STATUS OF THE TILEFISH, *LOPHOLATILUS CHAMAELEONTICEPS*, FISHERY OFF SOUTH CAROLINA AND GEORGIA AND RECOMMENDATIONS FOR MANAGEMENT

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ABSTRACT

We used a sex- and age-structured model and CPUE data from commercial and research vessels to assess the current status of the tilefish, *Lopholatilus chamaeleonticeps*, substock off South Carolina and Georgia. Based on commercial CPUE data and assumed natural mortality (M) rates of 0.10–0.25, we estimated that adult population density prior to fishing ranged from 603 to 950 per km^2 and stock biomass ranged from 1,130 to 1,570 tonnes (t). Our estimates of the recommended fishing mortality rate ranged from 0.10 (M = 0.10) to 0.48 (M = 0.25), resulting in sustainable yields of 40 (M = 0.10) to 82 t (M = 0.25) per year. We obtained higher estimates of virgin population density (883–1,710 per km^2) when research CPUE data were used. Sustained yield estimates also were higher, ranging from 55 (M = 0.10) to 148 t (M = 0.25) per year. Average estimates of recommended yield from commercial and research CPUE data were 58 and 95 t, respectively. Observed yields in the developing fishery exceeded 100 t in 1981–84 and in 1986; however, current observations indicate that fishing effort has declined to a low level in response to reduced catches. Based on the assumption that commercial CPUE data better reflect population trends, we recommend that the annual harvest not exceed about 50 t, which should result in a stock biomass of about 400–800 t. Apparent limitations on sustainable yield from the fishery probably can be attributed to the long lifespan, slow growth rate, and sedentary nature of tilefish.

The tilefish, *Lopholatilus chamaeleonticeps*, is a large demersal species found along the outer continental shelf of North America from Nova Scotia to Key West, FL, along the Gulf coast to Campeche Bank, and off South America from Venezuela to Surinam (Freeman and Turner 1977). Tilefish are long-lived and have relatively slow growth rates (Harris and Grossman 1985). They are most common at depths of 100–400 m and water temperatures of about 9°–14°C (Freeman and Turner 1977). Abundance is greatest in areas where substrates are suitable for burrow construction (Able et al. 1982; Grossman et al. 1985) or afford other shelter such as scour depressions around boulders (Valentine et al. 1980) or rubble piles (Low and Ulrich 1983).

Katz et al. (1983) described two genetically distinct tilefish stocks through use of morphometric and electrophoretic data: one composed of tilefish from the Middle Atlantic Bight (MAB), and one composed of tilefish from the South Atlantic Bight (SAB) and Gulf of Mexico. Larval transport from the Gulf of Mexico to the SAB may be responsible for similarities in electrophoretic results for these two areas (Katz et al. 1983). Katz et al. (1983) suggested, however, that it may be necessary to manage these substocks separately because of their wide geographic separation. If true, this should be done with the understanding that Gulf of Mexico populations may serve as a source of recruits to SAB populations (Katz et al. 1983).

Tilefish have been harvested commercially in the MAB since 1915, with annual landings ranging from <1 tonne (t) to 4,500 t (Turner et al. 1983). Landings from the SAB and Gulf of Mexico were small prior to 1980 (Low et al. 1983). A limited number of tilefish were caught incidentally in the deepwater grouper fishery off South Carolina (Low and Ulrich 1982). Recreational catches were small because of the depth at which tilefish occur (Low and Ulrich 1982). Commercial fisheries have since developed in both the SAB and Gulf of Mexico, due in part to an interest in diversification within the shrimp industry (Low et al. 1983).

For the segment of the SAB tilefish fishery operating off South Carolina and Georgia, increased fishing effort has resulted in a substantial increase in tilefish landings since 1978 (Table 1). In addition, a considerable number of tilefish caught off Georgia

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TABLE 1.—South Carolina and Georgia tilefish, *Lopholatilus chamaeleonticeps*, landings from 1978 to 1986. Georgia landings of tilefish and blueline tilefish, *Caulolatilus microps*, were not reported separately routinely prior to 1985. Landings by gear type were available for 1980–85, however, so rod and reel and electric reel catches of unclassified tilefish (which are almost exclusively blueline tilefish) were excluded to yield a more accurate estimate of Georgia tilefish landings.

	Landings (metric tons)		
Year	South Carolina[1]	Georgia[2]	Total
1978	2.59	[3]0.10	2.69
1979	10.08	[3]0.02	10.10
1980	43.89	(confidential)	>43.89
1981	103.74	0.35	104.09
1982	163.78	7.99	171.77
1983	252.55	6.67	259.22
1984	190.44	39.49	229.93
1985	70.49	13.04	83.53
1986	142.96	(confidential)	>142.96

[1]Andy Jennings, Fisheries Statistics Office, South Carolina Wildlife and Marine Resources Department, Charleston SC, pers. commun. 1987.
[2]S. Gordon Rogers, Fisheries Statistics Coordinator, Georgia Department of Natural Resources, Brunswick, GA, pers. commun. August 1987.
[3]Georgia Department of Natural Resources. 1983. Georgia landings annual summary 1980. Ga. Dep. Nat. Resour., Coastal Resour. Div., Brunswick, GA.

from about 1982 to 1984 were landed in Florida; therefore, landings in Table 1 are a conservative estimate of removals from these grounds.

Low et al. (1983) provided a preliminary estimate of maximum sustained yield (MSY = 162 t) for the developing fishery. Their estimate was derived from Gulland's (1971) model MSY = $0.5MB_0$, where M was the natural mortality rate and B_0 was an estimate of virgin biomass. Our objective was to provide updated yield estimates for use in managing the tilefish fishery off South Carolina and Georgia. We base these estimates on the 9-yr sequence of catches from the developing fishery as well as recently obtained information on the growth, mortality, and reproductive biology of tilefish from this area.

METHODS

We used a deterministic sex- and age-structured model to simulate the developing tilefish fishery and to calculate sustainable yields. The model was based on the following assumptions and data sources. We assumed that the natural mortality rate (M) ranged from 0.10 to 0.25 (Harris and Grossman 1985). We used sex-specific estimates of weight-at-age because the von Bertalanffy growth curves and length-weight relationships used to calculate weight-at-age differed significantly by sex (Harris and Grossman 1985). We used maturity-at-length data (Erickson and Grossman 1986) to estimate maturity at age by using a logistic model:

$$p_{s,a} = 1/(1 + \exp(-b_{Mat}(L_{s,a} - L50_{Mat}))) \quad (1)$$

where $p_{s,a}$ was the proportion of sex-s, age-a fish that were sexually mature, b_{Mat} was a parameter affecting the steepness of the curve, $L_{s,a}$ was the standard length (SL) of sex-s fish at age a, and $L50_{Mat}$ was a parameter representing the length at which 50% of the fish were sexually mature. We assumed that the total biomass of sexually mature females (S_f) was an adequate measure of spawning potential.

We used a logistic model to relate selectivity to length:

$$sel_{s,a} = 1/(1 + \exp(-b_{Sel}(L_{s,a} - L50_{Sel}))) \quad (2)$$

where $sel_{s,a}$ was the proportion of sex-s, age-a fish that were vulnerable to fishing, b_{Sel} was a parameter affecting the steepness of the curve, and $L50_{Sel}$ was a parameter representing the length at which 50% of the fish were vulnerable to fishing. Based on length-frequency data (Harris and Grossman 1985), we assumed that female and male tilefish reached 50% vulnerability at about 475–500 and 500–525 mm SL, respectively. We used a slope parameter (b_{Sel}) of 0.05 so that selectivity-at-age in the simulated fishery ranged from about 0 at age 5 to 1.0 at age 11 (Harris and Grossman 1985). Parameter estimates used in the model are summarized in Table 2.

We assumed that the relationship between spawning stock size and subsequent recruitment was weak or nonexistent because 1) tilefish produce pelagic larvae (Fahay and Berrien 1981); 2) there may be substantial egg or larval transport between the Gulf of Mexico and SAB (Katz et al. 1983); and 3) tilefish are dependent on the availability of shelter (Valentine et al. 1980; Able et al. 1982; Low and Ulrich 1983; Grossman et al. 1985). To represent the stock-recruitment relationship, we used a Beverton-Holt curve of the following form (Kimura 1988):

$$N_{s,6}[t + 6] = \frac{0.5N_6[0]S_f[t]/S_f[0]}{1 - A(1 - S_f[t]/S_f[0])} \quad (3)$$

where $N_{s,6}[t + 6]$ was the number of sex-s, age-6 recruits in year $t + 6$, $N_6[0]$ was the virgin recruitment level for both sexes combined, and $S_f[t]$ and $S_f[0]$ were the biomass levels for spawning females in year t and prior to fishing, respectively. The pa-

rameter A controlled the degree of density-dependence. We assumed that recruitment was either constant (A = 1.000) or decreasing by 10% when the spawning stock was reduced by 50% (A = 0.889). Few studies have shown a statistically significant relationship between spawning stock and recruitment (Hennemuth 1979); nevertheless, recruitment would be expected to decline at high Fs. For that reason, we used the latter assumption to explore the effect of the stock-recruitment relationship on the form of the yield curve. Other investigators have used this approach to obtain conservative estimates of equilibrium yield when information on the stock-recruitment relationship was unavailable (Lenarz and Hightower 1985; Henry 1986; Hightower and Lenarz 1986).

We simulated the fishery using virgin recruitment levels of 10,000–200,000 6-yr-old fish. This range would result in virgin population sizes of 45,000–2.1 million fish, depending on the assumed level of natural mortality. Assuming that the area inhabitated by tilefish off South Carolina and Georgia is about 476 km^2 (Low et al. 1983), these population sizes correspond to adult densities of 95–4,400 per km^2. This appeared to be an adequate range of densities, given that estimates of tilefish burrow density in the Hudson and Veatch Canyons off southern New England ranged from 119 to 2,434 per km^2 in 1980 (Grimes et al. 1986). As Low et al. (1983) noted, the 1974–78 catch rates off southern New England (0.49–0.93 kg/hook; Grimes et al. 1980) were similar to the 1981–82 catch rate in the expanding fishery off South Carolina and Georgia (0.86 kg/hook).

TABLE 2.—Parameter estimates for the sex- and age-structured model of the tilefish fishery off South Carolina and Georgia.

	Female	Male
von Bertalanffy[1]		
L_∞	[2]792	922
k	0.090	0.086
t(zero)	−1.774	−0.920
Length-weight[1]		
b(1)	2.28572E-8	7.92693E-9
b(2)	2.974	3.141
Maturity-at-age		
b_{Mat}	0.030	0.018
$L50_{Mat}$	495	458
Selectivity-at-age		
b_{Sel}	0.05	0.05
$L50_{Sel}$	475, 500	500, 525

[1]Harris and Grossman (1985). Length-weight relationship: $w = b(1)L^{b(2)}$.
[2]The estimate of L_∞ in Harris and Grossman (1985) (895 mm) was incorrect.

Because tilefish catches were negligible prior to 1978, the starting (1978) number-at-age vector at each recruitment level was assumed to be the equilibrium vector obtained at an F of 0. We assumed that our estimates of total landings were much more reliable than our estimates of fishing effort. For that reason, we solved iteratively for the sequence of fishing mortality rates that would produce the observed 1978–86 catches (Methot in press). For example, we began by solving for the 1978 F that would produce the 1978 catch biomass, and then used that F to project the number-at-age vector remaining in 1979. [We assumed that the final (1986) F should not exceed 2.0 (an exploitation rate of 80–84%), in order to rule out those cases where the 1986 harvest was attained by removing essentially all remaining tilefish.] Using this approach to estimate F, the observed and simulated catch biomass levels match exactly, although the observed and simulated age distributions may be different. Note that if we had a similar degree of confidence in our estimates of catch and fishing effort, it might be more appropriate to minimize differences between observed levels and model estimates of both catch and effort (see for example, Deriso et al. 1983), rather than forcing the model to reproduce the catches exactly.

At each virgin recruitment level, we calculated the correlation between the estimated 1978–86 Fs and estimates of total effort based on CPUE data. We used two sources of CPUE data: 1) commercial snapper reel CPUE from 1980 to 1982 South Carolina vessels (Low and Ulrich 1983); and 2) mean longline CPUE from 1982 to 1985 research cruises aboard the RV *Georgia Bulldog*. Based on commercial snapper reel kg/landing (figure 13 in Low and Ulrich 1983), we estimated that observed annual landings would have required more than 22 trips in 1980, 89 in 1981, and 445 in 1982 (Table 3). Using research cruise estimates of longline kg/hook, we estimated that observed annual landings would have required 351,000 hooks fished in 1982, 1.9 million in 1983, 1.6 million in 1984, and 380,000 in 1985 (Table 3). The research catches were made using standard commercial longline gear (Harris and Grossman 1985). We also obtained a composite 1980–85 effort series using the ratio of hooks fished to trips in 1982 (Table 3), but our results were the same as when only research CPUE data were used.

At each level of natural mortality, we selected the virgin recruitment level that maximized the correlation between estimates of F and fishing effort. The selected recruitment level was used in the equilib-

TABLE 3.—Estimates of total effort based on commercial and research catch per unit effort (CPUE) and total commercial landings. Estimates of 1980–82 commercial CPUE (kg/landing) were based on landings by snapper reel vessels (figure 13, Low and Ulrich 1983). Research CPUE estimates (kg/hook) were based on longline sets aboard the RV *Georgia Bulldog*; each estimate is an average of seasonal averages from spring, summer, and fall cruises. Estimates of hooks fished in 1980 and 1981 were based on the commercial CPUE data, using the ratio of trips to hooks fished in 1982.

Year	CPUE		Total landings (kg)	Estimated trips	Estimated hooks fished
	Commercial (kg/landing)	Research (kg/hook)			
1980	1,950	—	>43,890	>22	(>17,331)
1981	1,174	—	104,090	89	(70,110)
1982	386	0.490	171,770	445	350,551
1983	—	0.137	259,220		1,892,117
1984	—	0.140	229,930		1,642,357
1985	—	0.220	83,530		379,682

rium yield calculations. Our approach for selecting virgin recruitment levels was based on the "tuning" process used in cohort analysis (Mohn 1983; Rivard 1983). In that approach, auxiliary information is used to "adjust" or "fine-tune" the estimates iteratively so that the output from cohort analysis "matches" some series of observations (Rivard 1983). The level of agreement between the observations and model predictions can be measured using correlation or regression techniques (Mohn 1983).

We obtained estimates of equilibrium yield by expressing the number of sex-s fish in each age class ($N_{s,a}$, $a = 6, \ldots, n$, where n refers to fish ages 30 and older) as a function of the number of age-6 female fish ($N_{f,6}$). Following Getz (1980), we assumed that

$$N_{s,a+1} = \left[\prod_{j=6}^{a} \exp(-Z_{s,j})\right] N_{f,6},$$

$$a = 6, \ldots, n-2 \quad (4)$$

$$N_{s,n} = \left[\prod_{j=6}^{n-1} \exp(-Z_{s,j})/(1 - \exp(-Z_{s,n}))\right] N_{f,6} \quad (5)$$

where $Z_{s,j}$ was the total mortality rate for sex-s, age-j fish. Using Equations (4) and (5), female spawning stock can be redefined as a function of $N_{f,6}$:

$$S_f = \sum_{a=6}^{n} N_{f,a}\, w_{f,a}\, p_{f,a} \quad (6)$$

$$= N_{f,6}\left[w_{f,6}\, p_{f,6} + \sum_{a=7}^{n-1} w_{f,a}\, p_{f,a} \prod_{j=6}^{a-1} \exp(-Z_{f,j}) + w_{f,n}\, p_{f,n} \prod_{j=6}^{n-1} \exp(-Z_{f,j})/(1 - \exp(-Z_{f,n}))\right] \quad (7)$$

$$= N_{f,6}\, \phi(F) \quad (8)$$

where $\phi(F)$ is the bracketed expression in Equation (7) for a specified F. We then substituted $(N_{f,6}\, \phi(F))$ for S_f and solved Equation (3) for the equilibrium recruitment level as a function of F:

$$N_{f,6} = (0.5\, N_6[0]\, \phi(F) - S_f[0] + AS_f[0])/(A\, \phi(F)). \quad (9)$$

The virgin spawning stock $S_f[0]$ was calculated from Equations (4) to (6) for the specified level of M and virgin recruitment. We used Equations (4)–(9) to calculate the equilibrium number-at-age vector and associated yield for Fs from 0.0 to 0.5.

Following Francis (1986), we defined the target fishing mortality rate as $F_{0.1}$ for the constant recruitment case and F_{msy} for the density-dependent case. $F_{0.1}$ was the fishing mortality rate at which the slope of the yield curve was one-tenth the slope of the curve at the origin (Gulland and Boerma 1973). Compared to managing for maximum sustained yield, the $F_{0.1}$ policy usually results in greater economic efficiency when constant recruitment is assumed (Gulland and Boerma 1973; Sissenwine 1981; Francis 1986). An additional advantage is that a larger spawning stock would be maintained (Sissenwine 1978). The less conservative F_{msy} policy was assumed to be appropriate for the more conservative density-dependent case. The recommended yields for the constant recruitment and density-dependent cases were the equilibrium yields at $F_{0.1}$ and F_{msy} respectively.

RESULTS AND DISCUSSION

Our approach for estimating virgin recruitment level was similar to stock reduction analysis (SRA) (Kimura et al. 1984; Kimura 1985) except that we used a more general model to represent stock dynamics. In both approaches, a model is fully specified and the sequence of Fs used to drive the model are those that would have produced the observed sequence of catches. A range of solutions can be obtained corresponding to a range of virgin recruitment levels, but the solution set can be restricted by comparing model predictions to auxiliary data.

We obtained similar 9-yr patterns of F at different levels of virgin recruitment, particularly at higher recruitment levels where Fs were low in all years (Fig. 1). For that reason, correlation coefficients were similar over a wide range of recruitment levels (Fig. 2). Stronger conclusions about the true level of virgin recruitment may be possible once additional years of catch and CPUE data become available.

Based on commercial snapper reel CPUE data, the virgin recruitment level that maximized the correlation between estimates of F and fishing effort ranged from 30,000 to 100,000, depending on the assumed selectivity parameters and level of natural mortality (Table 4, Fig. 2). Correlations were high at all virgin recruitment levels, with maximum values obtained at the lowest recruitment levels capable of sustaining the 1978–86 observed catches (in order to match the sharp decline in CPUE from 1980 to 1982). Estimates based on research cruise CPUE data were higher, ranging from 40,000 to 180,000 (Table 5, Fig. 2). In both cases, the results were much more sensitive to M than to the $L50_{Sel}$ parameter of the selectivity function (Tables 4, 5).

Based on these estimates of the virgin recruitment level, the adult population prior to fishing would have ranged from 287,000 to 452,000 fish (commercial CPUE) or 420,000 to 814,000 fish (research CPUE). Assuming 476 km^2 of tilefish habitat off South Carolina and Georgia (Low et al. 1983), the estimated density prior to fishing would have been 603–950 (commercial CPUE) or 883–1,710 (research CPUE) per km^2. We are not aware of other estimates of tilefish density prior to fishing. Submersible dives were made on the South Carolina tilefish grounds after the period of (assumed) heavy exploitation; unfortunately, no density estimates are currently available. Comparisons with the exploited MAB stock are of some interest because MAB catch rates in the late 1970s were similar to initial catch rates off South Carolina and Georgia (Low et al. 1983). Our density estimates were similar to the burrow density estimates from the MAB. Grimes et al. (1986) reported that burrow density in Hudson Canyon ranged from 1,815 per km^2 in 1980 to 1,132 in 1982. Estimates for Veatch Canyon ranged from 772 per km^2 in 1981 to 1,531 in 1984. Tilefish density in the MAB may be lower than these estimates because not all burrows may be occupied (Able et al. 1982). In addition, burrow density is highly variable (Able et al. 1987) and some burrows may be inhabited only during certain seasons, depending on water temperature (Grimes et al. 1986). Nevertheless, these comparisons suggest that the density estimates we generated from catch data were reasonable.

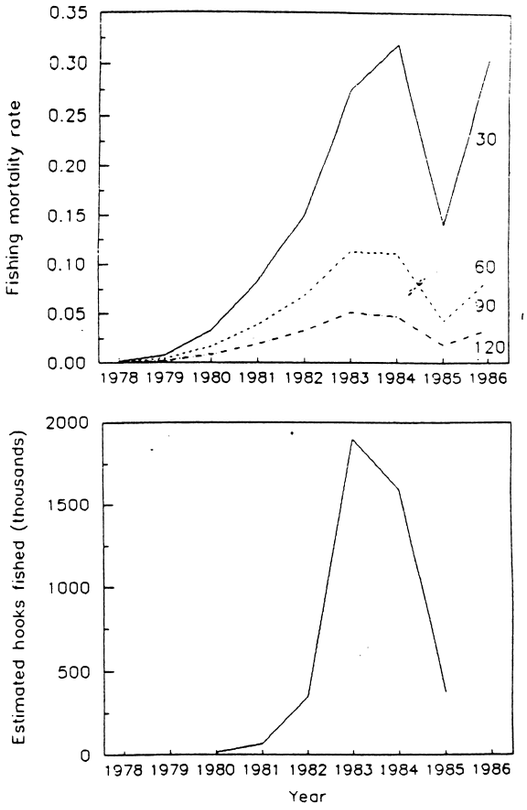

FIGURE 1.—Upper panel: estimated fishing mortality rates (F) from 1978 to 1986 at four (arbitrarily selected) levels of virgin recruitment (30,000–120,000 age-6 tilefish), assuming a natural mortality rate (M) of 0.10. Year-to-year changes in F were similar at other levels of M. Lower panel: estimates of fishing effort (hooks fished) based on commercial (1980–81) and research (1982–85) CPUE data.

TABLE 4.—Estimates of virgin levels of recruitment, adult population density, and biomass; recommended levels of fishing mortality, biomass, and yield; and 1987 biomass. Estimates were obtained from commercial CPUE data, using two sets of selectivity ($L50_{Sel}$) parameters, four levels of natural mortality (M), and two assumptions about the stock-recruitment relationship (A = 0.889 - recruitment dependent on spawning stock, A = 1.000 - recruitment constant).

	Female/male selectivity parameter $L50_{Sel}$							
	475/500 mm SL				500/525 mm SL			
M:	0.10	0.15	0.20	0.25	0.10	0.15	0.20	0.25
Virgin recruitment level (thousands)	30	40	70	90	30	40	70	100
Virgin population density (#/km^2)	662	603	811	855	662	603	811	950
Virgin biomass (t)	1,574	1,128	1,266	1,160	1,574	1,128	1,266	1,288
Recommended F (A = 0.889)	0.10	0.15	0.23	0.33	0.13	0.20	0.30	0.48
Recommended F (A = 1.000)	0.10	0.16	0.23	0.32	0.11	0.17	0.25	0.34
Recommended biomass (t) (A = 0.889)	553	437	511	485	509	408	504	535
Recommended biomass (t) (A = 1.000)	678	524	636	628	700	551	680	753
Recommended yield (t) (A = 0.889)	41	40	57	62	42	42	58	70
Recommended yield (t) (A = 1.000)	51	51	72	78	52	51	70	82
Estimated 1987 biomass (t)	624	247	468	435	636	261	484	584

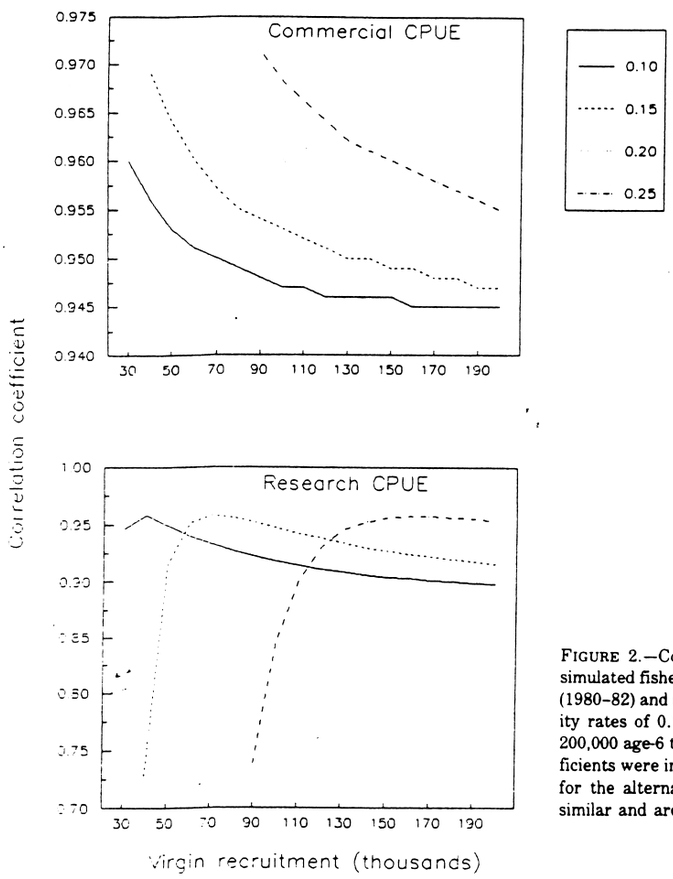

FIGURE 2.—Correlation between fishing mortality rates in the simulated fishery and estimates of fishing effort from commercial (1980–82) and research (1982–85) CPUE data, at natural mortality rates of 0.10–0.25 and virgin recruitment levels of 30,000–200,000 age-6 tilefish. Recruitment levels without correlation coefficients were inadequate to sustain the observed catches. Results for the alternative set of selectivity parameters ($L50_{Sel}$) were similar and are not shown here.

TABLE 5.—Estimates of virgin levels of recruitment, adult population density, and biomass; recommended levels of fishing mortality, biomass, and yield; and 1987 biomass. Estimates were obtained from research CPUE data, using two sets of selectivity ($L50_{Sel}$) parameters, four levels of natural mortality (M), and two assumptions about the stock-recruitment relationship (A = 0.889 - recruitment dependent on spawning stock, A = 1.000 - recruitment constant).

	Female/male selectivity parameter $L50_{Sel}$							
	475/500 mm SL				500/525 mm SL			
M:	0.10	0.15	0.20	0.25	0.10	0.15	0.20	0.25
Virgin recruitment level (thousands)	40	70	110	160	40	70	120	180
Virgin population density (#/km^2)	883	1,056	1,275	1,520	883	1,056	1,391	1,710
Virgin biomass (t)	2,098	1,974	1,989	2,062	2,098	1,974	2,170	2,319
Recommended F (A = 0.889)	0.10	0.15	0.23	0.33	0.13	0.20	0.30	0.47
Recommended F (A = 1.000)	0.10	0.16	0.23	0.32	0.11	0.17	0.25	0.34
Recommended biomass (t) (A = 0.889)	738	765	802	863	679	713	864	962
Recommended biomass (t) (A = 1.000)	904	917	999	1,117	932	965	1,165	1,355
Recommended yield (t) (A = 0.889)	55	71	89	109	56	73	100	126
Recommended yield (t) (A = 1.000)	69	90	114	139	70	89	120	148
Estimated 1987 biomass (t)	1,152	1,107	1,203	1,354	1,164	1,121	1,400	1,627

The two sets of CPUE estimates resulted in different conclusions about the current status of the stock. Based on commercial CPUE data, 1987 stock biomass was 22–45% of virgin biomass and 51–105% of the recommended level (Table 4). Estimated fishing mortality rates increased from about 0.1 in 1981 to a range of 0.3–1.4 in 1986 (Fig. 3). Based on research CPUE data, 1987 stock biomass was 55–70% of virgin biomass and 132–145% of the recommended level (Table 5). Estimated fishing mortality rates were much lower than from commercial CPUE data, increasing from about 0.08 in 1981 to 0.2 in 1986 (Fig. 3).

We believe that the results obtained from commercial CPUE data are far more likely, given recent reported declines in directed fishing. The decrease in landings observed in 1985 was attributed in part to reduced fishing pressure. A large group of boats from the Port Canaveral, FL area left the fishery, and a number of Georgia vessels began fishing further north (M. V. Rawson[3]). As of April 1988, most South Carolina longline vessels had switched to other fisheries and little directed tilefish fishing was occurring (R. Low[4]).

The difference in results for commercial and research CPUE estimates may be due to differences in areas fished. The RV *Georgia Bulldog* cruises were exploratory in nature, and catches were obtained primarily in the southern section of tilefish habitat off the Georgia coast (Harris and Grossman 1985). Early commercial effort was concentrated in the more northerly part of the tilefish habitat (Low et al. 1983). We recognize the commercial catch data provide a biased measure of abundance. Nevertheless, because South Carolina landings predominated in the developing fishery, we believe that commercial catch data from the primary fishing grounds will be a better overall measure of changes in abundance. For that reason, we restrict our remaining comments to results from the commercial CPUE data. Declines in commercial CPUE may underrepresent actual declines in abundance because fishermen presumably would change tactics over time in order to maintain high catch rates. If so, our use of commercial catch data may result in an optimistic estimate of current abundance.

We obtained equivalent estimates of 1987 biomass for the constant recruitment and density-dependent cases because of the short length of the data series, relative to the 6-yr lag between a reduction in spawning stock and subsequent lower recruitment to the fishery. Equilibrium yield curves differed substantially for the two recruitment assumptions (Fig. 4). Despite differences in equilibrium yield, recommended Fs were very similar for the two cases because of the different criteria used to develop F and yield recommendations (Table 4). Recommended yield was moderately higher under the optimistic constant recruitment assumption (Table 4). Recommended F was higher when $L50_{Sel}$ was increased; however, differences in recommended yield were negligible.

Estimated Fs differed substantially for the four levels of natural mortality (upper panel, Fig. 3). The large differences in 1984–86 Fs probably were due

[3]M. V. Rawson, University of Georgia Marine Extension Service, Brunswick, GA 31523, pers. commun. March 1987.
[4]R. Low, South Carolina Wildlife and Marine Resources Department, Charleston, SC 29412, pers. commun. April 1988.

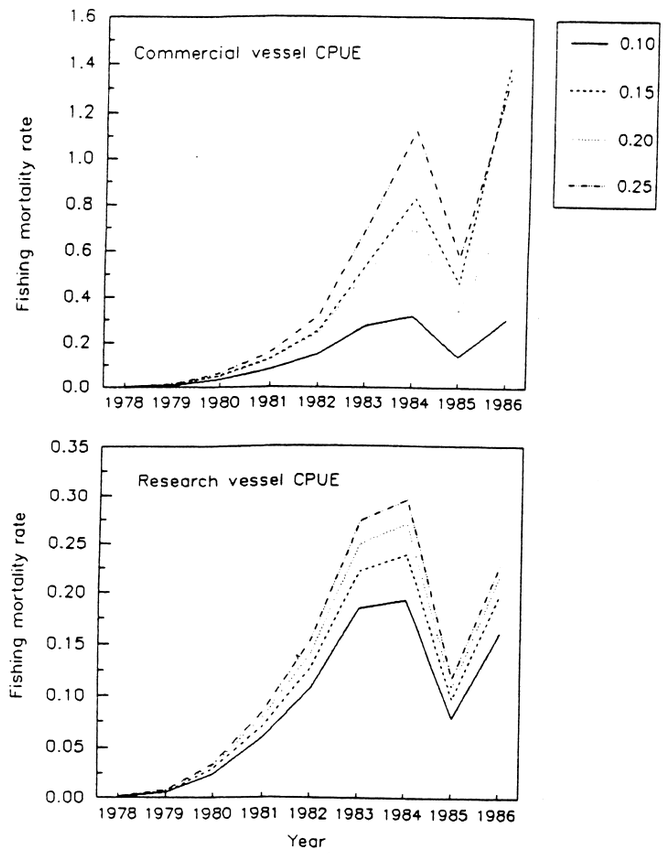

FIGURE 3.—Estimated fishing mortality rates (F) from 1978 to 1986 at natural mortality rates of 0.10–0.25. At each level of natural mortality, the virgin recruitment level was determined based on the correlation between F and estimated fishing effort, where estimates of effort were based on commercial vessel or research vessel CPUE. Results for the alternative set of selectivity parameters ($L50_{Sel}$) were similar and are not shown here.

to the lack of CPUE estimates for those years. Virgin biomass levels were similar at different levels of M, ranging from 1,130 t at M = 0.15 to 1,570 t at M = 0.10 (Table 4). Estimates of 1987 biomass were somewhat similar and relatively low, ranging from 247 t at M = 0.15 to 636 t at M = 0.10 (Table 4). Equilibrium yield curves differed in a predictable way at different levels of M (Fig. 4). Except at low Fs (<0.10), equilibrium yield increased as M increased, due to the higher estimates of virgin recruitment at higher levels of M. Recommended F was higher at higher levels of M, ranging from 0.10 at M = 0.10 to 0.48 at M = 0.25 (Table 4). Recommended yield increased from 41–52 t at M = 0.10 to 62–82 t at M = 0.25.

These results demonstrate that an important source of uncertainty in assessing tilefish stock status is the estimate of M. Harris and Grossman (1985) obtained 1982–83 catch curve estimates of Z equal to 0.25 for both female and male tilefish. Because the areas sampled by the RV *Georgia Bulldog* were thought to have received little fishing pressure, M could be as high as 0.25. Catch curve estimates of Z would be biased, however, if vulnerability to fishing increased with size. Turner et al. (1983) reported a decline in size at recruitment in the expanding MAB fishery and suggested that when larger tilefish were present, smaller ones either were less vulnerable to the gear or were avoided by fishermen. Z (and M) could be underestimated if vulnerability to fishing increased with size. Alternatively, Z (and M) could be overestimated if significant catches of predominantly older fish were made in the areas sampled by the RV *Georgia Bulldog*.

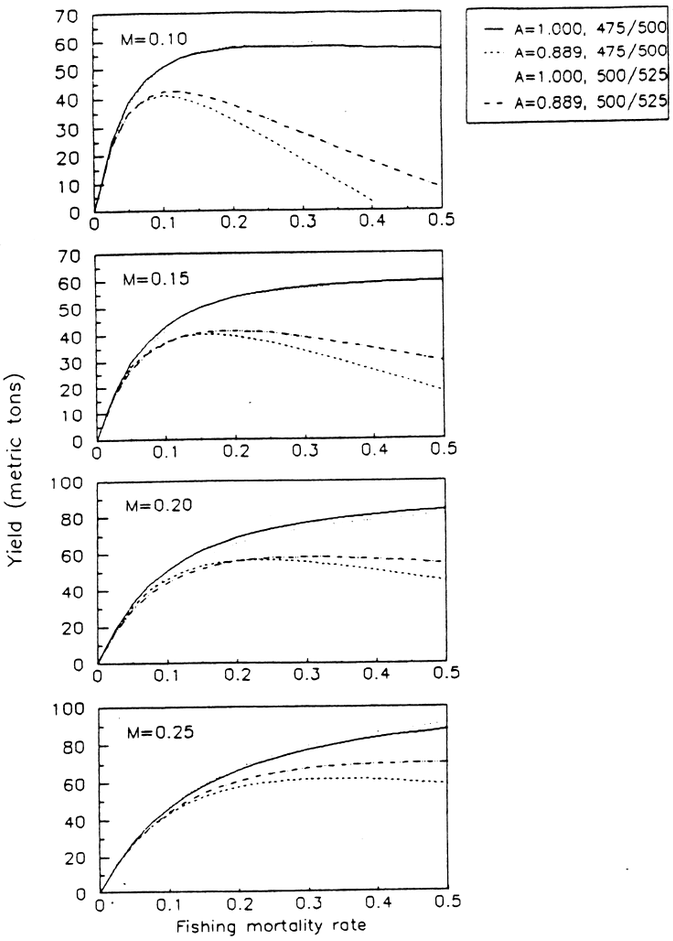

FIGURE 4.—Estimated equilibrium yield at four rates of natural mortality (M), two assumptions regarding the stock-recruitment relationship (A = 0.889 - recruitment dependent on spawning stock, A = 1.000 - recruitment constant), and two values for the female and male (F/M) selectivity parameter $L50_{Sel}$.

Evidence that M is less than 0.25 was provided by predictive models used to estimate M from the growth rate (k) and maximum age (Alverson and Carney 1975) or from k, L_∞, and mean water temperature (Pauly 1980). Estimates from the Alverson-Carney model were 0.107 (female) and 0.118 (male), whereas estimates from Pauly's method were 0.175 (females) and 0.163 (males) (Harris and Grossman 1985). Furthermore, Hoenig (1983) provided a model that predicts total mortality rate (Z) as a function of maximum age. Maximum observed age from May 1982 to August 1983 samples was 32 for female and 33 for male tilefish (Harris and Grossman 1985). Using Hoenig's model, Z would be 0.13 for each sex; therefore, that would be a maximum estimate of M.

A potential source of error in this assessment is the assumption that the selectivity pattern is constant over time. Recent observations (R. Low, fn. 4) indicate that the size at first vulnerability to fishing has decreased from about 1 kg (Harris and Grossman 1985) to about 0.45 kg. The decreasing size at recruitment increases the likelihood of recruitment overfishing because fish are being harvested well before the size at maturity (about 2–3 kg for females). Thus, the current model probably underestimates the impact of fishing. Higher Fs could be sustained if small tilefish were not vulnerable to fishing; unfortunately, it is difficult to regulate age at entry for hook-and-line gear (Myhre 1974) and discard mortality under a minimum size regula-

tion would likely be substantial (Huntsman and Manooch 1978a).

A second potential source of error is the use of a deterministic model to represent recruitment. Changes in population size and CPUE are due not only to the impact of fishing but also to fluctuations in year-class strength. Because the estimates of virgin recruitment were based on changes in CPUE, fluctuations in recruitment that increase (decrease) the decline in CPUE would result in a lower (higher) estimate of virgin recruitment. Based on size-frequency data from the MAB tilefish fishery, Turner et al. (1983) suggested that fluctuations in tilefish year-class strength may be substantial. Using size- and age-frequency data collected off Georgia, Harris and Grossman (1985) found little evidence for strong fluctuations in year-class strength. Tilefish are somewhat difficult to age, however, so differences in year-class strength could be hidden by ageing errors.

A third source of error is the unknown number of fish caught off South Carolina or Georgia, but landed in Florida. The impact on the assessment would depend on the magnitude of the catches and the years in which the catches occurred. If we arbitrarily assume that actual annual removals were 25% higher than combined South Carolina-Georgia landings, recommended Fs would be unchanged, whereas estimates of virgin recruitment and recommended yield would increase by about 25%. Thus, if Florida removals could be accounted for, estimates of stock size would be more accurate, but the increase in recommended yield would be offset by the increased catches, and would not result in increased overall landings.

CONCLUSIONS

The results of this study provide estimates of the relationship between yield and fishing mortality and of the recommended level for F. Results obtained using commercial CPUE estimates indicate that sustainable harvests from the fishery are quite low, and would be obtained at Fs considerably lower than observed in the developing fishery. We obtained higher estimates of population size and sustained yield using research CPUE data; however, we believe that the commercial CPUE data better reflect population trends. We estimate that current stock size is about 200–600 t, compared with a recommended level of 400–800 t. If the stock could be rebuilt to the recommended level, it should support an annual harvest of about 50 t. A rebuilding strategy is feasible for tilefish because catches are low except when directed fishing occurs (G. Ulrich[5]). At present, however, there are no restrictions on the tilefish fishery and despite reductions in effort, catches are probably large enough to prevent the stock from rebuilding (G. Ulrich fn. 5).

Apparent limitations on sustainable yield of the tilefish fishery probably can be attributed to the demographic characteristics of the stock. In a typical fishery for a long-lived, slow-growing species, a few years of high catches are followed by a sharp decline and a subsequent period of low yield (Huntsman and Manooch 1978b; Leaman and Beamish 1984; Francis 1986). Long-lived, sedentary species, such as reef fishes, may be particularly vulnerable to overfishing, even though fishing intensity may be low or the method inefficient (Huntsman and Manooch 1978b). Because tilefish are long-lived, slow-growing, and sedentary (due to their dependence on the availability of shelter), a similar pattern of exploitation can be expected for the tilefish fishery off South Carolina and Georgia.

Leaman and Beamish (1984) recommended that conservative harvest strategies be developed for long-lived species until the evolutionary implications of longevity are better understood. They suggested that extreme longevity (>50 years) may be an adaptive response to ensure population persistence under reproductive uncertainty. For example, a long reproductive life might enable a species to inhabit deeper water (200–1,000 m) where few competitors or predators are found, even though recruitment into such areas may be highly variable (Leaman and Beamish 1984). If variability in recruitment has a significant effect on tilefish stocks, a conservative management strategy emphasizing maintenance of a range of age classes may be appropriate.

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[5]G. Ulrich, South Carolina Wildlife and Marine Resources Department, Charleston, SC 29412, pers. commun. July 1987.

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