

IMPROVING MODELS OF COVARIATION
BETWEEN MARINE COMMUNITIES AND THEIR HABITATS
BY INCORPORATING PELAGIC FEATURES
CAPTURED BY COASTAL OCEAN OBSERVATORIES

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ABSTRACT OF THE THESIS

Improving models of covariation
between marine communities and their habitats
by incorporating pelagic features
captured by coastal ocean observatories

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Fisheries habitats are spatially and temporally variable in the Mid-Atlantic Bight. Therefore, understanding how fisheries species respond to habitat change is important for developing effective management strategies. In this study, we use canonical correspondence analysis (CCA) to determine which habitat variables are most important in explaining variation in fish and invertebrate communities sampled using bottom trawls. Using partial CCA we also quantify the relative explanatory power of benthic factors, pelagic factors measured *in situ*, and pelagic factors measured remotely for describing species variability. Results show that pelagic habitat factors are as important as benthic habitat factors in determining species distributions, and that remote sensing can accurately represent many characteristics of fisheries habitats. Cross-shore and seasonal variation in environmental variables were the major predictors of fisheries habitats, accounting for 71.3% of the total explained community variation. We generated seasonal

spatial maps for these key gradients and fit response curves for 6 species along each gradient. Future possibilities for fisheries management are discussed.

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1. INTRODUCTION

Animal distributions are influenced by environmental factors that constrain physiology and environmental factors that are behaviorally favored. However, we still know little regarding which factors are important in defining habitat and how and why animals respond to these factors. Marine and terrestrial environments are often treated in similar ways when studying habitat and executing management strategy, even though they are very different. In terrestrial landscapes bottom structure is very important, habitat is slow to change, and primary producers are large and long-lived. In marine seascapes bottom structure is not as important, habitat can change more quickly, and primary producers are small and short-lived. Considering only the benthos in marine management is akin to treating a three-dimensional seascape as a two-dimensional landscape.

1.1 Benthic Habitat

In the marine environment, habitat is often defined by only a few environmental characteristics. Fisheries managers and scientists tend to focus on benthic features such as depth, sediment type, and bottom temperature (e.g. Chatfield et al. 2010). Benthic studies have demonstrated that these types of characteristics are important for defining the habitats of marine animals (Chatfield et al. 2010, Ysebaert et al. 2002), but consideration of solely the benthos excludes many of the other potentially important marine habitat characteristics. While benthic structure is certainly essential for defining habitat, pelagic features are also crucial because these animals are living in a three-dimensional seascape characterized by a fluid that varies in several ways that strongly influence metabolism (Fry 1971). These features are less stable and therefore not as

easily measured or studied. However, advances in observational technology have allowed us to include the pelagic environment in habitat models.

1.2 Pelagic Habitat

While the pelagic environment is more difficult to study, it is important to the habitat of benthic and pelagic marine species at various life stages; the abundance, distribution, and composition of marine life is to a large extent explained by physical processes such as currents, fronts, eddies, upwelling and downwelling regions, and wind-driven mixing, all of which are highly dynamic in both space and time (Game et al. 2009). Some of the most important environmental factors affecting the metabolism and growth of fish are features such as temperature, dissolved oxygen, food, predators, salinity, and pollutants, most of which involve pelagic processes (Fry 1971, Yamashita et al. 2001). These and several other pelagic features affect the distribution of marine species by varying degrees at each life history stage. Even though pelagic features are important at all life stages, more research has been done regarding how larvae are affected by pelagic processes than has been for juveniles or adults (Katz et al. 1994, Terceiro 2007).

The larvae of many marine species, including those that are benthic when mature, are often pelagic and therefore rely heavily on water column characteristics. Their survival is constrained by features such as water temperature and salinity, but they also need to have a sufficient amount of food available for growth and to sustain them until settlement and metamorphosis. Surface currents are also crucial to the larvae of many species (Bakun 2010, Katz et al. 1994, Leis 2006). Many species have narrow habitat ranges that can serve as acceptable nursing grounds for juvenile fishes. Whether larvae

reach one of these areas depends on when and where the larvae are released, where the ocean currents carry them, and the presence or absence of larval behavior (Bakun 2010, Katz et al. 1994, Leis 2006). Bakun (2010) describes three major classes of physical processes that create an ideal reproductive habitat for coastal fishes. Enrichment processes such as upwelling and mixing can provide food for larvae, and concentration processes such as convergence and frontal formation would have a similar effect. Lastly, currents could also contribute to processes that favor retention within or drift toward an appropriate larval or settlement habitat.

Less research has been done on adult fish responses to pelagic processes than has for larval responses. Despite this, it is clear that both benthic and pelagic species continue to rely on the pelagic environment as they mature. Even the distributions of benthic infauna can be related to pelagic habitat variables (Ysebaert et al. 2002). Population distributions fundamentally depend on the survival and metabolism of the individuals making up that population (Neill et al. 1994). We know that pelagic features like temperature (Marsh et al. 1999) and dissolved oxygen (Falkowski et al. 1980) can have significant impacts on mortality of many fish and invertebrate species. However, it is likely that these extreme events are not the only pelagic conditions that drive species distributions.

1.3 The Dynamic Ocean

Compared to pelagic characteristics, benthic characteristics are used more often in habitat models, partly because they are assumed to be relatively stable over time. While the benthos is not static, the stability assumption generally holds in the absence of benthic data with finer time-scale resolution. The pelagic environment is, however, more

dynamic, especially in temperate coastal areas such as the Mid-Atlantic Bight (MAB), and the stability assumption is less acceptable in models of pelagic habitats. The MAB exhibits particularly high seasonal variability: for example, sea surface temperature varies seasonally by about 23°C (Shearman & Lentz 2010), and average cross-shore flow reverses during the autumn (Gong et al. 2010). Pelagic habitat in the region is also patchy and highly dynamic on time scales much shorter than whole seasons, many features being dependent on storms, variable winds, river runoff, sunlight, and many others (e.g. Glenn et al. 2008). The rapid change in pelagic habitat has made it difficult to incorporate these features into habitat models. However, advances in ocean observatories have allowed us to remotely measure many of these characteristics, including surface currents and SST. Several of these factors can be used to calculate other features, such as divergence and chlorophyll. Certain other characteristics that are neither directly measured nor calculated can relate to features that are measured. For example, remotely sensed currents can affect mixing, which in turn relates to features such as oxygen and productivity. This technology enables us to observe large regions with the fine spatial and temporal resolution necessary to develop fisheries-based habitat models.

1.4 Advancing Science and Management

With the increasing availability of data, it is becoming more important to create habitat models that merge the environment and species abundance and distribution. Understanding how fish respond to dynamic habitat characteristics is important both because it provides the opportunity to gain scientific understanding of the ecosystem and because it may improve fisheries management and economics. Better understanding of

the relationships between marine species and their environment can lead to the application of habitat models in management decisions, which would ideally lead to more sustainable fisheries (Game et al. 2009).

This study analyzed benthic and pelagic environmental characteristics to determine which factors were most important to the Mid-Atlantic Bight fish and invertebrate community. We also examined how remotely sensed variables contributed to the habitat characteristics important to the community. Using these results we can begin to define habitat and consider how we can measure and use important environmental characteristics in management decisions.

2. IMPROVING HABITAT MODELS BY INCORPORATING PELAGIC FEATURES CAPTURED BY OCEAN OBSERVATORIES

2.1 Introduction

Spatial distributions of many species are largely a result of habitat selection based on behavior and environmental constraints. The factors that define habitat, including temperature, benthic structure, and productivity, can impact the growth, survival, and reproductive success of individuals and these effects in turn influence the productivity and stability of entire regional populations (Fry 1971; Neill et al. 1994, Yamashita et al. 2001). In temperate areas like the Mid-Atlantic Bight (MAB) a diverse array of habitat characteristics can be observed within a single region over the course of a year. These include seasonal variation as well as environmental variation occurring over much shorter time scales. Many species in these regions are highly migratory, allowing them to respond to the frequent changes in the environment and also allowing them to use a variety of habitats at different times in their life cycles (Bakun 2010). Populations experience increased vulnerability to fishing pressure at certain times and in certain areas, especially over migration routes and in breeding and foraging areas (Game et al. 2009). In order to develop effective space- and time-based conservation strategies, it is important to understand how habitats change over time and how animal populations respond to changes in major environmental cues like temperature (Yamashita et al. 2001) and currents (Bakun 2010, Ysebaert et al. 2002).

There is a tendency to concentrate on benthic characteristics when describing the habitats selected by marine species (e.g. Chatfield et al. 2010). However, both pelagic and benthic species depend on the pelagic environment for a variety of reasons. Many

species spend at least part of their life cycles living in the water column, or have prey that rely on water column characteristics (Yamashita et al. 2001). Because the vertical water column is heavily used by fish species, seascapes should ideally be evaluated in three-dimensions. Including water column (pelagic) variables, such as currents and water column stability, in addition to benthic variables in habitat models gives a more complete view of the ecosystem and can be extremely beneficial for ecosystem analysis and development of management strategies. Pelagic features such as maximum tidal current velocities, for example, help predict the distributions for even macrobenthic infauna in an estuary (Ysebaert et al. 2002). Until recently, it has been very difficult to measure pelagic habitat factors over large spatial and temporal scales because of the difficulty and cost in regularly sampling the ocean on synoptic scales.

The Integrated Ocean Observing System (IOOS) now provides information about many of the pelagic features that can influence population and community dynamics over these synoptic scales. IOOS data includes pelagic variables detected remotely via satellite (i.e. sea surface temperature and ocean color), high-frequency (HF) radar (i.e. sea surface currents), and gliders (i.e. water column temperature, salinity, optical backscatter). These data streams are analyzed to produce derived variables such as chlorophyll, water mass, divergence, and vorticity. Satellites and HF radar currently provide the greatest amount of spatial coverage, including synoptic maps of surface currents, temperature, and chlorophyll. These fields can be combined to map the location and relative strength of water mass boundaries. While these observations are confined to the near surface of the ocean, they are often indicative of the sub-surface environment.

For the past several years, these pelagic features and processes have been well-documented in the MAB through the use of remotely sensed data from the Mid-Atlantic Regional Association Coastal Ocean Observing System (MARACOOS, www.maracoos.org), a regional subdivision of IOOS. Remote sensing has been used to help define habitat and biological responses in other regions (e.g. Hardman-Mountford et al. 2008, Palacios et al. 2006). However, the increasing availability and coverage of various types of remotely sensed data in the MAB allow us to examine relationships between fish and the pelagic environment that until now couldn't be studied.

Even benthic species are strongly linked to many pelagic habitat features and processes that are described by ocean observatories. For example, Bakun (2010) describes three major classes of physical processes that are important for yielding ideal reproductive habitat for coastal fishes: enrichment processes such as upwelling and mixing, concentration processes such as convergence, formation of fronts, and water column stability, and processes that favor retention within or drift toward proper habitat, most of which can be described by remotely sensed data streams. By considering the comparatively stable benthic features along with the dynamic pelagic features that can be measured both *in situ* and remotely with IOOS, we can more precisely describe the three-dimensional structure of the environment to which marine species respond (Game et al. 2009).

In this study we combined benthic, pelagic, and remote measures of the physical habitat in the Mid-Atlantic Bight. We built statistical relationships between habitat characteristics likely to affect the growth, survival, dispersal, and reproduction of marine species, and fish abundances available from the National Marine Fisheries Service,

Northeast Fisheries Science Center's (NMFS-NEFSC) bottom trawl survey data. The study consisted of three major components (Fig. 1). First, we determined which environmental variables were most strongly correlated with fish and invertebrate abundance using the multivariate ordination technique canonical correspondence analysis (CCA). Second, we used partial CCA to quantify the relative importance of three categories of environmental variables: benthic, *in situ* pelagic (CTD), and remotely sensed pelagic. Third, for each of the first three CCA axes we generated spatial maps of the environmental features as well as response curves for six species well-explained by the CCA model whose habitat distributions differed by latitude and by depth in the water column. Our goals in this analysis were to establish habitat-defining environmental characteristics, to determine the effectiveness of remote sensing technology in habitat models, and to use the response curves to infer any difference in response between species with differing latitudinal ranges or water column preferences.

2.2 Methods

2.2.1 Study Area

The Mid-Atlantic Bight (MAB) extends from Cape Cod, MA to Cape Hatteras, NC, and is an ideal location to study the impact of pelagic features on fish and invertebrate populations. Because the habitats in this region are patchy and can change over short time scales, many of the fish and invertebrates in the region are highly migratory. Many of these species are also of great interest to both commercial and recreational fisheries. There is high benthic biomass in this region, but small pelagic species are still very important (Link et al. 2008). These species could respond to many pelagic conditions that exhibit particularly high spatial and temporal (especially seasonal)

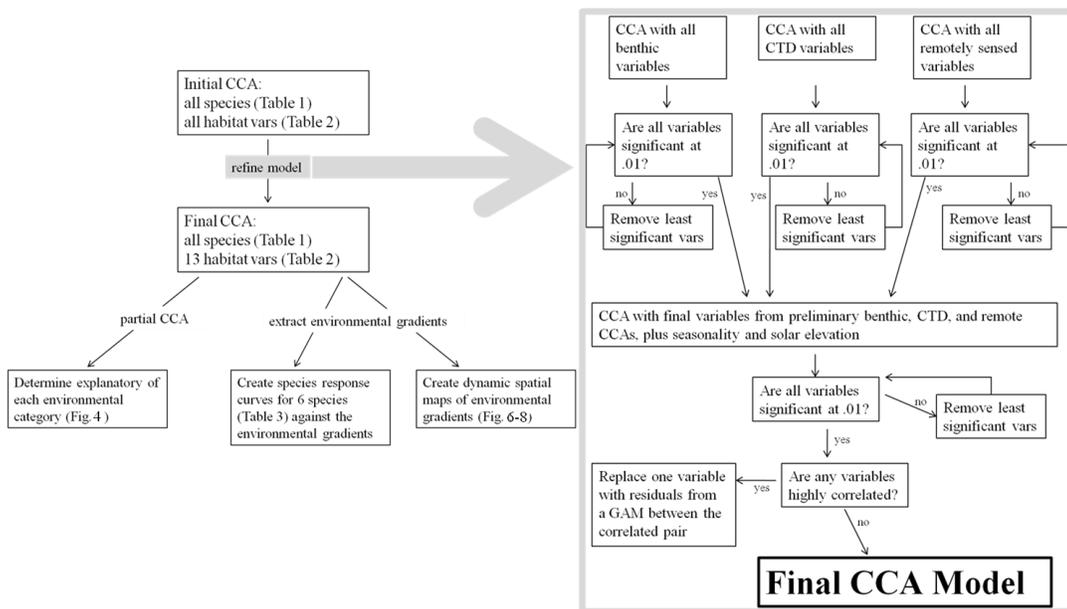


Figure 1. Flow chart of the analysis. The sequence of steps used to create the final model, and the subsequent analyses, are shown.

variation in this area, such as surface and bottom temperature, stratification, and surface currents (Gong et al. 2010, Shearman & Lentz 2010). Because of the high variation, the location of a species' chosen habitat can be highly dynamic. Now that we have a robust ocean observation system to capture these habitats, this region is well-suited to conduct this type of research.

2.2.2 Species Abundance Data

Abundance estimates for fish and invertebrate species were collected in the National Marine Fisheries Service, Northeast Fisheries Science Center's (NMFS-NEFSC) autumn, winter, and spring fisheries bottom trawl surveys (Table 1, Fig. 2). The survey design and trawl characteristics are described in detail by Azarovitz (1981). Winter cruises occurred in February (year day [yd]=39-57), spring cruises between March and the beginning of May (yd=63-123), and autumn cruises from the beginning of September through late October (yd=243-313), when the water column was still relatively stratified (Gong et al. 2010). Survey tows were made with a #36 Yankee trawl (12.7 cm stretched mesh opening, 11.4 cm stretched mesh cod end, 1.25 cm stretched mesh lining in cod end and upper belly) equipped with rollers and a 10.4 m wide x 3.2 m high opening. The net was towed at ~3.5 knots over the bottom for 30 minutes. Distances a net was towed over the bottom at each station averaged 1.9 km (95% Confidence limits 1.75-2.01 km). Trawls tows occurred throughout the 24 hour day.

We selected a spatial and temporal domain for analysis based upon the availability of remotely sensed data collected by MARACOOS. NEFSC bottom trawl samples collected from February 2003 through October 2007, between latitudes 37.14 &

Table 1. Common and scientific names of the 65 species included in the multivariate analysis. Included species were those observed in at least 10 of the trawls used in the analysis

Common Name	Scientific Name
Blueback Herring	<i>Alosa aestivalis</i>
Alewife	<i>Alosa pseudoharengus</i>
American Shad	<i>Alosa sapidissima</i>
Northern Sand Lance	<i>Ammodytes dubius</i>
Deepbody Boarfish	<i>Antigonia capros</i>
Striated Argentine	<i>Argentina striata</i>
Jonah Crab	<i>Cancer borealis</i>
Atlantic Rock Crab	<i>Cancer irroratus</i>
Black Sea Bass	<i>Centropristis striata</i>
Shortnose Greeneye	<i>Chlorophthalmus agassizi</i>
Gulf Stream Flounder	<i>Citharichthys arctifrons</i>
Atlantic Herring	<i>Clupea harengus</i>
Conger Eel Uncl.	<i>Congridae</i>
Barndoor Skate	<i>Dipturus laevis</i>
Smallmouth Flounder	<i>Etropus microstomus</i>
Red Deepsea Crab	<i>Geryon quinquedens</i>
Witch Flounder	<i>Glyptocephalus cynoglossus</i>
Blackbelly Rosefish	<i>Helicolenus dactylopterus</i>
Sea Raven	<i>Hemitripterus americanus</i>
American Lobster	<i>Homarus americanus</i>
Northern Shortfin Squid	<i>Illex illecebrosus</i>
Fawn Cusk-Eel	<i>Lepophidium profundorum</i>
Little Skate	<i>Leucoraja erinacea</i>
Rosette Skate	<i>Leucoraja garmani</i>
Winter Skate	<i>Leucoraja ocellata</i>
Yellowtail Flounder	<i>Limanda ferruginea</i>
Atlantic Seasnail	<i>Liparis atlanticus</i>
Longfin Squid	<i>Loligo paeleii</i>
Goosefish	<i>Lophius americanus</i>
Ocean Pout	<i>Macrozoarces americanus</i>
Longspine Snipefish	<i>Macrorhamphosus scolopax</i>
Grenadier Uncl.	<i>Macrouridae</i>
Spider Crab Uncl.	<i>Majidae</i>
Haddock	<i>Melanogrammus aeglefinus</i>
Atlantic Silverside	<i>Menidia menidia</i>
Offshore Hake	<i>Merluccius albidus</i>
Silver Hake	<i>Merluccius bilinearis</i>
Smooth Dogfish	<i>Mustelus canis</i>
Lanternfish Uncl.	<i>Myctophidae</i>
Bullnose Ray	<i>Myliobatis freminvillei</i>
Longhorn Sculpin	<i>Myoxocephalus octodecemspinosus</i>

Atlantic Hagfish	<i>Myxine glutinosa</i>
Snake Eel Uncl.	<i>Ophichthidae</i>
Summer Flounder	<i>Paralichthys dentatus</i>
Fourspot Flounder	<i>Paralichthys oblongus</i>
Butterfish	<i>Peprilus triacanthus</i>
Armored Searobin	<i>Peristedion miniatum</i>
Sea Lamprey	<i>Petromyzon marinus</i>
Sea Scallop	<i>Placoepecten magellanicus</i>
Bluefish	<i>Pomatomus saltatrix</i>
Northern Searobin	<i>Prionotus carolinus</i>
Striped Searobin	<i>Prionotus evolans</i>
Winter Flounder	<i>Pseudopleuronectes americanus</i>
Clearnose Skate	<i>Raja eglanteria</i>
Windowpane	<i>Scophthalmus aquosus</i>
Atlantic Mackerel	<i>Scomber scombrus</i>
Chain Dogfish	<i>Scyliorhinus rotifer</i>
Bobtail Uncl.	<i>Sepiolidae</i>
Spiny Dogfish	<i>Squalus acanthias</i>
Scup	<i>Stenotomus chrysops</i>
Tonguefish	<i>Symphurus</i>
Red Hake	<i>Urophycis chuss</i>
Spotted Hake	<i>Urophycis regia</i>
White Hake	<i>Urophycis tenuis</i>
Buckler Dory	<i>Zenopsis conchifera</i>

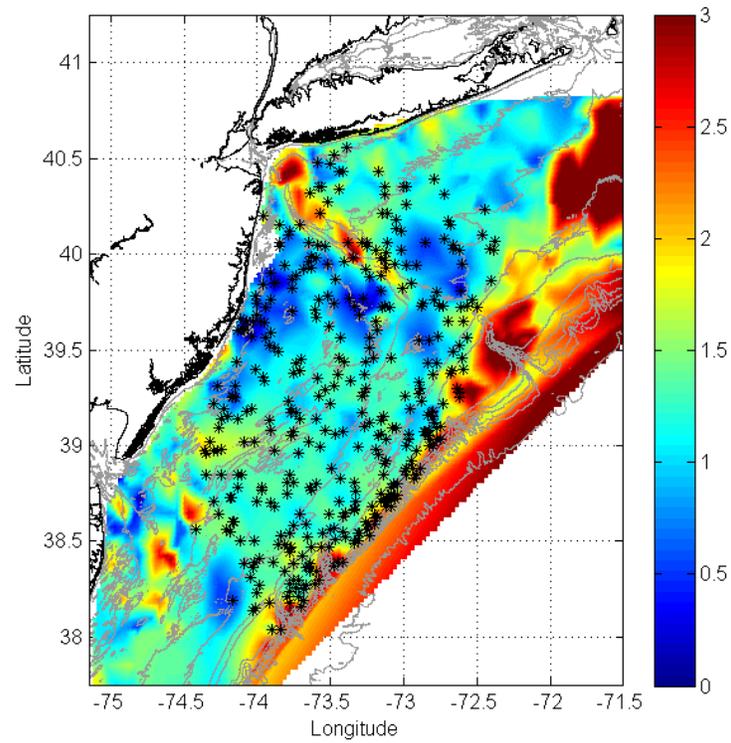


Figure 2. Locations of samples. The locations of the trawls included in the analysis are shown overlapping a map of sediment grain size on a phi scale.

40.85 N and Longitudes -70.83 & -75.16 fit within that domain. An average of 101 stations was sampled during spring and autumn cruises. An average of 70 stations was sampled during the winter.

2.2.3 Habitat Data

2.2.3.1 Benthic data

We computed topographic bottom habitat characteristics from the 3-arc-second NGDC Coastal Relief Model (<http://www.ngdc.noaa.gov/mgg/coastal/coastal.html>; 93m cell size; Table 2). We used circular moving window analysis in GRASS GIS software to calculate median and standard deviations of bottom depth, aspect, slope, and curvature from the relief model (Neteler & Mitasova 2008). We selected a window diameter of 1950 meters to correspond to the median length of NEFSC trawl tows (1910 meters). Profile and tangential bottom curvature measured the concavity (i.e. valleys, negative values) and convexity (i.e. ridges, positive values) of the surface parallel and tangential to major axes of slope, respectively (Neteler & Mitasova 2008). Sediment grain sizes (ϕ) for the trawl samples were selected from a map interpolated from records in the usSEABED data base (Reid et al. 2005). The map of sediment grain size had a spatial resolution of 2000 meters and was constructed using sampling bias correction, maximum-likelihood resampling, and a spline-in-tension algorithm described in Goff et al. (2005 & 2008).

2.2.3.2 Pelagic data

We used conductivity, temperature, and depth (CTD) profiles collected during NEFSC bottom trawl surveys to describe water column characteristics including bottom temperature, salinity, water column structure and stability (Table 2). We considered

Table 2. Data sources and possible ecological impacts of environmental variables considered in the CCA. Unless otherwise noted, the source of benthic variables is <http://www.ngdc.noaa.gov/mgg/coastal/coastal.html>, the source of CTD variables is the shipboard CTD, and the sources of remotely sensed data are HF radar for surface current data and Moderate Resolution Imaging Spectrometer (MODIS) for satellite data. Geographic coordinates were recorded at the time of the trawl, and solar elevation was calculated using the maptools library in R.

*variable is included in the final CCA model

*¹residuals of a GAM with log-transformed depth are included in the final CCA model

*²anomalies from MAB 7-year monthly averages are included in the final CCA model

Habitat Variable	Spatial Resolution	Effect or Process
Solar elevation	n/a	Vertical migration/catchability
Seasonality	n/a	Various
Benthic Data		
Depth (μ^* & SD)	1.95 km	Structural/spatial refuge
Slope (μ^{*1} & SD)	1.95 km	Structural/spatial refuge
Aspect (SD)	1.95 km	Structural/spatial refuge
Profile curvature (μ & SD)	1.95 km	Structural/spatial refuge
Sediment grain size (μ^* , from USSeabed)	2 km	Structural/spatial refuge/enrichment
Pelagic Data: CTD		
Bottom temperature*	n/a	Metabolic rate
Bottom salinity	n/a	Proximity to freshwater source
Surface salinity* ¹	n/a	Proximity to freshwater source
Mixed-layer depth	n/a	Mixing/primary productivity
Stratification*	n/a	Mixing/primary productivity
Simpson's PE (upper 30 m)	n/a	Mixing/primary productivity
Pelagic Data: Remotely Sensed (HF Radar)		
Cross-shelf velocity (raw μ & SD, detided μ & SD, filtered μ^* & SD)	10 km radius	Advection/movement cost/mixing
Along-shelf velocity (raw μ & SD, detided μ & SD, filtered μ & SD)	10 km radius	Advection/movement cost/mixing
Variance in raw velocities (cross-shelf* and along-shelf)	10 km radius	Tidal mixing/episodic forcing
Divergence/convergence (μ & SD)	10 km radius	Advection/movement cost/mixing
Divergence/convergence tendency*	n/a	Advection/movement cost/mixing
Vorticity (μ & SD)	10 km radius	Eddy development/retention
Vorticity tendency	n/a	Eddy development/retention
Pelagic Data: Remotely Sensed (Satellite)		
Sea surface temperature (μ^{*2} & SD)	10 km radius	Metabolic rate/seasonality
Chlorophyll- <i>a</i> (μ & SD)	10 km radius	Primary productivity/organic matter

Water leaving radiances at 412, 443, 488, 531, 551, 667 nm (μ & SD)	10 km radius	Water clarity & brightness/organic matter
Water leaving radiance divided by the maximum at each trawl: 412, 443, 488*, 531, 551* ¹ , 667 nm	10 km radius	Water clarity/organic matter
Water mass class	n/a	Various
Gradient strength & distance to gradient (frontal index)	n/a	Enrichment/concentration

“mixed layer” depth at which density was 0.125 kg/m^3 higher than at the surface layer (Levitus 1982), a stratification index calculated as the density difference between 50 m and the surface, and Simpson’s potential energy anomaly (PE; Simpson 1981) in the models. The stability index for the entire water column was positively correlated with bottom depth. To avoid its being confounded with depth, a measure of Simpson’s PE was calculated within only the upper 30 meters.

Surface features were observed remotely using shore- and space-based sensors. High Frequency (HF) radar (Barrick et. al. 1977) provided remotely sensed surface current measurements for our analysis (Table 2). A network of HF radars (frequency = 5 MHz) maintained by MARACOOS measures radial current vectors that are geometrically combined to produce total vector surface current maps each hour with a resolution of 6 km from Cape Hatteras, NC to Cape Cod, MA and from the shore to the edge of the continental shelf (www.maracoos.org, Roarty et al. 2010). These data have been used to describe seasonal (Gong et al. 2010) and event-scale surface dynamics (Dzwonkowski et al. 2009, 2010) in the MAB. For this analysis the entire raw time series for each HF radar grid point was de-tided using a least-squares fit of the five strongest tidal constituents (M2, S2, N2, K1, and O1). This de-tided data was then low pass filtered with a cutoff period of 30 hours. We only used data for grid points with > 25% return over the annual records. Surface divergence, represented as vertical velocity at 1 m depth, and vorticity, normalized by the local coriolis parameter of the lowpass filtered fields, were calculated using finite difference. The same processing was used as in Gong et al. (2010) and Dzwonkowski et al. (2009, 2010). We considered one-day and eight-day mean raw, de-

tided, and filtered cross-shore and along-shore velocity, as well as divergence, vorticity, and the variance of the raw fields within 10 km of each trawl sample in our modeling.

In addition to considering short-term upwelling and downwelling, we wanted to test the species response to regions with more consistent upwelling and downwelling. To quantify this we calculated a new “divergence tendency” variable by assigning a new value of -1 to instantaneous divergence (vertical velocity) values that were <-0.1 m/day (downwelling), 0 to those between -0.1 and +0.1 m/day (neither), or +1 to values $>+0.1$ m/day (upwelling). These new values were averaged for each grid point to produce a mapped index of upwelling and downwelling potential for each season and year. We calculated divergence tendency for each site by averaging all seasonal means within 10 km of the survey site. The same processing was performed to generate vorticity tendencies using threshold values of ± 0.02 . The thresholds chosen were in approximately the 25th and 75th percentile of the entire set of values.

Satellite remote sensing provided maps of surface temperature, chlorophyll-*a*, and water-leaving radiance within 10 km of each NEFSC trawl tow over both the 24 hours previous to the tow and the 8 days previous (Table 2). We used data from the Moderate Resolution Imaging Spectrometer (MODIS) binned to 1km spatial resolution with the standard data quality flags using Seadas v5.3 for sea surface temperature (SST) and ocean color (oceancolor.gsfc.nasa.gov). SST can range from less than 3 °C to about 28 °C in the MAB, especially in shallower water (Shearman & Lentz 2010), and we wanted to examine spatial anomalies independent of the strong seasonal signal. To do this, anomalies of these values based on monthly 7-year composites averaged over the entire study site were used rather than raw SST. To account for this adjustment, we also

included season as a factor in the analysis. We considered measurements of chlorophyll (mg m^{-3}), and normalized water-leaving radiance ($\text{W m}^{-2} \text{st}^{-1} \mu\text{m}^{-1}$) at 412, 443, 488, 531, 551, and 667 nm (nlw412, nlw443, ...) for our models. In addition to raw channel values, we also considered each wavelength divided by the maximum radiance on a survey by survey basis (from here on we refer to the wavelengths relative to the maximum for each survey as rnlw412, rnlw443, ...).

Ensemble clustering was applied to satellite sea surface temperature and reflectance measured at 490 and 555 nm to objectively classify water masses, and gradient strengths along frontal boundaries between water masses were determined using methods described in Oliver et al. (2004) and Oliver & Irwin (2008). We used maps of gradient strength along frontal boundaries of 27 water masses identified to compute the distance (d km) to, and gradient strength (∇G) of the nearest frontal boundary for each bottom trawl sample. We then calculated a frontal index (FI) for each trawl using the equation:

$$\text{FI} = \ln(\nabla G / d \text{ km} + 1).$$

Many of the 27 water masses contained fewer than 5 NEFSC trawl samples. As a result, we agglomerated the 27 water masses into 8 water masses using k-means clustering and the satellite data used in the original ensemble clustering. Each of the 8 water masses included at least 20 samples.

Since the species selected for analysis can exhibit day-night differences in behavior, including vertical migration, we expected capture efficiencies in bottom trawls to vary with the time of day of the sampling (Powell et al. 2004). We used the Maptools library in R (Lewin-Koh & Bivand 2009) to estimate solar elevations for the times and

locations of each trawl, which we considered in our model for partial analysis. All of the environmental variables except for season and solar elevation were divided into one of three categories: CTD (*in situ* pelagic), IOOS (remotely sensed pelagic), or benthic (Table 2).

2.2.4 Model Development

All statistical analysis was performed using R software (R Development Core Team 2008, Legendre & Legendre 1998, Bolker 2008, Jongman et al. 1995, McGarigal et al. 2000). The canonical correspondence analysis (CCA), used for variable selection and model partitioning, was done using the *vegan* library (Oksanen et al. 2008). The *vegan* library was also used in the goodness-of-fit tests to determine how well each species was explained by the different axes defined by the CCA. Generalized additive models (GAM), used in variable selection and to plot species responses to habitat gradients derived from the CCA were done using the *mgcv* library (Wood 2004, 2006, 2008). We used backward selection of variables within each category of habitat data and with all habitat categories combined to create the final CCA model, used a partial CCA to determine the relative explanatory value of each category, and used GAM analysis of species responses to the habitat gradients extracted from the full CCA. Figure 1 shows the sequence of the model development.

2.2.4.1 Variable selection for models

We used canonical correspondence analysis (CCA) for our model because it allowed us to simultaneously ordinate both the environmental and log-linear species responses, and also allowed for partial analysis (Oksanen et al. 2008). This technique determines how the environmental variables can be combined to best explain the total

community variation. It reduces the number of factors that need to be considered to predict community variation by taking several environmental variables and creating fewer factors (called axes) made up of linear combinations of the original environmental variables, which better explain the community variation than one environmental variable alone would.

The 65 species we used for this analysis were observed in at least 10 of the bottom trawls (Table 1). Species abundance was normalized to the trawl distance and log-transformed. Initially, we calculated three separate CCAs: one for each category of environmental variables (benthic, CTD, and remotely sensed). Because there was a large left-skew to depth, we used log-transformed depth in the model. We used variables from these analyses that were significant at the 0.01 level in a CCA containing environmental variables from all three categories, along with season and solar elevation. We tested the significance of the model terms in the CCA and the least significant environmental variables were removed from the analysis. This process was repeated until all environmental variables were significant to the model at a level of 0.01. We further culled variables by only including those with possible mechanistic effects on the physiology or behaviors of the animals (Table 2). For variables that provided the same information as others, the less noisy and more ecologically meaningful variables were used; remotely sensed 8-day means were used in place of 1-day means, divergence and vorticity tendencies instead of means, filtered current velocities instead of de-tided or raw velocities, and water-leaving radiances normalized to the maximum water-leaving radiance in place of the original water-leaving radiance values.

Any environmental variables included in the resulting CCA model that were ecologically meaningful but highly correlated with each other were modified to eliminate redundancy. To achieve this we fit a generalized additive model (GAM) to the two variables, and the values of one of the correlated variables were replaced with the differences (residuals) between the observed values and those predicted by the GAM. We performed another CCA using residuals instead of the raw variable, and if the residuals were no longer significant we removed them from the model. This was necessary for bottom slope, surface salinity, mixed-layer depth, and rnlw551, all of which were strongly correlated with depth. Residuals of mixed-layer depth were highly correlated with stratification, and were removed from the final model.

The final CCA model included the 65 species listed in Table 1 and 13 environmental variables: season, 3 benthic variables, 3 CTD variables, and 6 remotely sensed variables (Table 2).

2.2.4.2 Model partitioning

We determined relative explanatory power of each category of environmental data (benthic, CTD, and remotely sensed) and overlap in explanatory power between categories using a partial CCA (Borcard & Legendre 1992). The variables included in each category are listed in Table 2. We calculated partial CCAs to determine the amount of variation explained by all three categories together (which included all variables in the final model except for season) and by each of the three categories separately. We also calculated constrained CCAs for each category using the variables from the other two categories as constraints, as well as two additional constrained CCAs for each category using the variables from each of the other categories individually as constraints. The

amount of variation explained by each of the partial and constrained CCAs could be considered together to calculate the relative explanatory power of each category and how redundant the categories are with each other (Fig. 3).

2.2.4.3 *Species responses to environmental variability*

Scores for the first three CCA axes were calculated for each trawl survey included in the model. These scores were matched to the corresponding survey's time and location, and the scores were seasonally mapped. The color maps were derived using bilinear interpolation and the contours using linear interpolation, both on a grid with a cell size of 0.025° lat (2.8 km) by 0.025° lon (2.1 km). Species response curves were considered in tandem with these spatial maps to infer where a species would be most likely to occur.

To describe species responses to habitat, we chose six species of the 65 included in the CCA to be analyzed in relation to the environmental gradients extracted from the CCA. These species represented different latitude (north and south) and water column preferences (pelagic fish, pelagic squid, and benthic flatfish), and included Atlantic herring (*Clupea harengus*), witch flounder (*Glyptocephalus cynoglossus*), Northern shortfin squid (*Illex illecebrosus*), scup (*Stenotomus chrysops*), summer flounder (*Paralichthys dentatus*), and longfin squid (*Loligo paeleii*) (Table 3). Each of these is common in the MAB and is generally well-explained (as shown by a goodness-of-fit test) by the final CCA model. GAM (Wood 2004, 2006, 2008) was used to fit a response curve for the abundance of each of these six species to the score of the first three CCA axes. To place species on the same scale, abundances were standardized to maximum observed abundance.

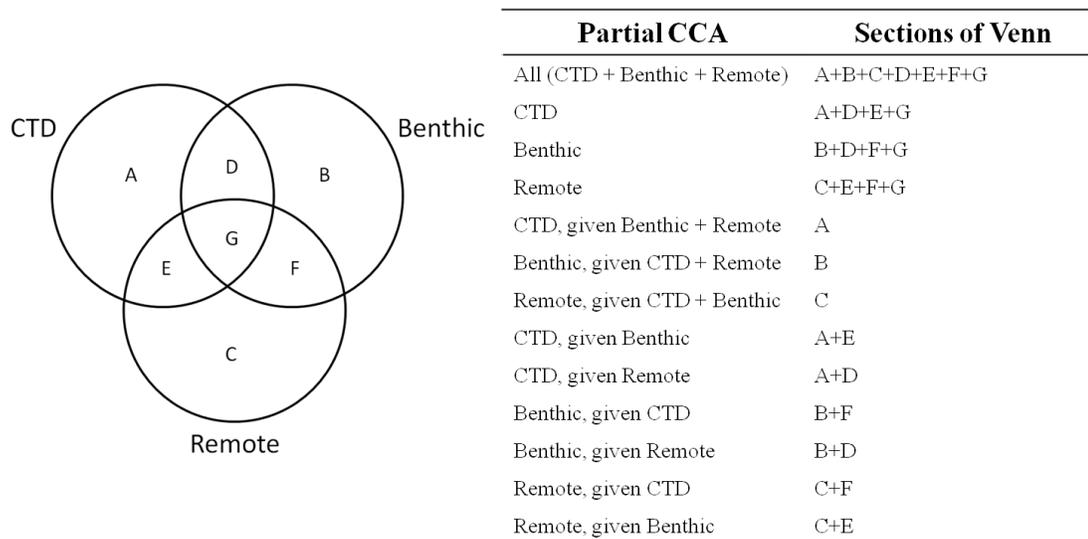


Figure 3. Partial CCA. Calculation of the relative explanatory power for each category of data.

Table 3. The 6 species analyzed in response to the environmental gradients extracted from the CCA.

Common Name	Scientific Name	Latitudinal Region	Water Column Preference
Atlantic herring	<i>Clupea harengus</i>	Northern	Pelagic fish
Witch flounder	<i>Glyptocephalus cynoglossus</i>	Northern	Benthic flatfish
Northern shortfin squid	<i>Illex illecebrosus</i>	Northern	Pelagic squid
Scup	<i>Stenotomus chrysops</i>	Southern	Pelagic fish
Summer flounder	<i>Paralichthys dentatus</i>	Southern	Benthic flatfish
Longfin squid	<i>Loligo paeleii</i>	Southern	Pelagic squid

2.3 Results

2.3.1 Variable Selection

The habitat variables included in the final analysis were season, 3 benthic variables (log-transformed depth, bottom slope residuals vs. depth, sediment grain size), 3 CTD variables (bottom temperature, surface salinity residuals vs. depth, stratification), and 6 remotely sensed variables (rnlw488, rnlw551 residuals vs. depth, sea surface temperature anomalies, filtered cross-shore velocity, variance in raw cross-shore velocity, and divergence tendency).

2.3.2 Community Variance Partitioning

The 13 variables included in the final CCA model accounted for 26.0% of the species variation. When the effects of seasonality were removed from the model in order to look at spatial variation in community response without the temporal aspect (season), 23.7% of the community response is explained by the model. Figure 4 shows how much of this 23.7% is due to each of the three categories of environmental data considered (benthic, CTD, remotely sensed) and how redundant they are with each other. Each of the three categories individually explained approximately the same proportion, but the pelagic characteristics (remotely sensed: 46.9%, CTD: 45.1%) explained slightly more than the benthic characteristics (40.9%). Remotely sensed variables had a high degree of redundancy with both benthic and CTD variables (16.7% and 16.0%, respectively), while there was little correlation between benthic and CTD (3.0%). Figure 5b shows which variables are likely to be responsible for this redundancy; the correlation between the remotely sensed category and the benthic category appeared to be due to a correlation

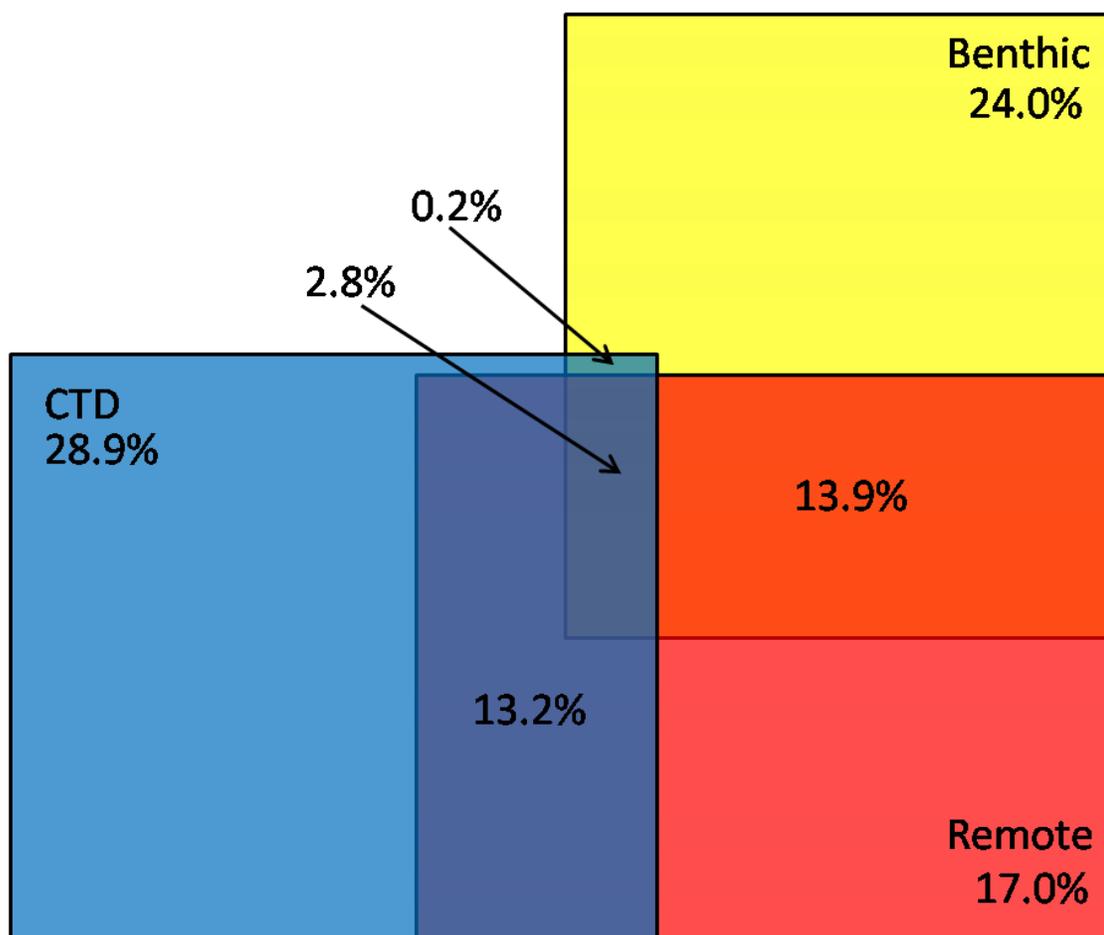


Figure 4. Relative explanatory power of categories of habitat data. Venn diagram depicts the proportion of the total 23.7% of the community response explained by spatial variation divided into three categories. Overlap between categories indicates redundancy between those categories. Pelagic categories were as effective at explaining community response as the benthic category was. The remotely sensed category showed high redundancy with both other categories.

with log-transformed depth and SST anomaly, while the correlation of remotely sensed data with the CTD data was probably due to the correlations of surface salinity residuals and stratification with cross-shore velocity, variance in cross-shore velocity, and rnlw551 residuals.

2.3.3 Species Response to CCA Axes

The first three axes of the final CCA model accounted for 71.3% of the explained community variation. Because all subsequent axes had only small contributions, species response GAM models were only fit to the first three axes (Fig. 5). Figures 6-8 show the species responses to each of these axes as well as spatial maps of the axis scores for winter, spring, and fall of 2006. We can use these to see at which locations during each season we would be most likely to find each of the six species considered in the GAM models; the peak of the response curves indicates at which axis score a species is likely to be most abundant, and the corresponding locations of those scores can then be found on the maps.

The first axis was defined by a cross-shore gradient. The most important environmental factors on each axis are listed here, with a (+) following the variable if it is positively correlated with the axis scores and a (-) if it is negatively correlated. The most influential variables on the first axis were log-transformed depth (-), sea surface temperature anomaly (-), bottom temperature (-), sediment grain size (- on phi scale), and rnlw551 (+). Axis scores tended to be low all around in the fall due to high SST but shallow water inshore, and low SST but deep water farther offshore. In the winter and spring, low SST in shallow inshore waters and high SST in deeper offshore waters created a gradient with high axis scores close to shore that decrease farther offshore.

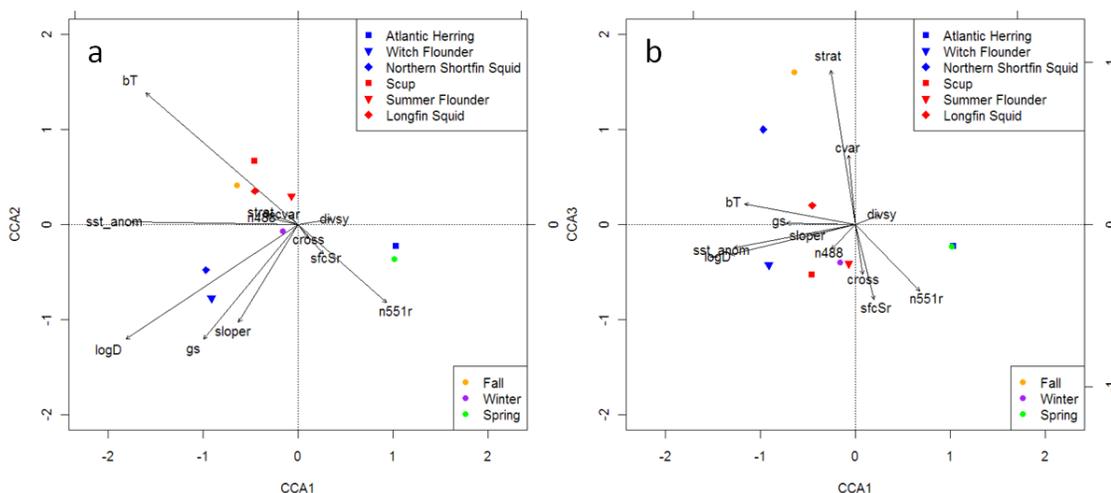


Figure 5. CCA biplots for the final model. Axes 1 and 2 (a) and 1 and 3 (b) are shown. Points correspond to median axis scores for a season or species, and arrows correspond to spatial environmental variables (logD = log-transformed depth, sloper = slope residuals vs. depth, gs = sediment grain size; bT = bottom temperature, sfcSr = surface salinity residuals vs. depth, strat = stratification; n488 = rnlw488, n551r = rnlw551 residuals vs. depth, sst_anom = SST anomaly, cross = filtered cross-shore velocity, cvar = variance in raw cross-shore velocity, divsy = divergence tendency). Variables corresponding to arrows reaching far along an axis are important on that axis.

Species that were most abundant in areas with high scores on this axis show a preference for shallow, cold areas with coarse-grained sediment and anomalously high green reflected. Witch flounder, Northern shortfin squid, longfin squid, and scup all tended to be most abundant for very negative axis values, while Atlantic herring and summer flounder were more abundant at slightly more positive values (Fig. 5, 6). Scup and summer flounder were not very well-explained on this axis.

The second axis was also a cross-shore gradient, but was mostly comprised of bottom variables, including bottom temperature (+), log-transformed depth (-), sediment grain size (- on phi scale), and bottom slope residuals (-). Shallow water with a warm bottom, coarse-grained sediment, and an anomalously small slope for that depth would produce high scores here. Spatial maps of this axis show high scores inshore and low scores offshore in the fall (from shallow water with a warm bottom to deep water with a cold bottom). In the winter and spring bottom temperature and depth balance each other on the axis and result in maps that are neutral across the entire region. On this axis, southern species (scup, summer flounder, longfin squid) were most abundant where axis values were very positive, while northern species (Atlantic herring, witch flounder, Northern shortfin squid) tended to be most abundant where axis values were more negative (Fig. 5, 7). Atlantic herring and Northern shortfin squid were not very well-explained on this axis, and southern species were better explained than northern species.

The third axis was characterized mostly by stratification (+), but variance in raw cross-shore velocity (+), surface salinity residuals (-), and rnlw551 (-) were also heavily weighted on the axis. A site with high scores on this axis would exhibit high stratification, high variance in cross-shore velocity, and low surface salinity and low

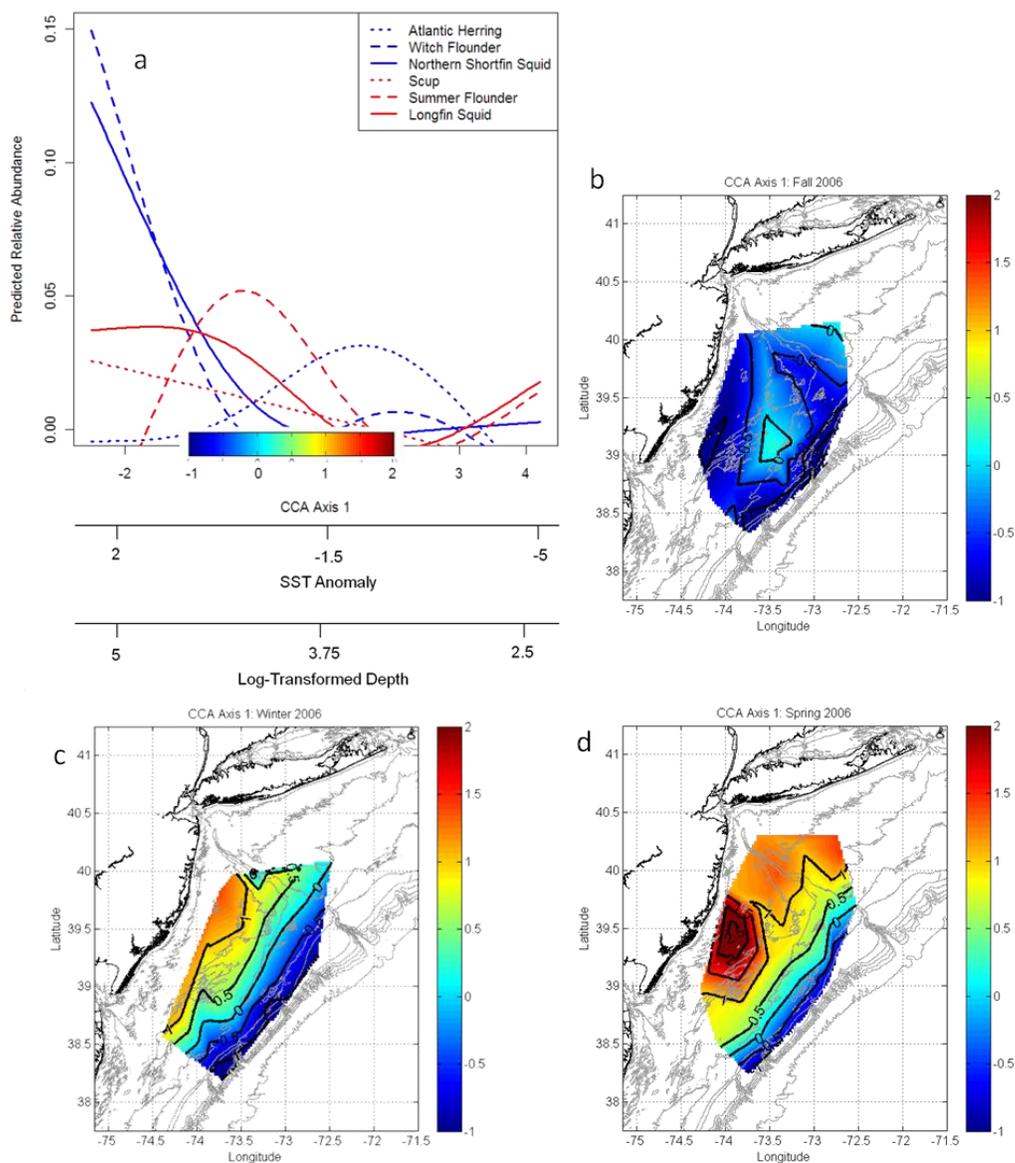


Figure 6. Response curves and Spatial Maps for CCA Axis 1. Abundance, relative to the maximum observed abundance, is plotted for six species as predicted by a GAM dependent on axis 1 scores, correlated with SST anomaly and depth (blue: northern, red: southern, solid: pelagic squid, dotted: pelagic fish, dashed: benthic flatfish) (a). Color maps and contours show how axis 1 scores are distributed spatially for fall (b), winter (c), and spring (d) of 2006.

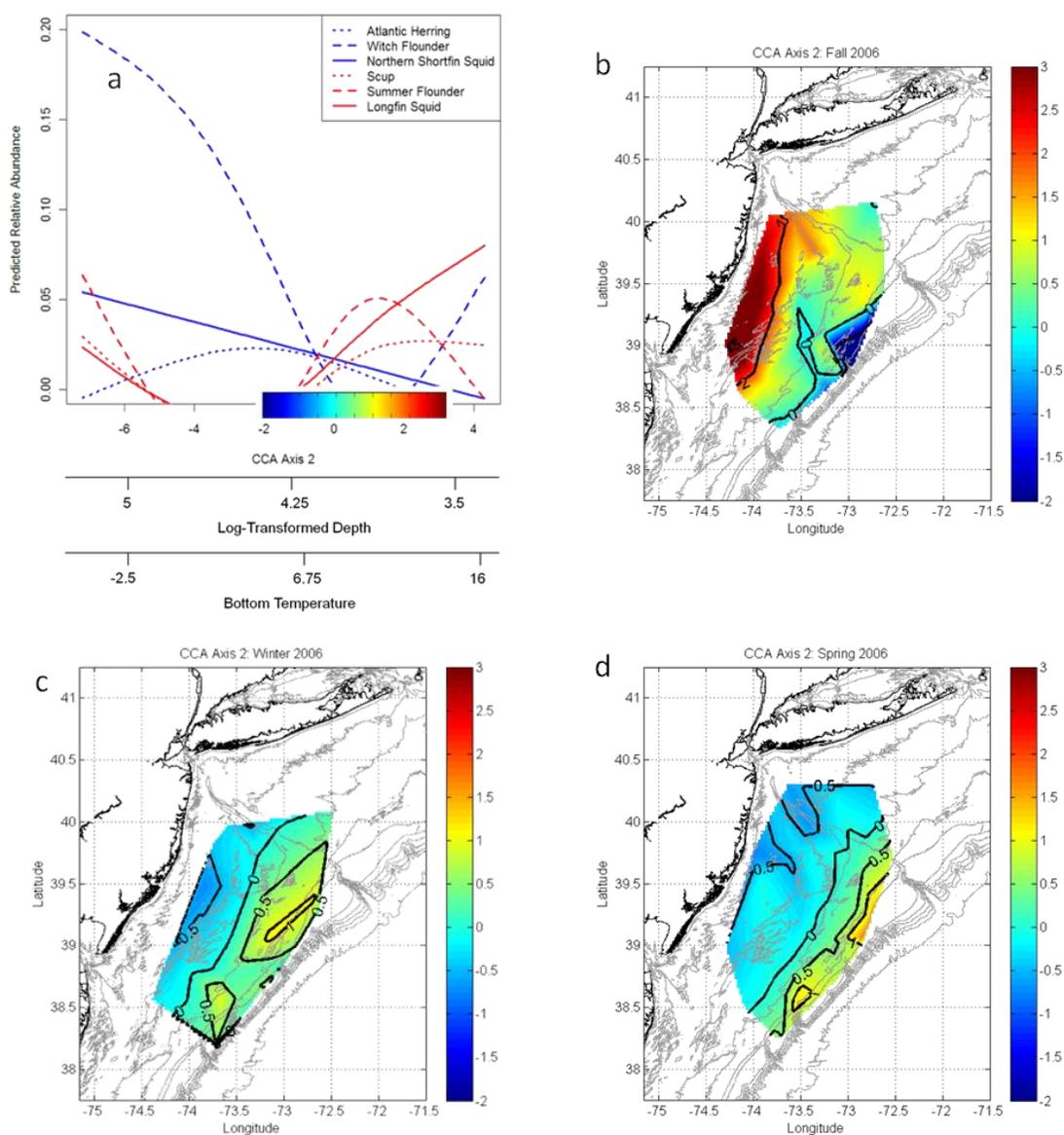


Figure 7. Response curves and spatial maps for CCA Axis 2. Abundance, relative to the maximum observed abundance, is plotted for six species as predicted by a GAM dependent on axis 2 scores, correlated with depth and bottom temperature (blue: northern, red: southern, solid: pelagic squid, dotted: pelagic fish, dashed: benthic flatfish) (a). Color maps and contours show how axis 2 scores are distributed spatially for fall (b), winter (c), and spring (d) of 2006.

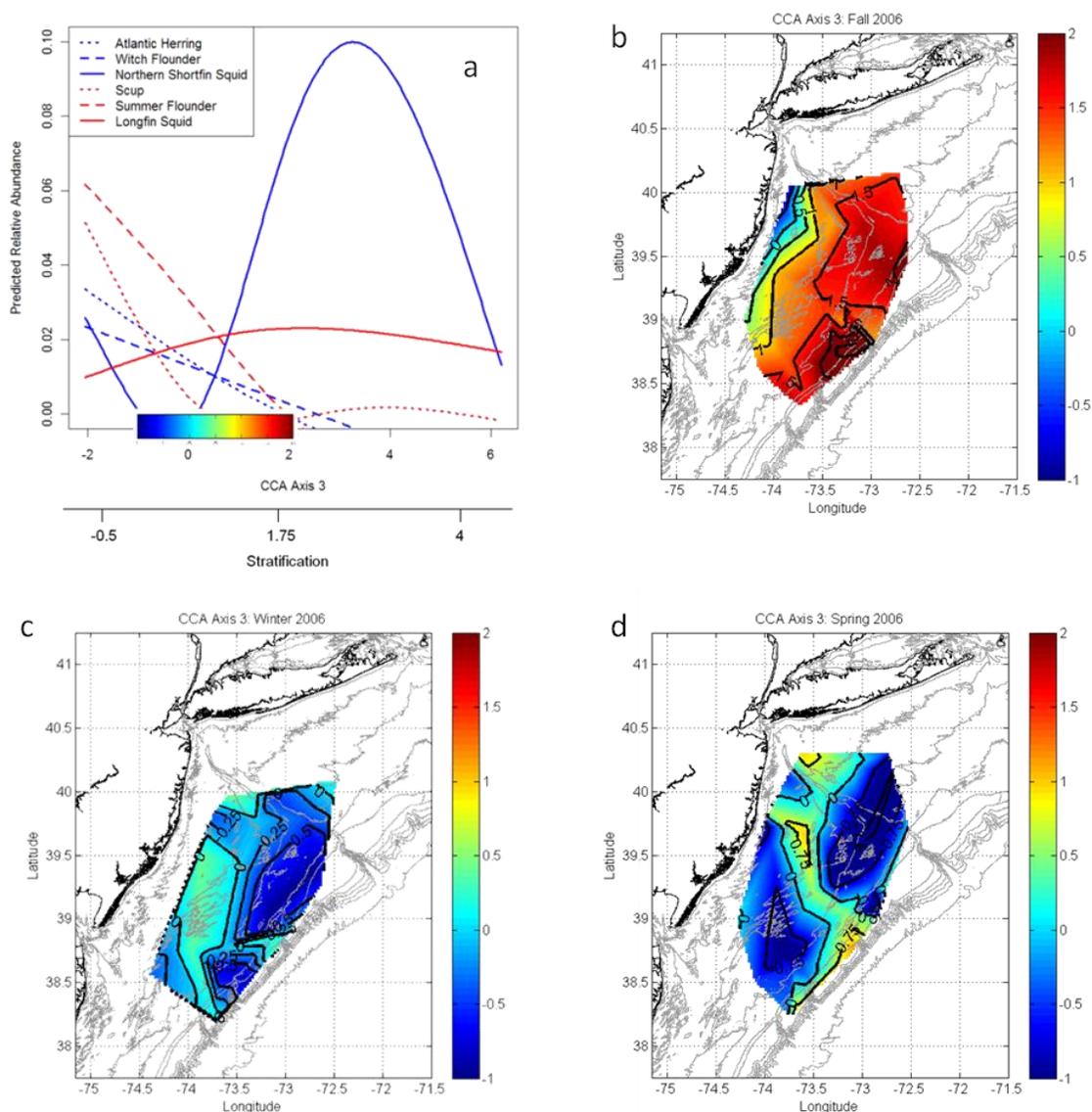


Figure 8. Response curves and spatial maps for CCA Axis 3. Abundance, relative to the maximum observed abundance, is plotted for six species as predicted by a GAM dependent on axis 3 scores, correlated with stratification (blue: northern, red: southern, solid: pelagic squid, dotted: pelagic fish, dashed: benthic flatfish) (a). Color maps and contours show how axis 3 scores are distributed spatially for fall (b), winter (c), and spring (d) of 2006.

rn1w551 (greenness) for that depth. This axis seems to describe seasonal variation, the major environmental factors all exhibiting strong seasonal dependence. High values on this axis are very characteristic of early fall features: high stratification, variable onshore flow, and relatively clear, fresh water; fall maps of this axis show scores that are low very near the coast but increase steeply in relatively shallow water and are high throughout the majority of the region. Low values throughout the entire region are more representative of winter and early spring. Scup, summer flounder, and Atlantic herring were most abundant with negative values on Axis 3, while Northern shortfin squid was most abundant with positive values (Fig. 5, 8). Longfin squid, witch flounder, and Atlantic herring were not well-explained on this axis.

2.4 Discussion

We found that the environmental features considered in this study are useful when defining important habitats for common fish and invertebrate species in the MAB. Both benthic and pelagic features were influential to the community. Additionally, many of the pelagic variables deemed important were described by ocean observing systems, and these remotely sensed characteristics increased the explanatory power of the model beyond what was given by benthic variables and those measured *in situ* using CTD.

2.4.1 Pelagic Habitat

Many management strategies tend to focus almost exclusively on the benthic habitat. While bottom structure serves as a refuge for many species and is important to consider, we find that the pelagic habitat is at least as important as the benthic in describing the distribution of many fish and invertebrate species in the MAB. The CTD and remotely sensed categories of variables each individually explained about as much

community variation as the benthic category did, and only 24% of the variation accounted for was not explained by either the CTD or remotely sensed habitat categories (Fig. 4). Also, pelagic variables came into play strongly in both the first and third CCA axes; sea surface temperature and rnlw551 residuals were important on the first axis, and all major variables on the third axis were pelagic features: stratification, variance in current velocity, surface salinity residuals, and rnlw551 residuals. These observations support the concept that seascapes need to be viewed as three-dimensional environments in which the entire vertical water column is just as important as the bottom structure.

2.4.2 Ocean Observing Systems Describe Pelagic Habitat

There was a high degree of redundancy between remotely sensed variables and both benthic and CTD variables; approximately a third of each of these two categories was also described by remotely sensed variables (Fig. 4). This suggests that the methods employed for measuring sea surface characteristics are effective at describing characteristics measured *in situ* throughout the water column. The redundancy with benthic variables was most likely due to the inclusion of SST anomalies in the remotely sensed category; SST in deep water is less likely to vary as much as it does in shallow water. The redundancy with the CTD variables, however, is more likely to be due to correlations between stratification, surface salinity residuals, cross-shore velocity and variance in velocity, and rnlw551 residuals. This may be due to currents affecting the stratification of the water column, which in turn may impact surface salinity and rnlw551 (greenness, possibly suggesting primary productivity). Although differences in redundancy between categories during different seasons were not considered in this study, it is likely that redundancy – particularly between remotely sensed variables and

CTD variables – does vary over the seasons, especially in the MAB. In the winter and early spring when the water column is unstratified, surface characteristics are more likely to be similar to bottom characteristics even in relatively deep water. In summer and early fall, however, when the water column is highly stratified, surface characteristics are less likely to represent bottom conditions.

2.4.3 Ocean Observing Systems Enhance Habitat Models

The power that remote sensing can have in describing the associations between the community and environmental gradients is demonstrated by the fact that IOOS comes into play in both the first (cross-shore) and third (seasonal) CCA axes, Axis 1 being heavily weighted with both sea surface temperature and rnlw551, and rnlw551 and variance in currents coming into play relatively strongly in Axis 3. With the growing possibilities that remote sensing can offer, several of the other variables that are most important on these axes could potentially be predicted using remote sensing equipment in the near future: bottom temperature, stratification, and salinity data can be gathered using gliders, and other features (surface salinity, for example) could potentially be inferred using algorithms that include surface characteristics measured via satellite and HF radar.

In the final CCA model, we also see that 17% of the explained community variation was explained solely by remotely sensed variables (Fig. 4). This indicates that ocean observatories not only give us information about habitat features we routinely measure *in situ*, but also on features not routinely measured *in situ*. Furthermore, six habitat variables were included in the remotely sensed category of data: twice as many as in either the CTD or benthic category. While this tells us that there are many remotely sensed variables that give us important information about habitat, it is important to note

that there were also many remotely sensed variables available to be used in this analysis and only a few that were available in the benthic and CTD categories. The explanatory power of the category was increased simply due to the number of variables used. The remotely sensed category explained approximately the same amount of community variation as either of the other two categories (CTD and benthic) (Fig. 4), so even though twice as many variables were included they did not seem to contribute proportionately to the explanation of community variation.

2.4.4 Other Conclusions

Twenty-six percent of the variability in species abundance was explained by the 13 environmental factors included in the model, but even though this percentage may seem small the results still tell us a lot about how fish and invertebrate species respond to their environment. In analyses such as this one the total variance explained should not be given much value because even an ordination with a relatively small amount of variance explained can still provide a lot of valuable information (Palmer 1993). We eliminated most of the environmental variables that were initially considered in the model because they were either shown to be unimportant or redundant with other variables. By doing this we were able to narrow several potentially important factors down to the final 13 (Table 2) that seemed to be most important to the community as a whole and that should be considered in future studies concerning communities in areas with several migratory fish species. These 13 factors were further condensed into two major gradients described by the first three axes, the first two axes defined mainly by a cross-shore gradient and the third defined by seasonal changes, especially in stratification. Analyses like this one allow us to look at the ecosystem holistically and focus less on individual species. If we

can determine the environmental variables that are important to the entire community we can make steps toward identifying what characteristics lead to “good conditions” for the ecosystem as a whole. This would then allow us to define areas in which it would be beneficial to focus future process studies.

Studies like this one can be very useful for fisheries management, and research looking at the data in other ways (for example, by using smaller target groups of species) can be a helpful supplement to our results. Similar research can, for instance, help to define essential fish habitat and reduce by-catch. Figures 6-8 include, in addition to species response curves, seasonal spatial maps for 2006 for each of the CCA axes discussed. The combination of these maps and response curves are an example of what can be done using results from this type of study. Looking at them together allows us to see at which locations in the MAB each of the axes in the model predicts high abundance for each species. If maps like these can be created and updated over frequently and used to predict the locations of groups of species relevant to fisheries, they may be helpful in developing dynamic management strategies. The growing applicability of remote sensing can be very helpful in increasing our ability to apply the results to fisheries with relative ease, and may allow for designation of dynamic MPAs which would require less area than static MPAs (Game et al. 2009). These developments also give us the opportunity to implement adaptive management. Because this management strategy requires constant adjustments to the practices of fishermen, managers, and scientists based on the observations of all involved (Kar & Matsuda 2006), it is important to be able observe environmental features long-term and on fine spatial and temporal scales. Now that ocean observatories make this possible, if we can strengthen collaborations

between fishermen, managers, and scientists, widespread use of adaptive management may be feasible in the near future. This would allow for continuous improvement on fishing practices, paving the way for more sustainable fisheries.

Because of the design of the study, and the limited data available, several questions are still left unanswered and deserve further study. The nature of the benthic structure should be reconsidered; here, benthic variables were assumed to be static over time, but in fact they can be very dynamic (Glenn et al. 2008). Also, because of the timing of the cruises, even though there are several survey sites for each season (winter, spring, and fall), those surveys take place over a limited time period and the entire season is not covered. No trawl surveys were collected during the summer, and therefore these results should be used cautiously if at all to consider species distributions during summer. We need to exercise caution in making inferences about pelagic species when using data collected by bottom trawl, since presumably these species would not most commonly occur at the same depths as the bottom trawls. We also cannot assume fish are in a “preferred” environment; fish collected may be in the process of moving to a favorable environment, if spawning they may be in (or moving to/from) an environment that is optimal for their young but unfavorable to them as adults (Terceiro 2007, Katz et al. 1994), etc. While we believe our major conclusions will hold across all seasons and for the ecosystem as a whole, the more specific details are likely to vary from our results depending on the seasons and species in question.

Future ecosystem models may also benefit by including other data that was not available for this study. We only had data available for adult individuals, but to fully understand the ecosystem we need to know about the abundance and distribution of all

life stages, including eggs and larvae. In order to understand adult fish distributions it may also be beneficial to include a time lag in models; knowing what environmental conditions were experienced when adults were in younger, more vulnerable life stages can help determine the present abundance and distribution of adult species. Determining appropriate time lags would be easiest with short-lived species, but having information on the size/age class of collected individuals could also help with this. Research suggests that size-selective fishing can negatively affect the resilience of populations and that it is important to maintain the age and spatial structure of populations as well as the biomass (Hsieh et al. 2010), further emphasizing the need to for data on size/age of fish collected. Studies similar to this one would also benefit from benthic data with a finer spatial resolution; many species depend on features that vary over scales much smaller than the 2 km grid used in this study, especially for refuge. Any reliance on these features would not have been revealed in this study. Having more remotely sensed variables available would also be extremely useful to fisheries studies. In the future, the ability of remote sensing equipment to replace *in situ* measurements can be increased further by measuring new characteristics or by finding new applications available with present equipment and by increasing the spatial and temporal coverage of the present equipment (between 2007 and 2008, the HF Radar network was expanded to cover the entire MAB). Other ocean observing assets not considered in this study, such as gliders, can also provide more continuous measures of pelagic characteristics (including but not limited to those that are measured using CTDs) remotely at depths spanning the entire water column. We already have a lot of great data sources, many of which were used in this study, that are useful resources for fisheries research and management. As technology develops further, the

possibilities are unlimited.

3. FUTURE OPPORTUNITIES

3.1 Technology is Sufficient, and Still Evolving

For years ecologists have known that the pelagic habitat is important in determining the distribution of marine species and until recently have not had the data necessary to model the pelagic habitat and how marine species respond to it. We now have satellites that measure – either directly or through the use of algorithms utilizing measured variables – sea surface temperature, water leaving radiances, chlorophyll, and locations and strengths of frontal boundaries, among others. HF radar provides maps of surface current velocity, vertical velocity, and vorticity. Coastal coverage in the MAB has grown from small subregions in 2003 to the entire MAB in 2008. Autonomous gliders extend the surface coverage provided by satellites and HF radar to the water column beneath the surface.

The remotely sensed characteristics that we considered were sufficient to describe many of the important features measured *in situ*, and several even contributed habitat-defining information that was not provided by either the *in situ* CTD factors or the benthic factors. With the constantly growing capabilities of ocean observatories, we should soon be able to remotely observe even more of the environmental factors that today we are still only able to measure by going out to sea. We now have the capability to make great strides in our understanding of the complicated interactions that define coastal ecosystems.

3.2 Application to Adaptive Fisheries Management

This new capacity to measure highly dynamic features with a fine spatial and temporal resolution makes the implementation of adaptive management strategies more

feasible. Adaptive management consists of a constant accumulation of knowledge and systematic feedback learning by scientists, fishermen, and managers (Kar & Matsuda 2006). It involves experimentation of different policies followed by monitoring of the results; any observations can be used quickly to adjust and inform new management and research decisions. With the capabilities we currently have for remote sensing, habitat models, and field observations, the tools are finally in place to make adaptive management possible, but in order to make it successful all user groups involved must work together as partners and be willing to share their knowledge and observations with one another.

The use of remote sensing in combination with habitat models allows us to create dynamic habitat maps that we can update frequently and as they are needed to aid in adaptive management. Game et al. (2009) suggest that remote sensing can be used to designate dynamic MPAs based on the constantly changing habitat, a strategy that would require less total area than static MPAs. We can do studies similar to this one but more focused on target groups of species, and potentially use the results from those studies in adaptive management for specific fisheries.

For example, the results from this study have contributed to the obtainment of funding for research that is currently underway for the longfin squid fishery in the MAB. This fishery has had considerable problems with butterflyfish bycatch, and has even been threatened to be shut down due to those issues. This new study will use habitat models to predict co-occurrence between squid and butterflyfish, and will use those models to speculate on how to best limit bycatch in the fishery. Dynamic maps based on habitat

variables obtained through ocean observatories, similar to those in figures 6-8, can be created for these co-occurrence models and used in adaptive management.

Cooperation and sharing of knowledge is an integral part of adaptive management. Currently we are collaborating with commercial fishermen and managers to ensure their input is part of the model development. In order to ensure the final product has relevance, we need information on how they fish and on what environmental cues they look for. We have already shared results from this multivariate study as well as one considering only longfin squid, butterfish, summer flounder, and spiny dogfish with the Mid-Atlantic Fisheries Management Council, and once we have results from the squid/butterfish co-occurrence model we intend to share it with and get further input from both fishermen and managers. As with any adaptive strategy, it will be an iterative process that should improve and provide us with valuable knowledge and experience at each step.

3.3 Future Research Possibilities

Game et al. (2009) note that marine species tend to exhibit increased vulnerability to fishing pressure in certain areas such as breeding grounds, foraging areas, and migration routes. It is especially important to understand the habitat dynamics in these regions and what controls the fish response. If the relationship between animals and the environment is misunderstood or misused, especially in these areas of increased vulnerability, the population (or even the entire community) could face potentially devastating effects. Habitat models that focus specifically on these vulnerable areas (for example, spawning habitat models) and the effects of fishing in these regions would be extremely beneficial.

We can also focus studies on specific species or small groups of species, which would allow us to get a more defined picture of which environmental factors best predict the distributions of those species. Marine species abundances may relate more closely to environmental factors that change on time scales similar to their generation times than they would to those that change more or less frequently (Hsieh & Ohman 2006). This leads us to predict that short-lived species are likely to respond to environmental features that change on very short time scales, such as currents and temperature, and long-lived species are more likely to respond to environmental features that change less frequently, including several benthic characteristics. Focusing on specific species could also make it easier to incorporate time lag into habitat models. Because the abundance of adult species depends partly on successful recruitment of the young, having a picture of the past habitat (when current adults would have been recruited) may help explain the present abundance and distribution of marine species. Incorporating this time lag may be difficult for many species, but can be very beneficial and feasible, at least for annuals and other short-lived species.

Other studies have indicated that size-selective fishing can negatively affect the resilience of populations (Hsieh et al. 2004). They suggest that managers should aim to conserve not only the viable spawning biomass of a population, but also the age and spatial structure. We did not have this data available on individuals for this study, but when possible it may be useful to incorporate age and/or size of individuals into habitat models as well as simple abundance or biomass.

Lastly, these results have strong implications for climate change. Nye et al. (2009) showed that many species exhibit temporal trends in spatial shifts consistent with

the environmental variations that are associated with climate change. The authors suggest many mechanisms for which climate change could have resulted in these spatial shifts, but it is still unclear which of those most impacts the fish. This study showed that fish respond strongly to habitat variations and defined some of the key habitat-defining benthic and pelagic characteristics, many of which have been impacted by climate change (e.g. temperature, wind-driven circulation). Future studies could look more deeply into just which habitat features are likely to be responsible for the spatial shifts that Nye et al. (2009) observed in many species and attributed to climate change.

Based on this study, we conclude that marine species respond to variations in not only the benthic habitat, but also in the pelagic habitat, and we are able to determine some of the major environmental factors that contribute to habitat. We also establish that ocean observatories can describe many important pelagic features that should be included in habitat models. This knowledge has enormous potential to lead to advances in management strategies, and the possibilities it opens up for new research opportunities are endless.

REFERENCES

- Azarovitz TR (1981) A brief historical review of the Woods Hole Laboratory trawl survey time series. In: Doubleday WG, Rivard D (eds) Bottom trawl surveys. *Can Spec Publ Fish Aquatic Sci* 58:62-67.
- Bakun A (2010) Linking climate to population variability in marine ecosystems characterized by non-simple dynamics: Conceptual templates and schematic constructs. *Journal of Marine Systems* 79:361-373.
- Barrick DE, Evans MW, Weber BL (1977) Ocean surface currents mapped by radar. *Science* 198:138-144.
- Bolker BM (2008) *Ecological models and data in R*. Princeton University Press: Princeton, NJ.
- Borcard D, Legendre P, Drapeau P (1992) Partialling out the spatial component of ecological variation. *Ecology* 73:1045-1055.
- Chatfield BS, Van Niel KP, Kendrick GA, Harvey ES (2010) Combining environmental gradients to explain and predict the structure of demersal fish distributions. *J Biogeogr* 37:593-605.
- Dzwonkowski B, Kohut JT, Yan X (2009) Seasonal differences in wind-driven across-shelf forcing and response relationships in the shelf surface layer of the central Mid-Atlantic Bight. *J Geophys Res* 114, C08018, doi:10.1029/2008JC004888.
- Dzwonkowski B, Lipphardt BL, Kohut JT, Yan XH, Garvine RW (2010) Synoptic measurements of episodic flow events in the central Mid-Atlantic Bight. *Continental Shelf Research* 30:1373-1386.
- Falkowski PG, Hopkins TS, Walsh JJ (1980) An analysis of factors affecting oxygen depletion in the New York Bight. *Journal of Marine Research* 38:479-506.
- Fry FEJ (1971) The effect of environmental factors on the physiology of fish. *Fish Physiology* 6:1-98.
- Game ET, Grantham HS, Hobday AJ, Pressey RL, and others (2009) Pelagic protected areas: the missing dimension in ocean conservation. *Trends in Ecology and Evolution* 24:360-369.
- Glenn SM, Jones C, Tawrdowski M, Bowers L, and others (2008) Glider observations of sediment resuspension in a Middle Atlantic Bight fall transition storm. *Limnology and Oceanography* 53:2180-2196.
- Goff JA, Mayer LA, Traykovski P, Buynevich I, and others (2005) Detailed investigation of sorted bedforms, or “rippled scour depressions,” within the Martha’s Vineyard Coastal Observatory, Massachusetts. *Cont Shelf Res* 25:461-484.
- Goff JA, Jenkins CJ, Williams SJ (2008) Seabed mapping and characterization of sediment variability using the usSEABED data base. *Cont Shelf Res* 28:614-633.
- Gong D, Kohut JT, Glenn SM (2010) Seasonal climatology of wind-driven circulation on the New Jersey Shelf. *J Geophys Res* doi:10.1029/2009JC005620.
- Hardman-Mountford NJ, Hirata T, Richardson KA, Aiken J (2008) An objective methodology for the classification of ecological pattern into biomes and provinces for the pelagic ocean. *Remote Sensing of Environment* 112:3341-3352.
- Hsieh C, Ohman MD (2006) Biological responses to environmental forcing: The linear tracking window hypothesis. *Ecology* 87:1932-1938.

- Hsieh C, Yamauchi A, Nakazawa T, Wang W (2010) Fishing effects on age and spatial structures undermine population stability of fishes. *Aquat Sci* 72:165-178.
- Jongman RHG, Ter Braak CJF, Van Tongeren OFR (1995) Data analysis in community and landscape ecology. Cambridge University Press: New York, NY.
- Kar TK, Matsuda H (2006) An overview of bioeconomic analysis and management in fisheries. *Journal of Fisheries and Aquatic Science* 1:218-234.
- Katz CH, Cobb JS, Spaulding M (1994) Larval behavior, hydrodynamic transport, and potential offshore-to-inshore recruitment in the American lobster *Homarus americanus*. *Mar Ecol Prog Ser* 103:265-273.
- Legendre P & Legendre L (1998) Numerical ecology, second English edition. Elsevier Science BV: Amsterdam.
- Leis JM (2006) Are larvae of demersal fishes plankton or nekton? *Advances in Marine Biology* 51:57-141.
- Levitus S (1982) Climatological atlas of the world ocean. US Government Printing Office: Washington, DC.
- Lewin-Koh NJ, Bivand R, contributions by Pebesma EJ, Archer E, and others (2008) mapproj: Tools for reading and handling spatial objects. R package version 0.7-16.
- Link J, Overholtz W, O'Reilly J, Green J, and others (2008) The Northeast U.S. continental shelf Energy Modeling and Analysis exercise (EMAX): Ecological network model development and basic ecosystem metrics. *Journal of Marine Systems* 74:453-474.
- Marsh R, Petrie B, Weidman CR, Dickson RR, and others (1999) The 1882 tilefish kill – a cold event in shelf waters off the north-eastern United States? *Fisheries Oceanography* 8:39-49.
- McGarigal K, Cushman S, Stafford S (2000) Multivariate statistics for wildlife and ecology research. Springer-Verlag: New York, NY.
- Neill WH, Miller JM, Van Der Veer HW, Winemiller KO (1994) Ecophysiology of marine fish recruitment: A conceptual framework for understanding interannual variability. *Netherlands Journal of Sea Research* 32:135-152.
- Neteler M, Mitasova H (2008) Open source GIS: A GRASS GIS Approach, third edition. Springer Science and Business Media, LLC: New York, NY.
- Nye JA, Link JS, Hare JA, Overholtz WJ (2009) Changing spatial distribution of fish stocks in relation to climate and population size on the Northeast United States continental shelf. *Mar Ecol Prog Ser* 393:111-129.
- Oksanen J, Kindt R, Legendre P, O'Hara B, and others (2008) vegan: Community Ecology Package. R package version 1.15-0. <http://cran.r-project.org/>, <http://vegan.r-forge.r-project.org/>.
- Oliver MJ, Glenn SM, Kohut JT, Irwin AJ, and others (2004) Bioinformatic approaches for objective detection of water masses on continental shelves. *Journal of Geophysical Research* 109:12PP.
- Oliver MJ, Irwin AJ (2008) Objective global ocean biogeographic provinces. *Geophysical Research Letters* 35, 10.1029/2008GL034238, 032008.

- Palacios DM, Bograd SJ, Foley DG, Schwing FB (2006) Oceanographic characteristics of biological hot spots in the North Pacific: A remote sensing perspective. *Deep Sea Research Part II: Topical Studies in Oceanography* 53:250-269.
- Palmer MW (1993) Putting things in even better order: The advantages of canonical correspondence analysis. *Ecology* 74:2215-2230.
- Powell EN, Bonner AJ, Muller B, Bochenek EA (2004) Assessment of the effectiveness of scup bycatch-reduction regulations in the *Loligo* squid fishery. *Journal of Environmental Management* 71:155-167.
- R Development Core Team (2008) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org>.
- Reid JM, Reid JA, Jenkins CJ, Hastings ME, and others (2005) usSEABED: Atlantic coast offshore surficial sediment data release. US Geological Survey Data Series 2005-118, version 1.0.
- Roarty H, Glenn S, Kohut J, Gong D, and others (2010) Operation and application of a regional HF radar network in the Mid-Atlantic Bight. *Marine Technology Society Journal* (submitted).
- Shearman RK, Lentz SJ (2010) Long-term sea surface temperature variability along the US east coast. *J Phys Oceanogr* 40:1004-1017.
- Simpson J (1981) The shelf-sea fronts: implications of their existence and behaviour. *Phil Trans R Soc Lond A* 302:531-546.
- Terceiro M (2007) Modeling environmental factors and summer flounder recruitment success. SAW 47 Working Paper 11(TOR 6) – Modeling Environmental Factors, 2068-2074.
- Wood SN (2004) Stable and efficient multiple smoothing parameter estimation for generalized additive models. *Journal of the American Statistical Association* 99:673-686.
- Wood SN (2006) *Generalized additive models: An introduction with R*. Chapman and Hall/CRC.
- Wood SN (2008) Fast stable direct fitting and smoothness selection for generalized additive models. *Journal of the Royal Statistical Society (B)* 70(2): - .
- Yamashita Y, Tanaka M, Miller JM (2001) Ecophysiology of juvenile flatfish in nursery grounds. *Journal of Sea Research* 45:205-218.
- Ysebaert T, Meire P, Herman PMJ, Verbeek H (2002) Macrobenthic species response surfaces along estuarine gradients: prediction by logistic regression. *Mar Ecol Prog Ser* 225:79-95.