

Reproductive Demography of Tilefish from the South Atlantic Bight with a Test for the Presence of Protogynous Hermaphroditism

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Abstract.—Length and age at maturity were determined for tilefish *Lopholatilus chamaeleonticeps* collected off the Georgia coast during the reproductive season. Fifty percent of the females were mature at a total length (TL) of 500 mm and an age of 6 years (the youngest female collected), whereas 50% of males were mature at 450 mm TL and 5 years of age (the youngest male collected); true sizes and ages of median maturity may be less. Fecundity estimates increased nonlinearly with tilefish weight, length, and age and ranged from approximately 0.85×10^6 to 8.5×10^6 eggs for fish ranging from 573 mm TL (2.0 kg, 8 years) to 899 mm TL (8.9 kg, 20 years), respectively. The relationship between fecundity (F) and length was: $\log_e F = (4.749 \log_e TL) - 16.508$; $r^2 = 0.93$; $N = 31$. We observed disproportionately large numbers of females at smaller lengths and of males at larger lengths. This would be expected if protogynous hermaphroditism were common among tilefish in the South Atlantic Bight. Skewed sex ratios, however, may have been caused by sex-specific differential growth rates because (1) transitional ovotestes were not observed; (2) although previtellogenic oocytes were present in approximately 1% of testes examined, neither vitellogenic nor early stage atretic oocytes were present; and (3) testes never contained evidence of an ovarian lumen.

Tilefish *Lopholatilus chamaeleonticeps* support a substantial commercial fishery on the eastern and Caribbean seaboard of the United States. Previous research conducted in the South Atlantic Bight (south Florida to Cape Hatteras, North Carolina) indicated that females reproduce between April and June (Erickson et al. 1985). Little is known, however, about fecundities or the size or age at maturity for tilefish. Morse (1981) examined several aspects of the reproductive biology of tilefish in the Middle Atlantic Bight (Cape Hatteras to Cape Cod, Massachusetts); however, because tilefish from this region represent a distinct stock (Katz et al. 1983), differences may exist in reproductive characteristics of tilefish from the South and Middle Atlantic bights. Such interstock differences in demography are common in marine fishes (Cushing 1981). Hence, we attempted to quantify several reproductive variables for tilefish from the South Atlantic Bight. In addition, we tried to determine whether tilefish were protogynous hermaphrodites, reproducing first as females and later as males (Atz 1964). Dooley (1978) suggested that tilefish exhibit protogynous hermaphroditism because small individuals are disproportionately female and a majority of larger fish are male. Turner et al. (1983) also observed skewed

sex ratios at lengths for Middle Atlantic Bight tilefish but concluded that this phenomenon probably was attributable to differential growth rates, rather than to protogynous hermaphroditism. Consequently, the purposes of our research were to estimate age and length at maturity for both sexes, to determine the relationship between fecundity and female size and age, and to evaluate whether tilefish are protogynous hermaphrodites.

Methods

Fifteen collections were made monthly or bi-monthly from May 1982 to December 1983 with benthic longlining gear deployed from the R/V *Georgia Bulldog*. Sampling occurred off the Georgia coast in two areas along the 180-m depth contour: an 18-by-5-km area centered on latitude 31°39'N, longitude 79°28'W; and an 8-by-5-km area centered on 31°52'N, 79°14'W. Captured tilefish were measured for total length (TL) to the nearest millimeter and weighed in the round to either the nearest 0.1 kg (fish ≤ 10 kg) or 0.5 kg (fish > 10 kg). Gonads were removed from 2,242 tilefish, preserved immediately in 10% formalin, and later stored in 45% isopropanol. Histological sections were made of 571 testes and 399 ovaries. Histologically processed tissues were dehydrated with ethanol, cleared with histosol, embedded in paraplast, and sectioned to approximately 7 μ m thickness. Tissue sections were stained with Gill's

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TABLE 1.—Maturity estimates for Georgia tilefish by length and age.

Length groups			Age groups		
Total length (mm)	Percent mature (N)		Age (years)	Percent mature (N)	
	Females	Males		Females	Males
450–474		50 (2)	5		67 (3)
475–499	33 (3)	50 (2)	6	75 (4)	91 (11)
500–524	67 (3)	67 (3)	7	100 (11)	100 (10)
525–549	50 (2)		8	100 (18)	81 (26)
550–574	93 (14)	100 (1)	9	92 (24)	97 (30)
575–599	100 (13)	81 (16)	10	92 (13)	94 (36)
600–624	95 (19)	96 (23)	11	100 (14)	100 (29)
625–649	100 (34)	89 (27)	12	100 (15)	89 (26)
650–674	92 (13)	97 (32)	13	100 (8)	100 (14)
675–699	100 (12)	89 (18)	≥ 14	100 (11)	100 (46)
700–724	100 (1)	94 (32)			
≥ 725	100 (18)	100 (119)			

hematoxylin and counter-stained with eosin. Aging data used in this paper were presented by Harris and Grossman (1985). Ages were determined from fin-ray cross sections examined under a compound microscope with transmitted light.

Maturity.—Estimates of length and age at maturity were obtained through histological examination of 132 female and 275 male gonads collected during the period of spawning and late gonadal development: May 1982 and March, April, and June 1983 (Erickson et al. 1985). Specimens collected during reproductive quiescence were not included in the maturity estimates due to the difficulty of staging resting gonads. Ovaries of immature females were identified by the presence of basophilic, previtellogenic oocytes (Moe 1969; Waltz et al. 1982); active vitellogenesis did not occur in the ovaries of immature fish, and post-ovulatory follicles were absent, indicating no prior ovulation. Immature males were defined as those with testes containing little spermatocyte development (Waltz et al. 1982); much of the testis contained spermatogonia and connective tissue. Limited spermatogenesis occurred in testes of immature fish.

Fecundity.—Ripe ovaries from 31 fish captured during March 1983 were used for fecundity estimates. Fecundity could not be estimated volumetrically (Bagenal and Braum 1978) because prior fixation in formalin and storage in isopropanol prevented Gilson's fluid from breaking down ovarian connective tissue. Hence, we used a gravimetric technique (Bagenal and Braum 1978). Ovaries were blotted dry and weighed to the nearest 0.001 g on an analytical balance. Because oocyte development appeared to be similar throughout

the ovary (Erickson et al. 1985), three replicate samples (Bagenal and Braum 1978) were taken from one ovarian lobe for each fecundity estimate. Each sample was weighed to the nearest 0.001 g and placed on a glass slide. Oocytes were teased free from the ovigerous lamellae and counted under a dissecting microscope at 30× magnification. We counted only developing oocytes (including the follicular layer), defined as opaque oocytes with diameters larger than approximately 0.18 mm (Erickson et al. 1985). Counts were summed across triplicate sections and extrapolated to both ovaries by weight proportion.

Protogynous hermaphroditism.—We tested for the presence of protogynous hermaphroditism by examining sex ratios of 2,240 measured and 1,093 aged tilefish and histological sections from 970 gonads. These data were collected monthly or bi-monthly from May 1982 through December 1983. All tilefish were sexed macroscopically. We used the criteria suggested by Sadovy and Shapiro (in press) to detect the presence of protogynous hermaphroditism. The presence of significantly more females than males in smaller size and younger age classes suggests that protogynous hermaphroditism may be present (Moe 1969; Manooch 1976; Waltz et al. 1979, 1982; Ross and Merriner 1983; Turner et al. 1983). This can be verified histologically if (1) gonads progress from predominantly ovarian tissue to testicular tissue (transitional ovotestis), usually after the spawning season (Smith 1965; Bruslé and Bruslé 1975; Fishelson 1975), (2) atretic, vitellogenic, and perhaps previtellogenic oocytes occur in testes (Smith 1965; Bruslé and Bruslé 1975), and (3) an ovarian lumen persists within the testis (Reinboth 1970).

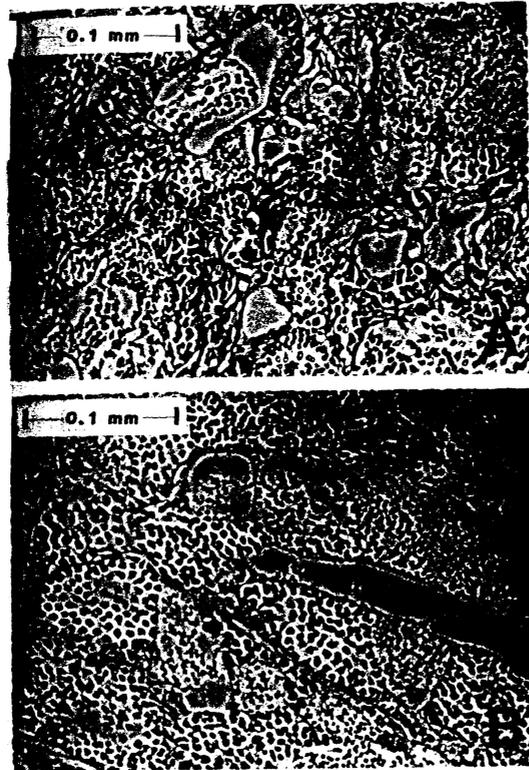


FIGURE 1.—Photomicrographs of cross-sectioned tilefish testes (hematoxylin and eosin). A. Gonad obtained from a mature, 664-mm total length (TL), 10-year-old fish captured in May 1982. Although spermatozoa are present, spermatogenesis is incomplete. B. Gonad obtained from a mature (unageable, 828-mm TL) fish captured in May 1982. Spermatogenesis is incomplete.

Results

Immature female tilefish ranged from 494 to 652 mm TL and 6 to 10 years of age (Table 1). More than 50% of the females were mature in each of the age groups collected. Immature males ranged from 463 to 725 mm and 5 to 12 years of age. At least 50% of the males were mature in each size and age class; however, spermatogenesis frequently appeared incomplete until males reached approximately 725 mm (Figure 1). It is unclear whether the majority of males less than 725 mm were functionally mature.

Tilefish less than 550 to 575 mm were uncommon in our samples and tilefish less than 463 mm were not captured. Hence, we were unable to determine the exact onset of sexual maturity in tilefish. In addition, sample sizes for age-at-maturity estimates were lower than sample sizes for length-at-maturity estimates. This was due to an inability

TABLE 2.—Numbers of Georgia tilefish caught in 50-mm length groups and in age groups. Within each length or age group, asterisks mark the significantly more common sex (chi-square tests of 1:1 sex ratio; * $P \leq 0.05$; ** $P \leq 0.005$).

Total length (mm)	Size groups		Age (years)	Age groups	
	Female (N)	Male (N)		Female (N)	Male (N)
450-499	5	5	5	0	4
500-549	18**	5	6	14	24
550-599	85**	53	7	46	32
600-649	197**	148	8	75	94
650-699	225	250	9	112	148*
700-749	68	277**	10	103	167**
750-799	30	193**	11	79	178**
800-849	73	137**	12	52	155**
850-899	36	115**	13	35	117**
900-949	5	119**	14	22	85**
950-999	0	65**	15	18	62**
≥1,000	0	100**	16	17	51**
			17	12	41**
			18	9	33**
			19	11	21
			20	6	18**
			21	4	8
			22	5	10
			23	3	7
			≥24	3	26**

to age all fish, primarily because of deterioration of the fin-ray core in some specimens (Harris and Grossman 1985).

Fecundity estimates ranged from 847,000 eggs (in a 573-mm, 2.0-kg, 8-year-old fish) to 8,453,000 eggs (899 mm, 8.9 kg, 20 years) and were significantly correlated with weight, length, and age. Least-squares regressions were used to obtain the following parameter estimates for log-transformed models (F = fecundity; W = body weight, kg; A = age, years):

$$\begin{aligned} \log_e F &= 1.497 \log_e W + 12.590; & r^2 &= 0.95; N = 31; \\ \log_e F &= 4.749 \log_e TL - 16.508; & r^2 &= 0.93; N = 31; \\ \log_e F &= 1.802 \log_e A + 10.407; & r^2 &= 0.77; N = 25. \end{aligned}$$

None of the untransformed relationships were linear (t -tests; $P < 0.05$ for null hypotheses of linearity). Error variances for fecundity-weight and fecundity-length relationships did not differ significantly (F -tests; $P > 0.05$; $df = 29, 29$; Neter and Wasserman 1974), which is surprising because typically it is more difficult to obtain accurate field measurements for weights than for lengths. The error variance of the fecundity-age relationship was significantly greater than those for fecundity-weight ($P \leq 0.05$; $df = 23, 29$) and fecundity-length ($P \leq 0.05$; $df = 23, 29$).

Sex ratios were skewed (Table 2). Tilefish small-

er than 650 mm were predominantly female and those larger than 700 were predominantly male, based on chi-square deviations from 1:1 sex ratios. When fish were grouped by age, there was no female preeminence among younger fish, but males dominated the sex ratios (usually significantly) after age 8. These data suggest either the presence of protogynous hermaphroditism in tilefish or differential growth and mortality rates between the sexes. It is unlikely that sex-specific immigrations or emigrations could have produced these patterns because tilefish appear to be sedentary (Grimes et al. 1983).

Protogynous hermaphroditism can be confirmed only through histological examination of gonads. Transitional ovotestes were not observed in the 970 gonads examined during all phases of the reproductive cycle; however, previtellogenic oocytes were observed in six of 571 testes (Figure 2). Two of these males (699 mm and 736 mm, age undeterminable) were mature, and the remainder (580–675 mm, 8–12 years) were immature. These testes were collected between December—period of recrudescence—and May—period of active spawning (Erickson et al. 1985). Vitellogenic or atretic oocytes were not observed in tilefish testes. We occasionally observed structures that resembled vestiges of atretic oocytes (Figure 2), usually within the connective tissue and the tunic of both ovaries and testes. These structures (diameter = 0.028–0.104 mm; mean = 0.065 mm; $N = 33$) were identified as melanin-macrophage centers (V. Blazer, University of Georgia, Athens, personal communication). Hematoxylin and eosin staining produced yellow-brown coloration, indicating the presence of ceroid. The melanin-macrophage centers also contained granules that were positive for Perl's stain, indicating the presence of hemosiderin. Finally, ovarian lumens were not observed in testes. Although previtellogenic oocytes were present in approximately 1% of the testes examined (of which 66% were from immature fish), these data suggest that protogynous hermaphroditism, if present in tilefish, is rare. The status of tilefish gonads prior to sexual maturation is unknown, for specimens smaller than 463 mm were not collected.

Discussion

Sample sizes of immature fish were small, indicating either that the gear selected for sexually mature fish, or that immature tilefish primarily reside in different areas from adults. Relationships between migration and sexual maturity have been

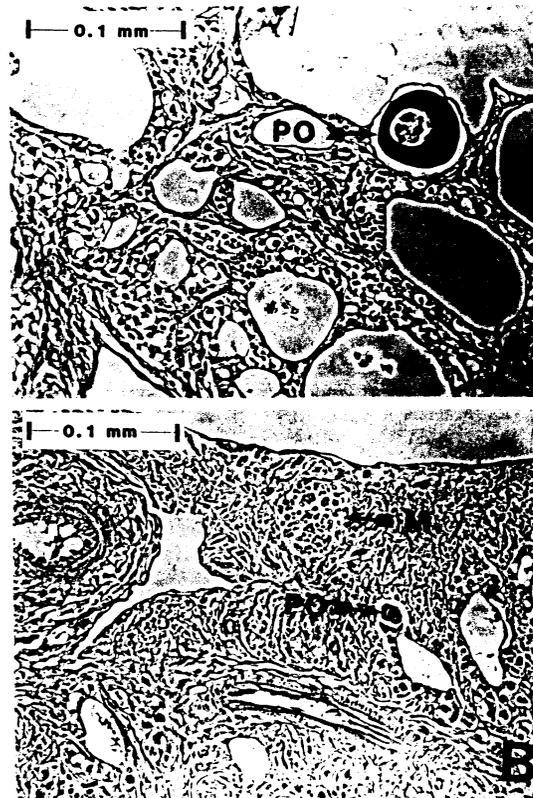


FIGURE 2.—Photomicrographs of cross-sectioned testes containing previtellogenic oocytes (PO) and a melanin-macrophage center (M) (hematoxylin and eosin). A. Gonad taken from a 580-mm total length (TL), 12-year-old immature fish during May 1982. B. Gonad obtained from an unageable, 736-mm TL, mature male in December 1983.

documented for red grouper *Epinephelus morio* (Moe 1969) and suggested for snowy grouper *E. niveatus* (Moore and Labisky 1984). We favor gear selectivity as the most likely explanation for our data because tilefish less than 200 mm have been observed in areas with adult tilefish in both the Middle and South Atlantic bights (personal communications: C. Grimes, National Marine Fisheries Service; R. Jones, University of Texas Marine Science Center). In addition, small tilefish also have been found in adult tilefish stomachs (Freeman and Turner 1977). If migration is not a factor, these data indicate that catchability of immature tilefish with commercial longline gear is low. A larger sample of small specimens will be required to accurately determine the onset of sexual maturity in tilefish from the South Atlantic Bight.

Morse (1981) indicated that lengths at maturity

for tilefish in the Middle Atlantic Bight were 600–650 mm for females and 650–700 mm for males, considerably greater than our upper estimates of 500 mm for females and 450 mm for males. The discrepancies probably are due to methodology. Although tilefish in the Middle Atlantic Bight represent a separate stock (Katz et al. 1983), and have been commercially harvested for a longer time than have southern tilefish (landings were small prior to 1980: Low et al. 1983), differential harvest is an unlikely cause of these discrepancies because size at maturity typically decreases with increased exploitation (Ricker et al. 1978; Beacham 1983a, 1983b). Morse (1981) estimated maturity macroscopically, whereas we did so histologically. Ross and Merriner (1983) found that testes of macroscopically staged “immature” blue-line tilefish *Caulolatilus microps* exhibited active spermatogenesis when examined histologically; we also observed this in small tilefish. Histological estimates of tilefish maturity almost certainly are more accurate than macroscopic ones. Our maturity estimates for males, however, are somewhat tentative because many specimens smaller than 725 mm showed active yet incomplete spermatogenesis, and whether or not these fish were functionally mature is problematical.

Follicular development is asynchronous in tilefish (Erickson et al. 1985); therefore, we may have underestimated fecundity if previtellogenic oocytes developed after the collection date or if batches were spawned prior to the collection date. We selected ripe ovaries to minimize the first possibility. Spent ovaries were not observed in March (Erickson et al. 1985), so spawning probably had not occurred before our sampling date. Fecundity also may have been overestimated if all developing oocytes were not ovulated and subsequently degenerated. It is difficult to quantify preovulatory oocyte degeneration (Macer 1974); consequently, our estimates represent maximum fecundities rather than actual fecundities.

Fecundity estimates for tilefish in the Middle Atlantic Bight ranged from 1.9×10^6 (in a 631-mm, 3.5-kg fish) to 7.8×10^6 eggs (809 mm, 9.0 kg) (Morse 1981). Morse (1981) assumed that fecundity increased linearly with both weight and length, and was best predicted by:

$$F = -996.471 + 887,000W \text{ and} \\ F = -15,020,043 + 26,865L;$$

F = fecundity; L = total length (mm); W = weight (kg). In most fishes, fecundity increases nonlinearly with fish length (Bagenal and Braum 1978).

Depending on the species, fecundity may increase linearly (Pitt 1964; Dietrich 1979; Lewis and Roithmayr 1980) or nonlinearly (de Martini and Fountain 1981; Waltz et al. 1982; Ross and Merriner 1983) with fish weight. Fecundity increased nonlinearly with length, weight, and age for South Atlantic Bight tilefish.

The percentage abundance of female tilefish decreased with increasing length and age in this study. Such skewed sex ratios are characteristic of species exhibiting protogynous hermaphroditism (Moe 1969; Manooch 1976; Waltz et al. 1979; Waltz et al. 1982; Ross and Merriner 1983). Skewed sex ratios, however, may be the result of other factors such as differential mortality or growth rates, or differential catchability between sexes. Turner et al. (1983) and Harris and Grossman (1985) showed that growth rates for tilefish were different between sexes, but could not detect statistical differences in mortality rates.

The occurrence of protogynous hermaphroditism in fishes can be confirmed only through histological sectioning of gonads. The best evidence for protogynous hermaphroditism is the observation of transitional ovotestes. We did not observe transitional ovotestes in tilefish, but this, in itself, is not sufficient evidence to reject the possibility of hermaphroditism. For example: sex reversal may be rapid; it may be restricted to a short time span; and it may not occur in all individuals in the population. We did collect, however, 970 specimens in 15 sample periods during 1982 and 1983 (representing all calendar months), and we should have been able to detect transitional ovotestes had they been present.

Many authors have regarded the presence of previtellogenic oocytes in teleost testes as evidence of protogynous hermaphroditism (review in Atz 1964). Previtellogenic oocytes were present in six of 571 testes examined. In the absence of other supporting data, however, this is not strong evidence for hermaphroditism (Atz 1964; Mehl 1973; Bruslé and Bruslé 1975; Peters 1975). Previtellogenic oocytes may persist for a long time in testes (Bruslé and Bruslé 1975) and may be the result of a juvenile bisexual stage (Mehl 1973). The occurrence of a juvenile bisexual stage in tilefish is uncertain, because we were unable to capture specimens less than 463 mm long. Ross and Merriner (1983) concluded that blue-line tilefish undergo “prematurational sex reversal” but they could not determine whether individuals of this species were “functional hermaphrodites.” Collections of small tilefish will be necessary before conclusions can be

reached about sex reversal during the juvenile period.

The presence of atretic bodies in the testis occurring due to the breakdown of vitellogenic oocytes also has been used as evidence for protogynous hermaphroditism in fishes. Unless early stages of follicular atresia are observed, however, this criterion may be misleading (Sadovy and Shapiro, in press). Smith (1965) found structures resembling late follicular atresia in the liver, gut, and other body parts in serranids. We also observed structures resembling a late stage of follicular atresia in some tilefish testes and ovaries; however, these structures were melanin-macrophage centers. The significance of these structures in tilefish gonads is uncertain.

Finally, no evidence of an ovarian lumen was detected in tilefish testes. This structure usually is present in functional males that have previously transformed from functional females (Reinboth 1970).

Although sex ratios were skewed, and some tilefish testes contained previtellogenic oocytes, our data strongly suggest that mature tilefish from the South Atlantic Bight are not protogynous hermaphrodites. If hermaphroditism exists in the South Atlantic Bight, it is either extremely rare or transitory or occurs only during the juvenile period and, consequently, should not greatly affect the population reproductive potential.

Leaman and Beamish (1984) argued that a long reproductive lifespan and iteroparity evolved to compensate for variability in recruitment. These demographic characteristics have been observed in tilefish, and variability in recruitment seems likely because tilefish produce pelagic larvae (Fayhay and Berrian 1981). Leaman and Beamish (1984) outlined the implications of managing long-lived fish species, such as tilefish, and concluded that "the production-growth oriented management strategies derived for shorter-lived species may result in rapid over-exploitation of accumulated biomass and a prolonged period of rehabilitation for the long-lived fish." This caveat certainly applies to tilefish, and a comprehensive management plan urgently is needed for this species because of the rapid development of the fishery in the South Atlantic Bight.

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