Importance of shoreface sand ridges as habitat for fishes off the northeast coast of the United States

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Abstract—To determine if shoreface sand ridges provide unique habitats for fish on the inner continental shelf, two cross-shelf trawl surveys (23 km in length) were conducted in southern New Jersey (July and September 1991–95 with a beam trawl and July and September 1997–06 with an otter trawl) to assess whether species abundance, richness, and assemblages differed on and away from the ridge. The dominant species collected with both gears were from the families Paralichthyidae, Triglidae, Gobiidae, Serranidae, Engraulidae, Stromateidae, and Sciaenidae. Overall abundance (n=41,451 individuals) and species richness (n=61 species) were distributed bimodally across the nearshore to offshore transect, and the highest values were found on either side of the sand ridge regardless of gear type. Canonical correspondence analysis revealed three species assemblages: inshore (<5 meters depth), near-ridge (9–14 meters depth), and offshore (>14 meters depth), and variation in species composition between gear types. Environmental factors that corresponded with the assemblage changes included depth, temperature, distance from the top of the ridge, and habitat complexity. The most abundant near-ridge assemblages were distinct and included economically important species. Sand ridges of the inner continental shelf appear to be important habitat for a number of fish species and therefore may not be a suitable area for sand and gravel mining.

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Shoreface sand ridges are common features within the inner continental shelf of the northeast Atlantic coast, although the importance of these sand ridges as fish habitat has received little attention. These topographic features consist of unconsolidated fine- to medium-grain sand, typically have vertical relief up to 10 meters, and are generally oriented obliquely to the adjacent shoreline (Stahl et al., 1974; McBride and Moslow, 1991). Over 200 shoreface sand ridges have been identified from Montauk Point, New York, to Miami Beach, Florida, and over 71 are found along the coast of New Jersey (McBride and Moslow, 1991).

These sand ridges may be important bathymetric features for commercial and recreational fishing areas if they provide important fish habitat; however, there is little evidence to refute or support that possibility. Adults, settled juveniles, and larvae of a number of fish species have been documented on sand ridges and in the immediate vicinity of sand ridges, indicating that these features are used by multiple fish at various life history stages (Able et al., 2006). Although sand ridges may provide habitat for important fish species, sand ridges from Massachusetts to North Carolina, including ridges off New Jersey (Byrnes et al., 2004), have gained attention as potential locations from which to extract sand and gravel for ongoing beach nourishment projects and to provide construction materials (Drucker et al., 2004). Extraction of sand and gravel reduces the complexity of a ridge, rendering it similar to the surrounding bottom.

Recent research on the effects of sand mining at ridges has focused on physical oceanographic processes (Nairn et al., 2004), and others with a focus on benthic invertebrates and their role in providing trophic support to fishes have provided limited evaluation of the biological response to sand mining (Diaz et al., 2004; Nairn et al., 2004). Although seasonal and spatial patterns of aquatic organisms near sand ridges have been examined for the presence of decapod crustaceans (Viscido et al., 1997) on and near sand ridges off New Jersey and for juvenile fish off Delaware and Maryland (Diaz et al., 2003), there have been no evaluations of correspondingly varying spatial patterns in the fish community or of their causal relationships with sand ridges.

If sand ridges provide unique habitat within inner continental shelf

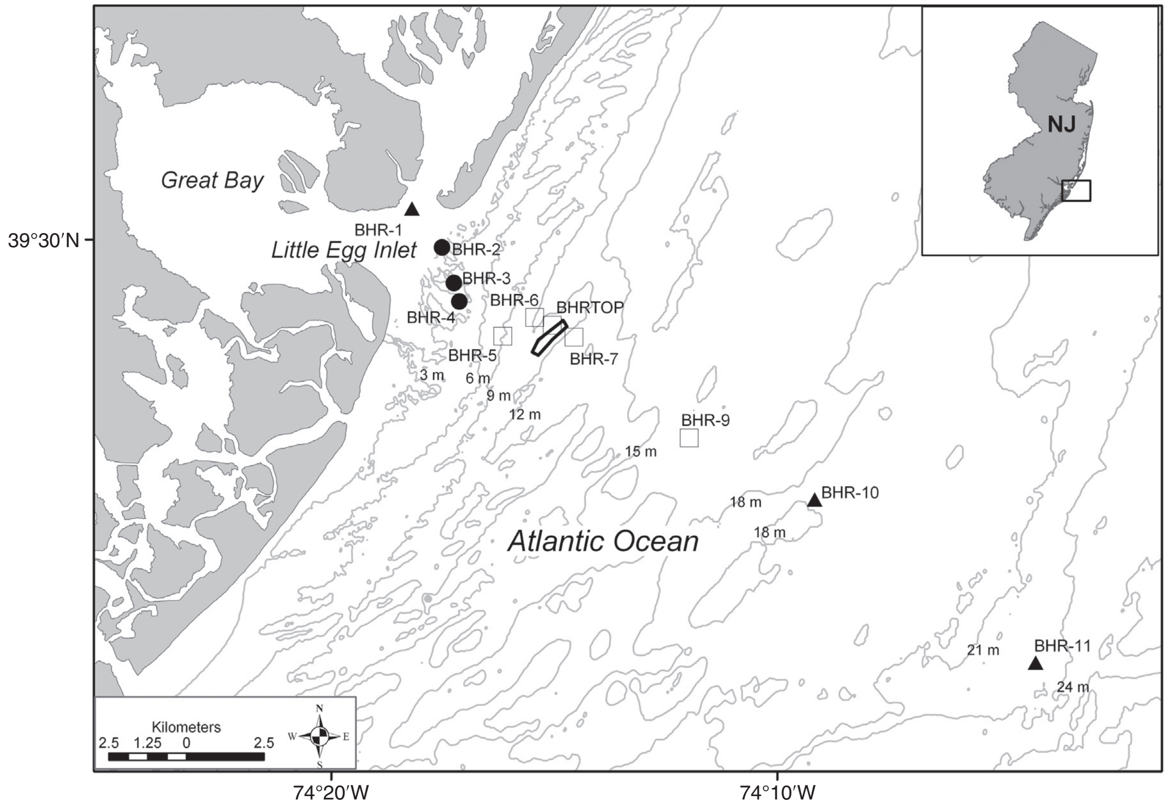

Figure 1

Station locations for the 1991–95 beam trawl surveys and 2001–06 otter trawl surveys off Little Egg Inlet off southern New Jersey. Locations sampled only by beam trawl are denoted by (●), those sampled only by otter trawl, by (▲), and those sampled with both gears, by (□). The thick black line delineates the top contour of Beach Haven Ridge.

ecosystems, then changes to fish assemblages associated with changes in the structure of sand ridges could be excellent indicators of the effects of sand and gravel mining or other habitat alterations. Additionally, sand ridges may not be the optimal choice for sand and gravel mining if it is shown that sand ridges act as strategic ecological features (whether in their influence on increased fish abundance or species richness) or provide essential fish habitat (EFH) for economically important species. The purpose of this study was to determine how use of habitat by fish varies between shoreface sand ridges and the surrounding inner continental shelf through an analysis of abundance and species assemblage patterns. The specific objectives were 1) to ascertain if there is a difference in fish abundance and species richness between the sand ridge and adjacent areas; 2) to determine if there are spatial or temporal patterns in species assemblages that are different between the sand ridge and adjacent areas; and 3) to describe any relationships between the species assemblages and environmental factors. Collectively, this information can provide resource managers a better understanding of the potential impacts of the mining of sand ridges on fishes.

Materials and methods

Study area

The study area encompassed the inner continental shelf waters off southern New Jersey between Barnegat Inlet and Brigantine Inlet (Fig. 1). Sampling was conducted along a 23-km transect across a shoreface sand ridge, Beach Haven Ridge (BHR). Beach Haven Ridge extends northeastward from the ebb tidal delta of Little Egg Inlet; it has a maximum relief of 8 m between the ridge crest and the trough on the seaward side, and the relief on the shoreward side is 4–5 m (Stahl et al., 1974). The substrate on top of the ridge is composed primarily of coarse sand (Craghan, 1995). The seaward side of the ridge has two major substrate types: 1) coarse sand with shells of the surf clam (*Spisula solidissima*) and 2) areas with a mixture of semilithified clay and sand. The landward side of the ridge is characterized as having two major substrate types: 1) areas of sand and clay mixture and 2) patches of semilithified clay and sand mixture. Mounds composed of tubes of the polychaete worm *Asabellides occulata* can also be found landward of the ridge, but are temporally variable. Bedforms (ripples) are

Table 1

Physical attributes of individual sampling stations along the Beach Haven Ridge (BHR) transect. Distance to ridge top is the distance (m) from that station to the station located on top of the ridge, plus signs indicate distances seaward of the ridge top, negative signs indicate distances landward of the ridge top. Habitat complexity index is an index of complexity from 1 to 3 and is based on the amount and type of substrate and macroalgae or other structural components present. See Figure 1 for station locations.

Sampling Station	Distance to ridge top (m)	Distance from shore (m)	Water depth (m)	Trawl type	Number of samples	Type of habitat	Habitat complexity index
BHR-1	–6000	0	2.8	Otter	67	Bare sand	1
BHR-2	–4600	300	3.1	Beam	4	Bare sand	1
BHR-3	–3700	750	5.1	Beam	8	Bare sand	1
BHR-4	–3200	1250	4.7	Beam	8	Bare sand	1
BHR-5	–1400	3050	9.4	Beam	10	Sand with patches of macroalgae and *Diopatra* tubes; clay+silt	3
				Otter	66		
BHR-6	–500	3950	11.5	Beam	22	Clay and sand with *Diopatra* tubes; clay+silt	3
				Otter	64		
BHRTOP	0	4450	10.3	Beam	16	Bare sand	1
				Otter	18		
BHR-7	1100	5550	13.6	Beam	27	Sand with shell hash and *Diopatra* tubes; clay/sand	3
				Otter	61		
BHR-9	5300	9750	16.3	Beam	2	Shell hash	2
				Otter	62		
BHR-10	10000	14450	18.0	Otter	29	Shell hash	2
BHR-11	19000	23450	19.9	Otter	22	Shell hash	2

consistently largest on the crest and flanks of the ridge. The crests are often bare, but the troughs are filled with varying amounts of shell valves and shell hash, which are frequently buried and uncovered. Although patches of *Diopatra cuprea* (plumed worm) tubes were found along the flanks and base of the ridge, they were never identified on the crest of the ridge.

Field sampling

Data from two independent sampling surveys, one with a beam trawl (1991–95), and the other with an otter trawl (1997–2006), were analyzed. Although the data sets were not collected concurrently, they did overlap both temporally (sampling months) and spatially (four sampling stations). This overlap between gear types provided the opportunity to observe temporal and spatial variation in species abundance and richness both within and between gears.

Beam-trawl sampling Sampling for fishes was conducted at eight stations along a transect from Little Egg Inlet across Beach Haven Ridge with a 2 meter (3-mm bar mesh) beam trawl (Fig. 1; Table 1). Both midsummer (July or the first few days in August) and late summer (September) samples were collected. The number of tows conducted at each station varied from 2 to 22 (Table 1). Tow speed was approximately 2.8–3.7 km/h and each tow was one minute in duration in an attempt to sample from discrete habitat types. All fish captured were identified to species where possible and measured to the nearest millimeter. Surface and bottom water samples were obtained with a Nansen bottle. Temperature and salinity were obtained from the water samples by using a stem thermometer and hand-held refractometer, whereas oxygen concentrations were determined by using Winkler titration for samples collected from 1991 through 1995.

Otter trawl sampling Eight stations on and within the vicinity of Beach Haven Ridge were sampled in midsummer (July or the first few days in August) and late summer (September) (Fig. 1; Table 1). Samples were collected with an otter trawl (4.9-m head rope, 19-mm mesh wings, 6-mm-mesh codend) in four replicate tows at the inlet station (BHR-1) with various small boats (4–7 meters) and in three replicate tows at each of the deeper stations with RV *Arabella* (15 meters). Sampling at BHR-10 and BHR-11 did not commence until September 2001. Tow speed varied depending on the prevailing ocean conditions, but duration of tows never exceeded two minutes in an attempt to ensure that fish were collected from discrete habitat types. For each tow, a random selection of up to 20 individuals of each species were measured to the nearest millimeter fork length (FL) or total length (TL), and the remainder were counted. Beginning in 2001, bottom and surface salinity, temperature, dissolved oxygen, and pH were measured with a YSI model 85 handheld dissolved oxygen and conductivity instrument (Yellow Springs Instruments, Yellow Springs, OH) and recorded after the first tow. Depth and bottom topography were determined with a Furuno model 256 video depth recorder (Furuno, Hyogo, Japan). Water transparency was measured with a Secchi disk at each station.

Habitat characteristics

To assess the importance of habitat complexity to the structure of fish assemblages, the substrate was characterized qualitatively. Because Beach Haven Ridge and its vicinity have been intensively studied in the past, it was possible to identify habitat characteristics for each station from previous research where SCUBA, submersible, and remotely operated vehicle, or sidescan sonar were used, or where structural samples of the habitat were collected during trawl sampling. Additionally, any benthic material (clay and silt clods, sea stars, sand dollars, algae, shell hash, *Diopatra* tubes, *Asabellides* mounds) retained by the 2006 otter trawl sampling was categorized and quantified to evaluate if any changes in substrate had occurred over time. Stations were assigned an index of complexity of 1, 2, or 3 based upon the type and amount of substrate and macroalgae or other structural components present, with 1 being the least complex (bare sand) and 3 being the most complex (one or more substrate types present with multiple biogenic components). Habitat complexity was lowest inshore, peaked on the sides of the ridge, and was of an intermediate value offshore (Table 1). Stations BHR-5, BHR-6, and BHR-7 had multiple substrate types and structural components and were given an index value of 3. Station BHRTOP and the inlet stations were all dominated by bare sand substrates and had no structures and were assigned a value of 1. The offshore stations varied in their substrates but had some complexity owing to biogenic features and were assigned a value of 2. In addition, the distance from a sampling location to the station located at the top of the ridge (BHRTOP), as well as the distance from a sampling location to the shore, were determined by using ArcGIS (Environmental Systems Research Institute, Inc., Redlands, CA).

Data analyses

A number of univariate and multivariate techniques were used to calculate population measures and assemblage structure. Catch per unit of effort (CPUE), or the number of fish captured per tow, was determined for each species at each station. Significant differences in patterns of CPUE among stations were tested by using ANOVA procedures. CPUE data were log transformed before analysis to correct for heterogeneity of variance (Underwood, 1997). Mean species richness per unit of effort (RPUE), or the number of different species caught in a tow, was also calculated for each sampling station. ANOVA and Tukey multiple comparison tests were used to assess the differences in mean species richness (RPUE) between stations. Frequency of occurrence was calculated for each species across tows at each sampling station. All univariate statistics were performed with SAS (vers. 9.1, SAS Inst., Inc., Cary, NC).

To determine the structure of the assemblages in the different habitats, two related ordination techniques were employed. Canonical correspondence analysis (CCA) is a constrained ordination technique in which the sample scores are constrained to be linear combinations of the explanatory variables (Van den Brink and Ter Braak, 1999). This technique is one of the most widely used gradient analysis tools in ecology because of its capacity to handle highly skewed species distributions, high noise levels, complex sampling designs, and the fact that it does not create an artificial arch effect (Palmer, 1993). Canonical correspondence analysis was performed on a subset of the overall data matrix for which environmental information was available for all stations. For the beam trawl data this "subset" was the entire data set, whereas for the otter trawl samples, the subset was limited to Beach Haven Ridge from 2001 to 2006. The data were arranged in a species-by-sample matrix, where the samples were the combination of all tows for a given location and date, and the CPUE represented the value fields. The data were log ($CPUE$+1) transformed to reduce the influence of abundant species. Any species whose abundance did not exceed five percent from at least one station was removed from the matrix.

Because CCA orders species only along gradients of the measured environmental variables, it may not, depending on the environmental variables available, be representative of the assemblages encountered. Therefore, the CCA was checked for bias by using correspondence analysis (CA), an unconstrained ordination method (McGarigal et al., 2000). The species-by-sample matrices were treated in the same manner as in the CCA.

Results

Environmental gradients

Summer temperature tended to decrease with increasing distance from the shoreline, and depth, salinity, and water transparency generally increased with increasing distance (Fig. 2). Average station depth increased with increasing distance from the shoreline (range: 2.8–19.9 m), with the exception of the station located on the top of the ridge (BHRTOP) (Table 1). Within the Beach Haven Ridge transect there was a change in depth from BHR-4 to BHR-5 of 4.7 m, indicating the transition from the Little Egg Inlet to nearshore coastal waters.

Although a number of previous studies incorporating a variety of techniques were used to determine habitat homogeneity, the similarity in descriptions when the same station was sampled by multiple sources provided confidence in the accuracy of the habitat descriptions, as well as the stability of the habitat over time.

Species abundance and richness

The specific patterns in species abundance and richness varied with sampling gear and habitat. The locations near the ridge typically had the largest number of species and individuals and the inshore, top of ridge, and locations offshore of the ridge had the least, regardless of sampling gear (Fig. 3). Fish abundance was higher in late summer than mid-summer for both gears, but the spatial patterns in species abundance were similar between seasons. There was no difference in species richness between seasons for either gear. Beam trawl catches were dominated by demersal fish families including Triglidae, Gobiidae, and Serranidae, whereas the dominant families found in the otter trawl consisted of Engraulidae, Stromateidae, Sciaenidae, Triglidae, and Bothidae (Tables 2–4).

In beam-trawl tows during 1991–95 (n=97), 2049 individuals were collected (primarily demersal but also some pelagic fishes) belonging to 34 species. Fish abundance (CPUE) was lowest inshore, increased slightly towards BHR-5, increased significantly (df=94, P<0.0001) at the stations on either side of the ridge (BHR-6<BHR-7), and was highest at the offshore station (BHR-9) (Fig. 3). The station on top of the ridge (BHRTOP) had significantly lower fish abundance than the stations on either side of the ridge and offshore (df=89, P<0.0001), but higher abundance than at the inshore stations. In otter-trawl tows during 1997–2006 (n=389), 39,402 benthic and pelagic fishes from 52 species were captured. Fish abundance (CPUE) was highest near the ridge (BHR-5> BHR-7>BHR-6) and significantly lower (df=381, P<0.0001) at all other stations (Fig. 3). Fish abundance at the top of the ridge was not significantly different from that at the inshore station or the offshore stations. The beam trawl typically captured smaller individuals (mean=38.8 mm, standard error [SE]=1.2) than did the otter trawl (mean=104.1 mm, [SE=1.1] Tables 2–4; Fig. 4).

Species richness was highest at the near-ridge stations and decreased offshore across both gear types (Fig. 3). The mean species richness per tow (RPUE) for the beam trawl was significantly higher (df=89, P<0.0001) at the sides of the ridge and offshore than at the other beam-trawl stations. The RPUE for the otter trawl was significantly higher (df=312, P<0.0001) at the near-ridge stations than at all other remaining stations.

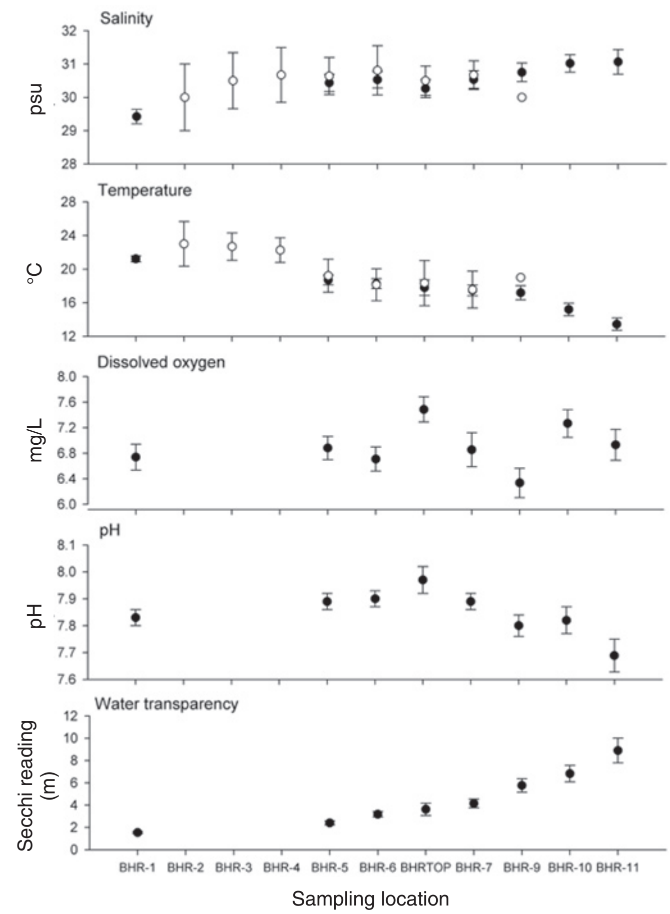

Figure 2

Environmental data (mean bottom values) for the 1991–95 beam trawl samples (○) and 2001–06 otter trawl samples (●). Vertical lines represent standard error. Sampling with a beam trawl at BHR-2 was conducted in midsummer 1995 only and at BHR-9 in midsummer 1993 only. Otter-trawl data at BHRTOP was collected in 2005 and 2006 only. Dissolved oxygen, pH, and a Secchi reading were not recorded at BHR-2, BHR-3, or BHR-4 during sampling with a beam trawl. See Figure 1 for station locations.

Fish-assemblage structure based on beam-trawl samples

Canonical correspondence analysis revealed no discernible pattern in fish-assemblage structure at the stations in midsummer (Fig. 5A), which is in contrast to late summer when there were two distinct, discrete assemblages: the inshore locations (BHR-2, BHR-3, BHR-4, BHR-5) and the near-ridge+offshore stations (BHR-6, BHRTOP, BHR-7, BHR-9) (Fig. 5B). However, within the midsummer samples there was variability in the species associated with each station between years (Fig. 5C). In late summer the near-ridge+offshore stations shared a number of dominant species, whereas the assemblage of inshore stations varied along both axes. The species composition at each inshore station was not only different from the near-ridge+offshore stations but also from each other (Table 2, Fig. 5D). Within the inshore group, BHR-3 was characterized by American sand lance (*Ammodytes americanus*) and gobies (*Gobiosoma* spp.), and BHR-5 was differentiated as the only station with weakfish (*Cynoscion regalis*). The remaining inshore stations were differentiated from other stations, and to some degree each other, by the abundance of Atlantic croaker (*Micropogonias undulatus*) and kingfish (*Menticirrhus* spp.). Less than half (39%) of the species identified were captured in both assemblages (Table 2), and no species were shared among the top five species loading scores for each assemblage.

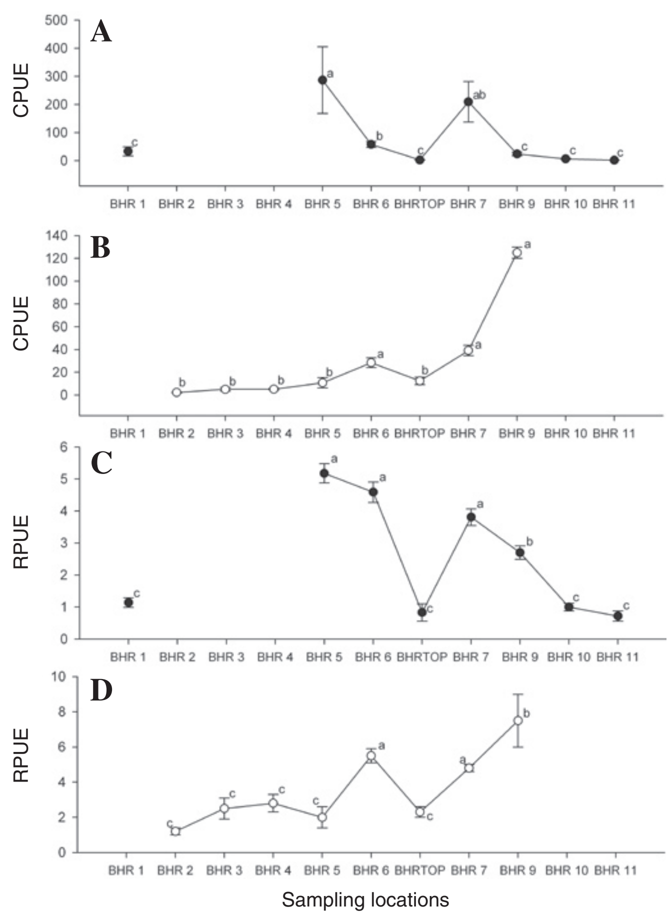

Figure 3

Mean abundance per tow (CPUE) and mean number of species per tow (RPUE) by sampling location for the otter trawl surveys (**A** and **C**) in 2001–06 and beam-trawl surveys (**B** and **D**) in 1991–95. Vertical lines represent standard error. Sampling locations with different superscripts are significantly different from each other at the alpha=0.05 level. See Figure 1 for station locations.

Over 60% of the variance in the species-environment interaction was reflected in both the mid- and late summer ordinations (Table 5). Temperature and habitat complexity were the dominant environmental variables shaping the late summer ordination (Table 6). The arrangement of the species assemblages in relation to the station assemblages was similar to that produced with correspondence analysis (CA), providing confidence that constrained ordination gave a satisfactory picture of realized distribution.

Fish-assemblage structure based on otter-trawl samples

Three assemblages were apparent in the otter-trawl data regardless of season: inshore (BHR-1), near-ridge (BHR-5, BHR-6, BHRTOP, and BHR-7), and offshore (BHR-9, BHR-10, and BHR-11) (Fig. 6). Seasonally, the near-ridge and offshore assemblages overlapped little in midsummer (Fig. 6A) and were discrete in late summer (Fig. 6B). In midsummer, the near-ridge assemblage was spread along both axes, indicating differences between samples, and the offshore assemblage was more compact, indicating a greater similarity in samples (Fig. 6A). In late summer the assemblage configurations were reversed (Fig. 6B). All three assemblages shared a majority of species, although there were some differences in the abundance of each species (Tables 3 and 4; Fig. 6, C and D).

The seasonal difference in assemblages resulted from a change in both the number and identity of species present in the study area (Tables 3 and 4; Fig. 6, C and D). In midsummer the inshore assemblage was composed predominately of northern pipefish (*Syngnathus fuscus*) and other species were present in lesser numbers (Table 3; Fig. 6C). The near-ridge assemblage was dominated by butterfish (*Peprilus triacanthus*) and bay anchovy (*Anchoa mitchilli*), and only striped anchovy (*Anchoa hepsetus*) and spotted hake (*Urophycis regia*) were present with a mean catch per tow greater than one (Table 3). Although butterfish was also the dominant species in the offshore assemblage, its abundance was one third of what was found in near-ridge trawls (Table 3). Of particular interest in the midsummer analysis was a group of species (weakfish, bluefish [*Pomatomus saltatrix*], northern puffer [*Sphoeroides maculatus*], bay anchovy, and striped anchovy) separated along the primary axis from the rest of the species centroids in the near-ridge assemblage. These species were associated with samples from near-ridge stations taken in 2001 and 2005 (Fig. 6A). During late summer, the abundance of bay anchovy increased substantially within the inshore assemblage, as did the abundance of northern pipefish (Table 4, Fig. 6C). At that time, bay anchovy was the most abundant species in the near-ridge assemblage by nearly two orders of magnitude, and Atlantic

Table 2

Catch per unit of effort (CPUE, with standard error in parentheses) and mean size (mm, with standard error in parentheses) for species captured during late summer beam trawl sampling from 1991 through 1995. Station assemblages were determined by using canonical correspondence analysis as shown in Figure 5B. Taxa were measured to total length (†), fork length (*), or body width (‡). A dash indicates that no data were available.

	Station assemblage			
	Inshore		Near-ridge+offshore	
Species	CPUE	Size	CPUE	Size
Syngnathus fuscus †	0.61 (0.27)	108 (13)	0.37 (0.11)	128 (11)
Prionotus carolinus †	0.17 (0.09)	55 (9)	4.16 (0.95)	24 (2)
Scophthalmus aquosos †	0.28 (0.18)	114 (14)	0.23 (0.09)	233 (7)
Sphoeroides maculatus †	0.11 (0.08)	105 (5)	0.40 (0.12)	47 (9)
Etropus microstomus †	0.5 (0.25)	45 (10)	17.79 (3.39)	27 (1)
Micropogonias undulatus †	1.06 (0.61)	15 (2)	0.81 (0.54)	25 (1)
Prionotus evolans †	0.17 (0.12)	48 (14)	0.53 (0.24)	74 (18)
Hippocampus erectus †	0.11 (0.08)	68 (17)	0.05 (0.03)	59 (4)
Centropristis striatus †	0.11 (0.11)	52 (8)	4.09 (1.58)	38 (1)
Cynoscion regalis †	0.22 (0.17)	75 (4)	—	—
Ammodytes americanus *	0.06 (0.06)	76 (–)	—	—
Ammodytes spp. *	0.06 (0.06)	81 (–)	—	—
Menticirrhus sp. †	2.83 (1.2)	39 (3)	—	—
Gobiosoma sp. †	0.39 (0.33)	34 (2)	—	—
Urophycis regia †	—	—	0.35 (0.09)	201 (15)
Urophycis chuss †	—	—	1.3 (0.40)	30 (1)
Gobiosoma ginsburgi †	—	—	5.28 (1.71)	30 (1)
Ophidion marginatum †	—	—	0.16 (0.09)	189 (12)
Paralichthys dentatus †	—	—	0.16 (0.09)	165 (51)
Raja erinacea ‡	—	—	0.09 (0.04)	251 (25)
Bothus sp. †	—	—	0.02 (0.02)	22 (–)
Raja eglanteria ‡	—	—	0.02 (0.02)	420 (–)
Tautogolabrus adspersus †	—	—	0.02 (0.02)	29 (–)

croaker, weakfish, and silver perch (*Bairdiella chrysoura*) were all present at relatively high abundances (Table 4). Bay anchovy and butterfish were the dominant species in the offshore assemblage (Table 4). The preponderance of species found near the ridge compared to offshore was reflected in the ordination by the number of species centroids associated with the near-ridge assemblage. However, some species were found at similar abundances in more than one assemblage (i.e., scup [*Stenotomus chrysops*]), and their centroids may have been located closer to, but not within, any one assemblage (Fig. 6D).

The percentage of variance of the species-environment interaction reflected in the midsummer (54%) and late summer (67%) ordinations was substantial across both time periods (Table 5). Temperature, depth, and dissolved oxygen were significant environmental variables that explained the species assemblages in midsummer; whereas distance from the ridge and depth were the primary factors in late summer (Table 6).

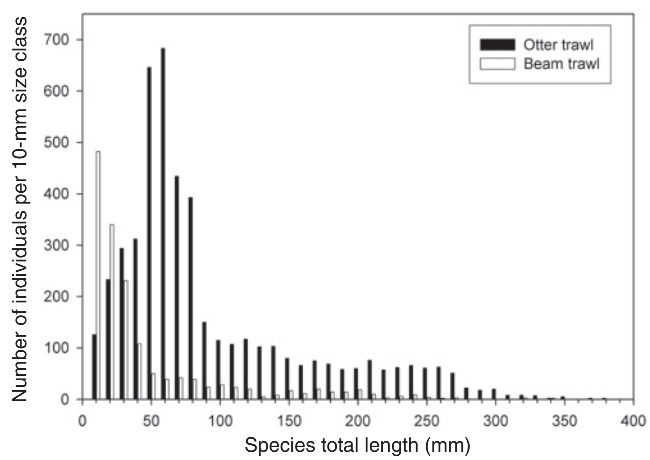

Figure 4

Length frequency (total length in millimeters, in 10-mm bins) of fishes captured by the beam and otter trawls. Seven individuals larger than 400 mm (all *Mustelus canis* [smooth dogfish]) captured in the otter trawl are not shown.

Table 3

Catch per unit of effort (CPUE, with standard error in parentheses) and mean size (mm, with standard error in parentheses) for species captured during mid-summer otter trawl sampling for 2001–06. Station assemblages were determined with canonical correspondence analysis as shown in Figure 6A. Taxa were measured to total length (†) or fork length (*). A dash indicates that no data were available.

	Assemblage					
	Inshore		Near-ridge		Offshore	
Species	CPUE	Size	CPUE	Size	CPUE	Size
Syngnathus fuscus †	0.64 (0.20)	116 (9)	0.03 (0.03)	127 (6)	—	—
Prionotus carolinus †	0.18 (0.18)	47 (2)	0.38 (0.13)	189 (13)	0.75 (0.26)	224 (8)
Scophthalmus aquosos †	0.18 (0.12)	62 (19)	0.25 (0.07)	129 (12)	0.08 (0.04)	270 (7)
Sphoeroides maculatus †	0.18 (0.18)	38 (23)	0.61 (0.28)	71 (3)	—	—
Anchoa mitchilli *	0.09 (0.09)	30 (–)	16.11 (9.15)	68 (1)	—	—
Etropus microstomus †	0.09 (0.09)	95 (–)	0.88 (0.24)	93 (3)	0.38 (0.10)	94 (10)
Menidia menidia *	0.09 (0.09)	55 (–)	—	—	—	—
Anchoa hepsetus *	—	—	1.92 (0.98)	65 (2)	—	—
Pomatomus saltatrix *	—	—	0.03 (0.02)	123 (7)	—	—
Peprilus triacanthus *	—	—	26.55 (15.8)	40 (1)	9.8 (3.2)	37 (1)
Urophycis regia †	—	—	1.2 (0.35)	173 (4)	0.08 (0.04)	157 (32)
Stenotomus chrysops *	—	—	0.47 (0.14)	111 (5)	0.05 (0.05)	106 (3)
Cynoscion regalis †	—	—	0.12 (0.14)	131 (11)	—	—
Prionotus evolans †	—	—	0.28 (0.12)	179 (13)	0.6 (0.41)	215 (6)
Menticirrhus saxatilis †	—	—	0.03 (0.02)	279 (25)	—	—
Centropristis striatus †	—	—	0.02 (0.02)	114 (–)	0.03 (0.03)	265 (–)
Paralichthys oblongus †	—	—	0.05 (0.03)	29 (2)	0.03 (0.03)	181 (–)
Urophycis chuss †	—	—	0.02 (0.02)	70 (–)	0.03 (0.03)	92 (–)
Hippocampus erectus †	—	—	—	—	0.03 (0.03)	53 (–)
Merluccius bilinearis †	—	—	—	—	0.05 (0.03)	175 (±21)
Citharichthys arctifrons †	—	—	—	—	0.03 (0.03)	68 (–)

Discussion

Species abundance and richness

The dominant fish families (Engraulidae, Paralichthyidae, Gadidae, Triglidae, Serranidae, Sciaenidae, and Stromateidae) and to some degree species (butterfish, spotted hake, northern searobin [*Prionotus carolinus*], black sea bass [*Centropristis striatus*], weakfish) captured by the two gears in the study area were similar to those previously found in inner continental shelf waters off of the northeast United States (Colvocoresses and Musick, 1984; Mahon et al., 1998) and southeast United States (Walsh et al., 2006). Previous comparisons between beam and otter trawls similar in size to those used in our study have shown that otter trawls collect more species and more individuals and that beam trawls catch smaller fish (Vasslides, 2007). This difference is reflected in the length-frequency histogram for all species (Fig. 4), as well as for the dominant species collected in both gears.

Overall species abundance (CPUE) and richness (RPUE) displayed a bimodal distribution across the inlet to the offshore transects, and the highest values occurred on either side of the ridge regardless of gear type (Fig. 3). This bimodal pattern has been previously suggested for fish (Martino and Able, 2003) and decapod crustaceans (Viscido et al., 1997) at Beach Haven Ridge but is in contrast to the findings from a number of studies of larger scale cross-shelf transects, where abundance has been shown to decrease linearly with depth in the Mid-Atlantic Bight (Colvocoresses and Musick, 1984), Chukchi Sea (Barber et al., 1997), and Mediterranean Sea (Colloca et al., 2003), but not in the Bering Sea (Mueter and Norcross, 1999).

The species composition and richness, and thus assemblage structure, varied between sampling gears. This was expected because beam trawls sample fishes on the bottom better than otter trawls (Wennhage et al., 1997) and thus capture more demersal species, including small, recently settled fish and small juveniles. This selectivity may explain the differences at certain sampling stations in regard to both abundance and species richness between the two trawl types. In the beam trawl, both abundance per tow and richness per tow at

Table 4

Catch per unit of effort (CPUE, with standard error in parentheses) and mean size (mm, with standard error in parentheses) for species captured during late summer otter trawl sampling during 2001–06. Station assemblages were determined using canonical correspondence analysis as shown in Figure 6B. Taxa were measured to total length (†) or fork length (*). A dash indicates that no data were available.

	Assemblage					
	Inshore		Near-ridge		Offshore	
Species	CPUE	Size	CPUE	Size	CPUE	Size
Syngnathus fuscus †	1.55 (0.62)	133 (3)	0.16 (0.07)	132 (7)	—	—
Prionotus carolinus †	0.07 (0.07)	47 (2)	0.23 (0.08)	230 (9)	0.12 (0.06)	131 (45)
Scophthalmus aquosos †	0.07 (0.04)	62 (19)	0.05 (0.03)	247 (33)	—	—
Sphoeroides maculatus †	0.21 (0.10)	89 (25)	0.08 (0.03)	98 (12)	0.03 (0.03)	90 (–)
Anchoa mitchilli *	4.69 (2.9)	51 (2)	372.15 (134.37)	58(1)	11.76 (9.49)	65 (1)
Etropus microstomus †	0.03 (0.03)	95 (–)	0.05 (0.03)	71 (4)	—	—
Menidia menidia *	0.41 (0.24)	71 (3)	—	—	—	—
Anchoa hepsetus *	0.24 (0.18)	76 (3)	2.02 (1.04)	86 (1)	—	—
Pomatomus saltatrix *	0.21 (0.13)	141 (17)	0.14 (0.06)	98 (2)	0.03 (0.03)	100 (–)
Peprilus triacanthus *	—	—	0.68 (0.17)	70 (5)	2.52 (0.80)	55 (3)
Urophycis regia †	—	—	0.08 (0.04)	217 (19)	0.06 (0.04)	187 (68)
Stenotomus chrysops *	—	—	0.52 (0.14)	152 (6)	0.35 (0.13)	126 (23)
Cynoscion regalis †	—	—	4.26 (0.66)	190 (4)	—	—
Prionotus evolans †	—	—	0.06 (0.03)	110 (13)	—	—
Menticirrhus saxatilis†	—	—	0.05 (0.03)	182 (54)	—	—
Centropristis striatus †	—	—	0.03 (0.02)	58 (24)	0.03 (0.03)	35 (–)
Micropogonias undulatus †	—	—	5.58 (2.29)	209 (4)	0.35 (0.21)	309 (9)
Bairdiella chrysoura †	—	—	1.09 (0.62)	131 (2)	—	—
Hippocampus erectus †	—	—	0.02 (0.02)	63 (–)	—	—
Merluccius bilinearis †	—	—	0.02 (0.02)	79 (–)	—	—

stations BHRTOP and BHR-9 were of intermediate and high values, respectively, whereas in the otter trawl these stations accounted for the lowest and intermediate values, respectively. Over 70% of the individuals captured at stations BHRTOP and BHR-9 during the beam trawl were young of the year (YOY) smallmouth flounder (*Etropus microstomus*), and the majority of these averaged 27 mm and 35 mm TL, respectively. During previous direct comparisons between beam and otter trawls it was found that CPUE and frequency of occurrence for smallmouth flounder were greater in beam trawls and that mean length was substantially less. Because this single species accounted for such a large proportion of the abundance at BHRTOP and BHR-9 as compared to the abundance at other stations, it appears that the selectivity of beam trawls plays a large role in estimating fish abundance and thus the fish assemblages in general.

The seeming discrepancies in RPUE between gear types at particular locations can be partially explained by the limited numbers of tows. At station BHR-9, data were collected from only two beam-trawl tows. Although ten species were collected, five species were represented by one individual and two species were represented by two individuals. Given this apparent patchiness, there is a possibility that additional sampling at this station would yield a RPUE that would more closely reflect the pattern observed in the otter-trawl tows. Even though a limited number of samples were taken with an otter trawl at BHRTOP ($n=6$), our previous opportunistic surveys with the same gear at other locations on the top of Beach Haven Ridge yielded low numbers of species per tow. However, twice the number of species were caught during midsummer sampling in 2006 at this station, but abundance of each new species was five individuals or less.

Fish-assemblage structure and environmental relationships

The number of assemblages and their constituent members varied by both gear and season. Two general groups were identified in the beam trawl (inshore and near-ridge+offshore) and three in the otter trawl (inshore,

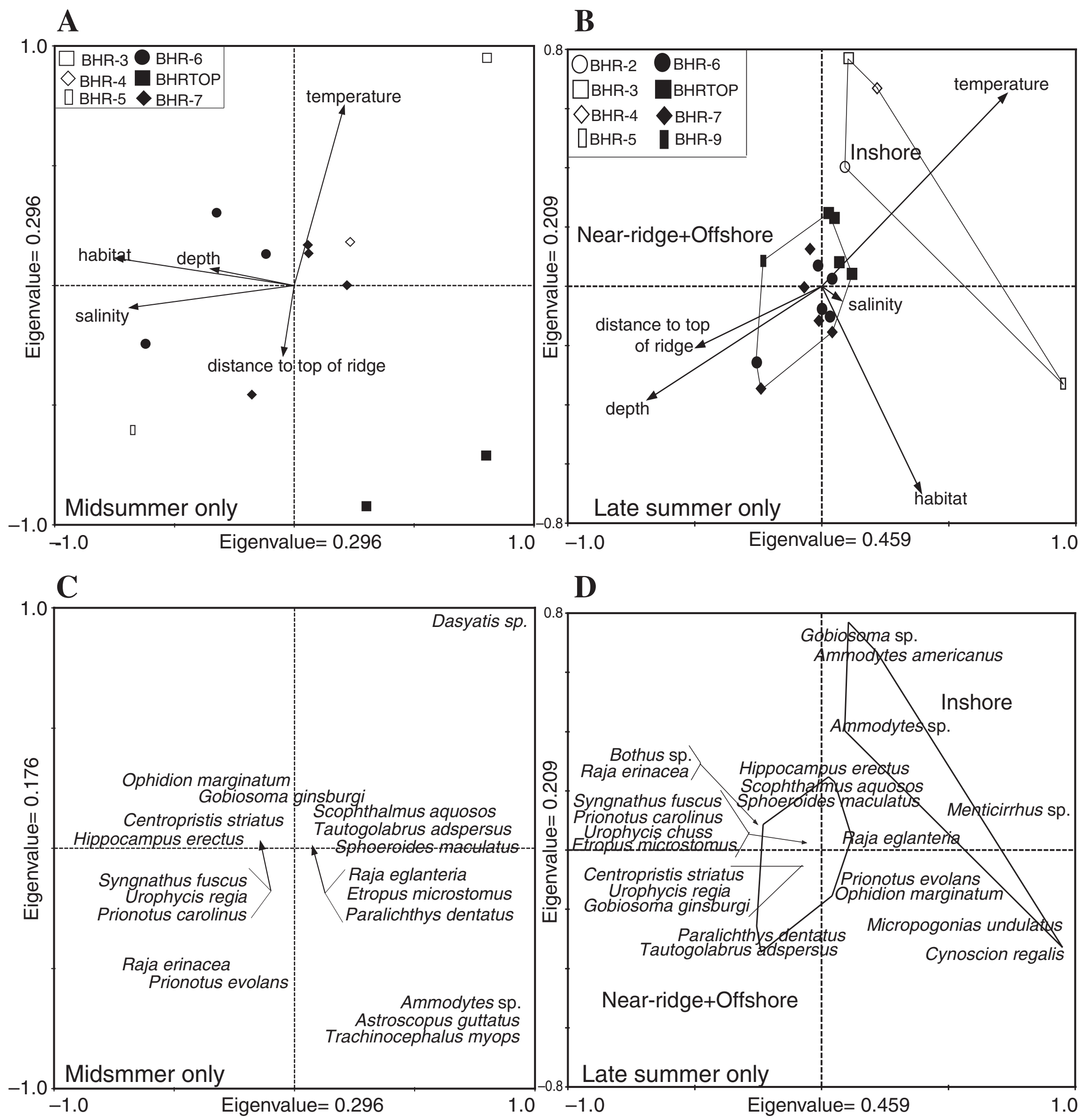

Figure 5

Canonical correspondence Analysis (CCA) ordinations of the beam trawl survey data (1991–95) displaying the station assemblages for midsummer only (**A**), late summer only (**B**), and the species assemblages for midsummer only (**C**) and late summer only (**D**). Solid lines within each figure box (A–D) enclose the boundaries of the identified assemblages. In A and B, each sampling station is identified by a different symbol and the arrows depict the gradient of each environmental variable. In C and D, species that occupy the same area of the graph are grouped by short lines and arrows denote their true locations.

near-ridge, and offshore). Within the Beach Haven Ridge beam trawl samples, 55% of the fish used in the analysis were found in both species assemblages, leaving nearly half of the species captured to be found in only one assemblage or the other. This is in stark contrast to the 2001–06 Beach Haven Ridge otter-trawl data subset, where 82% of the species were found in at least two of the three assemblages and only 18% of the species (silver perch, Atlantic silverside [*Menidia menidia*], northern kingfish [*Menticirrhus saxatilis*], and Gulf stream flounder [*Citharichthys arctifrons*]) were present in only one assemblage. Thus it appears that there is a definite gradient along the transect, represented by changes in species present in the beam trawl and by the relative abundances of shared species in the otter trawl.

Although cross-shelf gradients in demersal fish assemblages have been identified along the northeast United States (Sullivan et al., 2000), northwest United States (Mueter and Norcross, 1999), southwest United States (Johnson et al., 2001), and worldwide (Gray and

Table 5

Eigenvalues and cumulative percentage variance for each axis analyzed by season for the 1991–95 beam trawl data and 2001–06 otter trawl data by using canonical correspondence Analysis (CCA). The eigenvalues are a relative measure of the importance of each axis.

		CCA axis			
		1	2	3	4
1991–95 beam trawl data					
Midsummer	Eigenvalue	0.296	0.176	0.145	0.117
	Cumulative percentage variance				
	of species data	21.3	34.0	44.4	52.8
	of species environment	39.1	62.3	81.4	96.8
Late summer	Eigenvalue	0.459	0.209	0.153	0.132
	Cumulative percentage variance				
	of species data	17.2	25.0	30.8	35.7
	of species environment	46.8	68.1	83.8	97.2
2001–06 otter trawl data					
Midsummer	Eigenvalue	0.572	0.356	0.277	0.176
	Cumulative percentage variance				
	of species data	10.5	17.0	22.0	25.3
	of species environment	33.0	53.6	69.6	79.8
Late summer	Eigenvalue	0.343	0.236	0.128	0.067
	Cumulative percentage variance				
	of species data	10.7	18.1	22.1	24.3
	of species environment	39.8	67.2	82.0	89.9

Table 6

The *P* values from Monte Carlo permutation tests on the significance of the environmental variables in each data set. Significant *P* values ($P<0.05$) are shown in bold. A dash indicates that the variable was not measured.

	1991–95 beam trawl		2001–06 otter trawl	
Variable	Midsummer	Late summer	Midsummer	Late summer
Salinity	**0.036**	0.874	0.200	0.996
Temperature	0.212	**0.002**	**0.002**	0.360
Depth	0.120	0.266	**0.004**	**0.090**
Distance from ridge	0.062	0.094	0.406	**0.002**
Habitat complexity	0.796	**0.028**	0.132	0.112
Dissolved oxygen	—	—	**0.022**	0.654
Water clarity	—	—	0.218	0.824
pH	—	—	0.212	0.172

Otway, 1994), these gradients were all at substantially larger spatial scales. Few studies of either juveniles or adults have been conducted at a resolution similar to that of our study in inner continental shelf waters. Juvenile fish assemblages of the nearshore (<40 km) coast of Georgia exhibited a cross-shelf pattern in winter and spring, and a shallow group (8 m in depth) was separated from the other stations (12–18 m in depth) (Walsh et al., 2006). Fish assemblages in northern Argentina in the spring were identified as either those of the inner, central, or middle regions of the coastal shelf (Jaureguizar et al., 2006).

Analyses of fish assemblages across continental shelves often point to depth as the primary environmental variable correlated with the changes in fish-assemblage structure (Mahon et al., 1998; Walsh et al., 2006), whereas studies focused on shorter distances indicate a combination of environmental and physi-

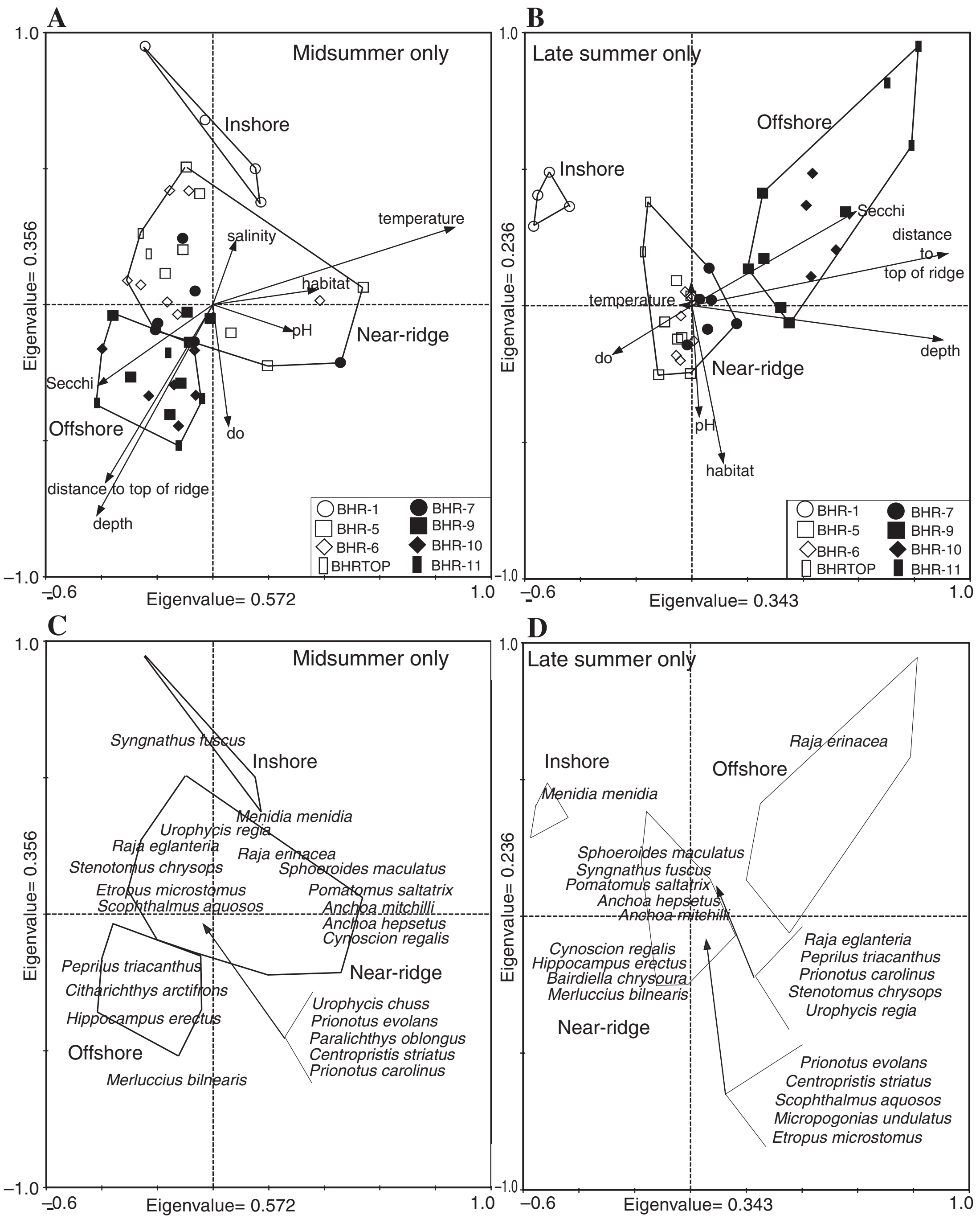

Figure 6

Canonical correspondence analysis (CCA) ordinations of the otter trawl survey data (2001–06) displaying the station assemblages for midsummer only (**A**), late summer only (**B**), and the species assemblages for midsummer only (**C**) and late summer only (**D**). Solid lines within each figure box (A–D) enclose the boundaries of the identified assemblages. In A and B, each sampling station is identified by a different symbol and the arrows depict the gradient of each environmental variable. In C and D, species that occupy the same area of the graph are grouped by short lines and arrows denote their true locations.

cal variables (Martino and Able, 2003; Jaureguizar et al., 2006). The results of our study point to the latter case. Temperature and distance from the top of the ridge were often as important explanatory factors as depth, and habitat complexity and dissolved oxygen were also correlated with the distribution of fish along the transect. Temperature has played an important role in regulating fish distribution in temperate waters (e.g., Colvocoresses and Musick, 1984; Able et al., 2006), and it may explain the variation in the species assemblages between mid- and late summer for both the beam and otter trawl. Furthermore, the temperature differences along a transect can also shape the species assemblages within a season, as seen in the significance levels for temperature between seasons in the otter trawl CCA (Table 6). In midsummer, when the CCA identified temperature as a statistically important environmental variable, there was a large temperature gradient from BHR-1 to BHR-5 and a slightly smaller change from BHR-7 to BHR-9. These temperature gradients are coincident with the three assemblages identified for the otter trawl midsummer samples in the CCA (Fig. 6A). In contrast, the late summer temperatures were fairly constant across the transect, and this constancy was reflected in the nonsignificant *P*-value for temperature in the CCA.

Although we examined seasonal and annual temporal scales, episodic events can also have a dramatic effect on species assemblages. The study area is well known as a region of upwelling during the summer months; it often has up to five upwelling events each year, typically lasting a week or more (Glenn et al., 2004). These upwelling events bring cooler water generally found at the offshore sampling locations onto the near-ridge stations. When sampling occurred during an upwelling event, similar species were captured at all stations along the transect (excluding BHR-1). However, in years where the bottom temperatures during sampling were higher than the average study temperature (1997, 1998, 2001, and 2005), the near-ridge species assemblage included weakfish and northern puffer, species more commonly associated with late summer when temperatures are warmer (Fig. 6C). It is interesting to note that upwelling events of 2001 were some of the most intense recorded during a 9-year study (Glenn et al., 2004). However, when the samples of 2001 were collected, the water temperatures had returned to the seasonal norm, thus illustrating the rapidity with which upwelling events break down and fish assemblages can change.

Although dissolved oxygen appears to be a significant factor in the arrangement of species assemblages along the sampling transect, its importance may be confounded by its relationship with temperature and depth. As expected, the highest mean dissolved oxygen levels were found at the stations with the coldest mean temperatures, which were also the deepest stations. However, the lowest mean dissolved oxygen value was found at a station in the same assemblage that had the highest value; thus the importance of dissolved oxygen remains unclear.

The trend toward less well-defined species assemblages when the environmental gradients were less pronounced lends some support to the idea that cross shelf patterns in species distributions are attributable to environmental gradients (Jaureguizar et al., 2006; Walsh et al., 2006). However, the importance of habitat complexity in the analyses of assemblages from both gear types (Table 6) indicates selection of specific habitats by some species within a large-scale environmental gradient (see Stoner and Abookire, 2002). This has been shown in many laboratory and field experiments for flatfishes (Neuman and Able, 1998; Stoner and Abookire, 2002) and other demersal fishes (Sullivan et al., 2000; Diaz et al., 2003). As suggested by Mueter and Norcross (1999), this difference may be due to differences in how juvenile or small fishes use benthic habitat compared to larger adult fishes.

The selection of habitat within the study area changed with ontogenetic stage; this is particularly true for the sandy substrate found on the top of the ridge. The beam trawl samples, which contained smaller, presumably younger juveniles, had greater species richness and abundance values on the ridge top than did the otter trawl, which captured larger juveniles and adults. The sandy substrate on the top of the ridge provided important habitat for species that bury themselves, such as northern stargazer (*Astroscopus guttatus*) (Able and Fahay, 1998) and snakefish (*Trachinocephalus myops*) (Sulak, 1990). These species were found only on the top of Beach Haven Ridge, although admittedly in small numbers. Sand lances, another group that buries itself in sand, was also found predominantly in the sandy substrates. In a paired video sled and beam trawl survey (where a video camera sled was towed along the bottom and then a beam trawl was dragged along the same area) on sand ridges off the coast of Maryland and Delaware, a substantially larger number of sand lances were captured in the video sled than in the beam trawl (Diaz et al., 2003), indicating that sand lance may be more important to the assemblage at Beach Haven Ridge than expected from the trawl results.

Time of day also affects the abundance, species richness, and identity of species captured in various habitats. A study of sand ridges offshore of Maryland and Delaware found that when complex habitats were located in proximity to simple habitats, fish abundance was twice as great in the complex habitats during the day, and the pattern was reversed at night (Diaz et al., 2003). This pattern is most likely due to 1) changes in foraging behavior over a diel period and to 2) smaller demersal fish selecting refuge from predators in complex habitats. The fact that all of the trawls in this study were conducted during daytime may explain why the stations located on either side of the top of the ridge, which had more complex habitats, had the highest values for abundance and richness.

There are a number of other possible explanations for the patterns in species abundance and assemblages identified herein that were not explored as part of this study. Investigations into the abundance and distribution of planktonic larvae around Beach Haven Ridge have revealed physical processes as important mechanisms in concentrating mollusk larvae on either side of the sand ridge (Ma et al., 2006). These same processes may be causing the increased abundance of pelagic fish species seen on the flanks of the sand ridges. The availability of preferred prey items, such as pelagic fishes like bay anchovy and butterfish, may also be affecting the abundance and distribution of fish species (Vasslides, 2007).

In summary, shoreface sand ridges may have a distinct influence on fish abundance and assemblages. The near-ridge habitats have higher species abundances and richness compared to the surrounding inner continental shelf and also possess a distinct species assemblage, including both recreationally and commercially important species. Additionally, the fish found at the top of the ridge were typical prey species (sand lances, anchovies, smallmouth flounder) favored by both resident and transient piscivores in the Mid-Atlantic Bight (Chao and Musick, 1977; Chase, 2002; Walter et al., 2003; Gartland et al., 2006) and thus sand ridges may influence the distribution of these economically important piscivores. As such, sand ridges appear to be important features of the inner continental shelf and may not be suitable areas for resource extraction activities.

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