

NOAA Technical Memorandum NMFS-NE-152

Essential Fish Habitat Source Document:

Tilefish, *Lopholatilus chamaeleonticeps*, Life History and Habitat Characteristics

U. S. DEPARTMENT OF COMMERCE National Oceanic and Atmospheric Administration National Marine Fisheries Service Northeast Region Northeast Fisheries Science Center Woods Hole, Massachusetts

September 1999

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Tilefish, *Lopholatilus chamaeleonticeps*, Life History and Habitat Characteristics

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Editorial Notes on Issues 122-152 in the NOAA Technical Memorandum NMFS-NE Series

Editorial Production

For Issues 122-152, staff of the Northeast Fisheries Science Center's (NEFSC's) Ecosystems Processes Division have largely assumed the role of staff of the NEFSC's Editorial Office for technical and copy editing, type composition, and page layout. Other than the four covers (inside and outside, front and back) and first two preliminary pages, all preprinting editorial production has been performed by, and all credit for such production rightfully belongs to, the authors and acknowledgees of each issue, as well as those noted below in "Special Acknowledgments."

Special Acknowledgments

David B. Packer, Sara J. Griesbach, and Luca M. Cargnelli coordinated virtually all aspects of the preprinting editorial production, as well as performed virtually all technical and copy editing, type composition, and page layout, of Issues 122-152. Rande R. Cross, Claire L. Steimle, and Judy D. Berrien conducted the literature searching, citation checking, and bibliographic styling for Issues 122-152. Joseph J. Vitaliano produced all of the food habits figures in Issues 122-152.

Internet Availability

Issues 122-152 are being copublished, *i.e.*, both as paper copies and as web postings. All web postings are, or will soon be, available at: *www.nefsc.nmfs.gov/nefsc/habitat/efh*. Also, all web postings will be in "PDF" format.

Information Updating

By federal regulation, all information specific to Issues 122-152 must be updated at least every five years. All official updates will appear in the web postings. Paper copies will be reissued only when and if new information associated with Issues 122-152 is significant enough to warrant a reprinting of a given issue. All updated and/or reprinted issues will retain the original issue number, but bear a "Revised (Month Year)" label.

Species Names

The NMFS Northeast Region's policy on the use of species names in all technical communications is generally to follow the American Fisheries Society's lists of scientific and common names for fishes (*i.e.*, Robins*et al.* 1991^a), mollusks (*i.e.*, Turgeon *et al.* 1998^b), and decapod crustaceans (*i.e.*, Williams *et al.* 1989^c), and to follow the Society for Marine Mammalogy's guidance on scientific and common names for marine mammals (*i.e.*, Rice 1998^d). Exceptions to this policy occur when there are subsequent compelling revisions in the classifications of species, resulting in changes in the names of species (*e.g.*, Cooper and Chapleau 1998^e).

^aRobins, C.R. (chair); Bailey, R.M.; Bond, C.E.; Brooker, J.R.; Lachner, E.A.; Lea, R.N.; Scott, W.B. 1991. Common and scientific names of fishes from the United States and Canada. 5th ed. *Amer. Fish. Soc. Spec. Publ.* 20; 183 p.

^bTurgeon, D.D. (chair); Quinn, J.F., Jr.; Bogan, A.E.; Coan, E.V.; Hochberg, F.G.; Lyons, W.G.; Mikkelsen, P.M.; Neves, R.J.; Roper, C.F.E.; Rosenberg, G.; Roth, B.; Scheltema, A.; Thompson, F.G.; Vecchione, M.; Williams, J.D. 1998. Common and scientific names of aquatic invertebrates from the United States and Canada: mollusks. 2nd ed. *Amer. Fish. Soc. Spec. Publ.* 26; 526 p.

^cWilliams, A.B. (chair); Abele, L.G.; Felder, D.L.; Hobbs, H.H., Jr.; Manning, R.B.; McLaughlin, P.A.; Pérez Farfante, I. 1989. Common and scientific names of aquatic invertebrates from the United States and Canada: decapod crustaceans. *Amer. Fish. Soc. Spec. Publ.* 17; 77 p.

dRice, D.W. 1998. Marine mammals of the world: systematics and distribution. Soc. Mar. Mammal. Spec. Publ. 4; 231 p.

^eCooper, J.A.; Chapleau, F. 1998. Monophyly and interrelationships of the family Pleuronectidae (Pleuronectiformes), with a revised classification. *Fish. Bull. (U.S.)* 96:686-726.

One of the greatest long-term threats to the viability of commercial and recreational fisheries is the continuing loss of marine, estuarine, and other aquatic habitats.

Magnuson-Stevens Fishery Conservation and Management Act (October 11, 1996)

The long-term viability of living marine resources depends on protection of their habitat.

NMFS Strategic Plan for Fisheries Research (February 1998)

The Magnuson-Stevens Fishery Conservation and Management Act (MSFCMA), which was reauthorized and amended by the Sustainable Fisheries Act (1996), requires the eight regional fishery management councils to describe and identify essential fish habitat (EFH) in their respective regions, to specify actions to conserve and enhance that EFH, and to minimize the adverse effects of fishing on EFH. Congress defined EFH as "those waters and substrate necessary to fish for spawning, breeding, feeding or growth to maturity." The MSFCMA requires NMFS to assist the regional fishery management councils in the implementation of EFH in their respective fishery management plans.

NMFS has taken a broad view of habitat as the area used by fish throughout their life cycle. Fish use habitat for spawning, feeding, nursery, migration, and shelter, but most habitats provide only a subset of these functions. Fish may change habitats with changes in life history stage, seasonal and geographic distributions, abundance, and interactions with other species. The type of habitat, as well as its attributes and functions, are important for sustaining the production of managed species.

The Northeast Fisheries Science Center compiled the available information on the distribution, abundance, and habitat requirements for each of the species managed by the New England and Mid-Atlantic Fishery Management Councils. That information is presented in this series of 30 EFH species reports (plus one consolidated methods report). The EFH species reports comprise a survey of the important literature as well as original analyses of fishery-

JAMES J. HOWARD MARINE SCIENCES LABORATORY HIGHLANDS, NEW JERSEY SEPTEMBER 1999 independent data sets from NMFS and several coastal states. The species reports are also the source for the current EFH designations by the New England and Mid-Atlantic Fishery Management Councils, and have understandably begun to be referred to as the "EFH source documents."

NMFS provided guidance to the regional fishery management councils for identifying and describing EFH of their managed species. Consistent with this guidance, the species reports present information on current and historic stock sizes, geographic range, and the period and location of major life history stages. The habitats of managed species are described by the physical, chemical, and biological components of the ecosystem where the species occur. Information on the habitat requirements is provided for each life history stage, and it includes, where available, habitat and environmental variables that control or limit distribution, abundance, growth, reproduction, mortality, and productivity.

Identifying and describing EFH are the first steps in the process of protecting, conserving, and enhancing essential habitats of the managed species. Ultimately, NMFS, the regional fishery management councils, fishing participants, Federal and state agencies, and other organizations will have to cooperate to achieve the habitat goals established by the MSFCMA.

A historical note: the EFH species reports effectively recommence a series of reports published by the NMFS Sandy Hook (New Jersey) Laboratory (now formally known as the James J. Howard Marine Sciences Laboratory) from 1977 to 1982. These reports, which were formally labeled as *Sandy Hook Laboratory Technical Series Reports*, but informally known as "Sandy Hook Bluebooks," summarized biological and fisheries data for 18 economically important species. The fact that the bluebooks continue to be used two decades after their publication persuaded us to make their successors – the 30 EFH source documents – available to the public through publication in the *NOAA Technical Memorandum NMFS-NE* series.

JEFFREY N. CROSS, CHIEF ECOSYSTEMS PROCESSES DIVISION NORTHEAST FISHERIES SCIENCE CENTER

Contents

1
1
5
6
7
7
8
8

Tables

Table 1.	ood items of tilefish, Lopholatilus chamaeleonticeps, in the Middle Atlantic Bight1	1
Table 2.	ummary of life history and habitat characteristics for tilefish, Lopholatilus chamaeleonticeps1	2

Figures

Figure 1.	The tilefish, Lopholatilus chamaeleonticeps (from Goode 1884).	13
Figure 2.	Abundance of the major prey taxa in the diet of juvenile tilefish collected during NEFSC bottom trawl surveys	.14
Figure 3.	Abundance of tilefish eggs relative to water temperature and bottom depth from NEFSC MARMAP surveys	.15
Figure 4.	Abundance of tilefish larvae relative to water temperature and bottom depth from NEFSC MARMAP surveys	.16
Figure 5.	Abundance of juvenile and adult tilefish relative to bottom temperature and depth based on NEFSC surveys	.17
Figure 6.	Distribution and abundance of tilefish eggs collected during NEFSC MARMAP surveys	.18
Figure 7.	Distribution and abundance of tilefish larvae collected during NEFSC MARMAP surveys	.21
Figure 8.	Seasonal distribution and abundance of juvenile and adult tilefish collected during NEFSC bottom trawl surveys	.22
Figure 9.	Tilefish distribution and relative abundance, 1973-1982, based on the long-line fishery effort	.24
Figure 10.	Comparison of "rough bottom" topography on either side of Hudson Canyon with tilefish fishing effort	.27
Figure 11.	Commercial weighout distributions of tilefish by seasonal quarters in Georges Bank and Middle Atlantic Bight	.28
Figure 12.	Commercial landings and catch-per-unit-effort data for tilefish from Georges Bank and Middle Atlantic Bight	.30

INTRODUCTION

Lopholatilus chamaeleonticeps (Goode and Bean 1879) (Figure 1) is the largest and longest lived of the tilefishes (Malacanthidae); it reaches 30 kg, grows to 120 cm TL, and lives over 45 years (Bigelow and Schroeder 1953; Turner *et al.* 1983; Turner 1986). The first recorded major catch of the species occurred in 1879 in 38 m of water south of Nantucket shoals (Collins 1884; Dooley 1978); it was identified as a new species at that time (Goode and Bean 1880).

Tilefish have a "unique spatial and temporal behavior" (Warner 1987). Their habitat is a relatively restricted band, approximately 80-540 m deep and 8-17°C, known as the "warm belt" (Verrill 1882) on the outer continental shelf and upper slope of the northwest Atlantic coast. Within this band, tilefish are more abundant near the 15° C isotherm which occurs between 100-240 m (Bigelow and Schroeder 1953; Freeman and Turner 1977; Dooley 1978), which includes the shelf break (120-145 m) (Stanley *et al.* 1972).

Tilefish are most abundant from Georges Bank to Key West, Florida and throughout much of the Gulf of Mexico (Matlock et al. 1991). They are occasionally reported from as far north as Banquereau Bank (44°26' N, 57°13' W) at depths between 50-150 m off Nova Scotia (Markle et al. 1980; Scott and Scott 1988) and off the coast of Surinam, but not in the Caribbean Sea (Bigelow and Schroeder 1953; Dooley 1978). Their distribution, which appears discontinuous, may be controlled by temperature, depth, and the availability of shelter or fine, semi-consolidated sediments that support their shelter burrows (Grossman et al. 1985; Jones et al. 1989; Matlock et al. 1991). A sibling species (L. villarii) occurs in the South Atlantic from Brazil to Argentina; the distributions of these species are not known to overlap (Freeman and Turner 1977; Dooley 1978).

Dooley (1978) speculated that tilefish recently colonized the outer continental shelf off southern New England because there are no reported catches of the species in the deep-water, longline cod fishery prior to 1879 (although the fishery probably was focused in shallower water because of the time and effort required to retrieve the gear by hand). Freeman and Turner (1977) suggest that tilefish are not restricted to a specific burrow, but may move within a local area (based on how quickly a fishing site can stop or start being productive). They noted that larger fish are less abundant at depths greater than 238 m, which is also true of the population south of Cape Hatteras (Low et al. 1983). The mean size of tilefish was greatest at intermediate depths (approximately 200-240 m) for both the northern and southern stocks (Low et al. 1983).

LIFE HISTORY

EGGS

Tilefish eggs are non-adhesive and buoyant (Bigelow and Schroeder 1953; Freeman and Turner 1977). Eggs that were fertilized artificially and reared at 22.0-24.6°C hatched in 40 hours (Fahay and Berrien 1981).

LARVAE

The larvae were not identified in ichthyoplankton samples until recently. Newly hatched larvae are 2.6 mm long and well formed at 5.0 mm; the largest pelagic larva found was 8.7 mm TL. Larvae occur in the plankton from July to September over the outer continental shelf in the Middle Atlantic Bight. The center of abundance lies between Hudson and Baltimore canyons (Fahay and Berrien 1981).

If post-larval tilefish are primarily sedentary and nonmigratory, except perhaps seasonally off southern New England (Freeman and Turner 1977; Grimes *et al.* 1987), then the recruitment of tilefish to support or re-establish local populations is dependent on larval settlement (Bumpus 1899). The habitat criteria for larval tilefish settlement and the transition to juveniles are unknown. If transitional tilefish larvae and early juveniles are unable to excavate burrows, they may be dependent on other sources of shelter.

JUVENILES (< 50 CM TL)

The smallest juveniles collected in bottom trawls were 15.5 mm SL (Fahay and Berrien 1981). Early juveniles (51-82 mm) were collected at 100-200 m during April-July along the outer edge of the Middle Atlantic Bight shelf (Bigelow and Schroeder 1953; Dooley 1978). The smallest fish collected in the Northeast Fisheries Science Center (NEFSC) bottom trawl surveys was approximately 140 mm [see Reid *et al.* (1999) for methods]. Bigelow and Schroeder (1953) reported that 60-90 mm specimens were collected off southern New England in April and 100-105 mm specimens were collected in July. Freeman and Turner (1977) suggested that particular juvenile size classes favor certain areas; some of these areas were avoided by the long-line fishery because of the low market value of small fish at that time.

Juveniles often occupy simple vertical shaft burrows in semi-lithified clay (Able *et al.* 1982). According to Freeman and Turner (1977), divers observed tilefish using American lobster (*Homarus americanus*) pots as shelter; in deeper waters, red crab (*Chaceon quinquedens*) traps may also be used. Anthropogenic material, such as ship wrecks and other solid structures, are also used (e.g., Cooper *et al.* 1987b), possibly by juveniles that have not found or excavated burrows.

ADULTS (> 50 CM TL)

Tilefish are shelter-seeking and adults have been observed and photographed using rocks, boulders, and the scour depressions beneath them, exposed rocky ledges, and horizontal and vertical burrows in semi-lithified clay outcrops on the upper slopes, flanks, and shoulders of submarine canyons such as Oceanographer Canyon (southern Georges Bank) and Hudson Canyon (off New Jersey) (Valentine et al. 1980; Able et al. 1982, 1987b). Tilefish burrows can be tubular or funnel-shaped, up to 5 m wide at the mouth, and several meters deep. The main burrow often contains a complex of smaller burrows created and used by decapod crustaceans (Able et al 1982; Grimes et al. 1986). The hydrographical, geological, and biological characteristics of this habitat were described by Valentine et al. (1980). The complex of burrows in clay outcrops along the slopes and walls of submarine canyons, and elsewhere on the outer continental shelf, have been called "pueblo" habitat, because of their similarity to human structures in the southwestern United States (Cooper and Uzmann 1977).

Twichell et al. (1985) speculated that the largest burrows are the product of a lifetime of the activities of individual tilefish. They gradually widen and deepen the burrows as they grow. Burrows are modified by decapod crustaceans, which sometimes join adjacent burrows with their activities, or collapse part or all of a burrow complex (Able et al. 1982; Twichell et al. 1985; Grimes et al. 1986). Able et al. (1987a) suggested that sidescan sonar could be used to assess the occurrence and density of burrows and other shelter on the seafloor (and possibly to estimate tilefish density). Using sidescan imagery, Grimes et al. (1986) estimated that the density of burrows was about 2,500/km² near Hudson Canyon and as high as 13,000/km² in the South Atlantic region (Barans and Stender 1993), but lower (approximately 1,600/km²) in the Gulf of Mexico (Matlock et al. 1991). Able et al. (1987b) reported that the density of burrows varied more than ten-fold among different areas inhabited by tilefish.

Tilefish are important modifiers or creators of habitat on the outer continental shelf (Able *et al.* 1982). Twichell *et al.* (1985) suggest that the burrowing habitats of tilefish and their associated crustaceans significantly alter the topography and that the irregular, hummocky topography found on either side of Hudson Canyon may be the product of tilefish activity. They also discuss how creation, expansion, and use of burrows, vertical pits, and horizontal pueblos in the semi-lithified clay enhances the erosion of the exposed clay. Grimes *et al.* (1987) suggest that since each generation of tilefish may excavate a new burrow, the habitat modification and erosion caused by tilefish is significant. It is reasonable to assume that small tilefish will use an existing burrow if it is in good shape and unoccupied. The current, relatively high fishing levels and low adult population levels may have reduced the need of recruiting tilefish to create new burrows and reduced erosion rates.

The initial methods of burrow excavation are not completely known, although several hypotheses have been proposed, including the activities of galatheid crabs and tilefish (Grimes et al. 1986, 1987). According to Cooper et al. (1987b), tilefish are a "tertiary borer and nestler that further enlarge excavations and occupy existing burrows"; they believe that the burrows are started by smaller crustaceans. Grimes et al. (1986) and Able et al. (1993) conclude that tilefish maintain the burrows and burrow associates. The use of burrow, pueblo, and intermixed habitats was described by Able et al. (1982) and Grimes et al. (1986). Tilefish are relatively inactive and usually only one tilefish occurs in a burrow (Able et al. 1982), although several tilefish were observed using boulders off southern New England (Grimes et al. 1987). There seems to be no preference for shelter size or shape. Some fish appear to be residents of certain burrows or shelter sites and retreated to these shelters when disturbed by researchers (Grimes et al. 1983, 1986). Tilefish may move away from their shelter to feed and their feeding activity may organize the activity of other species in the habitat; thus tilefish fit the definition of a "keystone" species (Grimes et al. 1986).

Tilefish are not unique in their modification of sediments. Stanley (1971) and Auster *et al.* (1995) reported depressions in sediments made by fish (e.g., red hake, *Urophycis chuss*) and crustaceans on the outer continental shelf that were used by other species for shelter.

Tilefish habitat in the northern Middle Atlantic Bight (Georges Bank to just south of Hudson Canyon) occurs on the shelf between 100-200 m, at 9-14°C, and contains rock or clay boulders, or clay outcrops with burrows (Grimes et al. 1986). In the southern part of the Bight, Levy et al. (1988) found tilefish using rocky ledge or burrow shelter south to Norfolk Canyon, off Virginia. Some of the biogenic habitat (cavernous hollows in clay) and poorly identified fish noted by Stanley (1971) in early video explorations in Wilmington Canyon (off Delaware) may include tilefish and their burrows. Tilefish were collected by trawl southwest of Norfolk Canyon in March during the winter fishery off Virginia and North Carolina in the early 1930s (Pearson 1932). The shelf area off southern New England and on Georges Bank may be used seasonally or if suitable temperatures persist through the coolest hydrographic periods (Grimes et al. 1986).

Tilefish habitat is used by other fish and invertebrates, especially crustaceans, including rare species (Williams 1988), those new to science (Bowman 1986), and those whose known range may extend in this habitat; e.g., yellowfin bass, *Anthias nicholsi* (Grimes *et al.* 1986; Bowman 1986; Cooper *et al.* 1987b). Several of these community members are of interest to fisheries, including American lobster, conger eel (*Conger*)

oceanicus), ocean pout (*Macrozoarces americanus*), cusk (*Brosme brosme*), redfish (*Sebastes* spp.), and hake (*Urophycis* spp.) (Grimes *et al.* 1986; Hood *et al.* 1988). Near Norfolk Canyon, tilefish overlap with the smaller blueline or blackline tilefish *Caulolatilus* sp. (Pearson 1932), with which it may share burrows (Able *et al.* 1987b). Some of the larger fish and lobster that co-exist with tilefish in their burrows compete with tilefish for food; e.g., conger eel (Freeman and Turner 1977; Levy *et al.* 1988).

The relatively flat seafloor among the tilefish burrows and in submarine canyons can be inhabited by species typical of unstructured, open bottom, such as Jonah crab (Cancer borealis), red crabs, skates (Raja spp.), dogfish (Squalus *sp.*), witch flounder (Glyptocephalus cynoglossus), Gulf Stream flounder (Citharichthys arctifrons), goosefish (Lophius americanus), shortnose greeneye (Chlorophthalmus agassizi), armored searobin (Peristedion miniatum), and faun cusk-eel (Lepophidium profundorum). These species are caught on longlines with tilefish or have been trawled, dredged, and observed during surveys (Goode 1881; Collins 1884; Bumpus 1899; Haedrich et al. 1975, 1980; Cooper et al. 1987a). The armored searobin may be confined to the same Middle Atlantic Bight shelf break "warm zone" as tilefish; it was also found dead during the great tilefish mortality event of 1882 (Collins 1884; Bigelow and Schroeder 1953).

Middle Atlantic Bight tilefish of both sexes grow about 10 cm/yr to age 4 after which growth rates slow and males grow faster than females (Turner *et al.* 1983; Turner 1986). Males grow larger than females (Freeman and Turner 1977; Morse 1981; Turner *et al.* 1983); the maximum size of females was 100 cm FL and the maximum size of males was 112 cm FL, but females tended to be older than males (Turner *et al.* 1983).

REPRODUCTION

The length at sexual maturity of tilefish collected off New Jersey in 1971-1973 was 60-65 cm TL in females and 65-70 cm TL in males (Morse 1981). Idelberger (1985) reported that 50% of females were mature at about 50 cm FL. This finding is consistent with studies of the South Atlantic stock, where some males delayed participating in spawning for 2-3 years when they were 10-15 cm longer (Erickson and Grossman 1986). Grimes et al. (1988) reported that in the late 1970s and early 1980s, both sexes were sexually mature at about 48-61 cm FL and 5-7 years of age; the mean size at 50% maturity varied with the method used and between sexes. Grimes et al. (1986) estimated that 50% of the females were mature at about 48 cm FL using a visual method and about 58 cm FL using a histological method. For males, the visual method estimated 50% maturity at 61 cm FL while the histological method estimated 50% maturity at 52 cm FL. The visual method is consistent with NEFSC estimates for other species (O'Brien *et al.* 1993).

Grimes *et al.* (1988) reported that the mean size and age of maturity in males (but not females) was reduced after 4-5 years of heavy fishing effort. This may be evident when comparing their findings (in late 1970s-early 1980s) with those of Morse (1981) for the early 1970s which was near the beginning of the renewed fishing effort for the species and which estimated maturity at a larger size. Although Morse used total length and Grimes used fork length, the shallow caudal indentation (forking) in tilefish probably does not account for all of the ~5-10 cm difference in length for visually estimated maturity.

Tilefish are not thought to be schooling fishes, but they do aggregate in their preferred habitat (Freeman and Turner 1977). Spawning behavior is unknown, but may be pair specific; female and male pairs are often observed sharing a burrow and pair-bonding behavior was reported by Grimes *et al.* (1986). Pair bonding would insure that a male was available to fertilize the eggs that are periodically released by the female. Mating may be socially mediated with dominant males controlling access to several females within a restricted area (Grimes *et al.* 1988) and may explain delayed maturity in some males. Idelberger (1985) suggested that the size and color of the dorsal head flap might play a role in females selecting a mate.

Idelberger (1985), Erickson *et al.* (1985), and Grimes *et al.* (1988) classified tilefish as serial or fractional spawners from March to November with a peak in activity between May and September. This encompasses the July-August spawning period reported by Collins (1884), Bigelow and Schroeder (1953), Freeman and Turner (1977), and Morse (1981). Dooley (1978) observed "ripe" females in February-June (locations not stated, but possibly South Atlantic).

Grimes *et al.* (1988) estimated that females 53-91 cm produce 195 x 10^3 to 10 x 10^6 eggs; the mean fecundity for 49 fish was 2.28 x 10^6 . This fecundity range is consistent with estimates by Morse (1981) and Erickson and Grossman (1986). However, these authors noted that with serial or fractional spawners there is some doubt whether all of the eggs in the ovaries are released during a single seasonal spawning cycle. Residual eggs could be resorbed during the winter.

Dooley (1978) suggested the possibility of a sex change at a small size based on a high ratio of females to males among smaller individuals and the fact that the largest fish are mostly males. Idelberger (1985), Erickson and Grossman (1986), and Grimes *et al.* (1988) found weak histological evidence for such a change. Turner *et al.* (1983) suggested that the ratio is the product of differential growth and mortality rates between the sexes.

FOOD HABITS

Nothing is known about the diets and feeding habits of tilefish larvae, but they probably prey on zooplankton. Dooley (1978) terms the post-larval stage "omnivorous" because Linton (1901), Bigelow and Schroeder (1953), and Freeman and Turner (1977) reported benthic organisms, such as crabs (spider, galatheids, pagurids), dominated their diets; they also ate conger eels, Atlantic hagfish (Myxine glutinosa), other fish, bivalve mollusks (Yoldia spp.), polychaetes, holothurians (Thyone spp.), and sea anemones (Table 1). They also eat near-bottom or pelagic prey such as salps (Salpa zonaria), squid, hyperiid amphipods, small spiny dogfish (Squalus acanthias), Atlantic mackerel (Scomber scombrus), Atlantic herring (Clupea harengus), and silver hake (Merluccius bilinearis). Human trash (potato peels, meat bones, and shiny hardware) were also eaten (Collins 1884; Freeman and Turner 1977). Tilefish stomachs examined off Georgia also contained non-benthic myctophid fish, butterfish (Peprilus triacanthus), deep-sea shrimp, and benthic spotted hake (Urophycis regia) (Dooley 1978). The NEFSC food habits database included data from nine juvenile tilefish, which ate primarily echinoderms (brittlestars) and unidentified crustaceans (Figure 2). Freeman and Turner (1977) reported that juveniles ate more echinoderms and mollusks than larger tilefish. Cooper et al. (1987b) called tilefish the apex predator of the "pueblo village" submarine canyon community.

In terms of availability of potential benthic prey, Wigley and Theroux (1981) and Theroux and Grosslein (1987) found that polychaetes dominated the biomass of the benthic fauna at the shelf break (~200 m) and upper slope from Georges Bank to North Carolina. Brittlestars (Ophiuroidea) were important in slightly shallower depths from western Georges Bank to the Hudson Canyon, and crustaceans were important on Georges Bank. However, the biomass on the upper slope was generally < 25 g/m² and this was usually substantially less than that found on the outer continental shelf.

Freeman and Turner (1977) and Low *et al.* (1983) reported that tilefish are visual daytime feeders, but Grimes *et al.* (1986, 1987) reported that tilefish were most active at night (~2000-0800 hrs). Tilefish appear to be attracted to the bait on longline hooks at some distance from their shelters (Grimes *et al.* 1982) suggesting that food detection is more than visual and tilefish may be effective scavengers on fresh material like many deep-sea megafauna. Freeman and Turner (1977) noted that there was no evidence that feeding is inhibited during spawning, which is consistent with an extended, serial spawning strategy.

In the winter, the shelf edge south of New Jersey supports several populations of wintering fish; e.g., black sea bass (*Centropristis striata*), scup (*Stenotomus chrysops*), butterfish, spotted hake, summer flounder (*Paralichthys dentatus*), small pelagic fishes, and squid (Pearson 1932) that may be a seasonal source of prey for tilefish.

PREDATION

Able et al. (1982) and Grimes et al. (1986) concluded that a primary function of tilefish burrows was predator avoidance. The NEFSC food habits database notes only goosefish as a predator. Grimes et al. (1982, 1987) reported attacks on hooked tilefish that they attribute to dusky sharks (Carcharhinus obscurus), but it is not known if free-swimming tilefish are attacked by this or other sharks, as suggested by Freeman and Turner (1977). Stillwell and Kohler (1992) did not find tilefish in the stomachs of sandbar shark (C. plumbeus) collected offshore in the Middle Atlantic Bight. Freeman and Turner (1977) reported that small juvenile tilefish are sometimes preyed on by spiny dogfish and conger eels, but by far the most important predator of small tilefish was cannibalism by larger tilefish. They also reported that sea lampreys (Petromyzon marinus) parasitize tilefish, especially in the winter and spring.

There are no recent studies of tilefish diseases and parasites, but Linton (1901) found that they were infected with a variety of parasites and Freeman and Turner (1977) reported nematodes in about 75% of the fish they examined, with the frequency of occurrence increasing with fish size. Low levels of toxic metal and organic contaminants have been found in several tissues of individuals from the Middle Atlantic Bight population, although the source of the contaminants is unknown (Steimle *et al.* 1996).

Hoenig (1983) used longevity estimates of 40-50 years for "unexploited" tilefish population in a regression model to predict total annual mortality M = 0.09-0.11. Shepherd (1998) noted that M is now estimated at 0.15.

MIGRATION

Based on a few tagging studies and the decade or so needed to re-colonize the southern New England grounds after the great mortality of 1882, it appears tilefish migrate little or not at all (Freeman and Turner 1977; Grimes *et al.* 1983, 1986). The seasonal variability in the presence of a band of warm water near Nantucket Shoal and southern Georges Bank during the winter/spring suggests that there is some migration along the outer shelf within the preferred habitat or, alternatively, that tilefish may reduce their activity or hibernate in their burrows at low water temperatures.

STOCK STRUCTURE

Two tilefish stocks have been identified in United States waters based on morphometric and electrophoretic similarities: in the Middle Atlantic Bight and south of Cape Hatteras into the Gulf of Mexico (Katz *et al.* 1983). Sulak and Ross (1996) reported that the ichthyofauna on the upper continental slope off Cape Hatteras was less diverse than on the upper slope off Virginia, and that individuals of many species off Cape Hatteras were smaller and less active than their conspecifics off Virginia. This community (which they termed "Lilliputian") was associated with low oxygen at the sediment surface and a high flux of particulate organic carbon from surface waters. This upper slope, hypoxic area may be the cause of tilefish stock separation. Management of the stock south of Cape Hatteras is covered by the South Atlantic Fishery Management Council's Snapper Grouper Fishery Management Plan.

HABITAT CHARACTERISTICS

Tilefish habitat is restricted to the continental shelf break south of the Gulf of Maine. The following description, based largely on Warner (1987), applies to juveniles and adults. The outer continental shelf, shelf break, and upper slope (approximately 100-500 m) that contain suitable habitat for tilefish are the product of several processes. The topography developed during repeated cycles of glacial advance and retreat that caused major changes in sea levels. The outer shelf of the Middle Atlantic Bight slopes gently $(1-2^{\circ})$ and is generally flat except for relict submerged river valleys (e.g., the Hudson Shelf Valley leading to the Hudson Canyon), submerged beach fronts, and submarine canyons. At the edge of the continental shelf, the slope increases to 5-7° and greater in the current-washed canyons, where there are near vertical walls. Sediments on the outer shelf-upper slope in the area used by tilefish are medium to fine sands and silt, with isolated areas of exposed clays and other consolidated sediment near the heads or along the sides of submarine canyons. Off southern New England, glacial erratic boulders randomly occur and coarser sediments are found in the current-washed channels of many canyons. The topography on either side of Hudson Canyon is irregular and hummocky (Twichell et al. 1995).

Current patterns and water mass dynamics at the shelf break are partially affected by wind, Rossby waves moving upslope, and lateral variation in the location of the Gulf Stream and its loops and gyres. Residual water mass movement on the shelf and upper slope is to the southwest. A "warm belt" (9-14°C) occurs at the shelf break where shelf and slope water meet. The width and linear extent of this band varies seasonally; it extends beyond Nantucket Shoal and along southern Georges Bank in the summer and fall, but retreats to off Long Island in the winter and spring (Colton and Stoddard 1973).

Flagg (1987) summarized the hydrography of the shelf for southern Georges Bank and his description

applies south to Virginia (Schmitz et al. 1987). Seasonal fluctuations in bottom temperatures affect the water column down to about 200 m on the continental shelf (including shallow parts of Georges Bank) and shelf break. There is a persistent cold pool or band of residual winter bottom water (usually $< 10^{\circ}$ C) along the mid-outer shelf that parallels the shelf break. Beyond the warm band at the shelf break (> 500 m), the bottom temperature on the slope declines gradually to about 4°C. There is a seasonally variable pycnocline on the outer shelf at about 50 m that deepens to 70-100 m at the shelf break; salinities above the pycnocline tend to be < 35 ppt and below the pycnocline, in the tilefish warm band, they are approximately 35-36 ppt. Dissolved oxygen (DO) at the shelf break varies seasonally between 3-7 ml/L in the winter and 3-5 ml/L in the summer; the lowest values occur in the oxygen minimum zone around 200-400 m. Movement of Gulf Stream gyres and meandering loops over the slope temporarily affect hydrographic conditions and biological communities at the shelf break.

The oceanographical, geological, and biological changes that occur at the shelf break, and the specialized community that exists in this zone, has been described as a unique ecotone with the characteristics of an edge effect (enhanced productivity and diversity), although the boundaries and environmental sensitivity of this zone/community are still in question (Church *et al.* 1984; Warner 1987). Warner *et al.* (1983) considered tilefish a good indicator species for delineating the shelf break "warm belt" community and for monitoring the sensitivity of this ecosystem to disturbance (e.g., oil and gas development).

EGGS

Tilefish eggs collected during the NEFSC Marine Resources Monitoring, Assessment and Prediction (MARMAP) program surveys [see Reid *et al.* (1999) for methods] were associated with mean water column (to 200 m) temperatures of 8-19°C with a trend following the seasonal rise in temperatures (Figure 3). This eggtemperature distribution suggests that Fahay and Berrien (1981) hatched eggs at a slightly higher than normal temperature (22.0-24.6°C vs. < 19.0°C). The hatching time they measured (40 hrs) may be longer under cooler conditions where eggs were collected.

The depths over which the eggs were collected during the NEFSC MARMAP surveys ranged from approximately 80-1250 m; most eggs were collected between 80-800 m (Figure 3). The November data was for one tow in deep water off Chesapeake Bay and suggests an unusual situation.

LARVAE

Tilefish larvae were rarely collected during the NEFSC MARMAP surveys. The survey data suggest that larvae prefer a narrow range of fairly warm temperatures (approximately 13-18°C) and relatively shallow depths (approximately 50-150 m) (Figure 4).

JUVENILES

The NEFSC groundfish surveys collected few juvenile tilefish in more than 30 years of operation. Spring trawl collections contained the highest number of samples (91). Approximately 24% of the collections occurred at bottom temperatures below the limit $(> 8^{\circ}C)$ reported in previous studies; most of these low temperature data came from surveys in the 1970s. The maximum temperature of juvenile occurrence in the NEFSC trawl surveys (approximately 15°C) was also lower than the preferred maximum (approximately 18°C) reported in previous studies (Figure 5; Table 2). Temperature data from other seasons were within the range of the spring collections, with a weak mode at 9-11°C (Figure 5). This suggests that juveniles are more tolerant of low temperatures than adults, which could help recruits survive in marginal habitat conditions.

The depth range of juveniles collected in the spring during NEFSC bottom trawl surveys was 90-264 m; most were collected at < 170 m (Figure 5); however, the maximum depth of the NEFSC trawl surveys was 366 m (see Reid *et al.* 1999). The juvenile tilefish depth of capture in other seasons was similar to that for spring.

ADULTS

Except for the spring, there are insufficient data on adult tilefish in the NEFSC bottom trawl surveys to estimate their bottom temperature and depth preferences. One adult (2% of total) was collected at 6.5° C (Figure 5) which is below the published temperature preference range (approximately 8-18°C). The maximum temperature at which adult tilefish were collected during the NEFSC bottom trawl surveys was lower (approximately 14°C) than the maximum reported in previous studies (Table 2). The association of adult tilefish with temperature was similar to juveniles with a weak mode at 10-11°C (Figure 5).

In the spring of 1882, an estimated 1.5 billion tilefish weighing over 7 million tons were found dead and dying in surface waters offshore between Nantucket Shoal and Maryland. This was followed by a collapse of the fishery and the population (Collins 1884; Bumpus 1899; Bigelow and Schroeder 1953; Dooley 1978). Many other organisms associated with the tilefish habitat also died (Bigelow and Schroeder 1953), including armored

searobin, "red snappers," galatheid crabs, and deep-water spider and hermit crabs (Collins 1884). The mortality is presumed due to thermal shock from a rapid drop in temperature, which may have been caused by meanders of the Gulf Stream or unusually heavy sea ice off Nova Scotia associated with upwelling of the deep, cold Labrador Current; undersea volcanism was also suggested (Collins 1884; Bumpus 1899; Bigelow and Schroeder 1953; Dooley 1978). Collins (1884) reported no evidence of disease or excessive parasite infestations; most freshly dead or dying fish had empty stomachs and their air bladders extruding from their mouths. Some fish found at the surface off southern New England during the event were identified by seamen as cod and hake (Collins 1884), which are moderately cold tolerant. This observation suggests that if temperature change was the cause, it was probably rapid.

The depth range of adults collected in the spring was 105-274 m with a weak mode at about 140 m; most fish were collected shallower than 210 m (Figure 5). Data for adult tilefish from other seasons were consistent with the spring with a mode at 160-170 m (all from winter collections), which is consistent with previous studies, although tilefish have been collected to 540 m (Table 2).

GEOGRAPHICAL DISTRIBUTION

EGGS

Based on the NEFSC MARMAP surveys (1978-1987), tilefish eggs were collected from March to November on the outer continental shelf from North Carolina to southern Georges Bank; the highest densities were found from Hudson Canyon to Block Canyon (south of Rhode Island) (Figure 6). In March, a few eggs were collected between these canyons. From April to October, eggs were collected broadly on the outer shelf. In November, eggs were only collected off Chesapeake Bay (Berrien and Sibunka 1999).

LARVAE

From the NEFSC MARMAP surveys, the center of larval abundance lies between Toms Canyon (just south of Hudson Canyon) and the "Mud Patch" (south of Nantucket Island) (Figure 7). Larvae were also collected off North Carolina and on eastern Georges Bank. However, this distribution is based on only those 12 tows that contained larvae over the entire survey period [see Reid *et al.* (1999) for methods].

JUVENILES

The NEFSC bottom trawl surveys collected few

juvenile tilefish. Those that were caught occurred mostly off southern New England in all seasons except summer (Figure 8).

ADULTS

The NEFSC bottom trawl surveys also collected few adult tilefish. Those that were caught occurred along the continental shelf break between Nantucket Shoals and Hudson Canyon primarily in spring (Figure 8).

Warner (1987) generated a series of relative CPUE maps for the fishery from Toms Canyon (south of Hudson Canyon) to Hydrographer Canyon (on western Georges Bank) for 1973-1982 (Figure 9). Because the fishery concentrated on areas with the highest catches (apparent abundance), the resulting data are biased and probably underestimate the distribution of the stock. At the time of this analysis, the fishery was still expanding and all areas of tilefish abundance may have not been located or reported. The eastern expansion noted in this time series was due mostly to the expansion of the fishery and not the tilefish stock. Effort in the tilefish fishery (used here as a surrogate for tilefish relative abundance) is associated with topographically rough bottom (Figure 10).

Chang (1990) examined commercial landings data for 1977-1988 when the tilefish fishery was mature and found that tilefish were more widely distributed (Figure 11) than during the early period of the fishery analyzed by Warner (1987). The highest landings in the mature fish were concentrated south of Martha's Vineyard and near Hudson Canyon, especially in the winter and spring (Figure 11).

STATUS OF THE STOCKS

The fishery for tilefish began in 1879, but collapsed shortly thereafter with the mass mortalities of 1882. It began to recover in the late 1890s with an abundance of young fish (Bumpus 1899) and by 1915 the species was again being fished and promoted by United States Bureau of Commercial Fisheries (Bigelow and Schroeder 1953; Dooley 1978). The reported fishery landings have been highly variable with peaks in 1914-1915, the late 1920s, mid-1950s, and mid-1970s. Catches were reduced or minimal in the early 1930s, during World War II, during 1961-1972 (Freeman and Turner 1977), and low but relatively stable since 1984 (Shepherd 1998). Most of the tilefish harvest until recently came from the Middle Atlantic Bight stock. In the early 1980s, recreational and commercial fisheries also developed for the stock south of Cape Hatteras (Low et al. 1983; Hightower and Grossman 1988; Parker and Mays 1998).

Shepherd (1998) notes low landings and a significant decline in CPUE of the northern stock since about 1981 as evidence of over-exploitation (Figure 12). Some of the variability in early landings was probably due to a decline

in consumer demand and a corresponding reduction in fishing effort (Bigelow and Schroeder 1953). Turner *et al.* (1983) also noted variability in stock recruitment during the 1970s. The resurgence of this offshore fishery in the early 1970s, partly as a recreational fishery (Morse 1981; Grimes *et al.* 1980, 1986), may be a response to the decline of inshore fisheries because of habitat degradation and overfishing (McHugh 1977). Barans and Stender (1993) reported similar declines in stock size and mean individual size as the South Atlantic Bight fishery developed, and harvests have also declined since the late 1980s (Parker and Mays 1998).

According to Turner (1986), the effects of fishing have been "drastic" and that stock size has been reduced by half to two-thirds, a level that continued into the mid-1990s (Shepherd 1998). High fishing mortality has truncated the size structure of the population; fewer large fish (> 70 cm) have been landed (Grimes *et al.* 1980; Turner *et al.* 1983).

RESEARCH NEEDS

- Are tilefish protogynous (a size-related sex change from female to male) at pre-maturation (Dooley 1978; Idelberger 1985; Grimes *et al.* 1988)? If so, how is it affected by the social structure of a local population (sex ratio of mature fish) and how is that affected by fishing?
- Do tilefish off southern New England and Georges Bank leave suitable habitats during the winter and where do they go (Grimes *et al.* 1986)?
- Assume that the boundaries of tilefish habitat are flexible and dictated by physical (sediments, shelter, temperature), biological (burrow builders, prey, competition, recruitment), and fishery (stock size, harvest intensity, and population size structure) processes. Can a probabilistic model be developed that identifies the size and shape of suitable habitat (after Warner 1987)?
- Are adult male tilefish territorial? If so, how does the removal by the fishery of large, dominant males effect the social structure of a local population (Grimes *et al.* 1988)?
- If vertical burrows, the primary habitat of tilefish according to Able *et al.* (1982) and Grimes *et al.* (1986), are filled with loose sediments because of intensive trawling (Churchill 1989), offshore sediment disposal, or a major storm, can the burrows be cleared and reused by the tilefish? By other organisms?
- What degree of symbiosis or mutualism exists between tilefish and other developers/users of burrow habitats; e.g., galatheid crabs (Grimes *et al.* 1987)?
- Do tilefish form long-term associations with individuals of the opposite sex (pair bonds) (Grimes *et al.* 1986)? How does harvesting affect the social

structure and breeding potential of the population?

- Peak activity and feeding in tilefish has been reported to be daytime (Freeman and Turner 1977) or nighttime (Grimes *et al.* 1987). Peak activity and feeding are usually coincident (for energetic reasons) unless feeding grounds are well away from resting grounds; why the difference in conclusions?
- The Katz *et al.* (1983) study of stock identification between the Middle and South Atlantic Bights did not examine tilefish between Toms Canyon (south of Hudson Canyon) and the border between North Carolina and South Carolina. Do tilefish from near Cape Hatteras (e.g., Norfolk Canyon) support separating the population into two biologically distinct stocks?
- More information on the age structure of the population in different years is needed to improve estimates of mortality rate and to determine sexual differences in mortality rate (Turner *et al.* 1983).
- The attributes of habitat that trigger larval tilefish settlement and juvenile transition are unknown. These are especially important for recruitment and maintenance of local, non-migratory populations.
- The range of environmental parameters for tilefish egg survival and development are unknown.
- Are tilefish affected by the relatively low levels of anthropogenic contaminants that are in their tissues (Steimle *et al.* 1996)?
- Do juvenile tilefish aggregate in certain areas? If so, where and what are the habitat characteristics (Freeman and Turner 1977)?
- Does the oxygen minimum band on the upper slope affect tilefish distribution?
- Is tilefish cannibalism caused by inadequate shelter habitat for small juveniles or the territoriality of adults? If so, can juvenile shelter and survival be increased artificially?
- Do juveniles tolerate lower temperatures than adults?

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Table 1. Food items of tilefish, *Lopholatilus chamaeleonticeps*, in the Middle Atlantic Bight [from Freeman and Turner (1977)].

MOLLUSCA (mollusks)

Gastropoda (univalve mollusks) Unidentified Pelecypoda = Bivalvia (bivalve mollusks) Protobranchia Nuculanidae Naculana acuta Pteroconchidae Mytilidae Musculus discors Pectinidae Cyclopecten nanus Eudesmodontida Pandoridae Pandora inflata Cephalopoda (squids, octopuses) Unidentified

ANNELIDA (segmented worms)

Polychaeta (sandworms, tube worms) Eunicida Lumbrinereidae Unidentified

ARTHROPODA (joint-footed animals)

Crustacea (crabs, barnacles, lobsters) Stomatopoda Lysiosquillidae Heterosquilla armata Isopoda Cirolanidae Cirolana polita Unidentified isopoda Decapoda Crangonidae Crangon septemspinosa Nephropsidae Homarus americanus Galatheidae Munida iris Paguridae Catapagurus sherreri Calappidae Acanthocarpus alexandri Majidae Euprognatha rastellifera Callodes robustus Cancridae Cancer borealis Cancer irroratus Cancer sp. Unidentified decapods Unidentified crustaceans

ECHINODERMATA (echinoderms) Stelleroides = Asteroidea (starfishes) Unidentified Ophiuroida (brittle stars) Ophiurida Amphiuridae Axiognathus squamata Amphiura centiculata **CHORDATA** (chordates) Tunicata = Urochordata (tunicates) Ascidiacea (ascidians) Unidentified ascidian Agnathostomata Agnatha (jawless fishes) Myxinidae Myxine glutinosa (Atlantic hagfish) Gnathostomata (jawed vertebrates) Chondrichthyes (cartilaginous fishes) Squalidae Squalus acanthias - spiny dogfish Osteichthyes (bony fishes) Clupeidae Brevoortia tyrannus - Atlantic menhaden Clupea harengus – Atlantic herring Myctophidae Ceratoscopelus maderensis - "lantern fish" Congridae Conger oceanicus – conger eel Ophichtidae Ophichthus cruentifer - margined snake eel Gadidae Merluccius albidus - offshore hake Serranidae Hemanthias aureorubens - streamer bass Branchiostegidae Lopholatilus chamaeleonticeps - tilefish Scombridae Scomber scombrus – Atlantic mackerel Scorpaenidae Helicolenus dactylopterus - blackbelly rosefish Ammodytidae Ammodytes americanus - American sand lance Stromateidae Peprilus triacanthus - butterfish Peuronectidae Paralichthys oblongus - fourspot flounder *Limanda ferruginea* – yellowtail flounder Lophiidae Lophius americanus - goosefish

SIPUNCULOIDEA (peanut worms) Unidentified

Page 12

Table 2. Summary of life history and habitat characteristics for tilefish, Lopholatilus chamaeleonticeps.

Life Stage	e Time of Year Size and Geogram Growth Locati		Geographic Location	Habitat	Substrate	Temperature
Eggs	Serial spawning March-Nov; peaks April- Oct	1.16-1.25 mm	Shelf break; Georges Bank to Cape Hatteras	Water column, 80- 800 m	Water column	8-19°C
Larvae	Feb-Oct; peaks July– Oct	2.6 to ~9.0 mm	Outer continental shelf; Georges Bank to Cape Hatteras	Water column, 50- 150 m	Water column	13-18°C
Juveniles (≤ 50 cm)	All year; may leave Georges Bank in winter	~15-500 mm	Shelf break, submarine canyon walls and flanks; Georges Bank to Cape Hatteras	Rough bottom, shelter, small burrows, 80-540 m	Rocky, stiff clay, human debris	~8-18°C
Adults (> 50 cm)	All year; but may leave Georges Bank in winter	Females: 50- ~100 cm; Males: 50- ~120 cm	Shelf break, submarine canyon walls and flanks; Georges Bank to Cape Hatteras	Rough bottom, shelter, larger burrows, 80-540 m	Rocky, exposed ledges, stiff clay	~8-18°C

Life Stage	Salinity	Dissolved Oxygen	Prey	Predators	Notes
<i>Eggs</i> ~34-36 ppt ~4-8 ml/L					
Larvae	~33-35 ppt	~4-8 ml/L			
<i>Juveniles</i> ≤ 50 cm	~33-36 ppt	~3-6 mg/L	Decapod crustaceans, small fish, benthic epifauna, human trash.	Tilefish, goosefish, sharks, dogfish, and conger eel.	
Adults > 50 cm	~33-36 ppt	~3-6 mg/L	Juvenile tilefish, other fish, decapods, benthic epifauna	Sharks, lampreys	Pair-bonding possible.



Figure 1. The tilefish, Lopholatilus chamaeleonticeps (from Goode 1884).



Figure 2. Abundance (percent volume) of the major prey taxa in the diet of juvenile tilefish collected during NEFSC bottom trawl surveys [see Reid *et al.* (1999) for details]. Echinodermata are mostly brittlestars (*Amphiura* sp.) and Arthropoda are crustaceans. The category "animal remains" refers to unidentifiable animal matter.



Figure 3. Abundance of tilefish eggs relative to water column temperature (to a maximum of 200 m) and bottom depth from NEFSC MARMAP ichthyoplankton surveys (1978-1987, all years combined). Open bars represent the proportion of all stations surveyed, while solid bars represent the proportion of the sum of all standardized catches (number/10 m^2).



Figure 4. Abundance of tilefish larvae relative to water column temperature (to a maximum of 200 m) and bottom depth from NEFSC MARMAP ichthyoplankton surveys (1977-1987, all years combined. Open bars represent the proportion of all stations surveyed, while solid bars represent the proportion of the sum of all standardized catches (number/10 m^2).







Figure 5. Abundance of juvenile and adult tilefish relative to bottom water temperature and depth based on NEFSC spring bottom trawl surveys. Open bars represent the proportion of all stations surveyed, while solid bars represent the proportion of the sum of all standardized catches (number/10 m^2).



Figure 6. Distribution and abundance of tilefish eggs collected during NEFSC MARMAP ichthyoplankton surveys, March to November, 1978-1987 [see Reid *et al.* (1999) for details].



Figure 6. cont'd.



Figure 6. cont'd.



Figure 7. Distribution and abundance of tilefish larvae collected during NEFSC MARMAP ichthyoplankton surveys from 1977-1987 [see Reid *et al.* (1999) for details].



Figure 8. Seasonal distribution and abundance of juvenile and adult tilefish collected during NEFSC bottom trawl surveys [1963-1997, all years combined; see Reid *et al.* (1999) for details].



Figure 8. cont'd.

Page 24



Figure 9. Tilefish distribution and relative abundance, 1973-1982, based on the long-line fishery effort; i.e. tubs of gear deployed within areas as surrogates for total catch; 1-43 tubs deployed = low-medium effort, 44-387 tubs deployed = medium-high effort (from Warner 1987).



Figure 9. cont'd.

Page 26



Figure 9. cont'd.



Figure 10. Comparison of "rough bottom" topography on either side of Hudson Canyon with 1973-1981 tilefish fishing effort (from Warner 1987).



Figure 11. Commercial weighout distributions of tilefish by seasonal quarters in the Middle Atlantic Bight and Georges Bank for 1977-1988 (from Chang 1990). 1^{st} = January-March, 2^{nd} = April-June, 3^{rd} = July-September, 4^{th} = October-December. Symbols indicate a range and GE = Greater/Equal, LT = Less Than.



Figure 11. cont'd.



Georges Bank - Middle Atlantic

Figure 12. Commercial landings and catch-per-unit-effort data (from the NEFSC bottom trawl surveys) for tilefish from Georges Bank and the Middle Atlantic Bight.

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