

DISTRIBUTION, ABUNDANCE, REPRODUCTION, FOOD HABITS, AGE, AND GROWTH OF ROUND SCAD, *DECAPTERUS PUNCTATUS*, IN THE SOUTH ATLANTIC BIGHT¹

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ABSTRACT

Five years of bottom trawling indicated that round scad were abundant and widely distributed throughout the South Atlantic Bight in summer and fall, but less abundant and restricted to deeper (28-110 m), warmer (>15°C) waters in winter and spring. Adults and juveniles were spatially segregated, with adults dominating catches in inner and outer shelf regions and juveniles dominating midshelf regions year round. Catches over sponge-coral habitat were significantly greater than catches over sand bottom in winter, whereas catches over the two bottom types were similar in other seasons. This seasonal change in distribution may relate to higher productivity and temperature stability of live bottom habitats. Stomach contents indicated that round scad are diurnally feeding zooplanktivores; diets changed seasonally and increased in prey diversity with growth. Round scad spawn repeatedly from March through September. Daily growth analysis revealed that both sexes mature in 4-5 months at approximately 11 cm fork length. The life span of round scad could not be determined because the growth record of otoliths of most adults was irregular.

Fishes of the genus *Decapterus* occur in most neritic and some oceanic waters of tropical, subtropical, and temperate latitudes. Little is known of the biology of most species, except for those species which support fisheries in the Hawaiian Islands, the Philippines, Japan, and the west coast of Africa (Yamaguchi 1953; Tiews et al. 1970; Akaoka 1971; Boely et al. 1973). Although the taxonomy of Indo-Pacific species is unclear (Berry 1968), three species are recognized in the western North Atlantic: the red-tail scad, *Decapterus tabl* Berry; the mackerel scad, *D. macarellus* (Cuvier); and the round scad, *D. punctatus* (Agassiz).

The round scad occurs in the western Atlantic from Nova Scotia to Rio de Janeiro, Brazil, and throughout the West Indies and Bermuda (Berry 1968); however, little information is available concerning its basic biology. The distribution of the species has been determined from purse seine catches in the Gulf of Mexico (Klima 1971), where it supports a bait fishery, and from bottom trawl catches over sand bottom habitat in the South Atlantic Bight (Wenner et al. 1979a, b, c, d, 1980). The location and duration of the spawning season has

been ascertained from ichthyoplankton surveys in the eastern Gulf of Mexico (Aprieto 1974; Leak 1981). In addition, Leak (1981) determined larval mortality and production, and estimated biomass and potential yield of round scad in the eastern Gulf of Mexico. The objectives of this study were to provide information on seasonal distributions, relative abundance, reproduction, feeding habits, age, and growth of round scad in the South Atlantic Bight.

METHODS

Seasonal Distribution and Relative Abundance

A stratified random sampling design (Grosslein 1969) was used to assign trawling stations within six depth zones (9-18 m, 19-27 m, 28-55 m, 56-110 m, 111-183 m, 184-366 m) on nine seasonal cruises (Table 1). A total of 739 stations were completed on the continental shelf and upper continental slope between Cape Fear, NC and Cape Canaveral, FL. Fishes were captured in a 3/4 scale version of a "Yankee No. 36" otter trawl (Wilk and Silverman 1976) with a 11.9 m headrope, a 16.5 m footrope, and a 1.3 cm stretch mesh cod end liner. Although catches of pelagic fishes by bottom trawls seldom provide accurate estimates of absolute abundance of these species, they probably do reflect relative

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TABLE 1.—Catch statistics for *Decapterus punctatus* in the South Atlantic Bight. n = number of trawls; \bar{x}_{st} = stratified mean catch tow⁻¹; \bar{x}_{ln} = stratified mean catch tow⁻¹ for $\ln(x + 1)$ transformed data; \bar{x}_{Bliss} = Bliss (1967) estimate of the stratified mean catch tow⁻¹; CV = coefficient of variation for untransformed data; CV_{ln} = coefficient of variation for $\ln(x + 1)$ transformed data.

Cruise	n	\bar{x}_{st}	\bar{x}_{ln}	\bar{x}_{Bliss}	CV	CV _{ln}
Fall 1973 (23 Oct.-16 Nov.)	67	2.83	0.59	1.86	31.6	1.68
Spring 1974 (1 Apr.-9 May)	89	1.21	0.25	0.58	35.8	1.70
Summer 1974 (13 Aug.-19 Sept.)	69	3.13	0.59	1.97	25.5	1.69
Winter 1975 (16 Jan.-2 Feb.)	52	0.24	0.11	0.79	0.8	2.02
Spring 1975 (31 Mar.-10 Apr.)	40	0.08	0.06	0.07	0.4	1.31
Summer 1975 (30 Aug.-19 Sept.)	68	1.17	0.37	0.89	7.9	1.47
Winter 1976 (12 Jan.-7 Feb.)	69	1.73	0.17	0.52	62.4	2.81
Summer 1976 (28 Aug.-21 Sept.)	69	1.51	0.34	0.87	25.7	1.70
Winter 1977 (17 Jan.-9 Mar.)	72	3.30	0.14	1.18	197.0	9.01

abundance and distribution (Wenner et al. 1979a). All trawling was conducted from the RV *Dolphin*, a 32.6 m converted tug, for approximately 30 minutes at 6.5 km/hour. Weight and fork length (FL) were measured for each individual, except for large catches which were subsampled. Surface and bottom temperatures were taken after each tow.

Length-frequency distributions were compared by season and by depth zone. An index of relative abundance (IRA = $1/n \sum \ln(x + 1)$; n = # trawls in each depth zone, x = weight of fish for each tow) was calculated from the catches for each depth zone (Musick and McEachran 1972). The stratified mean catch per tow and the estimated variance of the stratified mean catch per tow (Cochran 1977) were calculated from untransformed and $\ln(x + 1)$ transformed data to reduce the effects of contagion (Elliott 1971). The coefficient of variation was used to compare variation in catches (Clark and Brown 1977). The Bliss (1967) approximation retransformed the data from logarithmic to arithmetic units. The Wilcoxon rank sum statistic (Hollander and Wolfe 1973) was used to compare catches, depths, and temperatures of sponge-coral (Wenner 1983) and sandy open-shelf (Struhsaker 1969) habitats. Habitat designations of Wenner et al. (1979a) were used. Catches collected north and south of lat. 31°30'N were compared for winter and summer cruises to determine if seasonal migration occurred.

Reproductive Biology

Specimens used for reproductive analyses were collected in 1980 by several research and commercial vessels, frozen, and examined in the laboratory. Specimens were measured (nearest mm) and weighed (nearest 0.1 g). Ripe ovaries were fixed in Gilson's solution (Bagenal and Braum 1978) for fecundity determination. All other gonads were fixed in formol-alcohol, stained with a modified Harris hematoxylin and counterstained with eosin (Humason 1972). Maturity stages for testes follow Hyder (1969); maturity stages for ovaries were based on Wallace and Selman (1981) and the frequency distributions of oocyte diameters. Frequency distributions of oocyte sizes were determined from randomly selected ovaries in each maturity stage. Analysis of variance revealed no differences in means and variances of oocyte diameters taken from different regions of ovaries in any stage. Therefore, oocyte distributions for each ovary were determined from two or three randomly selected sections.

Proportions of fish in each maturity stage were determined bimonthly, and gonadosomatic indices [GSI = gonad wt/(body wt - gonad wt)] were determined for each maturity stage (except stage 1 when gonadal tissues weighed <0.1 g).

Ova numbers were estimated by modifying the methods of Macer (1974). Both ripe ova and developing oocytes with diameters >0.115 mm were counted. Developing oocytes were included in fecundity estimation because they exhibited characteristics of secondary growth phase (Wallace and Selman 1981) and were atretic in spent ovaries.

Feeding Habits

Stomach contents of 457 fish collected in 1980 were fixed in 20% formalin, and stored in 50% isopropyl alcohol. Frequency of occurrence (%FO) and percentage composition by number (%N) were computed for major prey categories. Volumetric displacement (%VOL) of prey categories from a representative subsample of 30 stomachs were determined by using a 0.1 cm² grid (Windell 1971). Seasonal and ontogenetic change in diets were compared with an index of relative importance [IRI = (%N + %VOL)(%FO)], computed from the sums of each prey category (Pinkas et al. 1971).

Feeding periodicity was determined by plotting the percentage of empty stomachs collected per time period, using 377 stomachs with known collection times. Distributions of fish lengths collected in dif-

ferent time intervals were compared to evaluate size bias that may occur with this method (Jenkins and Green 1977).

Age and Growth

Utricular otoliths (lapilli) of specimens collected in 1980 were used for age determination. Otoliths were stored in 95% ethyl alcohol and prepared for viewing using a modification of the methods of Haake et al. (1981), which resulted in a thin sagittal section containing the core of the otolith embedded in "Spurr" (Spurr 1969). Otolith length was measured to the nearest 0.1 mm at 100 \times with an ocular micrometer. Otolith images were projected on a high resolution television screen with a high resolution camera, which produced a total viewing magnification of 1088 \times or 2176 \times . Otoliths examined by scanning electron microscopy were prepared by the methods of Haake et al. (1981). Two counts of growth increments were made by the author, and an additional count was made by other experienced readers. Mean counts were used in all analyses, and specimens were discarded if individual counts for a specimen differed by more than 10%. Different readers usually showed agreement between counts: percentage difference between readers averaged 8%.

Counts of otolith increments were obtained from 71 juvenile and adult round scad, 13-143 mm FL. Sixty specimens (121-180 mm FL) could not be assigned ages because of the numerous growth interruptions in outer regions of the otolith. Increment formation was validated by examination of the margins of otoliths of juveniles (13-55 mm FL) collected at different times of day. Consistent measurements of the marginal increment could not be made because of the irregular shape of the lapilli; thus, only the occurrence of an incremental or discontinuous zone (terminology of Mugiyi et al. 1981) could be noted.

The SAS NLIN regression procedure with DUD and Marquardt options (Helwig and Council 1979) was used to determine parameters for the von Bertalanffy (1957) and Gompertz (Zweifel and Lasker 1976) growth equations. Because similar patterns of variation were observed in plots of the residuals of both models, r^2 values were used to evaluate model performance (Grossman et al. 1985). Instantaneous growth rates (%FL d⁻¹ and %WT d⁻¹) were calculated according to Ricker (1979). Weights were converted from lengths by using the least squares regression (Sokal and Rohlf 1981), $\ln wt$ (in g) = 2.96 $\ln FL$ (in mm) - 11.2 ($r^2 = 0.99$), deter-

mined from 156 individuals (13-185 mm FL) randomly selected within 10 mm size classes from all specimens (total = 1047) collected in 1980.

RESULTS

Seasonal Distribution and Relative Abundance

A total of 57,460 round scad were captured at 230 of the 739 stations in depths from 11 to 267 m; over 99% of the catch came from <92 m. Fish ranged from 2 to 26 cm FL ($\bar{x} = 11.4$), with 99% of the fish 6-17 cm FL.

Round scad were more widely distributed and abundant in summer and fall than in winter and spring. Indices of relative abundance (Fig. 1) were consistently high in summer and fall at shallow depths (<55 m) where *D. punctatus* were captured at 121 of 220 trawl stations. Indices of relative abundance during summer and fall in 56-110 m depths were quite variable, and catches in waters >110 m were rare (3 of 78 trawls), small (52 individuals captured), and occurred only in summer. The highest indices in winter and spring occurred in 19-110 m depths (usually 19-27 m), but were lower than values in summer and fall. Round scad were rarely collected in 9-18 m depths and never collected in waters >110 m in winter.

Differences among untransformed (\bar{x}_{st}), transformed (\bar{x}_{ln}), and Bliss (\bar{x}_{Bliss}) estimates of the stratified mean catch per tow (Table 1) revealed additional seasonal changes in the distribution of round scad. Transformed and Bliss estimates of the stratified mean catch per tow were higher in summer and fall than in winter and spring. However, untransformed values (\bar{x}_{st}) indicated that total catches in winter often exceeded total catches in summer. Such differences in catch statistics resulted from the relatively high frequency and low variability of catches in summer and fall, and the relatively low frequency and high variability of catches in winter and spring. This result was generally consistent with the coefficients of variation (CV and CV_{ln}), which indicated increased clumping in the winter catches.

The seasonal distribution of round scad appeared affected by temperature (Table 2). Over 97% of winter catches occurred in waters warmer than 15°C, over 99% of spring catches were made in waters warmer than 17°C, and over 99% of summer and fall catches occurred in waters warmer than 20°C.

Habitat affected the distribution of round scad in

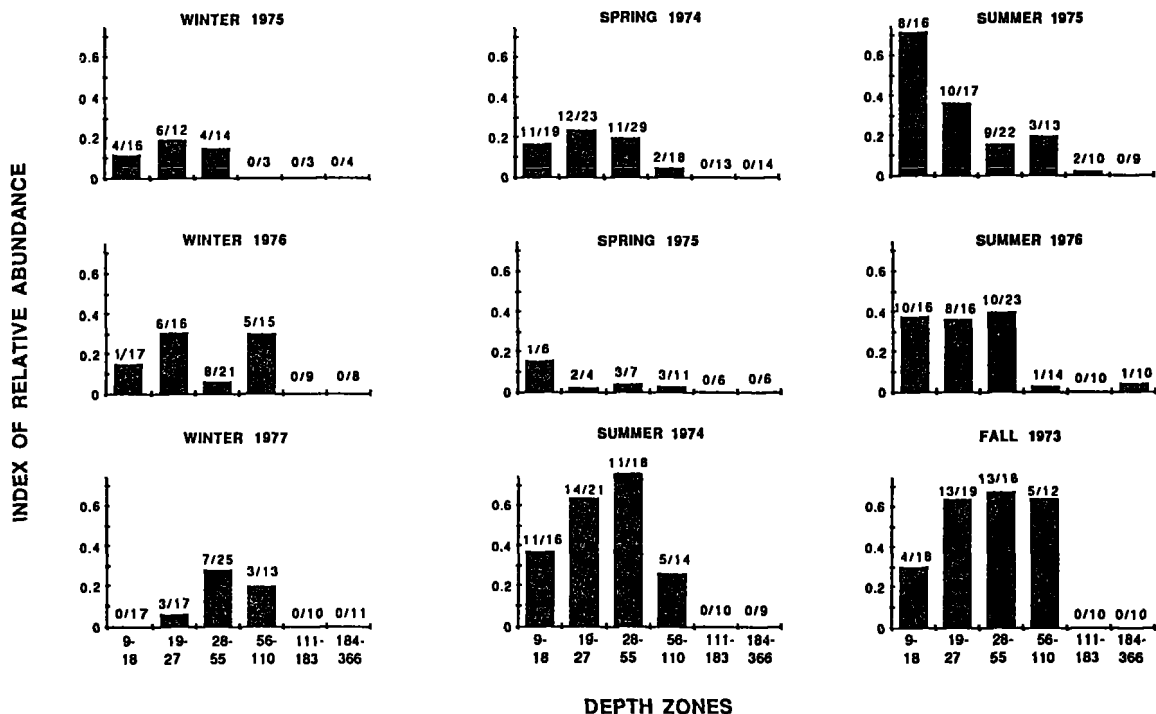


FIGURE 1.—Indices of relative abundance (Musick and McEachran 1972) of *Decapterus punctatus* by depth zone from MARMAP trawl survey for all cruises. Fractions are the number of trawls with round scad/total number of trawls.

TABLE 2.—Surface and bottom temperatures where *Decapterus punctatus* was collected in the South Atlantic Bight. Upper figure of each pair is surface value, lower figure is bottom value; \bar{x} = mean, s = variance.

	Winter			Spring			Summer			Fall
	1975	1976	1977	1974	1975	1974	1975	1976	1973	
\bar{x}	17.4	19.1	17.9	19.6	18.7	27.9	28.1	26.0	23.8	
	17.2	17.0	16.4	19.1	17.4	25.5	25.4	25.4	23.7	
s	2.5	3.5	2.5	1.5	2.7	0.5	0.6	0.6	1.9	
	2.0	2.8	2.1	1.3	1.3	1.9	4.9	3.5	1.9	
mini-	13.3	12.1	11.5	17.4	14.9	26.9	26.9	26.0	17.2	
mum	13.3	12.3	11.6	17.0	14.9	19.3	9.8	8.5	17.2	
maxi-	21.7	23.3	18.9	23.2	23.8	29.1	29.3	28.7	26.5	
mum	19.9	22.8	18.9	22.0	19.2	28.2	29.2	27.4	26.3	

winter. Catches over sponge-coral habitat were significantly larger than catches over sandy habitat in winter during 1976-77, whereas catches over the two bottom types were similar in other seasons (Table 3). Habitat types did not differ in temperature during either winter (Wilcoxon rank sum tests, $P = 0.25$ and 0.20 , $df = 19$ and 12 , respectively). Thus, temperature alone did not appear to account for the observed difference in winter catches over the two bottom types.

TABLE 3.—Comparison of catches of *Decapterus punctatus* over sponge-coral and sand habitats by cruise. If the Wilcoxon rank sum (Z) is significant (*), the direction of the difference is indicated. ΣC_i = sum of catches over sponge-coral habitats (n_i = # trawls), ΣC_s = sum of catches over sand habitats (n_s = trawls).

Cruise	ΣC_i	n_i	ΣC_s	n_s	Z
Winter					
1975	3	(3)	672	(49)	0.23
1976	7,201	(11)	597	(75)	3.57* (L>S)
1977	10,936	(11)	39	(82)	5.40* (L>S)
Spring					
1974	239	(11)	4,717	(91)	0.05
1975	2	(6)	46	(34)	0.36
Summer					
1974	445	(14)	8,023	(74)	0.61
1975	614	(18)	4,805	(69)	0.92
1976	663	(8)	5,094	(81)	0.86
Fall					
1973	215	(10)	13,139	(77)	0.74

Round scad did not appear to undertake seasonal longshore migrations in the South Atlantic Bight. Catches north and south of lat. $31^{\circ}30'N$ (which roughly bisects the South Atlantic Bight) showed occasional differences (Table 4), but no consistent

seasonal pattern. Catch differences indicative of a southward migration in winter and northward in summer (either $N < S$ in winter and spring or $N > S$ in summer and fall) occurred only in winter 1975 and summer 1976. Distributions opposite to the above patterns occurred in summer 1975. Similarity in the numbers (Chi-square test, $P = 0.50$, 1 df) of gill rakers, a variable character (Berry 1969), from specimens collected off South Carolina in winter ($\bar{x} = 37.2$, $s^2 = 1.2$, $n = 33$) and summer ($\bar{x} = 36.9$, $s^2 = 1.4$, $n = 38$) also suggested that discrete stocks were not migrating through the South Atlantic Bight.

Although adults and juveniles were caught at all depths throughout the year, length-frequency distributions by depth (Fig. 2) showed a similar pattern for nearly every cruise: fish size decreased from 9-18 m to 19-27 m depths, then increased with increasing depth to 110 m. Catches in 9-18 m consisted primarily of adults in fall and winter, whereas both juveniles and adults were captured in spring and summer. Juveniles predominated in 19-27 m, whereas adults composed most of the catch in deeper waters.

TABLE 4.—Comparison of catches of *Decapterus punctatus* north and south of lat. 31°30'N by cruise. If the Wilcoxon rank sum (Z) is significantly different (*), the direction of the difference is indicated. ΣC_n = sum of the catches north (n_n = # trawls north), ΣC_s = sum of the catches south (n_s = # trawls south).

Cruise	ΣC_n	n_n	ΣC_s	n_s	Z
Winter					
1975	8	(17)	667	(35)	561.80* (S>N)
1976	6,149	(42)	1,649	(44)	0.07
1977	10,728	(48)	247	(45)	0.31
Spring					
1974	993	(62)	3,963	(40)	0.33
1975	44	(36)	4	(4)	0.25
Summer					
1974	1,892	(47)	6,576	(41)	0.15
1975	1,915	(49)	3,504	(38)	1.35* (S>N)
1976	4,395	(46)	1,362	(43)	2.52* (N>S)
Fall					
1973	6,184	(47)	7,170	(40)	0.85

Reproductive Biology

All stages of ovarian maturity had different frequency distributions of oocyte diameters (Fig. 3). Resting ovaries contained primary or first growth phase oocytes approximately 25-115 μm in diameter. Few larger (>115 μm) developing or atretic oocytes occurred. Oocytes in developing ovaries ranged from 30 to 375 μm in diameter, and exhibited characteristics of first or second growth phase. Either one or two modes were present in the frequency distri-

butions of the sizes of second growth phase oocytes, 100-375 μm in diameter. Germ cells in ripe ovaries ranged from 30 to 495 μm in diameter. Ripe ovaries contained oocytes in both growth phases and maturing ova. Two or three modes were present in the frequency distribution of germ cells of ripe ovaries. Spent ovaries contained small oocytes in primary growth phase and occasionally larger oocytes undergoing atresia. Germ cells in these flaccid ovaries were usually 30-255 μm in diameter, although larger cells were observed. Gonadosomatic indices (Table 5) changed as expected: indices increased from resting through ripe stages, then decreased for spent fish.

Maturity stages of testes were more difficult to distinguish because testes often contained all stages of spermatogenesis; therefore, stage determination was based upon subjective interpretation of the relative quantities of spermatocytes, spermatids, and sperm. Although more variable, gonadosomatic indices of males (Table 5) were similar to those of females.

TABLE 5.—Gonadosomatic indices (gonad wt/(total body wt - gonad wt)) of *Decapterus punctatus* by stage maturity. \bar{x} = mean, s = variance, n = sample size.

	Testes			Ovaries		
	\bar{x}	s	n	\bar{x}	s	n
Resting	0.008	0.004	64	0.007	0.003	60
Developing	0.018	0.012	103	0.027	0.011	49
Ripe	0.028	0.014	74	0.045	0.019	64
Spent	0.015	0.009	18	0.016	0.008	13

Seasonal occurrence of maturity stages showed good agreement between males and females (Fig. 4), and indicated a protracted spawning period. Developing gonads were found from February through August, and ripe individuals of both sexes were collected from March through August.

Examination of gonads indicated that both species mature at approximately 110 mm FL. Frequency distributions of length by sex (Fig. 5) indicate that both sexes mature over a narrow size range. Specimens <100 mm FL were immature, whereas more than 90% of fish 110-119 mm FL were mature. Both ripe males and females were collected in the size range at which gonadal development begins (100-109 mm FL).

Fecundity estimates (# ova female⁻¹ yr⁻¹) for 32 ripe females (119-174 mm FL) ranged from 6,200 to 51,000 per female and were highly variable for specimens of similar sizes. The distribution of the sizes of the oocytes in these ovaries was not deter-

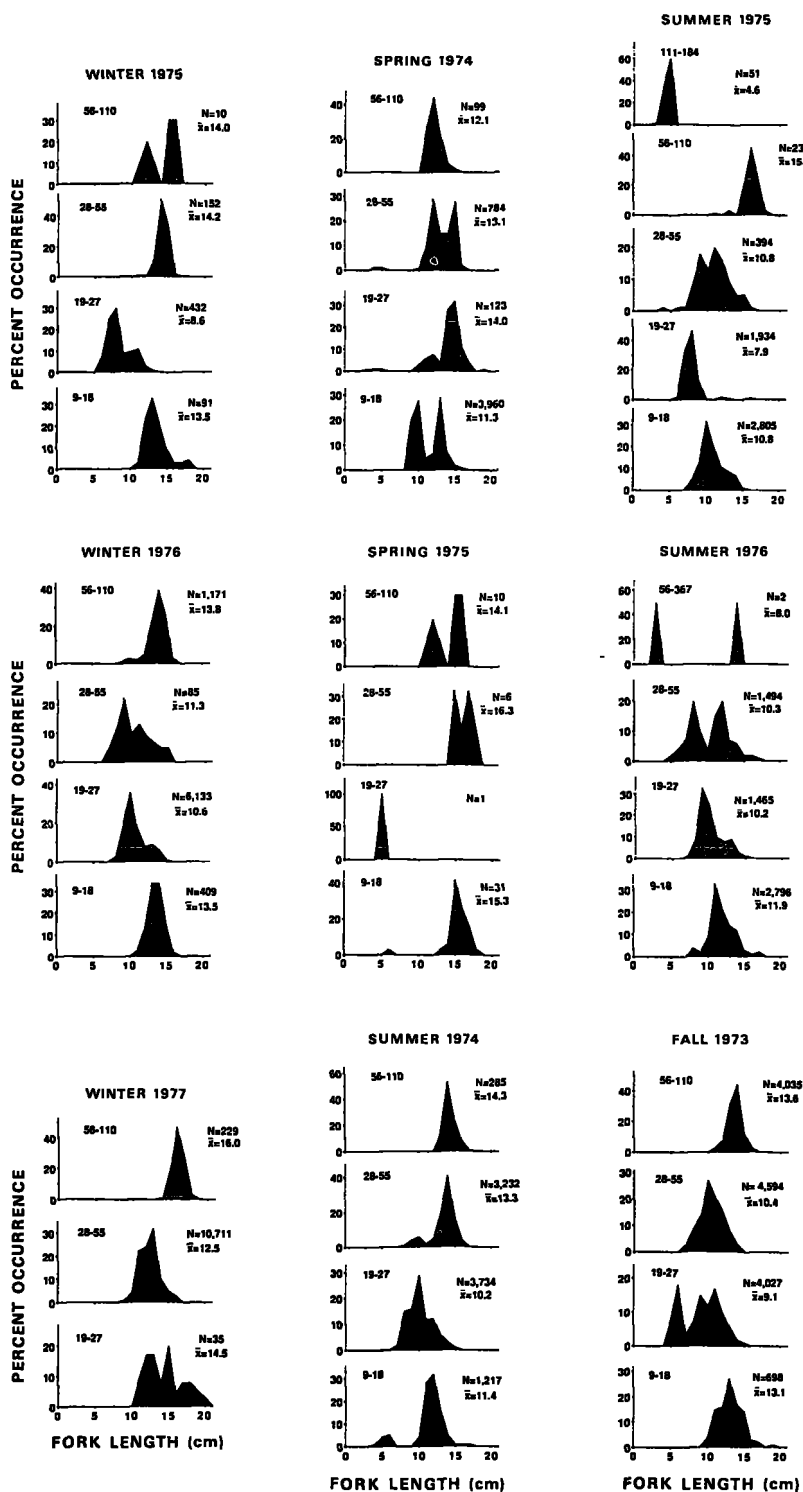


FIGURE 2.—Frequency distributions of fork lengths of *Decapterus punctatus* by depth zone, for all cruises. Numbers above each distribution indicate range of the depth zone in m; N is sample size; \bar{x} is mean length of individuals.

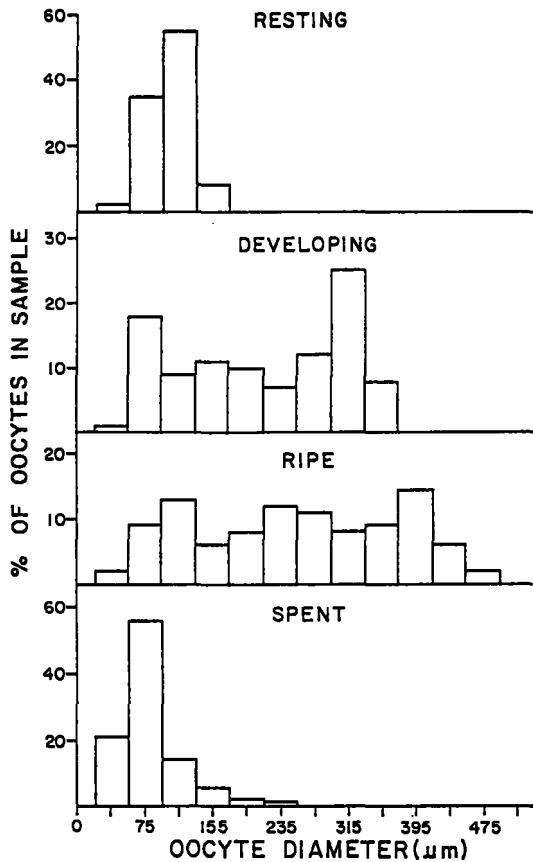


FIGURE 3.—Frequency distributions of oocyte diameters from four randomly selected ovaries of *Decapterus punctatus* in each maturity stage. The total number of oocytes measured in each ovary was 306 (oocytes from 3 sections within the anterior, central, and posterior regions of each ovary).

mined, and it was unknown if these individuals had spawned. The regression equations of fecundity on length and weight for 33 specimens were as follows: $\log_{10} \text{ fec} = -10.9 + 5.63 \log_{10} \text{ FL}$ ($r^2 = 0.46$); and $\log_{10} \text{ fec} = -1.14 + 1.56 \log_{10} \text{ wt}$ ($r^2 = 0.55$).

Feeding Habits

Approximately 91% of round scad (39-189 mm FL) contained identifiable prey. The highest indices of relative importance for all specimens were for copepods (0.37), mollusk larvae (0.19), amphipods (0.06), and ostracods (0.04). The most numerous prey groups were mollusk larvae (29%, predominantly gastropod and pelecypod veligers), copepods (25%), barnacle cyprids (14%), and ostracods (10%). Chaetognaths (35%), copepods (28%), mollusk larvae

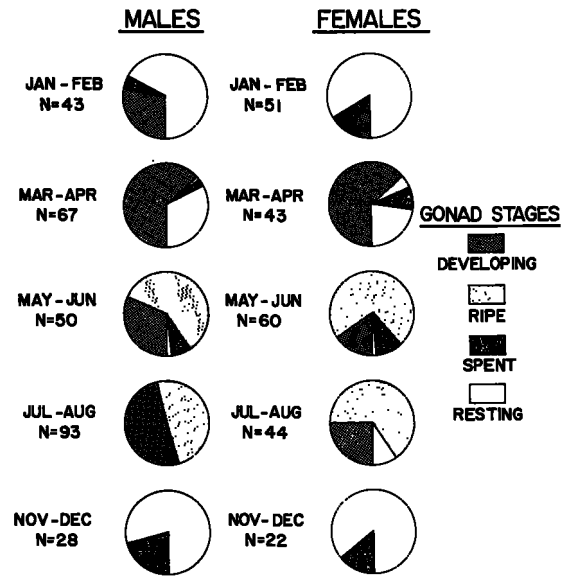


FIGURE 4.—Seasonal occurrence of maturity stages of gonads of *Decapterus punctatus*. N is sample size for each bimonthly period. No gonads were examined from specimens collected in September and October 1980-81.

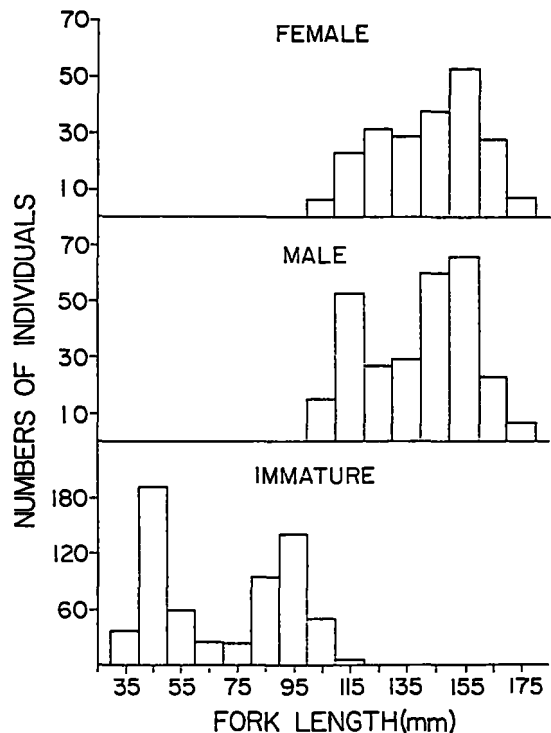


FIGURE 5.—Frequency distributions of fork length of *Decapterus punctatus* by sex. Both sexes mature at approximately 110 mm FL.

(12%), and amphipods (10%, predominantly hyperiids and caprellids) contributed the greatest volumes of prey. Copepods (70%), mollusk larvae (47%), amphipods (30%), and decapod larvae (25%) occurred most frequently.

Some differences were found in stomach contents of fishes of different size (Table 6). Small fish preyed almost exclusively on copepods. Medium-sized fish preyed predominantly on copepods, but less frequently and to a lesser extent than small fishes. Large fish fed on a variety of prey and consumed large prey items (such as chaetognaths).

Mollusk larvae and copepods dominated the diets in all seasons except spring (Table 7). In spring, round scad fed on copepods, ostracods, chaetognaths, and barnacle cyprids. The preponderance of copepods in diets of round scad in summer is due in part to the large number of juveniles included in the analysis. The mean size of fish in the summer sample was smaller than the mean size of fish in all other seasons (Student-Newman-Keuls tests; $q_{453,4} = 14.1$ for winter vs. summer, $q_{453,3} = 13.2$ for summer vs. spring, and $q_{453,2} = 11.1$ for summer vs. fall). In all other seasons, dietary analyses (Table 5) were based on fish samples with similar size distributions (Student-Newman-Keuls tests; $q_{453,3} = 0.7$ for winter vs. fall, $q_{453,2} = 0.7$ for winter vs.

spring, and $q_{453,2} = 0.1$ for fall vs. spring). The mean number of prey items showed considerable seasonal variation from 4.6 in fall to 104 in spring.

The percentage of empty stomachs varied as a function of time of day (Fig. 6). Few empty stomachs (2-7%) were collected from midmorning to early evening, whereas 13-29% of stomachs were empty from early evening to midmorning. Size effects are unlikely to have caused the observed differences in the percentages of empty stomachs: samples with lower (2, 5, and 7) and higher (13, 20, and 29) percentages were comprised of fish of similar size (ANOVA, $F_{(1,4)} = 0.01$, $P > 0.75$).

Age and Growth

Validation of the daily growth marks on otoliths of round scad was provided in two ways. Examination of marginal increments of lapilli from small specimens (13-55 mm FL) collected at different times of day suggested daily periodicity of increment formation. The margin consisted of the transparent incremental zone from midafternoon until early morning and the dark discontinuous zone in midmorning (Table 8). The allometric relationship between otolith and fish length also validates the use of otoliths for age determination. Otolith length (OL)

TABLE 6.—Index of relative importance (IRI), frequency of occurrence (%FO), volumetric displacement (%VOL), and relative abundance of prey (%N) by sizes. N = sample size (# empty stomachs), \bar{x} = mean fork length in mm, s = variance of fork lengths, and n = total number of prey.

Length/prey	N %	VOL %	FO %	IRI
40-89 mm FL: $N = 82(12)$, $\bar{x} = 50$ mm, $s = 13$ mm, $n = 1,272$				
Copepoda	74	80	75	1.15
Mollusca	13	5	24	0.04
Decapoda	3	7	27	0.03
Amphipoda	2	2	15	0.01
Eggs	3	2	24	0.01
Ostracoda	1	1	10	<0.01
Other	4	3	32	0.02
90-139 mm FL: $N = 192(15)$, $\bar{x} = 114$ mm, $s = 13$ mm, $n = 8,003$				
Copepoda	34	57	74	0.67
Mollusca	20	13	47	0.16
Cirripedia	31	13	20	0.09
Ostracoda	9	8	22	0.04
Amphipoda	2	3	28	0.01
Decapoda	1	3	25	0.01
Other	3	3	32	0.02
140-189 mm FL: $N = 183(14)$, $\bar{x} = 156$ mm, $s = 10$ mm, $n = 12,850$				
Mollusca	36	12	59	0.28
Copepoda	14	12	64	0.17
Amphipoda	14	12	31	0.08
Chaetognatha	15	53	10	0.07
Ostracoda	11	5	30	0.05
Cirripedia	4	2	25	0.02
Decapoda	1	1	32	0.01
Other	5	4	48	0.04

TABLE 7.—Frequency of occurrence, volumetric displacement, and relative abundance of prey of *Decapterus punctatus* by season. Abbreviations as in Table 6; r = range of fork lengths.

Season/prey	N %	VOL %	FO %	IRI
Winter: $N = 116(10)$, $\bar{x} = 140$ mm, $s = 25$ mm, $r = 85-185$ mm, $n = 4,357$				
Mollusca	47	32	48	0.38
Copepoda	17	31	52	0.25
Ostracoda	15	14	31	0.09
Cirripedia	12	5	33	0.06
Decapoda	2	7	35	0.03
Amphipoda	1	2	17	0.01
Other	6	9	47	0.07
Spring: $N = 112(5)$, $\bar{x} = 135$ mm, $s = 18$ mm, $r = 97-175$ mm, $n = 10,999$				
Copepoda	21	18	92	0.36
Amphipoda	17	15	52	0.16
Ostracoda	13	6	45	0.09
Chaetognatha	17	51	13	0.09
Cirripedia	22	5	25	0.07
Mollusca	6	2	67	0.05
Decapoda	1	2	26	0.01
Other	3	2	45	0.02
Summer: $N = 161(16)$, $\bar{x} = 87$ mm, $s = 40$ mm, $r = 35-163$ mm, $n = 6,505$				
Copepoda	55	73	79	1.01
Mollusca	37	18	43	0.24
Decapoda	1	3	22	0.01
Amphipoda	1	1	21	<0.01
Ostracoda	1	1	10	<0.01
Cirripedia	1	1	9	<0.01
Other	2	2	28	0.01
Fall: $N = 68(10)$, $\bar{x} = 138$ mm, $s = 33$ mm, $r = 48-180$ mm, $n = 264$				
Mollusca	65	44	21	0.23
Copepoda	19	34	42	0.22
Other	16	22	36	0.14

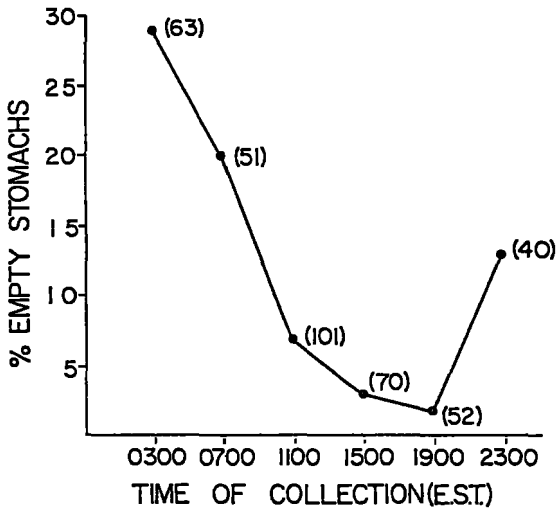


FIGURE 6.—Percent of empty stomachs of *Decapterus punctatus* collected at different times of day. Samples were pooled over 4-h intervals, of which midpoints are given. (n) is sample size.

TABLE 8.—Appearance of marginal increments of otoliths of *Decapterus punctatus* collected at different times of day. Data indicate increments are formed daily. N = number of specimens, times are Eastern Standard Time.

FL of specimens (N)	Time of capture	Marginal increment
42-55 mm (4)	0239-0257	wide, transparent
17-22 mm (11)	0812-0817	thin, dark
13-24 mm (4)	1506-1516	wide, transparent
35-53 mm (8)	2045-2053	wide, transparent

was proportional to fork length throughout the size range (14-143 mm FL) for which age determination was possible ($\log_{10} OL$ (in mm) = $0.82 \log_{10} FL$ (in mm) - 1.61; $r^2 = 0.99$, $n = 71$).

The thickness and structure of growth increments changed in consistent ways in lapilli (Fig. 7). Ten to twelve faint daily increments surrounded a central core, which contained the primordium (Fig. 8). The next 10-15 increments increased in thickness, and the following 20-25 increments gradually decreased in thickness. A distinct change occurred at this point, and increments became thinner and more regular. Increments appeared uniform in thickness

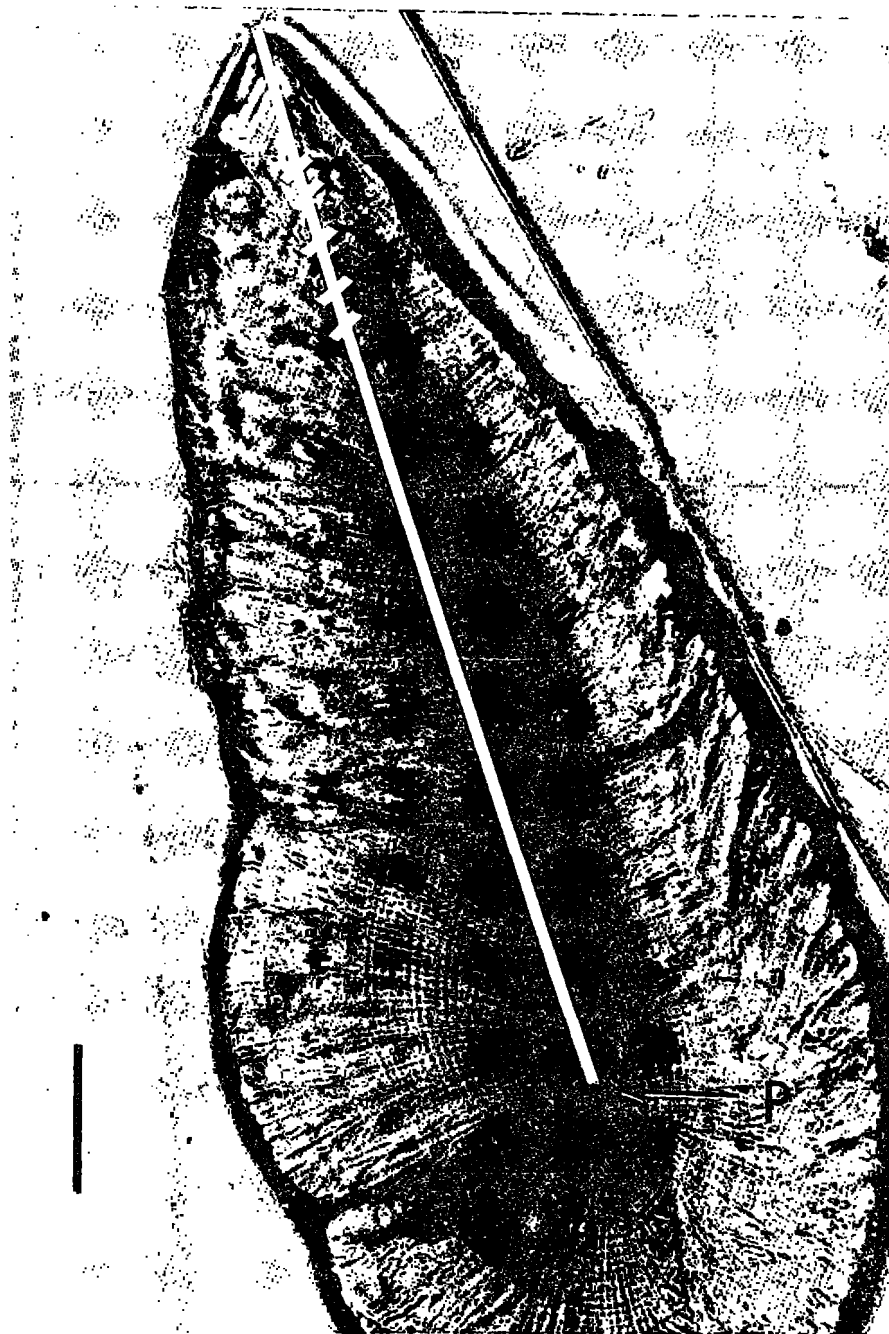


FIGURE 7.—Sagittal section through a lapillus of *Decapterus punctatus*. The pattern of fine, regular growth increments is interspersed increasingly with heavy, irregular growth interruptions (crosshatches) in outer regions of the otolith. Bar indicates 0.10 mm, P is the primordium.

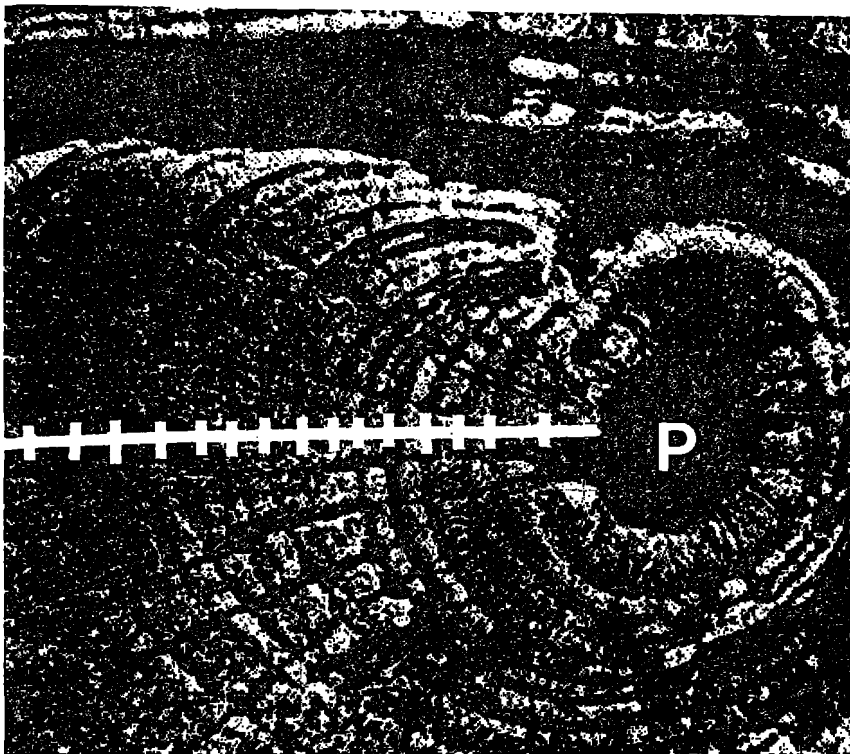


FIGURE 8.—Scanning electron micrograph of a sagittal section through the primordium of a lapillus of *Decapterus punctatus*. P is the primordium and crosshatches denote daily increments. The pattern of otolith growth of juveniles was consistent in most otoliths.

to approximately increment 100, then gradually became thinner and more difficult to count. Growth interruptions appeared in outer portions of otoliths of large fish, and growth records were more irregular.

Round scad grew rapidly for 120-150 days until reaching sexual maturity at approximately 110 mm FL (Fig. 9). The von Bertalanffy [FL = 161 (1 - exp (-0.012 (age - 29.5)))] and Gompertz [FL = 1.17 exp [4.76 (1 - e^{-0.026 (age)})]] growth equations provided good and nearly identical fits ($r^2 = 0.96$ and 0.97, respectively) to the observed data. Specific growth rates (Table 9) for juveniles were initially high, decreased sharply until sexual maturity, then decreased more gradually throughout the time period for which age determination was possible. The largest specimen for which reliable counts could be determined was 143 mm FL, although most specimens at that size could not be assigned an age.

The age of round scad for the entire size range (FL up to 21 cm) that was collected in the South

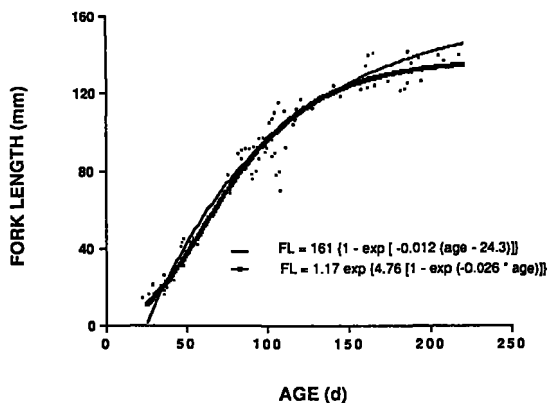


FIGURE 9.—Von Bertalanffy (thin line) and Gompertz (heavy line) growth equations. Sexual maturity of *Decapterus punctatus* is reached at approximately 110 mm FL in 120-150 days.

Atlantic Bight could not be determined from daily increments on the lapillus. The age of all specimens <120 mm FL could be determined, but only half of

TABLE 9.—Instantaneous growth rates (Ricker 1979) of *Decapterus punctatus* predicted from the von Bertalanffy equation (fig. 11). Weights were converted from lengths by using the regression: $\ln Wt (g) = 2.96 \ln FL (mm) - 11.2$.

Age (d)	FL d^{-1} (%)	Wt d^{-1} (%)
35-60	6.3	13.2
61-85	1.9	5.6
86-105	0.8	2.6
106-130	0.7	2.2
131-155	0.4	1.6
156-180	0.3	1.2

the specimens 121-143 mm FL and no individuals >143 mm FL could be assigned an age. Replicate counts of otolith increments from adults often differed by >10%, and were considered unreliable. In addition, frequent growth interruptions occurred in the outer portions of the otoliths of large specimens, and the timing of formation of such marks was not known.

DISCUSSION

Seasonal Distribution and Relative Abundance

Round scad apparently migrate shoreward across the continental shelf as sea temperatures increase in spring, then migrate into warm (>15°C) midshelf (28-110 m) depths as inshore temperatures decline in winter. Intermediate shelf depths in the South Atlantic Bight are fairly warm year round, unlike inshore waters which are seasonally cooled by cold fronts (Atkinson et al. 1983) and outer shelf waters which are intruded upon by cold-water upwellings (Blanton et al. 1981). Magnuson et al. (1981) reported that catches of round scad were proportional to temperature, and laboratory studies (Wyllie et al. 1976) have suggested a preferred temperature of 27°C. Seasonal onshore and offshore movements are made by round scad in the Gulf of Mexico (Klima 1971) and by other pelagic fishes in the South Atlantic Bight (Wenner et al. 1979a, b, c, d, 1980) and elsewhere (Allen and DeMartini 1983).

Longshore migration does not appear to be a consistent feature of the movements of round scad along the southeastern Atlantic states. Differences of catches (Table 4) made north and south of lat. 31°30'N are inconsistent, and limited meristic data (see Results) provides no evidence of movements by discrete stocks through the South Atlantic Bight.

Although fish communities of live bottom habitats may change (Chester et al. 1984), latitudinal differences in the distribution of demersal fishes in sandy, open shelf habitats of the South Atlantic Bight are not apparent (Wenner et al. 1979a). More substantive information (tag-recapture studies, etc.) than the limited data given above is needed to determine accurately the movement patterns of round scad. At the present time, available information suggests that seasonal migration in round scad involves mainly onshore or offshore movement.

The abundance of round scad in the South Atlantic Bight is undoubtedly underestimated by catch statistics (Table 2). First, benthic otter trawling is generally inadequate for determining the abundance of small, mobile pelagic species (Wenner et al. 1979a). Second, the attraction of round scad to sponge-coral habitats in winter may have exaggerated the apparently large fluctuations in the seasonal abundance of round scad in the South Atlantic Bight. The sampling protocol assumes equal probability of capture over the different habitat types, but the probability of capturing round scad over live-bottom habitats varies seasonally. An increased proportion of live-bottom areas should be sampled in winter to obtain more reliable estimates of the abundance of round scad. The distribution, extent, and adequacy of sampling of live-bottom habitats are not well known (Wenner 1983). Thus, sampling inadequacies and the seasonal attraction of round scad to live-bottom habitat result in underestimation of abundance.

Several factors may influence the attraction of round scad to live-bottom habitat in winter. First, round scad utilize live-bottom habitat in winter, when invertebrate biomass has peaked and potential competitors and predators have decreased (George and Staiger 1978³; Wenner et al. 1980, 1983, 1984; Sedberry and Van Dolah 1984). Second, winter temperatures at live-bottom stations, though not significantly different from temperatures at sand-bottom stations, tend to be warmer, and scad prefer warm waters. The greatest densities of round scad occur in the midshelf where seasonal temperatures are generally warmest and the most highly productive live-bottom areas are located (Miller and Richards 1980; Sedberry and Van Dolah 1984). Finally, the relief of live-bottom habitats (albeit low) may serve to attract round scad; many coastal pelagic fishes, including round scad, have an affin-

³George, R. V., and J. C. Staiger. 1978. Epifaunal benthic invertebrate and demersal fish populations in the Georgia Bight continental shelf environment. South Atlantic Benchmark program, Volume 3, Texas Instruments Inc. Draft Report, p. 211-254.

ity for structure (Klima and Wickham 1971; Feder et al. 1974; Hastings et al. 1976).

Although fish sizes within each depth zone overlapped, the observed pattern was fairly consistent and distinct for all cruises; adults composed the catch in 9-18 m depths, and fish in deeper waters (mostly juveniles) showed a positive size-depth correlation. Adults migrate inshore in spring to feed and spawn, and offshore in winter to avoid cold waters. However, the apparent movement of juveniles to deeper waters is not understood. Correlations between fish size and depth are numerous in aquatic habitats (Helfman 1978), but explanations based on changing physiological tolerances (Bullis and Struhaker 1970), foraging strategies (Polloni et al. 1979), and predation responses (Hobson 1972) have been difficult to demonstrate in most fishes.

Reproductive Biology

Although results (Fig. 3) indicate that *D. punctatus* spawn primarily from March through August, spawning probably occurs through September and to a lesser extent throughout the year. Collections were not made during September and October of 1980, but water temperatures in August and September in the South Atlantic Bight are generally similar (Atkinson et al. 1983). Round scad larvae have been collected in winter in the South Atlantic Bight (Fahay 1975; Powles and Stender 1976) and the eastern Gulf of Mexico (Leak 1981). Larval occurrence has been correlated with water temperature in the eastern Gulf of Mexico (Leak 1981), and sufficient water temperatures ($>20^{\circ}\text{C}$) occur throughout the year in parts of the South Atlantic Bight.

The pattern of oocyte development is generally quite variable and complex in serial spawners: oocytes develop asynchronously or synchronously in groups, and ova are released in batches. Three observations suggested that round scad are serial spawners: 1) the occurrence of three distinct modes in the frequency distributions of oocyte diameters from ripe ovaries collected in spring; 2) two modes in those distributions from ripe fish collected in late summer; and 3) evidence of spawning in ovaries having a frequency distribution of oocyte diameters similar to developing ovaries. Spawning was indicated by disorganized ovarian septa with conspicuous spaces, debris in the ovarian lumen, residual atretic oocytes, and brown bodies.

Although estimates of fecundity in round scad are comparable to those of *D. pinnulatus* (Yamaguchi 1953), *D. macrosoma*, and *D. russelli* of similar size

(Tiews et al. 1970), the conventional method applied here probably underestimated fecundity. Because gonads used in fecundity estimation were not examined histologically, it was not possible to determine if spawning had occurred recently in specimens used for fecundity measures. In addition, sufficient numbers of specimens were not examined to determine spawning frequency from running-ripe (DeMartini and Fountain 1981) or postovulatory (Hunter and Goldberg 1979) females. Previous studies on other serial spawning fishes (Hunter and Goldberg 1979; Hunter and Leong 1981; DeMartini and Fountain 1981; Conover 1985) have shown that estimates of annual fecundity (total number of ova spawned in 1 year) can differ from conventional fecundity estimates (which ignore multiple spawning) by an order of magnitude. Serial spawning fishes generally have low relative ovary weights (Martinez and Houde 1975; Smith and Lasker 1978; DeMartini and Fountain 1981), but can expend over 100% of their body weight per year in eggs (Hubbs 1976; DeMartini and Fountain 1981). If observed fecundity in round scad (6,200-51,000) is extrapolated from the 4.3% relative ovary weight (Table 7) to total body weight, then fecundity estimates of 142,000-1,173,000 would result. If observed fecundity is divided by the proportion of oocytes in the most advanced developmental mode (32%, from Figure 3), then batch fecundities of approximately 2,000-16,000 per female (130-230 eggs/g body weight) and annual fecundity estimates (based on 10 d spawning cycle for 6 months) of 36,000-288,000 would result. Both estimates are entirely speculative, but support the contention that the conventional method underestimated fecundity, and emphasize the need for additional studies on the fecundity of round scad.

Round scad mature at a smaller size than reported for other species of *Decapterus*, which reach maturity at 18-20 cm (Yamaguchi 1953; Tiews et al. 1970). The small size at which round scad become sexually mature suggests that they are under strong selection pressure to mature rapidly. The natural mortality of round scad in the eastern Gulf of Mexico is high (Houde et al. 1983). Compared with temperate and boreal species, many tropical clupeoids also mature at small sizes, seldom attain large size and have high adult mortality rates (Blaxter and Hunter 1982; Houde et al. 1983).

Feeding Habits

Zooplanktivores feed during the day or at night, but seldom during both periods (de Silva 1973; Hob-

son and Chess 1976; Helfman 1986), probably due to visual limitations (Durbin 1979). The absence of nocturnal prey and the strongly diurnal periodicity of stomach fullness (Fig. 6) indicate that *D. punctatus* feeds during the day. Round scad rarely consumed mysids, tanaids, and cumaceans, which are abundant in the water column at night but dwell in the benthos during the day (Kaestner 1970; Hobson and Chess 1976). The diel periodicity in empty stomachs (Fig. 6) is not biased by sizes of fish differing among collection times (see Results). Individuals of different sizes have similar gut evacuation rates (Perrson 1981) but different gut capacities; therefore, small individuals empty their guts more quickly than large individuals. The lack of a size difference in this analysis substantiates the daily feeding period by round scad.

Scales were a common item in round scad stomachs, but were deleted from analyses because several observations indicated that round scad were feeding on debris (including scales) generated by trawling: 1) oral chambers of specimens often contained scales; 2) scale size and type varied; and 3) the extent of presumed lepidophagy was not correlated with fish size. In addition, scales were seldom found in latter portions of the gut. Most other lepidophages generally prey on a small number of species (Sazima 1983), or for only a portion of their life history (Carr and Adams 1972). Thus, round scad probably consume scales on occasion, but not to the extent that the data would indicate. It seems likely that round scad were feeding on scales abraded from fishes during their avoidance of or capture by the trawl. Yamaguchi (1953) also attributed the occurrence of scales in the stomachs of *D. pinnum* to gear bias.

Ontogenetic changes in the diet occurred with growth. Larger individuals had more diverse diets which included larger prey. Small fish fed primarily on small, abundant copepods and copepodites. Stomach contents of several (10) small juveniles (13-26 mm FL) collected during an ichthyoplankton survey in 1973 also contained mostly copepods (S. Hales pers. obs.). Data from these specimens were not included in previous analyses due to the possibility of differential prey digestion.

Seasonal changes in the diets of round scad probably reflect fish size and the relative abundance of zooplankton components. Copepods and mollusks were the most important prey in all seasons except during spring when barnacle cyprids were the most numerous and chaetognaths contributed the greatest volume of prey. Zooplankton volumes and diversity reach their peak in the spring (Deevey 1960;

Reeve 1964), and cyprids are more abundant in the spring than in any other season (Lang and Ackenhausen-Johns 1981). The preponderance of copepods in the diet of round scad in summer partially reflects the abundance of juvenile round scad, which appear to feed primarily on small abundant copepods.

Molluscan veligers may be an exception to the general pattern of prey selection. They have not been reported to be abundant in the zooplankton of the South Atlantic Bight (Paffenhöfer 1980, 1981) or elsewhere (Deevey 1960; Reeve 1964), yet occurred frequently in the diets of round scad. Shells of both gastropods and bivalves and the opercula of gastropods were all that remained in the stomachs of round scad on occasion; such parts are apparently digested slowly and retained in the stomach. However, such an explanation alone does not account for the frequency and abundance of mollusk veligers. Brewer and Kleppel (1986) have reported the paradox of low bivalve density yet frequent occurrence in the guts of some larval fishes, and suggested that bivalve veligers may occur in microscale patches just above the bottom. Planktonic stages of gastropods are important prey for horse mackerel (*Trachurus trachurus*), which school near the bottom (Macer 1977). Thus, the frequency and abundance of mollusk veligers in the stomachs of round scad may be attributed to both the abundance of mollusk veligers being greater than generally recognized and their low digestibility and long retention in stomachs.

Age and Growth

Round scad grow rapidly to sexual maturity at 11 cm FL in 4-5 months, and apparently achieve a major proportion of their total size in their first year. Because of the problems encountered in age determination in this study, little can be said about the age of most adults. The asymptote predicted by the von Bertalanffy model (161 mm FL) is much shorter than the maximum size observed in the South Atlantic Bight. Thus, the growth rates observed in this study should not be extrapolated to older and larger fish. Houde et al. (1983) reported the mean size of round scad in the eastern Gulf of Mexico to be 136 mm FL at age 1, 160 mm FL at age 2, and 177 mm FL at age 3. In addition, they reported considerable variation (10-20 mm) in the mean lengths at age. Differences in the growth rates observed in the two studies are believed to be due mainly to methodology, but may also be due to slight differences in the growth of round scad between the two areas.

Growth rates reported in this study for juvenile round scad are similar to those of juvenile *Selar crumenophthalmus* (Kawamoto 1973) and *Trachurus trachurus* (Macer 1977), and would enable spring-spawned round scad encountering favorable conditions to spawn in the fall (Leak 1981). Other species of *Decapterus* are reported to grow more slowly (Yamaguchi 1953; Tiews et al. 1970; Ingles and Pauly 1984), but such studies used length-frequency information only and may have underestimated growth. These species (*D. pinnulatus*, *D. russelli*, *D. macrosoma*) reach sexual maturity at 17-20 cm FL in their first or second year, and attain 25-35 cm FL in 3-5 years (Yamaguchi 1953, Tiews et al. 1970). The rapid growth of round scad to sexual maturity suggests that this species is under strong selection to mature early. Mortality estimates for round scad (Leak 1981; Houde et al. 1983) are high even in comparison with other coastal pelagic fishes, which do not achieve as large a size as round scad during their first year.

Daily growth increments were easily distinguished in juveniles and small adults, but could not be used to determine ages of most adults. Frequent spawning involving the high energetic expenditures reported for other pelagic fishes (Hubbs 1976; DeMartini and Fountain 1981) would result in slow growth of adults. Specific growth rates based on Houde et al. (1983) (0.04% FL d⁻¹ for 1-2 yr olds, and 0.03% FL d⁻¹ for 2-3 yr olds) are much slower than the rate of young adults (0.28% FL d⁻¹) observed in this study. A reduction in increment thickness with growth (Brothers 1979; Campana 1985) might result in the exceedingly fine increments observed in the outer portions of the otoliths of adults. Another possibility is that growth of adults is insufficient to maintain the pattern of daily increment formation. McGurk (1984) has reported that daily increment formation in larval *Clupea harengus* may be altered when absolute growth rates are <0.36 mm d⁻¹.

Occurrence of growth interruptions in the outer portions of otoliths of most adults also hindered age determination. The period of formation of such marks was not known. If such marks are not formed in 1 day, then inclusion of such marks as daily increments would result in underestimation of the ages of adults. Growth interruptions may result from spawning (Panella 1974), lunar or tidal rhythms (Rosenberg 1982), or stress (Ralston and Miyamoto 1983); however, correlations between such events and the growth record of round scad could not be determined.

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