GROWTH, MORTALITY, AND AGE/SIZE STRUCTURE OF THE FISHERIES FOR TILEFISH, *LOPHOLATILUS CHAMAELONTICEPS*, IN THE MIDDLE ATLANTIC-SOUTHERN NEW ENGLAND REGION

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ABSTRACT

Otoliths of tilefish taken in 1978 from the Middle Atlantic Bight and Southern New England region were used to determine length at age and growth rates. Marginal increment analysis revealed that annuli were formed once each year between March and May, and modes in the length-frequency histogram for small tilefish (<31 cm FL) in March-May agreed with back-calculated lengths at ages 1-3. Tilefish (sexes combined) grew about 10 cm FL per year for the first 4 years, and beyond that age males grew more rapidly than females. Maximum size of females was 95 cm FL and of males 112 cm FL, and maximum ages were 35 and 26 years, respectively. Von Bertalanffy growth formulae for both sexes were found to be significantly different with Hoetelling's T^2. Sex ratios at age generally were not significantly different from 1:1, and skewed sex ratios at length were attributed to differential growth rates. No significant differences were found between males and females in the regressions of both whole and eviscerated weights on length.

Length-frequency histograms of tilefish from the longline fishery in 1974-80 showed truncation of the size structure accompanied by a decrease in the size at full recruitment in more recent years. In 1974, 71% were >70 cm FL, while in 1980 these larger fish made up about 19% of the catch. Length frequencies from three fisheries in 1978 had a similar modal size (51-55 cm FL), but some differences in size structure. The recreational and longline fisheries caught larger fish (37 and 53%, respectively, between 56 and 75 cm FL) than the foreign trawl fishery (17% at 56-75 cm FL and 51% at 26-50 cm FL). The differences in length frequencies were reflected in the age structures of the three fisheries, with the foreign trawls exploiting 3-7 year olds (91% of the catch), recreational anglers 4-9 year olds (98%), and longline 4-9 year olds (90%).

The catch curve for the longline fishery was concave, probably the result of increased fishing pressure in recent years. Estimates of the instantaneous rate of total mortality were 0.46 for the more linear portion of the longline catch curve and 0.60 for the catch curve from the foreign trawl fishery.

Tilefish, *Lopholatilus chamaeleonticeps*, are large [to about 120 cm FL (fork length) and 30 kg], demersal branchiostegids found along the outer continental shelf in 80-540 m from Nova Scotia to Surinam (Dooley 1978; Markle et al. 1980). In the Middle Atlantic Bight and Southern New England waters they have usually been found in temperatures of 9°-14°C and depths of 100-240 m.[4] After a brief period as pelagic larvae (Fahay and Berrien 1981; Berrien in press), tilefish settle to the bottom. Both juvenile and adult tilefish ranging in size from 10 or 20 cm FL to >1 m FL have been observed occupying vertical burrows (Able et al. 1982), horizontal excavations in submarine canyon walls called "pueblo villages" (Cooper and Uzmann 1977; Warme et al. 1978), and scour depressions around boulders (Valentine et al. 1980). Tilefish excavations appear to be local centers of abundance for several species of crustaceans and fish; thus through their burrowing activity, tilefish may have considerable impact on outer continental shelf communities (Able et al. 1982).

Commercial exploitation of Middle Atlantic-Southern New England tilefish began in 1915, and landings have been made in nearly all years since that time. Annual landings from this unit stock (Katz et al. 1983) have fluctuated from a peak of 4,500 metric tons (t) landed in 10 mo in 1916 to <1 t reported for several years since then. Commercial landings have risen during the 1970's, due to the development of a longline fishery currently centered in New Jersey and New York. Landings in 1977-80 (2,061, 3,412, 3,840, and 3,575 t, respectively) have exceeded all years except 1916 for which information is available (Freeman and Turner footnote 4; U.S. Department of

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Commerce 1980a-c; Christensen[5]), and the tilefish fishery has been the most valuable finfish fishery in New Jersey during 1978-80 and New York in 1979-80 (U.S. Department of Commerce 1980a-c; Grimes et al. 1981; Christensen footnote 5). Small fisheries which exploit another stock of tilefish (Katz et al. 1983) exist off South Carolina (Creel 1981; Christensen footnote 5), southeastern Florida, and in the Gulf of Mexico (Grimes et al. 1980)

Despite the economic and ecological importance of tilefish, little is known about its life history or the impact of fishing on the Middle Atlantic-Southern New England population (Freeman and Turner footnote 4; Grimes et al. 1980). The purpose of this paper is to present age, growth, and mortality information on tilefish from that region, to compare size and age structure of the catch of some of the recently active tilefish fisheries, and to examine changes in the size structure of longline catches during 1974-80.

MATERIALS AND METHODS

Samples of tilefish from the Middle Atlantic-Southern New England region were obtained from domestic longline and recreational fisheries, National Marine Fisheries Service (NMFS) trawl surveys, and the foreign trawl fishery. Sample information included the nature of the sample (random or nonrandom), capture method, location, and date. Length (FL in cm) was recorded for individual fish and often sex and weight (whole and/or eviscerated) were noted as well. It was often impossible to determine the sex of some small tilefish by macroscopic examination of the gonads so that three sex classifications—male, female, and unknown—were used. No males were identified <50 cm FL, and most of the fish of unknown sex were <55 cm FL, though some were as large as 71 cm FL.

After preliminary examination of scales and sections of sagittal otoliths and third dorsal rays, otoliths were selected as primary aging structure. Up to five sections (0.15-0.35 mm thick) were taken from the center of each otolith in the dorsoventral plane using a diamond blade saw. Sections were examined with a dissecting microscope at 10X with reflected light and a dark background. The transition from the translucent (hyaline) to opaque tissues was most pronounced, and was defined as the edge of an annulus. It was usually impossible to follow annuli around an entire section of a tilefish otolith, so that, when the

number of rings was in doubt, rings were counted on each side of the sulcus acusticus (Fig. 1). We made measurements to each annulus and to the otolith edge in the medioventral region of the section which passed through or closest to the center of the otolith. We used a filar micrometer and recorded distances in ocular micrometer units (one unit = 0.082 mm). Because tilefish otoliths grow allometrically in the medioventral region, measurements were made from the core of the otolith to the furthest point from the core on each annulus and on the edge of the section (Fig. 1B). Hayashi (1976a) made similar measurements, though in a different plane, on the whole otoliths of the red tilefish, *Branchiostegus japonicus japonicus.*

All otoliths of *Lopholatilus chamaeleonticeps* were read once, and one-third were reexamined. All of the first 120 otoliths were read twice. Close agreement between first and second readings occurred in a subsample of 50 from the next 150 otoliths; therefore, routine second readings were discontinued for fish with <10 annuli. Otoliths with 10 or more annuli were assigned an age only after agreement was reached between several counts; when agreement was not achieved, the median number of annuli from at least five counts was used.

Empirical lengths at age were used in constructing an age-length key; however, a few fish did not form annuli by the end of the usual period of annulus formation. To reduce bias which would result from assigning such fish to a younger age, we adopted the following rule: Any fish captured in the 3 mo after the end of the usual annulus formation period with hyaline tissue at the edge of the otolith and a marginal increment at least half as large as the increase in size of the otolith in the previous full year was assigned an age corresponding to its number of rings plus one.

Least-squares linear regression was used to describe the otolith size (OS): fork length (FL) relationship and the length:weight relationships. The final regression lines were converted to functional regression equations (Ricker 1973). We added a factor to the OS:FL equation which compensated for variation in otolith size at a given fork length. The distance to each annulus was adjusted by the ratio of the average otolith size for fish of the fork length in question to the observed otolith size for that fish (Bagenal and Tesch 1978). The resulting equation was used to compute back-calculated lengths.

Analysis of covariance (ANCOVA) was used to compare slopes of regression lines between sexes, and analysis of variance (ANOVA) was used for comparison of mean marginal increments, mean growth increments, and mean lengths at age. The SAS
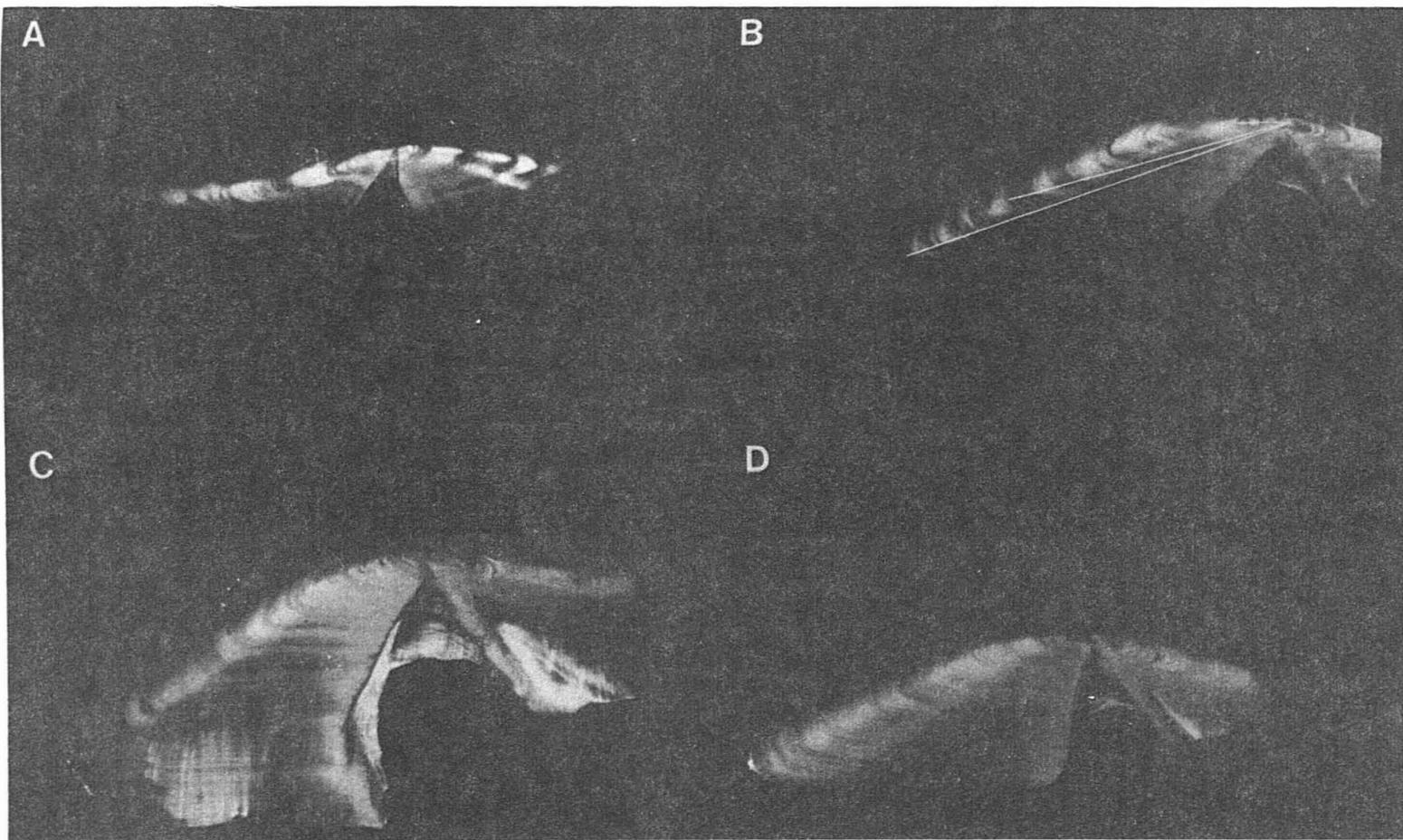
FIGURE 1.—Four sections of tilefish otoliths. The medioventral region is on the right in A and on the left in B, C, and D. The medial edge is the lower edge of each section, and the sulcus acusticus is the notch seen in the middle of the medial face. A) Section of an otolith from a 3-yr-old tilefish of 33 cm FL and of unknown sex. B) An otolith section from an 8-yr-old male tilefish of 77 cm FL. White lines indicate lines used to measure from the core to the edge of the first and fifth annuli and to the edge of the otolith. C) An otolith section from an 89 cm FL female tilefish aged 30 yr showing the aberrant otolith growth pattern with tissue only being deposited on the medial edge. D) Section of an otolith from an 89 cm FL male aged 8 yr.

general linear model (Helwig and Council 1979) was used for these analyses, and the partial sums of squares (Type IV) were used as test criteria.

The von Bertalanffy growth formula was fit to the data from each fish with SAS nonlinear regression, using Marquardt's method (Helwig and Council 1979). This provided repeat observations of length at each age, allowing us to estimate variance about the regression line and to compare curves with Hoetelling's T^2 (Morrison 1976; Bernard 1981).

We divided the fishing grounds into two areas, Hudson Canyon and Southern New England (Fig. 2), to consider differences in the length frequency of

tilefish. A weighting procedure was used in calculating length frequencies to eliminate bias introduced by excessively large samples collected during a season. Equal weight was given to each large sample ($n > 50$) from an area in a year and season, and seasonal longline landings (Christensen footnote 5) were used to weight the seasonal length frequencies when computing the annual length frequency. If a year and area had <200 observations, no weighting was used in calculating the length frequencies.

The total instantaneous mortality rates (Z) were calculated through least-squares regression of the natural log of the number in an age group on age.
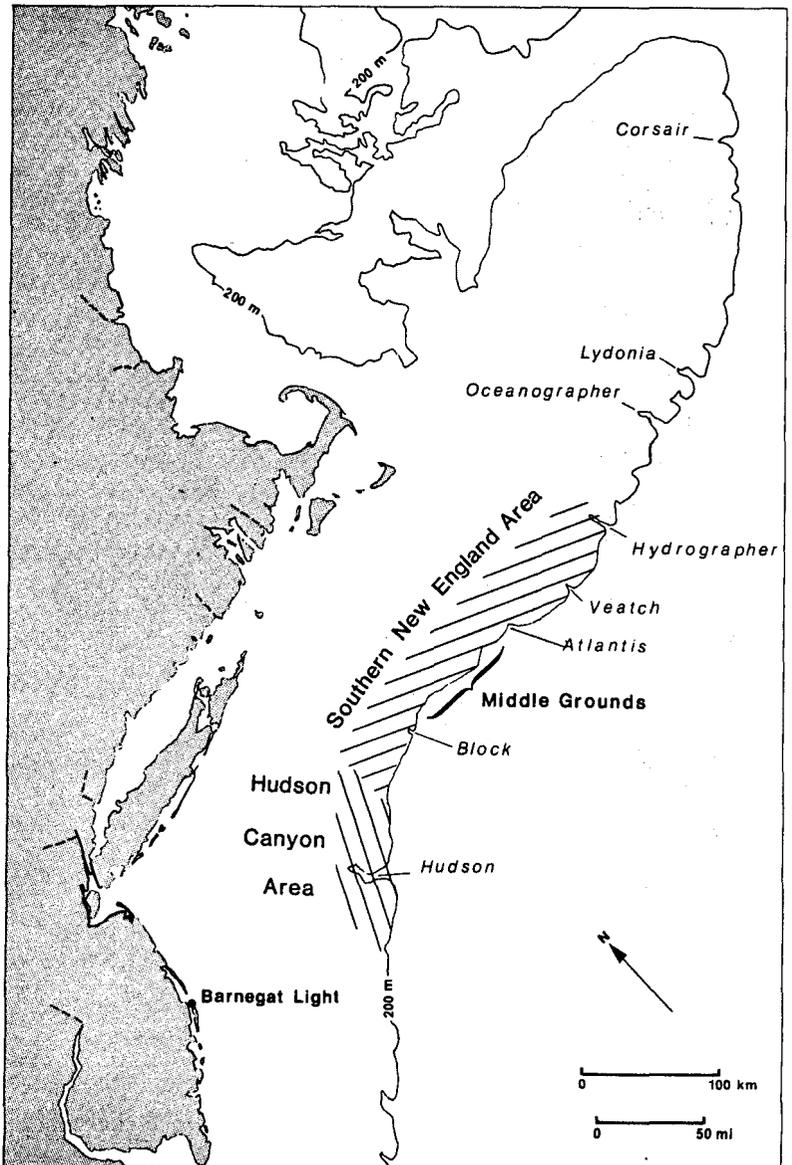

FIGURE 2.—Map of the continental shelf from New Jersey to Maine showing some of the major submarine canyons from the Middle Atlantic Bight to Georges Bank. Two primary fishing areas are labeled, Hudson Canyon (long. 71°55'-72° 42'W) and southern New England (long. 67°00'-71°54'W).

RESULTS

Otoliths were collected from 755 tilefish in 1978. Ninety percent of the sections (682) were readable and used for age and growth studies. Of these, 305 were females, 233 were males, and 144 were of unknown sex. Changes in growth pattern of the otolith of some of the largest fish presented problems for analysis of growth rates. Thirteen fish (11 females and 2 males) of 84-108 cm FL stopped depositing tissue on the ventral side of the otolith but continued to grow on the medial face (Fig. 1C). Fish with this aberrant otolith growth pattern were not included in marginal increment analysis or in estimation of the OS:FL relationship. However, measurements were made to annuli formed before the otolith growth change.

Validation

Mean marginal increments in ocular micrometer units were lowest in June and increased to a maximum in January and February (Fig. 3). ANOVA indicated highly significant differences between monthly means ($P < 0.01$). We concluded that annuli were formed once and only once each year, and most fish completed annulus formation by 1 June. Younger tilefish apparently formed annuli later than
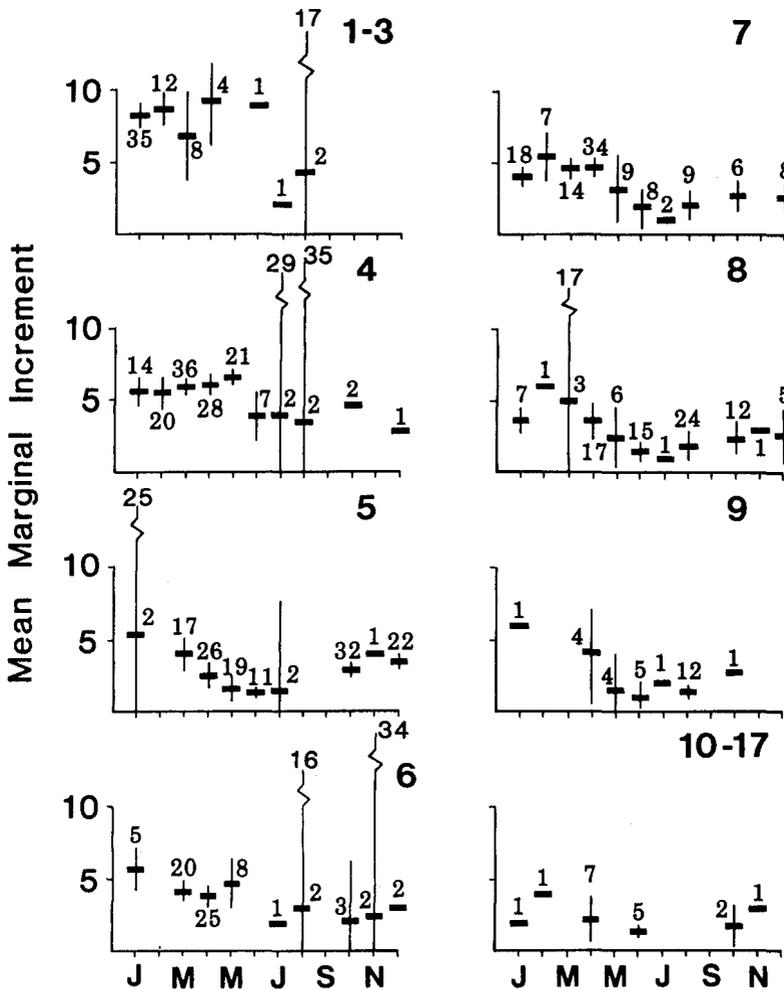
FIGURE 3.—Mean marginal increment in ocular micrometer units by month for eight age groups of tilefish, based on number of annuli formed. Number of annuli is in the upper right corner of each graph, the horizontal bar is the mean, the number just above or below the mean is the sample size, and the vertical line is the 95% confidence interval. Some confidence intervals exceed the size of the graph with their smallest values <0 and their largest values given above the end of the interval.

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older tilefish; the mean marginal increment for fish with 1-3 and 4 bands did not decline until late in spring, while the mean marginal increment of older fish usually began to decline in March (Fig. 3). Eleven fish apparently had not formed annuli by 1 June. They had hyaline edges and marginal increments equal to 50-120% of the increase in their otolith size in the previous year. Four of these fish (one female and three of unknown sex) had formed 3 or 4 annuli, six were females with 7-9 annuli, and one was a male with 6 annuli.

Otolith size increased with fish size and thus provided added evidence for the validity of using the otoliths for aging tilefish. A log-log regression model fit the data best. ANCOVA showed no significant differences in slope or elevation between males and females ($P > 0.05$) in the 50-73 cm FL range for which there were nearly equal numbers of each sex. Therefore, one least-squares regression line was derived for all fish ($r^2 = 0.90, n = 663$) and converted to a functional regression equation [ln (FL) = −0.4369 + 1.1112 ln (OS)].

Seasonal length-frequency analysis of small tilefish (2-30 cm FL) taken over several years (Fig. 4) showed modes near the time of annulus formation that agreed closely with the back-calculated lengths
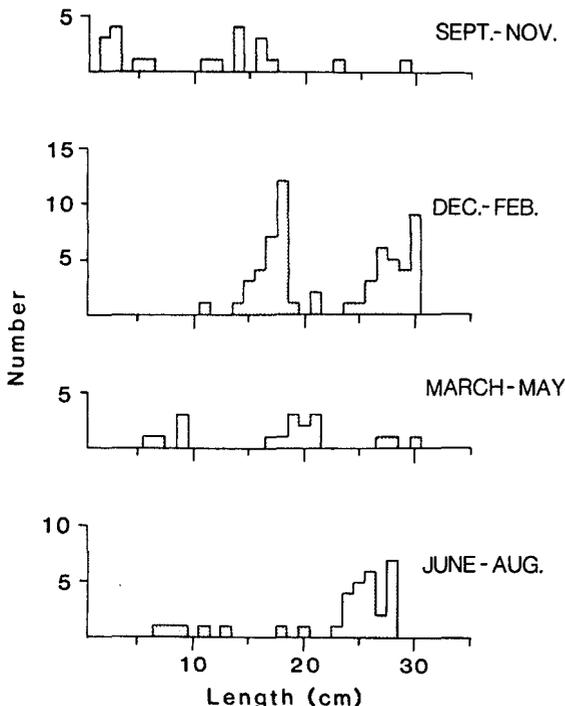

FIGURE 4.—Length frequency of small tilefish sampled by various researchers (see text) in 3-mo intervals.

(Table 1). These histograms were compiled from our data, other published data (Bigelow and Schroeder 1953; Fahay and Berrien 1981), and unpublished data (Fahay and Berrien[6]). In the winter and spring, three distinct modes occurred at 6-11, 17-21, and 27-30 cm FL which approximated the mean back-calculated lengths (see below) at ages 1, 2, and 3 yr, respectively. Tilefish spawn from at least May into October (Freeman and Turner footnote 4; Idelberger et al. 1981; Fahay and Berrien 1981), and the smallest fish observed were in the fall. The progressive increase in size of the smallest fish from the fall through the summer, and the progressive increase of other modes, also indicated that these modes represented age groups.

Progressive increase of modes in the longline length frequencies for 1977-79 (Fig. 5) also suggested that age data were valid. In 1977 a mode existed at 41-45 cm FL; in 1978 there was a more pronounced mode at 51-55 cm FL; and in 1979 there was one at 56-60 cm FL. The sizes of these fish in 1977-79 compared well with mean empirical lengths at ages 4-6 of fish we aged (see below).

Longevity and Length at Age

Length-at-age data suggested that males grow faster than females, but females live longer. On average, tilefish (sexes combined) grew about 10 cm FL/yr for the first 4 yr and thereafter growth slowed, especially for the females (Table 1). After age 3, mean back-calculated lengths of males were larger than those of females. At age 4, males and females averaged 43 and 41 cm FL, respectively, and by the ninth year males averaged 74 cm FL while females averaged 64 cm FL. The oldest fish was a 35-yr-old female of 89 cm FL, and the largest female was 95 cm FL at 32 yr. The largest male was 112 cm FL at 20 yr old, and the oldest male was 96 cm FL at 26 yr.

Back-calculated growth increments for males and females were significantly different in years 3-16 (ANOVA: $P < 0.05$). For years 17-25, they were either not significantly different ($P > 0.10$) or not comparable because of small sample sizes. Statistical analyses were not performed on data involving back-calculated lengths at age 1, because the OS:FL conversion formula was fit to fish >16 cm FL so back-calculations below that size (including nearly all back-calculated lengths at age 1) may have been inaccurate. Males achieved significantly more growth than females in all years (3-16) except the third (Dun-
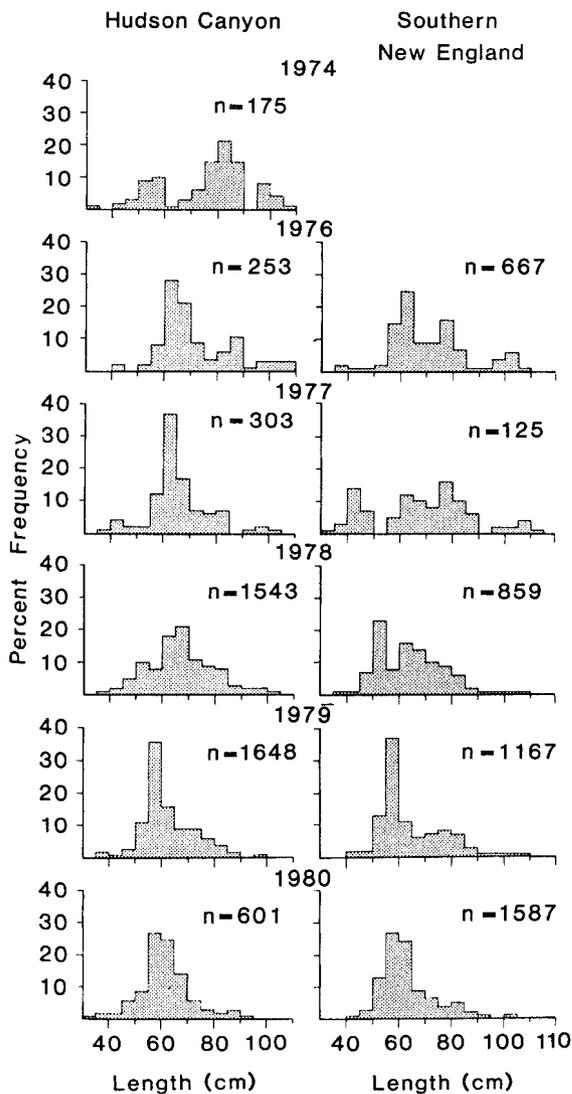
FIGURE 5.—Length frequency of tilefish caught by longline in the Hudson Canyon and Southern New England areas, 1974-80. If there were 200 or more observations in a year and area, the data were weighted equally by trips within a season and by percentage of annual landings made in each season; no weighting was used if there were <200 observations in a year and area. n = sample size.

can's multiple range test: $P = 0.05$), and these differences exceeded 1 cm FL after the fifth year (Fig. 6). Fish of unknown sex grew more slowly than females through their fifth year (significantly slower at ages 3-4, Duncan's test: $P = 0.05$), and they always grew more slowly than males (significantly so for ages 3-5, Duncan's test: $P = 0.05$).

ANOVA and Duncan's multiple range test on last back-calculated lengths for fish caught in different locations and by different fishing gears showed no significant differences between areas ($P > 0.05$) and indications of gear selection for only some ages. Sex was included as an effect in the ANOVA to account for differential growth rates. Foreign trawl and long-line caught fish were equal or nearly equal (within 1 cm) in size at ages 3, 4, 6, and 7, when their average lengths were 29, 41, 53, and 63 cm FL, respectively. Recreationally caught fish were significantly larger at age 4 (Duncan's test: $P = 0.05$) when they averaged 46 cm FL and at age 5 when all gears were significantly different (ANOVA: $P < 0.01$ and Duncan's test: $P = 0.05$) with the recreational catch averaging 51 cm FL, the longline catch being intermediate in size (49 cm FL), and the foreign trawl-caught fish being smallest (46 cm FL). The recreational catch at age 7 was significantly smaller (Duncan's test: $P = 0.05$) than the catch by the other gears (63 cm FL). In all other years, differences in size were not significant.

Growth Models

Growth models (von Bertalanffy 1938) for males and females were found to be significantly different with Hoetelling's T^2 ($P < 0.01$). Curves were fit using last back-calculated length at age, except for the 13 fish with aberrant otolith growth patterns for which empirical length was used. Females had a much smaller L_∞ (90 cm FL) and a larger K (0.153) than males ($L_\infty = 111$ cm FL and $K = 0.130$). To describe growth of the entire population, a von Bertalanffy curve was also fit for all tilefish (Fig. 7).

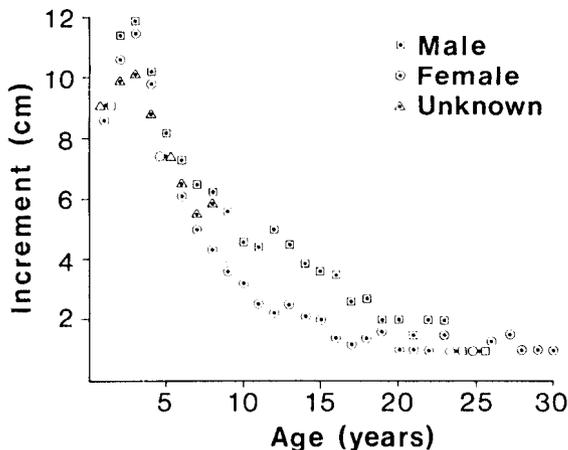Ricker's (1975) population growth statistic (G)

FIGURE 6.—Annual growth increment of tilefish by age and sex. Data for the first year may be inaccurate, because the back-calculation formula was fit to tilefish that were at least 1 yr old. The mean of each increment is shown by the point (·).

calculated for each sex reflected the length-at-age data with similar values for both sexes through age 4

and faster growth rates for males of age 5 and older (Table 1).

Length and Weight Relationships

The length:weight regressions for both whole and eviscerated weights were not significantly different between males and females. Log-tansformed regressions were most appropriate. The data were examined with ANCOVA between 50 and 95 cm FL where there were about equal numbers of observations for each sex. Differences between slopes for males and females were more nearly significant for the whole weight regressions than the eviscerated weight regressions (ANCOVA, $P = 0.08$ and 0.26, respectively). Final regressions were therefore computed for all tilefish combined and converted to Ricker's (1973) functional regression equations. These were

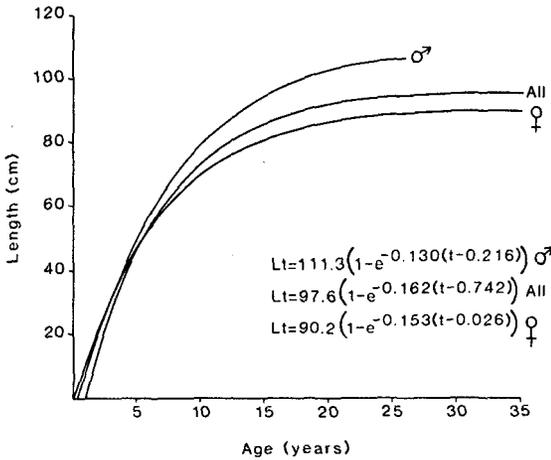$$\ln (wt) = -5.32 + 3.26 \ln (FL)$$

and

FIGURE 7.—von Bertalanffy growth formulae for male, female, and combined tilefish.

$$L_t = 111.3\left(1-e^{-0.130(t-0.216)}\right) \, \male$$
$$L_t = 97.6\left(1-e^{-0.162(t-0.742)}\right) \, \text{All}$$
$$L_t = 90.2\left(1-e^{-0.153(t-0.026)}\right) \, \female$$

TABLE 1.—Mean back-calculated fork length (cm) at age[1], empirical length at age, annual increment, and population growth rate (exponential) for female, male, and all tilefish combined in 1978.

	Age																	
	1[2]	2[2]	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Female																		
Mean back-calculated length	9	19	31	41	48	54	59	62	64	67	70	72	73	75	77	78	79	80
Mean empirical length	—	—	38	47	52	58	64	65	66	68	—	90	—	—	84	77	—	84
Mean increment	9	11	11	10	7	6	5	4	4	3	3	2	2	2	2	1	1	1
Population growth rate ($\times 10^{-2}$)	261	153	91	55	39	30	17	10	16	12	10	6	8	7	3	5	6	7
n	—	—	14	47	61	40	65	52	11	1	—	1	—	—	1	1	—	1
Male																		
Mean back-calculated length	9	21	32	43	51	58	64	70	74	77	79	83	87	91	94	97	99	101
Mean empirical length	—	—	40	50	53	60	71	74	79	86	89	93	—	—	99	102	104	—
Mean increment	9	11	12	10	8	7	6	6	6	5	4	5	4	4	4	4	3	3
Population growth rate ($\times 10^{-2}$)	264	150	90	55	43	37	25	22	11	8	18	16	14	12	10	6	5	6
n	—	—	4	51	55	17	44	41	23	5	1	1	—	—	5	1	1	—
Combined																		
Mean back-calculated length	9	20	31	41	49	55	62	66	71	73	75	78	81	84	87	86	89	88
Mean empirical length	18	25	37	48	52	58	67	69	75	83	89	92	—	—	97	90	104	84
Mean increment	9	11	11	10	8	7	6	5	5	4	4	4	4	3	3	2	2	2
Population growth rate ($\times 10^{-2}$)	258	149	92	56	42	35	24	22	11	7	14	13	12	10	-2	11	-4	6
n	7	5	60	131	135	67	112	95	34	6	1	2	—	—	6	2	1	1

	Age																
	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
Female																	
Mean back-calculated length	82	83	83	84	85	86	87	89	90	91	92	90					
Mean empirical length	82	—	—	—	—	—	—	—	—		92	89	91	89	95	—	88
Mean increment	2	1	2	1	2	1	1	1	2	1	1	1	—	—	—	—	—
Population growth rate ($\times 10^{-2}$)	4	1	4	6	4	4	5	6	4	4	-7	—	—	—	—	—	—
n	1	—	—	—	—	—	—	—	—	—	1	1	1	3	1	—	2
Male																	
Mean back-calculated length	103	105	101	103	105	106	107	—									
Mean empirical length	96	109	—	108	—	—	108	96									
Mean increment	2	2	1	2	2	1	1	—									
Population growth rate ($\times 10^{-2}$)	6	-12	6	6	3	3	—	—									
n	2	2	—	1	—	—	1	1									
Combined																	
Mean back-calculated length	90	91	86	88	89	90	91	89	90	91	92	90	—	—	—	—	—
Mean empirical length	91	109	—	108	—	—	108	96	—	—	92	89	91	89	95	—	88
Mean increment	2	1	1	1	2	1	1	1	2	1	1	1	—	—	—	—	—
Population growth rate ($\times 10^{-2}$)	5	-17	5	6	4	4	-10	6	4	4	7	—	—	—	—	—	—
n	3	2	—	1	—	1	1	1	—	—	1	1	1	3	1	—	2

[1]Because of apparent otolith growth patterns; back-calculations were not possible for females above age 30 or males above age 25.
[2]Back-calculated lengths of <18 cm FL may be inaccurate because no otoliths from fish <18 cm FL were used to fit the otolith size: fork length regression line.

$$\ln (\text{eviscerated wt}) = -5.18 + 3.21 \ln (\text{FL}).$$

Overall, whole weights were 7% greater than eviscerated weights. However, this percentage increased from about 5% for 40-54 cm FL females to 14% for 90-94 cm females, while it increased only from 5% for males of 50-54 cm FL to 8% for males of 90 cm FL or more.

Size Structure

Randomly collected length measurements from longline, recreational, and foreign trawl fisheries showed differences in sizes of tilefish exploited. All three fisheries had similar modal sizes, but the majority of the foreign trawl catch was smaller than the modal size, while the majority of the longline and recreational catches exceeded the modal size (Fig. 8). Size structure was available for the longline and recreational landings in 1977 and for all three fisheries in 1978. Because sample sizes were often small, no weighting was used in preparing length-frequency histograms and all fishing areas were combined. In 1977 the longline and recreational fisheries had one mode at 61-65 cm FL, and similar size distributions (65-70% of the fish between 56 and 75 cm FL, Fig. 8). In 1978 there was a mode for all three fisheries at 51-

55 cm FL. Foreign trawl catches were most distinct; the majority of the catch was below the modal size (51% from 26 to 50 cm FL), and only 17% was in the 56-75 cm FL interval. The longline and recreational catches were similar in that most of the catch exceeded the modal size, but the longline landings had a second mode (61-70 cm FL) while the recreational catch did not. Fifty-three percent of the longline catch was in the 56-75 cm FL interval, and 37% of the recreational catch was in that size range.

Size structure in the longline fishery became truncated between 1974 and 1980. In some years, the size structure differed between the two fishing areas (Fig. 5). The earliest length-frequency histogram (1974) for the Hudson Canyon area showed what Grimes et al. (1980) considered to be a relatively unexploited population, and the first histogram for the Southern New England fishing area (1976) showed smaller modal sizes than the 1974 data for the Hudson Canyon. In 1974, 71% of the tilefish from the Hudson Canyon area were >70 cm FL. In 1976, 43% of the fish from the Hudson Canyon area and 46% from the Southern New England area were >70 cm FL. These percentages declined in 1978 to 36 and 30%, respectively, and in 1980 to 16 and 21%, respectively.

Size at complete recruitment to the longline fishery (occurring just above the modal size in the length-
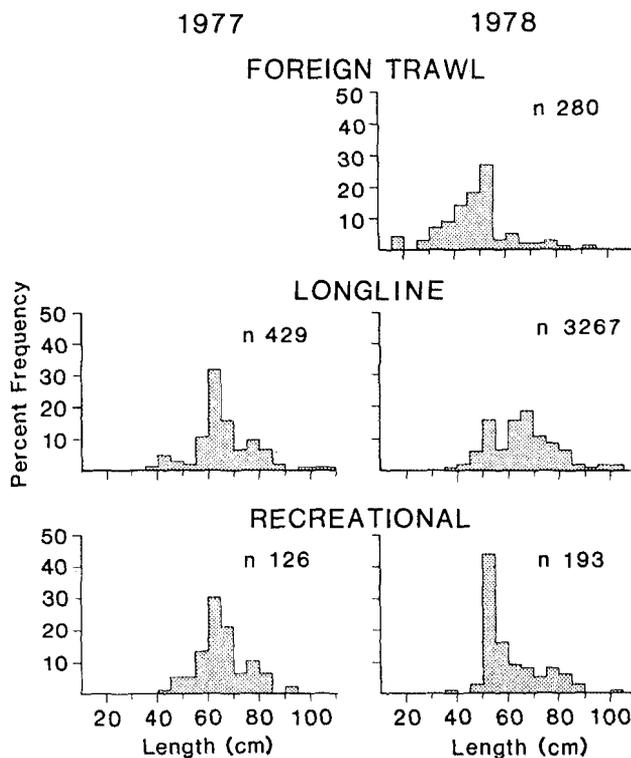

FIGURE 8.—Length frequencies of tilefish caught during 1977 and 1978 in all fishing areas by recreational and longline fishermen and foreign fishing vessel trawls. n = sample size.

frequency data) decreased in 1974 to 1980. The 1974 data indicated that complete recruitment occurred after 81-85 cm. By 1976 the peak frequency occurred at 61-65 cm, and this continued to be the case in 1977 and nearly so in 1978 in the Hudson Canyon area. In the Southern New England area, the lowest modal size occurred during 1978 at 51-55 cm FL. In succeeding years the modal size was generally 56-60 cm FL for both areas.

Strong modes at successively larger sizes in consecutive years were apparent in the longline length-frequency data, suggesting the presence of strong year classes and variable recruitment. The presence of such modes in both fishing areas indicated that they were not simply a result of discovering new concentrations of tilefish as the fishery expanded. Particularly noticeable was a mode at 41-45 cm FL in 1977, 50-55 cm FL in 1978, and 56-60 cm FL in 1979. These sizes were similar to our empirical lengths at age in 1978 of 4-, 5-, and 6-yr-old fish suggesting that these modes represented the 1973 year class.

Age Structure and Mortality

Age composition of the longline, recreational, and foreign trawl fisheries was quite different in 1978. Longline landings were dominated by 7 and 8 yr olds which represented 24 and 25% of the catch, respectively, and 90% of the catch were 4-9 yr olds (Fig. 9). The recreational catch was comprised mainly of 5 yr olds (32%), and 98% of the catch were 4-9 yr olds. Four-yr-old tilefish accounted for 33% of the foreign trawl catches; 72% of the catches were 3-5 yr olds, and 91% were 3-7 yr olds. Age at full recruitment was clearly different for each fishery—age 9 for longline, 6 for recreational, and 5 for the foreign trawl. The differences in length frequencies of longline catches in the Hudson Canyon and Southern New England areas resulted in higher percentages of 7 yr olds in the former area and more 4-6 yr olds in the latter.
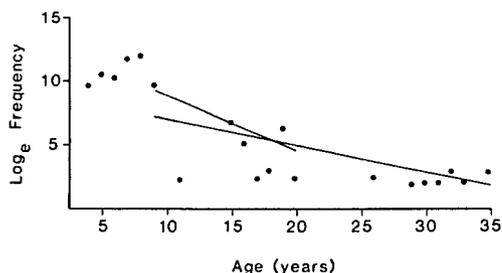

FIGURE 9.—Catch curve for tilefish caught by longline during 1978 in the Middle Atlantic-Southern New England region. Regression lines from data for fish age 9-20 yr and 9-35 yr are shown.

Total mortality rates (Z) computed for the longline and foreign trawl fisheries were found to be similar. ANCOVA revealed no significant differences between sex-specific catch curves in total mortality rates in the 1978 longline fishery ($P > 0.05$), thus Z was computed for all tilefish combined. The number at age in the longline fishery (Fig. 9) was typical of both fisheries in that there were numerous fish at the younger ages (<10 yr) and few fish between 10 and 35 yr. This resulted in a concave catch curve indicating either a lower rate of mortality for the oldest fish, or that those fish had not been subjected to fishing pressure for their entire lives, or both. The total mortality estimate from the longline data was 0.17 ($r^2 = 0.416$) for all ages; however, the effect of the curvilinearity in the catch curve was considered significant, and a more representative age range was selected. The instantaneous rate of total mortality was reestimated to be 0.46 for ages 9-20 from the longline fishery (the number at age 11 was considered an outlier and not included, $r^2 = 0.52$). The rate of total mortality for the foreign trawl fishery was estimated to be 0.60 for ages 5-8 ($r^2 = 0.84$).

DISCUSSION

Growth

All branchiostegids studied to date exhibit differences in growth rates between sexes with the females growing more slowly than males. *Lopholatilus chamaeleonticeps*, the largest and longest lived branchiostegid, shows the most pronounced difference in this regard with males reaching 105-115 cm FL in 20-26 yr and females ranging from 85 to 95 cm FL in 29-35 yr. Hayashi (1976b) reported that the average male *Branchiostegus japonicus japonicus* from the East China Sea was 32 cm TL (reported as body length) at 8 yr while females averaged only 29 cm TL at 8 yr. Ross (1978) demonstrated similar, though proportionally less pronounced, differences for *Caulolatilus microps* from North Carolina and South Carolina. Differences in mean back-calculated length at age between the sexes during the oldest ages were on the order of 15-20% of the average male's length for *L. chamaeleonticeps* (this study), 10-12% for *B. japonicus japonicus* (Hayashi 1976b), and from −1 to 5% for *C. microps* (Ross 1978).

The divergence of growth rates in branchiostegids is correlated with sexual maturation of females. Pronounced differences in growth between the sexes in *L. chamaeleonticeps* was evident at 5 yr (Fig. 6) when the average female was slightly smaller (51 cm empirical FL) than the observed size of maturation (52-57 cm

FL) based on visual staging of gonads (Idelberger et al. 1981). Both sexes of *B. japonicus japonicus* and *C. microps* exhibited similar prematurational growth rates, and the rates diverged in association with the maturation of females (Ross and Huntsman 1982). The divergence of growth rates of the sexes simultaneous with female maturation presumably reflects earlier and higher energetic costs of reproduction for females. The relatively slow growth of the *L. chamaeleonticeps* of unknown sex suggests that they may be among the smaller members of their year class, and their more rapid growth than females at ages 6-8 suggests that at least the older ones may be males.

Differential growth rates of males and females should lead to skewed sex ratios at size as Wenner (1972) had demonstrated. Idelberger et al.[7] have shown that in 1978-80 the sex ratio of tilefish >55 cm FL was disparate (Table 2). Fewer males than females occurred between 56 and 65 cm FL (38-42% males), males predominated between 71 and 85 cm FL (64-84% males), nearly equal numbers of each sex occurred in the 86-95 cm FL range (50-58% males), and only males were above 95 cm FL. Dooley (1978) suggested that the skewed sex ratios of tilefish might have been caused by either protogynous sex reversal or differential growth. Idelberger et al. (footnote 7) have examined histological sections of tilefish gonads and reported that adult tilefish do not undergo sex reversal. Additionally we tested sex ratio at age (for ages 4-10 and all ages above 10 combined) and found significant deviations from 1:1 only at age 7 (log-likelihood test: $G = 5.32$, $P < 0.05$). We concluded that differential growth rates probably caused the skewed sex ratios at length. We believe

that more rapid growth of males out of the 56-65 cm FL range causes the initial, smaller percentages of males. The greater numbers of males in the 71-85 cm FL range is a result of their younger age and thus shorter exposure to mortality. The males in this size range were 9-12 yr olds, while the females were 12-23 yr olds. Continued rapid growth of males through the 86-95 cm FL interval (only males age 13-15 yr fall within the range) and the much slower growth of females, in conjuction with their greater longevity, result in an accumulation of old females between 86 and 95 cm FL (50-58% males). Ross (1978) also hypothesized that differential growth rates, not protogynous sex reversal among adults, caused skewed sex ratios in *Caulolatilus microps*. Clearly, mortality rates influence sex ratio at length in *L. chamaeleonticeps* and, if mortality is increased by fishing, the proportion of females in the larger size intervals will decrease.

Size Structure and Mortality

The prominence and progression of strong modes through the length-frequency data from the longline fishery indicate that strong year classes were present and recruitment of tilefish has varied. Evidence of weak year classes may be seen in the relatively low frequencies of 61-65 cm FL fish in 1974 and of 56-60 cm FL fish in 1978, especially in the Southern New England area (Fig. 5). Such fluctuations in year-class strength will cause variations in population size and thus create problems in estimating allowable catches.

The truncation in size structure of longline catches, which Grimes et al. (1980) attributed to the effect of fishing, has continued. The proportion of fish >70 cm FL declined from 71% in 1974 to 16-21% in 1980 (Fig. 5). This was accompanied by an increase in the longline fleet size from about five vessels in 1974 (Grimes et al. 1980) to about 30 vessels in 1980 and increased effort per vessel at least through 1980[8].

The difference in size structure of the foreign trawl and the longline catches (Fig. 8) shows that longlines select for larger fish. In addition, the reduction in size at full recruitment in the longline landings since 1974 suggests that when larger tilefish are present, smaller ones are either less vulnerable to the gear or they are avoided by the fishermen. If this is true, longline length frequencies show higher relative frequencies of large fish than actually exist in the population, which would lead to an underestimation of mortality rates.

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[7]Idelberger, C. F., C. B. Grimes, and K. W. Able, Rutgers University, New Brunswick, NJ 08903, unpubl. data, 1982.

TABLE 2.—Percentage of male tilefish > 50 cm FL in 1978-80 (from Idelberger et al. text footnote 7) and results of log-likelihood tests of the hypothesis that sex ratio did not differ from 1:1 (G).

Length (cm)	n	% males	G
51-55	268	54	1.976
56-60	140	38	8.844*
61-65	166	42	3.779
66-70	180	46	0.940
71-75	117	64	8.865*
76-80	116	84	55.745*
81-85	80	71	14.028*
86-90	24	58	0.376
91-95	10	50	0.100
96-100	6	100	—
101-105	3	100	—
106-110	1	100	—
Total	989	48	Pooled 0.369

*$P < 0.01$.

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[8]Grimes, C. B., K. W. Able, and S. C. Turner, Rutgers University, New Brunswick, NJ 08903, unpubl. data, 1982.

The estimate for instantaneous total mortality rate (0.17) from the longline fishery in 1978 using all fully recruited ages was undoubtedly too low. Estimates of 0.46-0.60 derived from more linear portions of the longline catch curve and the foreign trawl catch curve, respectively, are considered by us to more realistic. The difference between the two estimates may be due to a variety of factors, including variation in year-class strength, gear selection, and increased mortality rates. The longline estimate may be low if the selectivity for larger sized tilefish noted above applies to fully recruited age groups as well. The foreign trawl estimate may be high because the strong 1973 year class was the first fully recruited year class in 1978, and trawls appear to be biased towards smaller tilefish. Alternately, the estimate of total mortality rate from 5 to 8 yr olds from the foreign trawl fishery may more accurately represent recently increased mortality rates than the estimate from 9 to 20 yr olds taken in the longline fishery, because catch curve estimates of Z reflect the history of mortality rates over the lifetime of the year classes sampled (Ricker 1975; Csirke and Caddy 1983). More information on the age structure in different years and for the older members of the tilefish population (>10 yr) is needed to improve the estimates of mortality rate. While our results showed no significant differences in mortality rates in 1978, the older ages of the females suggest that they may have a lower mortality rate than males. The question of sexual differences in mortality should be addressed in greater detail.

ACKNOWLEDGMENTS

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