

The Importance of Physical and Biogenic Structure to Juvenile Fishes on the Shallow Inner Continental Shelf¹

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ABSTRACT: Fish-habitat relationships on the shallow inner continental shelf were quantified with video sled and metered beam trawl on Fenwick and Weaver shoals offshore of Maryland and Delaware, U.S. These areas provide megascale physical relief and habitat complexity, but for juvenile fishes, mesoscale and microscale habitat is very important particularly as refuge from predation. At these smaller scales, much of the relief on the inner continental shelf is contributed by bedforms or sand waves and biogenic structures such as tubes, shell beds, or pits. A quantitative association for juvenile fishes between and within benthic habitats was found and related primarily to bedform size and amount of biogenic structure. The incidence of fishes was about four-times higher for large bedforms (> 30 cm wavelength and about 10 cm crest height) relative to smaller bedforms (< 30 cm wavelength and about 5 cm crest height). For biogenic structure, going from high patch-mat tube densities to lower densities or no biogenic structure increased fish incidence by 5.4 and 3.3 times, respectively. The significant relationships of fishes with bedform size and density of biogenic structure indicated that seemingly small differences in physical structure of a habitat can make the difference between unacceptable and essential habitat for juvenile fishes. Proximity of complex and simple habitats was important in the diel use of habitat and in balancing pressure of refuge from predation provided by complex habitats with foraging for increased resources available in simpler habitats. During the day, spatially complex habitats comprised of *Diopatra* and *Asabellides* tube mats had about twice as many fishes relative to bare sandy habitats (8.3–9.9 versus 4.0–4.1 fishes 100 m⁻², respectively). At night, the pattern was reversed with more fishes present in the bare sandy habitats (12.4–13.5 versus 5.6–8.7 fishes 100 m⁻²). Some fish, such as *Ammodytes* spp., were very habitat specific and occurred only on dynamic coarser sands near the top of the shoals. Others, such as *Urophycis regia*, showed less habitat preference and occurred in all habitats during both day and night. Combining the effects of physical relief and biogenics, the habitat with the highest incidence of fishes had large bedforms with some biogenic structure. More emphasis needs to be placed on quantifying the relationship between fishes and their habitats for the fisheries management concept of essential fish habitat to develop into an effective tool on the inner continental shelf. The juvenile life history stages need to be emphasized because fish-habitat interactions are the strongest for these stages and may be the most ecologically important.

Introduction

In assessing the quantitative relationship between fishes and benthic habitat, particular emphasis needs to be placed on juvenile life history stages for several reasons. As the adult stage is reached benthic fishes become increasingly mobile and less habitat specific in both continental shelf and estuarine

systems (see Able and Fahay 1998; Steves et al. 1998 for examples). The juvenile period is longer in duration than the larval period for most fishes, and small changes in habitat quality that affect growth and survival of juveniles may have large impacts on the number of fish produced by a specific habitat. Most species of economic importance along the east coast of the U.S. use estuarine and nearshore habitats as juveniles (Hoss and Thayer 1993; Able and Fahay 1998) and are susceptible to declining habitat quality. A primary source of mortality for juvenile fishes is predation (Sissenwine 1984; Smith 1985; Houde 1987; Doherty 1991; Beverton and Iles 1992), which is mediated by habitat characteristics (Bartholomew et al. 2000). Recruitment and year-class strength are established at the postlarval and

¹ Presented within two symposia dealing with essential fisheries habitat and implications of global climatic change at the American Fisheries Society's 24th Annual Larval Fish Conference at Gulf Shores, Alabama, November 6–10, 2000. Symposium and meeting conveners were Richard F. Shaw and James H. Cowan, Jr.

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early juvenile stage (Beverton et al. 1984; Sissenwine 1984; Rothschild 1986; Sinclair 1988; Fogarty et al. 1991; Cushing 1996).

Previous studies on the U.S. east coast that characterized fish abundance versus habitat relationships dealt mostly with adults and mesoscale patterns (Colvocoresses and Musick 1984; Gabriel 1992) even though benthic habitat relationships in these studies were masked by changes in environmental parameters not related to physical habitat, such as temperature and seasonality. In some fishes, distribution can be related to sediment type or habitat characteristics using large-scale sampling (e.g., Auster et al. 1997; Norcross et al. 1997), but it is still often difficult to derive quantitative relationships between physical and biological aspects of the habitat and abundance of fishes (Able 1999). Higher resolution small-scale sampling is required to determine microhabitat associations of fishes that can then be extended to mesoscale (> 1 km) habitat characteristics (Langton et al. 1995; Caley et al. 1996; Hewitt et al. 1998; Sullivan et al. 2000).

Spatial variability in topography and substrate characteristics do influence biological community attributes at very small (cm) to regional (km) scales (Langton et al. 1995; Huston 1999; Schneider 2001). Because regional sampling at very high densities is often not feasible, we chose to use techniques that would allow varying spatial scales to be addressed. Continuous long (> 10 km) transect sampling with video cameras provided centimeter-scale coverage and estimates of rates of meter-scale spatial change that could be combined to address spatial variation at larger spatial scales. A metered beam trawl was used to estimate fish density in various habitats.

Our study was centered on the Fenwick Shoal region, the primary set of detached sand ridge features offshore of the border between Maryland and Delaware, U.S. These topographic features are believed to be long-term accretional and erosional responses to storm-related hydraulic regimes in combination with sea-level rise since the last deglaciation (Swift and Field 1981; McBride and Moslow 1991; Goff et al. 1999). They apparently formed as shore-attached ridge features produced during shoreline erosion of mixed sands and some coarser components by storm generated flows (Swift et al. 1973) and were drowned and detached from shore as sea level rose.

Materials and Methods

The study area was located on the inner continental shelf in the central portion of the mid-Atlantic Bight. Most of our effort was concentrated on Fenwick Shoals (38°27.5'N, 74°55.9'W) with

lesser effort on Weaver Shoal (38°25.5'N, 74°55.5'W; Fig. 1). Sampling conducted in June 1998 for classification of benthic habitats in and around the Fenwick Shoal region led us to hypothesize that there were quantitative relationships between the presence of juvenile fishes and benthic habitat characteristics, and that a combination of video transect and beam trawl data could be used to test our hypothesis. In May 1999 we concentrated our sampling effort in the areas where major sedimentological and biological transitions were identified from the 1998 data.

The video sled was towed on the bottom at 2 to 3 knots when the vessel was under power and as low as 0.8 knots when drifting in order to acquire more detailed images at slower speeds. The video camera was set obliquely to the bottom, about a 45° angle, and about 15 cm from the bottom in order to resolve smaller surface details and biological structures. The area viewed by the camera was a trapezoid about 10 cm along the baseline closest to the camera and 40 cm along the far baseline. The total field of view was about 0.2 to 0.4 m² depending on sled orientation. The sled was linked to the surface via two cables that provided power to the camera and incandescent lamps and transmitted the video signal to the surface where sled performance and bottom features could be viewed in real time. The video signal was multiplexed with differential global positioning system (DGPS) data and recorded to videotape for later analysis.

For analysis, sled video images were transferred from analog to digital video format. The digital video was then played back at 1/3 speed with substrate configuration, fish and invertebrate fauna, and biogenic feature occurrence, both quantity and type, scored by an observer at 1-s intervals. Video times were translated to position using recorded DGPS logs. Where position data were missing due to slowed DGPS data logging, positions were estimated using an average of the two nearest positions. Habitats were classified in terms of visible physical and biological characteristics. Bottom relief was classified as being large (bedforms > 30 cm wavelength and about 10 cm wave height as estimated from the video images), small (bedforms < 30 cm wavelength and < 5 cm wave height), and flat (no bedforms and relief < 1 cm). Biological features were classified as patch-mat (dense patches of tubes or organisms to continuous cover of tubes), some (single tube, organism, or biogenic structure), and None (no obvious biogenic structures). Shell hash was classified by percent coverage of the sediment surface into three categories: < 10%, 10–50%, and > 50%. Bottom with > 50% shell coverage was considered to be shell bed habitat. In addition to benthic habitat classifications, each fish

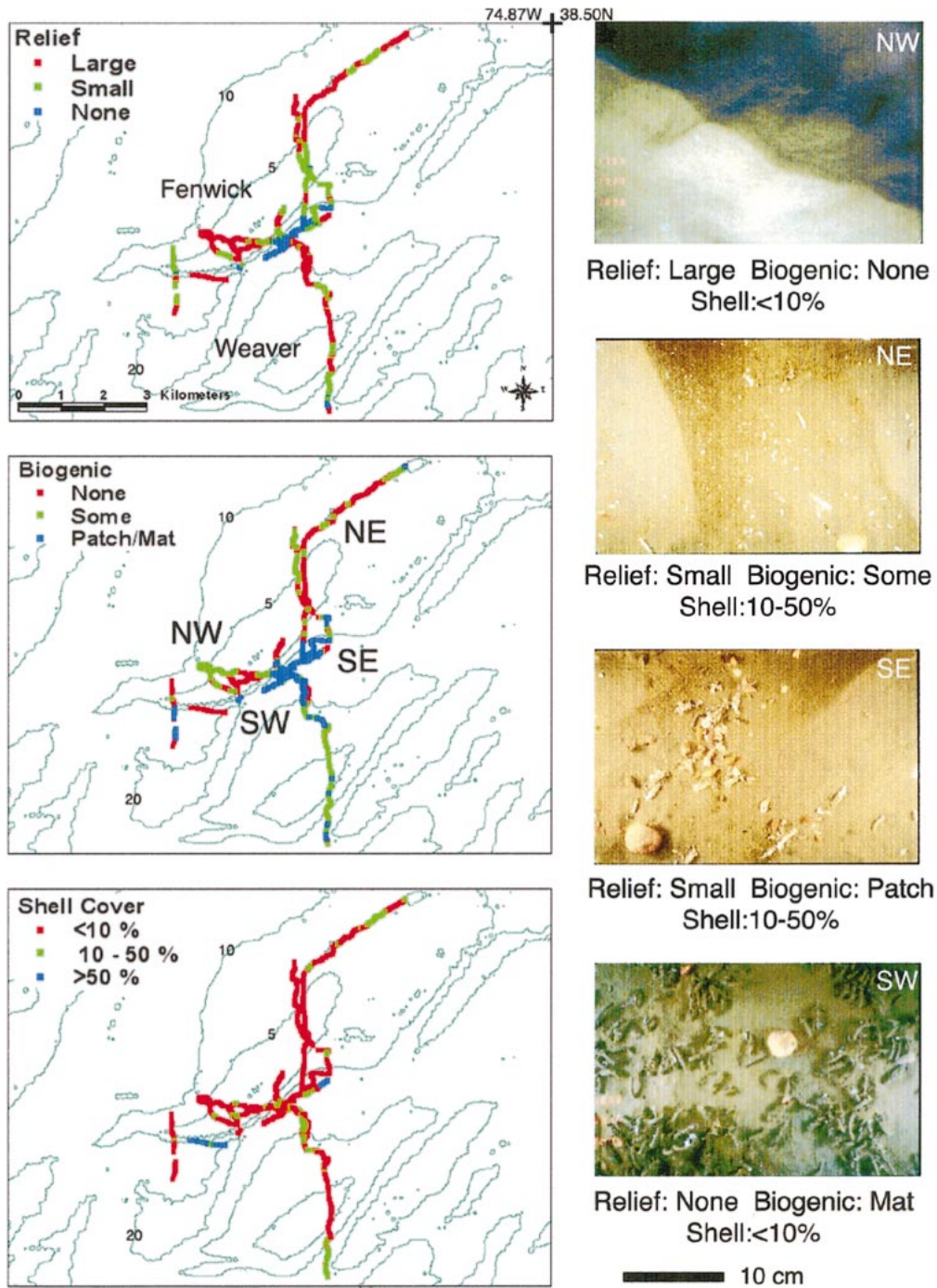


Fig. 1. Spatial distribution of benthic habitats in the Fenwick Shoal area classified by relief or bedform size (Large = > 30 cm wavelength and about 5 cm wave height, Small = < 30 cm wavelength and < 5 cm wave height, None = flat bottom), Biogenic Structure (None = none obvious, Some = occasional structure, Patch/Mat = patchy to uniform cover of tubes), and Shell Cover over the bottom. Approximate location of beam trawls are indicated in the center map as: NW (larger bedforms, coarser sands with gravel and slightly more shell cover, little biogenic structure), NE (smaller bedforms, medium and fine sands with less shell, little biogenic structure), SE (small bedforms to flat bottom, medium and fine sands, dominated by *Diopatra cuprea* tubes), SW (flat bottom, finer sands with some silt, dominated by *Asabellides oculata* tubes). Images from each of the trawled areas are included to give an impression of habitats and classification criteria.

TABLE 1. Summary of benthic habitat variables used in the Poisson regression analysis. Only 22 of the possible 27 combinations of habitat characteristics occurred. Data are based on 1-s interval videotape data.

Bedform Size	Biogenic Structures	Shell Cover	Total Intervals	Percent of Track Line	Juvenile Fishes
Large	None	<10%	6,820	22.1 ²	316
	None	10–50%	1,613	5.2	24
	None	>50%	46	0.1	0
	Some	<10%	4,762	15.5	251
	Some	10–50%	748	2.4	117
	Patch-mat ¹	<10%	735	2.4	1
Small	Patch-mat	10–50%	698	2.3	13
	None	<10%	5,085	16.5	58
	None	10–50%	780	2.5	3
	Some	<10%	1,503	4.9	29
	Some	10–50%	520	1.7 ²	1
	Patch-mat	<10%	1,541	5.0	6
None	Patch-mat	10–50%	653	2.1 ²	1
	Patch-mat	>50%	316	1.0	1
	None	<10%	83	0.3	3
	None	10–50%	24	0.1	0
	None	>50%	10	<0.1	0
	Some	<10%	94	0.3	1
	Some	10–50%	43	0.1	0
	Patch-mat	<10%	3,840	12.5 ²	28
	Patch-mat	10–50%	327	1.1	2
	Patch-mat	>50%	560	1.8	1

¹ Tubes in small to large patches to mats that completely cover the bottom.

² Examples of these habitat classes shown in Fig. 1.

observed in the video was reviewed at slow speed until species, or lowest practical taxonomic level, identification could be determined. Seafloor habitats were then identified based on the relative amounts of the three variables: bottom relief, biological features, and shell hash.

A beam trawl (2 m wide, 3 mm mesh) was used to assess fish occurrence and ground-truth the video image identifications in the major habitat types delineated by the video sled. The trawl was fitted with a meter-wheel (Kuipers et al. 1992) to measure distance trawled so that fish abundance per unit area could be estimated. In each area of relatively homogeneous habitat type, eight 2-min trawls were collected, four during the day and four during the night. Fish collected in each trawl were sorted to major taxa, counted and recorded, and preserved in formalin for laboratory processing. In the laboratory, preserved fishes were identified to species or lowest practical taxonomic level, weighed, and measured.

Cluster analyses of the trawl data was performed with the program COMPAH96 (Gallagher personal communication) originally developed at the Virginia Institute of Marine Science in the early 1970s. The bottom habitat and fish species clusters were generated using flexible sorting with β of -0.25 and Bray-Curtis similarity, also known as Pielou's (1984) percentage similarity, calculated from si-

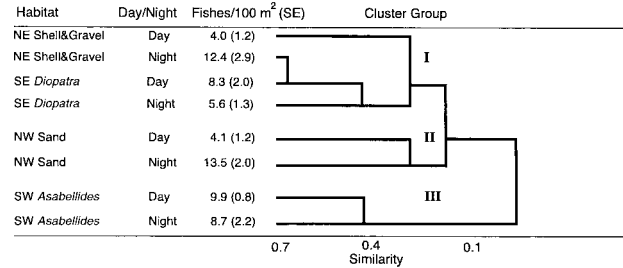


Fig. 2. Dendrogram of the relationships between benthic habitats and diel occurrence of fishes in beam trawl collections in the Fenwick Shoal region, May 1999. Fishes in the highest biogenic structure SW *Asabellides* habitat were the most distinct, followed by the highest energy NW sandy habitat. The two intermediate structure and energy sites, NE shell and gravel and SE *Diopatra* habitat, grouped together.

multaneous standardization of abundance (Boesch 1977):

$$Y = X / \sqrt{(\text{sample total} \times \text{species total})}$$

where Y is the standardized value of abundance (X).

To test the hypothesis that juvenile fish were related to physical and biological aspects of habitat, we used a Poisson loglinear model (Poisson regression) that modeled the abundance of fishes, the dependent variable in our observational study, relative to the benthic habitat variables. We assumed that for each 1-s video data interval, fish presence or absence was a Bernoulli trial. The explanatory variables thought to affect fish incidence were size of bedforms (large, small, none), abundance of biogenic structures (patch-mat, some, none), and density of shell cover (< 10%, 10–50%, > 50%) on the bottom. Data were not autocorrelated (Durbin-Watson D = 1.9, first order autocorrelation = 0.04), and the Poisson model was generated with PROC GENMOD (Stokes et al. 1995) using ln (n) as the canonical link for a General Linear Model with a Poisson random component, where n is the observed sample size for each cell in the model. To correct for overdispersion, the Poisson variance was scaled based on the Pearson Chi-Square statistic, which brought the deviance to 1.00 and Pearson Chi-Square to 0.96, and the offset parameter set to ln (number of 1-s intervals).

Results

IN SITU IMAGING OF HABITATS

Analysis of the May 1999 videotapes produced 30,801 1-s interval data points, representing about 37 km of track line. Each data point represented about 0.2 to 0.4 m², for a total area of about 7,400 to 14,800 m². These data were combined to arrive at a benthic habitat classification for the video track lines (Table 1, Fig. 2). The most extensive

benthic habitat encountered 50% of the total area surveyed was large bedforms (typically > 30–40 cm wavelength and about 10 cm crest height) with little to no obvious biogenic activity. Smaller bedform habitat (< 30 cm wavelength and < 5 cm crest height) comprised about 34% of the area surveyed and flat, generally featureless bottom 16% (Table 1). Physically dominated habitats with low levels of biogenic activity comprised about 72% of the track line. Biogenic activity in these habitats consisted of occasional tubes, megafauna, pits, or fecal mounds. Biologically dominated habitats had greater amounts of biogenic structure and activity, mostly tube patches and beds of the polychaetes *Diopatra cuprea* and *Asabellides oculata*, and were about 25% of the track line. Both polychaetes construct large tubes; *D. cuprea* uses fragments of organic debris and shell, and *A. oculata* uses fine sand. Shell beds made up of empty valves of the surf clam *Spisula solidissima*, with > 50% coverage of the bottom, occurred over 3% of the area surveyed.

The distribution of benthic habitats, as delineated by our three variables, presented a complex two-dimensional spatial pattern within any defined geographic area (Fig. 1). Four relatively homogeneous areas were recognized based on habitat composition. The northeast seaward flank of Fenwick Shoal (NE) was primarily coarser sands with gravel and slightly more shell cover. The northwest shoreward face of the shoal (NW) was primarily medium and fine sands with less shell than the other habitats. The southeast seaward trough (SE) where surface sediments were medium and fine sands and dominated by *D. cuprea* tubes. The southwest shoreward trough (SW) where surface sediments were finer sands with some silt and dominated by *A. oculata* tubes. The first two habitats represent physically dominated bottom with little evidence of biological control over habitat characteristics and the last two habitats represent biologically dominated bottom. Much of the large bedform, low biogenic structure habitat flanked the two shoal features (Fenwick and Weaver) with increased amounts of biogenic structure found in the trough between these shoals. This pattern was correlated with water depth and sediment grain size. Shallower shoal flanks, about 9 to 10 m deep, were coarser grained than the trough that had depths to 19 m and finer grained sediments. The tops of the shoals were about 4 to 5 m deep.

A total of 2,403 individuals comprising 14 bony fish and four elasmobranch taxa were recorded from the videotape (Table 2). When first observed, all of these were on or within a few centimeters of the bottom and exhibited little avoidance reaction until the sled was within several centimeters. The

TABLE 2. Fish taxa observed with the video sled. All individuals were singular occurrences except *Ammodytes* spp. Taxa marked with x were excluded from the Poisson regression.

Taxa	Total Number	Excluded
<i>Ammodytes</i> spp. ¹	2,259 ²	
<i>Anchoa mitchilli</i> ¹	11	x
<i>Conger oceanicus</i> ¹	1	x
Carcharhinidae	2	x
<i>Centropristis striata</i> ¹	1	
<i>Cynoscion regalis</i> ¹	8	
<i>Lophius americanus</i>	1	x
<i>Menticirrhus saxatilis</i>	2	
<i>Mustelus canis</i>	1	x
<i>Ophidion marginatum</i> ¹	3	
<i>Paralichthys dentatus</i> ¹	1	
<i>Prionotus carolinus</i> ¹ , <i>P. evolans</i> ¹	12	
<i>Raja eglantaria</i> ¹	6	x
<i>Raja</i> spp. ¹	9	x
Sciaenidae	1	
<i>Stenotomus chrysops</i> ¹	4	
Unidentified fish, flat ³	8	
Unidentified fish, not flat	70	
<i>Urophycis regia</i> ¹	2	
<i>Urophycis</i> spp. ¹	1	

¹ Species and taxa also collected in the trawls.

² Occurred in 712 1-s video samples.

³ Likely juvenile *E. microstomus*.

exception was the bay anchovy, *Anchoa mitchilli*, which was distributed higher in the water column and swam away as the sled approached. We were able to identify almost all (90%) taxa that were observed in the images because of their shape or behavior.

The species composition was dominated by benthic forms with the exception of *A. mitchilli* and the numerically dominant *Ammodytes* spp. which uses both pelagic and benthic habitats. The latter were easy to distinguish as they entered or left the substrate, a characteristic behavior (Able and Fahay 1998), when disturbed by the approach of the sled. The taxonomic identity of these individuals is somewhat problematic because two species (*Ammodytes americanus* and *Ammodytes dubius*) can occur on inner continental shelf shoals or ridges (Able personal observation) from the Middle Atlantic Bight (Nizinski et al. 1990). The other species identified from video (Table 2) were common to the region.

The fish were distributed over the entire Fenwick Shoal region and many species and taxa did show habitat preferences. *Ammodytes* spp., 94% of all individuals encountered, were the most habitat specific and occurred mainly on the top and flanks of Fenwick Shoal that was dominated by coarse sands and larger bedforms. *Ammodytes* spp. were highly aggregated with as many as 28 individuals in a single 1-s video sample (mean 3.2 ind \pm 3.8 SD). Of the 712 video samples with *Ammodytes* spp.,

TABLE 3. Fishes collected with beam trawl in the four major benthic habitat types present in the Fenwick Shoal area. See text for habitat descriptions.

Fish	NE Sand	NW Shell	SE Diopatra	SW Asabellides	Total
<i>Ammodytes</i> spp. ¹	9	1	—	—	10
<i>Anchoa mitchilli</i> ¹	—	1	1	—	2
<i>Centropristis striata</i> ¹	—	0	1	—	1
<i>Conger oceanicus</i> ¹	—	1	—	1	2
<i>Cynoscion regalis</i> ¹	—	—	—	1	1
<i>Enchelyopus cimbrius</i>	—	—	—	6	6
<i>Etropus microstomus</i>	22	23	30	10	85
<i>Mugil curema</i>	—	—	—	1	1
<i>Ophidion marginatum</i> ¹	—	3	1	—	4
<i>Paralichthys dentatus</i> ¹	—	—	—	1	1
<i>Prionotus carolinus</i> ¹	4	14	8	—	26
<i>Prionotus evolans</i> ¹	—	—	—	1	1
<i>Pseudopleuronectes americanus</i>	—	—	1	4	5
<i>Raja eglantaria</i> ¹	—	2	2	15	19
<i>Raja erinacea</i>	—	—	—	6	6
<i>Scomber scombrus</i>	—	1	—	—	1
<i>Scophthalmus aquosus</i>	—	—	—	2	2
<i>Stenotomus chrysops</i> ¹	—	4	—	—	4
<i>Syngnathus fuscus</i>	—	—	—	1	1
<i>Urophycis regia</i> ¹	21	2	37	95	155

¹ Species and taxa also seen in the video.

43% contained > 1 individual. All other fish occurrences were single individuals, except *A. mitchilli*.

FISH FROM TRAWL SAMPLES

The beam trawls from all four sampled habitats collected a total of 333 individuals representing 18 bony fish and two elasmobranch taxa (Table 3). The species composition from the beam trawl samples was similar to that from video images with 60% of the species in common. Species that were collected by trawl but not on video included pelagic (*Scomber scombrus*, *Mugil curema*), relatively rare (*Enchelyopus cimbrius*, *Syngnathus fuscus*) or cryptic forms which are known to bury in the substrate (*Scophthalmus aquosus*, *Pseudopleuronectes americanus*, *Urophycis regia*).

The most abundant fish was the hake, *U. regia*,

followed by the smallmouth flounder, *Etropus microstomus*. Together they were about 70% of the fish caught and are common members of shallow continental shelf fish assemblages (Able and Fahay 1998) but neither was commonly observed on video. It is likely that most of the 78 small, unidentified fishes in the video were these two species. Length frequency measurements indicated the median size of *U. regia* was 75 mm (range 45 to 215 mm) and *E. microstomus* was 65 mm (range 45 to 125 mm) both size ranges were well within the size range of the unidentified fishes on the video.

FISH-HABITAT ASSOCIATIONS

The association of fishes with habitats, as identified from video images, appeared to be related to sediment grain size, physical relief or bed roughness, and presence of biogenic structure. Both the NE coarser sand-gravel and SE *Diopatra* tube habitats, which had about the same habitat characteristics as the NE trawl site except for higher densities of *Diopatra* tubes, had similar fish assemblages (Cluster group I, Fig. 2). The NW sand habitat (group II) fish assemblage had the highest similarity with the dynamic sandy habitats represented in group I (Fig. 2). The SW *Asabellides* tube habitat (group III) was the most dissimilar of the four habitat types and also represented the most biogenically complex habitat sampled and had no diel difference in fish abundance. The NE and NW sites, which had lowest levels of biogenic structure, were the only habitats to show a strong diel difference in fish abundance with about four times as many fish present at night. The SE *Diopatra* habitat that clustered with the NE habitat had more biogenic structure and no diel difference.

Cluster analysis of the fishes grouped by habitat and diel trawls indicated that there were day and night differences in numbers of fish caught and species composition in collections from the SW *Asabellides* tube and NW sand habitats (Fig. 3). Two of the five species groups were associated with the

TABLE 4. Results of Poisson regression analysis for video data habitat classification using bedform size, biogenic structure, and shell cover.

Parameter	Value	DF	Estimate	SE	χ^2	p
Intercept		1	-4.4277	0.6018	54.13	<0.0001
Bedform	None	1	-0.6341	0.7286	0.76	0.3841
	Small	1	-1.3946	0.3514	15.75	<0.0001
	Large	0	0.0000	0.0000		
Biogenic	None	1	1.1991	0.6081	3.89	0.0486
	Some	1	1.6840	0.6083	7.66	0.0056
	Patch-mat	0	0.0000	0.0000		
Shell	>50%	1	-1.1809	2.3291	0.26	0.6121
	10-50%	1	0.1236	0.2863	0.19	0.6658
	<10%	0	0.0000	0.0000		
Scale		0	3.2548	0.0000		

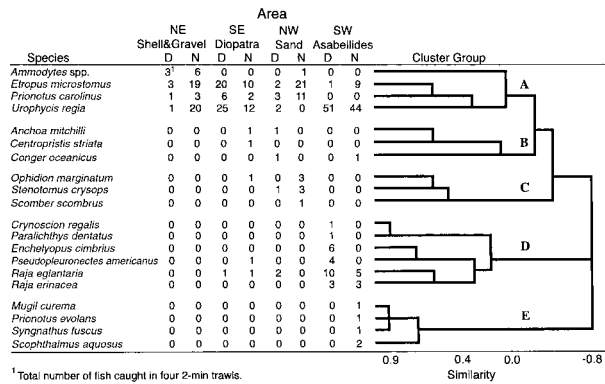


Fig. 3. Dendrogram of the relationships between fish grouping based on beam trawl collections in the Fenwick Shoal region, May 1999. Group A fishes tended to be the common species that were distributed across all habitat types, both day and night, with the exception of *Ammodytes* spp. The other four species groups were more specific to a habitat or time of day. Groups D and E were associated with SW *Asabellides* habitat during the day and night, respectively.

SW *Asabellides* tube habitat (groups D and E). Species group D was six species mostly associated with day trawls and Group E was four species caught only at night in the SW *Asabellides* tube habitat. Group C was primarily a nighttime group of three species mostly associated with the NW sand habitat. Species group B were diel species from the NW sand and SE *Diopatra* habitat. Group A was the numerically dominant species that occurred in all habitats both day and night (Table 3, Fig. 3).

The Poisson regression included only juvenile demersal fishes. Rare species such as rays and sharks, and several large individuals were excluded (Table 2). The model was parameterized such that estimated changes in fish incidence would be referenced to large bedforms, patch-mat tubes, and < 10% shell cover. The model intercept then represented the incidence of fishes in a habitat that was represented by these characteristics. The overall fit of the model was good with the physical relief ($p = 0.0003$) and biogenic variables ($p = 0.006$) producing significant parameters. Shell cover parameters were not significant ($p = 0.796$), which may have been related to the limited amount of high density shell hash or shell beds. Only 3% of the total area surveyed had > 50% shell coverage. Analysis of standardized residuals (Agresti 1990) indicated the model had good fit over the entire range of data.

The abundance of juvenile fishes varied among habitats. Changes in physical relief, going from large to small bedforms, resulted in a significant decline in the incidence of fishes. Fishes were 4 times more likely to be in large (≈ 10 cm crest height) than small (≈ 5 cm) bedform habitats. The

difference in fishes between large bedform and flat bottom habitats was not significant, but the negative sign of the parameter estimate points to a possible decline in fish relative to large bedforms. Both parameters estimated from the biogenic variable were significant, with a shift from patch-mat tube densities to only the presence of some biogenic structure increasing fish incidence by a ratio of 5.4. Differences among patch-mat tubes and no biogenic structure was marginally significant and also associated with higher fish incidence by a ratio of 3.3. With most of the video track being sampled at night, these parameter estimates are consistent with the trawl data that showed an increase in fishes at night in habitats with little or no biogenic structure. Combining the effects of physical relief and biogenics, the habitat with the highest incidence of fishes had large bedforms with some biogenic structure.

Discussion

We predicted that there would be a quantitative relationship between habitat complexity and fish abundance. Complexity on the low relief Middle Atlantic Bight inner continental shelf was measured as size of bedforms and density of biogenic structures. A quantitative association for fishes among and within benthic habitats did exist and was related primarily to bedform type and amount of biogenic structure. Another factor we considered, shell cover, did not contribute significantly to the abundance of fishes even though other studies have shown a close association of juvenile fishes with shell (Auster et al. 1991; Able et al. 1995). Shell was not a significant determinant of fish occurrence in our studies because of its low spatial abundance and possibly because it was correlated with bedforms and biogenic structures. About 40% of the shell beds around Fenwick Shoal were found in the troughs of large and small bedforms. The other 60% were found on flat bottom with patch-mat densities of biogenic structures. Visibility may have also been a problem in the spatially complex shell and tube mat habitats where juvenile fishes could avoid detection.

Shoal fields, like Fenwick Shoal, provide much of the megascale physical relief or complexity on the otherwise flat inner continental shelf. But detecting fish-habitat associations at these scales is complicated by changes in other variables such as temperature and depth as other investigators have shown (Colvocoresses and Musick 1984). Another complicating factor seems to be the decline in habitat specificity as fishes grow, mature to adults, and migrate (Able and Fahay 1998; Steves et al. 1998; Sullivan et al. 2000). For juvenile fishes it is often the mesoscale and microscale habitats that are

most important as refugia for local populations. At these smaller scales much of the relief on the inner continental shelf is contributed by bedforms or sand waves and biogenic structures such as tubes, shell beds, or pits. The significant relationships of fishes with bedform size and density of biogenic structure demonstrates that small changes in physical habitat can make the difference between unacceptable and essential habitat for juvenile fishes. Demersal fishes may be exhibiting a tactile response and prefer to use slopes of larger bedforms as feeding grounds at night. We found the incidence of fishes to be about 4 times higher for large bedforms relative to smaller bedforms.

Proximity of complex and simple habitats may be important in diel use and in balancing refuge from predation provided by complex habitats with increased resources available in simpler habitats. Estimates of fish abundance from the trawl data suggested that during the day the more spatially complex SE *Diopatra* and SW *Asabellides* habitats (Fig. 1) had about twice as many fishes relative to the barer sandy NE and NW habitats. At night the pattern was reversed with more fishes present in the bare sandy habitats. Smallmouth flounder (*E. microstomus*) and hake (*U. regia*) were the best examples being 8.3 and 6.4 times more likely to be found in complex habitats during the day. The more spatially complex biogenic habitats tended to have more fishes during the day and simpler physically structured habitats more fishes at night. The Poisson model also predicted the shift in fishes from biogenically complex to simpler habitats.

Sandeels, *Ammodytes* spp., were the most habitat specific of all the fishes sampled and occurred only on dynamic sands near the top of Fenwick Shoal where sediment grain size was medium to coarse sand. Similar coarse sediment preference was shown for the European species *Ammodytes marinus* (Wright et al. 2000). The other fishes showed less preference for a particular habitat, such as *U. regia*, which occurred in all habitats during both day and night.

As Sullivan et al. (2000) indicated, it is difficult to define the habitats actually occupied by a fish. Juvenile life history stages need to be emphasized because that is when fish-habitat interactions are the strongest. The combined use of video sled and metered trawl was effective at quantitatively defining the nature of juvenile fish-habitat relationships for the study area and could be used over much of the continental shelf in the Middle Atlantic Bight as well as other areas. This effectiveness derived from the strength of one technique that offset the weakness of the other. The video sled was able to locate fishes in their habitat at microscales over large areas of the bottom and map the habitat

at the same time. The video was often unable to resolve species identity, particularly for small juveniles or detect several cryptic, but often abundant, species because many of these buried in the substrate. The beam trawl provided samples that allowed us to ground-truth the identification and provided size measurements as well as an independent, quantitative measure of abundance per unit area, as in other studies (Kuipers et al. 1992). The disadvantage of the trawl is that it homogenizes the importance of microhabitat by sampling over large spatial scales, even with short tow times, and often across habitat types based on our preliminary observations with a trawl mounted video camera.

Quantifying fish-habitat relationships will assist in determining what is termed essential fish habitat by the Magnuson-Stevens Fishery Conservation and Management Act that currently guides fishery management in the U.S. (Benaka 1999; Rosenberg et al. 2000). Essential fish habitat is broadly defined to include the water column and substrate necessary for spawning, breeding, feeding, or growth to maturity for fishes.

ACKNOWLEDGMENTS

We present part of a larger study funded by Minerals Management Service to evaluate existing living resources and the potential for impacts on those resources associated with mining of sand for beach nourishment from the shallow inner-continental shelf (Cutter and Diaz 2000). We would like to thank the crews of the M/V *Atlantic Surveyor* from Toms River, New Jersey (1998 cruise) and the University-National Oceanographic Laboratory System vessel R/V *Cape Henlopen* of the University of Delaware (1999 cruise). Stacy Hagan and Roger Hoden assisted with sampling at sea. This study was supported by the Department of the Interior, Minerals Management Service under the guidance of Barry Drucker (Contract No. 1435-01-97-CT-30853). New Jersey Sea Grant provided additional support for analysis of data. This paper is Virginia Institute of Marine Science contribution number 2513 and contribution number 2003-01 of the Rutgers University Institute of Marine and Coastal Sciences.

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SOURCE OF UNPUBLISHED MATERIALS

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Received for consideration, May 21, 2001

Revised, April 19, 2002

Accepted for publication, April 26, 2002