American Fisheries Society Symposium 23:17–26, 1999

The Complex Life History of Tilefish *Lopholatilus chamaeleonticeps* and Vulnerability to Exploitation

CHURCHILL B. GRIMES[1]
National Marine Fisheries Service, Southeast Fisheries Science Center, Panama City Laboratory, 3500 Delwood Beach Road, Panama City, Florida 32408-7403, USA

STEPHEN C. TURNER
National Marine Fisheries Service, Southeast Fishery Science Center 75 Virginia Beach Drive, Miami, Florida 33149, USA

Abstract.—Tilefish stocks along the Atlantic coast of the United States have a history of rapidly becoming overfished. Since 1916 when the unexploited southern New England–mid-Atlantic stock yielded 4,500 metric tons (mt), there have been three 20- to 25-year cycles of rapidly increasing landings followed by equally rapid declines to very low levels of catch. Landings have exceeded the long-term potential yield (approximately 1,200 mt) during each of the periods of high catches, especially from 1977 and 1982 when the fishing mortality rate was three times that necessary to obtain maximum yield per recruit.

The complex life history of tilefish may have made them exceptionally vulnerable to exploitation. They are relatively long lived, slow growing and late maturing; for example, females attain 35 years and 95 cm fork length (FL), and mature in 5–7 years. Adults construct shelters (e.g., burrows) in portions of the continental shelf where there is both malleable substratum and relatively warm temperature (9–14°C). Thus, stocks are restricted to specific identifiable portions of the outer continental shelf, making them especially vulnerable to fishing. Reproductive and fishery data indirectly indicate that sexually dimorphic and behaviorally dominant males receive higher fishing mortality resulting in unusually rapid declines in reproductive success of the stock.

Tilefish is a demersal gonochoristic species found in the western Atlantic Ocean along the outer continental shelf from Nova Scotia south to Surinam, but exclusive of the Caribbean Sea (Dooley 1978; Markle et al. 1980). Within the U.S. Mid-Atlantic Bight (Cape Cod, Massachusetts, to Cape Hatteras, North Carolina), they inhabit a narrow zone of relatively warm bottom temperatures (9–14°C) in 80–240 m depth (Able et al. 1982; Grimes et al. 1986). They are long lived and slow growing, maximum size and age being 95 cm fork length (FL) and 35 years and 112 cm FL and 26 years in females and males, respectively (Turner et al. 1983). Tilefish spawn during summer utilizing a complex breeding system featuring behaviorally dominant males (Grimes et al. 1988). Both sexes are functionally mature (i.e., produce gametes) at about 50 cm FL and 5 years, but some males do not develop ripe testes for 2–3 years and 10–15 cm in additional length; that is, they appear to delay participation in spawning. Adults are sexually dimorphic, with males attaining larger sizes and developing conspicuously enlarged adipose flaps (an apparent indictor of male breeding status) at 65–70 cm FL (6–7 years), the size and age by which virtually all males develop ripe testes. Based upon the timing of the development of large ripe testes and enlarged adipose flaps, Grimes et al. (1988) reasoned that this is the size and age when males begin to participate in spawning, not when, based upon histology of the testes, they begin producing sperm. Following a brief period as pelagic larvae (Fahay and Berrien 1981; Berrien 1982), juveniles settle to the bottom.

Tilefish select sedimentary substrata, constructing a variety of shelter habitats. Grossman et al. (1985) found a strong correlation between soft sediment composition and tilefish occurrence. Both juveniles and adults occupy contagiously distributed vertical burrows, the primary habitat, in Pleistocene clay (Able et al.1982;

---

[1] New address: National Marine Fisheries Service, Southwest Fisheries Science Center, Santa Cruz/Tiburon Laboratory, 3150 Paradise Drive, Tiburon, California 94920, USA

Grimes et al. 1986). Adults also inhabit horizontal excavations into more vertically oriented clay sediments in submarine canyons called "Pueblo Habitats" (Cooper and Uzmann 1977; Warme et al. 1977; Grimes et al. 1986) and scour depressions under and around glacial erratic boulders (Valentine et al. 1980; Grimes et al. 1986).

Tilefish in the mid-Atlantic–southern New England stock (Katz et al. 1983) have long supported important fisheries, and annual commercial catches have varied widely since 1916 when 4,500 metric tons (mt) were landed in 10 months (Freeman and Turner 1977). In the early 1970s an important long-line fishery developed, centered in New York and New Jersey, and became one of the most valuable fin fisheries in both states during most years since 1978 (Grimes et al. 1980; NOAA, NMFS 1997). A small recreational headboat fishery that developed in New York and New Jersey during the 1980s landed less than 100 mt per year and is now essentially nonexistent.

The purpose of this paper is to review past trends in the commercial fisheries, pointing out that tilefish have a history of becoming rapidly overfished. Furthermore, we argue that the complexity of their life history, in particular long life, slow growth, habitat specificity, and a complex breeding system featuring behaviorally dominant males have made them especially vulnerable to overfishing.

Historical Trends in Landings

Historical landings show three 20- to 25-year cycles of rapidly increasing landings followed by equally rapid declines to very low levels of catch (Figure 1). Catches were first recorded in 1915. In 1916 a record 4,500 mt were landed, but then catches rapidly declined to about 500 mt in 1920. Landings then steadily increased to about the 200-mt level in 1930, but crashed thereafter; and by 1942 less than 100 mt were recorded. Catches again increased during the late 1940s and attained the 1,500-mt level during the early- to mid-1950s, but declined to about 30 mt in 1969. In the early 1970s, with the development of the long-line fishery in New York and New Jersey, landings again increased, reaching 3,700 mt in 1979, but once again declining to about 500 mt by 1988. Perhaps entering yet a fourth cycle, land-

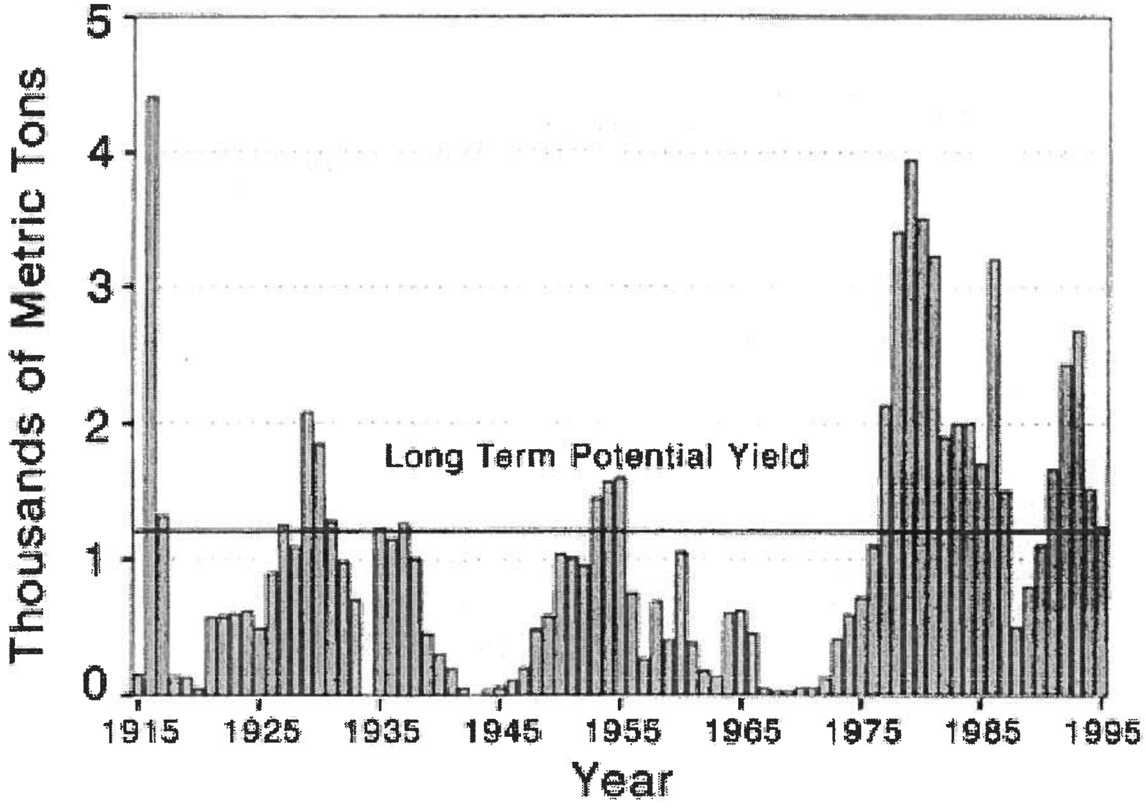

FIGURE 1.—Commercial landings of tilefish in the Mid-Atlantic–southern New England region and the long-term potential yield estimated by Shepherd (1994).

ings have increased since 1988 to a recent high of about 2,700 mt in 1993, but have declined to 1,200 mt in 1995. While the decline in landings during the 1940s can also be attributed to low fishing effort during World War II, the 20- to 25-year cycles of increasing and declining catches are clear and most likely attributable to overfishing.

Contrasting the trend in commercial landings of tilefish with those of Atlantic cod *Gadus morhua* from Georges Bank for roughly the same period (Figure 2), the cod fishery has not experienced a boom and bust pattern, let alone any trend suggesting a cyclic period of high and low catches.

Both age-based and biomass models were used to assess the stock status during the early 1970s to early 1980s (Turner 1986), and more recent analysis of catch and effort and surplus production was done (Shepherd 1994). Based upon nonequilibrium surplus production analysis, long-term potential yield is estimated to be about 1,200 tons (Shepherd 1994). According to the criterion of the catch exceeding the long-term potential yield, the stock has been overfished during each of the four periods of high catch, especially the latter two periods, and rapid declines in catch have followed. Trends in catch rate indicated that during the latter period of high catches, the population level continuously declined, that is, from 1975 to 1993 catch-per-unit of effort declined by 80% (Shepherd 1994).

Age-based analysis also indicated that the stock was overfished during the late 1970s and early 1980s (Turner 1986). Yield-per-recruit analysis showed that the maximum (1.75 kg per recruit) was available at the instantaneous fishing mortality rate of 0.23 at the assumed instantaneous natural mortality of 0.10. Virtual population analysis showed that weighted mean fishing mortality rate in 1982 for all recruited ages was 0.69, threefold higher than the rate required to harvest maximum yield per recruit.

Life History

Longevity and Growth

Because tilefish are long lived and slow growing, stock productivity is relatively low. Age estimates of tilefish from transverse sections of saggital otoliths indicated that females reached 35 years of age and 89 cm FL, and the oldest males 26 years at 96 cm FL. Both sexes grew about 10 cm per year for the first five years of life after which growth slowed, but more so in females than males. For example, in 15 years females reached 75 cm and males 90 cm FL. Apparent greater longevity of female tilefish may be a result of more rapid growth of males causing them to reach harvestable size sooner than females, and thus expose males to fishing mortality longer than females. This process would reduce the probability of males attaining old ages. Alternatively, males may be behaviorally dominant, at least during the breeding season, as will be discussed in a subsequent section of this paper. Behaviorally dominant males may have preferential access to baited hooks on longlines and

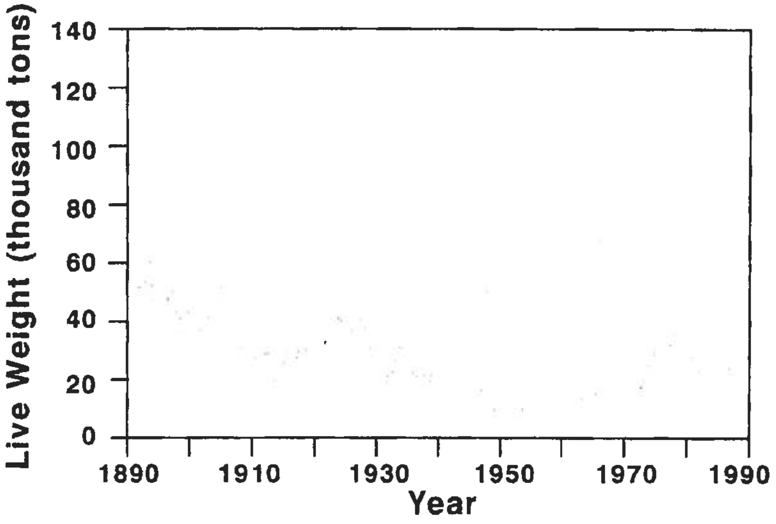

FIGURE 2.—Commercial landings of Atlantic cod from Georges Bank. Redrawn from Serchuck and Wigley (1992).

thus receive a higher rate of fishing mortality than females.

Tilefish generally occur along the outer continental shelf in depths of 100–300 m. Within that depth zone, their spatial distribution pattern is defined by substratum type and temperature. Wherever tilefish have been observed, they had constructed habitats in the seafloor. The simplest habitat they occupied were scour depressions under glacial erratic boulders and under slabs of sedimentary rock. Boulder habitats occurred mostly in the New England area, a region subjected to late Pleistocene glaciation, the source of the boulders. Rock slab habitats were observed in Baltimore Submarine Canyon at the southern end of the Mid-Atlantic Bight. Pueblo habitats occupied by tilefish are horizontal excavations into vertically oriented outcrops of stiff gray Pleistocene clay deposits in the walls of submarine canyons off New England.

The primary habitat of tilefish in the mid-Atlantic and southern New England region are vertically oriented burrows. These funnel-shaped excavations into Pleistocene clay deposits were secondarily burrowed by associated crustaceans and small fishes. The size, structure, spatial distribution, and other species associated with the different habitat types have been described in detail (see Grimes et al. 1986).

Sediment type is a critical factor in allowing successful construction of shelters. Only sediments with sufficiently high degrees of malleability and cohesiveness would allow excavations to be constructed and persist. Stiff semilithified silty clay deposits of Pleistocene origin (e.g., around Hudson Submarine Canyon) were ideal (Twichell et al. 1985; Grimes et al. 1986), but burrows were also found in other soft substrata composed of sand, silt, and a relatively high percentage (approximately 30% by weight) of clay (Able et al. 1987). The importance of sediment type in determining the distribution of tilefish was demonstrated using side-scan sonar (100 kHz) to identify individual burrows, and a 3.5 kHz depth sounder to profile upper bottom sediments and identify clay (Figure 3). Burrows were found where stiff Pleistocene clay was exposed near the surface of the substrata. For example, at a site in Hudson Canyon, the sidescan sonogram and sub-bottom profiler records indicated a transition from burrowed to smooth bottom and different sediment profiles on each side of the transition. On the bur-

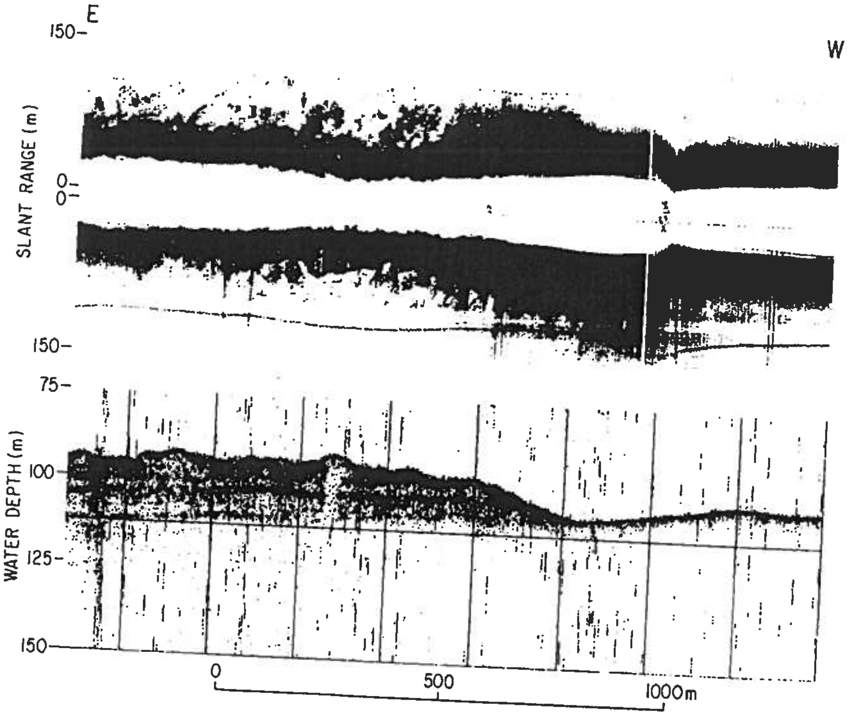

FIGURE 3.—Sidescan sonogram (upper) and sub-bottom profile (lower) at a submersible dive location near Hudson Canyon showing heavily burrowed and unburrowed bottom. Individual burrows are points of strong acoustic reflectance and clay sediments are represented by several layers of weak acoustic reflectance atop a layer of strong reflectance (sand). Redrawn from Grimes et al. (1986).

rowed side, there was a 20-m thick poor acoustic-reflecting layer (clay) above a strong acoustic-reflecting layer (sand). The nonburrowed surface was a strongly reflective sand bottom. This interpretation was validated by direct observation during submersible dives.

The second critical habitat defining factor is temperature; in the mid-Atlantic–southern New England region, tilefish are always associated with a narrow zone of 9–14°C bottom water along the outer continental shelf (Freeman and Turner 1977; Dooley 1978; Grimes et al. 1986). This "warm belt" (Verrill 1882) represents the interface between distinct continental shelf and slope water masses. The area of the mid-Atlantic–southern New England continental shelf bathed by 9–14°C water varied seasonally (Figure 4). The hatched area in the figure shows the shelf area bathed in 9–14°C water for a representative month in each season. Continental cooling of shelf water in winter (represented by January) reduced the 9–14°C area resulting in minimum coverage in spring (March). Vernal warming of shelf water increased the size of the "warm belt" during the summer (July), eventually reaching the seasonal maximum in fall (October).

Vulnerability to Fishing

The extreme habitat specificity of tilefish makes them unusually vulnerable to fishing because characteristics like bottom temperature and sediment type are easily measured and identified allowing concentrations of fish to be accurately located using modern navigational electronics. Vulnerability to fishing is demonstrated by statistically significant seasonal trends in catch rates in the long-line fishery for tilefish from 1974 to 1978 (Grimes et al. 1980; Figure 5). Trends reflected the seasonal changes in the shelf area bathed in 9–14°C bottom water. Catch rate was high in winter when available 9–14°C habitat was declining, and highest in spring when 9–14°C habitat was at a minimum and fish were concentrated. Conversely, catch rates were low in summer and fall when available 9–14°C habitat was expanded and fish were more dispersed. Our interpretation that seasonally varying catch rates reflect limited movements by tilefish in response to seasonal variation in the shelf area bathed in 9–14°C water is supported by submersible observations. Smaller and less structurally complex burrow habitats were observed in areas of the southern New England continental shelf

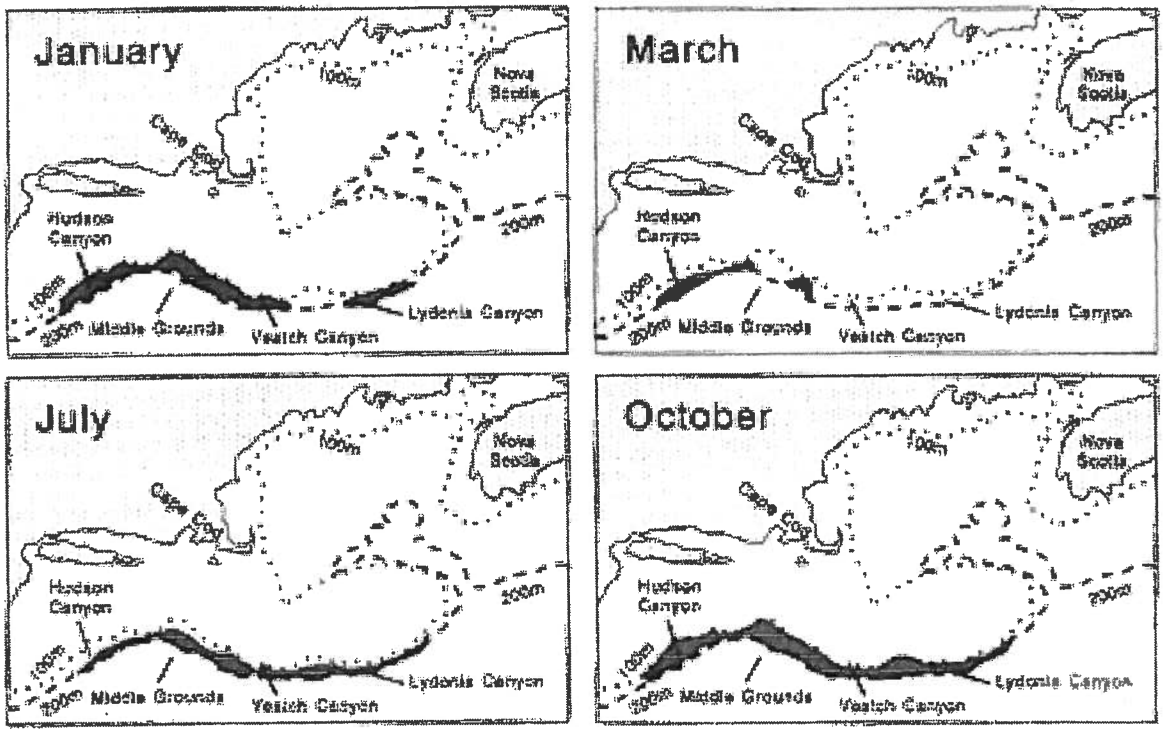

FIGURE 4.—Area of the Mid-Atlantic–southern New England continental shelf between 100 and 200 m bathed by 9–14°C bottom water (shaded and cross hatched) during a representative month in each season. Redrawn from Grimes et al. (1986).

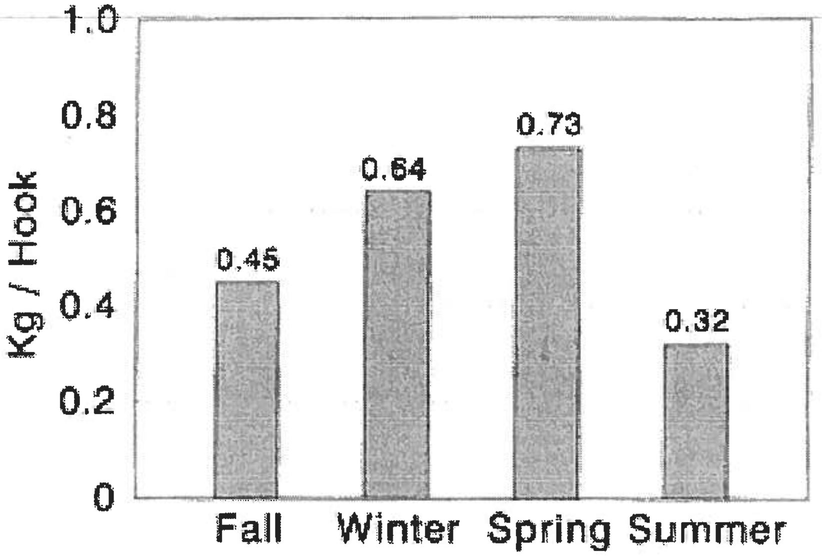

FIGURE 5.—Seasonal mean catch rates from the Mid-Atlantic–southern New England long-line fishery for tilefish from 1974 to 1978. Plotted from Grimes et al. (1980).

that were not bathed by 9–14°C water year round. Lower occupancy rates of burrows were also observed in these seasonal habitats, that is, burrows occupied only at certain times of the year (Grimes et al. 1986).

Breeding System

Tilefish appear to have a complex mating system, featuring behaviorally dominant males, that can be disrupted by fishing. Based upon time-lapse camera observations made during the summer spawning season that showed a female in a burrow during the night while the male remained active nearby, Grimes et al. (1988) suggested that behaviorally dominant, sexually dimorphic males (larger adipose flaps than females) may spawn with females in association with burrows. Sexual maturity was determined by both visual inspection of gonads (presence of ripe-appearing gonads) and histological examination of gonadal tissues (presence of mature gonad structure and vitellogenic ova or sperm). All females were determined to be mature by both methods at about 60 cm FL. On the other hand, all males were determined to be mature at 60 cm FL by histological examination; however, they did not develop a large testicular mass until 2–3 years later at about 80 cm FL (Figure 6). These analyses may indicate that males were physiologically mature and capable of spawning (producing sperm) 20 cm smaller and 2–3 years before they became behaviorally dominant spawning males with a large testicular mass (Grimes et al. 1988).

The timing of the expression of sexual dimorphism in relation to gonad development is additional evidence suggesting a behaviorally mediated breeding system. Adipose flap height increased with size in both sexually mature and immature (determined by visual staging) male tilefish, but adipose flaps were larger for all mature males at least 60 cm FL. Furthermore, flaps became markedly larger for mature males greater than 75 cm FL, and these large males all had large well-developed testes (Figure 7). Grimes et al. (1988) interpretation of these results was that adipose flap size may be a signal of male reproductive status. Large spawning males have large flaps while smaller, perhaps subordinate, males may be physiologically mature (as determined histologically), but do not have enlarged testes or large adipose flaps.

We hypothesize that fishing was selective for large dominant males. During the period of time when the long-line fishery in the Mid-Atlantic Bight was rapidly expanding, catch rate (abundance) diminished by 70% (Turner 1986), and the size of recruitment to the fishery declined from about 90 cm FL in 1974 to 45–50 cm FL in 1982 (Figure 8). The size of recruitment to long-line fisheries is usually determined by hook size (i.e., larger fish take larger hooks). That was apparently not the case for the tilefish fishery at this time, because there were no changes in hook size on

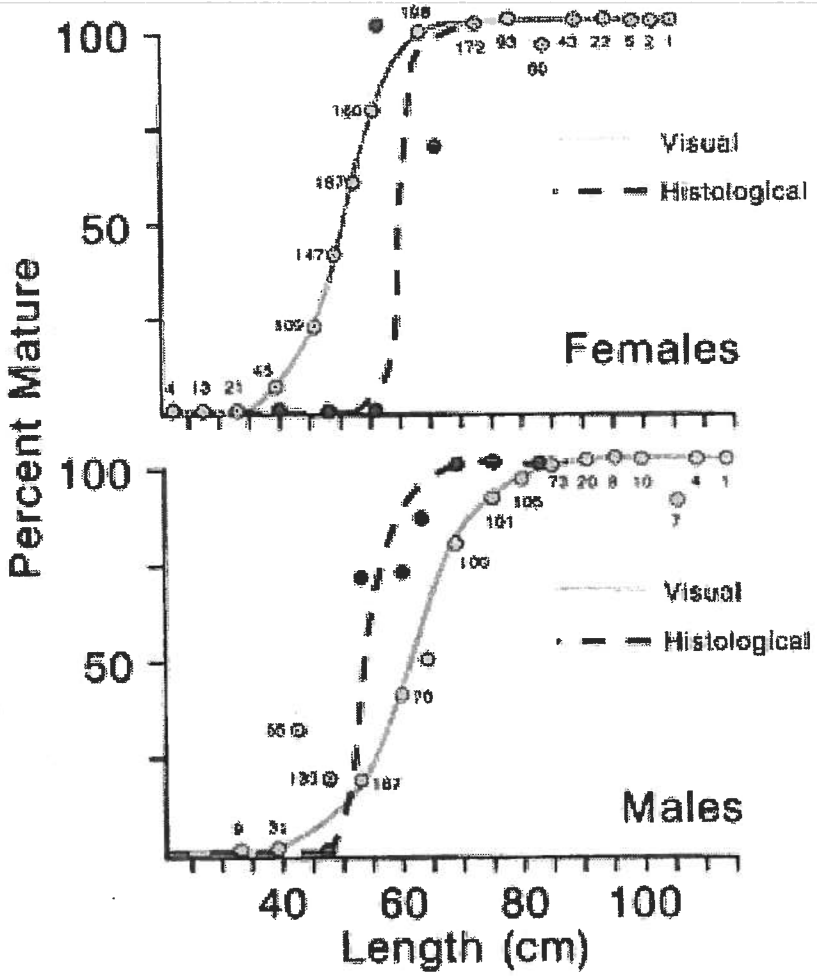

FIGURE 6.—The relationship of sexual maturity (assessed by visual staging and histological methods) and size for female and male tilefish, sample size is given for each data point. Redrawn from Grimes et al. (1988).

longlines used in the fishery during this period. We suggest that the size of recruitment declined because as large dominant fish were removed from the stock by fishing, the smaller and less behaviorally dominant fish gained access to baits.

A second line of evidence supporting the contention that long-line fishing was selective for large dominant males comes from sex-specific instantaneous fishing mortality rates estimated by virtual population analysis (Turner 1986). Fishing mortality increased from 1974 to 1982 when the long-line fishery rapidly expanded as previously described, but the rate was usually higher for males (Figure 9). Although direct evidence of sex-selective fishing is meager, it has been reported for hermaphroditic species, but not gonochores. Male gag *Mycteroperca microlepis*, (Gilmore, Harbor Branch Oceanographic Institution, personal communication) and scamp *M. phenax*, (Gilmore and Jones 1992) were reported to be selectively caught from spawning aggregations observed from a submersible. Gilmore and Jones (1992) postulated that fishing selection was based on male behavior and that it would result in differential fishing mortality for males. However, gag and scamp are protogynous hermaphrodites that breed in aggregations and are suspected to have haremic breeding systems (Gilmore and Jones 1992; Coleman et al. 1996). Thus, these species may be more likely to develop strong behavioral dominance in males, making them more susceptible to selective fishing than the gonochoristic tilefish.

We hypothesize that selective removal of large dominant spawning males may disrupt the

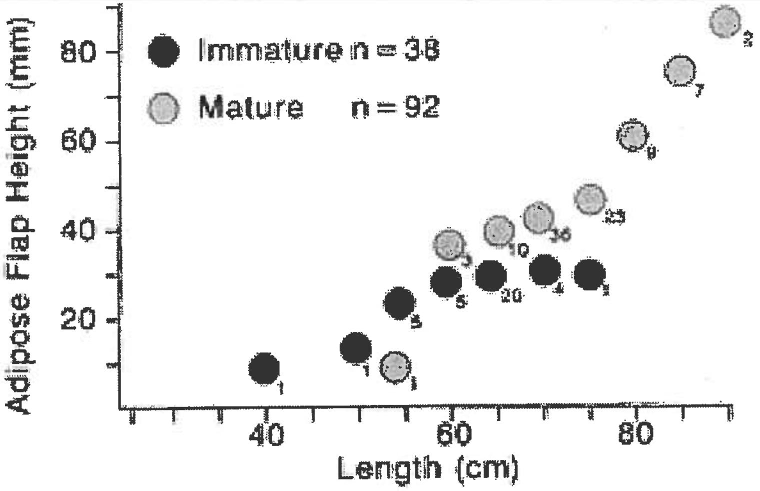

FIGURE 7.—The relation between mean predorsal adipose flap size and fork length in sexually mature and immature tilefish. Maturity was assessed by visual staging. Sample size is given for each data point. Redrawn from Grimes et al. (1988).

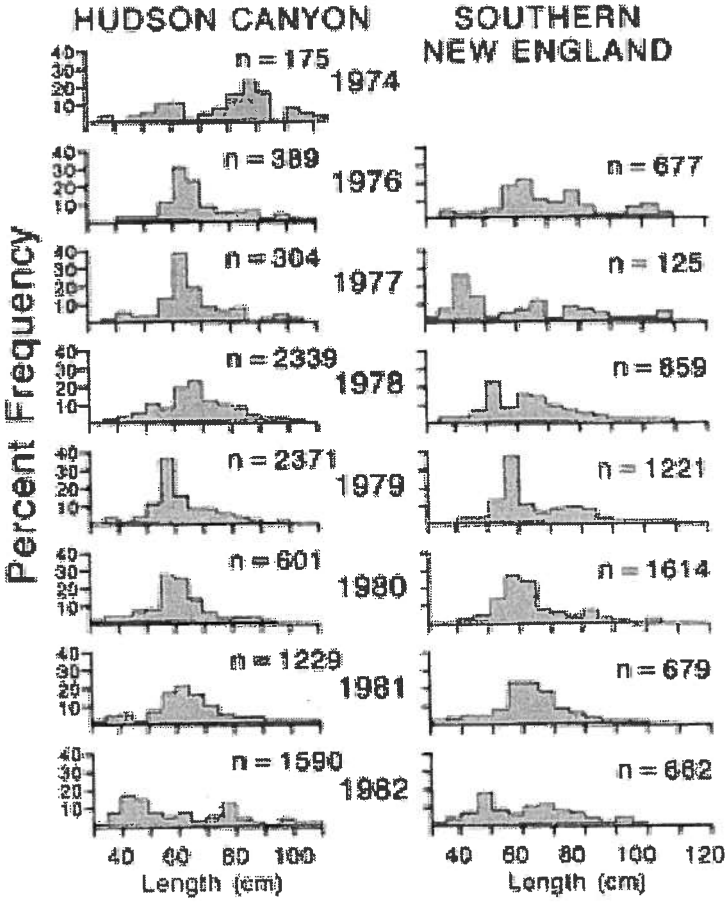

FIGURE 8.—Size-frequency distribution of tilefish long-line catches during the years of rapid development of the fishery. Redrawn from Turner (1986).

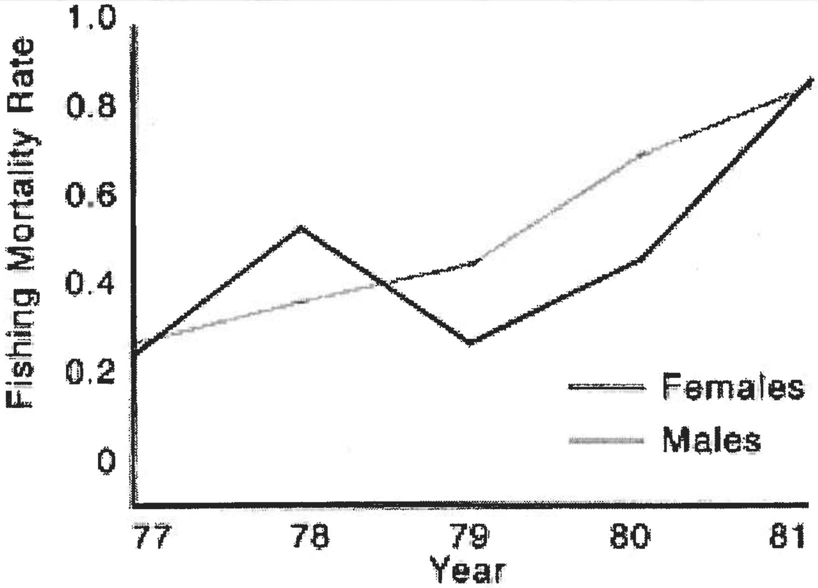

FIGURE 9.—Instantaneous fishing mortality rates (from virtual population analysis) for male and female tilefish during years of rapid development of the long-line fishery. Plotted from Turner (1986).

mating system because the remaining smaller subordinate males with small testes could not fertilize all the eggs produced by females. This sperm limitation could result in reduced reproductive success. Alternatively, reduction in the number of dominant males could result in the potential for lower reproductive success by reducing spawning opportunities for ripe females. Observation of natural spawnings, field experiments, and theoretical models all suggest that sperm limitation is a regular occurrence in several marine taxa including fish (Levitan and Petersen 1995). Furthermore, Coleman et al. (1996) suggested that in gag a dramatic reduction in the proportion of males from fishing may have resulted in some females not spawning, or alternatively in sperm limitation if males attempted to apportion spawning among all available females. Either scenario would result in lowered reproductive success.

Conclusion

A brief review of the history of the commercial long-line fisheries for tilefish suggests that the stock is especially vulnerable to exploitation, showing several 20- to 25-year cycles of rapidly increasing landings, then overfishing followed by precipitously declining catches. The extreme susceptibility of tilefish to overfishing is most likely due to their complex life history. Long life and slow growth result in relatively low stock productivity, and thus are contributing factors. More importantly, the extreme habitat specificity of tilefish, that is, restriction to sites defined by narrow temperature limits and burrowable substratum, allow fishermen to easily locate concentrations of fish and very efficiently impose fishing effort (i.e., catchability of tilefish is high). An additional factor causing susceptibility to overfishing is that fishing may disrupt the breeding system by selectively removing large behaviorally dominant spawning males, resulting in sperm limitation or reduced spawning opportunities for females, either or both reducing reproductive success.

References

Able, K. W., C. B. Grimes, R. A. Cooper, and J. R. Uzmann. 1982. Burrow construction and behavior of tilefish, *Lopholatilus chamaeleonticeps*, in Hudson Submarine Canyon. Environmental Biology of Fishes 7:199–205.

Able, K. W., D. C. Twichell, C. B. Grimes, and R. S. Jones. 1987. Tilefishes of the Genus *Caulolatilus* construct burrows in the seafloor. Bulletin of Marine Science 40(1):1–10.

Berrien, P. 1982. Larval fish distribution in the

Middle Atlantic Bight. Pages 23–44 *in* M. D. Grosslein and T. R. Azarovitz, editors. Fish distribution. MESA (Marine Ecosystem Analysis) New York Bight Atlas Monograph 15.

Coleman, F. C., C. C. Koenig, and L. A. Collins. 1996. Reproductive styles of shallow-water groupers (Pises: Serranidae) in the eastern Gulf of Mexico and the consequences of fishing spawning aggregations. Environmental Biology of Fishes 47(2) 129–141.

Cooper, R. A., and J. R. Uzmann. 1977. Ecology of juvenile and adult clawed lobsters, *Homarus americanus*, *H. gammarus* and *Nephrops norvegicus*. Pages 187–208 *in* B. F. Phillips and J. S. Cobb, editors. Workshop on lobster and rock lobster ecology and physiology. Commonwealth Scientific and Industrial Organization, Division of Fisheries and Oceanography, Circular 7.

Dooley, J. K. 1978. Systematics and biology of tilefishes (Perciformes: Branchiostegidae and Malacanthidae), with descriptions of two new species. NOAA (National Oceanic and Atmospheric Administration) Technical Report NMFS (National Marine Fisheries Service) Circular 41.

Fahay, M. P., and P. Berrien. 1981. Preliminary description of larval tilefish, *Lopholatilus chamaeleonticeps*. Rapports et Proces-Verbaux des Reunions Conseil Internationale pour l'Exploration de la Mer 178:600–602.

Freeman, B. L., and S. C. Turner. 1977. Biological and fisheries data on tilefish, *Lopholatilus chamaeleonticeps* Goode and Bean. NOAA (National Oceanic and Atmospheric Administration) NMFS (National Marine Fisheries Service) Northeast Fisheries Center, Sandy Hook Laboratory Technical Service Report 5.

Gilmore, R. G., and R. S. Jones. 1992. Color variation and associated behavior in the epinepheline groupers, *Mycteroperca microlepis* (Goode and Bean) and *M. phenax* Jordan and Swain. Bulletin of Marine Science 51:84–103.

Grimes, C. B., K. W. Able, and R. S. Jones. 1986. Tilefish, *Lopholatilus chamaeleonticeps*, habitat, behavior and community structure in Mid-Atlantic and southern New England waters. Environmental Biology of Fishes 15:273–392.

Grimes, C. B., K. W. Able, and S. C. Turner. 1980. A preliminary analysis of the tilefish, *Lopholatilus chamaeleonticeps*, fishery in the Mid-Atlantic Bight. U.S. National Marine Fisheries Service Marine Fisheries Review 42(11):13–18.

Grimes, C. B., C. F. Idleberger, K. W. Able, and S. C. Turner. 1988. The reproductive biology of tilefish, *Lopholatilus chamaleonticeps* Goode and Bean, from the United States Mid-Atlantic Bight, and the effects of fishing on the breeding system. Fishery Bulletin 86(4):745–762.

Grossman, G. D., M. J. Harris, and J. E. Hightower. 1985. The relationship between tilefish (*Lopholatilus chamaeleonticeps*) abundance and sediment composition off Georgia. Fishery Bulletin 83:443–447.

Katz, S. J., C. B. Grimes, and K. W. Able. 1983. Delineation of tilefish, *Lopholatilus chamaeleonticeps*, stocks along the United States east coast and in the Gulf of Mexico. Fishery Bulletin 81:41–50.

Levitan, D. R., and C. Petersen. 1995. Sperm limitation in the sea. Trends in Ecology and Evolution 10(6):228–231.

Markle, D. F., W. B. Scott, and A. C. Kohler. 1980. New and rare records of Canadian fishes and the influence of hydrography on resident and nonresident Scotian Shelf ichthyofauna. Canadian Journal of Fisheries and Aquatic Science 37: 49–65.

NOAA (National Oceanic and Atmospheric Administration), NMFS (National Marine Fisheries Service). 1997. Fisheries of the United States 1996. Current Fisheries Statistics 9600.

Shepherd, G. 1994. Tilefish. Pages 96–97 *in* Status of the fishery resources off the northeastern United States for 1994. NOAA (National Oceanic and Atmospheric Administration) NMFS (National Marine Fisheries Service) Technical Memorandum NMFS-NE-108.

Turner, S. C. 1986. Population dynamics of and impact of fishing on tilefish, *Lopholatilus chamaeleonticeps*, in the Mid-Atlantic-Southern New England region during the 1970s and early 1980s. Doctoral dissertation. Rutgers University, New Brunswick, New Jersey.

Turner, S. C., C. B. Grimes, and K. W. Able. 1983. Growth, mortality and age/size structure of the fisheries for tilefish, *Lopholatilus chamaeleonticeps*, in the Middle Atlantic-Southern New England region. Fishery Bulletin 81:751–763.

Twichell, D. C., C. B. Grimes, R. S. Jones, and K. W. Able. 1985. The role of erosion by fish in shaping topography around Hudson Submarine Canyon. Journal of Sedimentary Petrology 55(5):712–719.

Valentine, P. C., J. R. Uzmann, and R. A. Cooper. 1980. Geology and biology of Oceanographer Submarine Canyon. Marine Geology 38:283–312.

Verrill, A. E. 1882. Notice of the remarkable marine fauna occupying the outer banks off the southern coast of New England. No. 7 and some additions to the fauna of Vineyard Sound. The American Journal of Science 124:360–371.

Warme, J. E., R. A. Slater, and R. A. Cooper. 1977. Bioerosion in submarine canyons. Pages 65–70 *in* D. J. Stanley and G. Kelling, editors. Sedimentation in submarine canyons, fans, and trenches. Dowden, Hutchinson and Ross Publishers, Stroudsburg, Pennsylvania.