STUDIES ON TILEFISH FISHERY BIOLOGY, ECOLOGY AND BIOEROSION ON THE MIDDLE ATLANTIC AND SOUTHERN NEW ENGLAND CONTINENTAL SHELF

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ABSTRACT

Manned submersibles were used in the vicinity of submarine canyons of southern New England and the mid-Atlantic Bight during the summers of 1979 through 1984 to evaluate the performance of commercial bottom longline gear, document the abundance and distribution of tilefish shelters and define the ocean floor fauna associated with the tilefish shelters. Time-lapse photography documented tilefish behavior relative to the shelters. Coordinated submersible, sidescan sonar and seismic profiling operations were conducted to define the role of bioerosion by tilefish in shaping seafloor topography. Sidescan sonographs showed individual tilefish burrows whose distribution were highly contagious. At Hudson Canyon, tilefish had created an 800 km^2 area of rough topography through bioerosion which has probably been occurring over the past 12-13,000 years.

INTRODUCTION

Because of the major ecological and economic significance of tilefish, we have studied them since 1979 using manned submersibles. Our studies have provided information relevant to the rational exploitation of their valuable fisheries, and discovered their important role in sea floor processes. In this paper we summarize the results of these *in situ* studies; for further details refer to the original papers on commercial fishing gear performance (Grimes et al. 1982); behavior, community structure and habitat (Able et al. 1983; Grimes et al. 1986); the role of tilefish bioerosion in shaping bottom topography (Twichell et al. 1985); and use of sidescan sonar as a fishery tool (Able et al. in prep.).

Tilefish, *Lopholatilus chamaeleonticeps*, are large (to 120 cm and 27 kg) demersal branchiostegid fishes found along the edge of the continental shelf in 80-540 m depths from Nova Scotia to Surinam (Dooley 1978; Markle et al. 1980). In the Middle Atlantic Bight and Southern New England waters they have usually been found from 80-240 m. This species is long lived and slow growing, reaching at

least 112 cm FL and 35 years (Turner et al. 1983). Batch spawning occurs during summer, with females producing pelagic eggs; reproduction is socially mediated (Grimes et al. in prep.). Tilefish are benthic carnivores, the diet consisting mostly of crustaceans and fishes and secondarily of polychaetes and echinoderms (Turner and Freeman in prep.). In addition, the investigations we summarize here suggest that tilefish are "keystone" species, critical to the organization and maintenance of their community.

Commercial exploitation of the Middle Atlantic-Southern New England tilefish stock (Katz et al. 1983) began in 1915, and landings have been reported nearly every year since. Annual landings have fluctuated between a peak of 4,500 metric tons (t) in 1916 to 1 t for several years since. Landings have increased dramatically since the 1970's, due to the development of an important longline fishery centered in New York and New Jersey. Landings from 1977-1982 (2,000, 3,400, 3,800, 3,600, 3,200 and 1,900 t, respectively) exceeded all previous years for which information is available except 1916 (Freeman and Turner 1977; U.S. Dept. Comm. 1980 a-c; Christensen pers. comm.). Tilefish have been the most valuable finfish fishery in New Jersey and New York in most years since 1978.

METHODS AND PROCEDURES

Study sites and submersibles used

We conducted a series of submersible cruises along the east coast of the U.S. (Fig. 1) during the summers of 1979-1984 (Table 1). In 1979 we used the two man submersible Nekton Gamma, a 4.9 m long vessel that could operate to a depth of 300 m. Support for Nekton Gamma was provided by the R/V Atlantic Twin. All other dives reported here were conducted with the Harbor Branch Oceanographic Institution's four-man submersible Johnson-Sea-Link, operated from the support ship R/V Johnson.

Habitat, behavior and community structure

Dives were made along straight line transects (across or along depth contours), or in accordion shaped tracks for more detailed mapping (see Grimes et al. 1986). On other dives, when specific tasks (behavior observations, burrow measurement and dissection, etc.) were planned, the submersible moved very little. During a typical dive, physical (bottom temperature, depth, topography, visibility, current speed and direction and substrate type) and biological (tilefish abundance, size, sex, behavior, burrow number and dimensions, and associated fish and macroinvertebrates) parameters were recorded on audio tapes. Photographs were taken with one or two externally mounted 35 mm cameras and a bow-mounted video camera with the recorder located in the submersible.

Estimates of tilefish length, habitat dimensions and densities of associated fish and macroinvertebrates were made from 35 mm photographs projected onto grids of known dimensions. The grids were

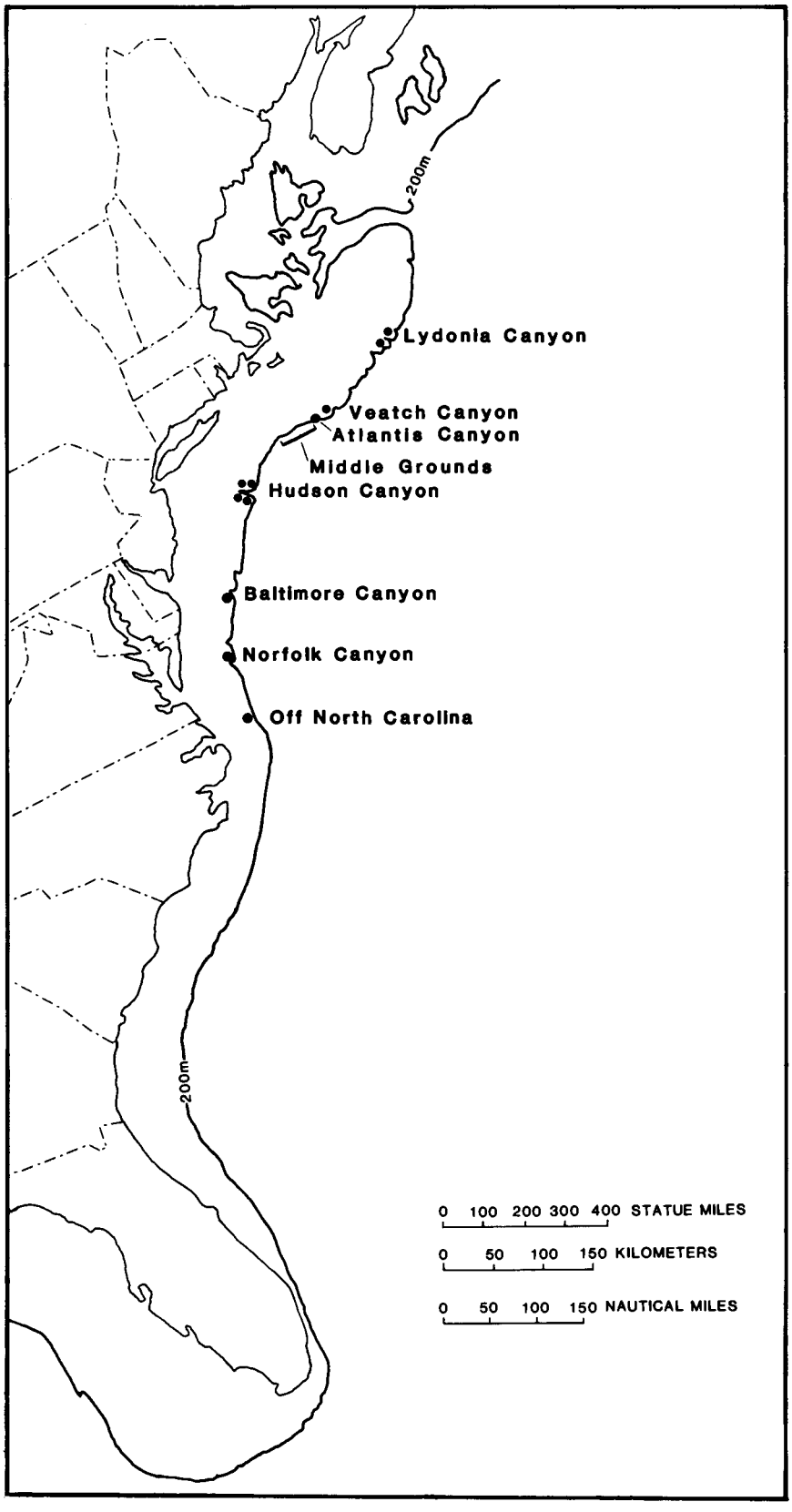

Figure 1. Map of U.S. east coast showing study sites.

Table 1. Summary of submersible operations for tilefish studies along the east coast of the U.S. during 1979-84. See Figure 1 for locations. Major locations include Lydonia (LC), Veatch (VC) and Hudson (HC) Canyons. Habitat types indicated as vertical burrow (VB), Pueblo habitat (PH), boulder field (BF) or other (OH).

	1979	1980	1981	1982
Locations	Hudson Canyon	Lydonia, Veatch Hudson Canyons	Lydonia, Veatch Hudson Canyons	Hudson Canyon
Cruise dates	23-27 August	6-18 August	23-28 July	22-30 July
Number of dives	12	12	12	9
Depth range of observations	85-299 m	LC = 139-192 m VC = 117-229 m HC = 146-156 m	LC = 134-268 m VC = 122-213 m HC = 144-241	129-227 m
Types of habitats observed	VB	LC = VB, PH, BF VC = VB, PV, BF HC = VB	same as 1980	VB

	1983			1984		
Locations	Hudson Canyon	Baltimore Canyon	Norfolk Canyon	Middle Grounds	Atlantis Canyon	Veatch Canyon
Cruise dates	15-16 August	17 August	18 August	29 July-	3 August	4 August
Number of dives	4	2	2	10	2	1
Depth range of observations	119-175 m	204-253 m	175-247 m	102-243 m	183-337 m	130-132 m
Types of habitats observed	VB	OH	OH	VB	OH	VB

originally photographed with the submersible ashore. Estimates for the above measurements were then corrected to reflect the differences in light transmission from air to water. These estimates were validated with in situ measurements of objects from Johnson-Sea-Link using rods and weighted lines marked in known increments and checked against photographic estimates of the same objects. Density estimates for tilefish and burrow abundance were determined using the numbers of fish and habitats seen, the length

of the submersible transects and the width observed along the tracks (based on visibility estimates by the submersible pilot and the observer). Interpretation and description of habitat types, tilefish behavior, etc., were aided by reviewing video tapes made during the dives.

We collected small organisms and made additional observations using equipment unique to Johnson-Sea-Link. Fishes and macroinvertebrates associated with tilefish habitat were collected by injecting rotenone directly into burrows. Fishes and macroinvertebrates were sucked into a collecting box through a nozzle attached to the end of the manipulator arm. Tilefish burrows were dissected with the jaws of the manipulator arm or by blowing sediments away with the submersible bow thruster.

A 35 mm camera and strobe, controlled by an intervalometer, was mounted on a tripod and used to take time-lapse photographs of tilefish and their burrows near Hudson Canyon. Photographs were taken every 2.0 minutes over a 24 hour period.

Fishing Gear Performance

This study was conducted near Hudson Submarine Canyon (Fig. 1) in cooperation with the commercial longline vessel Lori-L from Barnegat Light, N.J. While longlines were being set, hooks were marked with a series of colored ribbons and numbered plastic tags. This made it possible to coordinate our in situ observations with those made by colleagues and the Lori-L crew as the gear was retrieved. The longline was observed using Nekton Gamma. To determine the importance of bait predation we calculated the percentage of hooks observed with predators and without baits at successive time intervals (High 1980). See Grimes et al. (1982) for additional details of this procedure.

Sea Floor Processes

In 1982, 1983 and 1984 we investigated the role of sea floor bioerosion by tilefish in the formation of an area of rough topography around Hudson Canyon. We employed coordinated submersible, sidescan sonar and subbottom profiling operations. Sidescan sonar images (sonographs), 3.5 kHz subbottom profiles and echo sounding profiles were collected from R/V Johnson between dives. The Johnson-Sea-Link was used to "ground truth" features observed on sonographs and to collect sediment samples for grain size analysis. In selected areas we constructed detailed maps of the bathymetry and burrow distribution using closely spaced echo sounding profiles, sidescan sonographs, and many submersible dives.

The extent of rough sea floor topography mapped with seismic profiles was compared to the spatial distribution of commercial fishing for tilefish. Data on the commercial fishery for tilefish was obtained through cooperation with commercial longline fisherman from Barnegat Light, N.J. and Montauk, N.Y. during a study of the biological basis of management of the fishery (Grimes et al. 1980; Turner et al. 1983). Cooperating fishermen maintained logs providing necessary catch information (e.g., catch location and date, and amount of gear fished). We used these data to produce a point distribution map of fishing locations (Robertson 1967; Cesney 1972) for comparison to the geological data.

RESULTS AND DISCUSSION

Performance of Commercial Fishing Gear

We made two daytime dives in August 1979 to observe baited longlines (Grimes et al. 1982) and saw 42 hooked fish; most were alive and in good condition. Only four tilefish were dead; two had swallowed the bait and were hooked internally and two fish were bitten off just behind the operculum, presumably by sharks (probably the dusky shark, *Carcharhinus obscurus*).

The burrowing behavior of tilefish may have caused loss of catch. Seven (17%) of the 42 tilefish observed on marked longlines on the bottom were not accounted for on the *Lori-L*. It is likely that hooks were pulled free from fish partially in their burrows, because we observed several attempts by hooked fish to enter burrows.

Apparently baited longlines attracted tilefish from a wider area than just the immediate vicinity of the longline. During five dives made on tilefish grounds (but not along baited longlines) to investigate behavior and ecology there was a strong positive correlation ($r = 0.91$) between the number of tilefish seen and the number of burrows encountered; few tilefish were away from burrows (see Fig. 1 in Grimes et al. 1982). Along a baited longline we observed many more hooked tilefish (42) than would have been predicted from the number of burrows sighted (3), which suggested that tilefish foraged some distance away from their burrows to take a baited hook.

Benthic invertebrate predators on bait were an important factor affecting catch and optimum soak time. Starfish (*Astropecten* sp.) accounted for 70% of bait predators observed; the crabs *Cancer* sp. and *Acanthocarpus alexandri* accounted for 26% and 6%, respectively. Predation began soon after the longline was set and increased linearly with soak time until all hooks observed were preyed upon after 190 minutes (Fig. 2). Complete removal of bait took longer; all hooks had bait at 78 minutes, but the percent of hooks with bait began to decrease, falling to 70% (excluding hooks with tilefish) after 190 minutes. After 8 hours all hooks were bare (Fig. 2).

We could not determine optimum soak time very precisely. No fish were caught during the first 60 minutes of the longline set, so the minimum soak time may be around 2 hours. When 42 tilefish were caught, all baits were gone after 8 hours (and 90% gone after 7 hours), which gives the maximum useful time.

Most of this assessment would not have been possible without the submersible. Information on burrowing behavior and the resulting catch loss, foraging behavior and its relevance to the area fished by longlines, and the identification of bait predators and the predation rate could only have been acquired by traversing a baited longline with a submersible. The presumed rate of bait loss from predation (because bait predators could not be directly observed) and the rate of catch loss from predation could have been determined from a commercial fishing vessel, the former only with repeated longline settings and retrievals at time intervals. Repeated longline settings would have required chartering the vessel because normal fishing operations would have been precluded. We

believe these factors made the submersible a particularly effective and efficient sampling platform.

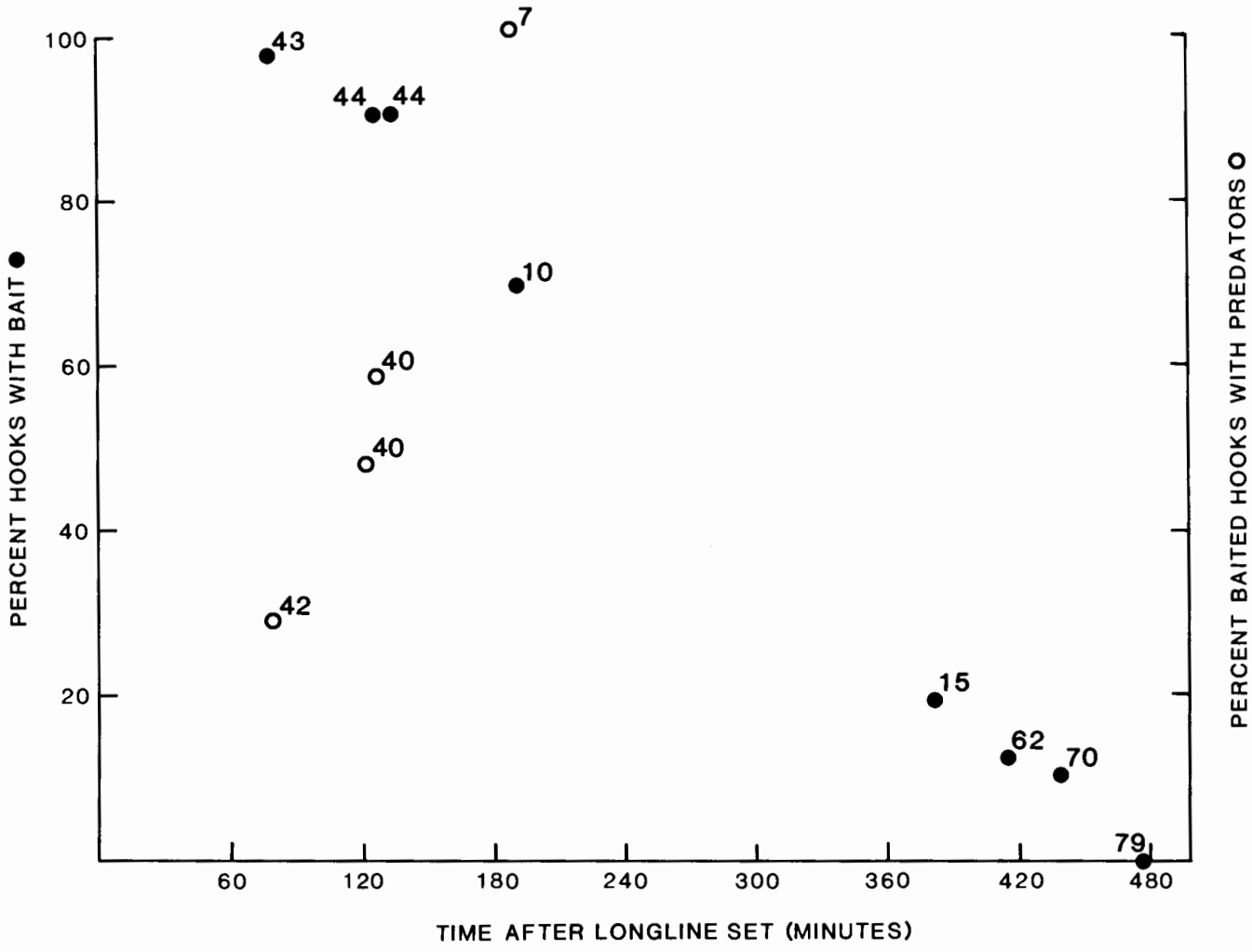

Figure 2. Predation on baited longline hooks by benthic invertebrates and rate of bait loss. Numbers of hooks observed between successive time intervals are shown above data points (from Grimes et al. 1982).

Sidescan Sonar As a Fishery Tool

Using sidescan sonar in conjunction with submersible operations we determined that it was possible to identify individual tilefish burrows on sidescan sonographs (see subsequent Sea Floor Processes section). This finding suggested to us that high resolution sidescan sonar (100 kHz) might have more general utility as a fishery tool. Because individual burrows were identified it could be used to find new tilefish grounds, and determine abundance in unfished areas. It may also be possible to identify critical habitats of other fishery resources as well, for example boulder and Pueblo habitats and rock outcroppings, etc. We conducted further

studies in 1984 to establish if some of these other habitats were identifiable with sidescan sonar, and also determined that the lower size limit of burrows that could be resolved on relatively flat bottom was about 0.5 m diameter (Able et al. in prep.).

Habitat, Behavior and Community Structure

Observations from submersibles have shown that tilefish are shelter seeking fishes that occupy a variety of habitats (Warme et al. 1977; Uzmann et al. 1978; Valentine et al. 1980; Cooper and Uzmann 1980; Able et al. 1982; Cooper et al. in press). We currently recognize three more or less distinct types along the northeast coast of the U.S.: rocks and boulders, Pueblo habitats and vertical burrows (Grimes et al. 1986). These habitats have certain characteristics in common. They were all found within the "warm belt" (Verrill 1882), a narrow zone of relatively warm 9-14° C water which represents the interface between distinct continental slope and continental shelf water masses (Christ and Chamberlain 1976). Temperature and salinity data obtained during our dives were in agreement (Grimes et al. 1986). In addition, the presence of exposed clay that provided a malleable substrate for burrowing was critical to burrow construction and distribution (Able et al. 1983; Twichell et al. 1985). However, the occurrence and utilization of the different habitats varied with geological setting, latitude and season. Fish behavior, residency, and community interactions and structure differed both between and among habitat types.

Boulders and Rocks

The association of tilefish with large boulders was the simplest type of tilefish habitat observed. The boulders, either singly or in clumps, were observed on the rims and along the walls of submarine canyons. The boulders were variable in size and shape and ranged from 0.3 - 5 m in diameter. As described by Valentine et al. (1980) boulders were often in shallow scour basins, probably of combined physical and biological origin.

Tilefish have been observed utilizing this habitat in depths from 149-242 m in Veatch, Lydonia, Hudson and Baltimore Canyons (Able et al. 1982; Grimes et al. 1986) and in Oceanographer Canyon (Valentine et al. 1980). This habitat for tilefish appears to be more common in the northern canyons which were closer to the late Pleistocene glaciers, the source of these boulders (Valentine et al. 1980; Cooper et al. In press).

Tilefish evidently use boulders for shelter. Typically, tilefish rested motionless against or, if possible, under a portion of a boulder. In most instances a single adult tilefish was observed at a boulder, but on occasion as many as three could be seen simultaneously. Utilization of boulder habitats appears to be random and temporary. On several occasions we chased tilefish away from boulders with the submersible and followed them to note their subsequent choice of habitats. Fish stopped at various other boulders and showed no inclination to return to to the original boulder. Furthermore, on later dives to the same boulder we could not establish that the same fish was present.

We observed four tilefish occupying excavations under rock slabs among anemone fields at a dive site along the southwest wall of Baltimore Canyon. Numerous rock slabs about 1 x 2 m, with their

axes at varying angles to the slope, covered the bottom for a distance of over 150 m on a steeply sloping (30°) canyon wall from 204 to 253 m depth. Excavations in the grey sediment under and adjacent to rock slabs were common and appeared to be of biological origin. Fish appeared to orient to a particular habitat; they would not leave their habitat when prodded with the manipulator arm of the submarine, as they did at boulder habitats.

Certain crustaceans and other fishes were commonly associated with rock and boulder habitats (Table 2). Most of these associates were ubiquitous with tilefish in these habitats, except for Macrozoarces americanus and Brosme brosme which were only observed at southern New England sites and Sebastes sp. which was seen only at Baltimore and Norfolk Canyons.

Pueblo Habitats

These habitats have been illustrated and described (Warme et al. 1977; Cooper and Uzmann 1977, 1980) by the former as "a relatively localized area of submarine canyon wall where megabenthic crustaceans and finfish have intensively bioeroded depressions and borings into the substrate and have occupied these sites." Pueblo habitat, occupied by tilefish, was commonly observed in Lydonia, Veatch (the latter also by Warme et al. 1977) and Oceanographer Canyons (Valentine et al. 1980). During our dives these habitats were found from 170 to 245 m depth. We have never observed Pueblo habitats around Hudson Canyon, even though we have made many more dives there (Table 1). We observed, as did Warme et al. (1977) and Valentine et al. (1980), that Pueblo habitats always occurred in the stiff grey clay found as outcrops along the walls of many of the submarine canyons in the study area. The excavations in the substrate occupied by tilefish were variable in shape and size. The smallest were just large enough to admit the girth of the tilefish, while others were as much as 1 m wide by 3 m long, and 1 m deep. They often had multiple openings into a single layer space (grotto). Dye marker experiments revealed that large and small openings into the grottos from the substrate surface were common and numerous. The openings not constructed by tilefish result from the burrowing activity of several associated species (Table 2).

The behavior of tilefish occupying Pueblo habitats was similar to those in excavations under rock slabs, but different from boulders. When approached by the submersible, tilefish always entered head first, and then usually pressed themselves against the back of the grotto and remained motionless. Exits from the grotto were tail first or head first. Following acclimation to the submersible, tilefish would leave the grotto but remained in the immediate vicinity (within 2-3 m). If disturbed, they moved directly back into the grotto and became motionless again.

Individual tilefish may be long-term residents of the same Pueblo habitat. We independently identified (using fish size and various body scars and marks) the same two adult tilefish at the same location approximately one year apart.

Habitat very similar to Pueblo habitat was observed on the north wall of Norfolk Canyon between 175 and 247 m. This habitat consisted of extensive, heavily bioeroded areas of stiff grey clay that was topographically complex, with several large clay blocks thrust up above the substrate with vertical walls and overhangs 25 m

Table 2. Fishes and crustaceans observed at various tilefish habitats along the northeast coast of the U.S. during 1980-1983. Each species was observed every year (see Table 1) unless otherwise noted. HC = Hudson Canyon, VC = Veatch Canyon, LC = Lydonia Canyon, BC = Baltimore Canyon, and NC = Norfolk Canyon (from Grimes et al. 1986).

Species	Boulders and rocks	Pueblo habitats	Vertical burrows
Crustaceans			
Munida sp.[a]	VC,LC	VC,LC	VC,LC
Munida longipes	BC	NC	--
Cancer sp.	VC,LC	VC,LC	VC,LC,HC
Acanthocarpus alexandria	--	--	HC
Homarus americanus	VC,LC	VC,LC	VC,LC,HC
Bathynectes superba	BC	NC	HC
goneplacid (possibly *Chacellus filiformis*)	--	--	VC,HC
Fishes			
Conger oceanicus	VC,LC	VC,LC	VC,HC
Macrozoarces americanus	VC,LC	VC,LC	--
Brosme brosme	VC,LC	--	--
Anthias nicholsi	VC,LC,BC	VC,LC,NC	VC,LC,HC
Helicolenus dactylopterus	VC,LC,BC	VC,LC,NC	VC,LC,HC
Sebastes sp.	VC	NC	--
Urophycis sp.	--	VC	HC
Laemonema sp. (possibly *L. barbatum*)	--	NC	--

a. Three species have been identified from collected specimens: *M. iris*, *M. valida*, and *M. forceps*. However, it is not possible to distinguish them from submersible sightings or photographs.

high. Tilefish were observed inhabiting the largest of the grotto-like excavations (up to 2 m greatest distance across the opening).

Although these Norfolk Canyon habitats were physically very similar to Pueblo habitats, they were quite different biologically (Table 2). Numerous anemones (*Halcurias pilatus*) living attached to the burrowed clay characterized the community in Norfolk Canyon. *Anthias nicholsi* was common, along with *Sebastes* sp., the galatheid crab *Munida longipes* and the portunid crab *Bathynectes superba*.

Vertical Burrows

We believe vertical burrows are the primary habitats of tilefish in the Middle Atlantic and southern New England area (Able et al. 1982; Grimes et al. 1986). Vertical burrows, especially larger ones, were funnel-shaped and extensively secondarily burrowed by associated species along the upper margin. The larger secondary burrows located at the burrow margin were connected to the main burrow shaft. Burrows were contagiously distributed. By compiling the frequency distributions of distances between all adjacent

burrows observed on transect dives we determined that 27% of all burrows seen at Hudson Canyon were less than 20 m apart (Grimes et al. 1986).

Burrows were observed over greater depth ranges around Hudson Canyon (120-225 m) and at the Middle Grounds (102-243 m), than at the two more northern submarine canyons (Veatch Canyon 120-165 m; Lydonia Canyon 125-183 m). At Veatch Canyon and Lydonia Canyons, where boulder and Pueblo habitats also occurred, vertical burrows were in shallower water. Largest burrows were observed at Hudson Canyon (Table 3; mean depth = 1.7 m, range = 1.25-2.3 m, n = 6). Burrows estimated to be up to 5.0 m in diameter were observed but not measured because they were too large to appear entirely within

Table 3. Diameter (mean and range in m) of tilefish burrows near submarine canyons in the Mid-Atlantic-Southern New England area; n = number of burrows measured (from Grimes et al. in press).

Study Area	1980	1981	All
Hudson Canyon	1.57 (0.8-3.5) n = 26	1.6 (0.3-3.0) n = 25	1.6 (0.3-3.5)* n = 51
Veatch Canyon	0.89 (0.4-2.0) n = 20	0.84 (0.3-1.5) n = 20	0.88 (0.3-2.0)* n = 40
Lydonia Canyon	-	0.88 (0.5-1.2) n = 6	0.88 (0.5-1.2) n = 6

*Mean burrow diameters for Hudson and Veatch canyons are significantly different [t = 6.73, t(.05) = 0.99].

the photographic field of view. Burrows were generally smaller (Table 3), less secondarily bioeroded, less funnel shaped and less dense (Table 4) at dive locations north of Hudson Canyon. In fact, burrows at Hudson Canyon were on the average twice as large (upper cone diameter), over eight times more dense and much more complex than burrows at Lydonia Canyon. We believe that geographic differences in burrow habitats indicated that habitats at the more northern dive locations were less temporally stable. The temporal instability probably resulted from the greater seasonal variations in bottom temperatures at more northern dive locations (Grimes et al. 1986).

We hypothesized that the conical upper portion of larger burrows results from the combined activity of tilefish and the associated species that inhabit burrow margins. Galatheid crabs, which inhabit the smallest secondary burrows in burrow cones, displace sediments into burrows and these sediments are forced out

Table 4. Density (mean and range) of tilefish burrows per km^2 near submarine canyons of the Mid-Atlantic-Southern New England area based on submersible transects; n = number of transects (from Grimes et al. in press).

Study area	1980	1981	1982	All
Hudson Canyon	1815 (952-2434) n = 4	1239 (1011-1548) n = 2	1132 (592-1646) n = 6	1234 (592-2434) n = 12
Veatch Canyon	958 (119-1429) n = 4	772 (748-798) n = 2	-	624 (119-1429) n = 6
Lydonia Canyon	233 n = 1	130 (67-164) n = 2	-	145 (67-322) n = 3

of the central shaft by tilefish swimming movements. Secondary burrows that interconnect to the main burrow make the upper portion of some tilefish burrows "honey combed" and prone to eventual collapse. Additionally, we observed clay clumps near occupied burrows that suggested to us that oral excavation by tilefish was an important means of burrow construction. These mechanisms explain the formation of conical shaped burrows, but do not account for the larger diameter (estimated up to 9-10 m across) crater-like features that we observed. These U-shaped features were secondarily eroded like funnel-shaped burrows, and had as many as three individual burrow shafts dug into their lower portions. Craters probably formed by the coalescence of closely spaced vertical burrows that widened and deepened.

Some burrows may be very old, if they are occupied by successive generations of tilefish (individuals live in excess of 30 yrs, Turner et al. 1983, and the clay into which they are dug is Pleistocene). However, a recent experiment suggested that if a burrow were unoccupied it would fill with sediment in maximum time of one year. We removed the fish from a large burrow (2 m diameter), marked the burrow location with an acoustic transponder. When we returned one year later the burrow was almost completely silted in and unoccupied.

Species that are sparse over open bottom are concentrated in and around burrows, forming a definite "tilefish community" (Table 2). Approximately 60-80% of all galatheid crabs, cancrid crabs and blackbellied rosefish counted in photographs were associated with burrows. At times of peak activity as many as 2 galatheids, 5 goneplacids, 5 Anthias sp., 1 Urophycis sp. and 1 Helicolenus dactylopterus were photographed at a single large (2 m diameter) burrow.

Time-lapse photography revealed distinct activity patterns for some associated species listed in Table 2 (Fig. 3). Galatheid crabs were more frequently photographed during the day, as were Anthias

nicholsi. H. dactylopterus may be crepuscular because they were most frequently photographed during early morning and late afternoon. Urophycis sp. activity showed no particular periodicity. Goneplacid crabs were clearly nocturnal, never appearing in photographs exposed after 0810 hr and before 1910 hr.

Small crabs and fishes probably concentrate around burrows for several reasons. They all appear to be shelter seeking and the complex topography of the burrow provides that. The goneplacid and galatheid crabs are also burrowers and the exposed clay in burrows may be the best malleable substrate available. Also, the swimming actions of tilefish probably keep their small secondary burrows at least partially free of fine silt. Finally, if tilefish feeding and excretion make the burrow a more resource rich environment, then associated species may gain trophic rewards. Whatever the exact nature of the benefits of burrows, the advantages gained must exceed the disadvantages of danger from predation, because some associates (in particular galatheid crabs, cancrid crabs and probably Helicolenus dactylopterus) are components of the diet of tilefish (Turner and Freeman in prep.).

As in the case of Pueblo habitats, tilefish seemed to orient to a particular burrow, especially around Hudson Canyon. In numerous instances when rotenone was injected into burrows fish exited but remained nearby, and in some instances attempted to re-enter the burrow. These fish had not been incapacitated by the rotenone as they quickly swam away when touched by the submersible manipulator arm.

Most direct in situ observations have indicated single occupancy of burrows. However, time-lapse photographs showed a male and female (sexes distinguished by larger adipose crest in males) utilizing the same burrow and displaying definite temporal activity patterns (Fig. 3). The female was seen repeatedly in photographs

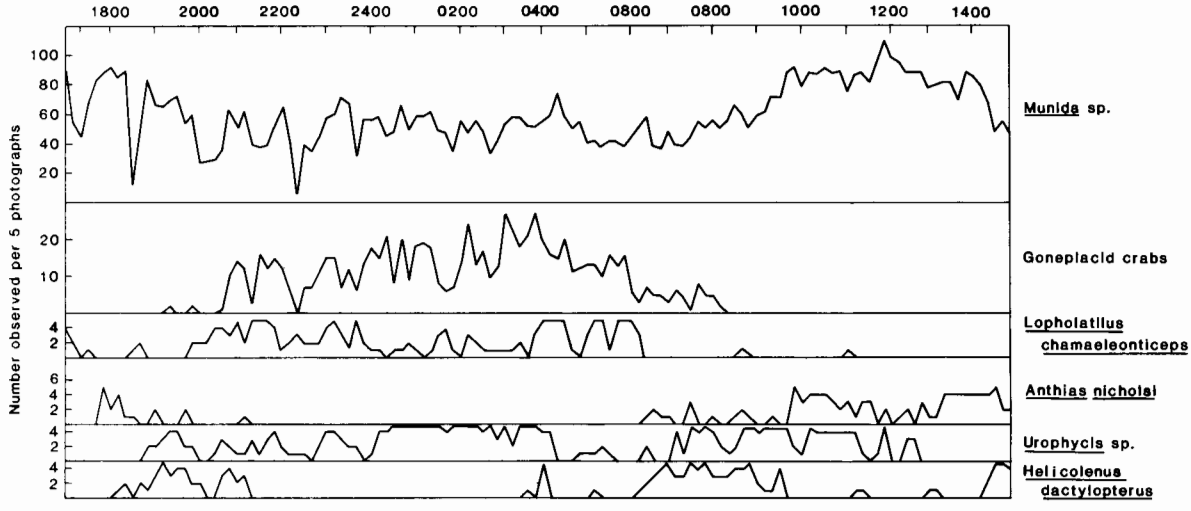

Figure 3. Temporal activity of tilefish and several associated species at a vertical burrow in Hudson Canyon, determined from time lapse photographs (from Grimes et al. 1986).

from about 1630 to 2230 hr. mostly entering and/or exiting the burrow, and seldom hovering above or around the burrow. At about 2230 hr the male appeared and was observed until 0700 hr, usually above the burrow margin or central shaft. We do not know if the female was in the burrow. However, because the male was not seen entering or exiting the burrow may suggest this was so. From 0700 hr until 1500 hr the female was observed near the burrow in very few photographs taken between 0900-1000 hr and 1100-1200 hr. This may suggest that for the most part both sexes were away from the burrow foraging during the day.

The non-corresponding temporal activity patterns of tilefish and some associated species (galatheid crabs, A. nicholsi, Urophycis sp. and H. dactylopterus) and the knowledge that these species are prey of tilefish (Turner and Freeman in prep.) suggested that predation was a powerful organizing force in communities associated with burrows, and probably Pueblo habitats as well. The burrow and Pueblo village associated communities are complex ecological systems featuring physical and biological interactions with tilefish acting as a keystone (Paine 1966) species. They shape the habitat and provide a physically suitable environment (perhaps trophically advantageous as well) for other members of the community. They interact with galatheid and goneplacid crabs to further structure and develop the habitat. Finally, they enjoy a symbiosis (probably mutualistic) with at least galatheid crabs, and through predation probably influence community structure. Clearly, the exact nature of the relationships between tilefish and associated species (i.e. trophodynamics and the possibility of an unusually efficient flux of nutrients through the community) are fertile areas for future research.

Sea Floor Processes

Bioerosion is increasingly recognized as an important process generating sediment and shaping bottom topography along the continental margin (Warme and Marshall 1969; Dillon and Zimmerman 1970; Stanley 1971; Warme et al. 1971; Rowe et al.1974; Cacchione et al. 1978; Ryan et al. 1978; Warme et al. 1978; Valentine et al. 1980; Malahoff et al. 1981; Hecker 1982). On the outer continental shelf tilefish play an active role in eroding the sea floor as described in previous sections of this paper.

The outer continental shelf off New Jersey and Long Island is mostly shaped by an evenly spaced linear northeast-southwest trending ridge and swale topography. However, around Hudson Canyon this regular topography is replaced by an irregular hummocky topography (Fig. 4; Ewing et al. 1963; Knebel 1979). The area covers about 800 km and occurs mostly at depths between 120 and 500 m. Hummocks are irregularly spaced and have 1-10 m relief. The hummocks are clearly erosional because horizontal reflectors are truncated at the flanks. Because of the proximity of the rough topography to Hudson Canyon the features have been attributed to canyon related processes (Ewing et al. 1963; Knebel 1979). Our knowledge of tilefish, habitat, ecology and behavior has led us to hypothesize that bioerosion by tilefish may be the cause of the rough bottom topography (Twichell et al. 1985).

There is a close correspondence between the fishing grounds for tilefish and the extent of the rough topography: Fig. 4 outlines the

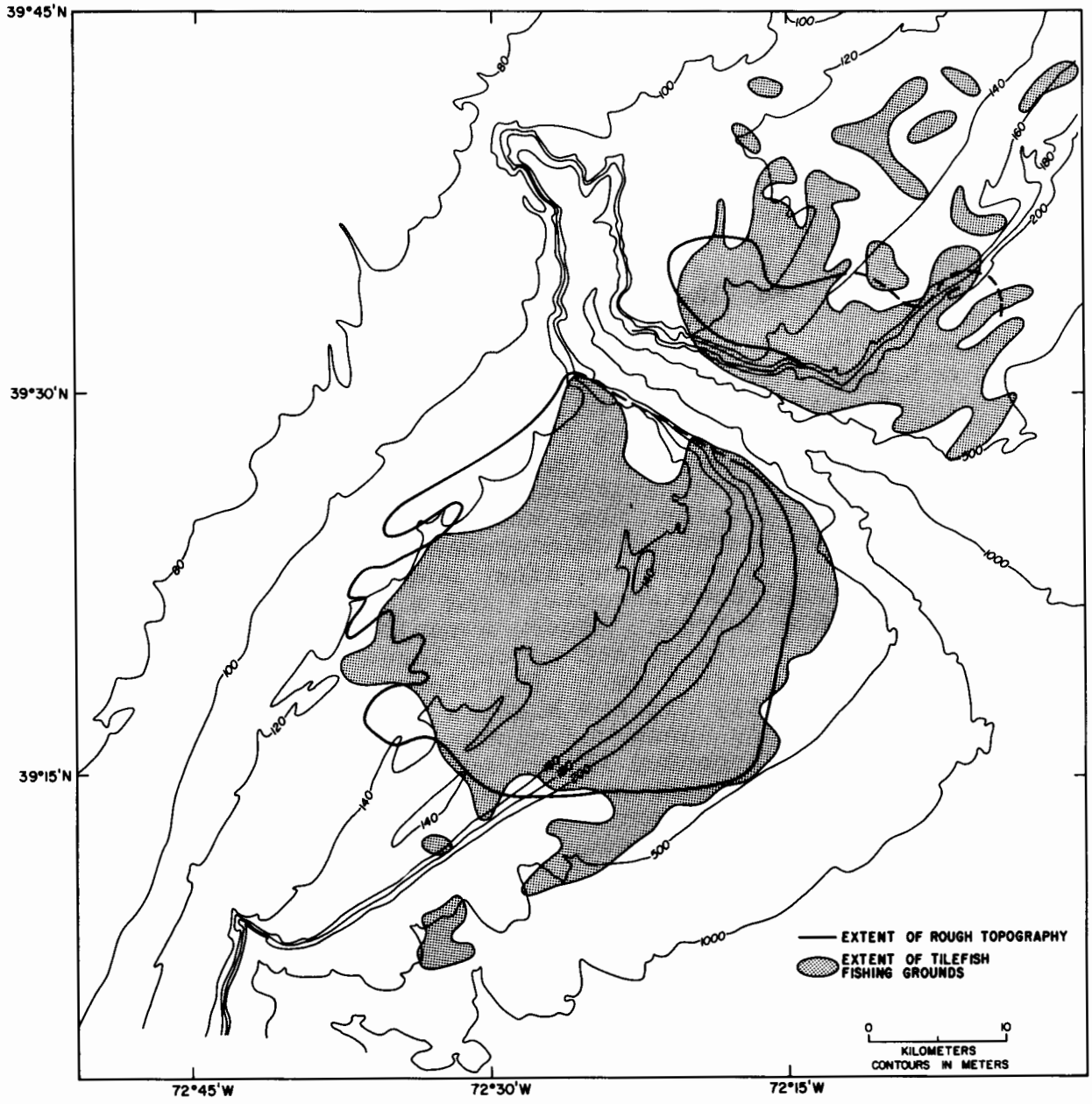

Figure 4. Comparison of the extent of the rough topography around Hudson Canyon with the extent of the tile fish grounds (from Twichell et al. in press).

location of 1634 individual longline sets made from 1978-1982, as well as the extent of the rough topography.

Stratigraphic data supported our contention that the hummocky topographic features were Holocene rather than Pleistocene in age. Seismic profiling showed three distinct layers. The oldest layer, an acoustically massive layer that was exposed north of Hudson Canyon, consisted of medium to coarse sand. Overlying the massive layer was a well laminated layer that observations from a submersible showed to be stiff grey clay, and it was this layer that

was burrowed by tilefish. The uppermost layer was composed of Holocene sand (13,000 yrs old) that was only seen shoreward of the area of rough topography. The rough topography coincided with the area where the laminated clay layer was exposed on the sea floor. Where the clay was buried by Holocene sand, the upper surface of the clay was smooth, indicating that the rough topography was younger than 13,000 yrs, otherwise the clay surface that was buried would also be rough (Twichell et al. 1985).

Grain size analysis of sediment samples taken across the three stratigraphic layers indicated three distinct sediment populations. The largest and smallest size fractions were medium to coarse sand that characterized the Holocene sand sheet shoreward of the rough topography, and silty-clay that characterized the burrowed substrate. The third sediment type was a thin veneer (less than 1 m) of sediment that covered much of the rough topography away from burrows; it was a mixture of the silt-clay excavated by tilefish, and sand transported offshore from the Holocene sand sheet.

The basic process of burrow construction and maintenance through the combined activities of tilefish and associated species over time may provide the mechanism for forming the rough topography. Considerable maintenance of the burrows is required; the vacant burrow we revisited after one year was silted in. Thus, sedimentation was considerable, and a fish must do considerable work to maintain a burrow. Such a rapid rate of filling suggests that juveniles probably do not occupy large existing burrows because they could not maintain them. Therefore, successive generations of tilefish would mostly dig new burrows rather than occupy old ones. Also, we frequently observed clouds of fine sediment coming from burrows, and once suspended it was evidently transported away by the current because there were not sediment mounds around burrows. Much of the suspended sediment may have been lost to the upper continental slope because mean drift in the area is 8 cm/sec to the south.

Having identified a mechanism for sea floor bioerosion we evaluated its extent by using sidescan sonar to determine the spatial distribution of tilefish burrows. Sidescan sonographs showed burrows only in areas where the clay layer was exposed at the surface of the substrate (Fig. 5 - upper panel). Our interpretation of burrows seen on sonographs was validated by direct observation during submersible dives.

We also used sidescan sonar to estimate mean burrow density ($2500/km^2$), and combined that information with the calculated sediment volume in a 2 m diameter burrow (1.3 m assuming a perfect conical shape 1.5 m deep) to estimate the amount of sediment removed from the 800 km area; that amount was 2.6 million m^3 Since each generation of fish mostly dig their own burrows, rather than occupy existing ones, the amount of sediment removed would be much more than the amount removed to form the present burrows.

Thus, tilefish effectively remove large sediment volumes. However, how can burrowing form large scale hummocky topography given that individual burrows and the rough topography were of very different scales? We believe that the larger scale hummocky topography is a consequence of spatially differential erosion rates over a long time period. Our analysis of the spatial distribution of burrows, i.e., frequency distribution of the distances between

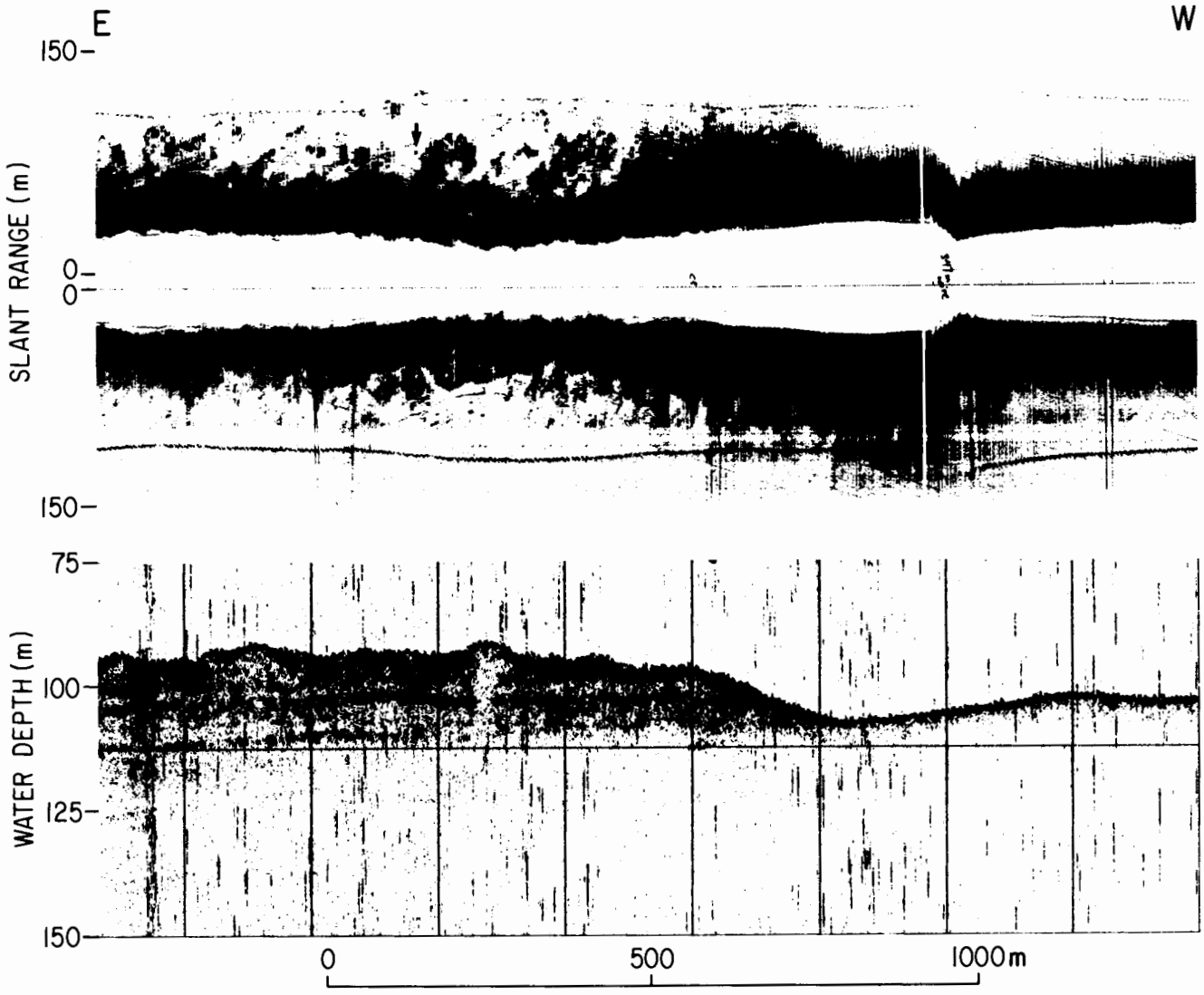

Figure 5. Sidescan sonograph (upper panel) and 3.5 kHz profile (lower panel) on the eastern side of the Hudson Canyon. On the sonograph, tilefish burrows are evident as points of strong acoustic reflectance with a shadow in front of them. The 3.5 kHz profile shows the rough topography and laminated clay substrate on the left portion of the record, its erosional truncation, and the exposure of the underlying sand on the right part of the record. Note the disappearance of tilefish burrows at the boundary of the clay substrate (from Twichell et al. 1985).

adjacent burrows (taken from sidescan sonographs and from direct measurements along submersible transects), showed that burrows were contagiously distributed (Twichell et al. 1985). In areas where burrows were clustered, bioerosion should be more rapid than where burrows were scarce. Furthermore, the dimensions of burrow clusters (up to 200 m across) were similar to the size of the larger

depressions separating the hummocks.

In summary, we have proposed that tilefish are responsible for the extensive bioerosion of bottom sediments around Hudson Canyon. By burrowing (and individual burrows coalescing to form craters) in clusters for the past 8 to 10 thousand years they have created the large scale hummocky topography.

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