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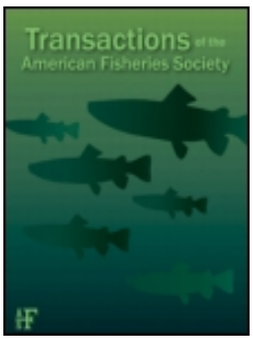

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Age, Growth, and Reproductive Biology of Blueline Tilefish along the Southeastern Coast of the United States, 1982–1999

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Abstract.—The blueline tilefish *Caulolatilus microps* is a long-lived, slow-growing deepwater demersal species patchily distributed along the outer continental shelf of North America from Cape Lookout, North Carolina, to Campeche Bank, Mexico. Commercial landings of blueline tilefish for the southeastern United States peaked in 1983 at 530 metric tons (mt), fell to 31 mt by 1985, and exceeded 100 mt only once between 1986 and 1999. We collected blueline tilefish off North Carolina and South Carolina (approximately 32°N to 33°N) during 1982–1987 and 1996–1999 with fishery-independent gear, and whole tilefish were sampled from commercial catches during 1996–1998. Specimens were assigned an age from counts of increments on a transverse section of the left sagitta. Sex and reproductive state of all individuals were determined from histological sections of the gonad. The mean size of males was significantly larger than that of females (583 versus 537 mm total length), and the mean lengths of males and females declined significantly between the periods 1982–1987 and 1996–1999. Mean ages throughout the study were 11.2 years for males and 15.2 years for females. The mean ages of both males and females decreased significantly between the periods 1982–1987 and 1996–1999 (from 15 to 8.6 years for males and from 17.7 to 11.2 years for females). Males were significantly larger than females for most ages sampled during 1982–1987 (ages 6, 8–27, 31); however, during 1996–1999 males were significantly larger than females only among the younger ages (ages 5–14). The overall male : female sex ratio for blueline tilefish during 1982–1987 was 1:2.12, which was significantly different from 1:1. However, the sex ratio during 1996–1999 was 1:0.85, which was not significantly different from 1:1. Increased fishing mortality during 1980–1983 may have cropped off the largest specimens (predominantly males, i.e., the fishing-up effect), which may explain the predominance of females in the 1980s. The shift to a predominance of males in the 1990s does not suggest a decrease in fishing mortality because the mean size of fish sampled decreased significantly between the 1980s and 1990s. Spawning occurred during the evening from February through October in females, and the gonadosomatic index reached a peak in May. Spawning males were collected during January and March through October. Monthly estimates of total fecundity and the lack of a size gap between stage-3 yolked oocytes and earlier stages of oocytes indicate that annual fecundity is indeterminate. With an extended spawning season of approximately 240 d, a female could spawn 120 times in a season. Multiplying the number of spawning events by batch fecundity estimates for specimens 366–629 mm total length produced estimates of potential annual fecundity that ranged from 1,972,300 to 11,397,700 oocytes. The loss of larger and older blueline tilefish from the population and the significant relationship between female size and batch fecundity suggest that the fecundity of the population is currently much less now than it was during 1970s and 1980s.

The blueline tilefish *Caulolatilus microps* is a long-lived, slow-growing deepwater demersal species patchily distributed along the outer continental shelf of North America from Cape Lookout, North Carolina, to Campeche Bank, Mexico (Dooley 1978). Blueline tilefish appear to move little as adults and are found along the outer continental shelf, shelf break, and upper slope on irregular bottom. Usual habitats are ledges or crevices and around boulders or rubble piles at depths of 48–236 m, where temperatures are 15–23°C (Struhsaker 1969; Ross 1978; Ross and Huntsman 1982; Parker and Mays 1998). Blueline tilefish have been observed hovering near or entering burrows under rocks (Parker and Ross 1986), a characteristic associated with many malacanthids (Able et al. 1982; Able et al. 1987; Baird and Baird 1992).

Commercial and recreational fisheries have harvested blueline tilefish, although only the commercial fishery has reported significant catches since 1985 (Parker and Mays 1998). Blueline tilefish share their habitat with many other deepwater species, including snowy grouper *Epinephelus niveatus*, red porgy *Pagrus pagrus*, vermilion snapper *Rhomboplites aurorubens*, blackbelly rosefish

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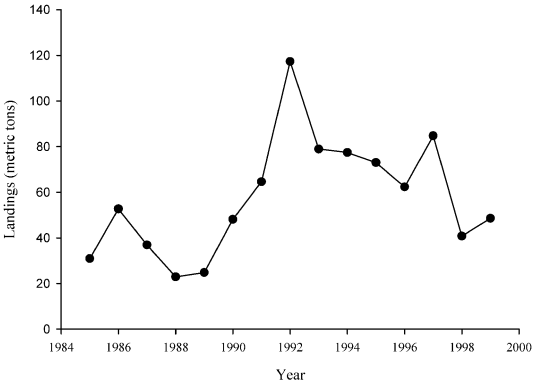


FIGURE 1.—Commercial landings of blueline tilefish for the U.S. southeast Atlantic coast, 1985–1999.

Helicolenus dactylopterus, Warsaw grouper *E. nigritus*, and yellowedge grouper *E. flavolimbatus*. Although recreational and commercial fisheries have extensively exploited this deepwater community, these fisheries may have been targeting species other than blueline tilefish (Ross and Huntsman 1982; Parker and Mays 1998). Commercial landings for blueline tilefish for North Carolina, South Carolina, Georgia, and the east coast of Florida peaked in 1983 at 530 metric tons (mt) and fell to 31 mt by 1985; landings increased to 117 mt in 1992 but were less than 50 mt by 1999 (Parker and Mays 1998; National Marine Fisheries Service, Fish Statistics and Economic Division, personal communication; Figure 1). Landings from the Carolinas have predominated, averaging 87% of the annual total since 1985.

Recent studies have attributed changes in life history patterns of deepwater reef fishes to increases in fishing effort over the last 3 decades (Buxton 1993; Harris and McGovern 1997; Harris et al. 2001; Wyanski et al. 2000). The purpose of this study was to assess the age structure, growth, sex ratio, size and age at maturity, spawning season, spawning frequency, and fecundity of the blueline tilefish population off North Carolina and South Carolina during two periods (1982–1987 and 1996–1999) to determine any changes in the life history and to estimate annual fecundity.

Methods

Sampling

Blueline tilefish were collected during 1982–1987 and 1996–1999 with fishery-independent gear by the Marine Resources Monitoring, Assessment, and Prediction (MARMAP) program of the South Carolina Department of Natural Resources between 32°N and 33°N. In addition, whole tilefish were sampled from commercial catches off North Carolina and South Carolina (approximately 32°N to 33°N) during 1996–1998. Samples were collected at the fish house, and the entire catch of the vessel was sampled.

Blueline tilefish habitat was identified with electric snapper reels, bottom longline gear, and bottom grab samples during research cruises conducted by MARMAP in 1980–1981. During 1982–1987, MARMAP used electric snapper reels (1982–1983), Kali poles (Russell et al. 1988), and longline gear to sample blueline tilefish. Twenty Kali poles (5 hooks/pole; number 6 and 7 circle hook sizes) were set over a bottom of rocky outcrops and soaked for 90 min. Longlines of 100 tuna circle hooks (numbers 5, 7, and 9) tied to gangions and placed at 3.7-m intervals on 366 m of 6.4-mm solid braid dacron groundline were set over mud and sand bottom where temperatures exceeded 9°C. Each 100-hook set was buoyed to the surface with polypropylene line.

During 1997–1999, longlines of 100 tuna circle hooks (numbers 5 and 7) tied to gangions placed at 12 m intervals on 1,219 m of galvanized cable groundline buoyed to the surface were used. Each 100-hook set was soaked for 90 min. A short longline, consisting of a 30-m groundline with 20 gangions (numbers 5 and 7 tuna circle hooks) spaced at 1.5-m intervals and 457 m of polypropylene buoyed to surface, was used during 1996–1999 to sample areas of rough bottom and rocky outcrops at depths exceeding 80 m. Each short longline was also soaked for 90 min. Hooks of Kali poles and all longlines were baited with squid. Some blueline tilefish were captured in Florida traps and Chevron traps (see Harris and McGovern 1997 for methodology).

Total and fork lengths (TL and FL; mm) and total body weight (TBW; g) were measured for most specimens. Sagittae were removed (only the left sagitta from commercial samples), fresh gonad weight was measured (± 1 g) in some specimens, and a posterior section of each gonad was preserved in 11% formalin buffered with marble chips for histological analysis. Only total lengths were recorded for blueline tilefish caught during 1982–1983, and otoliths were extracted and gonad samples taken from a random subsample of the catch. Samples of ovarian tissue for fecundity analysis were collected during 1997–1999. To reduce the amount of formalin used, ovaries were not preserved whole. For each specimen, a longitudinal section of tissue from one ovarian lobe, repre-

senting the anterior through posterior portions, was preserved in 10% formalin.

Age and growth

Sagittae were stored dry in coin envelopes; the left sagitta was used in age determination. Sagittae were marked through the core along the dorsoventral axis and embedded in epoxy resin. A transverse section (0.7–1.0 mm thick) was made through the core with a Buehler Isomet low-speed saw. Sections were mounted on glass slides with Accumount mounting medium and viewed under a dissecting microscope at 20–70× magnification using transmitted light. Increments (one translucent and one opaque zone) were counted independently by two readers who lacked knowledge of specimen length or date of capture. Frequently, we observed a group of increments with very narrow translucent and opaque zones, separated from the next group by a larger translucent zone; this was particularly prevalent in the first few increments of older fish. Each group of increments was counted as a single increment. If counts differed, otoliths were reread by both readers simultaneously and discarded from analyses if disagreements persisted.

Mean lengths, ages, and observed lengths at age within each collection period (1982–1987 and 1996–1999) were compared between sexes, gear type, and data source using Student's *t*-test and analysis of variance (ANOVA). Based on the results of these tests, data from all sources were then pooled for each period, and the same comparisons were made between periods. Von Bertalanffy growth curves were fit to unweighted mean observed lengths at age for males, females, and both sexes of blueline tilefish for each period because these were the only data for which realistic fits were obtained for both sexes and periods.

Reproduction

Reproductive tissues were vacuum infiltrated and blocked in paraffin, and then sectioned (7-μm thickness) on a rotary microtome. Three sections from each sample were placed on a glass slide, stained with double-strength Gill's hematoxylin, and counter-stained with eosin Y. Sections were viewed under a compound microscope at 40–400× magnification, and two readers independently assigned sex and reproductive state (Table 1) via criteria modified from Schmidt et al. (1993) and Harris et al. (2001). Date of capture, specimen length, and specimen age were unknown to the readers. If the assessments differed, the slide was viewed simultaneously by both readers and omitted from analyses if disagreement persisted. Specimens with developing, ripe, spent, or resting gonads were considered sexually mature.

Spawning season for female tilefish was estimated based on the presence of hydrated oocytes and postovulatory follicles (POFs). Because the rate of POF degradation is a function of water temperature, POFs were assigned approximate ages according to the criteria developed by Hunter and Goldberg (1980) for northern anchovy *Engraulis mordax*. Blueline tilefish spawn in slope waters with summer bottom temperatures that average 13.7°C (range = 8.5–20.8°C; Mathews and Pashuk 1986), similar to the temperatures (13–19°C) at which northern anchovy spawn (Hunter and Macewicz 1985). A female gonadosomatic index (GSI; Nikolsky 1963) was calculated to quantify the reproductive cycle: GSI = (ovary weight/TBW)(100). Sex ratios (male: female) were examined for each period, size-class, and age-class via a chi-square goodness-of-fit test to determine if the ratios differed from the expected 1:1. A comparison was made only if the expected frequency was greater than 5.

Fecundity

We used four definitions of fecundity that followed Hunter et al. (1992): (1) ''total fecundity'' is standing stock of stage-3 yolked oocytes, (2) ''batch fecundity'' is number of hydrated oocytes released in one spawning event, (3) ''determinate fecundity'' is when potential annual fecundity (i.e., in our study, the number of hydrated oocytes matured per year, uncorrected for atretic losses) is fixed before the spawning season, (4) ''indeterminate fecundity'' is when potential annual fecundity is not fixed before the spawning season.

Three stages of yolked (vitellogenic) oocytes—migratory nucleus (MN) oocytes, hydrated oocytes, and atretic oocytes (Hunter et al. 1992)—were identified in samples from formalin-preserved gonads. Oocyte size distributions from eight specimens were used to elucidate temporal patterns in oocyte development. The average radius of each oocyte in a subsample of 300–700 whole oocytes was measured with Global Lab Image software and then doubled for diameter.

Densities of hydrated and MN oocytes combined from three locations (anterior, middle, and posterior) in the left ovaries of nine fish without evidence of ovulation were compared to determine whether oocytes were randomly distributed. Two 75-mg samples of ovarian tissue, each consisting

TABLE 1.—Histological criteria used to assess reproductive state in male and female blueline tilefish, as modified from Schmidt et al. (1993) and Harris et al. (2001).

Reproductive state	Male	Female
Immature	Smaller transverse section than in resting male; spermatogonia and little or no spermatocyte development.	Oogonia and primary growth oocytes (<60 μm in diameter) only; no evidence of atresia. Compared with resting females, transverse section of ovary is smaller; lamellae lack muscle and connective tissue bundles and are not as elongate, oogonia abundant along margin of lamellae, and ovarian wall is thinner.
Developing	Development of cysts containing primary and secondary spermatocytes through some accumulation of spermatozoa in lobular lumina and ducts.	See below.
Ripe	Predominance of spermatozoa in lobules and ducts; little or no occurrence of spermatogenesis.	Completion of yolk coalescence and hydration in most advanced oocytes; zona radiata becomes thinner.
Spent	No spermatogenesis; some residual spermatozoa in shrunken lobules and ducts.	More than 50% of vitellogenic oocytes undergoing alpha or beta stage of atresia.
Resting	Larger transverse section compared with immature male; little or no spermatocyte development; empty lobules and ducts; some recrudescence (spermatogonia through primary spermatocytes) possible at end of stage.	Oogonia and primary growth oocytes (>60 μm in diameter) only and traces of atresia possible. Compared with immature females, transverse section of ovary is larger, lamellae have muscle and connective tissue bundles, lamellae are more elongate and convoluted, oogonia less abundant along margin of lamellae, and ovarian wall is thicker and exhibits varying degrees of expansion because of previous spawning.
Developing, recent spawn		Vitellogenic oocytes predominant and postovulatory follicles (POFs) <24 hours old (Hunter and Goldberg 1980).
Developing, recent spawn		Vitellogenic oocytes predominant and POFs ≥24 but <48 hours old (Hunter and Goldberg 1980).
Developing, recent spawn		Vitellogenic oocytes predominant and POFs ≥48 hours old.
Early developing, cortical alveoli		Most advanced oocytes in cortical–alveoli stage.
Developing, vitellogenesis		Most advanced oocytes in yolk granule or yolk globule stage.
Final oocyte maturation		Most advanced oocytes in migratory nucleus stage; partial coalescence of yolk globules possible.

of 50–150 MN oocytes and hydrated oocytes, were taken per specimen. The effects of location and individual fish on density were assessed with a two-factor ANOVA.

We used the gravimetric method to estimate total fecundity and batch fecundity. To estimate total fecundity, two 25-mg samples were taken from random locations in 39 ovaries, of which 34 were in a developing stage (Table 1); in each sample all stage-3 yolked oocytes were counted. In five specimens, vitellogenic oocytes and a partial batch of hydrated oocytes were present, the results of ongoing ovulation. Total fecundity was calculated as the preserved ovary weight (g) times oocyte density (i.e., the number of stage-3 oocytes per sample weight [g]; Hunter et al. 1992)

Because we did not preserve whole ovaries, fresh weight (FW; g) of ovaries was converted to preserved weight (PW; g) with regression equations for reproductive states in scamp *Mycteroperca phenax*: for developing ovaries (FW = 17–59 g, $N = 10$, adjusted $r^2 = 0.992$)

$$PW = FW(0.966) - 1.860,$$

and for ripe ovaries (FW = 42–309 g, $N = 19$, adjusted $r^2 = 0.994$)

$$PW = FW(0.897) + 1.148.$$

The relationship between total fecundity and total length was described for three seasonal periods (April, July–August, and September–October), and the effect of time interval on total fecundity was examined using least-squares linear regression and analysis of covariance (ANCOVA).

Blueline tilefish exhibited evidence of indeterminate fecundity; therefore, batch fecundity and spawning frequency were estimated to calculate

TABLE 2.—Sample size by gear and period for blueline tilefish collected off North Carolina and South Carolina.

Gear	1982–1987		1996–1999	
	Fishery independent	Fishery dependent	Fishery independent	Fishery dependent
Hook and line	39	283	0	4
Trap[a]	18	0	53	0
Kali pole	391	0	0	0
Longline[b]	87	0	16	558
Trawl	0	2	0	0
Total	535	285	69	562

[a] Chevron, Florida, and experimental traps.
[b] Horizontal longline and short longline.

potential annual fecundity. We used the hydrated oocyte method of Hunter et al. (1985) to estimate batch fecundity, but we used of a larger sample weight and immersed samples in a 1–5% formalin solution to enumerate and measure oocytes. Two 35–75-mg samples were taken from random locations in the ovaries of 39 fishery-dependent specimens in the final oocyte maturation or ripe states collected during 1997–1998. The MN and hydrated oocytes were counted; both stages were present in 10 of 39 specimens.

We obtained three estimates of spawning frequency based on histological criteria (presence of MN or hydrated oocytes, <24-hour-old POFs, and 24 to <48-hour-old POFs) that indicate imminent or recent spawning. Our methods of estimating spawning frequency followed those of Hunter and Goldberg (1980). All females in fishery-dependent samples from 1996 to 1998 that were reproductively active (vitellogenic oocytes present, developing and ripe reproductive states) were examined for evidence of spawning. Two or three of the spawning criteria were present in the majority of specimens with histological evidence of spawning. Spawning frequency among reproductively active females was based on the proportions for each criterion. The three estimates of spawning frequency were averaged (see Fitzhugh et al. 1993) and the average was multiplied by the number of days in the spawning season to determine the number of spawning events in that season (see Cuellar et al. 1996). To calculate potential annual fecundity, batch fecundity was multiplied by the number of spawning events. All statistical tests were conducted with SAS (SAS Institute 1989), and the results were considered significant at $\alpha < 0.05$

Results

Sampling

A total of 1,451 blueline tilefish (820 in 1982–1987; 631 in 1996–1999) were sampled; most (65%) specimens taken during 1982–1987 were from fishery-independent sampling, whereas during 1996–1999 most (89%) were from fishery-dependent sampling (Table 2). There were no significant differences in the mean age, mean length, or length at age of males or females sampled using different gear types or from fishery-dependent and fishery-independent sources when compared within a period. Data were thereafter pooled by period for all analyses. Length frequencies of male and female blueline tilefish were significantly different in the two periods (Kolmogorov–Smirnov test: for males, D = 0.599 and $N = 517$, for females, D = 0.436 and $N = 704$, $P < 0.001$) and shifted to smaller fish for both sexes in 1996–1999 (Figure 2). The mean total length of fish sampled during 1982–1987 (591 mm, SD 79, range 334–784, $N = 816$) decreased significantly during 1996–1999 (524 mm, SD 72, range 333–734, $N = 628$; $t = 16.68$, df = 1,442, $P < 0.0001$). The mean total length of males (583 mm) sampled during the study was significantly larger than that of females (537 mm; $P < 0.0001$, $t = 9.65$, df = 911, unequal variances). From 1982–1987 to 1996–1999 the mean total lengths also decreased significantly ($P < 0.001$) for males (from 653 to 538 mm; $t = 16.76$, df = 369, unequal variances) and for females (from 559 to 500 mm; $t = 11.76$, df = 476, unequal variances).

Age and Growth

Only 923 of the 1,451 blueline tilefish sampled were successfully aged, and initial agreement between readers was only 24%, although there was 64% agreement within 2 years. Age frequencies of males and females differed significantly ($P < 0.001$) between the two periods sampled (Kolmogorov–Smirnov test: for males, D = 0.467, $N = 335$); for females, D = 0.424, $N = 464$), for both sexes shifting to younger fish in 1996–1999 (Figure 3). Age decreased significantly between

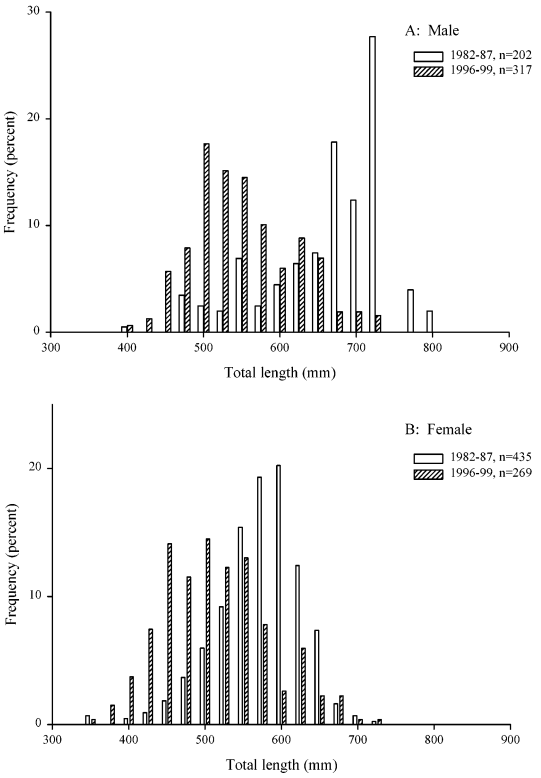


FIGURE 2.—Length frequency of **(A)** male and **(B)** female blueline tilefish sampled off North Carolina and South Carolina from fishery-dependent and fishery-independent sources during 1982–1987 and 1996–1999 (*n* = number of specimens).

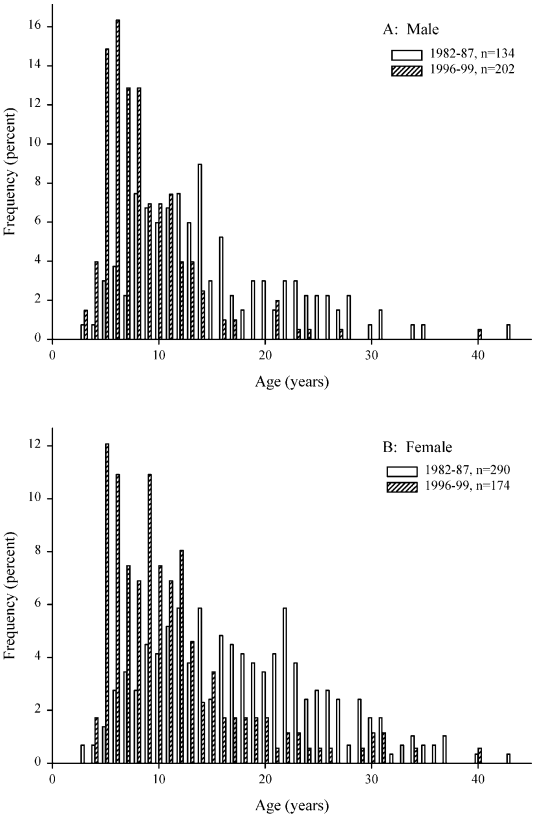


FIGURE 3.—Age frequency of **(A)** male and **(B)** female blueline tilefish sampled off North Carolina and South Carolina from fishery-dependent and fishery independent sources during 1982–1987 and 1996–1999 (*n* = number of specimens).

periods 1982–1987 (mean 16.9 years, SD 7.9, range 3–43; $N = 519$) and 1996–1999 (mean 10 years, SD 5.8, range 3–40; $N = 404$; $t = 16.68$, df = 917, unequal variances, $P < 0.0001$). Mean total length of males was always greater than that of females; however, mean age of males (11.2 years) was younger than that of females (15.2 years), and each sex showed significant decreases from 1982–1987 to 1996–1999 (from 15 to 8.6 years for males, $t = 8.97$, df = 199, unequal variances; from 17.7 to 11.2 years for females, $t = 9.53$, df = 421, unequal variances; $P < 0.001$). Males were significantly larger than females for most ages sampled during 1982–1987 (ages 6, 8–27, 31; $P < 0.01$); however, during 1996–1999 males were significantly larger than females for only younger ages (ages 5–14; $P < 0.01$; Figure 4). This change was the result of the decrease in length at age of male blueline fish from 1982–1987 to 1996–1999, which was significant for ages 8, 9, 13, 14 and 16 ($P < 0.01$), whereas the lengths at age of females between the two sampling periods did not differ significantly. However, the power of some of these tests was low due to the relatively small sample size of fish in some age-classes.

Von Bertalanffy growth parameters (Table 3) showed slight differences between sexes and periods, L_{inf} decreasing for males between periods and increasing for females. Values for *K* were lower for both sexes and sexes combined for 1996–1999, suggesting growth may have slowed in this period. The value of these results is questionable, however, as unweighted mean lengths were used to fit these curves.

Reproduction

The overall male: female sex ratio for blueline tilefish sampled during 1982–1987, at 1:2.12, differed significantly from 1:1 (Table 4). Females 650 mm TL or shorter were more abundant than males,

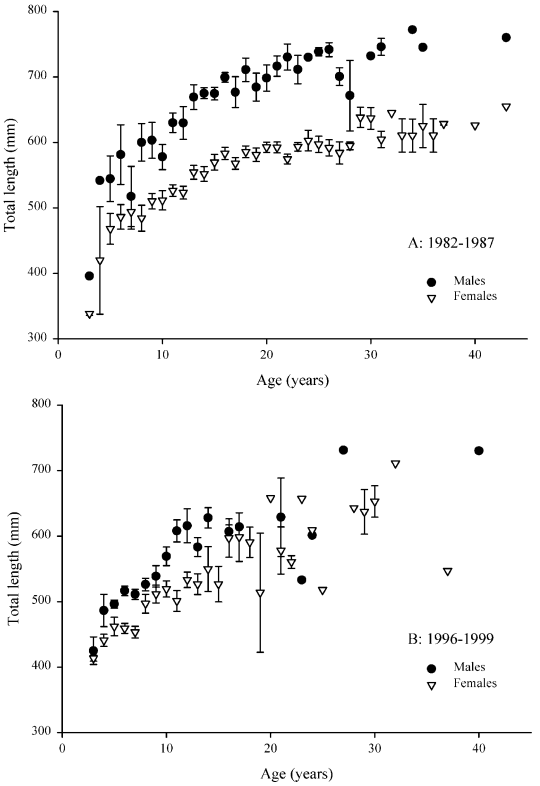


FIGURE 4.—Mean length at age for male and female blueline tilefish sampled off North Carolina and South Carolina during **(A)** 1982–1987 and **(B)** 1996–1999. Error bars represent one standard error.

and the sex ratio differed significantly from 1:1 for fish 451–650 mm TL. Males greater than 650 mm TL were more abundant than females, and the sex ratio of fish 651–750 mm differed significantly from 1:1.

The overall male: female sex ratio for blueline tilefish sampled during 1996–1999, at 1:0.85, did not differ significantly from 1:1 (Table 4). Females 450 mm TL or shorter were more abundant than males, and the sex ratio differed significantly from 1:1 for fish 351–450 mm TL. Males greater than 450 mm TL were more abundant than females, and the sex ratio of fish 501–650 mm differed significantly from 1:1.

The sex ratio at age data indicate that, for almost all age-classes, male abundance increased in the later period compared with females (Table 5). During 1982–1987, age-specific sex ratios favored males for only age-8 fish, whereas in 1996–1999, males predominated all age-classes except ages 9, 12, and 15 and older. The sex ratio of blueline tilefish age 15 and older changed very little between 1982–1987 and 1996–1999, although the number of individuals in this age-group decreased considerably. Chi-square analyses were not attempted for age-based sex ratios because of the large number of cells with an expected frequency of less than 5.

Only four immature blueline tilefish were sampled (three females, one male). Correct assignment of reproductive tissue to the immature and resting categories is indicated by the near or complete overlap in the left tail of length histograms for specimens that were definitely mature (i.e., developing, ripe, and spent) and specimens that were resting and by the minimal overlap in the histograms for immature and resting specimens. Immature females were age 3 (336 mm TL) and age 6 (333 and 387 mm), and the smallest mature female was age 4 (338 mm). An age could not be assigned to the only immature male, and the smallest mature male was age 3 (393 mm TL). Fifty percent of females were mature at 326–350 mm TL ($N = 4$) and 100% at 351–375 mm ($N = 4$), whereas 92% of the males were mature at 376–400 mm ($N = 12$) and 100% at larger sizes.

Based on the occurrence of hydrated oocytes and postovulatory follicles, spawning occurred from February through October (Figure 5A). The spawning season may extend beyond October, but no specimens were collected during November and December. Mean GSI values of females peaked in May and decreased progressively through September (Figure 6). The prevalence of hydrated oocytes still surrounded by a follicle cell layer during daylight hours indicated that blueline tilefish probably

TABLE 3.—Von Bertalanffy parameters for growth curves fitted to unweighted mean observed length at age for blueline tilefish sampled off North Carolina and South Carolina during 1982–1987 and 1996–1999.

	1982–1987				1996–1999			
Sex	L_∞	K	t_0	N	L_∞	K	t_0	N
Male	750	0.11	−5.45	104	716	0.07	−12.54	201
Female	626	0.12	−5.57	219	649	0.09	−7.58	172
Sexes combined	643	0.15	−3.88	406	651	0.08	−11.77	400

TABLE 4.—Chi-square analyses of sex ratio for blueline tilefish sampled off North Carolina and South Carolina during 1982–1987 and 1996–1999. Null hypothesis (H_0): male to female ratio is 1:1.

Total length (mm)	Males	Females	Male : Female	χ^2	P	H_0
			1982–1987			
301–350	0	3				
351–400	0	2				
401–450	0	10				
451–500	11	36	1:3.27	13.29	<0.001	Reject
501–550	18	84	1:4.66	42.71	<0.001	Reject
551–600	13	140	1:10.77	105.42	<0.001	Reject
601–650	22	60	1:2.73	17.61	<0.001	Reject
651–700	49	6	1:0.12	33.62	<0.001	Reject
701–750	42	1	1:0.04	39.09	<0.001	Reject
751–800	8	0				
No length		4				
Total	163	346	1:2.12	88.68	<0.001	Reject
			1996–1999			
300–350	0	1				
351–400	2	14	1:7	9.00	$0.005 > P > 0.001$	Reject
401–450	22	58	1:2.64	16.20	<0.001	Reject
451–500	81	70	1:0.86	0.80	$0.25 > P > 0.10$	Accept
501–550	93	68	1:0.73	3.88	$0.05 > P > 0.025$	Reject
551–600	51	28	1:0.55	6.69	$0.01 > P > 0.005$	Reject
601–650	50	22	1:0.44	10.89	<0.001	Reject
651–700	12	7	1:0.58	1.32	>0.25	Accept
701–750	4	1	1:0.25			
No length	2	1				
Total	317	270	1:0.85	3.76	$0.1 > P > 0.05$	Accept

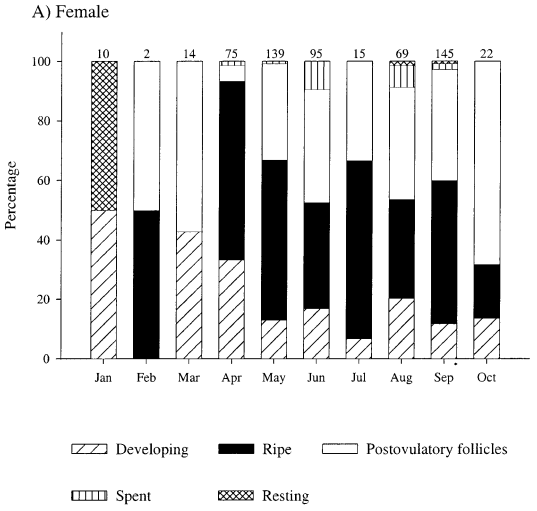
spawned in the evening (Figure 7). Spawning males were collected during January and from March through October (Figure 5B). Spawning females ($N = 279$) were captured on research cruises off North Carolina and South Carolina (32°04′N to 32°52′N) at depths of 48–232 m; only eight spawning females were captured at depths less than 163 m. Approximate fishing locations provided by fishermen showed that spawning females sampled from the commercial fishery ($N = 77$) were captured off North Carolina and South Carolina (32°47′ to 32°55′N) at depths of 165–199 m.

Fecundity

There was no significant difference in the density of hydrated and MN oocytes combined among three selected locations in the ovaries of nine specimens ($F = 0.36$, $P = 0.70$, df = 2), which indicated that samples for estimating total fecundity and batch fecundity could be taken from any lo-

TABLE 5.—Sex ratio by age for blueline tilefish sampled off North Carolina and South Carolina during 1982–1987 and 1996–1999.

Age (years)	1982–1987			1996–1999		
	Male	Female	Male : Female	Male	Female	Male : Female
4	1	2	1:2	8	3	1:0.38
5	4	4	1:1	30	21	1:0.7
6	5	8	1:1.6	33	20	1:0.61
7	3	10	1:3.33	23	13	1:0.57
8	10	8	1:0.8	26	12	1:0.46
9	9	13	1:1.44	14	19	1:1.36
10	8	12	1:1.50	14	13	1:0.93
11	9	15	1:1.67	15	12	1:0.8
12	10	17	1:1.7	8	14	1:1.75
13	8	11	1:1.38	8	8	1:1
14	12	17	1:1.42	5	4	1:0.8
≥15	54	171	1:3.17	12	35	1:2.92



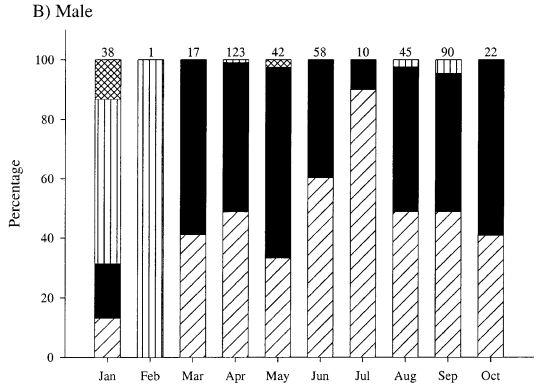


FIGURE 5.—Reproductive state percentages of **(A)** female and **(B)** male blueline tilefish collected off North Carolina and South Carolina during 1980–1999. The number of specimens examined by month is above each bar.

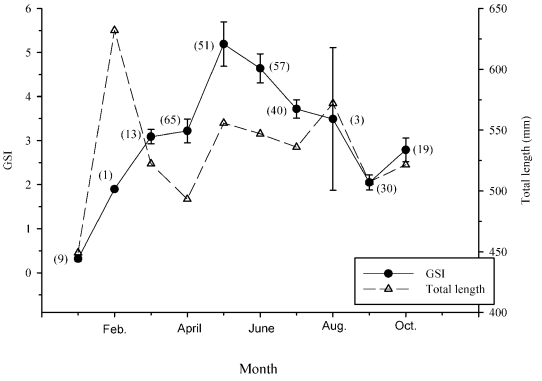


FIGURE 6.—Gonadosomatic index (GSI) by month and total lengths of female blueline tilefish collected off North Carolina and South Carolina during 1997–1999. The GSI = 100 × gonad weight/whole body weight. Error bars represent one standard error; numbers in parentheses are the number of ovaries examined.

cation without bias. Oocyte density ranged from 0.59 to 2.00 oocytes/mg of tissue.

Total fecundity ($\log_e$-transformed) as a function of total length was essentially constant throughout the spawning season (Figure 8) because the *y*-intercept did not decrease until September–October. The interaction term in an ANCOVA showed that the slopes of the equations were not significantly different among months ($F = 0.41$, $P = 0.6642$, df = 2; Table 6); however, the intercept of the September–October equation was lower than that for April ($P = 0.0020$). Atretic oocytes were not prevalent.

Annual fecundity in blueline tilefish is indeterminate because total fecundity did not decrease until the end of the spawning season and no size gap between stage-3 yolked oocytes and earlier stages of oocytes (Figure 9A) developed at any time during the spawning season (Figure 9B–D). Continuous production of oocytes was also evident in frequency plots of oocyte diameters because the percentage of stage-3 yolked oocytes did not progressively decrease over time (Figure 9). The small percentage (8–18%) of MN oocytes and hydrated oocytes relative to stage-3 yolked oocytes was evidence that blueline tilefish are batch spawners.

Estimates of spawning frequency and batch fecundity, necessary to estimate potential annual fecundity, were based on hydrated and MN oocytes because most fishery-independent sampling, and probably most commercial fishing, occurred during daylight, which concurred with the time of hydration (Figure 7). For comparative purposes spawning frequencies based on the occurrence of POFs were also estimated. The proportion of specimens with hydrated or MN oocytes among females with oocytes undergoing vitellogenesis was similar in fishery-dependent samples collected during 1996–1998 (0.64; Table 7) and in all samples from 1980 to 1999 (0.59; $N = 472$). One of the two proportions based on the occurrence of POFs (i.e., 24–48 hours old) in 1996–1998 matched the proportion based on hydrated and MN oocytes. The average of the three proportions based on 1996–1998 samples was 0.56, which corresponded to an approximate spawning periodicity of 2 d. With an extended spawning season of approximately 240 d (March–October), an individual female could spawn approximately 120 times in a spawning season. The short spawning periodicity

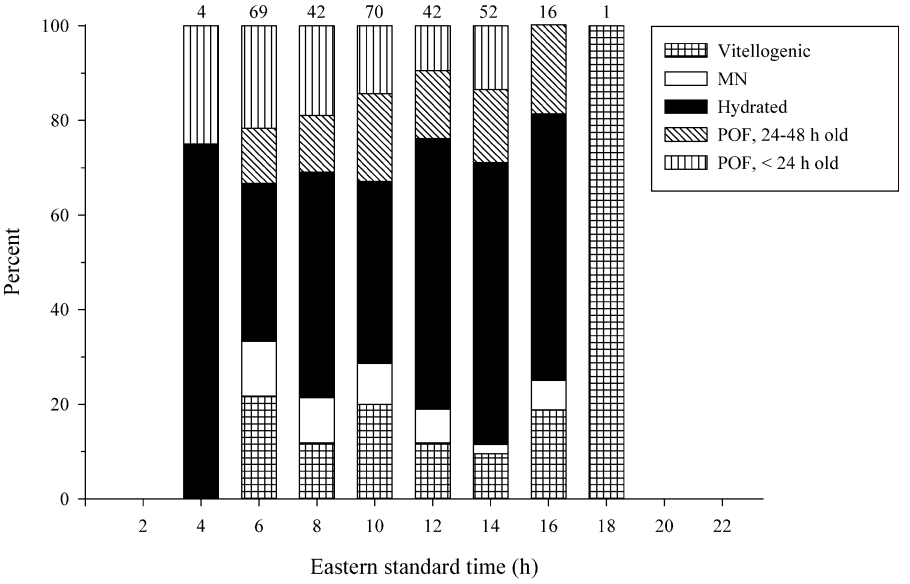


FIGURE 7.—Time of day (Eastern standard time) of spawning in female blueline tilefish collected off North Carolina and South Carolina during fishery-independent sampling in 1983–1999. All specimens were reproductively active and categorized according to dominant histological criterion (N = 296), where MN = migratory nucleus and POF = postovulatory follicle. Time of day noted includes the hour before and after (i.e., 0400 hours is from 0300 to 0459 hours).

in blueline tilefish was evident in histological sections from individual fish, which had as many as three batches of oocytes (i.e., MN or hydrated oocytes and POFs <24 and 24–48 hours old).

Statistically significant relationships were developed between batch fecundity ($\log_e$-transformed) and total length, fork length, whole body weight, and ovary-free body weight (Table 8).

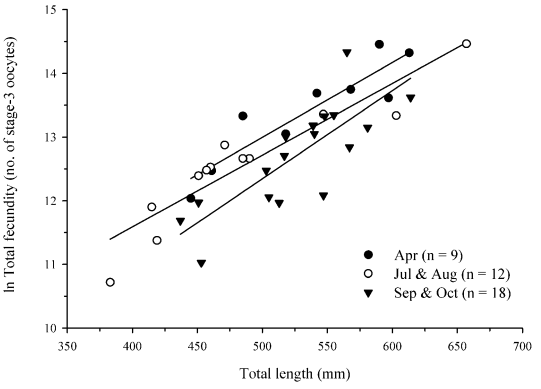


FIGURE 8.—Estimates of $\log_e$-transformed total fecundity (number of stage-3 oocytes) in 39 blueline tilefish relative to total length during three seasonal periods. The specimens were captured in fishery-dependent samples taken with longlines off North Carolina and South Carolina in 1997–1998.

Batch fecundity was not regressed against age because of the low number of specimens that were assigned an age (N = 10). Batch fecundity as a function of total length did not differ among seasonal periods (April, June–August, and September–October), as indicated by the lack of differences in slopes (F = 0.05, P = 0.952, df = 2) and intercepts (F = 2.45, P = 0.101, df = 2) among months. Given the similarity of the equations, data from all periods were combined to estimate the relationship between batch fecundity and total length (Figure 10). Batch fecundity ranged from 16,400–95,000 oocytes for specimens 366–629 mm TL. Multiplying the estimated number of spawning events (120) by batch fecundity (BF) estimates for blueline tilefish 366–629 mm TL (BF = 7.266 + 0.00667·TL; Table 8; Figure 10) produced estimates of potential annual fecundity that ranged from 1,972,300 to 11,397,700 oocytes.

Discussion

Blueline tilefish have small otoliths that were difficult to age from sections. The otolith core was difficult to identify clearly before sectioning—thus, many sections were off the core—and even good sections were difficult to age. We attempted to make all counts on the dorsal side of the otolith, but when patterns of increment formation were

TABLE 6.—Regression coefficients for the linear relationship between total length (TL; mm) and $\log_e$ total fecundity of blueline tilefish collected off North Carolina and South Carolina in 1997–1999. The effect of month on this relationship was evaluated with analysis of covariance. A single asterisk denotes $P < 0.001$; a double asterisk denotes $P < 0.0001$.

Month	*a*	*b*	Adjusted r^2	*F*	*n*
Apr	7.0345	0.011894	0.800	32.96*	9
Jul–Aug	7.0831	0.011260	0.850	63.40**	12
Sep–Oct	5.4343	0.013815	0.614	28.03**	18

observed, some counts were made on the ventral side of the otolith, and some counts were made using both sides. Frequently we observed a group of increments with very narrow translucent and opaque zones, separated from the next group by a larger translucent zone, particularly in the first few increments of older fish. We counted each group of increments as a single increment and assumed that our counts correctly represented age. Increment grouping and tightly packed increments at the otolith edge of older fish precluded validation of the periodicity of increment formation. Although Ross and Huntsman (1982) used marginal increment analysis (whole otoliths) to suggest the formation of one increment per year, we did not assign a birth date due to the uncertainty of the timing of increment formation.

Although the aging methodology we used had the potential to introduce error into ages, other species in the deepwater species complex have age ranges similar to those we report, suggesting that our estimated ages may be reasonable estimates of the real ages of the fish sampled (Turner et al. 1983; Harris and Grossman 1985; White et al.

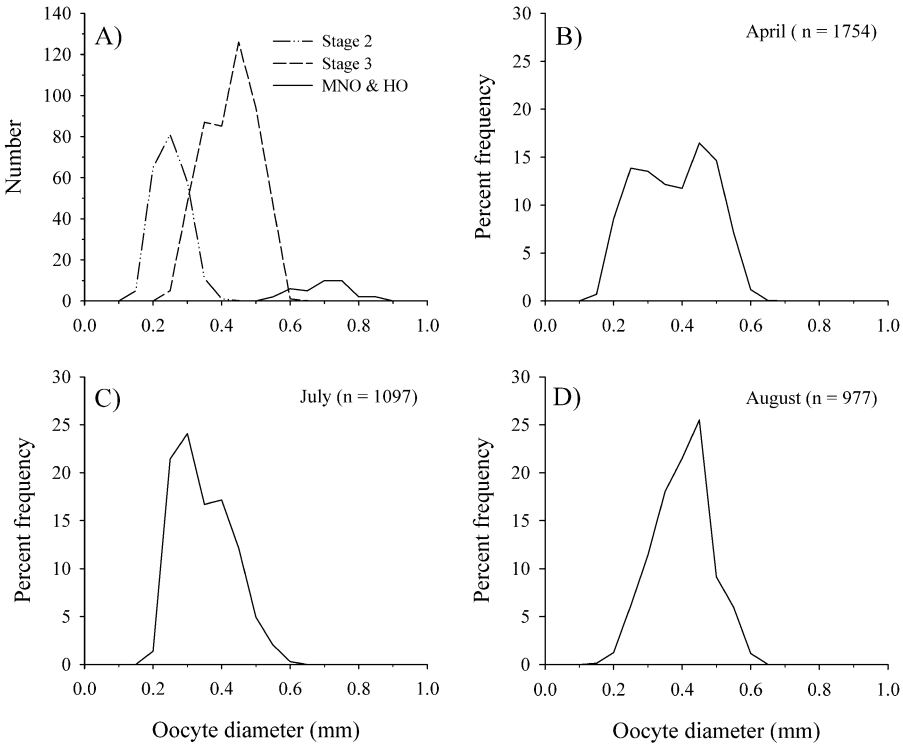


FIGURE 9.—**(A)** Number of oocytes by diameter for three stages of oocytes (Hunter et al. 1992; MNO = migratory nucleus oocyte, HO = hydrated oocyte) taken from eight blueline tilefish collected off North Carolina and South Carolina by commercial bottom longlines, 1997–1998. Oocyte-diameter frequency distributions for the three stages combined are presented for **(B)** April ($N = 3$), **(C)** July ($N = 2$), and **(D)** August ($N = 3$); the data for a single specimen in April was not included in this analysis but was included in the data for panel (A).

TABLE 7.—Number of female blueline tilefish with hydrated or migratory-nucleus (MN) oocytes, postovulatory follicles (POFs) less than 24 h old, and POFs 24 to less than 48 h old, as well as the total number of mature females with vitellogenic oocytes in samples collected off North Carolina and South Carolina with bottom longlines on commercial vessels during 1996–1998. The proportions were averaged to estimate spawning frequency.

Date	No. with hydrated or MN oocytes	POFs <24 h old	POFs 24–48 h old	Total mature females
Apr	40	17	24	53
May				
Jun	17	16	19	25
Jul	22	15	26	32
Aug	4	10	14	22
Sep	17	7	17	25
Total	100	65	100	157
Proportion of total	0.637	0.414	0.637	

1998; Wyanski et al. 2000). The increment groups observed during the first years of growth may have formed in response to short-term fluctuations in bottom temperature because it has been suggested that tilefish do not feed at temperatures below 9.5°C (Low et al. 1983). It is unlikely these subannual increments were spawning checks (Ross and Huntsman 1982) because they were evident in specimens younger than age 3 (age 3 is the age of first spawning).

Although several gear types were used to capture the blueline tilefish sampled for our study, the limited amount of blueline tilefish habitat along the southeast coast appears to have resulted in the same population of fish being sampled, regardless of the gear type used. All gear types were very similar (except traps, which accounted for 71 fish): comparable hook sizes, gear was fished on the bottom to 2 m off the bottom, similar locations fished. Therefore, gear selectivity was probably similar. Furthermore, the observed changes were evident for the samples from a single gear type, which was fished in the same manner for both periods. Although comparisons between gear types provided no evidence to suggest different selectivities among gear types within a period, sample size may not have been large enough to detect statistical significance among some gear types. However, we think that our samples probably provide an accurate representation of the population available to fishing gear in the sampled locations during the two periods.

Sexual dimorphism (i.e., males grow to larger sizes than females) was pronounced in the blueline tilefish sampled, particularly during 1982–1987. The reduction in sexual dimorphism in 1996–1998 was due to the loss of larger fish (predominantly males) from the population, which was presumably due to the fishing-up effect from substantially increased fishing effort during the early 1980s (Low et al. 1983). Since then, fishing mortality has remained high enough to preclude the reestablishment of large males in the population. The lack of change in the size at age of females in spite of a reduction in the mean size and age of females sampled over the study confirms the size-selective nature of the fishery.

The ratio of males to females collected with rod and reel off North Carolina and South Carolina during 1972–1977 was not significantly different from 1:1, although males outnumbered females (Ross and Merriner 1983). In our study, the ratio was highly skewed toward females during 1982–1987 and slightly, albeit not significantly, skewed toward males during 1996–1999. Although it is possible these differences were due to gear selec-

TABLE 8.—Linear regression coefficients and 95% confidence intervals (CIs) for the relationship between $\log_e$ batch fecundity (number of hydrated and migratory-nucleus oocytes) and total length, fork length, and whole and ovary-free weights in blueline tilefish collected from April through October off North Carolina and South Carolina. A single asterisk denotes $P < 0.001$; a double asterisk denotes $P < 0.0001$.

Dependent variable	Range	a	95% CI	b ($\times 10^{-3}$)	95% CI ($\times 10^{-3}$)	Adjusted r^2	F	N
Total length (mm)	366–629	7.266	5.557–8.975	6.67	3.45–9.89	0.306	17.71*	39
Fork length (mm)	341–591	7.310	5.609–9.012	7.01	3.61–10.41	0.302	17.43*	39
Whole weight (g)	560–2,880	9.509	8.943–10.076	0.743	0.431–1.055	0.369	23.22**	39
Ovary-free weight (g)	544–2,732	9.534	8.952–10.116	0.756	0.423–1.089	0.346	21.09**	39

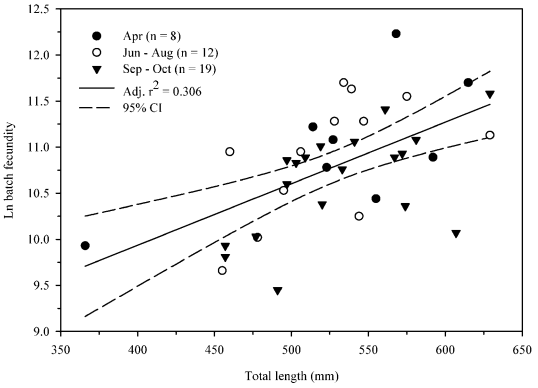


FIGURE 10.—Estimates of $\log_e$-transformed batch fecundity of blueline tilefish relative to total length during three seasonal periods. Migratory nucleus oocytes and hydrated oocytes were counted in 39 specimens captured collected off North Carolina and South Carolina by commercial bottom longlines in 1997–1998.

tivity, the range of lengths sampled by Ross and Merriner (1983) was similar to that in our study. So, it is unclear why the population would be biased towards females during 1982–1987, particularly if the fishery was targeting the larger fish, which tended to be males. Peak landings of tilefish occurred in 1983 (Harris et al. 2001), and it may be that the rapid development of the fishery in the early 1980s, combined with the fishing-up effect, removed many of the males before 1982, leaving mainly females remaining on the fishing grounds. The shift back to a slight skewing towards males by 1996–1999 was probably the result of time allowing the males removed during the early stages of the fishery to be replaced by new recruits, albeit sustained fishing mortality precluded reestablishing large males present in the population. Differences in sampling depths were not a factor because 79–90% of the specimens from each period in our study were collected at depths of 160–190 m.

With only four immature specimens, we could not estimate total length at 50% maturity for either sex. The size of mature females in our study generally agreed with the macroscopic maturity analysis done by Ross and Merriner (1983), who found one of five females mature at 376–400 mm TL. We only collected six mature females that were 375 mm TL or smaller. Male gonads were small and required the use of histological techniques to accurately assess their maturity. Ross and Merriner (1983) found spermatogenesis and collections of spermatozoa in histological sections of testes from males (390–500 mm TL; $N = 11$) that they had macroscopically assessed as immature. In our collections, nearly all (117 of 118) males that were 385–500 mm TL (3–21 years old) were mature. Females reached maturity as early as age 3 in both studies, but the oldest immature females in our study were age 6, compared with age 5 in Ross and Merriner (1983).

We found evidence of spawning in blueline tilefish off the Carolinas from February through October, which generally agrees with the results of Ross and Merriner (1983), but we lacked samples from November and December. Ross and Merriner (1983) found the GSI in both sexes and the percentage of ripe females off North Carolina exhibited a primary peak in May and a smaller peak in September, but monthly sample sizes were typically less than 20 specimens. Our sample sizes were larger, and the GSI for females off North Carolina and South Carolina exhibited only a May peak (Figure 6). No spawning peaks were evident in the histological data.

We found that oocyte densities were similar among three tested locations in ovaries of blueline tilefish, which concurs with Ross (1978). We agree with Ross and Merriner (1983) that blueline tilefish are multiple spawners because oocyte diameter frequency distributions have two or more modes of oocytes that are developing and the percentage of MN oocytes and hydrated oocytes relative to stage-3 yolked oocytes was less than 20%.

Annual fecundity in blueline tilefish is indeterminate because total fecundity does not decrease until the end of the spawning season, and a gap in size between stage-3 yolked oocytes and earlier stages of oocytes does not develop. Our estimates of total fecundity are one-third to one-half of the fecundity estimates of Ross and Merriner (1983) for three similar time intervals because they counted early yolked to hydrated oocytes, whereas our total fecundity estimates were based on only stage-3 yolked oocytes. Although the total fecundity estimates are different, there is a noticeable decrease in total fecundity at the end of the spawning season in both studies. Until the concepts of determinate fecundity and indeterminate fecundity were developed (Hunter et al. 1992), many investigators assumed that total fecundity represented the annual production of oocytes, even in nontemperate fish species. We found that blueline tilefish have indeterminate fecundity, and we used estimates of spawning frequency and batch fecundity (batch size) to estimate potential annual fecundity (as per Hunter et al. 1992). Our estimate could be improved by the addition of small and large specimens.

Loss of larger and older blueline tilefish from the population and the significant relationship between female size and batch fecundity suggest that the fecundity of the population is considerably less now than it was during 1972–1977 and 1982–1987. Nevertheless, blueline tilefish may be more resilient to the relatively high levels of fishing mortality than tilefish *Lopholatilus chamaeleonticeps* because the fishery is not harvesting immature individuals and a high number of egg batches are released during a spawning season. The population abundance appears to have recovered somewhat since the sharp decrease in landings in the mid-1980s (as reflected by a slight increase in landings) and is supporting consistent landings; however, the population may still be vulnerable to any increase in fishing mortality. As the management of this deepwater complex develops, all the species must be closely monitored to ascertain how each responds to management.

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