)	2(2)
Columbellidae Mitrella			Neopanope packardii	6(5)	
lunata	1(1)		Neopanope sp.	2(1)	
Turbinidae Turbo castanea	1(1)		Pilumnus dasypodus	1(1)	
Bivalvia			Pilumnus sayi		8(2+)
Cardiidae Laevicardium			Pilumnus spp.		2(2)
pictum		6(5)	Pinnotheridae Pinnixa		
Cephalopoda			sp.		1(1)
Decapoda		1(1)	Majidae		
Octopoda Octopus sp.		2(2)	Epialtus dilattatus for-		
Nematoda	2(1)		ma elongata	1(1)	
Polychaeta	1(1)		Libinia spp.	2(2)	
Eunice sp.	1(1)		Macrocoeloma septem-		
Stomatopoda		1(1)	spinosa		1(1)
Squillidae Squilla rugosa		1(1)	Metoporhaphis calcar-		
Gonodactylidae Gonodac-			ata	1(1)	
tylus bredini		18(7+)	Microphrys bicornutus		1(1)
Isopoda	1(1)		Mithrax forceps		8(2+)
Idoteidae Erichsonella sp.	1(1)		Mithrax pleuracanthus		3(3)
Sphaeromatidae Paracer-			Mithrax spp.		8(2+)
ceis sp.	3(2)		Pelia mutica	1(1)	
Amphipoda	21(8)		Pitho anisodon	2(2)	
Natantia	21(17)		Pitho lherminieri		1(1)
Penaeidae	1(1)		Pitho spp.		4(3)
Penaeus duorarum			Podochela riisei		1(1)
duorarum	4(4)		Ophiuroidea	1(1)	5(4)
Sicyonia laevigata	1(1)		Ophiodermatidae Ophio-		
Sicyonia sp.	1(1)		derma sp.		1(1)
Trachypenaeus con-			Ascidiacea		7(3)
strictus		4(3)	Osteichthyes	5(5)	22(7+)
Trachypenaeus sp.	1(1)		Ariidae Bagre marinus	2(1)	
Caridea	16(6)		Batrachoididae Opsanus	• •	
Palaemonidae	4(2)		pardus		1(1)
Brachycarpus sp.	1(1)		Ophidiidae		1(1)
Alpheidae	3(3)		Syngnathidae Hippocam-		()
Alpheus normanni	1(1)		pus erectus		1(1)
Alpheus spp.	4(4)		Centropomidae Centropo-		` '
Hippolytidae	9(3)		mus undecimalis	1(1)	
Hippolyte sp.	1(1)		Serranidae	-(-)	
Latreutes parvulus	1(1)		Diplectrum formosum		1(1)
Tozeuma carolinense	14(7)		Serraniculus pumilio		1(1)
Processidae	15(6)		Serranus subligarius		2(2)
Processa bermudensis	1(1)		Gerreidae		2(2)
Processa spp.	9(2)		Eucinostomus gula	1(1)	
Porcellanidae)(2)		Eucinostomus sp.	1(1)	
Petrolisthes armatus		4(2)	Apogonidae Apogon sp.	1(1)	1(1)
Petrolisthes galanthi-		7(2)	Ephippidae Chaetodipterus		1(1)
		2/2)	faber		1/1)
nus Patroliethas spp	2(1)	3(?)	Blenniidae		1(1)
Petrolisthes spp.	2(1)	2(1)			1(1)
Paguridae	2(2)	2(1)	Gobiidae Gobiosoma mac-		2/11
Albuneidae Albunea sp.	47.45	1(1)	rodon		2(1)
Brachyura	4(4)	5(5)	Scorpaenidae Scorpaena		
Leucosiidae Speloeopho-			calcarata		1(1)
rus nodosus	. ·	1(1)	Cynoglossidae Symphurus		
Portunidae	9(9)		plagiusa		1(1)

determined using otoliths and maximum lengths for Atlantic populations of black sea bass ranged from 9 to 10 yr and 340 to 430 mm (Cupka et al., 1973; Briggs, 1978; Mercer, 1978; Waltz et al., 1979; Link, 1980; Wenner et al., 1986). Ages of large males (350–450 mm) from off New York were determined (using scales) to be between 12 and 20 yr (Lavenda, 1949); however, the accuracy of these scale-determined ages is questionable because they were not validated (Mercer, 1978).

Gulf of Mexico black sea bass grew more rapidly during the first year than did Atlantic populations. Sizes of age I Atlantic fish reported by Cupka et al. (1973), Briggs (1978), Mercer (1978), Waltz et al. (1979), Link (1980), and Wenner et al. (1986) ranged from 73 to 115 mm compared to our mean back-calculated length at age I of 122 mm for Gulf fish. After age I, however, size at age of Atlantic fishes is apparently greater. By age VI, the reported mean lengths for Atlantic populations ranged from 298 to 404 mm (Cupka et al., 1973; Briggs, 1978; Mercer, 1978; Waltz et al., 1979; Link, 1980; Wenner et al., 1986) and are greater than the 232 mm reported in this study. Our L_∞ estimate for Gulf specimens (311 mm, all aged fish) was less than values estimated for Atlantic populations (341–625 mm); however, the growth coefficient from our study (0.17) was within the range given for Atlantic populations (0.088–0.231; Cupka et al., 1973; Mercer, 1978; Wenner et al., 1986).

Differences in calculated growth rates between populations of black sea bass have been attributed to sampling biases resulting from gear selectivity (Mercer, 1978) and different exploitation rates (Wenner et al., 1986). Using a variety of gear, as we did in this study, minimizes this bias. Furthermore, Godcharles (1970) determined that the heart-shaped trap used in this study was the least selective of the trap types evaluated for capturing black sea bass. Wenner et al. (1986) suggested that the larger mean sizes at age of black sea bass from South Carolina reported by Cupka et al. (1973) were due to low exploitation rates. For eastern Gulf of Mexico samples, the effect of exploitation on the size and age structure of the population was of minimal importance because this fishery was still developing at the time the study was initiated (Godcharles, 1970). The pattern of faster initial growth followed by a smaller size at age and shorter lifespan for Gulf populations when compared to Atlantic populations has been observed in other nearshore and reef fishes, including Micropogonias undulatus (White and Chittenden, 1977), Mycteroperca microlepis (Manooch and Haimovici, 1978), and Mycteroperca phenax (Godcharles and Bullock, 1984), and may reflect regional patterns of growth.

Reproduction.—Our observations on the development and structure of black sea bass gonads were similar to those of Mercer (1978), Link (1980), Wenner et al. (1986), Grier (1987), and Cochran and Grier (1991) and to those of Smith (1959, 1965) and Moe (1969) for other protogynous serranids. The size and age at which the sex ratio of Gulf black sea bass changed from predominantly females to predominantly males was similar to those for South Atlantic populations. For Mid-Atlantic and New York populations, fishes appear to change sex at larger sizes and at older ages. In our study, males >210 mm were more common than females >210 mm (age IV), a size similar to that reported for South Atlantic populations (210 to 230 mm; ages IV-V; Waltz et al., 1979; Wenner et al., 1986). For Mid-Atlantic and New York fish, males predominated at 260 to 290 mm (ages V to VI; Lavenda, 1949; Briggs, 1978; Mercer, 1978). Cupka et al. (1973) reported that males from the South Atlantic Bight became predominant at 290 mm, a size larger than that observed in other studies done there; however, Wenner et al. (1986) suggested that Cupka et al.'s (1973) results may reflect the fact that

the South Atlantic population was only lightly exploited at that time. Shapiro (1987) suggested that the smaller size at which males become numerically dominant (a reflection of the size when sex change occurs) is a response to increasing fishing mortality by a protogynous species whose sex change is under behavioral control.

Age at maturity in eastern Gulf populations was similar to that in Atlantic populations. We found vitellogenic oocytes (suggesting maturity) in age 0 fish and found no immature fish above age IV, a finding consistent with those of Atlantic studies (Mercer, 1978; Link, 1980; Wenner et al., 1986). Size and age of transitional Gulf fish (160–230 mm, ages I–V) were within ranges given for Atlantic populations (120 to >339 mm, ages I–VII; Kendall, 1977; Waltz et al., 1979; Link, 1980; Wenner et al., 1986). For Gulf populations, the frequency of occurrence of transitional fish was highest between ages II and IV, which is similar to ages II–V for Atlantic populations (Waltz et al., 1979; Wenner et al., 1986).

The spawning season of black sea bass in the eastern Gulf corresponded with those reported for Gulf and South Atlantic populations but was earlier than those of Mid-Atlantic Bight and New York populations. Gulf populations studied by us, Smith (1907), Reid (1954), Moe (1966), Hoff (1970), and Cochran and Grier (1991) and South Atlantic populations studied by Kendall (1977), Mercer (1978), Link (1980), and Wenner et al. (1986) spawned during December to April. Spawning of Mid-Atlantic and New York populations occurred during late spring through summer (Lavenda, 1949; Mercer, 1978).

Feeding Ecology.—Our finding that black sea bass consumed primarily decapod crustaceans and fishes is consistent with reports for Gulf (Goode, 1884; Reid, 1954; Miller, 1959) and Atlantic populations (Miller, 1959; Cupka et al., 1973; Link, 1980; Sedberry, 1988). Similar feeding habits are known for other serranids (Parrish, 1987). Inshore fish consumed primarily caridean and penaeid shrimps, amphipods, and xanthid crabs; similar food habits were reported by Reid (1954) for black sea bass taken near channels and on deeper flats off Cedar Key, Florida. Cupka et al. (1973) suggested that the presence of sessile organisms, such as colonial tunicates, in stomach contents of black sea bass indicated some grazing activity, and this may explain the seagrasses we found in the stomachs of some inshore fish.

We could not observe any feeding variations or periodicity in either the inshore or offshore fish because our samples were collected at irregular time intervals, but other authors have reported such observations. In laboratory-reared, wild black sea bass, Hoff (1970) noted decreased feeding from mid-January to mid-April during the spawning season. Cupka et al. (1973) noted that 50% of South Carolina black sea bass stomachs were empty during March and associated this with spawning activity. Cupka et al. (1973) also found a high percentage of empty stomachs during November and December, but they were not able to offer a plausible explanation for this decrease in feeding. These patterns may be present in Gulf black sea bass; however, these aspects of the feeding ecology could not be addressed.

ACKNOWLEDGMENTS

This paper has a long history, and the paths of many people are intertwined with it. We thank D. S. Beaumariage, R. M. Ingle, E. A. Joyce, Jr., F. A. Kalber, J. J. Kimmel, M. A. Moe, Jr., and K. A. Steidinger for supplying logistical support. We thank Capt. Earl Girard and crewmembers of the R/V HERNAN CORTEZ; Capt. Francis Clymer of the ATLANTIS II; and J. K. Rolfes and R. C. Baird of the Department of Marine Science, University of South Florida for collecting specimens and E. McManus

for sectioning otoliths. D. K. Camp and N. B. Whiting (crustaceans), C. R. Futch and P. L. Fore (fish), W. G. Lyons (mollusks), and T. Perkins (polychaetes) were very helpful in identifying dietary items. D. K. Camp, J. J. Kimmel, M. M. Leiby, R. E. Matheson, M. D. Murphy, F. C. Sutter, III, J. G. Leiby, L. C. French, and two anonymous reviewers provided valuable editorial assistance. M. J. Myers provided word processing assistance. Partial funding for this research was provided by Financial Assistance Awards 2-408-R and 2-IJ-2 from the National Oceanic and Atmospheric Administration funded through Public Laws 88-309 and 99-659.

LITERATURE CITED

- Bagenal, T. B. and F. W. Tesch. 1981. Age and growth. Pages 101-136 in T. B. Bagenal, ed. Methods for assessment of fish production in fresh waters. Blackwell Scientific Publ., Oxford.
- Baird, R. C., K. Rolfes, B. Causey, W. Fable, A. Feinstein and D. Milliken. 1972. Fish. Pages 176–199 in Anclote environmental project report, 1971. Mar. Sci. Inst., Univ. South Florida, St. Petersburg, Florida.
- ——, W. A. Fable, B. D. Causey, R. A. Dietz, A. Feinstein, D. M. Milliken and K. J. Rolfes. 1973. Fish. Pages 142–183 in Anclote environmental project report, 1972. Mar. Sci. Inst., Univ. South Florida, St. Petersburg, Florida.
- —, G. F. Mayer, K. J. Rolfes, R. A. Dietz and A. Feinstein. 1975. Fishes, Pages 359–448 in G. F. Mayers and V. Maynard, eds. Anclote environmental report, 1974. Dept. Mar. Sci., Univ. South Florida, St. Petersburg, Florida.
- Beaumariage, D. S. 1964. Returns from the 1963 Schlitz tagging program. Fla. Board Conserv. Mar. Lab. Tech. Ser. 43. 34 pp.
- —— and A. C. Wittich. 1966. Returns from the 1964 Schlitz tagging program. Fla. Board Conserv. Mar. Lab. Tech. Ser. 47. 50 pp.
- Bigelow, H. B. and W. C. Schroeder. 1953. Fishes of the Gulf of Maine. Fish. Bull. Fish Wildl. Serv. U.S. 53: 577 pp.
- Biosonics. 1987. Optical pattern recognition system. Biosonics, Inc., Seattle, Washington. 121 pp. Bortone, S. A. 1977. Osteological notes on the genus *Centropristis* (Pisces: Serranidae). Northeast Gulf Sci. 1: 23-33.
- Bowen, B. W. and J. C. Avise. 1990. Genetic structure of Atlantic and Gulf of Mexico populations of sea bass, menhaden, and sturgeon: influence of zoogeographic factors and life-history patterns.

 Mar. Biol. 107: 371-381.
- Briggs, J. C. 1958. A list of Florida fishes and their distribution. Bull. Fla. State Mus. Biol. Sci. 2: 223-318.
- Briggs, P. T. 1978. Black sea bass in New York waters. N.Y. Fish Game J. 25: 45-58.
- Chapman, R. W. 1977. Plasma proteins and systematics of the genus *Centropristis* (Pisces: Serranidae). M.S. Thesis, Univ. West Florida, Pensacola, Florida. 99 pp.
- Cochran, R. C. and H. J. Grier. 1991. Regulation of sexual succession in the protogynous black sea bass, *Centropristis striata* (Osteichthyes: Serranidae). Gen. Comp. Endocrinol. 82: 69-77.
- Collins, M. R., S. B. Van Sant and D. J. Schmidt. 1990. Age validation of tag-recaptured reef fish off South Carolina. Page 73 in The 70th Annual Meeting of the American Society of Ichthyologists and Herpetologists, 14-20 June, 1990, Charleston, South Carolina. (Abstract).
 Cupka, D. M., R. K. Dias and J. Tucker. 1973. Biology of the black sea bass Centropristis striata
- Cupka, D. M., R. K. Dias and J. Tucker. 1973. Biology of the black sea bass *Centropristis striata* (Pisces: Serranidae), from South Carolina waters. South Carolina Wildl. Mar. Res. Dept., Mar. Res. Ctr., Charleston, South Carolina. 93 pp.
- Frame, D. W. and S. A. Pearce. 1973. A survey of the sea bass fishery. Mar. Fish. Rev. 35: 19-26. Ginsburg, I. 1952. Eight new fishes from the Gulf coast of the United States, with two new genera and notes on geographic distribution. J. Wash. Acad. Sci. 42: 84-101.
- Godcharles, M. F. 1970. Exploratory fishing for southern sea bass, *Centropristis striatus melanus*, in the northeastern Gulf of Mexico, Fla. Board Conserv. Mar. Lab. Tech. Ser. 63. 26 pp.
- and L. H. Bullock. 1984. Age, growth, mortality and reproduction of the scamp, *Mycteroperca phenax* (Pisces: Serranidae). Fla. Dep. Nat. Resour. Bur. Mar. Res. PL 88-309 Annual Report FY 1982-1983 to NMFS Jan. 1984. 30 pp.
- Goode, G. B. 1884. The sea bass Serranus atrarius. Pages 407-410 in The fisheries and fishery industries of the United States. U.S. Govt. Print. Offices, Washington, D.C.
- Grier, H. J. 1987. Brown bodies in the gonads of the black sea bass, *Centropristis striatus*. Page 199 in Proc. 3rd Int. Symp. Reprod. Phys. Fish.
- Hastings, R. W. 1972. The origin and seasonality of the fish fauna on a new jetty in the northeastern Gulf of Mexico. Ph.D. Dissertation, Florida State Univ., Tallahassee, Florida. 555 pp.
- Hoff, F. H. 1970. Artificial spawning of the black sea bass, Centropristis striatus melanus Ginsburg, aided by chorionic gonadotrophic hormones. Fla. Dep. Nat. Resour. Mar. Res. Lab. Spec. Sci. Rep. 25. 17 pp.

- Hood, P. B., K. W. Able and C. B. Grimes. 1988. Biology of the conger eel *Conger oceanicus* in the Mid-Atlantic Bight: I. Distribution, age, growth, and reproduction. Mar. Biol. 98: 587-596.
- Humason, G. L. 1972. Animal tissue technique. W. H. Freeman & Co., San Francisco, California. 641 pp.
- Humm, H. J., R. C. Baird, K. L. Carder, T. L. Hopkins and T. E. Pyle. 1971. Fishes. Pages 63-77 in Anclote environmental project annual report 1970. Mar. Sci. Inst., Univ. South Florida, St. Petersburg, Florida.
- Joseph, E. B. and R. W. Yerger. 1956. The fishes of Alligator Harbor Florida, with notes on their natural history. Fla. State Univ. Stud. No. 22, Pap. Oceanogr. Inst. 2: 111-156.
- Joyce, E. A., Jr. 1968. Project Hourglass explores the continental shelf. Sea Frontiers. 14: 352-359.

 and J. Williams. 1969. Rationale and pertinent data. Mem. Hourglass Cruises 1(1), 20 pp.
- Kendall, A. W. 1977. Biological and fisheries data on black sea bass, *Centropristis striata* (Linneaus). NOAA/NMFS Sandy Hook Laboratory, Tech. Ser. Rep. 7. 29 pp.
- Lavenda, N. 1949. Sexual differences and normal protogynous hermaphroditism in the Atlantic sea bass, *Centropristis striatus*. Copeia 1949: 185–194.
- Lindall, W. N., W. A. Fable and L. A. Collins. 1973. Range extension of *Centropristis striata melana*. Fla. Sci. 36: 214-215.
- Link, G. W. 1980. Age, growth, reproduction, feeding, and ecological observations on the three species of *Centropristis* (Pisces: Serranidae) in North Carolina waters. Ph.D. Dissertation, Univ. North Carolina, Chapel Hill, North Carolina. 277 pp.
- Low, R. A. 1982. The South Carolina fishery for black sea bass (*Centropristis striata*), 1977–1981. South Carolina Mar. Res. Cent. Tech. Rep. No. 53. 17 pp.
- Manooch, C. S. and M. Haimovici. 1978. Age and growth of the gag *Mycteroperca microlepis* and size-age composition of the recreational catch off the southeastern United States. Trans. Am. Fish. Soc. 107: 234-240.
- Mercer, L. 1978. The reproductive biology and population dynamics of the black sea bass, *Centro-* pristis striata. Ph.D. Dissertation, College of William and Mary, Williamsburg, Virginia. 196 pp.
- Miller, R. J. 1959. A review of the seabasses of the genus *Centropristis* (Serranidae). Tulane Stud. Zool. 7: 35-68.
- Moe, M. A., Jr. 1963. A survey of offshore fishing in Florida. Fla. State Board Conserv. Mar. Lab. Prof. Pap. Ser. 4. 117 pp.
- ——. 1966. Tagging fishes in Florida offshore waters. Fla. Board Conserv. Mar. Lab. Tech. Ser. 49, 40 pp.
- . 1969. Biology of the red grouper *Epinephelus morio* (Valenciennes) from the eastern Gulf of Mexico. Fla. Dep. Nat. Resour. Mar. Res. Lab. Prof. Pap. 10. 95 pp.
- Mountain, J. A. 1972. Further thermal addition studies at Crystal River, Florida with an annotated checklist of marine fishes collected 1969–1971. Fla. Dep. Nat. Resour. Mar. Res. Lab. Prof. Pap. Ser. 20. 103 pp.
- Musick, J. A. and L. P. Mercer. 1977. Seasonal distribution of black sea bass, *Centropristis striata*, in the Mid-Atlantic Bight with comments on the ecology and fisheries of the species. Tran. Am. Fish. Soc. 106: 12-25.
- Parrish, J. D. 1987. The trophic biology of snappers and groupers. Pages 405-464 in J. J. Polovina and S. Ralston, eds. Tropical snappers and groupers; biology and fisheries management. Westview Press, Inc., Boulder, Colorado.
- Reid, G. K. 1954. An ecological study of the Gulf of Mexico fishes, in the vicinity of Cedar Key, Florida. Bull. Mar. Sci. Gulf Caribb. 4: 1-94.
- Ricker, W. E. 1973. Linear regressions in fishery research. J. Fish Res. Board Can. 30: 409-434.
- Rivers, J. B. 1966. Gear and technique of the sea bass trap fishery in the Carolinas. Commer. Fish. Rev. 28: 15-20.
- Rolfes, J. K., R. A. Dietz and R. C. Baird. 1974. Fish. Pages 120-132 in Anclote environmental project report, 1973. Mar. Sci. Inst., Univ. South Florida, St. Petersburg, Florida.
- SAS Institute, Inc. 1985. SAS user's guide: statistics. SAS Institute, Inc., Cary, North Carolina. 956 pp.
- Sedberry, G. R. 1988. Food and feeding of black sea bass, *Centropristis striata*, in live bottom habitats in the South Atlantic Bight. J. Elisha Mitchell Sci. Soc. 104: 35-50.
- Shapiro, D. Y. 1987. Reproduction in groupers. Pages 295-327 in J. J. Polovina and S. Ralston, eds. Tropical snappers and groupers; biology and fisheries management. Westview Press, Inc., Boulder, Colorado.
- Smith, C. L. 1959. Hermaphroditism in some serranid fishes from Bermuda. Pap. Mich. Acad. Sci. Arts Lett. 54: 111-119.
- ----. 1965. The patterns and the classification of serranid fishes. Am. Mus. Novit. 2207. 20 pp. Smith, G. B. 1976. Ecology and distribution of eastern Gulf of Mexico reef fishes. Fla. Mar. Res. Publ. No. 19. 78 pp.

Smith, H. M. 1907. The fishes of North Carolina. North Carolina Geol. Econ. Surv., Raleigh, North Carolina, II: 1-453.

Sokal, R. R. and F. J. Rohlf. 1981. Biometry, W. H. Freeman and Co., New York, 859 pp.

Springer, V. G. and K. D. Woodburn. 1960. An ecological study of the fishes of the Tampa Bay area. Fla. State Board Conserv. Mar. Lab. Prof. Pap. Ser. 1. 104 pp.

Topp, R. 1963. The tagging of fishes in Florida, 1962 program. Fla. State Board Conserv. Prof. Pap. Ser. 5. 76 pp.

Tyler, J. E. 1964. Preliminary exploratory fishing on the Florida west coast. Fla. Board Conserv. Mar. Lab. Spec. Sci. Rep. 8. 14 pp.

Waltz, W., W. A. Roumillat and P. K. Ashe. 1979. Distribution, age structure, and sex composition of the black sea bass, *Centropristis striata*, sampled along the southeastern coast of the United States. South Carolina Mar. Res. Cent. Tech. Rep. 43. 18 pp.

Wenner, C. A., W. A. Roumillat and C. W. Waltz. 1986. Contributions to the life history of black sea bass, *Centropristis striata*, off the southeastern United States. Fish. Bull. U.S. 84: 723-741.

White, M. L. and M. E. Chittenden. 1977. Age determination, reproduction, and population dynamics of the atlantic croaker, *Micropogonias undulatus*. Fish. Bull. U.S. 75: 109-123.

DATE ACCEPTED: December 1, 1992.

Addresses: (P.B.H.) Florida Marine Research Institute, Florida Department of Environmental Protection, 100 Eighth Ave. S.E., St. Petersburg, Florida 33701; (M.F.G.) National Marine Fisheries Service, NOAA, Regional Office, 9450 Koger Blvd., St. Petersburg, Florida 33702; (R.S.B.) 425 McDaniel, Tallahassee, Florida 32303.