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[Article]

Assemblage Structure in Shoal and Flat-Bottom Habitats on the Inner Continental Shelf of the Middle Atlantic Bight, USA

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Abstract.—Sand shoals provide both a potentially unique habitat resource for marine organisms and a source of sand for the replenishment of eroded beaches. Sand removal may negatively influence marine communities, so understanding how marine fauna utilize habitats at and around shoals would provide much-needed guidance in selecting sites for sand harvest. A 2-year study was conducted on the inner continental shelf of the Middle Atlantic Bight, U.S.A., to compare finfish and invertebrate assemblages at sand shoal and nearby flat-bottom habitats. Multiple sampling modalities were used to sample organisms across a range of sizes, living habits, and life history stages. There was a trend toward greater abundance, species richness, and species diversity in flat-bottom habitats than in shoal habitats, and all of these community measures were generally lower during winter than in spring, summer, or fall. Moreover, species groups, including pelagic finfish, pelagic invertebrates, benthic finfish, and benthic invertebrates, were all more abundant in the flat-bottom habitats. Particular species characterized each type of habitat and these associations varied with season. Sampling with a large commercial trawl indicated that shoal finfish assemblages were characterized by striped bass *Morone saxatilis* and little skate *Leucoraja erinacea* in the fall, by scup *Stenostomus chrysops* in the spring, and by American sand lance *Ammodytes americanus*, scup, and clearnose skate *Raja eglanteria* in the summer. Experimental trawl sampling, which targeted primarily smaller organisms, found that communities on shoals were characterized by gastropods in the winter, squid (class Cephalopoda), and right-handed hermit crabs (family Paguridae) in the spring, and right-handed hermit crabs and scup in the summer. Winter was the period of lowest finfish and invertebrate use of shoal habitat and thus would be the best time of year for dredging sand to minimize acute impacts.

Complex habitat structures on the ocean bottom provide unique habitat for some species of fish and invertebrates in continental shelf ecosystems (Malatesta and Auster 1999). In particular, structures that provide macroscale (tens to hundreds of meters) vertical relief can offer both enhanced forage for predators and refuge for prey species (Kohn 1967; Gilinsky 1984; Diaz et al. 2003). Shoals (also known as sand ridges) are common geologic features on continental shelves. Often occurring as a network of multiple linear shoals (also known as a "ridge and swale" system), these submerged, ripple-like plateaus of sediment vary with regard to grade of relief, height, and horizontal expanse and are often the dominant relief-forming structures in an otherwise flat environment (Steimle and Zetlin 2000). Shoal habitats may provide unique habitat for benthic or bentho-pelagic fish and invertebrates on the continental shelf.

Fields of sand shoals are distributed globally, occurring in the coastal waters of such places as The Netherlands (Van de Meene 1994), Germany (Antia 1996), South America (Swift et al. 1978; Parker et al. 1982), Korea (Lee and Chun 1994), Canada (Michel 2004) and the United States (Vasslides and Able 2008). Despite the wide occurrence of shoal fields, little is known about how marine organisms use this habitat or the benefits it provides them (Diaz et al. 2003, 2004; Vasslides and Able 2008). The body of literature that describes fish assemblages in relation to habitat is growing; however, most of these studies either focus on communities of the deep continental shelf (Auster et al. 1995, 2001; Langton et al. 1996) or are directed toward improving understanding of life-stage-specific habitat utilization for individual species (Diaz et al.

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2003). Few studies have addressed the relevance of specific habitats in the Middle Atlantic Bight for whole communities within inner continental shelf systems, and little information exists concerning the use of offshore shoals by fish and mobile benthos.

In addition to providing unique habitat, shoals are valuable sources of harvestable sand that can be used to mitigate the effects of erosion along nearby coastlines. One common strategy used to counteract erosion is beach nourishment, in which sand is dredged from offshore deposits or "borrow" sites, pumped to a beach or transported directly using the dredge, and placed along the shoreline to widen the beach. Sand harvesting from shoals is expected to modify habitat features utilized by marine fauna. At both meso- and micro-scales, features such as biogenic structures, bedforms, sand waves, and proximity to the shoal are believed to influence the distribution of finfish and invertebrates at shoals (Diaz et al. 2003, 2004; Vasslides and Able 2008). Environmental factors such as depth, temperature, salinity, and bottom habitat probably also play key roles (Vasslides and Able 2008). For infauna, distributional patterns at shoals are strongly influenced by sediment grain size (Byrnes et al. 2004). Despite the advances in shoal biology that these studies have provided, none used a replicated sampling design for comparison of shoal assemblages with those in nearby habitats or used multiple gear types to encompass the wide range of species groups that may be associating with these habitats.

Here we present a 2-year, all-season study of the finfish and macroinvertebrate communities on a network of linear shoals along the Middle Atlantic Bight of the United States. This study employed a multiple-sampling-gear approach to characterize the broad spectrums of organism size, living habit, and life stage that occur in these communities. Specifically, the goals of this study were (1) to determine whether species abundance, species richness, species diversity, or species group abundance differ between shoal habitat and nearby flat-bottom habitats, (2) to compare the composition of assemblages between these two habitats, and (3) to identify which species, if any, characterize each habitat.

Study Area

The study was conducted on the inner continental shelf of the Middle Atlantic Bight region off the coasts of Maryland and Delaware, which is known as the Delmarva shelf. In this region, networks of linear shoals occur between 16 and 25 km from the coast and encompass approximately 800 km^2 of the inner shelf (Figure 1). Surface sediments off the Maryland and Delaware coasts within the study region are mostly terrigenous sand and silt with locally abundant clays. Four sand shoals within this region (B, D, Fenwick, and Weaver) were identified by the U.S. Minerals Management Service a priori for sand mining to aid beach nourishment projects (Figure 1). The maximum grade of relief of each site was used to compare the differences in vertical macrostructure among sites. These data are available through the Maryland Geological Survey, which interpolates depth data using triangular irregular network models in a geographical information system (GIS). The depth data originate from the National Geophysical Data Center (NGDC) coastal relief model (Divins and Metzger 2003), which provides depth data for the coast of the United States. Based on these data, we found that the maximum grade of relief for Fenwick Island Shoal and Weaver Shoal was twice as great as that for shoals B and D (Table 1; Conkwright and Williams 1996; Conkwright et al. 2000). Four flat-bottom sites were identified by reviewing several sets of bottom habitat information available from other surveys conducted in the study area. This information included underwater video and profile camera imagery (Cutter and Diaz 2000), fisheries data (Musick 2000; Olney and Bilkovic 2000), and NGDC bathymetry data (Divins and Metzger 2003). The four flat-bottom sites selected were in the same general location as the shoals to eliminate confounding factors such as proximity to shore or influence of different water masses. In the vicinity of the shoals, the only areas of uniform bathymetry (flat bottom) were located in deeper waters, away from the shoals; therefore, flat-bottom sites generally occurred at greater depths than shoals (Table 1). Sand shoals were composed primarily of sand, whereas benthic sediments at flat-bottom sites were mainly silty sands (Table 1). A video survey (Slacum et al. 2006) confirmed that the shoal sites and flat-bottom sites selected for the study lacked any anomalous structures that could affect comparisons.

Methods

Sampling Design for Fish and Invertebrate Surveys

Sampling stations were initially chosen within the four shoal sites and four flat-bottom sites using a GIS-based random sample coordinate selection program. Within a station, sampling was restricted to the tops of the shoals and to the center of the areas chosen as reference sites. Sampling was conducted at these locations on each sampling date of the study. Fish sampling began in the fall of 2002 and was conducted seasonally (fall, winter, spring, and summer) for two consecutive years. Sampling was conducted using multiple gear types (small experimental demersal trawl, large commercial demersal trawl, and experimental gill

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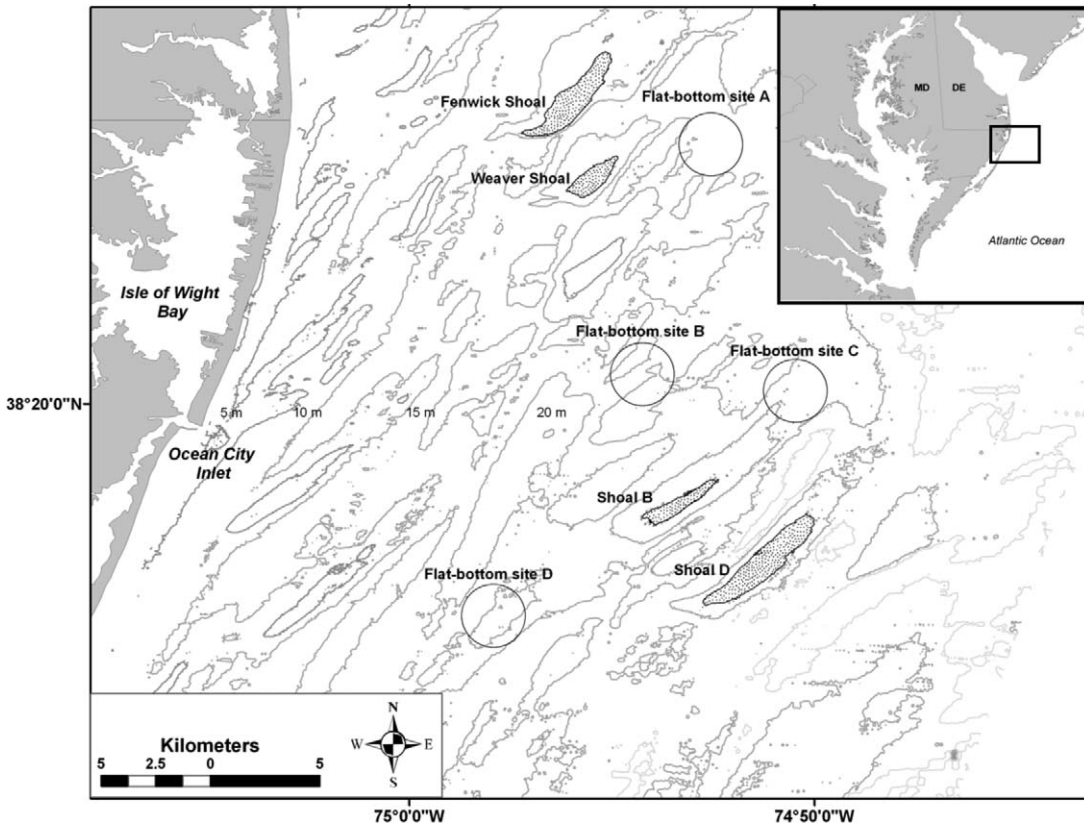


FIGURE 1.—Map of the four shoals and four flat-bottom sites sampled for marine biota off the coast of Maryland and Delaware using trawls and gill nets from November 2002 until September 2004.

nets) that are selective for different species and sizes to ensure that all finfish and mobile macrobenthic species could be sampled. Two replicate samples were collected at each of the eight sites during each season. This resulted in a total of 384 samples being collected during the course of the survey (i.e., 2 replicates per site × 8 sites × 8 seasons × 3 types of gear). The average catch of the two replicates was used to represent the catch at a given site. After sampling, all organisms were identified to the lowest practical taxon and counted, and 25 randomly selected specimens of each fish and crab species were measured to the nearest

TABLE 1.—Sampling depth, sediment grain size, and grade of relief for shoal and flat-bottom sampling sites off the coasts of Maryland and Delaware (see Figure 1).

Site	Depth (m)			Sediment grain size[a]	Grade of relief (%)
	Average	Minimum	Maximum		
Fenwick Shoal	7.0	5.2	9.1	Sand	>30
Weaver Shoal	8.6	7.3	10.4	Sand	>30
Shoal B	8.8	7.6	11.0	Sand	<15
Shoal D	13.0	10.4	16.2	Sand	<15
Flat-bottom					
A	16.6	14.3	19.2	Silty sand	0
B	17.0	12.8	22.3	Silty sand	0
C	17.0	12.2	21.9	Silty sand	0
D	15.2	12.5	18.3	Silty sand	0

[a] Shepard's class designations determined from grain size analysis of surface core samples collected from the top of the shoals and several samples from adjacent flat-bottom areas reported in Conkwright and Williams (1996) and Conkwright et al. (2000).

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millimeter standard length and carapace width, respectively. No other invertebrate species were measured.

Multiple gear types were used in order to sample species across spectrums of size, living habit, and life stage. Two trawl nets were used. A smaller 7.6-m, semiballoon, experimental otter trawl with a 4-cm stretch-mesh body fitted with a 3-mm stretch-mesh liner in the cod end was used to sample smaller benthic-oriented species and life stages. A larger 30.5-m "round net" commercial trawl with a 15-cm stretch-mesh body that tapered to a 5-cm stretch-mesh cod end was used to sample larger and more mobile epibenthic and pelagic individuals. The small trawl was towed at 1.5–2.0 knots from a 7.6-m research vessel, whereas the larger trawl was towed at 3.0–3.5 knots from a 16.5-m commercial trawling vessel. Both small and large trawls were towed for 10 min, resulting in an approximate tow length of 500 m by the small trawl and 1,000 m by the large trawl. Total distance trawled was calculated as the distance between the locations where the vessels reached trawling speed and those where they slowed for net retrieval. Geographic coordinates were recorded from shipboard differential Global Positioning Systems. Gill-net sampling was also conducted using a 182.9-m-long × 3-m-deep gill net. Each net consisted of two sets of equal-length panels that were randomly distributed throughout the net. Each set contained three panels of different mesh size: 7-, 9-, and 15-cm stretch mesh. The catch by each of the panels within a single set (three panels) was summed and then an average catch of the two sets was taken to represent the catch for a given site. Nets were deployed from a commercial fishing vessel and anchored on the bottom parallel to the current and fished for an average of 4 h.

Statistical Analysis

Univariate analysis of community measures.—The number of species collected in trawls was standardized to catch per unit effort (CPUE) for analysis. The area swept by the trawl was calculated by multiplying the towed distance by the trawl headrope size. For ease of comparison, catch for both trawl types is expressed as catch per 10,000 m^2, which is one-third the area of one large trawl tow (30,500 m^2) and 2.6 times the area of a single small trawl tow (3,800 m^2). Gill-net catch was standardized to catch per hour of soak time. Analysis of variance (ANOVA) was used to compare mean total species abundance (CPUE), mean total species richness, and mean total species diversity between shoals and flat-bottom sites. Species richness was the total number of species (average of two replicate tows) collected at a site, and diversity was calculated using the Shannon–Wiener index. Catch data were $\log_e(x + 1)$ transformed before analysis to meet the assumption of equal variance among treatments for ANOVA. In each ANOVA, log-transformed CPUE was the response variable; site and season were treated as blocks; and type of site (shoal or flat bottom) was the explanatory factor. One-way ANOVA was also used to examine differences in common species groups (benthic finfish, pelagic finfish, benthic invertebrates, and pelagic invertebrates) among habitats. Group assignments were based on habitat associations reported in the literature (Grosslein and Azarovitz 1982; Collette and Klein-MacPhee 2002). The pelagic invertebrate group was composed only of squid (class Cephalopoda) because no other pelagic invertebrates were collected. A one-way ANOVA was used to compare high- and low-relief shoals by pooling data across all sampling dates. Analyses were carried out for each kind of gear using the SAS GLM procedure (SAS 2004). Because of deployment problems with the small trawl during fall 2002, small-trawl data from this period were excluded from analyses.

Meta-analysis across gear types for species group associations.—Meta-analysis was used to determine whether there was an overall difference in species group abundance between habitat types with data pooled across both trawl gear types. Gear types were treated as separate "experiments" that were deployed to sample the same true differences in the abundances of fish and invertebrates. Using the method described by Hedges and Olkin (1985), the standardized mean differences in $\log_e(x + 1)$ transformed CPUE between shoals and flat-bottom sites for each species group was determined such that a negative standardized effect would indicate greater CPUE in flat-bottom habitats, a positive standardized effect would indicate greater CPUE in shoal habitats, and a standardized effect of zero would indicate no difference. A significant effect size is indicated by a standardized effect with upper and lower 95% confidence limits (the equivalent of ± 2 standard errors) that do not overlap with zero (Hedges and Olkin 1985). The gill-net survey offered little insight into differences in the use of benthic habitat because gill nets sample large, mobile fish that have weak affinities for benthic habitat; therefore, gill-net data were excluded from the meta-analysis.

Multivariate community analysis.—Multivariate analyses were used to identify seasonal differences in assemblage structure between shoal sites and flat-bottom sites using the routines in the PRIMER (Plymouth Routines in Multivariate Ecological Research) version 5 statistical package (Clarke and Gorley 2001). Species abundance data were log-transformed and subjected to group-average cluster analysis and nonmetric multidimensional scaling (MDS) ordination

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using a Bray–Curtis similarity matrix (Clarke and Warwick 2001). Species with strong school-forming tendencies have heterogeneous spatial distributions that obscure interpretation of multivariate analyses. Bay anchovy *Anchoa mitchilli* is such a species and therefore was excluded from analyses of small-trawl data.

Nonmetric MDS is an ordination technique that ranks samples according to their relative similarity. Nonmetric MDS is well suited for this type of community analysis because it lacks assumptions about species distributions and is able to represent complex relations among samples accurately. The stress reported with each nonmetric MDS ordination is a measure of how well the two-dimensional ordination depicts the relationships in the similarity matrix.

Two-way crossed analyses of similarity (ANOSIM) were used to test for differences in species composition between shoal and flat-bottom sites after blocking for the effects of season. Significant differences produced by the ANOSIM test are determined by the value of the *R*-statistic. The *R*-statistic reflects the observed differences between groups (in this case shoal sites versus flat-bottom sites) contrasted with differences among replicates within groups. For ANOSIM tests that were significant, the similarity percentages (SIMPER) procedure was used to identify which species were responsible for the separation of samples in the MDS ordination and thus to characterize the assemblages associated with shoal and flat-bottom sites, respectively. The analysis identifies which species contribute most to the average dissimilarity between habitats.

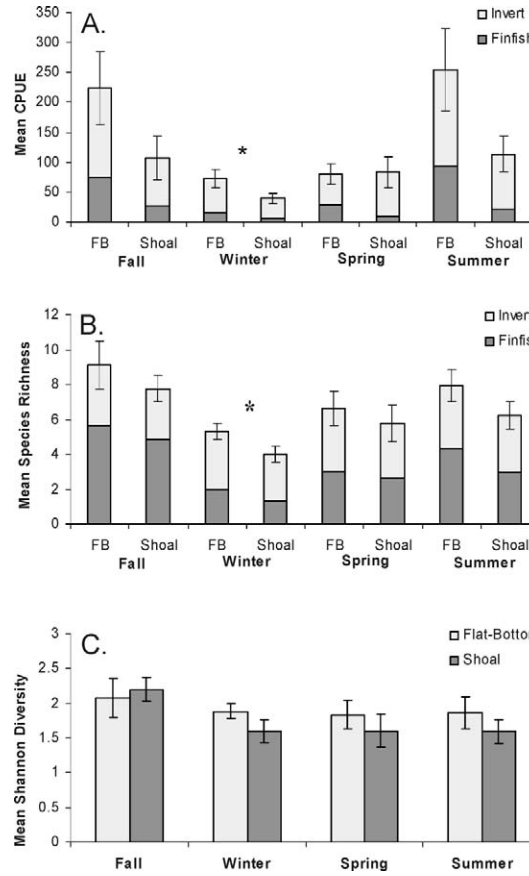


FIGURE 2.—Combined 2-year seasonal means and SEs of **(A)** CPUE (number/10,000 m^2), **(B)** species richness, and **(C)** species diversity (Shannon index) of fish and invertebrates collected in small trawls at four shoal sites and four flat-bottom sites (FBs) off the coast of Maryland and Delaware from November 2002 to September 2004. Untransformed means and SEs are shown; asterisks indicate significant ($P < 0.05$) differences between shoal and flat-bottom sites during particular seasons.

Results

Univariate ANOVAs for Community Measures

Small trawl.—During the fall, winter, and summer, mean total finfish and invertebrate CPUE and species richness were greater at flat-bottom sites than at shoal sites (Figure 2); however, this pattern was significant only during winter. During spring, both total CPUE and species richness were similar for both habitats. Total CPUE was greater during fall and summer regardless of habitat. Species diversity was similar between habitats in all seasons.

Small trawls collected a total of 41 different species of fish and invertebrates from shoal and flat-bottom sites during the course of the study (Table A.1 in the appendix). Twenty-four species of fish and 15 species of invertebrates were collected from flat-bottom sites, whereas 19 species of fish and 15 species of invertebrates were collected from the shoals. Among those species, 6 fish and 2 invertebrates collected from flat-bottom sites were never collected from shoal sites, and 2 species—blue crab and inshore lizardfish—were found only at the shoals. The CPUE for each species caught by each of the three gear types during each season is reported in Table A.1. The percentage contributions of the most abundant species during each season are reported in Table 2. Squids (23%) and right-handed hermit crabs (19%) represented the greatest proportion of the total catch across all sampling events. Right-handed hermit crabs were present at all stations during every season, and starfish were present at most stations during every season. The finfish species that made up the greatest proportion of the total catch over all seasons sampled was northern searobin (5%). More benthic finfish, pelagic finfish, and pelagic invertebrates (squid) were captured in the

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TABLE 2.—The five most abundant species (in terms of proportion of total CPUE) collected by each type of gear during each season.

	Small trawl		Large trawl		Gill net	
Season	Species	%	Species	%	Species	%
Fall	Starfishes	30	Spiny dogfish	30	Spiny dogfish	87
	Right-handed hermit crabs	19	Winter skate	22	Bluefish	5
	Squids	18	Striped bass	16	Starfishes	3
	Atlantic croaker	11	Windowpane	7	Striped bass	2
	Spotted hake	5	Starfishes	4	Winter skate	1
Winter	Sand shrimp	33	Winter skate	29	Spiny dogfish	75
	Moon snails	14	Windowpane	19	Smooth dogfish	7
	Right-handed hermit crabs	14	Little skate	17	Atlantic rock crab	6
	Spotted hake	11	Atlantic herring	10	Alewife	4
	Gastropods	10	Spiny dogfish	5	Northern pipefish	3
Spring	Squids	25	Scup	44	Smooth dogfish	56
	Right-handed hermit crabs	19	Butterfish	35	Atlantic menhaden	19
	Starfishes	14	Squids	9	Striped searobin	8
	Spotted hake	9	Winter skate	3	Winter skate	8
	Gastropods	9	Northern searobin	3	Portly spider crab	2
Summer	Squids	31	Scup	34	Atlantic menhaden	23
	Right-handed hermit crabs	21	Northern searobin	21	Atlantic croaker	18
	Bay anchovy	11	Atlantic croaker	14	Smooth dogfish	16
	Starfishes	10	American sand lance	8	Bluefish	13
	Northern searobin	9	Lady crab	7	Atlantic sharpnose shark	7
All seasons	Squids	23	Scup	32	Spiny dogfish	53
	Right-handed hermit crabs	19	Butterfish	20	Smooth dogfish	13
	Starfishes	15	Squids	7	Atlantic menhaden	8
	Sand shrimp	6	Winter skate	7	Bluefish	6
	Northern searobin	5	Northern searobin	6	Atlantic croaker	4

small trawl at flat-bottom sites than at shoal sites (Tables 3, 4). Small trawls caught benthic invertebrates in nearly equal numbers from shoal sites and flat-bottom sites.

Large trawl.—Mean total finfish and invertebrate CPUE was significantly greater at flat-bottom sites than at shoal sites during winter but was similar among habitats during fall, spring, and summer. It was greatest during spring and least during winter regardless of habitat. Mean total species richness was greater at flat-bottom sites than at shoal sites during fall, winter, and summer; there was no difference during spring (Figure 3). Species diversity was significantly greater at flat-bottom sites during fall and summer, and the trend was similar but not significant during winter. No difference was observed during spring.

Large trawls collected a total of 56 different species of fish and invertebrates from shoal and flat-bottom sites (Table A.1). Forty-one fish and 12 invertebrates were collected from flat-bottom sites, and 31 fish and 11 invertebrates were collected from shoal sites. Twelve fish and 1 invertebrate collected from flat-bottom sites were not collected from shoal sites, and three species—the blue crab, harvestfish, and Spanish mackerel—were found only at the shoals. The most abundant species for each season are shown in Tables 2 and A.1. Scup (32%) and butterfish (20%) represented the greatest percentage of the total catch over the 2-year study. Windowpane and winter skate were collected during every season from nearly every site. Squid was the most commonly collected and most abundant invertebrate over all the sites during the 2-year study. The CPUE of pelagic finfish and invertebrates (squid) captured in large trawls was significantly greater at flat-bottom sites than at shoal

TABLE 3.—Catch per unit effort (mean ± SE) for species groups caught by each gear type. Bold italics indicate significant ($P < 0.05$) differences between shoal and flat-bottom (FB) habitats.

Gear	Habitat	Benthic invertebrates	Benthic finfish	Pelagic finfish	Pelagic invertebrates
Small trawl	FB	55.47 ± 8.88	***34.46 ± 6.88***	***15.72 ± 8.26***	***42.00 ± 17.59***
	Shoal	57.95 ± 10.43	***12.59 ± 1.75***	***1.54 ± 0.62***	***10.62 ± 4.06***
Large trawl	FB	3.52 ± 0.56	50.06 ± 7.29	***32.85 ± 17.92***	***7.22 ± 1.56***
	Shoal	5.87 ± 1.67	80.25 ± 29.57	***8.74 ± 7.14***	***6.71 ± 2.63***
Gill net	FB	0.14 ± 0.05	5.10 ± 1.37	1.41 ± 0.59	0 ± 0
	Shoal	0.33 ± 0.17	4.19 ± 1.04	0.68 ± 0.17	0 ± 0

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TABLE 4.—Standardized mean differences in $\log_e$ (CPUE + 1) at shoal sites versus flat-bottom sites from a meta-analysis of large and small trawl surveys for each species group. Negative numbers indicate that more animals were captured at flat-bottom sites.

Species group	Standardized effect	95% confidence limits	
		Lower	Upper
Benthic finfish	−0.47	−0.73	−0.22
Benthic invertebrates	0.01	−0.24	0.27
Pelagic finfish	−0.58	−0.84	−0.32
Pelagic invertebrates	−0.44	−0.7	−0.18

sites (Tables 3, 4). More benthic finfish were captured at shoal sites than at flat-bottom sites.

Gill nets.—Overall, mean total CPUE, total species richness, and species diversity did not differ greatly between flat-bottom sites and shoal sites (Figure 4).

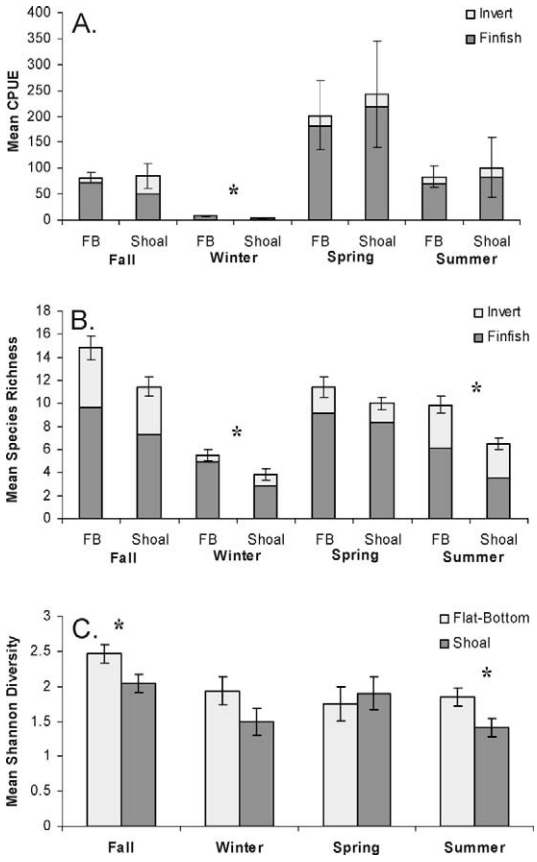


FIGURE 3.—Combined 2-year seasonal means and SEs of **(A)** CPUE (number/10,000 m^2), **(B)** species richness, and **(C)** species diversity (Shannon index) of fish and invertebrates collected in large trawls at four shoal sites and four flat-bottom sites off the coast of Maryland and Delaware from November 2002 to September 2004. See Figure 2 for additional details.

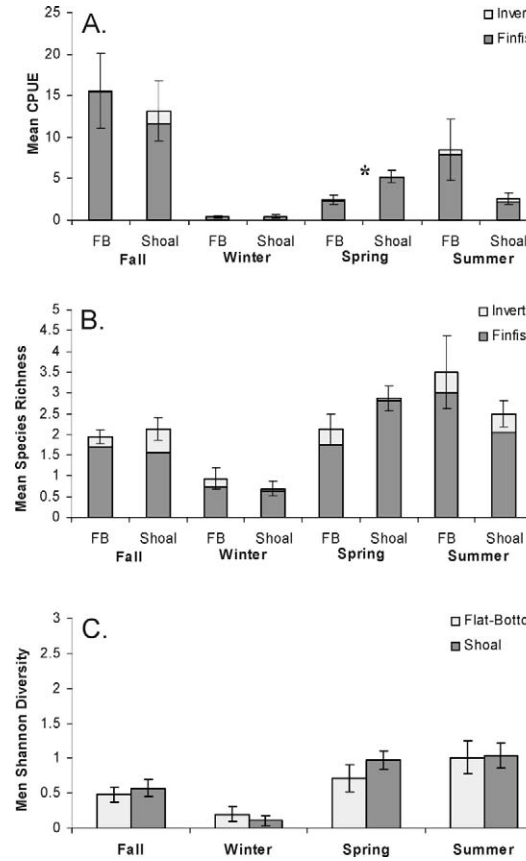


FIGURE 4.—Combined 2-year seasonal means and SEs of **(A)** CPUE (number/h), **(B)** species richness, and **(C)** species diversity (Shannon index) of fish and invertebrates collected in gill nets at four shoal sites and four flat-bottom sites off the coast of Maryland and Delaware from November 2002 to September 2004. See Figure 2 for additional details.

The only significant difference was during spring, when mean abundance was greater at shoal sites than at flat-bottom sites.

Gill nets collected a total of 36 different species of fish and invertebrates from shoal and flat-bottom sites (Table A.1). A total of 22 fish and 5 invertebrates were collected from flat-bottom sites, compared with 21 fish and 5 invertebrates from shoal sites. Nine fish and one invertebrate collected from flat-bottom sites were not collected from shoal sites, and eight fish and one invertebrate were found only at the shoals. The most abundant species for each season are shown in Tables 2 and A.1. Spiny dogfish (53%) and smooth dogfish (13%) made up the greatest proportion of the total catch over the 2-year study. These two species exhibited a seasonal transition in which spiny dogfish dominated the catch during fall and winter collections

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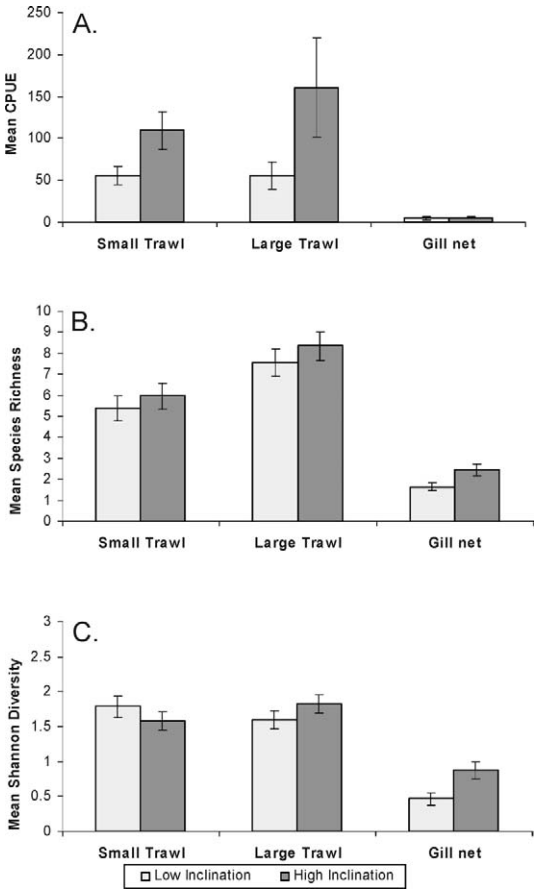


FIGURE 5.—Combined sampling means and SEs of **(A)** CPUE, **(B)** species richness, and **(C)** Shannon's index of diversity for shoals with a high grade of relief (Fenwick and Weaver) versus those with a low grade of relief (B and D).

and smooth dogfish dominated the catch during the spring and summer collections. Gill nets collected small numbers of invertebrate species throughout the survey (mostly tangled in the nets or attracted by fish caught in the nets). Among the invertebrate species collected, starfish and portly spider crab were caught most frequently and were the most abundant.

Comparisons among Shoals

When averaged across seasons and years, shoals with a greater vertical grade generally had greater mean total CPUE than shoals with a lesser grade, but this pattern was not statistically significant (Figure 5). This general pattern was evident for both small and large trawls, but not for gill nets. Species richness and species diversity were similar among all four shoals for all sampling gears.

Meta-analysis for Species Group Associations

Meta-analysis summarizing effects across both trawl types confirmed that for benthic finfish, pelagic finfish, and pelagic invertebrates greater CPUE occurred at flat-bottom sites than at shoal sites (Tables 3, 4). For benthic finfish, pelagic finfish and pelagic invertebrates, the standardized effect size was negative and the upper and lower 95% confidence limits did not overlap with zero. This indicates that CPUE was significantly greater in the flat-bottom habitats than in the shoal habitats (Hedges and Olkin 1985). Benthic invertebrate CPUE did not differ between shoal and flat-bottom sites, as indicated by the small standardized effect (0.01) with upper and lower 95% confidence limits that overlapped with zero.

Multivariate Analyses

The cluster analysis and MDS ordination showed a strong separation of sites that varied with season for both small and large trawls. Given the strong effect of seasonality, the data were examined within each season and ordination plots were constructed to determine whether sites tended to form groups according to type of habitat (shoal versus flat bottom). Assemblages at shoal and flat-bottom sites derived from the small-trawl data showed a tendency to form groups during spring and summer but not during fall or winter (Figure 6). Assemblages at shoal and flat-bottom sites derived from the large-trawl data separated clearly on the ordination during summer, fall, and winter but not during spring (Figure 7).

Two-way crossed ANOSIM tests using type of habitat as the main factor and seasons as blocks detected a significant difference in the R-statistic between sites for the large-trawl data and a narrowly significant difference (at the 10.9% level) for the small-trawl data. The results of the two-way crossed ANOSIM tests indicated that, despite the strong effect of seasons, differences in species composition between the shoal and the flat-bottom sites could be detected for the small and large trawls. SIMPER was then used for these two gears to determine which species typified the shoals and the flat-bottom sites.

Individual species that characterized either the shoal or flat-bottom habitat were evident in the SIMPER analysis, and these patterns varied with season and gear (Tables 5, 6). Four to seven species were responsible for about 50% of the dissimilarity between assemblages that associated with shoal and flat-bottom habitats. Among the species that distinguished assemblages during the fall, Atlantic croaker, windowpane, scup, squids, and right-handed hermit crabs were more abundant at flat-bottom sites than at shoal sites (Tables

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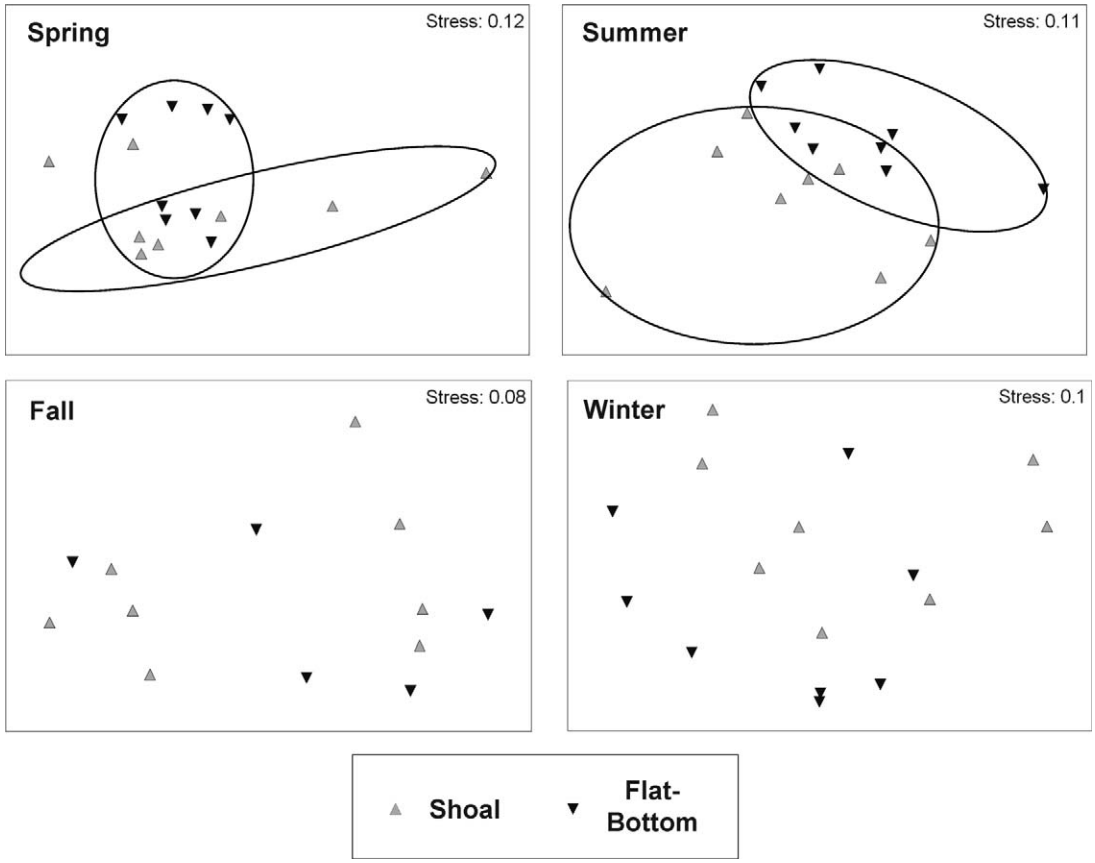


FIGURE 6.—Multidimensional scaling ordinations of data from shoal and flat-bottom sites collected by the small trawl in each of four seasons.

5, 6). Striped bass were more abundant at shoal sites than at flat-bottom sites during the fall. However, this pattern was strongly influenced by particularly large catches of striped bass from one sampling event at Fenwick Shoal. During the winter, sand shrimp, spotted hake, winter skate, and windowpane were among the species that distinguished assemblages between kinds of habitat and were more abundant at flat-bottom sites than at shoal sites. Gastropods were the only distinguishing organisms that were more abundant at shoal sites during winter. Scup and gastropods were more abundant at shoal sites than at flat-bottom sites during the spring. Spotted hake, butterfish, and northern searobin were more abundant at flat-bottom sites during the spring. During the summer, scup, right-handed hermit crabs, American sand lance, and clearnose skate were among the distinguishing species, and these were more abundant at shoal sites than at flat-bottom sites. Flat-bottom habitats were characterized by squid, northern searobin, and Atlantic croaker during the summer, when they were more abundant there than at the shoals.

Discussion

Shoals and deep, flat-bottom areas are macroscale habitats for finfish and macroinvertebrates on the inner continental shelf of the U.S. mid-Atlantic region. Unique faunal assemblages were associated with both habitats. Flat-bottom habitats generally had greater abundance, species richness, and species diversity than shoal habitats. Among shoals, a trend toward greater abundance at shoals with a steeper grade was evident. Three of the four species groups examined (benthic finfish, pelagic finfish, and pelagic invertebrates) were significantly more abundant at flat-bottom habitats than at shoals. At the individual species level, however, several macroinvertebrate and finfish species were responsible for most of the seasonal variability in assemblage structure in each of the habitats.

Greater availability of benthic forage at flat-bottom

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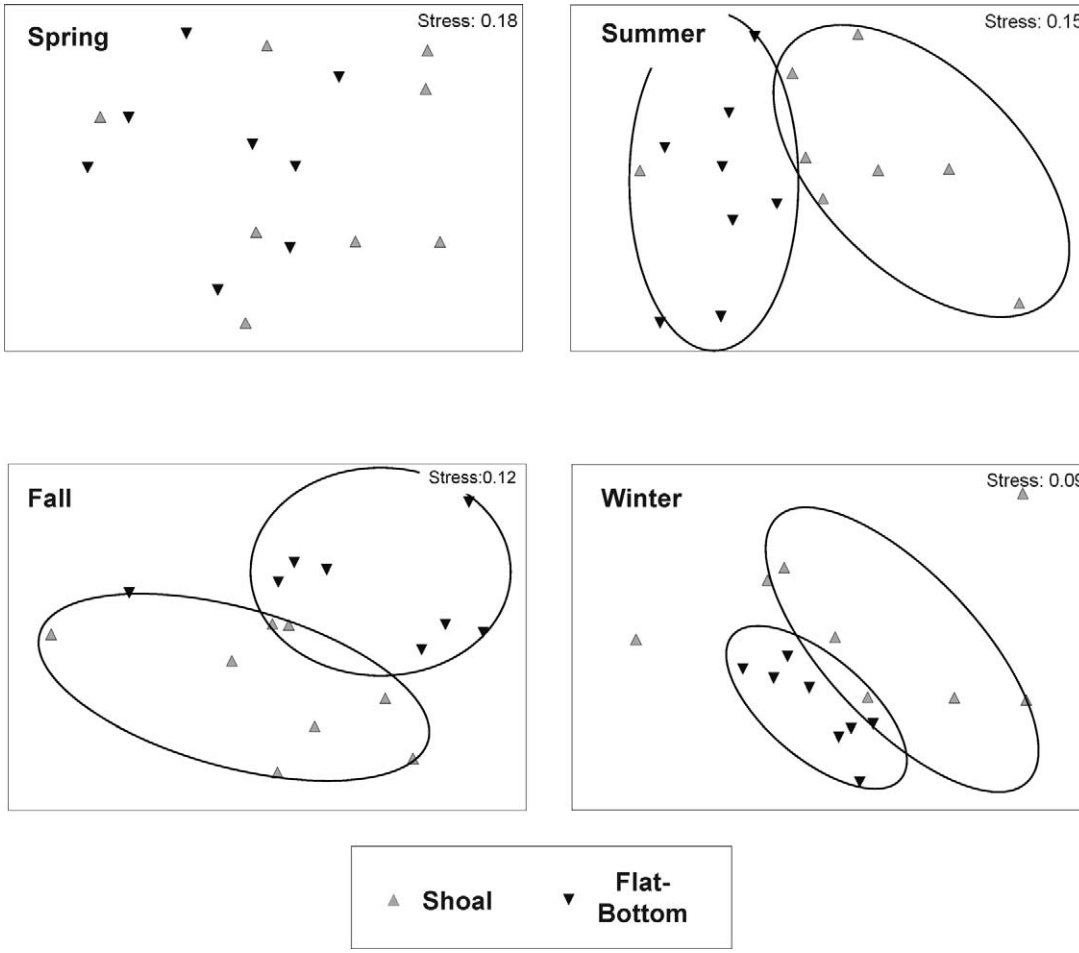


FIGURE 7.—Multidimensional scaling ordinations of data from shoal and flat-bottom sites collected by the large trawl in each of four seasons.

habitats may explain the greater abundance of fish in those areas. Previous work in the vicinity of two of the shoals studied here (Fenwick and Weaver) showed that the troughs adjacent to these shoals were more biologically productive (i.e., contained more benthic invertebrates) than the shoals themselves (Cutter and Diaz 2000). Similarly, a long-term, 23-km transect study of small fish off the coast of New Jersey found depauperate levels of abundance and species richness at the tops of shoals (8-m maximum vertical relief) but peak levels of these measures in the troughs located within 500–1,400 horizontal meters of the peak of the shoals (Vasslides and Able 2008). These areas of elevated productivity might represent an underwater ecotone (i.e., a zone of transition between major ecological features), but the mechanisms that form and maintain these biological patterns are unknown. The flat-bottom sites studied here could have overlapped with or could share some biological similarities with the transition areas around shoals.

Microhabitat features are known to influence local distributions of species (Lough et al. 1989; Auster et al. 1991, 1997) and may have contributed to the differences in assemblage structure that we observed between shoals and flat-bottom areas. Diaz et al. (2003) used a video sled to evaluate microhabitat such as bedforms (i.e., sand waves) and biogenic structures (e.g., tubes, shell beds, and pits) on two of the same shoals we studied (Fenwick and Weaver). They found four times as many juvenile fish in areas with larger bedforms (10-cm crest height) than in areas with smaller bedforms (5-cm crest height) and that habitat complexity (measured as biogenic tube densities) was associated with greater abundance of juvenile fish.

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TABLE 5.—SIMPER results for the small trawl showing the species that explained 50% of the dissimilarity between shoal and flat-bottom habitats. Average abundance (measured as CPUE) is given for each species for each kind of habitat. Average dissimilarity appears in parentheses for each season.

Species	Contribution to dissimilarity (%)	CPUE		Habitat of greater abundance
		Shoal	Flat bottom	
Fall (61.10)				
Squid	15.12	1.1063	56.844	Flat bottom
Starfishes	12.29	56.022	42.139	Shoal
Right-handed hermit crabs	11.09	20.668	43.157	Flat bottom
Atlantic croaker	10.96	2.4308	32.377	Flat bottom
Winter (48.54)				
Sand shrimp	14.14	11.033	25.738	Flat bottom
Spotted hake	13.91	2.2866	9.6859	Flat bottom
Moon snails	13.56	6.038	9.6603	Flat bottom
Gastropods	11.27	7.0792	3.8578	Shoal
Spring (65.48)				
Spotted hake	15.44	1.0105	13.75	Flat bottom
Squids	12.66	25.821	14.227	Shoal
Right-handed hermit crabs	10.59	19.077	11.901	Shoal
Starfishes	9.14	9.8147	12.828	Flat bottom
Gastropods	7.45	9.405	4.731	Shoal
Summer (64.08)				
Squids	14.39	10.79	104.2	Flat bottom
Right-handed hermit crabs	11.85	58.44	19.86	Shoal
Starfishes	10.88	8.686	27.16	Flat bottom
Northern searobin	9.18	2.579	31.47	Flat bottom
Scup	7.90	9.131	4.779	Shoal

TABLE 6.—SIMPER results for the large trawl showing the species that explained 50% of the dissimilarity between shoal and flat-bottom habitats. See Table 5 for additional details.

Species	Contribution to dissimilarity (%)	CPUE		Habitat of greater abundance
		Shoal	Flat bottom	
Fall (42.05)				
Striped bass	7.67	26.5919	0.19769	Shoal
Windowpane	7.64	1.32865	10.3903	Flat bottom
Scup	7.38	0.08619	1.71523	Flat bottom
Starfishes	6.94	4.80582	2.53113	Shoal
Little skate	6.72	3.76622	2.53948	Shoal
Spiny dogfish	6.15	18.3139	31.1487	Flat bottom
Squids	5.04	0.75403	2.35553	Flat bottom
Striped searobin	4.32	0.21406	1.81129	Flat bottom
Winter (58.78)				
Winter skate	20.1	0.50753	3.1302	Flat bottom
Windowpane	12.58	0.61537	1.73535	Flat bottom
Little skate	11.32	0.7482	1.32828	Flat bottom
Atlantic herring	7.85	0.50552	0.71458	Flat bottom
Spring (41.23)				
Scup	13.46	159.607	34.1772	Shoal
Butterfish	13.15	33.5495	123.138	Flat bottom
Squids	10.97	21.8023	18.4566	Shoal
Northern searobin	7.92	3.61385	8.89072	Flat bottom
Starfishes	5.71	1.5346	0.85051	Shoal
Summer (53.20)				
Northern searobin	10.13	8.56392	30.0131	Flat bottom
Scup	8.49	56.5869	6.24876	Shoal
Squids	8.37	4.26828	8.06429	Flat bottom
American sand lance	7.18	14.0127	0.2922	Shoal
Butterfish	6.63	0.13339	1.79157	Flat bottom
Atlantic croaker	6.47	0	26.2772	Flat bottom
Clearnose skate	6.24	3.68401	1.72599	Shoal

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Diaz et al. (2003), however, targeted small juvenile fish using different sampling gear than that used here: a much smaller trawl (2 m wide, 3-mm mesh) and a video sled. The presence of spatially varying benthic microhabitat features may have attracted macroinvertebrates and small juvenile finfish which, in turn, could have provided habitat and forage for the larger species collected in our study.

Differences in bottom depth may provide an alternative or additional explanation for the differences in habitat associations observed during our study. Many studies have shown that depth delineates the distributions of demersal fish along the northeastern U.S. continental shelf (Overholtz and Tyler 1985; Murawski and Finn 1988; Gabriel 1992; Perry and Smith 1994; Methratta and Link 2006). Depth is associated with temperature variations, migratory patterns, and prey distributions (Able and Fahay 1998; Grosslein and Azarovitz 1982). Depth was inextricably linked with the kinds of habitat considered in this study (i.e., all of the flat-bottom sites occurred at deeper bottom depths than the shoal sites); consequently, we could not separate the effect of depth from those of other factors. Rather, we considered depth to be an inherent characteristic of these habitats. The difference between the minimum depth of a shoal (5.2 m) and the maximum depth of a flat-bottom area (22.3 m) was 17.1 m in our study.

Seasonal migrations across a depth gradient probably played a strong role in the seasonal patterns we observed in the assemblage. The species collected from both habitats were comparable to those reported in other studies within the Middle Atlantic Bight region (Musick et al. 1986; Diaz et al. 2003; Slacum et al. 2008), where demersal fish use the shallow continental shelf seasonally as a nursery ground. This study area has one of the most extreme seasonal temperature ranges in the world, and most of the species collected in this study are highly migratory, boreal, or warm–temperate/subtropical species (Musick et al. 1986). The extreme seasonal fluctuations in distribution and abundance that we observed are consistent with previous work showing the greatest diversity during the late summer and fall and the least during the winter (Colvocoresses and Musick 1984). Our finding that only a small percentage of the species encountered (5 of 57 fish and 2 of 17 invertebrates) were present throughout all the seasonal surveys is suggestive of seasonal migrations into and out of the study area.

Many fish species move vertically through the water column on a diurnal basis (Neilson and Perry 1990). These species migrate upward at night under the cloak of darkness to avoid predators that rely on vision to detect prey. During the day, these species migrate downward and take refuge among complex microhabitat features on the bottom. All sampling for our study was conducted during the daytime; consequently, we could not discern diurnal patterns. Nighttime sampling using the same kinds of gear probably would show very different patterns. Diurnal migrations are ubiquitous across marine systems, including at subtropical sea mounts in the Atlantic Ocean (Fock et al. 2002), the open waters of the North Pacific (Ishida et al. 2002), and the shelves of Norway (Albert and Bergstad 2005) and Australia (Blaber et al. 1990). Diel differences also have been observed among benthic habitats of varying complexity. A study on Fenwick and Weaver shoals found that fish were more abundant on bare, sandy habitats at night than during the day, when abundance was greater in more complex habitats that presumably provided greater refuge from predation (Diaz et al. 2003).

Directed studies of the biology of shoals or sand ridges are rare in the published literature. Most, including this study, are compelled by federal agencies that are interested in mining sand from these macroscale seascape features for replenishing beaches (Diaz et al. 2004; Drucker et al. 2004; Byrnes et al. 2004). Other studies are likely to be found among the gray literature, which is more difficult to obtain (e.g., Cutter and Diaz 2000). Diaz et al. (2004) used a combination of grab sampling, sediment profile cameras, a video sled, and trawls to evaluate the communities of benthos, fish, and invertebrates associated with mid-Atlantic shoals. Although more limited in spatial (5 sites) and temporal (late spring and summer only) extent than our study, this study complements ours by providing information about habitat features on a finer scale, such as biogenic tube mats and small benthic invertebrates (e.g., annelids and amphipods). Furthermore, we found the two most dominant species in Diaz et al.'s (2004) study, spotted hake and smallmouth flounder, to be common at both shoal and flat-bottom sites. Similar methods have been used to study shoal habitats off the coast of Alabama in the Gulf of Mexico (Byrnes et al. 2004). Using grab samplers to study infaunal communities associated with five sand resource areas, Byrnes et al. (2004) found spatial and seasonal variation in assemblage structure both within and between potential borrow sites. Broad-scale zonation patterns were attributed to discharges from Mobile Bay and their effect on the chemistry of the water column and hydrographic structure, whereas finer-scale variation was attributed to sediment grain size and its direct effect on the infaunal community.

Another approach to assessing the role of sand ridges has been to mine sets of long-term monitoring

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data. Vasslides and Able (2008) analyzed data from two independent sampling surveys, one that used a 2-m beam trawl from 1991 through 1995 and another that used a 4.9-m otter trawl from 1997 through 2006. Data collected during this 16-year period from stations along a linear, 23-km transect (maximum depth, 24 m) were analyzed to evaluate how assemblages of finfish on the inner continental shelf associated with sand ridges on the face of the shore. The transect, which originated in shallow, inshore waters and extended into deeper waters, included one station on a single sand ridge and adjacent stations on either side of the ridge. Vasslides and Able (2008) found that both the abundance and species richness of finfish were lowest at sites near the shore and at a single site on the top of the sand ridge; the greatest levels of these measures were observed offshore and at areas just adjacent to the ridge (within 500–1,400 m). This pattern for an individual shoal is consistent with the results of our study, which involved sampling on multiple shoals (i.e., community measures are smaller at shoals). The changes in the structure of the assemblage throughout the summer and the underlying environmental drivers that Vasslides and Able (2008) observed also complement our study, which identified characteristic species for both shoals and adjacent habitats across all four seasons. Although Vasslides and Able (2008) did not report patterns for macroinvertebrates, many of the finfish species they sampled, including the species that were most abundant in their collections (i.e., smallmouth flounder and butterfish), were also common at our study sites. Also similar to the current study, they reported that environmental factors (depth, temperature, salinity, and habitat) are important for delineating the patterns we observed. Taken together, the results of both studies suggest a need for targeted studies at small spatial scales in the areas adjacent to shoals to identify local factors that might be contributing to the elevated levels of production observed in such areas.

The methodology employed here provided the opportunity to gain a holistic understanding of assemblages at shoals and flat-bottom areas and suggests a useful model for future studies of the ecology of subtidal habitats. A replicated experimental design at the level of habitat (four shoals and four flat-bottom habitats) allowed statistical analysis with sufficient degrees of freedom to discern significant differences. Sampling during each of the four seasons over 2 years allowed us to make seasonal comparisons, and using multiple types of gear allowed us to study organisms representing a spectrum of size, living habit, and life history patterns. Further refinements of such studies could include more detailed evaluations of microhabitat features, collection of continuous environmental data (e.g., temperature and salinity), sampling at night, and inclusion of a concurrent tagging study to determine the time spent and behavioral patterns exhibited within and among habitats. Such studies will become increasingly necessary as we continue to move toward spatial approaches for managing marine ecosystems.

Although we found several species to be more abundant either at shoal sites or at flat-bottom sites, asserting that these habitats are essential ("necessary to fish for spawning, breeding, feeding and growth to maturity"; NOAA 1996) for these species requires a greater mechanistic understanding of how and why fish are associating with particular habitats than we now have. Simply identifying that a species is abundant in a particular location does not necessarily indicate that the location affords the species an advantage in recruitment, growth, or survival. Incorporating essential fish habitat (EFH) approaches into fisheries management is fraught with challenges (Benaka 1999; Rosenberg et al. 2000). Chief among these is the fact that evaluating vital rates and production while linking those population-level properties to habitat characteristics is particularly difficult in a marine environment over the broad spatial scales at which species are managed. Nevertheless, such efforts are necessary if EFH designations are to become a truly useful tool for fisheries managers.

Changes in geophysical conditions caused by harvesting sand to replenish beaches are likely to affect the living marine resources that inhabit these areas. Mining can modify the texture of the sediment or cause the site to become a reservoir of fine sediments and organic material (NRC 1995) while increasing the bottom depth of borrow sites. Mining also reduces habitat complexity by removing microscale biogenic structures that can provide both refuge and forage (Diaz et al. 2004). Benthic invertebrates and finfish that associate with shoals probably are drawn to some aspect of the habitat, food resource, or thermal or bathymetric conditions provided by the shoal. Removing the shoal would eliminate those benefits. The magnitude of such effects is expected to be correlated with the duration and scale of sand mining activities (Pickett and White 1985). Recovery of the benthic resources and the organisms that rely on them after mining activity could take a few to many years, depending on the magnitude and duration of the perturbation and local rates of recruitment (Van Dolah et al. 1984; Newell et al. 1998). Although macroinvertebrates are expected to recruit rapidly into disturbed sediments in coastal systems (Simon and Dauer 1977), the original species composition is expected to take much longer to become reestablished and might never occur if the disturbance is severe.

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Opportunistic species are expected to colonize newly disturbed areas, followed by later successional species that have superior competitive abilities (Connell and Slatyer 1977). Similar patterns are expected for infauna. The recovery of infaunal abundance and diversity after sand mining can take between 1 and 3 years, and the recovery of species composition can take much longer (Byrnes et al. 2004).

Management Recommendations

Sand mining destroys benthic habitats and disrupts the local communities of benthos and finfish. Diaz et al. (2004) estimated that removing the top meter of sand from Fenwick Shoal could result in the loss of 150 million individuals or 300 kg (wet-weight) of biomass from the system. Assuming that sand mining will continue to be used for the replenishment of eroded beaches, the following recommendations could help to minimize the disturbance of natural assemblages. First, several individual species appear to be concentrated at shoals during spring, summer, and fall and the values of community measures (i.e., total species CPUE, species richness, and species diversity) are generally smallest during winter; therefore, harvesting sand during winter could minimize adverse ecological effects. Second, shoals should be mined only partially, such that some portion of the targeted shoal remains as a patch of habitat. For example, the depth of the mining cut could be limited or the crests of shoals where species diversity appears to be relatively low could be targeted for mining. Limiting the distance between the remaining patches of shoal habitat would reduce the distance and time a shoal-associating species would have to travel between patches (Söndgerath and Schröder 2002; Cowen et al. 2006). Further research would be required to identify the optimal geometric structure and design of shoal habitat patch networks for those species expected to be most affected by mining operations. Third, we found weak evidence that fewer fish are associated with shoals that have a shallower relief, suggesting that those shoals should be targeted for mining instead of steeper shoals when the option is available. Fourth, sand mining should be avoided during periods of peak recruitment (spring and summer) for species of benthic invertebrates that associate with shoals (Diaz et al. 2004). Fifth, mining should be avoided when demersal finfish are using the inner continental shelf as a nursery ground (Able and Fahay 1998; Manderson et al. 2003). Sixth, sand could be mined at night, when some species migrate vertically into the water column (Neilson and Perry 1990) to reduce the direct injury to fish that can result from mining activities. Seventh, shoals should be mined in rotation to allow shoal-associated assemblages to recover between mining events; this should be done in consideration of the rate at which sand accumulates at the particular shoal where sand is being harvested. Using one or a combination of these approaches could mitigate the effects of sand mining while allowing federal agencies to accomplish their management goals.

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References

Able, K. W., and M. P. Fahay. 1998. The first year in the life of estuarine fishes in the Middle Atlantic Bight. Rutgers University Press, New Brunswick, New Jersey.

Albert, O. T., and O. A. Bergstad. 2005. Temporal and spatial variation in the species composition of trawl samples from a demersal fish community. Journal of Fish Biology 43:209–222.

Antia, E. E. 1996. Shoreface-connected ridges in German and U.S. Mid-Atlantic bights: similarities and contrasts. Journal of Coastal Research 12:141–146.

Auster, P. J., K. Joy, and P. C. Valentine. 2001. Fish species and community distributions as proxies for seafloor habitat distributions: the Stellwagen Bank National Marine Sanctuary example (northwest Atlantic, Gulf of Maine). Environmental Biology of Fishes 60:331–346.

Auster, P. J., R. J. Malatesta, and C. L. S. Donaldson. 1997. Distributional responses to small-scale habitat variability by early juvenile silver hake, *Merluccius bilinearis*. Environmental Biology of Fishes 50:195–200.

Auster, P. J., R. J. Malatesta, and S. C. LaRosa. 1995. Patterns of microhabitat utilization by mobile megafauna on the southern New England (USA) continental shelf and slope. Marine Ecology Progress Series 127:77–85.

Auster, P. J., R. J. Malatesta, S. C. LaRosa, R. A. Cooper, and L. L. Stewart. 1991. Microhabitat utilization by the megafaunal assemblage at a low relief outer continental shelf site: Middle Atlantic Bight, USA. Journal of Northwest Atlantic Fisheries Science 11:59–69.

Benaka, L., editor. 1999. Fish habitat: essential fish habitat and rehabilitation. American Fisheries Society, Symposium 22, Bethesda, Maryland.

Blaber, S. J. M., D. T. Brewer, J. P. Salini, and J. Kerr. 1990. Biomasses, catch rates, and abundances of demersal fishes, particularly predators of prawns, in a tropical bay

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in the Gulf of Carpentaria, Australia. Marine Biology 107:397–408.

Byrnes, M. R., R. M. Hammer, T. D. Thibaut, and J. D. Snyder. 2004. Potential physical and biological effects of sand mining offshore Alabama, U.S.A. Journal of Coastal Research 20:6–24.

Clarke, K. R., and R. N. Gorley. 2001. PRIMER version 5: user manual/tutorial. PRIMER-E, Plymouth Marine Laboratory, Plymouth, UK.

Clarke, K. R., and R. M. Warwick. 2001. Change in marine communities: an approach to statistical analysis and interpretation, 2nd edition. PRIMER-E, Plymouth Marine Laboratory, Plymouth, UK.

Collette, B., and G. Klein-MacPhee, editors. 2002. Bigelow and Schroeder's fishes of the Gulf of Maine, 3rd edition. Smithsonian University Press, Washington, D.C.

Colvocoresses, J. A., and J. A. Musick. 1984. Species associations and community composition of Middle Atlantic Bight Continental Shelf demersal fishes. U.S. National Marine Fisheries Service Fishery Bulletin 82:295–313.

Conkwright, R. D., and C. P. Williams. 1996. Offshore sand resources in central Maryland shoal fields. Maryland Geological Survey, File Report 96-3, Baltimore. Available: mms.gov/SandAndGravel/MarineMineralResourceEvaluation.htm#Maryland. (April 2009).

Conkwright, R. D., C. P. Williams, and L. B. Christiansen. 2000. Offshore sand resources in northern Maryland shoal fields. Maryland Geological Survey, File Report 00-02, Baltimore. Available: mms.gov/SandAndGravel/MarineMineralResourceEvaluation.htm#Maryland. (April 2009).

Connell, J. H., and R. O. Slatyer. 1977. Mechanisms of succession in natural communities and their roles in stabilization and organization. American Naturalist 111:1119–1144.

Cowen, R. K., C. B. Paris, and A. Srinivasan. 2006. Scaling of connectivity in marine populations. Science 27:522–527.

Cutter, G. R., Jr., and R. J. Diaz. 2000. Benthic resource mapping and resource evaluation of potential sand mining areas, 1998–1999. *In* Environmental survey of potential sand resource sites offshore Delaware and Maryland, part 1. Final Report to the Minerals Management Service, International Activities and Marine Minerals Division, contract 1435-01-97-CT-30853, Herndon, Virginia. Available: gomr.mms.gov/homepg/espis/espismaster.asp?appid=1. (April 2009).

Diaz, R. J., G. R. Cutter, Jr., and K. W. Able. 2003. The importance of physical and biogenic structure to juvenile fishes on the shallow inner continental shelf. Estuaries 26:12–20.

Diaz, R. J., G. R. Cutter, Jr., and C. H. Hobbs, III. 2004. Potential impacts of sand mining offshore of Maryland and Delaware, part 2 Biological considerations. Journal of Coastal Research 20:61–69.

Divins, D. L., and D. Metzger. 2003. NGDC coastal relief model. National Oceanic and Atmospheric Administration, Washington, D.C.

Drucker, B. S., W. Waskes, and M. R. Byrnes. 2004. The U.S. Minerals Management Service outer continental shelf sand and gravel program: environmental studies to assess the potential effects of offshore dredging operations in federal waters. Journal of Coastal Research 20:1–5.

Fock, H., F. Uiblein, F. Köster, and H. von Westernhagen. 2002. Biodiversity and species–environment relationships on the demersal fish assemblage of Great Meteor Seamount (subtropical NE Atlantic) sampled by different trawls. Marine Biology 141:1432–1793.

Gabriel, W. L. 1992. Persistence of demersal fish assemblages between Cape Hatteras and Nova Scotia, northwest Atlantic. Journal of Northwest Atlantic Fisheries Science 14:29–46.

Gilinsky, E. 1984. The role of fish predation and spatial heterogeneity in determining benthic community structure. Ecology 65:455–468.

Grosslein, M. D., and T. R. Azarovitz. 1982. Fish distribution. New York Sea Grant Institute, MESA New York Bight Atlas Monograph 15, Albany.

Hedges, L. V., and I. Olkin. 1985. Statistical methods for meta-analysis. Academic Press, San Diego, California.

Ishida, Y., A. Yano, B. Masatoshi, and M. Ogura. 2002. Vertical movement of a chum salmon *Oncorhynchus keta* in the western north Pacific Ocean as determined by a depth-recording archival tag. Fisheries Science 67:1030–1035.

Kohn, A. J. 1967. Environmental complexity and species diversity in the gastropod genus *Conus* on Indo–West Pacific reef platforms. American Naturalist 101:251–259.

Langton, R., R. Steneck, V. Gotceitas, F. Juanes, and P. Lawton. 1996. The interface between fisheries research and habitat management. North American Journal of Fisheries Management 16:1–7.

Lee, H. J., and S. S. Chun. 1994. Landward migration of isolated shelly sand ridge (Chenier) on the macrotidal flat of Gomso Bay, west coast of Korea: controls of storms and typhoon. Journal of Sedimentary Research 64:886–893.

Lough, R. G., P. C. Valentine, D. C. Potter, P. J. Auditore, G. R. Bolz, J. D. Neilson, and R. I. Perry. 1989. Ecology and distribution of juvenile cod and haddock in relation to sediment type and bottom currents on eastern Georges Bank. Marine Ecology Progress Series 56:1–12.

Malatesta, R. J., and P. J. Auster. 1999. The importance of habitat features in low-relief continental shelf environments. Oceanologica Acta 22:623–626.

Manderson, J. P., J. Pessutti, C. Meise, D. Johnson, and P. Shaheen. 2003. Winter flounder settlement dynamics and the modification of settlement patterns by postsettlement processes in a NW Atlantic estuary. Marine Ecology Progress Series 253:253–267.

Methratta, E. T., and J. S. Link. 2006. Seasonal variation in groundfish habitat associations in the Gulf of Maine–Georges Bank region. Marine Ecology Progress Series 326:245–256.

Michel, J. 2004. Regional management strategies for federal offshore borrow areas, U.S. East and Gulf of Mexico coasts. Journal of Coastal Research 20:149–154.

Murawski, S. A., and J. T. Finn. 1988. Biological basis for mixed-species fisheries: species codistribution in relation to environmental and biotic variables. Canadian Journal of Fisheries and Aquatic Sciences 45:1720–1735.

Musick, J. A. 2000. Transitory species (vertebrate nekton). *In* Environmental survey of potential sand resource sites

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offshore Delaware and Maryland, part 2. Final Report to the Minerals Management Service, International Activities and Marine Minerals Division, contract 1435-01-97-CT-30853, Herndon, Virginia. Available: gomr.mms.gov/homepg/espis/espismaster.asp?appid=1. (April 2009).

Musick, J. A., J. A. Colvocoresses, and E. J. Foell. 1986. Seasonality and distribution, availability and composition of fish assemblages in Chesapeake Bight. Pages 451–474 *in* A. Yanez and Y. Arancibia, editors. Fish community ecology in estuaries and coastal lagoons: towards an ecosystem integration. University of Mexico Press, Mexico City.

Neilson, J. D., and R. I. Perry. 1990. Diel vertical migrations of marine fishes: an obligate or facultative process? Advances in Marine Biology 26:115–168.

Newell, R. C., L. J. Seiderer, and D. R. Hitchcock. 1998. The impact of dredging works in coastal waters: a review of the sensitivity to disturbance and subsequent recovery of biological resources on the sea bed. Oceanography and Marine Biology: An Annual Review 36:127–178.

NOAA (National Oceanic and Atmospheric Administration). 1996. Magnuson–Stevens Fishery Conservation Act. NOAA Technical Memorandum NMFS-F/SPO-23.

NRC (National Research Council). 1995. Beach nourishment and protection. National Academy Press, Washington, D.C.

Olney, J., Sr., and D. M. Bilkovic. 2000. Literature survey of reproductive finfish and ichthyoplankton present in proposed mining locations within the Middle Atlantic Bight. *In* Environmental survey of potential sand resource sites offshore Delaware and Maryland, part 3. Final Report to the Minerals Management Service, International Activities and Marine Minerals Division, contract 1435-01-97-CT-30853, Herndon, Virginia. Available: gomr.mms.gov/homepg/espis/espismaster.asp?appid=1. (April 2009).

Overholtz, W. J., and A. V. Tyler. 1985. Long-term responses of the demersal fish assemblages of Georges Bank. U.S. National Marine Fisheries Service Fishery Bulletin 83:507–520.

Parker, G., N. W. Lanfredi, and D. J. P. Swift. 1982. Seafloor response to flow in a southern hemisphere sand-ridge field: Argentine inner shelf. Sedimentary Geology 33:195–216.

Perry, R. I., and S. J. Smith. 1994. Identifying habitat associations of marine fishes using survey data: an application to the northwest Atlantic. Canadian Journal of Fisheries and Aquatic Sciences 51:589–602.

Pickett, S. T. A., and P. S. White. 1985. The ecology of natural disturbance and patch dynamics. Academic Press, London.

Rosenberg, A., T. E. Bigford, S. Leathery, R. L. Hill, and K. Bickers. 2000. Ecosystem approaches to fishery management through essential fish habitat. Bulletin of Marine Science 66:535–542.

Simon, J. L., and D. M. Dauer. 1977. Reestablishment of a benthic community following natural defaunation. Pages 139–154 *in* B. C. Coull, editor. Ecology of marine benthos. University of South Carolina Press, Columbia.

SAS (SAS Institute). 2004. SAS/STAT user's guide, version 9.00. SAS Institute, Cary, North Carolina.

Slacum, H. W., Jr., W. Burton, J. Vølstad, J. Dew, E. Weber, R. Llansó, and D. Wong. 2006. Comparisons between marine communities residing on sandshoals and uniform-bottom substrates in the mid-Atlantic Bight. Final Report for the Mineral Management Service. Available: gomr.mms.gov/homepg/espis/espismaster.asp?appid=1. (April 2009).

Slacum, H. W., Jr., J. H. Vølstad, E. Weber, W. Richkus, R. Diaz, and C. Tallent. 2008. The value of applying commercial fisher's experience with designed surveys to identify characteristics of essential fish habitat for adult summer flounder (*Paralichthys dentatus*). North American Journal of Fisheries Management 28:710–721.

Söndgerath, D., and B. Schröder. 2002. Population dynamics and habitat connectivity affecting the spatial spread of populations: a simulation study. Landscape Ecology 17:57–70.

Steimle, F. W., and C. Zetlin. 2000. Reef habitats in the Middle Atlantic Bight: abundance, distribution, associated biological communities, and fishery resource use. Marine Fisheries Review 62:24–42.

Swift, D. J. P., G. Parker, M. W. Lanfredi, G. Perillo, and K. Figg. 1978. Shoreface-connected sand ridges on American and European shelves: a comparison. Estuarine and Coastal Marine Sciences 7:257–273.

Van de Meene, J. W. H. 1994. The shoreface-connected ridges along the central Dutch coast. Royal Dutch Geographical Society, Netherlands Geographical Studies 174, Utrecht, The Netherlands.

Van Dolah, R. F., D. R. Calder, and D. M. Knott. 1984. Effects of dredging and open-water disposal on benthic macroinvertebrates in a South Carolina estuary. Estuaries 7:28–37.

Vasslides, J. M., and K. W. Able. 2008. Importance of shoreface sand ridges as habitat for fishes off the northeast coast of the United States. U.S. National Marine Fisheries Service Fishery Bulletin 106:93–107.

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Appendix A: Species Collected

TABLE A.1.—CPUE (SE) per 10,000 m^2 for all species collected in shoal and flat-bottom habitats for each gear type during each season. Gear abbreviations are as follows: G = gill net, L = large trawl, S = small trawl.

		Flat bottom			
Species	Gear	Fall	Winter	Spring	Summer
Benthic finfish					
American sand lance *Ammodytes americanus*	L	0.02 (0.02)		0.03 (0.03)	0.29 (0.29)
Atlantic angel shark *Squatina dumeril*	L				0.03 (0.03)
Atlantic cod *Gadus morhua*	L			0.02 (0.02)	
Atlantic croaker *Micropogonias undulatus*	G				1.99 (1.16)
	L	0.18 (0.13)			26.28 (15.96)
	S	32.38 (15.55)			0.74 (0.42)
Atlantic sharpnose shark *Rhizoprionodon terraenovae*	G				0.24 (0.12)
Barndoor skate *Dipturus laevis*	L		0.34 (0.15)		
Black sea bass *Centropristis striata*	G			0.02 (0.02)	
	L	0.16 (0.11)		0.07 (0.04)	0.09 (0.07)
	S			1.15 (1.15)	0.14 (0.14)
Bullnose ray *Myliobatis freminvillei*	G				0.11 (0.11)
	L				0.33 (0.14)
	S				0.14 (0.14)
Clearnose skate *Raja eglanteria*	G				
	L	1.11 (0.30)	0.02 (0.02)	0.05 (0.05)	1.73 (0.63)
	S	1.14 (0.61)			4.3 (1.45)
Cownose ray *Rhinoptera bonasus*	G				
Goosefish *Lophius americanus*	L			0.05 (0.04)	
Inshore lizardfish *Synodus foetens*	S				
Lined seahorse *Hippocampus erectus*	S				0.13 (0.13)
Little skate *Raja erinacea*	L	2.54 (0.91)	1.33 (0.28)	1.87 (0.40)	
	S		1.52 (0.59)	0.14 (0.14)	
Northern kingfish *Menticirrhus saxatilis*	G				
	L	0.02 (0.02)		0.2 (0.09)	0.07 (0.07)
Northern pipefish *Syngnathus fuscus*	G		0.02 (0.02)		
	S	0.29 (0.29)	0.16 (0.16)		
Northern puffer *Sphoeroides maculatus*	L			0.02 (0.02)	
	S	0.30 (0.30)			0.14 (0.14)
Northern searobin *Prionotus carolinus*	G			0.02 (0.02)	0.17 (0.06)
	L	0.61 (0.36)		8.89 (5.31)	30.01 (5.95)
	S	1.43 (0.85)		6.89 (5.53)	31.47 (15.85)
Northern stargazer *Astroscopus guttatus*	L	0.02 (0.02)		0.03 (0.03)	
Red hake *Urophycis chuss*	L	0.05 (0.05)		0.03 (0.03)	
	S		0.14 (0.14)		
Roughtail stingray *Dasyatis centroura*	L				0.02 (0.02)
Scup *Stenotomus chrysops*	L	1.72 (0.32)		34.18 (15.31)	6.25 (5.43)
	S	3.25 (2.03)		0.74 (0.62)	4.78 (1.56)
Smallmouth flounder *Etropus microstomus*	L	0.02 (0.02)			0.02 (0.02)
	S	5.38 (1.69)	1.27 (0.52)	3.29 (0.9)	3.38 (2.03)
Smooth butterfly ray *Gymnura micrura*	L				0.03 (0.03)
Smooth dogfish *Mustelus canis*	G	0.14 (0.11)	0.06 (0.06)	1.41 (0.27)	1.06 (0.33)
	L	0.26 (0.10)		4.05 (1.10)	0.02 (0.02)
Spiny dogfish *Squalus acanthias*	G	14.17 (4.49)	0.22 (0.09)		
	L	31.15 (9.57)	0.34 (0.15)		
Spot *Leiostomus xanthurus*	G				0.07 (0.07)
	L				0.75 (0.62)
Spotted hake *Urophycis regia*	L	0.14 (0.12)	0.04 (0.03)	0.66 (0.31)	0.77 (0.35)
	S	10.66 (5.00)	9.69 (3.1)	13.75 (3.1)	0.98 (0.58)
Striped bass *Morone saxatilis*	G	0.04 (0.04)			
	L	0.20 (0.10)			
Striped cusk-eel *Ophidion marginatum*	S				1.56 (1.07)
Striped searobin *Prionotus evolans*	G	0.04 (0.04)	0.02 (0.02)	0.22 (0.13)	0.09 (0.05)
	L	1.81 (0.97)		0.71 (0.27)	0.12 (0.10)
	S			0.39 (0.39)	
Summer flounder *Paralichthys dentatus*	L	1.51 (0.37)	0.14 (0.07)	0.49 (0.15)	0.26 (0.07)
	S			0.15 (0.15)	0.43 (0.30)
Weakfish *Cynoscion regalis*	G	0.04 (0.04)			0.07 (0.05)
	L	0.79 (0.36)			0.35 (0.25)
	S				0.57 (0.57)
Windowpane *Scophthalmus aquosus*	G		0.01 (0.01)		

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TABLE A.1.—Extended.

Species	Shoal			
	Fall	Winter	Spring	Summer
	Benthic finfish			
American sand lance *Ammodytes americanus*		0.42 (0.38)	0.24 (0.18)	14.01 (8.47)
Atlantic angel shark *Squatina dumeril*				
Atlantic cod *Gadus morhua*				
Atlantic croaker *Micropogonias undulatus*				
	2.43 (1.38)			
Atlantic sharpnose shark *Rhizoprionodon terraenovae*				0.54 (0.20)
Barndoor skate *Dipturus laevis*		0.16 (0.10)		
Black sea bass *Centropristis striata*				
			0.02 (0.02)	0.02 (0.02)
Bullnose ray *Myliobatis freminvillei*				
				0.05 (0.05)
Clearnose skate *Raja eglanteria*			0.05 (0.04)	0.02 (0.02)
	1.55 (0.28)		1.21 (0.47)	3.68 (0.95)
	1.67 (0.55)		0.58 (0.33)	3.04 (1.16)
Cownose ray *Rhinoptera bonasus*				0.04 (0.04)
Goosefish *Lophius americanus*				
Inshore lizardfish *Synodus foetens*				1.12 (0.57)
Lined seahorse *Hippocampus erectus*				
Little skate *Raja erinacea*	3.77 (1.39)	0.75 (0.17)	3.61 (0.49)	
	0.28 (0.28)	0.91 (0.43)	0.59 (0.26)	
Northern kingfish *Menticirrhus saxatilis*			0.05 (0.05)	
			0.24 (0.10)	0.04 (0.04)
Northern pipefish *Syngnathus fuscus*				
				0.16 (0.16)
Northern puffer *Sphoeroides maculatus*			0.03 (0.03)	
	0.28 (0.28)			
Northern searobin *Prionotus carolinus*				0.05 (0.03)
	0.06 (0.03)		3.61 (2.93)	8.56 (2.44)
	1.71 (0.72)		1.31 (0.52)	2.58 (0.76)
Northern stargazer *Astroscopus guttatus*				0.09 (0.09)
Red hake *Urophycis chuss*				
				0.05 (0.03)
Roughtail stingray *Dasyatis centroura*				
Scup *Stenotomus chrysops*	0.09 (0.04)		159.61 (100.37)	56.59 (56.28)
			0.30 (0.30)	9.13 (3.9)
Smallmouth flounder *Etropus microstomus*				
	4.00 (1.61)	0.68 (0.55)	1.91 (0.58)	1.20 (0.38)
Smooth butterfly ray *Gymnura micrura*				0.02 (0.02)
Smooth dogfish *Mustelus canis*	0.04 (0.04)		2.94 (0.41)	0.74 (0.28)
	0.17 (0.08)		6.44 (1.50)	
Spiny dogfish *Squalus acanthias*	10.89 (3.53)	0.41 (0.16)		
	18.31 (4.64)	0.31 (0.14)		
Spot *Leiostomus xanthurus*				
Spotted hake *Urophycis regia*			0.16 (0.05)	0.04 (0.03)
	6.39 (0.98)	2.29 (0.78)	1.01 (0.52)	0.14 (0.14)
Striped bass *Morone saxatilis*	0.56 (0.32)			
	26.59 (23.53)	0.05 (0.03)		
Striped cusk-eel *Ophidion marginatum*				
Striped searobin *Prionotus evolans*			0.41 (0.16)	
	0.21 (0.07)		1.42 (0.52)	0.02 (0.02)
			0.44 (0.32)	
Summer flounder *Paralichthys dentatus*	2.6 (0.61)	0.02 (0.02)	0.25 (0.12)	0.07 (0.04)
		0.61 (0.46)	0.14 (0.14)	
Weakfish *Cynoscion regalis*				
Windowpane *Scophthalmus aquosus*				

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TABLE A.1.—Continued.

Species	Gear	Flat bottom			
		Fall	Winter	Spring	Summer
	L	10.39 (3.02)	1.74 (0.23)	0.80 (0.14)	0.34 (0.08)
	S	4.57 (1.97)	0.74 (0.28)	0.42 (0.23)	0.15 (0.15)
Winter flounder *Pseudopleuronectes americanus*	L			0.03 (0.03)	
Winter skate *Leucoraja ocellata*	G	0.24 (0.15)		0.16 (0.12)	
	L	14.83 (1.88)	3.13 (0.43)	6.52 (1.41)	0.87 (0.49)
	S	3.4 (1.41)	0.15 (0.15)	0.43 (0.31)	
		Pelagic finfish			
Alewife *Alosa pseudoharengus*	G		0.01 (0.01)		
	L			0.18 (0.14)	
American shad *Alosa sapidissima*	G				
Atlantic bonito *Sarda sarda*	G				
Atlantic herring *Clupea harengus*	L		0.71 (0.6)		
Atlantic mackerel *Scomber scombrus*	G				
Atlantic menhaden *Brevoortia tyrannus*	G			0.45 (0.26)	2.49 (1.36)
	L		0.15 (0.06)		
Atlantic silverside *Menidia menidia*	L		0.05 (0.03)		
	S		1.65 (0.90)		
Bay anchovy *Anchoa mitchilli*	L	2.76 (2.61)			
	S	9.97 (7.88)			38.66 (27.35)
Blue runner *Caranx crysos*	L				0.09 (0.07)
Blueback herring *Alosa aestivalis*	G	0.04 (0.04)			
	L		0.14 (0.07)	0.02 (0.02)	
Bluefish *Pomatomus saltatrix*	G	0.74 (0.43)			0.84 (0.49)
	L	1.40 (0.43)			0.05 (0.04)
Butterfish *Peprilus triacanthus*	G	0.04 (0.04)		0.02 (0.02)	0.47 (0.31)
	L	0.85 (0.25)		123.14 (68.24)	1.79 (0.73)
	S	0.28 (0.28)		0.57 (0.39)	4.99 (1.64)
Cobia *Rachycentron canadum*	G				0.02 (0.02)
Dusky shark *Carcharhinus obscurus*	G				0.36 (0.2)
Harvestfish *Peprilus paru*	L				
Hickory shad *Alosa mediocris*	L		0.05 (0.04)		
Sandbar shark *Carcharhinus plumbeus*	G				
Silver hake *Merluccius bilinearis*	S	1.73 (1.13)		0.42 (0.23)	
Spanish mackerel *Scomberomorus maculatus*	G				0.14 (0.07)
	L				
Striped anchovy *Anchoa hepsetus*	S	0.26 (0.26)			2.60 (1.35)
Thresher shark *Alopias vulpinus*	G				
	L				0.02 (0.02)
		Benthic invertebrates			
Atlantic rock crab *Cancer irroratus*	G	0.07 (0.05)	0.03 (0.03)		
	L	0.13 (0.05)			0.09 (0.04)
	S	2.09 (1.79)	0.28 (0.28)	0.27 (0.18)	1.34 (0.68)
Blue crab *Callinectes sapidus*	L				
	S				
Channel whelk *Busycotypus canaliculatus*	L	0.20 (0.08)		0.27 (0.18)	
	S	1.80 (1.80)		0.13 (0.13)	
Coarsehand lady crab *Ovalipes stephensoni*	G				
	L	0.24 (0.13)			0.66 (0.28)
	S	0.29 (0.20)	0.59 (0.26)		
Common octopus *Octopus vulgaris*	L	0.02 (0.02)			
Gastropods Gastropoda	S		3.86 (3.71)	4.73 (1.71)	
Heart urchins Echinoidea	S			0.27 (0.19)	0.29 (0.29)
Horseshoe crab *Limulus polyphemus*	L	0.83 (0.4)	0.23 (0.10)	0.14 (0.07)	0.07 (0.05)
	S	0.15 (0.15)	0.14 (0.14)		
Knobbed whelk *Busycon carica*	L	0.07 (0.04)		0.19 (0.11)	0.02 (0.02)
	S				0.14 (0.14)
Lady crab *Ovalipes ocellatus*	G				0.02 (0.02)
	L	2.9 (0.53)			3.56 (0.55)
	S	1.75 (0.88)			4.51 (1.86)
Moon snails *Polinices* spp.	G			0.02 (0.02)	
	L			0.03 (0.03)	0.02 (0.02)
	S		9.66 (4.3)	2.88 (0.86)	
Nudibranchs Nudibranchia	S		0.42 (0.31)	0.43 (0.23)	
Portly spider crab *Libinia emarginata*	G			0.15 (0.07)	0.10 (0.06)
	L	0.07 (0.05)		0.05 (0.03)	
	S	0.28 (0.28)	0.38 (0.38)	1.01 (0.72)	0.18 (0.18)

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TABLE A.1.—Extended. Continued.

Species	Shoal			
	Fall	Winter	Spring	Summer
	1.33 (0.29)	0.62 (0.18)	1.04 (0.11)	0.13 (0.06)
	2.33 (1.32)	0.44 (0.24)	1.61 (0.63)	0.79 (0.39)
Winter flounder *Pseudopleuronectes americanus*		0.03 (0.03)		
Winter skate *Leucoraja ocellata*	0.18 (0.11)		0.45 (0.27)	
	21.41 (3.64)	0.51 (0.18)	7.39 (1.02)	0.09 (0.07)
	4.23 (1.82)		1.46 (0.56)	
Pelagic finfish				
Alewife *Alosa pseudoharengus*		0.02 (0.02)		
		0.03 (0.03)		
American shad *Alosa sapidissima*			0.14 (0.11)	
Atlantic bonito *Sarda sarda*			0.03 (0.03)	
Atlantic herring *Clupea harengus*		0.51 (0.45)		
Atlantic mackerel *Scomber scombrus*				0.06 (0.06)
Atlantic menhaden *Brevoortia tyrannus*			1.03 (0.56)	
Atlantic silverside *Menidia menidia*		0.02 (0.02)		
		0.45 (0.33)		
Bay anchovy *Anchoa mitchilli*				
Blue runner *Caranx crysos*				0.02 (0.02)
Blueback herring *Alosa aestivalis*				
		0.05 (0.05)		
Bluefish *Pomatomus saltatrix*	0.57 (0.20)		0.02 (0.02)	0.55 (0.3)
	0.45 (0.16)		0.02 (0.02)	
Butterfish *Peprilus triacanthus*				0.03 (0.03)
	0.07 (0.05)		33.55 (28.31)	0.13 (0.09)
	0.27 (0.27)			3.36 (1.93)
Cobia *Rachycentron canadum*				0.03 (0.03)
Dusky shark *Carcharhinus obscurus*			0.05 (0.03)	0.18 (0.08)
Harvestfish *Peprilus paru*				0.05 (0.05)
Hickory shad *Alosa mediocris*				
Sandbar shark *Carcharhinus plumbeus*			0.02 (0.02)	
Silver hake *Merluccius bilinearis*	2.58 (1.35)		0.15 (0.15)	
Spanish mackerel *Scomberomorus maculatus*				
	0.02 (0.02)		0.02 (0.02)	
Striped anchovy *Anchoa hepsetus*				
Thresher shark *Alopias vulpinus*			0.02 (0.02)	
Benthic invertebrates				
Atlantic rock crab *Cancer irroratus*		0.03 (0.03)		
	0.1 (0.06)	0.02 (0.02)		
			1.86 (1.72)	
Blue crab *Callinectes sapidus*	0.02 (0.02)			
				0.16 (0.16)
Channel whelk *Busycotypus canaliculatus*	0.21 (0.09)		0.07 (0.05)	
	0.27 (0.27)			
Coarsehand lady crab *Ovalipes stephensoni*				0.02 (0.02)
	0.16 (0.09)			2.97 (1.59)
Common octopus *Octopus vulgaris*				
Gastropods Gastropoda		7.08 (4.78)	9.41 (5.07)	6.97 (4.36)
Heart urchins Echinoidea			0.30 (0.30)	1.15 (0.58)
Horseshoe crab *Limulus polyphemus*	0.18 (0.07)	0.12 (0.06)	0.07 (0.05)	0.02 (0.02)
Knobbed whelk *Busycon carica*	0.04 (0.03)			0.03 (0.03)
Lady crab *Ovalipes ocellatus*				0.02 (0.02)
	2.19 (0.36)			9.34 (4.05)
	1.39 (1.11)			4.48 (2.42)
Moon snails *Polinices* spp.				
	0.14 (0.08)	0.05 (0.03)	0.40 (0.28)	
	0.89 (0.63)	6.04 (2.07)	3.06 (1.18)	0.30 (0.20)
Nudibranchs Nudibranchia				
Portly spider crab *Libinia emarginata*			0.02 (0.02)	0.06 (0.04)
			0.07 (0.04)	0.05 (0.03)
	0.32 (0.22)			

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TABLE A.1.—Continued.

Species	Gear	Flat bottom			
		Fall	Winter	Spring	Summer
Right-handed hermit crabs	L	0.06 (0.03)		0.02 (0.02)	0.06 (0.06)
Paguridae	S	43.16 (23.26)	7.6 (1.58)	11.9 (3.66)	19.86 (5.21)
Sand shrimp *Crangon septemspinosa*	S	0.83 (0.83)	25.74 (5.25)	3.33 (1.44)	
Starfishes Asteroidea	G				0.17 (0.17)
	L	2.53 (1.22)	0.16 (0.07)	0.85 (0.46)	0.61 (0.31)
	S	42.14 (19.47)	8.66 (5.36)	12.83 (6.44)	27.16 (6.44)
		Pelagic invertebrates			
Squids Cephalopoda	L	2.36 (0.94)		18.46 (4.60)	8.06 (2.33)
	S	56.84 (35.56)	0.16 (0.16)	14.23 (5.95)	104.18 (56.65)

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TABLE A.1.—Extended. Continued.

Species	Shoal			
	Fall	Winter	Spring	Summer
Right-handed hermit crabs	0.02 (0.02)			
Paguridae	20.67 (6.26)	7.82 (2.1)	19.08 (7.52)	58.44 (24.68)
Sand shrimp *Crangon septemspinosa*	0.28 (0.28)	11.03 (3)	4.38 (1.37)	
Starfishes Asteroidea	0.95 (0.65)			0.25 (0.17)
	4.81 (2.59)	0.22 (0.08)	1.53 (0.66)	0.69 (0.37)
	56.02 (29.63)	1.79 (0.91)	9.81 (4.05)	8.69 (3.34)
	Pelagic invertebrates			
Squids Cephalopoda	0.75 (0.23)		21.80 (9.24)	4.27 (3.07)
	1.11 (0.84)		25.82 (12.43)	10.79 (5.56)

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