THE REPRODUCTIVE BIOLOGY OF TILEFISH, *LOPHOLATILUS CHAMAELEONTICEPS* GOODE AND BEAN, FROM THE UNITED STATES MID-ATLANTIC BIGHT, AND THE EFFECTS OF FISHING ON THE BREEDING SYSTEM

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ABSTRACT

To investigate the reproductive biology of tilefish, *Lopholatilus chamaeleonticeps* Goode and Bean, we sampled the commercial longline fishery from 1978 to 1982. Results suggested that tilefish are fractional spawners from March to November with a spawning peak from May to September. Estimates of fecundity ranged from about 195×10^3 to 10×10^6 (for 53 cm FL, 2.1 kg and 91 cm FL, 13 kg females), but only 60–85% of the ovarian eggs appeared to have been released by the end of the spawning season.

Tilefish are apparently gonochoristic however, some adult males had slight amounts of ovarian tissue within the testicular mass. Sex ratios were skewed in favor of males at larger sizes; however, both sexes were present at most ages. All juveniles and unsexed fish (<400 mm FL) appeared to be female (i.e., gonad cell structure consisted of oogonia and previtellogenic oocytes), suggesting that some tilefish may undergo prematurational sex reversal, or that early gonad development involves an all female appearing stage.

Tilefish may have a complex breeding system that is behaviorally mediated. Both sexes are functionally mature at ca. 50 cm FL and 5 years, but some males appear to delay participation in spawning for 2–3 years and 10–15 cm in additional length. Tilefish are sexually dimorphic, with males attaining larger sizes and developing conspicuously enlarged predordal adipose flaps (an apparent indicator of male breeding status) at 65–70 cm FL (6–7 years), when males begin to participate in spawning (i.e., develop large testes), not when they are functionally mature (i.e., producing sperm).

The rapidly expanding fishery from 1978 to 1982, which reduced population density by one-half to two-thirds, may have altered the breeding system by causing males to spawn at smaller sizes (10 cm) and younger ages (2–2.5 years) in 1982 than in 1978.

Tilefish, *Lopholatilus chamaeleonticeps* (Branchiostegidae), is a demersal gonochoristic species found along the outer continental shelf from Nova Scotia south to Surinam (Dooley 1978; Markle et al. 1980). Within the Mid-Atlantic Bight (continental shelf between Cape Cod, MA and Cape Hatteras, NC), they inhabit a narrow zone of relatively warm temperatures (9°–14°C) in about 80–240 m depths. Following a brief period as pelagic larvae (Fahay and Berrien 1981; Berrien 1982), juveniles settle to the bottom. Adults are sexually dimorphic, males having larger adipose flaps (= predorsal crest of Dooley 1978) than females (Katz et al. 1983). Growth in both sexes is about 10 cm per year for the first four years, then it slows, but more so in females than males (Turner et al. 1983). Maximum size of females is about 100 cm FL and 112 cm FL in males, and maximum ages are 35 and 26 years, respectively (Turner et al. 1983).

Both juveniles and adults select sedimentary substrata, and seek shelter in a variety of habitats. Grossman et al. (1985) found a strong correlation between sediment composition and tilefish occurrence. Juveniles and adults occupy highly contageously distributed vertical burrows, the primary habitat, in Pleistocene clay substrata (Able et al. 1982; Grimes et al. 1986). Adults also inhabit horizontal excavations in more vertically oriented clay sediments of submarine canyon walls called "pueblo habitats" (Cooper and Uzmann 1977; Warme et al. 1977; Grimes et al. 1986), and scour depressions under and around glacial erratic boulders (Valen-

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tine et al. 1980; Grimes et al. 1986). Several crustaceans and fishes are concentrated in and near tilefish excavations, which are formed by the combined activity of tilefish and their associates (Able et al. 1982; Grimes et al. 1986). Several associates are important components of tilefish diets, suggesting close trophic linkages within the burrow community (Turner and Freeman MS[5]; Grimes et al. 1986). Limited mark-recapture data suggests that tilefish are sedentary (Grimes et al. 1983). Tilefish and their associates have definite temporal activity patterns, and male-female pairing may occur (Grimes et al. 1986). Habitat preference, contagious distribution within suitable clay substratum, definitive activity patterns, limited movement, and pair bonding provide opportunities for social interaction and organization within populations.

Commercial landings of the Mid-Atlantic–southern New England tilefish stock (Katz et al. 1983) have varied widely since 1916 when 4,500 metric tons (t) were landed in 10 months (Freeman and Turner 1977). In the early 1970s an important longline fishery developed, centered in New York-New Jersey, and landings increased. This fishery became one of the most valuable finfisheries in both states during most years since 1978 (Grimes et al. 1980; U.S. Department of Commerce 1980a–c; D. J. Christensen pers. commun.[6]). From 1977 to 1980, annual landings were 2,061, 3,412, 3,840, and 3,575 t, but catches declined to 3,200 and 1,900 t in 1981 and 1982 (U.S. Department of Commerce 1980a–c; D. J. Christensen fn. 6). Effects of fishing on the stock have been drastic, reducing stock size by one-half to two-thirds from 1978 to 1982 (Turner 1986).

The purpose of this paper is to describe the reproductive biology of tilefish in the northern stock, and present evidence that participation in spawning by males is socially mediated. Furthermore, we show that the mating system has been modified by commercial fishing.

MATERIALS AND METHODS

Samples of tilefish from the United States Mid-Atlantic–southern New England area were obtained from domestic longline and New Jersey recreational (headboat[7]) fisheries. Information gathered for each sample included the statistical nature of the sample (random or nonrandom), capture method, location (LORAN C), date, and length (FL, cm), sex, weight (whole and eviscerated), and height (mm) of the adipose flap of each animal. When possible, gonads were excised, weighed (0.1 g) and preserved in 10% formalin. We assigned each fish to one of three classifications (male, female, or unknown) and one of six stages of sexual maturity following visual examination (Nikolsky 1963). Some fish used for reproductive studies were aged using thin sections of their saggital otoliths (Turner et al. 1983).

Routine histological sectioning and staining (haemotoxylin and eosin) techniques and light microscropy (450× and 1000×) were used to examine gonad structure of six small fish (<50 cm), and assess the state of sexual maturity. Ovarian development corresponded to that described by Moe (1969) for red grouper, *Epinephelus morio*, and Yamamoto (1956) for the flounder *Liopsetta obscura*. Spermatogenic development was identical to that of *Tilapia leucosticta* (Hyder 1969) and toadfish, *Opsanus tau*, (Hoffman 1963). Females were assessed as immature when ovaries contained only previtellogenic and early vitellogenic oocytes (Yamamoto 1956; Moe 1969; Waltz et al. 1982; Ross 1978; Erickson and Grossman 1986). Males were considered mature when active spermatogenesis was occurring and spermatozoa were present in spermatogenic tubules (Ross 1978). Limited spermatogenesis occurred in the testes of some immature males (Erickson and Grossman 1986).

A gonosomatic index (GSI) was calculated for females according to the formula $GSI = \frac{GW}{BW} \times 100$, where GW = fresh gonad weight (g) and BW = fresh eviscerated body weight (g) (Nikolsky 1963), for describing spawning seasonality. The seasonal progression of mean ovum diameters was also used to establish the reproductive seasonality, and the ovum-diameter frequency distribution for ripe females was used to indicate spawning frequency (isochronal vs. heterochronal) (Hickling and Rutenberg 1936). Separated ova from each fish were placed in liquid and stirred; a random sample for measuring was then obtained by extracting three aliquots with a large syringe. Diameters of 500–1,000 ova from each female were measured (nearest ocular micrometer unit) using a binocular dissecting scope and a filar micrometer. We assumed

[5]Turner, S. C., and B. L. Freeman. Food habits of tilefish, *Lopholatilus chamaeleonticeps*. Unpubl. manuscr. Southeast Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Miami, FL 07732.

[6]D. J. Christensen, Northeast Fisheries Center Sandy Hook Laboratory, National Marine Fisheries Service, NOAA, Highlands, NJ 07732, pers. commun. 1983.

[7]Headboats are vessels which charge anglers for fishing on an individual, thus "per head", basis.

uniform ova size (developmental stage) distribution among anterior to posterior ovarian lobe locations, as has been demonstrated for *Lopholatilus chamaeleonticeps* from the South Atlantic Bight (Erickson et al. 1985).

To determine if the liver was being utilized to store energy in the form of fat reserves to be used in gonad maturation, we calculated a hepatosomatic index (HSI) = liver weight (g)/gutted body weight (g) × 100 (Htun-Han 1978).

Ovaries used to estimate fecundity (= ovarian egg count of Gale and Deutsch (1985)) were preserved in modified Gilson's fixative (Bagenal and Braum 1978). The ovarian tunic was removed and washed free of adhering ova. Developing ova were separated from folicular material and most oogonia by washings under a stream of water. Based upon initiation of yolk accumulation, all oocytes with diameters >0.15 mm were included in ovarian egg counts. Each sample of developing ova was diluted in water and stirred, then at least two subsamples pipetted; each subsample was placed in a 6 × 6 cm gridded Petri dish for counting. Ova were counted in six randomly selected grid squares, and the average number of ova in the six squares was then adjusted to the total subsample count by multiplying the average by the total number of grid squares in the dish. The sample and subsamples were oven dried at 40°C for at least 24 hours and weighed to the nearest 0.001 g on a Mettler[8] balance. Fecundity (total ovarian egg count) was estimated as the number in the subsample multiplied by sample weight divided by subsample weight.

Predictive equations of fecundity from length and weight were fit using least squares regression and converted to functional regressions (Ricker 1973). Fecundity was separately regressed on FL and gutted weight using all possible combinations of untransformed log and semi-log models. We inspected residuals, plots and coefficients of determination to evaluate fits.

RESULTS

Gonad Structure and Sex Determination

Males smaller than 600 mm FL were difficult to sex by gross gonadal structure because testes were small and undeveloped. However, in females larger than about 400 mm FL ovaries were sufficiently developed to visually determine sex easily. Therefore, we histologically examined gonadal tissues of 155 fish (50 males, 545–814 mm FL; 52 females, 241–678 mm FL; and 53 juveniles, 146–400 mm FL). Based upon gonad microstructure, seven fish between 467 and 592 mm FL that were macroscopically unsexable were males. All juveniles and unsexed fish <400 mm FL (79 fish 121–400 mm FL) appeared to be females, i.e., had cell structure consisting of only oogonia. These cells had slightly acidophilic cytoplasm and distinct, but irregular, cell membranes. The nuclear membrane was less obvious because it was masked by basophylic nuclear material located peripherally.

The paired ovaries of adult *L. chamaeleonticeps* are suspended below the swimbladder from the dorsal body wall in the extreme posterior of the body cavity. Ovarian microstructure and development are identical to *Caulolatilus microps* (Ross and Merriner 1983) and *L. chamaeleonticeps* (Erickson et al. 1985) from the South Atlantic Bight and are described in detail by Idelberger (1985).

The testes of tilefish are solid, smooth textured, and more elongate than ovaries. In males smaller than about 65 cm FL, testes were not obviously lobed and were pinkish in color. Only in large adult males were testes creamy white and heavily lobed. Microstructure of the testes was typical of teleosts (Hoffman 1963; Smith 1965; Hyder 1969) and was identical to *C. microps* (Ross and Merriner 1983), and, like the ovary structure, was described in detail by Idelberger (1985). Two males (604 and 609 mm FL) had slight amounts of ovarian tissue within the testicular mass (Fig. 1). That ovarian tissue consisted of several resting or previtellogenic (perinucleolar) oocytes located in testicular mass with definite spermatogenic tubules and crypt structure.

Sexual Dimorphism

The predorsal adipose flap is sexually dimorphic in adult tilefish and can easily be used to determine sex in animals larger than about 70 cm FL. The size of the predorsal flap was significantly larger in males than in females older than age 5 years and larger than 65 cm FL (Table 1). It was not possible to compare predorsal flap sizes of the largest males to those of females, because females do not grow as large as males (Turner et al. 1983; Harris and Grossman 1985).

Sexual Maturity

We determined the general pattern of age and size of sexual maturity using both visual staging and

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

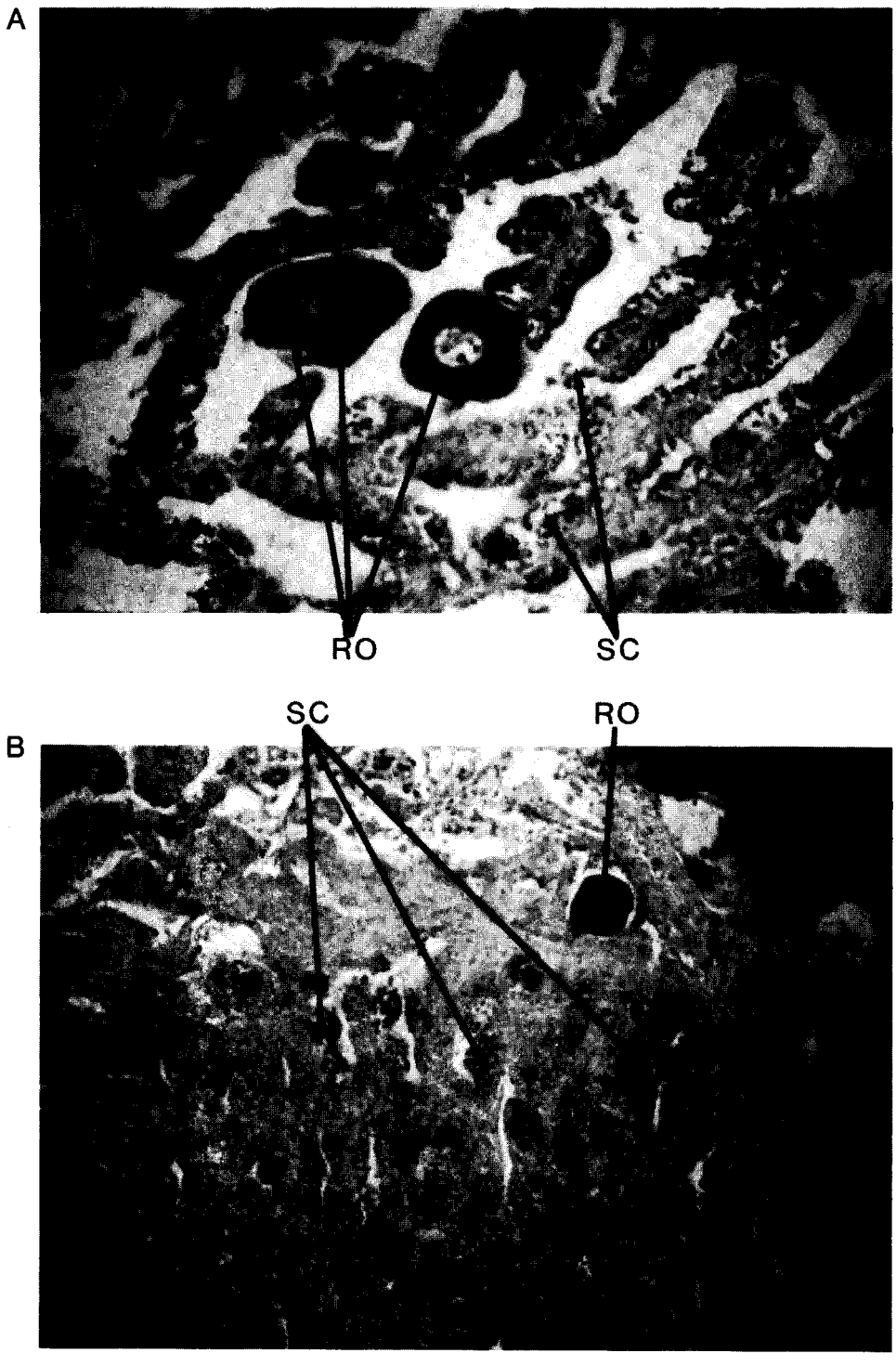

FIGURE 1.—Photomicrographs of histological sections of tilefish testes from a 60.4 cm FL male at ×400 (A) and a 60.9 cm FL male at ×100 (B) showing residual oocytes (RO) and spermatogenic cripts (SC).

TABLE 1.—Mean ($\bar{X}$) and sample size (N) for predorsal adiposal flap height at size and age for male and female tilefish, and students t-tests of flap height differences between sexes.

	Males		Females			
	$\bar{X}$ (mm)	N	$\bar{X}$ (mm)	N	t-value	Probability
Size (FL, mm)						
45–49	20.1	13	17.1	19	1.02	N.S.
50–54	23.1	29	23.6	49	0.33	N.S.
55–59	25.7	36	25.9	62	0.04	N.S.
60–64	30.6	40	27.6	105	0.91	N.S.
65–69	37.1	73	31.6	101	2.63	<0.01
70–74	49.8	67	31.7	51	3.58	<0.01
75–79	61.8	30	37.6	25	4.05	<0.01
80–84	72.3	30	37.7	11	1.90	<0.05
85–89	82.4	12	28.8	8	1.84	<0.05
90–94	68.0	1	38.5	2	Not testable	
95–99	63.0	1	—	0	Not testable	
100–104	98.0	8	—	0	Not testable	
Age (years)						
3	—	0	5.0	6	Not testable	
4	—	0	8.1	7	Not testable	
5	20.5	6	20.4	16	0.018	N.S.
6	36.2	23	21.6	32	6.63	<0.001
7	33.2	41	27.9	51	3.42	<0.01
8	44.0	40	30.1	42	5.64	<0.001
9	51.4	17	30.4	40	5.97	<0.001
10	57.4	8	32.9	35	5.45	<0.001
11	65.0	4	31.9	16	5.59	<0.001
12	—	0	30.9	9	Not testable	
14	—	0	36.5	2	Not testable	
15	112	1	36.8	14	Not testable	

histological data pooled over all years of the study. The two methods gave substantially different results for males; however, both visual and histological data suggested that all females matured at 60–65 cm FL and 8–9 years of age (Figs. 2, 3). Visual staging indicated that virtually all males were mature at 80–85 cm FL and 10–11 years. In contrast, histological results indicated almost all males were mature at 65–70 cm FL (estimated age 7–8 years, Turner et al. 1983) (Figs. 2, 3). That is, visual staging suggested that females matured about 20 cm smaller and 2–3 years younger than males; however, according to histological analysis, both males and females were mature and producing gametes at a similar size (60–70 cm FL). Thus, these results show that although males were producing sperm at 65–70 cm FL (estimated 7–8 years, Turner et al. 1983), they were not developing a large testicular mass until 80–85 cm FL and age 10–11 years.

We reasoned that predorsal adipose flap size might be a sign of maturity or reproductive status of males, because the height of the flap was larger in males than females above 65 cm and age 5 years (see previous section on Sexual Dimorphism). Additionally, the development of enlarged adipose flaps in males coincided with the size of 50% maturity (60–65 cm FL) as judged by development of enlarged testes (i.e., visual method), not at the smaller size of 50% maturity (50–55 cm FL) determined histologically (Fig. 2). Therefore, if predorsal adipose flap height were a sign of reproductive status in males, then mature males should have larger flaps than immature males; and this was so (Fig. 4). Furthermore, ANCOVA (with FL as the covariate) indicated that flap height was significantly larger in mature males than immature males (Table 2).

TABLE 2.—Mean and ANCOVA (with FL as the covariate) of predorsal adipose flap height in sexually mature and immature male tilefish. Flap height data set tested was restricted to a size range containing both mature and immature males (50–75 cm FL). df = degrees of freedom, ss = sum of squares, N = sample size, and $\bar{X}$ = mean.

MEAN			
	N	$\bar{X}$ flap height (mm)	X FL (cm)
Immature	94	28.7	59.4
Mature	87	42.7	68.6

ANCOVA				
Source	df	ss	F	$P > F$
Maturity	1	504.4	6.42	0.0121
FL	1	7,423.4	94.56	0.0001
FL X maturity	1	605.1	7.71	0.0061
Error	177	13,895.7		
Total	180	30,365.8		

Because we had studied reproduction during a period of rapid expansion of the fishery, i.e., the commercial longline fishery had decreased the tilefish population by one-half to two-thirds from 1978 to 1982 (Turner 1986), we decided to examine the data to determine if the fishery had affected the size at which tilefish were developing enlarged testes (i.e., attaining maturity as assessed by the visual method). A comparison of visually assessed sexual maturity at size and age for 1978 and 1982 suggested that females <50 cm FL were maturing at a smaller size in 1978 than in 1982, but that females >50 cm FL matured at very slightly larger sizes in 1978 than in 1982 (Table 3). Log-likelihood contingency tests of these data for females indicated that maturity-at-length was significantly different in 1978 and 1982, but the difference was due to the numbers of mature and immature fish between 41 and 55 cm (Table 3). The data for males <75 cm FL indicated that males matured at smaller size in 1982 than in 1978 (Table 4). A log-likelihood contingency

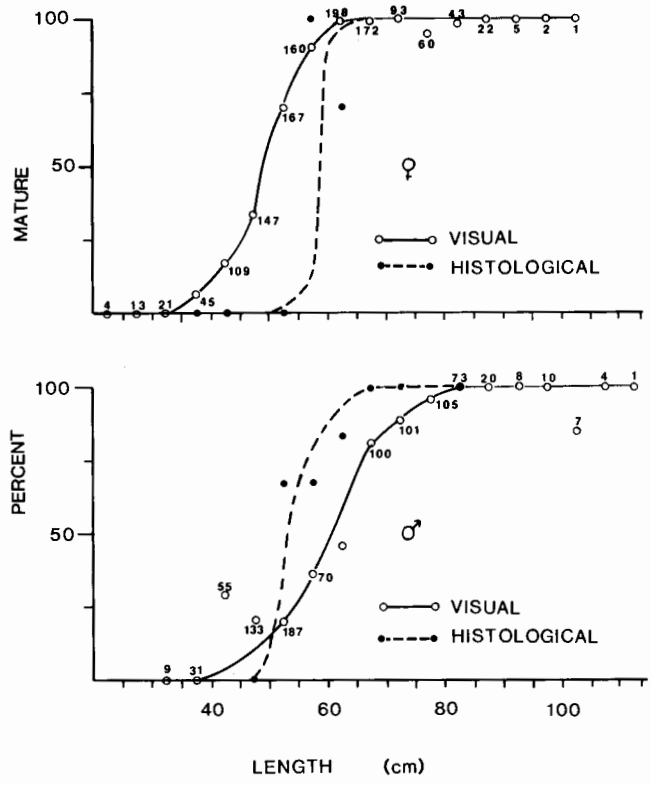

FIGURE 2.—The relationship of sexual maturity (by both visual staging and histological methods) and size (5 cm FL intervals) for female and male tilefish. Sample size is shown next to each point. Curves are fitted by eye.

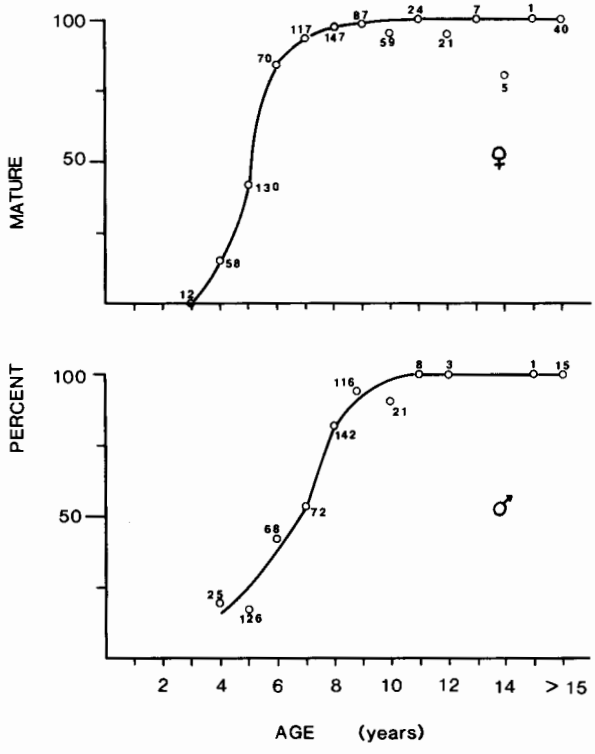

FIGURE 3.—The relationship of sexual maturity (by visual staging) and age for female and male tilefish. Sample size is shown next to each point. Curves are fitted by eye.

TABLE 3.—Female sexual maturity at length (visually determined) and log-likelihood contingency test that maturity at fork length (FL) in female tilefish was not different for 1978 and 1982. Critical chi-square values are $\chi^2_{0.05}$ (11 df) = 19.7 and $\chi^2_{0.01}$ (11 df) = 24.7. NT = not testable.

FL (cm)	1978 Maturity No.	1978 Maturity %	1978 Sample size	1982 Maturity No.	1982 Maturity %	1982 Sample size	G-statistic
26–30	No data			0	0	1	NT
31–35	0	0	7	0	0	3	0
36–40	3	21	14	0	0	17	0
41–45	11	49	23	4	7	60	30.4
46–50	34	81	42	11	15	72	89.6
51–55	54	59	92	41	89	46	56.5
56–60	40	80	50	35	100	35	0
61–65	63	98	64	49	100	49	0
66–70	57	100	57	27	100	27	0
71–75	12	100	12	29	100	29	0
76–80	12	92	13	14	93	15	0.2
81–65	10	100	10	4	100	4	0
86–90	6	100	6	No data			NT
91–95	3	100	3	1	100	1	0
96–100	No data			1	100	1	NT
Total			393			360	176.7

TABLE 4.—Male sexual maturity at length (visually determined) and log-likelihood contingency tests that maturity at fork length (FL) in male tilefish was not different for 1978 and 1982. Critical chi-square values are $\chi^2_{0.05}$ (10 df) = 18.31 and $\chi^2_{0.01}$ (10 df) = 23.2. NT = not testable.

FL (cm)	1978 Maturity No.	1978 Maturity %	1978 Sample size	1982 Maturity No.	1982 Maturity %	1982 Sample size	G-statistic
31–35	0	0	4	No data			NT
36–40	0	0	15	No data			NT
41–45	5	28	18	11	52	21	4.4
46–50	10	24	42	50	79	63	59.9
51–55	13	12	105	16	43	37	47.3
56–60	0	0	15	19	73	26	0
61–65	8	44	18	12	71	17	5.2
66–70	15	60	25	16	89	18	13.7
71–75	31	79	39	15	94	16	8.9
76–80	47	96	49	20	91	22	1.8
81–85	28	100	28	14	100	14	0
86–90	10	100	10	5	100	5	0
91–95	3	100	3	2	100	2	0
96–100	8	100	8	No data			NT
101–105	3	100	3	No data			NT
106–110	1	100	1	No data			NT
111–115	1	100	1	No data			NT
Total			384			241	141.2

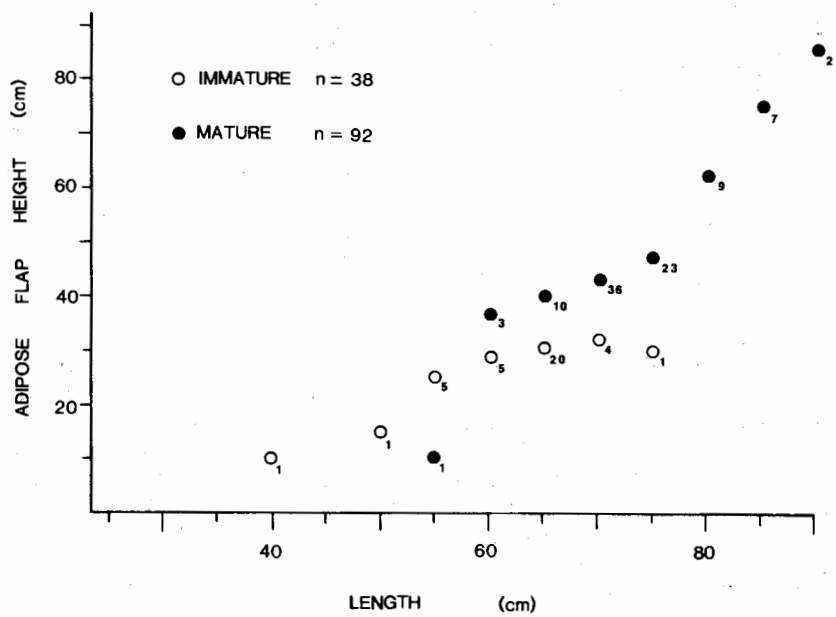

FIGURE 4.—Mean predorsal adipose flap height at length (5 cm FL intervals) for sexually mature and immature male tilefish. Maturity was assessed by visual staging. Sample size is indicated for each interval.

test indicated that maturity-at-age in males for the two years was highly significantly different (Table 4).

Analysis of visual maturity at age data gave less ambiguous results. Percent of females mature at age in 1978 and 1982 was not significantly different (Table 5). However, males matured at younger ages in 1982 than 1978, and the differences between years were highly statistically significant (Table 6).

TABLE 5.—Female sexual maturity at age (visually determined) and log-likelihood contingency tests that maturity at age in female tilefish was not different for 1978 and 1982. Critical chi-square values are $\chi^2_{0.05}$ (9 df) = 16.9 and $\chi^2_{0.01}$ (9 df) = 21.7. NT = not testable.

Age (yr)	1978 Maturity No.	1978 Maturity %	1978 Sample size	1982 Maturity No.	1982 Maturity %	1982 Sample size	G-statistic
3	0	0	1	0	0	3	0
4	1	8	13	1	5	19	0.3
5	35	43	82	5	33	15	3.1
6	19	83	23	3	75	4	0.6
7	47	90	52	8	100	8	0
8	68	97	70	20	95	21	0.7
9	14	100	14	14	100	14	0
10	2	100	2	12	100	12	0
11	No data			7	100	7	NT
12	1	100	1	8	100	8	0
13	No data			4	100	4	NT
14	No data			2	100	2	NT
≥15	9	100	9	4	100	4	0
Total			267			121	4.7

TABLE 6.—Male sexual maturity at age (visually determined) and log-likelihood contingency tests that maturity at age in male tilefish was not different for 1978 and 1982. Critical chi-square values are $\chi^2_{0.05}$ (8 df) = 15.5 and $\chi^2_{0.01}$ (8 df) = 20.1. NT = not testable.

Age (yr)	1978 Maturity No.	1978 Maturity %	1978 Sample size	1982 Maturity No.	1982 Maturity %	1982 Sample size	G-statistic
4	1	6	16	3	75	4	34.5
5	10	10	96	7	41	17	44.8
6	3	19	16	8	80	10	27.6
7	6	38	16	6	75	8	22.3
8	41	77	53	15	75	20	0.6
9	23	85	27	19	100	19	0
10	5	100	5	6	86	7	0
11	2	100	2	1	100	1	0
12	1	100	1	2	100	2	0
≥15	11	100	11	No data			NT
Total			246			88	129.8

TABLE 7.—Sex ratio at length and log-likelihood tests that sex ratio was not different from 1:1 at 5 cm FL intervals. All *G* scores were calculated using Yates correction for small sample sizes. Critical chi-square values are $\chi^2_{0.05}$ (1 df) = 3.84 and $\chi^2_{0.01}$ (1 df) = 6.64. NT = not testable.

Fork length (cm)	Number of females	Percent	Number of males	G-statistic
46–50	46	46	54	0.6
51–55	95	41	134	6.7
56–60	56	78	16	23.5
61–65	66	78	19	27.5
66–70	74	69	33	16.1
71–75	18	30	43	10.5
76–80	14	21	53	25.8
81–85	13	30	31	7.6
86–90	7	37	12	1.3
91–95	5	63	3	0.4
96–100	0	0	9	NT
101–105	0	0	4	NT
106–110	0	0	2	NT
111–115	0	0	1	NT

Sex Ratio

To minimize the chances of obtaining biased results caused by the effects of fishing we estimated sex ratio at size and age using only data collected in 1978 when the tilefish population was lightly exploited. Proportions of males and females were similar in the 46–50 and 51–55 cm FL intervals, although the ratio in the 51–55 cm FL interval tested significantly different at $P < 0.05$ (Table 7). Males were significantly predominant (70–80%) between 71 and 90 cm FL. At the 91–95 cm FL size females were predominant once again (>50%), although not significantly so (Table 7). Above 100 cm FL only males were collected.

The general pattern of sex ratio at age in 1978 seems to have been equal proportions of the sexes through about age 20 years, with only females present from ages 29 to 36 years. Log-likelihood tests of sex ratio at age showed no significant differences from equality except for ages 7 and 8 years; sex ratio at age was not testable for ages 29–36 years because only females were present (Table 8).

Although sex ratio was skewed with age and size, the estimated sex ratio for the entire population was different from 1:1 in 1978 (Table 9). We calculated the population to be 46.2% males, and could not reject the null hypothesis that sex ratio is not different from 1:1 ($\chi^2 = 0.15$, df = 1, $\chi^2_{0.05} = 3.84$) in the population ≥50 cm FL.

Spawning

Several lines of evidence suggest that tilefish in the Mid-Atlantic–southern New England area are

TABLE 8.—Sex ratio at age and log-likelihood tests that sex ratio at age was not different from 1:1. All *G* scores were calculated using Yates correction for small sample sizes. Critical chi-square values are $\chi^2_{0.05}$ (1 df) = 3.84 and $\chi^2_{0.01}$ (1 df) = 6.64. NT = not testable.

Age (yr)	Number of females	Percent	Number of males	*G*-statistic
4	1	100	0	NT
5	43	46	50	0.7
6	10	67	5	2.5
7	40	78	11	18.8
8	69	62	42	7.1
9	20	49	21	1.0
10	2	29	5	2.4
11	0	0	2	NT
16	2	40	3	0.8
19	2	50	2	Equality
29	1	100	0	NT
30	1	100	0	NT
31	1	100	0	NT
32	2	100	0	NT
33	1	100	0	NT
34	1	100	0	NT
35	1	100	0	NT
36	1	100	0	NT

TABLE 9.—The proportion of male tilefish in the 1978 population ≥50 cm FL, $P = \sum_{i}^{n} L_i M_i$ where L and M = the proportion of all fish and males, respectively, in the ith 5 cm FL interval, and n = the number of size intervals. L_i was determined from the 1978 commercial longline catch of tilefish.

Fork length (cm) *i*	Proportion of all fish *L*	Proportion of males *M*	Proportion of males in population *P*
<50	0.026	0	0
51–55	0.058	0.540	0.032
56–60	0.158	0.253	0.026
61–65	0.073	0.167	0.012
66–70	0.162	0.267	0.044
71–75	0.191	0.646	0.127
76–80	0.110	0.792	0.089
81–85	0.087	0.744	0.066
86–90	0.682	0.611	0.043
91–95	0.021	0.400	0.008
96–100	0.011	0.875	0.010
≥101	0.036	1.000	0.004
			= 0.462

fractional spawners from about March through November, although most of the reproduction evidently occurs from May to September. Some females with free ova in the ovarian lumen (running ripe) were present in March through August and in October and November. From May through August, 89–98% of the females were ripe or running ripe (Fig. 5). Running ripe or ripe males were not as frequently observed as were females in a similar reproductive state. In fact, only very large males (75–80 cm FL) were observed with a large creamy white swollen testicular mass. Ripe males were found in January, March, May through August, October, and November, but the highest proportions (23–46%) were present in May through August (Fig. 5).

GSI data for females indicated a similar seasonal spawning pattern (Fig. 6). Highest GSI values consistently occurred from May through August, when ovaries accounted for 3.5–8.3% of gutted body weight.

Analysis of ovum-diameter data also suggested that spawning occurred mostly from May to September, and indicated that spawning was fractional, i.e., ova were released in batches. Highest monthly mean developing ovum diameters (0.30–0.42 mm) occurred in May through August (Fig. 7). During these months mean ovum diameter was usually >0.35 mm (Fig. 7). During other months, mean ovum diameter was always ≤0.30 mm. The size-frequency distribution of ova from running ripe females was polymodal (Fig. 8), suggesting multiple spawnings by individual females during the reproductive season.

Tilefish may not utilize the liver and soma to store energy as fat for mobilization to the gonads in preparation for spawning as many species are thought to do (Hoar 1957). HSI for both males and females showed a distinct pattern of seasonal variation, but highest values occurred during summer (spawning season) and lowest in winter (Fig. 9). Somatic condition factor (eviscerated weight, g/FL^3) showed no discernable seasonal pattern in males or females.

Fecundity

Because tilefish are fractional spawners, fecundity (ovarian egg count) was estimated from females collected early in the spawning season (i.e., May to early June) to minimize the chance of using a partially spawned ovary and underestimating egg number. Estimates of fecundity ranged from approximately 195,000 for a 53 cm FL (2.1 kg) female to 10 million for a 91 cm FL (13 kg) female, with a mean egg count of 2.28 million (n = 49, SD = 1.02). The 91 cm FL female with 10 million eggs was exceptional; all other estimates were <4.1 million, even for other large females 80 and 86 cm FL. Therefore, we judged that the two largest fish, 91 and 86 cm FL, were outliers and developed predictive equations for egg count without using outlier data.

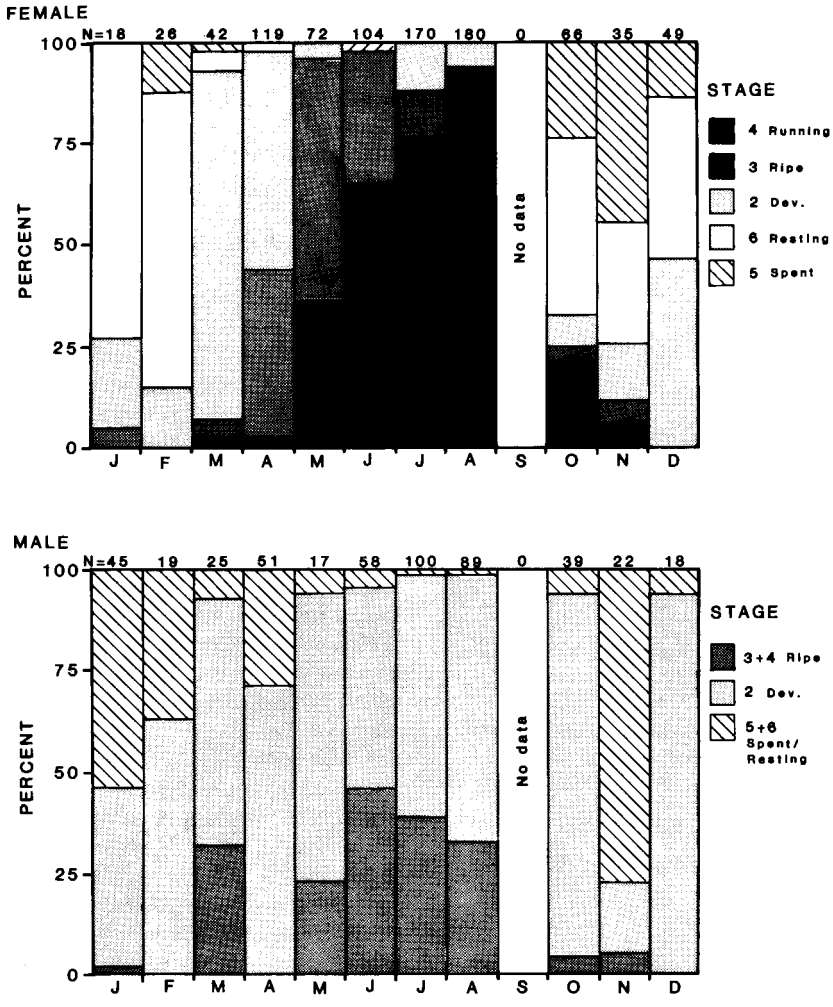

FIGURE 5.—Reproductive seasonality of female and male tilefish as indicated by the percent of various visual maturity stages collected by month from 1978 to 1982.

Log-transformed models produced slightly superior fits, with length proving a slightly better predictor of ovarian egg count than weight ($\log_e Y = 4.75 \log_e \mathrm{FL} - 5.2$, $r^2 = 0.62$, $n = 48$; $\log_e Y = 1.48 \log_e W + 2.48$, $r^2 = 0.59$, $n = 48$). Based upon our estimates, a first spawning female would produce <500,000 eggs.

DISCUSSION

Seasonality and Spawning

It seems clear that the northern stock of *Lopholatilus chamaeleonticeps* consists of fractional spawners over an 8 or 9 month season, with peak spawning from May to September. Our findings agree with the limited information previously reported. Collins (1884) reported ripe fish in July; Bigelow and Schroeder (1953) in August; Dooley (1978) in February, March, June, and July; Morse (MS)[9] March through August; and Freeman and Turner (1977) from mid-March to mid-September. Other members of the Branchiostegidae (*Caulolatilus microps*, *C. chrysops*, *C. princeps*, *C. affinis*,

[9]Morse, W. W. Length, weight, spawning and fecundity of the tilefish, *Lopholatilus chamaeleonticeps*, from New Jersey waters. Unpubl. manuscr. Northeast Fish. Cent. Sandy Hook Lab., Natl. Mar. Fish. Serv., NOAA, Highlands, NJ 07732.

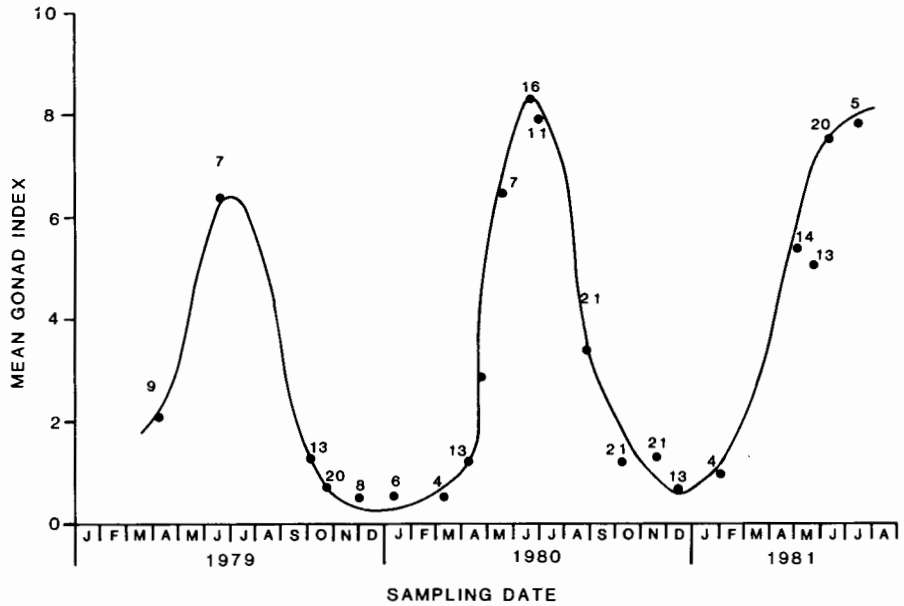

FIGURE 6.—Reproductive seasonality of female tilefish as indicated by monthly mean gonad index. Sample size is indicated for each month.

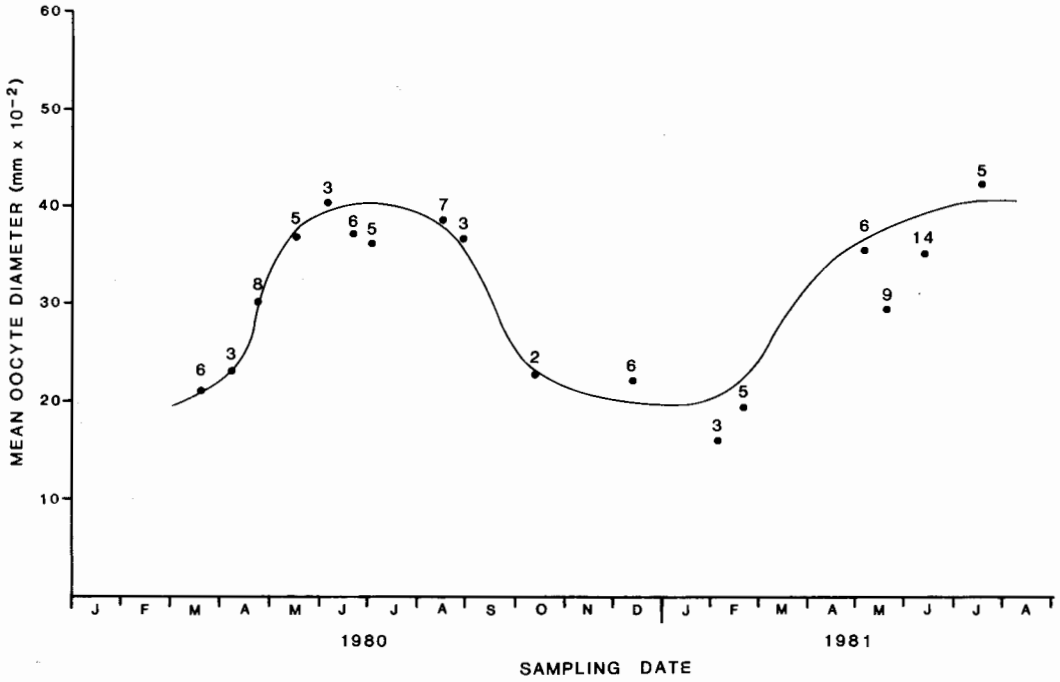

FIGURE 7.—Reproductive seasonality of female tilefish as indicated by monthly mean oocyte diameters. Sample size is indicated for each month.

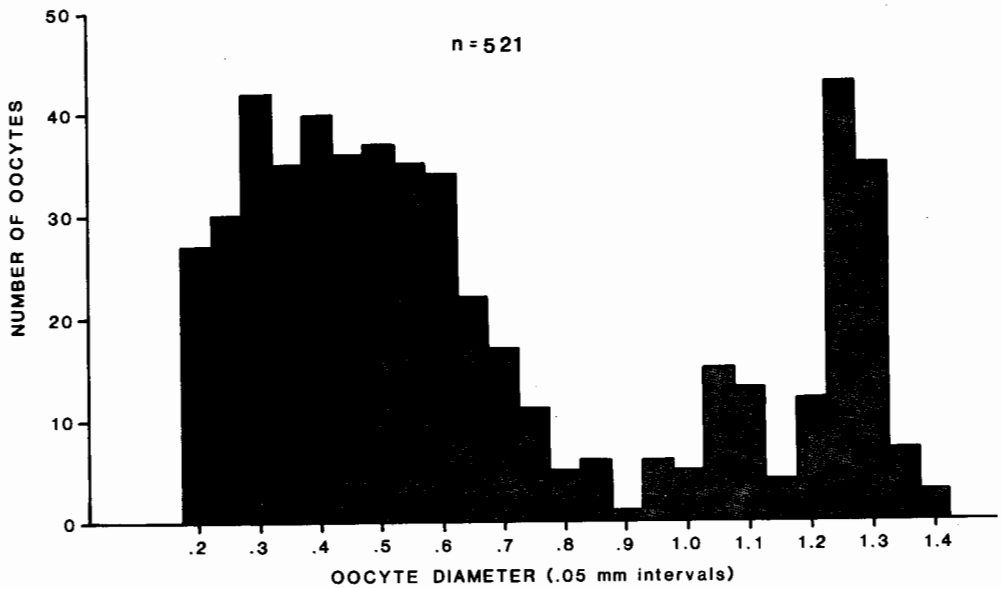

FIGURE 8.—Frequency distribution of oocyte diameters from a spawning 66 cm FL female tilefish (running ripe) collected in June 1979.

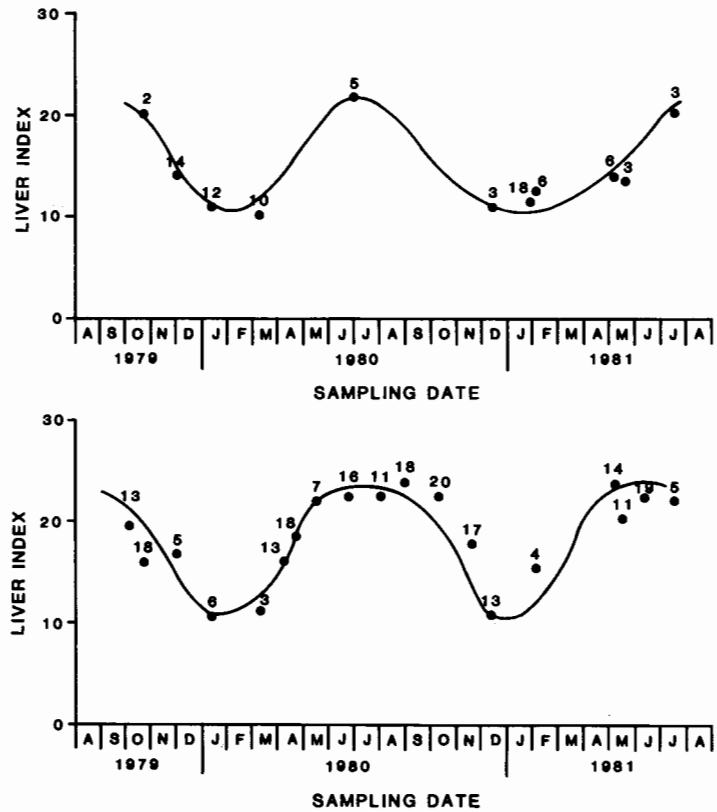

FIGURE 9.—Monthly mean heptosomatic index for male (upper) and female (lower) tilefish. Sample size is shown next to each mean.

Branchiostegus japonicus) all exhibit extended reproductive seasons centered around summer (Hayashi 1977, 1979; Dooley 1978; Ross and Merriner 1983). However, Erickson et al. (1985) reported that *L. chamaeleonticeps* spawned from March through June off Georgia in the South Atlantic Bight. The reason for the shorter reported spawning season for *L. chamaeleonticeps* in the South Atlantic Bight is uncertain.

Fractional spawning by individual females was indicated by the polymodal frequency distribution of ovum diameters. This asynchronous follicular development is typical of fractional spawning (deVlaming 1983), and has been reported for *L. chamaeleonticeps* in the South Atlantic Bight (Erickson et al. 1985) and Mid-Atlantic Bight (Morse fn. 9). Fractional spawning based upon polymodal ovum-diameter distributions has also been reported for the confamilials *C. microps* and *B. wardi* (Dooley 1978; Ross and Merriner 1983).

Our estimates of fecundity in tilefish are consistent with those in the literature. We agree with Gale and Deutsch (1985) that the term fecundity is incorrectly applied to many fishes, especially fractional spawners, because in most cases there is no reasonable means to determine which or how many oocytes or developing ova will be released, or how many ovarian ova will be resorbed after spawning and never released. Therefore, we recognize that our ovarian egg count data provides only a rough estimate of actual fecundity. Erickson and Grossman (1986) found the relationship between fecundity and weight to be best described by a log transformation ($\log_e F = 1.497 \log_e W + 12.59$, $r^2 = 0.93$); while Morse (fn. 9) found the relationship best fitted to a linear form ($F = -966{,}471 + 887\ W$, $r^2 = 0.61$). To compare our estimates further we calculated relative fecundity using extreme point estimates of fecundity reported by other authors (Erickson and Grossman 1986, $414 \cdot g^{-1}$ and $950 \cdot g^{-1}$ for 2.0 and 8.0 kg fish; Morse fn. 9, $543 \cdot g^{-1}$ and $867 \cdot g^{-1}$ for 3.5 and 9.0 kg fish) and this study ($119 \cdot g^{-1}$ and $769 \cdot g^{-1}$ for 2.1 and 13.0 kg fish), and using predictive equations (Table 10). Comparing the range of point estimates, the three studies are similar, however our findings agree more closely with Erickson and Grossman (1986) when the comparison is based upon predictive equations. The inconsistency in the comparison is because Morse (fn. 9) used a linear equation, thus assuming that egg production per gram of body weight was constant for all body weights, and Erickson and Grossman (1986) and this study chose curvilinear equations. It is possible to conclude that small tilefish, like some other fishes (Grimes 1987), produce fewer eggs per unit body weight than larger fish.

We compared numbers of ova actually found in ripe ovaries collected on 1 July ($n = 3$) and 28 August ($n = 6$) to ovarian egg numbers predicted for the same size females to estimate what proportion of ova had been spawned in the mid- and late-spawning season. The analysis suggested that approximately 25% of ovarian eggs were spawned by July and 50% by the end of August. The ovaries of two postspawning females collected on 10 October contained considerable quantities of ovarian eggs >0.15 mm in diameter. These ova accounted for 15–20% of the predicted ovarian egg number. By December 11 ($n = 3$) the number of ovarian eggs >0.15 mm in diameter had decreased to about 5% of the predicted maximum ovarian egg number. Since atretic ova were observed in histological preparations of ovaries in spent and resting stages, and resorption is well documented in other teleosts (Hoar 1957; Smith 1965; Combs 1969; Foucher and Beamish 1977; LaRoche and Richardson 1980; Waltz et al. 1982), it seems reasonable to conclude that at least 15–20% of the maximum ovarian egg number are never spawned and are resorbed during the winter.

Sexuality

Our results agree with Erickson and Grossman (1986) that tilefish are gonochoristic and that secondary gonochorism is a possibility. Gonad microstructure and development of adult (>50 cm FL) tilefish were typical of most male and female oviparous teleosts, and identical to that described for

TABLE 10.—Comparison of ovarian egg number and relative ovarian egg number for small (2.0 kg) and large (9.0 kg) female tilefish calculated following Erickson and Grossman (1986), Morse,[1] and this study.

	Body weight	Egg number	Relative egg number
Erickson and Grossman	2.0	828,723	414
	9.0	7,875,326	875
Morse	2.0	1,773,003	887
	9.0	7,982,003	887
This study	2.0	917,434	459
	9.0	8,498,245	944

[1]Morse, W. W. Length, weight, spawning and fecundity of the tilefish, *Lopholatilus chamaeleonticeps*, from New Jersey waters. Unpubl. manuscr. Northeast Fish. Cent. Sandy Hook Lab., Natl. Mar. Fish. Serv., NOAA, Highlands, NJ 07732.

male and female *Caulolatilus microps* (Ross and Merriner 1983) and female *Lopholatilus chamaeleonticeps* (Erickson et al. 1985). Like Ross and Merriner (1983) and Erickson and Grossman (1986), we also found a few adult males (2 of 50) with ovigerous tissue (previtellogenic residual oocytes) in the testicular mass. Histological sections of testes revealed no gross structural features that indicated prior functional female status (e.g., remnants of an ovarian lumen (Sadovy and Shapiro 1987)). Furthermore, no ovary was ever observed in transition to a testis (transitional ovotestes), however transition can occur within a matter of weeks. Similar to other branchiostegids (*C. microps*, Ross and Merriner 1983; *Branchiostegus wardi* and *B. serratus*, Dooley 1978; *L. chamaeleonticeps*, Erickson and Grossman 1986), sex ratios were skewed in favor of males at large sizes. However, both sexes were present at most sizes and ages (45–95 cm FL and 5–10, 16, and 19 years) and only females were present at ages 29–36 years, ruling out protogyny. Disparate sex ratios at size are apparently due to differential growth and mortality rates between sexes (Turner et al. 1983; Harris and Grossman 1985).

Our histological examination of juvenile gonads suggest that some *L. chamaeleonticeps* may undergo prematurational sex reversal. All juvenile gonads examined (63 fish, 146–400 mm FL) appeared to be female, based upon gonad cell structure (i.e., presence of only oogonia and previtellogenic oocytes). We are very tentative about the determination that all of these small fish (<400 mm FL) were females, because undifferentiated gonia, oogonia, and spermatogonia are very similar in appearance (Yamamoto 1956; Hoffman 1963; Hyder 1969; Ross 1978). Once a gonad has developed gross structure such as spermatogenic tubules and crypts, or an ovarian lumen, determining sex is straightforward. We found residual oogonia in 2 of 50 histologically examined testes. We found no juveniles with truly intersexual gonads, nor were we able to observe a lumen. Ross and Merriner (1983) suggested that the confamilial *C. microps* underwent prematurational sex reversal, and that gonochorism in *C. microps* might be a regression from monandric protogyny. Their conclusions were based upon findings from four juveniles (one specimen with a totally ovarian gonad and the remaining three with gonads that contained substantial amounts of testicular tissue), and adult males (8 of 41 examined) with residual oocytes in the testicular mass.

That prematurational sex reversal has been observed among several families and species of fish suggests that either prematurational sex reversal is more common among fishes than suspected, or that early gonad development in fishes involves an all-female or female-appearing stage. For example, the salmonid *Salmo gairdneri* (Mrsic 1923); the cyprinids *Brachydanio rerio* (Takahashi 1977), *Barbus tetrazona* (Takahashi unpubl. data cited in Takahashi 1977), *Rodeus ocellatus* (Shimizu 1979), *Cyprinus carpio* (Davis and Takashima 1980), and *Carassius auratus* (Stromsten 1931; Takahashi and Takano 1971); and the anabantids *Macropodus concolor* and *M. opercularis* (Schwier 1939) are hatched as all females having ovaries with no testicular characteristics. About one-half continue normal development to mature females and about one-half undergo a transitory intersexual stage before becoming adult males. The female juvenile cyprinids *Brachydanio rerio*, *Barbus tetrazona*, *Rhodeus ocellatus*, and *Carassius auratus* all develop an ovarian lumen, as well as oogonia and previtellogenic oocytes. Prematurational sex change is reportedly common among the hermaphroditic Sparismatinae (Scaridae) that spend their entire life as males (Robertson and Warner 1978).

Social Control

We interpret the data on sexual maturity and sexual dimorphism to suggest that some sexually mature males delay participation in spawning for up to 3 years and 10–15 cm, and that this mating system is socially mediated. Histological assessments of sexual maturity revealed that both males and females produced mature gametes by about 50 cm FL and 5–6 years. However, visual inspection of gonads to determine maturity gave the same result as the histological evidence in females, but indicated that males were not mature until attaining 65–70 cm FL and 7–8 years. Ross and Merriner (1983) also reported that some *Caulolatilus microps* males that were visually assessed as immature were later shown by histological methods to be producing mature gametes, and Erickson and Grossman (1986) found *L. chamaeleonticeps* off Georgia that showed active, yet incomplete spermatogenesis.

Sexual dimorphism in tilefish is manifested in the size of the adipose flap which is conspicuously larger in males than females and larger ultimate body size in males; size of the adipose flap may be an indication of male breeding status. The adipose flap of males became larger at 65–70 cm FL (7–8 years) when males were judged sexually mature by visual inspection (i.e., had developed large testes), not

when they were functionally mature at 50 cm FL as revealed by histological methods.

A nonrandom mating system of pairing, involving mate selection by females, is consistent with the both sexual dimorphisms observed in tilefish. Female mate selection can convey a reproductive advantage to large males (Ghiselen 1969; Howard 1979), but in randomly mating species, females are usually larger than males (Ghiselen 1969). Female ability to discriminate males is required to support female mate selection (Howard 1979), which often leads to development of specialized structures and colorations by males for display (Krebs 1972; Warner and Robertson 1978). The enlarged adipose flap in tilefish certainly represents a conspicuous, highly visible feature in some adult males that could serve as a visual cue to signal male breeding status.

The evolution of a female mate selection system requires that a male have the ability to control resources important to the female (Howard 1979; Krebs and Davies 1984), and several lines of evidence suggest that male tilefish may be territorial. Burrowing is apparently the rule in the family (Able et al. 1987). Direct observation from submersibles and mark-recapture data indicated that tilefish orient to particular burrows, and may be long-term residents of their habitats (Grimes et al. 1983, 1986). Furthermore, time-lapse photography showed the same male-female pair of tilefish utilizing the same burrow over a 26-h period (Grimes et al. 1986), and pair formation has been observed in the branchiostegids *Malacanthus plumieri* (Clark and Ben-Tuvia 1973), *Hoplolatilus* sp. (Thresher 1984), and *H. starcki* and *H. cuniculus* (Randall and Dooley 1974).

We believe that our data indicate that tilefish have a mating system consisting of two classes of sexually mature males, a category actively engaged in spawning and a category of satellite males that do not spawn. Similar breeding systems have been described for several species of hermaphroditic reef fish (Popper and Fishelson 1973; Fishelson 1975; Warner and Robertson 1978; Robertson and Warner 1978; Warner and Hoffman 1980; Shapiro 1984). For example, there are scarid and labrid populations with large territorial terminal phase males that have preferred mating status, and nonterritorial initial phase males that have nonpreferred breeding status (Warner and Robertson 1978; Robertson and Warner 1978). Hermaphroditic populations of the serranid *Anthias squamipinnis* in the Gulf of Eilat have two behaviorally distinct types of males, a dominant territorial male that actively courts, interacts, and spawns with females, and smaller males that do not interact or spawn with females in the social group. The latter male category have filamentous degenerative gonads (Popper and Fishelson 1973; Fishelson 1975). These mating systems are characterized by strong sexual selection and maintenance of reproductive territories by males, and by being reef systems in which fish are habitat limited. Tilefish are also severely habitat limited, i.e., to burrowable clay substrate generally (Able et al. 1982; Grossman et al. 1985; Grimes et al. 1986).

During the period we studied reproduction, the fishery for tilefish was rapidly expanding, and one effect of fishing seems to have been to alter the structure of the mating system. Based upon both age-structured and non-age-structured population modeling, tilefish population density was reduced by about one-half to two-thirds from 1978 to 1982, apparently due to the rapid expansion of the commercial longline fishery (Turner 1986). Female size, and particularly age, at maturity do not seem to have been altered in any consistent fashion by the population reduction from fishing. Males, on the other hand, appear to have experienced profound changes in visually assessed maturity; they clearly were mature at smaller size (10 cm) and younger age (2–2.5 years) in 1982 than in 1978.

We interpret the decrease in size/age of maturity in males to be the effect of fishing. Fishing lowered population density, and in so doing may have made mating territories available to smaller and younger males. This interpretation is supported by the findings of Warner and Robertson (1978) and Robertson and Warner (1978) that the ratio of the two categories of sexually mature males (initial and terminal phase) in western Caribbean scarid and labrid populations was density dependent; i.e., relatively more initial phase males were found in dense populations.

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