REPRODUCTIVE BIOLOGY OF THE BLUELINE TILEFISH, *CAULOLATILUS MICROPS*, OFF NORTH CAROLINA AND SOUTH CAROLINA[1]

JEFFREY L. ROSS[2] AND JOHN V. MERRINER[3]

ABSTRACT

Blueline tilefish, *Caulolatilus microps*, were obtained by hook and line fishing and port sampling operations off North Carolina and South Carolina from 1972 to 1977. *Caulolatilus microps* spawn off the Carolinas from April through October, with peak activity off North Carolina in May-June and September-October. Multiple spawnings by individual females were indicated by multimodel size distributions of ova; this is complemented by the continuous production of spermatozoa in testes, which is facilitated by dynamic spermatogenic tubules. Fecundity is best predicted by fish weight: ln.Fecundity = 0.016 + 1.832 ln Weight. Fecundity estimates ranged from 0.2 million ova for a 412 mm TL (0.82 kg) fish to 4.1 million ova for a 736 mm TL (4.85 kg) fish. Females attained sexual maturity between 425 and 450 mm TL (age IV-V). Males showed pronounced testicular development after age V (500 mm TL). Females were more abundant from 300 to 500 mm TL; the sex ratio was 1:1 between 500 and 600 mm TL; males predominated in size classes greater than 600 mm TL. Protogynous sex reversal in three juvenile specimens (156-202 mm TL) was indicated by transitional gonads or testes with residual oocytes. Previtellogenic oocytes in 8 of 42 mature males (436-700 mm TL) further suggest protogyny, although no adult fish with transitional gonads were observed. Whether blueline tilefish are strictly juvenile or functional hermaphrodites has yet to be determined.

The blueline tilefish, *Caulolatilus microps* Goode and Bean, is a semitropical demersal branchiostegid that constitutes a significant component of the deepwater grouper-snapper fishery off North Carolina and South Carolina (Huntsman 1976). It inhabits the outer continental shelf, shelf edge, and upper slope (70-235 m) from Cape Charles, Va., to Key West, Fla., and in the Gulf of Mexico from Pensacola, Fla., to Campeche, Mexico (Dooley 1978).

In 1972 scientists at the Southeast Fisheries Center of the National Marine Fisheries Service (NMFS) began studying the biology, community relationships, and population dynamics of the offshore demersal (reef) fishes off the southeastern United States, ultimately to provide effective management of this fishery (Huntsman 1976). The reproductive biology of blueline tilefish was investigated as part of that program, and is herein described with respect to 1) spawning seasonality, 2) descriptive gonadogenesis, 3) fecundity, 4) age/size of sexual maturity, 5) sex ratio with size, and 6) sexual transition.

The reproductive biology of *C. microps* is previously undescribed. Dooley (1978) reported the capture of ripe females in January and May through September off North Carolina. Brief notes on reproduction for other branchiostegids suggest protracted spawning seasons for *C. princeps* (Fitch and Lavenberg 1971), *C. affinis* (Dooley 1978), *Lopholatilus chameleonticeps* (Freeman and Turner 1977; Grimes[4]), and *Branchiostegus japonicus japonicus* (Hayashi 1977). Dooley and Paxton (1975) related the presence of several size classes of ova in maturing *B. wardi* and *B. serratus* to multiple spawning and found anomalous sex ratios within size classes. Pelagic eggs and larvae of *Caulolatilus* sp. and *L. chameleonticeps* have been collected off the Carolinas and in the northwest Atlantic (Freeman and Turner 1977; M. Fahay[5]).

MATERIALS AND METHODS

Blueline tilefish were captured over rugged precipitous bottoms as well as gently sloping sections of the shelf edge (Fig. 1). Specimens were obtained by hook and line fishing with electric reels and rods from

[1]Contribution No. 1083, Virginia Institute of Marine Science, Gloucester Point, Va. Based on a thesis by Jeffrey L. Ross, submitted to the School of Marine Science, College of William and Mary, Williamsburg, Va., December 1978.

[2]Virginia Institute of Marine Science, Gloucester Point, Va.; present address: North Carolina Division of Marine Fisheries, P.O. Box 967, Manteo, NC 27954.

[3]Virginia Institute of Marine Sciences, Gloucester Point, Va.; present address: Southeast Fisheries Center Beaufort Laboratory, National Marine Fisheries Service, NOAA, Beaufort, NC 28516.

[4]Churchill B. Grimes, Assistant Professor, Department of Environmental Resources, Rutgers University, P.O. Box 231, New Brunswick, NJ 08903, pers. commun. February 1982.

[5]Michael Fahey, Fishery Biologist, Northeast Fisheries Center Sandy Hook Laboratory, National Marine Fisheries Service, NOAA, Highlands, NJ 07732, pers. commun. February 1982.

Manuscript accepted November 1982.
FISHERY BULLETIN: VOL. 81, NO. 3, 1983.

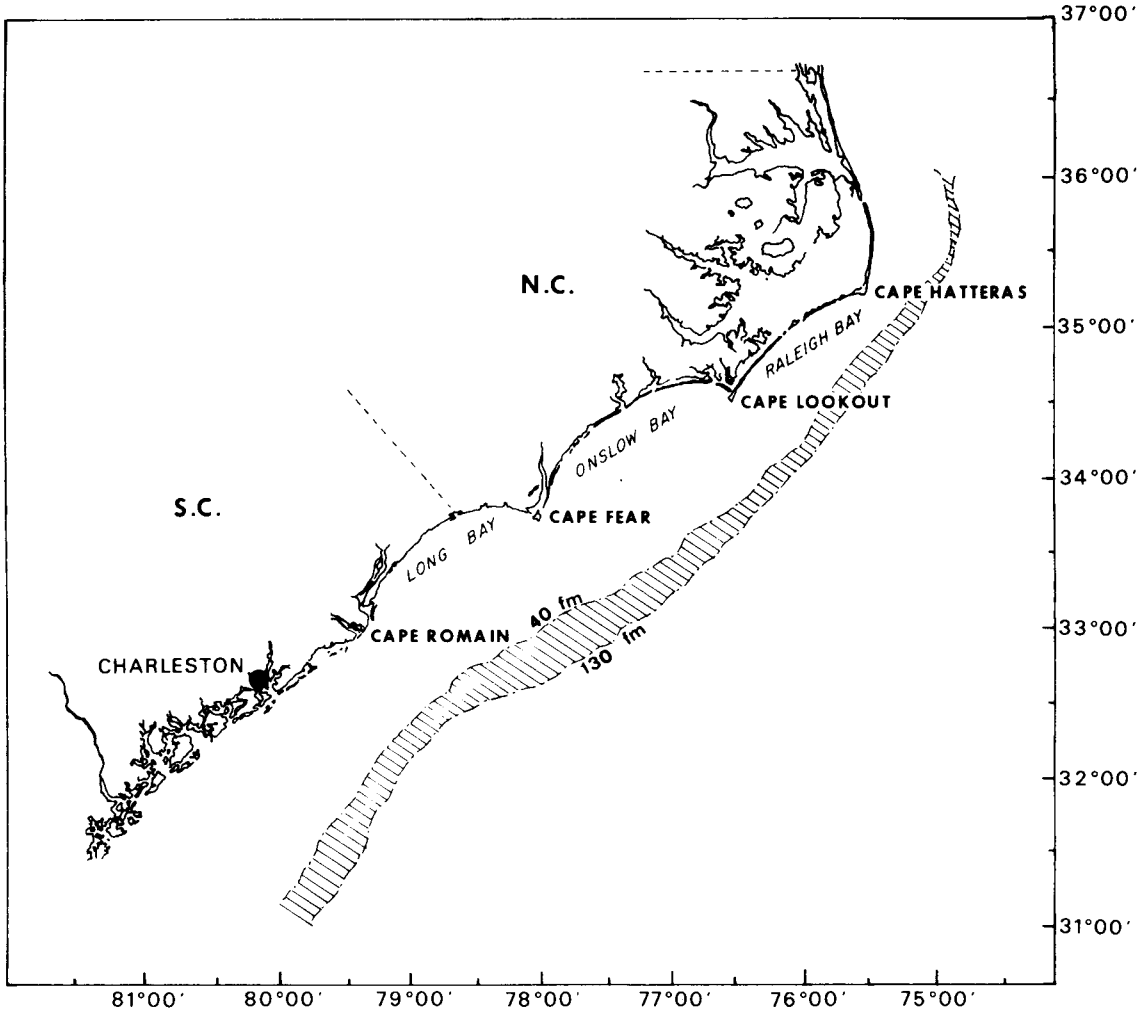

FIGURE 1.— Distribution of *Caulolatilus microps* off North Carolina and South Carolina (noted by hatch marked area).

1972 to 1977 in the northern and central portions of Onslow Bay aboard the RV *Onslow Bay* (NMFS). Fishing was most successful when baits were maintained as close to the bottom as possible. Total length (TL, mm) and total weight (W, g) were recorded for each fish, gonads excised and stored in 10% Formalin[6] and otoliths removed and stored in glycerine. Sampling of headboats fishing out of North Carolina and South Carolina ports provided ancillary records of total length and total weight, and samples of gonads and otoliths.

A gonosomatic index (GSI) was calculated according to the formula

$$GSI = \frac{GW}{W} \times 100$$

where GW = preserved gonad weight (0.1 g) and W = total body weight (g). GSI was used to determine spawning seasonality and sexual maturity.

Sex was determined by gonad examination since blueline tilefish apparently exhibit no sexually dimorphic characteristics. Ovaries and testes were staged macroscopically and histologically after preservation in 10% Formalin (Tables 1, 2). Ova stages corresponded to those described by Moe (1969) for red grouper, *Epinephelus morio*: oogonia, 2-8 μ; stage I, early oocytes, 20-50 μ; stage II, previtellogenic oocytes, 40-170 μ; stage III, early vitellogenic oocytes, 110-260 μ; stage IV, active vitellogenic oocytes, 215-650μ; stage V, mature ova, 735-910 μ

[6]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

with 140-196 μ oil globule. Spermatogenic stages were analogous to those described by Moe (1969) for red grouper and Hyder (1969) for *Tilapia*. Routine histological methods were used for slide preparations from Formalin-fixed gonads.

Frequency distributions of ova diameters were plotted by gonad stage to determine individual spawning patterns. Representative females were selected for each ovarian stage. The diameter of 50 ova from each occurring stage (previtellogenic, early vitellogenic, active vitellogenic, and mature oocytes) were measured from each sample using a gridded petri dish and a magnification of 70×. A ratio of the four stages was then determined by reducing the magnification to 20× and counting two or more entire grids until about 500 ova were counted. This ratio was reduced to a base of 200 and combined with ova diameter frequencies per stage data using the ratio

$$\frac{\text{frequency of ova stage}}{200} \times \frac{\text{ova diameter frequency}}{50}$$

to determine the relative frequency of each size group.

Well-Developed and Ripe ovaries from fish captured from April through September were used for fecundity estimates. One ovary randomly selected from each pair was weighed to the nearest 0.1 g. The ova were teased free of the ovarian tunic. Two subsamples were removed and all vitellogenic ova (stages III-V; determined by relative size and opacity of cytoplasm) were counted. The sample and subsamples were oven dried and weighed to the nearest 0.001 g. The formula

$$Y = \frac{(W)\ (w_i)}{(W_i)\ (w)}\ y$$

was used to estimate fecundity, with Y = total number of eggs in both ovaries, W = wet weight of both ovaries, W_i = wet weight of selected ovary, w_i = total dry weight, w = total dry weight of subsamples, and y = number of ova in subsamples (Manooch 1976).

TABLE 1.—Developmental stages of *Caulolatilus microps* ovaries.

Maturity stage	External appearance	Ova composition
Immature (stage 1) (>250 mm TL)	Small, maroon, sausage to teardrop shaped hollow organs.	Ovigerous lamellae composed of dense aggregations of undifferentiated oogonia and primary oocytes.
Resting (stage 2)	Flaccid triangular sacs with translucent tunic and dark reddish internal mass	Primarily early and previtellogenic oocytes with <1% early vitellogenic oocytes.
Developing (stage 3)	Ovary becomes increasingly rotund while maintaining a basic triangular shape; yellowish orange appearance due to granular ovigerous mass. tunic becomes more transparent, and ova are discernable.	Previtellogenic oocytes numerically dominant with some early and active vitellogenic oocytes. Well-developed ovaries contain an increasing number of vitellogenic oocytes evenly distributed over a large size range (215-650 μ).
Well-Developed (stage 4)	Ovarian tunic becomes nearly transparent yellowish ova densely packed and discernable.	Vitellogenic oocytes predominant and evenly distributed over a large size range (215-650 μ).
Ripe (stage 5)	May-August: Greatly distended, bulbous and occupying more than 1/3 of the peritoneal cavity; very light orange to white in color; 2-4% body weight. Ova clearly visible through delicate, nearly transparent tunic.	Broad size distribution of vitellogenic oocytes, with a mode of very large (420-640 μ) vitellogenic oocytes together with stage III and small (215-400 μ) stage IV oocytes. Mature oocytes (785-910 μ) characteristically contained in lumen, free of ovigerous lamellae.
	September-October: Ovaries comparatively smaller, firm, more triangular though rotund; 1-2.4% body weight.	A mode of large stage IV oocytes with stage V oocytes present and relatively few small (215-400 μ) stage IV oocytes.
Recently Spent-Redeveloping. (stage 6-3)	Resemble deflated early developing ovaries; distinguished by inflamed ventral, posterior portion, otherwise cream colored.	Stage III and small stage IV oocytes occur together with some very large stage IV and stage V oocytes, the latter often in an atretic state.
Spent (stage 6)	Flaccid, reduced in size; muscular tunic contracting and becoming firm, inflamed.	No evidence of vitellogenesis; stage IV and V oocytes are atretic; a few stage III oocytes occur.

TABLE 2.—Developmental stages of *Caulolatilus microps* testes.

Maturity stage	External appearance	Spermatogenic activity
Immature/Resting	Basically threadlike maroon organs with slight laterally compressed expansion posteriorly above sperm duct.	Spermatogenic tubules generally inactive, though spermatozoa may occur in lumen of spermatogenic tubules and collecting tubules.
Developing	Maroon, thin, elongate, laterally compressed, with widest portion directly above sperm ducts, tapering rapidly to filamentous anterior projection.	Spermatogenic tubules contain crypts at all developmental stages with spermatozoa collecting in the lumen and collecting tubules.
Well-Developed	More robust, triangular to nearly cornucopia shaped, tapering anteriorly. Maroon to creamy off-white color.	Extensive collections of spermatozoa in expanded lumens of actively developing spermatogenic tubules, with channeling of spermatozoa into medial collecting tubules.
Ripe	No running ripe testes observed	

Juvenile specimens were obtained for gonadal analysis from the Field Museum of Natural History, Chicago, Ill., and the Institute of Marine Science, University of North Carolina, Morehead City, N.C.

RESULTS

Gonadal Development

The paired ovaries of *C. microps* are suspended below the swim bladder by mesovarium in the most posterior portion of the body cavity. The mesovarium extends the length of the ovary and contains the ovarian arteries. Oogenesis and vitellogenesis occur within the ovigerous lamellae which are distributed evenly and project laterally and medially from the tunica albuginea. The absence of lamellae from a narrow band in the ventral portion of the ovary forms an ovocoel. This facilitates ovarian expansion and collection of ripe ova released from the lamellae prior to extrusion through the common oviduct (Moe 1969).

Testes of blueline tilefish are solid, smooth textured, compressed laterally, and relatively more elongate than ovaries. They are suspended from the swim bladder by the mesorchium, which has a wide base of attachment along the medial surface. Each testis enters the urinary papilla by a separate sperm duct.

The structure and developmental pattern of the testes are similar to that described by Smith (1965) as tubular. The primary spermatogenic units are radial spermatogenic tubules and spermatogenic crypts. In cross section, the spermatogenic tubules are essentially a ring, one spermatogonium or one spermatogenic crypt thick (Fig. 2). An elastic connective tissue, the Sertoli cells, encapsulates and maintains the integrity of the tubules and the individual developing crypts. It presumably serves as the site of steroidogenesis (Lofts 1968; Hoar 1969). Development proceeds at varying rates within each spermatogenic tubule, analogous to that in the ovigerous lamellae, so that active spermatogenic tubules usually contain crypts at all stages of development (Fig. 3). Spermatids were the most advanced stage observed within a crypt. Spermiogenesis, the morphogenesis of spermatid to spermatozoa, occurred around the time of passage from crypt to the lumen of the spermatogenic tubule.

Whereas in many fishes the interstitial tissue separating the developing tubules breaks down at later stages of development resulting in extensively

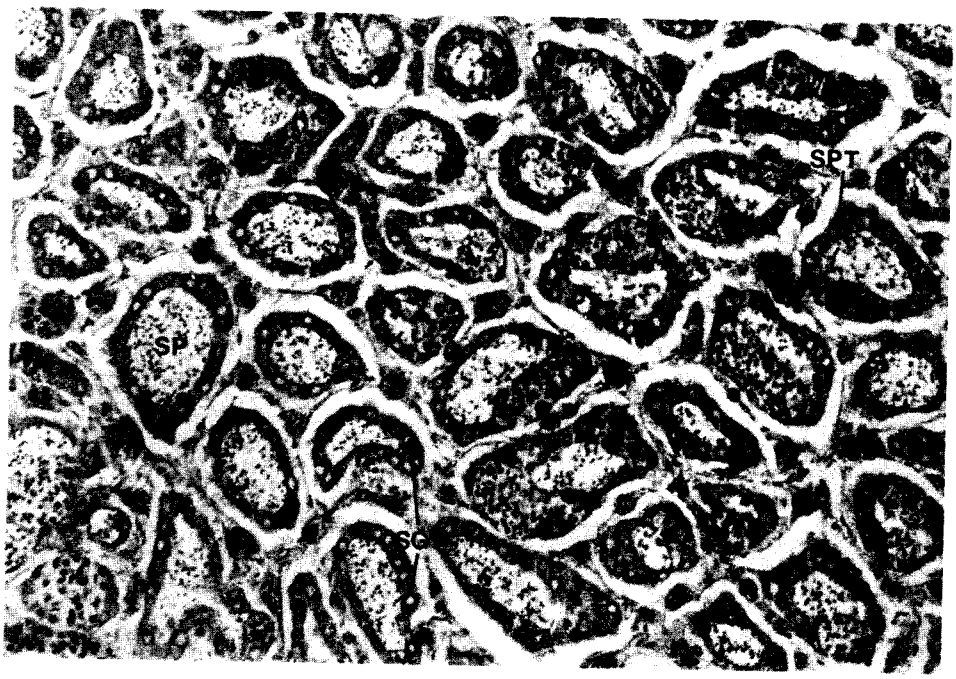

FIGURE 2.—Cross section of Early-Developing testes from a 530 mm TL *Caulolatilus microps* collected 15 March 1977. Note radial spermatogenic tubules (SPT) composed principally of primary spermatogenia (SG1) with few developing crypts, and the presence of spermatozoa (SP) in the lumen of the spermatogenic tubules (Haematoxylin × 200).

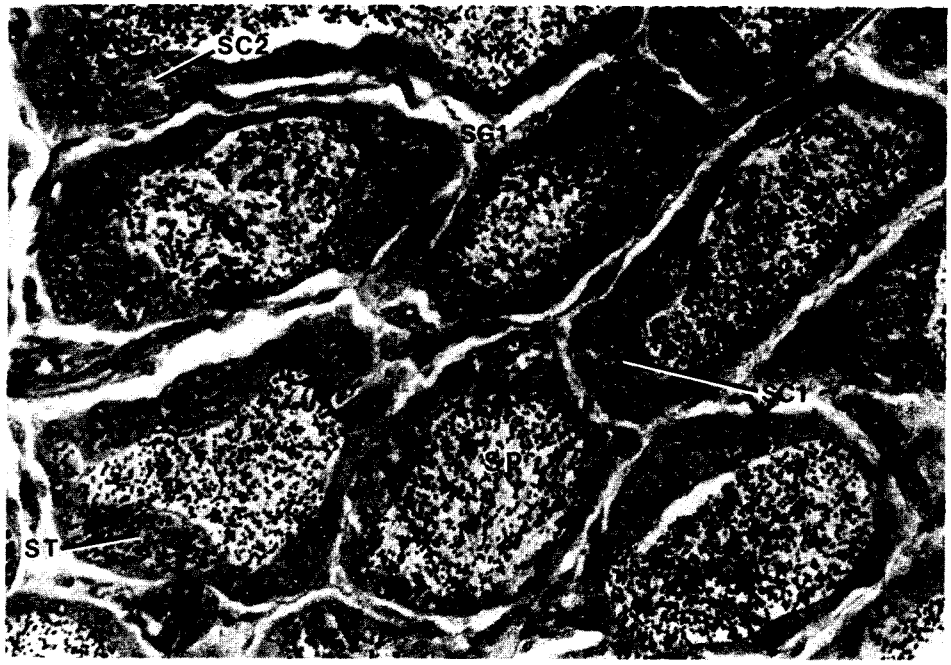

FIGURE 3.—Cross section of Developing testes from a 664 mm TL *Caulolatilus microps* captured 9 September 1974. Note spermatogenic tubules composed of the spectrum of developing crypt stages, with primary (SG1) spermatogonia; primary (SC1) and secondary (SC2) spermatocytes; spermatids (ST); and collections of spermatozoa (SP) in the lumen (Haematoxylin and eosin × 200).

packed sinuses of spermatozoa, the spermatogenic tubules of *C. microps* maintain their integrity. Drainage of spermatozoa from the testes results from the dynamic nature of the tubules. In the course of their development, they migrate medially from the lateral epithelium. Several observations support this hypothesis. In an early-developing male captured in May (Fig. 4), the lateral spermatogenic tubules are undeveloped and inactive with small amounts of spermatozoa in the lumen. Those adjacent to the dorsomedial portions of the testes are also generally inactive but contain larger collections of spermatozoa. This suggests that longevity of spermatogenic tubules exceeds one season and that spermatogenic tubules generate from the peripheral interstitium (Lofts 1968). The spermatogenic tubules adjacent to the dorsomedial connective tissue in developing testes are generally the most well developed, and can be seen merging with the medial collecting tubules (Fig. 5). The collecting tubules have boundary cells that are essentially connective tissue, and contain only spermatozoa. The spermatogenic tubules can be distinguished, since they are bordered by active spermatogenic crypts. Testicular drainage is thus accomplished by a dorsomedial migration of spermatogenic tubules and their merging with and releasing of spermatozoa into the collecting tubules. The collecting tubules channel the spermatozoa posteriorly and ventrally into the separate sperm ducts.

Spawning Seasonality

Caulolatilus microps spawn off North Carolina and South Carolina between April-May and September-October. Monthly mean GSI values for 138 females and 101 males captured off North Carolina exhibited peaks in May and September (Fig. 6). Early-Developing ovaries were predominant from February through April. High GSI values in May corresponded to the greatest incidence of Well-Developed and Ripe females (Fig. 7). The lower mean GSI values observed in June, July, and August corresponded with a diversity of gonad stages including Early-Developing, Well-Developed, Ripe, and Recently Spent-Redeveloping ovaries. Ovaries were again synchronously Well-Developed or Ripe in September though considerably smaller than gonads observed in May and June. Low GSI values from November through March reflect a period of gonad

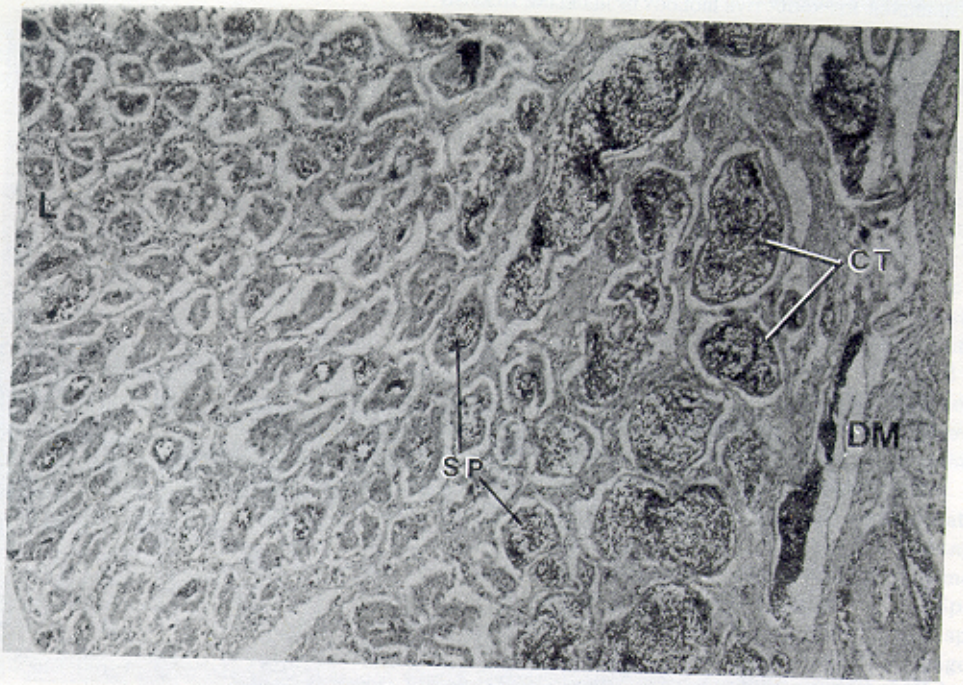

FIGURE 4.—Cross section of Resting testes from a 410 mm TL *Caulolatilus microps* collected 15 March 1977. Note undeveloped state of lateral (L) spermatogenic tubules and increased collections of spermatozoa (SP) in spermatogenic tubules and collecting tubules (CT) located along dorsomedial (DM) region (Haematoxylin and eosin × 78).

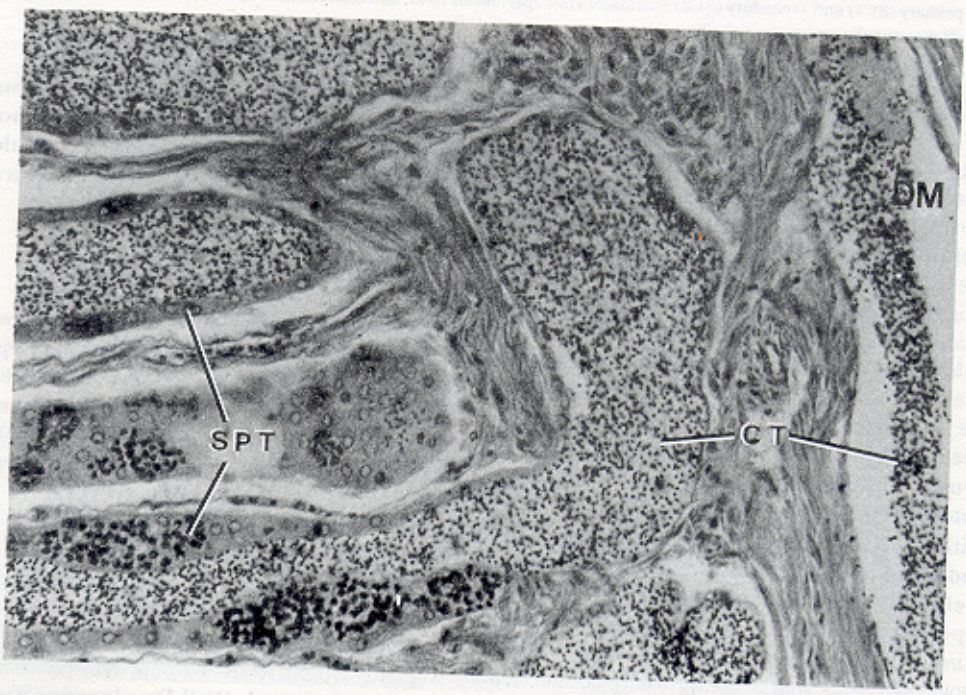

FIGURE 5.—Cross section of Developing testes from a 664 mm TL *Caulolatilus microps* collected 9 September 1974. Note spermatogenic tubules (SPT) composed of active crypts merging with and channeling spermatozoa into collecting tubules (CT) which occur along the dorsomedial (DM) tunica albuginea (Haematoxylin and eosin × 256).

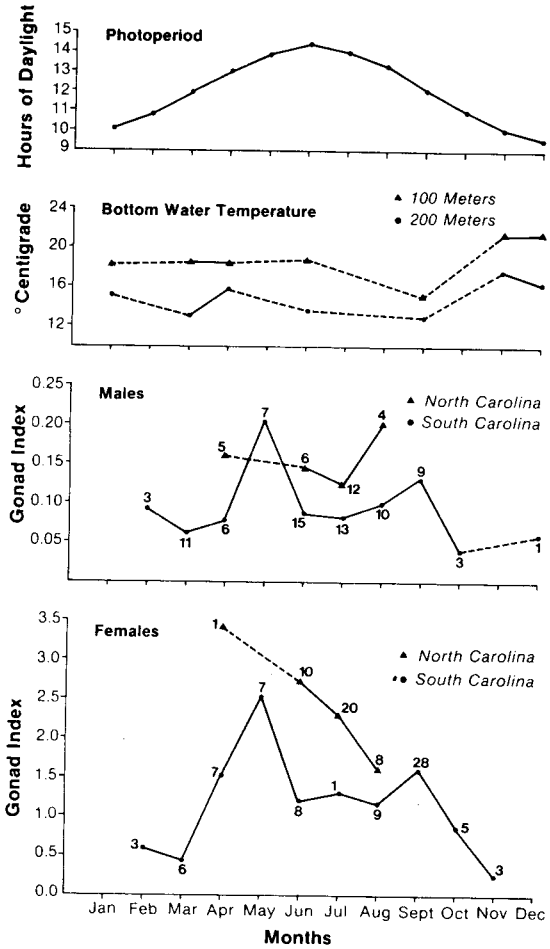

FIGURE 6.—Monthly mean gonad index values for male and female *Caulolatilus microps* from North Carolina and South Carolina, mean bottom temperatures off Beaufort, N.C. (Stefansson and Atkinson 1967), and photoperiod.

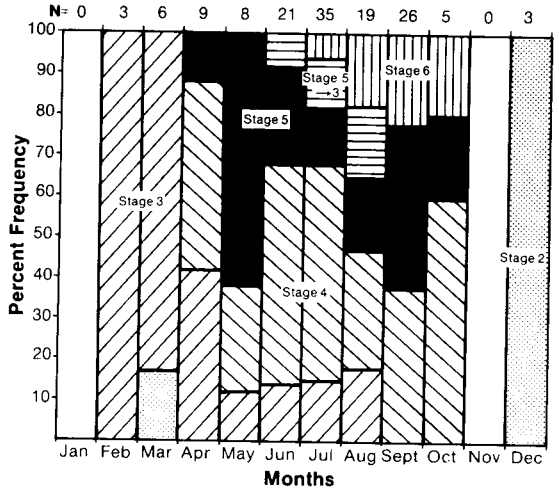

FIGURE 7.—Percent frequency histogram of gonad developmental stages observed each month for female *Caulolatilus microps* from North Carolina and South Carolina.

regression and early development. Ripe females were captured off South Carolina during April and July, which could indicate a more continuous or three-peaked spawning season. Monthly mean GSI as well as mean standard length were greater for females off South Carolina, but data are too limited to draw any further conclusions.

Analysis of ova development within individual ovaries suggested that blueline tilefish are multiple spawners (Fig. 8). Ovaries considered Resting characteristically contained primary oocytes and previtellogenic oocytes. Early-Developing ovaries showed a progression of early vitellogenic oocytes developing from the residual stock. Well-Developed ovaries in late April contained a mode of late vitellogenic oocytes cooccurring with previtellogenic and early vitellogenic oocytes (Fig. 9). Ripe females from May and June exhibited modes of previtellogenic oocytes, early vitellogenic oocytes, late vitellogenic oocytes, and mature eggs. This indicated continuous development from the residual stock of oocytes occurred when spawning was imminent. Early vitellogenic ova are predominant in Spent-Redeveloping ovaries and cooccur with residual mature, atretic mature, and late vitellogenic oocytes. Late vitellogenic oocytes were again the predominant oocytes in Well-Developed ovaries during September. There was also a decreased proportion of early vitellogenic oocytes in comparison with Well-Developed gonads from May.

Males accommodate the protracted season of oogenesis by maintaining a constant state of development during the spawning season. The two peaks in GSI of testes coincided with those observed for ovaries (Fig. 6). Testes contained some spermatozoa in all months sampled and observed histologically, while those from April through September generally contained large quantities of spermatozoa in the collecting tubules. However, we never captured any males with free-running milt.

Fecundity

We estimated the fecundity of blueline tilefish from three periods during their spawning season. Fecundity ranged from 210,000 ova (412 mm TL) to 3,220,000 ova (637 mm TL) for 18 fish captured from April to early June (Fig. 10). Fecundity was significantly correlated with both length and weight:

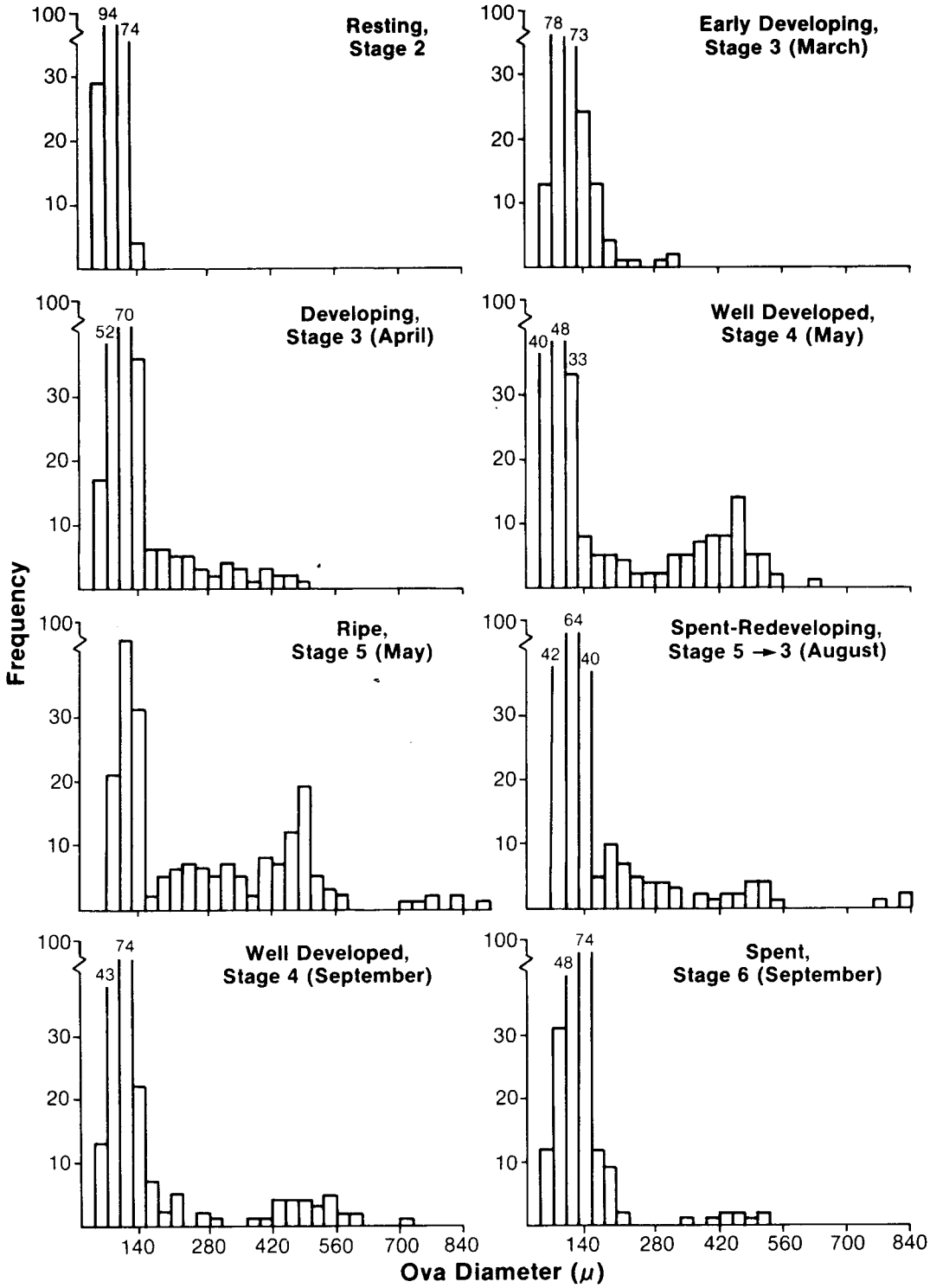

FIGURE 8.—Ova diameter frequency distributions for designated ovarian developmental stages for female *Caulolatilus microps* from North Carolina.

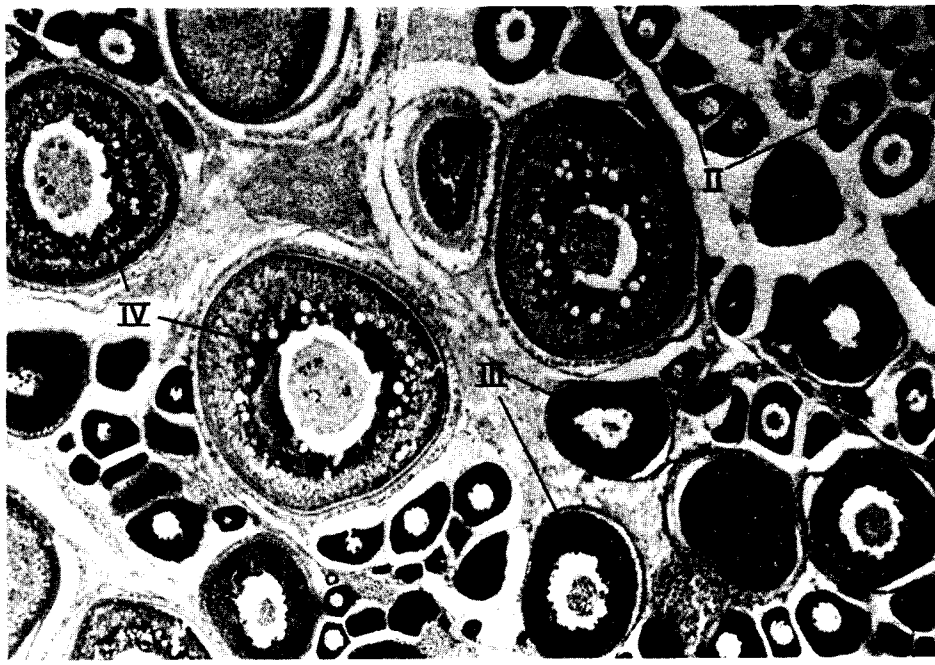

FIGURE 9.—Cross section of Well-Developed ovary from a 515 mm TL female *Caulolatilus microps* (21 April 1977) with lamellae composed of residual stock previtellogenic oocytes (II), early vitellogenic oocytes (III), and late vitellogenic oocytes (IV) (Haematoxylin and eosin × 63).

$$\ln \text{Fecundity} = 8.830 + 0.00986 \text{ Total length}$$
$$r^2 = 0.74, \text{ and}$$
$$\ln \text{Fecundity} = 0.016 + 1.832 \ln \text{Weight}$$
$$r^2 = 0.78.$$

Fecundity for 14 Ripe females captured in July basically agreed with the above fecundity relationship; the estimates ranged from 196,000 (436 mm TL) to 4,107,035 ova (736 mm TL). The estimated fecundity of 12 Well-Developed and Ripe females from September decreased approximately one-third to one-half. The production of vitellogenic ova appears greater during the late spring-early summer spawning peak than the early fall peak. However, insufficient data on the frequency of spawnings by individuals within age/size groups and the number of eggs released preclude further refinement of individual annual fecundity estimates.

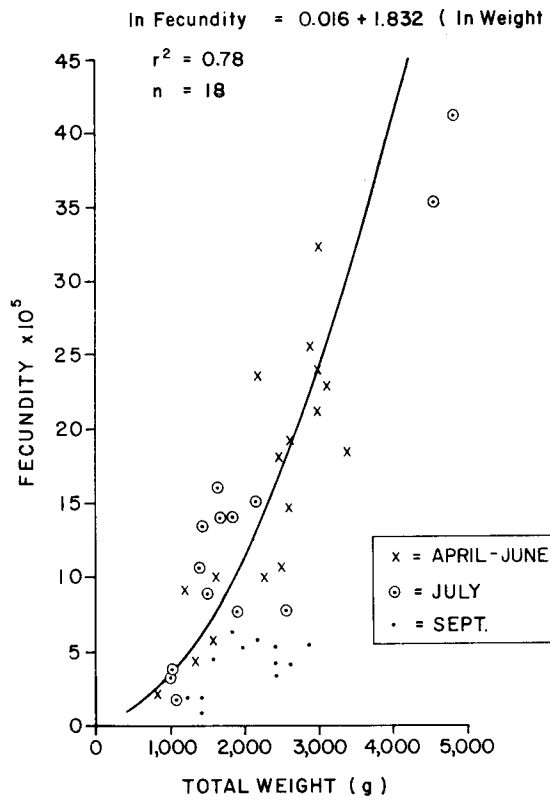

FIGURE 10.—Fecundity-weight relationship for *Caulolatilus microps* collected in April to June. Fecundity estimates are plotted for fish captured in July (South Carolina) and September (North Carolina).

Sexual Maturity

Maturity of females, defined as the size at which >50% of the individuals were gonadogenically active, occurred between 425 and 450 mm TL (Table 3) which is typically a 4- or 5-yr-old fish (Ross and Huntsman 1982). One of three age III females (387-421 mm TL), 50% of the age IV ($n = 8$; 427-506 mm TL), 73% of the age V ($n = 15$; 430-546 mm TL), and 100% of the age VI+ females were mature. The pattern of ovarian development corroborated the macroscopic maturity analysis. Relative gonad weight increased with total length after initial steep increases in relative gonad size between 400 and 500 mm TL. Mean GSI and maximum relative gonad weights were consistently greater for females captured off South Carolina than those captured off North Carolina, although the biological reason for this is unknown.

TABLE 3.—Percentage of sexually mature female and male *Caulolatilus microps* from North Carolina and South Carolina.

Total length	Females N	Females Percent mature	Males N	Males Percent mature
250-300	3	0		
301-325				
326-350	1	0		
351-375	2	0		
376-400	5	20.0	1	0
401-425	11	45.5	1	0
426-450	8	75.0	4	0
451-475	11	81.8	3	0
476-500	11	90.9	5	20.0
501-525	24	100.0	8	50.0
526-550	24	100.0	9	77.8
551-575	18	100.0	9	77.8
576-600	8	100.0	8	87.5
601-625	13	100.0	7	100.0
626-650	11	100.0	13	100.0
650+	4	100.0	41	100.0

Male *C. microps* show little gross testicular development under 500 mm TL (Table 3). Macroscopically, 50% were considered immature between 500 and 525 mm TL and 100% attained maturity above 600 mm TL. No age IV ($n = 4$; 436-453 mm TL) and only 12.5% of the age V males ($n = 8$; 485-574 mm TL) were considered mature, and a majority (62.5%) had not matured until age VI ($n = 8$; 520-556 mm TL). The initial and most pronounced increase in relative testis size occurred in males >500 mm off North Carolina and males >600 mm off South Carolina. Histological examination of testes from males 390-500 mm TL ($n = 11$) revealed spermatogenesis and collections of spermatozoa in fish macroscopically considered immature. These testes were very small (<0.08% body weight) and maroon in color. We could not determine whether this represented precocious development or functional maturity.

Sex Ratio and Sexual Transition

Males outnumbered females in the combined North Carolina and South Carolina collections (195 to 176), but this was not significantly different from a 1:1 ratio ($\chi^2 = 0.97$). However, sex ratios become skewed when size (Table 4) or age (Table 5) are considered. Females were more numerous between 300 and 500 mm TL, and in several cases there were significant deviations from 1:1. Between 500 and 600 mm TL

TABLE 4.—Frequency of male and female *Caulolatilus microps* from North and South Carolina within 25 and 100 mm TL intervals, with Chi-square values assuming a 1:1 sex ratio.

Length	Male	Female	Percent female/25 mm	χ^2	Percent female/100 mm	χ^2
101-200	3	1			25	1.0
201-300		1			100	
301-325						
326-350		1	100		88	5.4*
351-375		1	100			
376-400	1	6	86	3.57		
401-425	1	6	86	3.57		
426-450	7	12	63	1.32	67	9.89*
451-475	6	20	77	7.54*		
476-500	14	19	58	0.75		
501-525	20	23	53	0.21		
526-550	15	18	55	0.27	52	0.32
551-575	19	22	54	0.22		
576-600	18	16	47	0.12		
601-625	19	16	46	0.26		
626-650	16	8	33	2.67	30	16.9*
651-675	20	3	13	12.57*		
676-700	15	2	12	9.94*		
701-725	11	0	0			
726-750	5	1	17		9	15.6*
751-775	3	1	25			
776-800	2	0	0			

*$P \leq 0.05$.

TABLE 5.—Frequency of male and female *Caulolatilus microps* from North and South Carolina within age groups with Chi-square values assuming 1:1 sex ratio.

Age	Females	Males	χ^2
II	1		1.8
III	3	1	
IV	16	4	7.2*
V	26	15	2.95
VI	16	9	1.96
VII	11	7	0.89
VIII	11	16	0.93
IX	7	4	0.82
X	4	12	4.00*
XI	1	3	1.0
XII	0	6	6.0*
XIII	0	2	
XIV	0	2	3.57
XV	1	2	

*$P \leq 0.05$.

the sex ratio was essentially 1:1. In fish >600 mm TL, males became increasingly and significantly more abundant. Similarly, females outnumbered males in ages III through VII while males became predominant for ages X through XV.

Histological evidence from four juvenile blueline tilefish indicated prematurational sex reversal. The gonad from a 186 mm TL specimen was ovarian and composed of basophilic oogonia with some primary oocytes (Fig. 11). The remaining three specimens had gonads which exhibited progressive stages of sex reversal. The earliest stage (202 mm TL) was predominantly ovarian with an acidophilic germinal testicular mesothelium proliferating through the ovigerous lamellae from the dorsomedial connective tissue (Fig. 12). The proliferating mesothelium contained primary spermatogonia and would be the site of steroidogenesis, inducing atresia and the recycling of ovarian elements (Hoar 1969). Gonads of two specimens (178 and 184 mm TL) in advanced stages of sex reversal had differentiated into the basic testicular components with spermatogenic tubules present and spermatogenesis proceding (Figs. 13, 14). Both specimens revealed evidence of a previous ovarian stage in the form of atretic structures, residual oocytes, or proliferating testicular mesothelium along the peripheral epithelium. These specimens were all captured in March and were within the size range predicted for *C. microps* after one year of growth (Ross and Huntsman 1982). Residual oocytes were also observed in 8 of 41 developing testes from adult males (Fig. 15). These fish were 430-700 mm TL and had solid testes which exhibited no other remnant ovarian structures.

FIGURE 11.—Cross section of ovary from a juvenile 186 mm TL *Caulolatilus microps* collected 13 March 1961 with oogonia and primary oocytes (I) (Haematoxylin and eosin × 200).

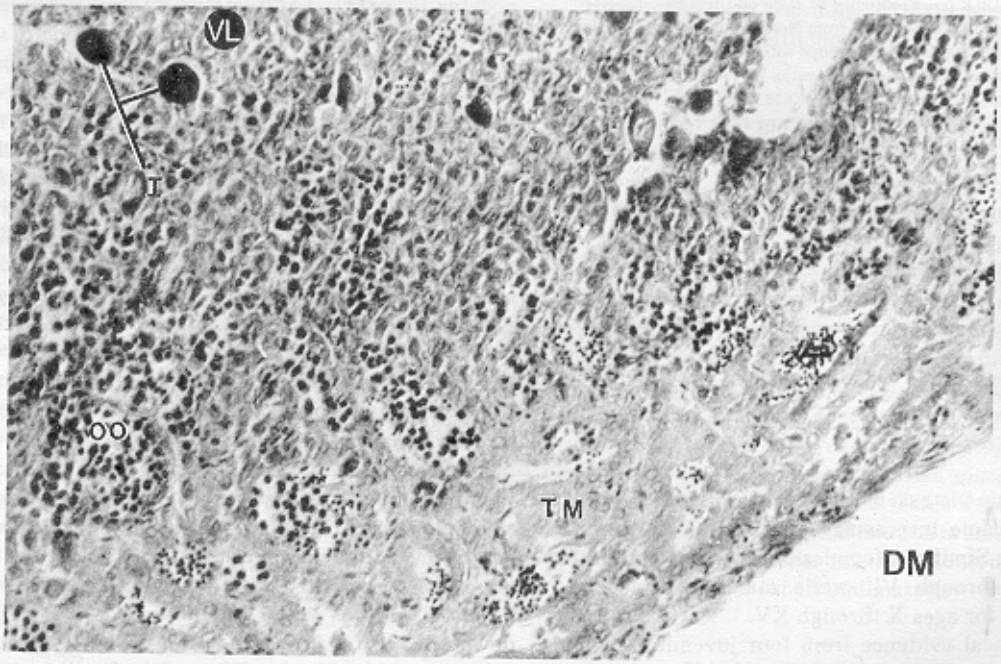

FIGURE 12.—Cross section of gonad from a juvenile 202 mm TL *Caulolatilus microps* collected 13 March 1961. Note occurrence of oogonia (OO) and primary oocytes (I) along ventrolateral region (VL) with proliferating testicular mesothelium (TM) originating from dorsomedial areas (DM) (Haematoxylin and eosin × 200).

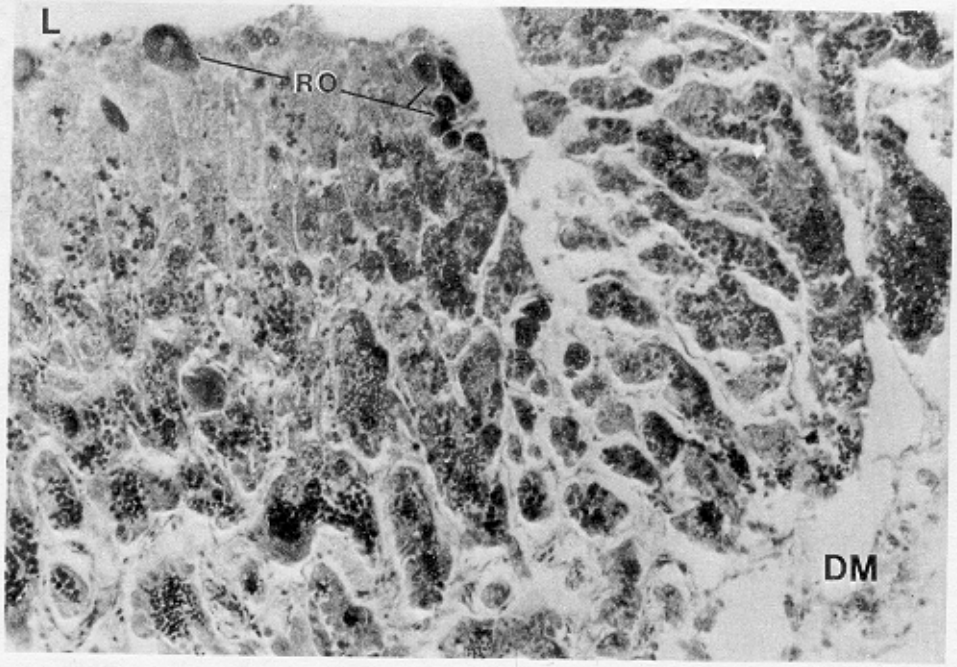

FIGURE 13.—Cross section of gonad from a juvenile 184 mm TL *Caulolatilus microps* collected 13 March 1961. Note spermatogenic tubules composing dorsomedial region (DM) and residual oocytes along lateral (L) gonadal margin (Haematoxylin and eosin × 200).

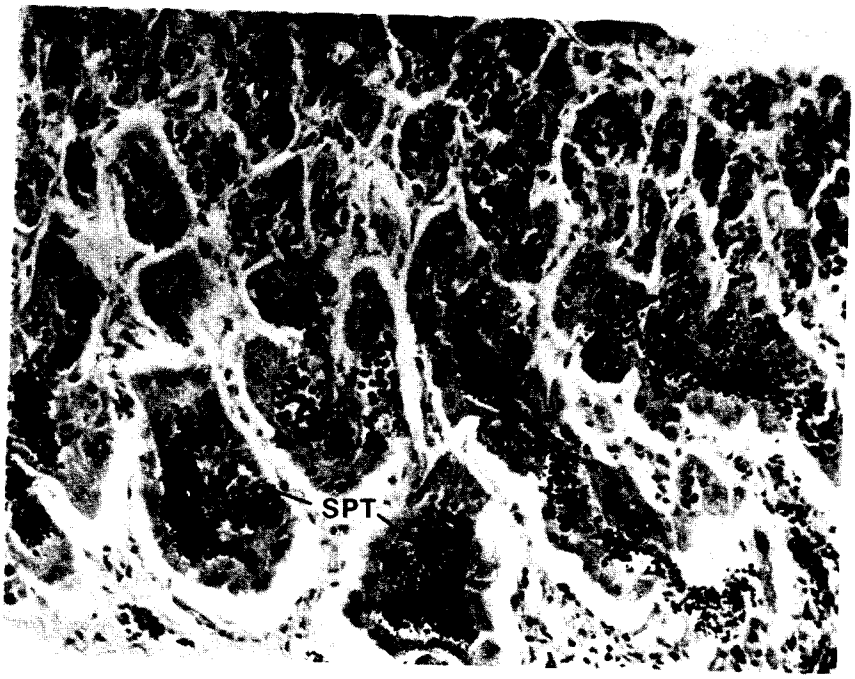

FIGURE 14.—Cross section of gonad from a juvenile 184 mm TL *Caulolatilus microps* collected 13 March 1961. Note in this closeup of previous gonad the well-defined spermatogenic tubules (SPT) (Haematoxylin and eosin × 400).

FIGURE 15.—Cross section of Well-Developed testes from a 562 mm TL *Caulolatilus microps* captured 22 April 1977. Note extensive collection of spermatozoa (SP) and occurrence of residual previtellogenic oocytes (RO) (Haematoxylin and eosin × 78).

DISCUSSION

The initiation of gonadogenesis in blueline tilefish during March and April and the termination in September-October coincide with the periods of rapidly increasing and decreasing photoperiods (Fig. 6). This is a more conservative environmental cue than temperature when considering the shelf edge habitat. Temperature fluctuations are not necessarily seasonal, but also subject to cold-water intrusions from outer continental shelf bottom waters and meanderings of the axis of the Gulf Stream (Stefansson and Atkinson 1967). The initiation of gonadal development has also been correlated with photoperiod for the cooccurring red porgy, *Pagrus pagrus*, (Manooch 1976). The protracted spawning of vermilion snapper, *Rhomboplites aurorubens*, was correlated with both photoperiod and water temperature (Grimes and Huntsman 1980); however, its occurrence over the continental shelf increases its susceptibility to seasonal temperature variation.

Blueline tilefish ovaries seasonally undergo a progressive maturation of residual stock oocytes to vitellogenic state with several modes generated and no sharp distinctions between residual and maturing eggs. The multimodal size distribution of oocytes observed is characteristic of fishes that spawn several times during a protracted spawning season (Clark 1934; Warner 1975a; Grimes and Huntsman 1980). Off North Carolina it appears that most *C. microps* spawn during May-June and September-October. The capture of large females (>600 mm TL) that were Ripe in July and August might indicate more frequent spawning by larger fish. The generally larger females captured off South Carolina might spawn earlier and more frequently than those off North Carolina, although data supporting this conclusion are incomplete. The continuous developmental pattern of male testes would certainly accommodate protracted spawning by females.

If local spawning is directed toward the maintenance of regional populations (Marshall 1966), the production of several batches of eggs during a protracted spawning season should improve chances of concurrence with favorable environmental conditions. Of particular relevance to *C. microps* spawning are the influence and extent of transport of eggs and larvae by the Florida Current (Gulf Stream). The ridge and trough bottom irregularity off South Carolina known as the Charleston Bump causes a seasonal deflection of the Gulf Stream and resulting inshore southwest setting eddy currents occurring as far north as Cape Hatteras (Brooks and Bane 1978). These are effective around the 50-100 fathom curves and could be an important means of regional retention of eggs and larvae produced by *C. microps* and other shelf edge inhabitants.

Whether *C. microps* are strictly prematurationally or also functionally protogynous cannot as yet be confirmed. Winter (between spawning periods) collections are needed to determine whether transitional adults occur. The skewed sex ratios with size and age could indicate that sex reversal occurs over an extended range of ages rather than just prematurationally. However, skewed sex ratios with size could be attributable to differential growth rates, which have been noted for *C. microps* (Ross and Huntsman 1982) as well as *L. chameleonticeps* (Turner et al.[7]) and other tilefishes (Dooley 1978). Skewed sex ratios with age could result simply by <50% of the juvenile females changing sex to males. Furthermore, functional protogyny is questionable since 1) all males possessed solid testes, whereas secondary males generally retained remnants of the hollow ovarian lumen (Smith and Young 1966; Warner 1975a) and 2) the existence of 400-500 mm males would have entailed their sex reversal prior to functioning as reproductive females.

Prematurational sex reversal, evidenced by histological examination of juvenile gonads, accounts for the presence of oocytes in developing testes. The development of remnant ovarian gonocytes to previtellogenic oocytes in a testis could result from the activation of estrogens, the presence of which is implicit had there been a juvenile female stage (Bruslé 1969; Bruslé and Bruslé 1975). The males with residual oocytes were captured in the spring, the period of maximum hormonal induction for initiating gonadogenic activity (Hoar 1969). The residual oocytes were previtellogenic oocytes which 1) are reported to be the most resistant oocytes to resorption and atresia (Bruslé and Bruslé 1975) and 2) were observed in medial connective tissue or in collecting tubules and not interspersed within active spermatogenic tissue.

The occurrence of prematurational sex reversal in *C. microps* should indicate protogyny elsewhere in its genus or family. This is possible though not yet confirmed for several related species. Atlantic goldface tilefish, *C. chrysops*, captured off North Carolina and in the Gulf of Mexico ($n = 20$) include 7 females 385-

[7]Turner, S. C., C. B. Grimes, and K. W. Able. In prep. Age, growth mortality and age/size structure of the fisheries for tilefish, *Lopholatilus chameleonticeps*, in mid-Atlantic and southern New England waters. Department of Environmental Resources, Rutgers University, P.O. Box 231, New Brunswick, NJ 08903.

503 mm TL and 13 males 503-562 mm TL (Ross unpubl. data). The sex ratio for anchor tilefish, *C. intermedius*, off Texas is 66 females:5 males between 100 and 270 mm TL, and 0 females:8 males >270 mm TL (Ross, Pavela, and Chittenden unpubl. data). Dooley (1978) reported anomalous sex ratios for *L. chameleonticeps*, *B. wardi*, and *B. serratus*. Clark and Ben-Tuvia (1973) reported pairs of *Malacanthus hoedtii* outside burrows including a large male and a smaller female. Prematurational sex reversal is also suspected of the tilefish, *L. chameleonticeps*, based on juvenile gonadal histology and adult sex ratio data (Grimes footnote 4).

Prematurational sex reversal in *C. microps* is likely a regression from monandric protogyny to functional gonochorism. The size-advantage model, which attributes protogyny to cases where an individual reproduces most efficiently as a female when young and a male when it gets older (Ghiselin 1969) is generally applicable when such things as inexperience, male dominance, mate selection, or territoriality lead to a differential in male reproductive success at older ages (Warner 1975b). Caulolatilids presumably evolved in the Caribbean and are often associated with reef-type habitat (Dooley 1978) where protogyny is widespread (Choat and Robertson 1975; Smith 1975; Warner 1975a, b). A radiation of *C. microps* (or ancestor) in the evolutionary past from a reef-type environment to more extensive outer continental shelf and upper slope habitats may have reduced the selection pressure favoring protogyny. The increase in utilizable habitat and more continuous distribution would allow more frequent opportunities for smaller males to engage in spawning, hence favoring sex reversal at an earlier age and ultimately tending toward secondary gonochorism.

ACKNOWLEDGMENTS

We wish to thank Gene Huntsman and the staff at the Southeast Fisheries Center Beaufort Laboratory, National Marine Fisheries Service (NMFS), Beaufort, N.C., for allowing access to their facilities and data, and particularly Robert Dixon, Charles Manooch, Pete Parker, Doug Willis (NMFS), Churchill Grimes (Rutgers University), and Robert Matheson (Duke University) for their assistance with field collections and enlightening discussions. We also thank the late Patricia Berry (Virginia Institute of Marine Science (VIMS)) for histological preparations, Ken Thornberry and Bill Jenkins (VIMS) for photographic assistance, and Joe Scott (College of William and Mary) for use of photomicroscopic equipment. Robert Karl Johnson (Field Museum of Natural History) and Frank Schwartz (Institute of Marine Science, University of North Carolina) kindly provided juvenile specimens. Finally Gene Huntsman, George Sedberry, and John Olney contributed much in their review of this and earlier versions of the manuscript.

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