

# Abiotic proxies for predictive mapping of nearshore benthic assemblages: implications for marine spatial planning

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**Abstract.** Marine spatial planning (MSP) should assist managers in guiding human activities toward sustainable practices and in minimizing user conflicts in our oceans. A necessary first step is to quantify spatial patterns of marine assemblages in order to understand the ecosystem's structure, function, and services. However, the large spatial scale, high economic value, and density of human activities in nearshore habitats often makes quantifying this component of marine ecosystems especially daunting. To address this challenge, we developed an assessment method that employs abiotic proxies to rapidly characterize marine assemblages in nearshore benthic environments with relatively high resolution. We evaluated this assessment method along 300 km of the State of Maine's coastal shelf (<100 m depth), a zone where high densities of buoyed lobster traps typically preclude extensive surveys by towed sampling gear (i.e., otter trawls). During the summer months of 2010–2013, we implemented a stratified-random survey using a small remotely operated vehicle that allowed us to work around lobster buoys and to quantify all benthic megafauna to species. Stratifying by substrate, depth, and coastal water masses, we found that abiotic variables explained a significant portion of variance (37–59%) in benthic species composition, diversity, biomass, and economic value. Generally, the density, diversity, and biomass of assemblages significantly increased with the substrate complexity (i.e., from sand-mud to ledge). The diversity, biomass, and economic value of assemblages also decreased significantly with increasing depth. Last, demersal fish densities, sessile invertebrate densities, species diversity, and assemblage biomass increased from east to west, while the abundance of mobile invertebrates and economic value decreased, corresponding mainly to the contrasting water mass characteristics of the Maine Coastal Current system (i.e., summertime current direction, speed, and temperature). Integrating modeled predictions with existing GIS layers for abiotic conditions allowed us to scale up important assemblage attributes to define key foundational ecological principles of MSP and to find priority regions where some bottom-disturbing activities would have minimal impact to benthic assemblages. We conclude that abiotic proxies can be strong forcing functions for the assembly of marine communities and therefore useful tools for spatial extrapolations of marine assemblages in congested (heavily used) nearshore habitats.

**Key words:** *abiotic proxies; benthic assemblages; demersal fishes; ecological principles; epifauna; marine spatial planning; mobile invertebrates; sessile invertebrates.*

## INTRODUCTION

The ocean is crowded with human use, especially in coastal areas where traditional (e.g., fisheries) and emerging industries (e.g., offshore renewable energy) increasingly compete for space and can create adverse effects to marine ecosystems (Worm et al. 2006, Halpern et al. 2008, Jackson 2008). Marine spatial planning (MSP) has long promised to alleviate this growing demographic pressure (Douvere 2008, 2010), with potential benefits both to multi-use management and conservation objectives. Providing a spatially explicit framework to

better organize human activities, MSP seeks to minimize user conflicts and protect natural ecosystems through the co-location of compatible uses and/or environments (Douvere 2008, 2010). MSP program development progresses worldwide (Douvere 2010, IOPTF 2010, Collie et al. 2013). However, program effectiveness (as management or conservation tools) will greatly depend on whether or not adopted MSPs were designed to promote foundational ecological principles that enhance important attributes of an ecosystem's structure, functions, services, and/or networks of connectivity (Crowder and Norse 2008, Gaydos et al. 2008, Foley et al. 2010).

A necessary first step toward determining the foundational ecological principles for an ecosystem is to characterize the spatial and temporal structure of marine assemblages contained (Brown et al. 2011, Lecours et al. 2015, Stamoulis and Delevaux 2015). This allows managers to consider the foundational ecology of the system

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relative to current patterns of human use and then to prioritize attributes and/or areas that may be either valuable or vulnerable under multi-use planning scenarios. Unfortunately distributions of marine assemblages (and their maintaining processes) are rarely characterized at scales relevant to MSP (Lecours et al. 2015). The expense and logistics of ecological sampling alone restricts observations to a limited number of survey stations. Especially in nearshore ecosystems, the complex nature of habitat and prevailing patterns of coastal use (e.g., boat traffic and fixed fishing gear) constrains sampling efforts further, by either limiting or preventing observations entirely. As a result, marine assemblages can be well defined in discrete easy-to-sample areas, yet largely unknown throughout a vast study region, making the equal characterization of ecosystems a significant barrier to effective coastal MSP.

Fortunately, several new technologies and analytical tools improve our ability to bridge the gap between ecological observations and the scale of marine spatial planning. Hydroacoustic mapping, remote sensing, oceanographic buoy arrays, and advanced hydrographic modelling frameworks make the rapid characterization of relatively fine-scale abiotic conditions increasingly feasible (e.g., Roberts et al. 2010, Brown et al. 2011, Diesing and Stephens 2015, Mamede et al. 2015, Shumchenia et al. 2015). Capabilities for multivariate predictive species and assemblage-level models have also improved, coinciding with the advent of powerful statistical programs and geographic information systems (GIS; e.g., Guisan and Zimmermann 2000, Elith and Leathwick 2009). Since many species are influenced by abiotic variables and GIS layers for abiotic conditions are more widely available, development of “abiotic proxies” could be a cost-effective approach for mapping the structure of marine ecosystems (McArthur et al. 2010, Brown et al. 2011).

Currently, no best practice method exists for employing abiotic proxies. The process broadly involves identifying abiotic variables to serve as simplified mappable representations of ecological attributes (McArthur et al. 2010, Brown et al. 2011). Most marine studies have focused thus far on characterizing assemblages through classification of continuous abiotic variables into discrete regions of similar abiotic conditions (i.e., for inferred shifts in species composition; McArthur et al. 2010, Brown et al. 2011). While relatively easy and inexpensive, this “abiotic only” method is imperfect as it often ignores complex underlying abiotic-biotic relationships (i.e., linear vs. non-linear) and can confine inherently continuous ecological patterns into discrete classifications, thereby producing maps with unknown, assumed, and/or simplified value (Brown et al. 2011, Sutcliffe et al. 2015). Some have used ecological observations to improve abiotic classifications through ground-truthing (Greene et al. 2010, Kerrigan et al. 2010, Monteiro et al. 2015). However, an increasingly preferred method is to examine abiotic-assemblage relationships first (e.g., Auster et al. 2002, Watling and Skinder 2007, Huang et al. 2014, Rees

et al. 2014, Gonzalez-Mirelis and Buhl-Mortensen 2015) and then to scale up robust ecological patterns using fitted model predictions and continuous layers of abiotic condition afterward (Brown et al. 2011, Sutcliffe et al. 2015). This method ensures that underlying complexities are preserved and that there is no loss of information through arbitrary classification.

Here we developed a novel assessment method that employs abiotic proxies to rapidly scale up marine assemblages in nearshore environments with relatively high spatial resolution. For demonstration purposes, we focused on nearshore benthic assemblages in the Gulf of Maine, a region where over 95% of the marine resource value (i.e., \$585 million in 2014) comes from benthic megafauna that live in relatively shallow (<100 m) coastal habitats (i.e., within about 20 km from the shore; DMR 2015). The dominant abiotic conditions within this nearshore area (hereafter referred to as the “Maine coastal shelf”) include a mosaic of differing seabed substrates, complex bathymetry, and two oceanographically distinct coastal currents that create strong physical gradients in water motion, temperature, and salinity during the summer months (Townsend 1991, Pettigrew et al. 2005). Therefore, we hypothesized that substrate type, depth, and differences between coastal water masses could be used as abiotic proxies for benthic assemblages in this system. We tested this by conducting remotely operated vehicle (ROV) surveys stratified by substrate, depth, and water mass along the Maine coastal shelf. Our study objectives were (1) to determine the proportion of variance explained by each abiotic variable, (2) to visualize their effect on ecological assemblage attributes, and (3) to explore potential foundational ecological principles for applying MSP within the study region. The small ROV was uniquely suited for working in the Maine coastal shelf because it could work around the myriad lobster traps and associated surface buoys that typically exclude traditional survey methods (e.g., otter trawls). This allowed us to relate specific organisms quantified to the substrate, depth, and water mass conditions where they live. Since our proposed abiotic proxies are likely to be important for defining MSP foundational ecological principles elsewhere, we also discuss how this study might be adapted to other systems.

## METHODS

### *Study area and design*

The Gulf of Maine is a semi-enclosed sea that stretches over 500 km along the northwestern Atlantic continental shelf from Cape Cod, Massachusetts, USA to Cape Sable, Nova Scotia, Canada, and is bounded on its seaward edge by Georges and Browns Bank (Fig. 1A). Its coastline is mostly dominated by bedrock with sandy pockets increasing south and westward along the shore. The Maine coastal shelf is narrow (25–50 km; Fig. 1B), extending to about 100 m depth and surrounding several deeper basins and rocky ledges. Its waters contain three distinct water

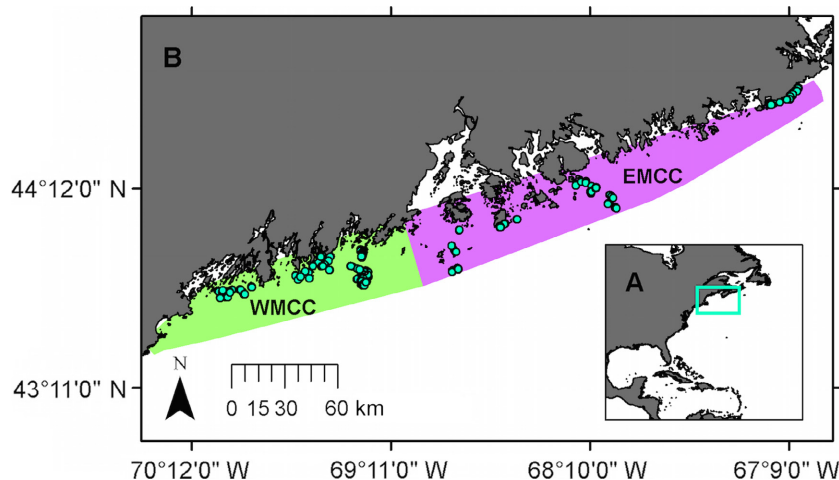


FIG. 1. The study area within (A) the northwestern Atlantic and sampling locations within (B) the Gulf of Maine. A blue polygon denotes the Maine coastal shelf. Blue points designate sites surveyed using small remotely operated vehicle systems during the summer months from 2010 to 2013. The Maine Coastal Current (MCC) system is highlighted in green and purple, where the green polygon designates the Western Maine Coastal Current (WMCC) and the purple polygon designates the Eastern Maine Coastal Current (EMCC). [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

mass layers: (1) a high salinity layer from the western North Atlantic that fills the deep ocean basins, (2) a perennially cool intermediate layer, and (3) a shallow surface layer whose characteristics vary spatially throughout the year (Brooks 1985). Flowing over the coastal shelf, this upper layer forms the Maine Coastal Current (MCC) system, which flows southwesterly in a counter-clockwise circulation pattern and diverges at Penobscot Bay, creating two oceanographically distinct water masses. In the Eastern Maine Coastal Current (EMCC), greater tidal energy and wind stress drive strong tidal currents that vertically mix the water column, bringing cold water to the surface and warmer waters to the benthos. Meanwhile, the Western Maine Coastal Current (WMCC) becomes thermally stratified during the summer months, fueling pulses of primary productivity (Pettigrew et al. 2005).

#### Survey data

We conducted ROV surveys along the Maine coastal shelf from 2010 to 2013 in order to characterize the summertime (June–August) structure of benthic assemblages with respect to patterns of nearshore abiotic conditions (Fig. 1B). Employed ROV systems included a Subsea Tuffcam (SVS Subsea Video Systems, inc. Elizabeth City, North Carolina, USA), a VideoRay Pro 3 (VideoRay LLC. Pottstown, Pennsylvania, USA), and a JW Fishers SeaLion-2 (JW Fishers, East Taunton, Massachusetts, USA). Each system possessed several main features that allowed for comparison, including a downward-facing camera (~450 lines resolution), a 10-cm laser-scaling system, an array of adjustable lighting, geo-referencing via timestamp to a handheld GPS, and a depth sensor.

The ROV survey design involved the completion of stratified random benthic drift transects at predetermined sites. We stratified the survey by three abiotic factors (i.e.,

substrate, depth, and water mass) and selected sites a priori using available nautical charts and satellite imagery (Table 1). Available nautical charts provided initial information regarding broad substrate characteristics (e.g., ledge, boulder, cobble, gravel, sand-mud) and the approximate depth range (e.g., 20–30 m, 40–60 m, 70–100 m) of each potential site. Meanwhile, remote sensing imagery for long-term average summertime thermal conditions provided a visual confirmation of the expected water mass conditions of each site (i.e., whether sites would be in the EMCC vs. WMCC; NOAA CoastWatch data [available online](http://eastcoast.coastwatch.noaa.gov/)).<sup>4</sup>

Due to the east-west orientation and length of the Maine coastline, as well as the narrowness of the coastal shelf, we used a longitudinal approach to site selection (e.g., Steneck and Wilson 2001). This ensured that we captured the greatest variation of sites east-to-west, as well as north-to-south. To start, we generated a total of 200 random longitudes across the study area that were of greater than 1 km apart, i.e., 100 in the WMCC and 100 in the EMCC. Then we selected an equal number of sites along each longitude that fit within our target strata (e.g., three transects at 20–30 m and on ledge, three transects at 20–30 m on boulder, etc.).

In the field, we conducted approximately 1 h of drift surveying per site. If buoyed lobster gear densities interfered with or prevented survey operations at a particular predetermined site, we substituted that site for another nearby location wherever possible to ensure we acquired a sufficient number of sites per target stratum. To minimize fish attraction and avoidance behaviors, the ROV lighting was always adjusted for low light conditions and ROV thruster use was minimized wherever possible (e.g., Stoner et al. 2008).

<sup>4</sup> <http://eastcoast.coastwatch.noaa.gov/>

*Quantifying benthic assemblages*

In the lab, we reviewed each ROV video to identify, measure, and enumerate all visible demersal and benthic taxa to species, including all megafauna (i.e., >10 cm) and all visible macrofauna (i.e., macrofauna 1–10 cm). Multiple reviewers viewed each video, and performed quality control checks at random to ensure consistency in enumerations and identifications between reviewers. We paid special attention to the enumeration of certain aggregating species (e.g., cunner and pollock) that exhibited following behaviors to minimize the overestimation of fish densities; where identification or enumeration uncertainty arose, we sent high definition video and/or still images to experts for quality control (e.g., Stoner et al. 2008).

For each video, we georeferenced species observation and prevailing abiotic conditions along each transect within an Excel spreadsheet (Microsoft, Redmond, Washington, USA) using the video time stamps and the GPS track time stamps. All species counts, body sizes, and abiotic conditions were aggregated to the nearest GPS time stamp. A substrate stratum was also visually assigned at each GPS time stamp based the dominant size of substrates observed (i.e., Table 1) (Brown 1993, Bell et al. 2004). The ROV pressure sensor provided a depth measurement at each GPS time stamp.

In order to quantify spatially explicit patterns of species assemblages, we also estimated the total area covered by each transect during video analysis, using transect length and width estimates derived from the GPS tracks and the laser scaling system, respectively. At the time of collection, the exact area of each transect varied due to drift time, current speed, and camera height. Each transect also often covered multiple substrate strata due to the patchy landscape of substrates in the Maine coastal shelf. Therefore following the completion of video analysis, we split the Excel data from each transect (i.e., the aggregated GPS

time points with associated species counts, body sizes, and abiotic conditions) into standardized 25-m<sup>2</sup> sub-transects of consistent area, continuous data coverage, and consistent strata; that way each sub-transect could be treated as one data point within one stratum. Then, we quantified average spatially explicit patterns of population density (individuals/m<sup>2</sup>) and species diversity ( $H'$ ) (Spellerberg and Fedor 2003) per sub-transect. We also derived spatially explicit estimates for species-specific and then assemblage-level biomass estimates (kg/m<sup>2</sup>) per sub-transect using published length–mass equations (e.g., Haynes and Wigley 1969, Krouse 1972, Wigley et al. 2003, Kelly 2012). Last, we multiplied the species-specific biomass estimates by the average landing price for each taxa so that we could derive a spatially explicit estimate of species-specific and assemblage-level economic value per sub-transect (DMR 2015).

*Developing abiotic proxies*

We used R statistical software (R Foundation for Statistical Computing, Vienna, Austria) to explore the univariate effect of each abiotic factor on ecological attributes of benthic assemblages, including assemblage density, demersal fish density, mobile benthic invertebrate density, sessile invertebrate density, species diversity, assemblage biomass, and economic value. In total, three abiotic factors were considered (Table 1), including substrate type, depth, and water mass. As our data were not amenable to the assumptions of analysis of variance, we tested the effect of each factor using a non-parametric one-way Kruskal-Wallis test and a pairwise Dunn Test for post-hoc comparison (Chan and Walmsley 1997). If abiotic factors produced significant univariate effects on assemblage attributes, abiotic variables were examined as potential multivariate proxies.

To allow our assessment method to scale for entire ecosystems, we then modeled the multivariate effect of

TABLE 1. Abiotic factors used for remotely operated vehicle (ROV) survey stratification and testing of the univariate effect of abiotic proxies on ecological attributes of summertime benthic assemblages.

Abiotic factors and survey strata	Strata values
Substrate (size structure of the seabed)†	
Ledge	>1 m
Boulder	0.25–1 m
Cobble	0.064–0.25 m
Gravel	0.0002–0.064 m
Sand-mud	<0.0002 m
Depth (distance from sea surface to the seabed)†	
Shallow	20–30 m
Intermediate	40–60 m
Deep	70–100 m
Water mass (persistent nearshore water masses differing in terms of their characteristics, i.e., temperature, salinity, current velocity and prevailing current direction, and delineated from satellite imagery)‡	
WMCC	>69° W longitude
EMCC	<69° W longitude

† From navigational charts.

‡ NOAA Coast Watch summertime climatological mean (June–August; <http://eastcoast.coastwatch.noaa.gov/>).



TABLE 2. Abiotic variables considered for use in scaling up ecological attributes of summertime benthic assemblages via canonical correlation analysis and generalized additive models.

Abiotic variables	Units and Abbreviation	Factor	Continuous	Fitting data source	Projection data source
Substrate	ledge (l), boulder (bo), cobble (co), gravel (g), sand-mud (sm)	x		visual assignment from ROV video analysis	Barnhardt et al. (1998)
Depth	m (d)		x	ROV depth sensor delineated from	GEBCO
Water mass	Western Maine Coastal Current (WMCC), Eastern Maine Coastal Current (EMCC)	x		HYCOM modeled and remote sensing imagery	NOAA Coast Watch summertime climatologic mean (June–August)
Bottom temperature	°C (t)		x	HYCOM real-time values	HYCOM summertime climatologic mean (June–August)
Bottom salinity	psu (s)		x	HYCOM real-time values	HYCOM summertime climatologic mean (June–August)
Bottom current velocity	m/s (mag)		x	HYCOM real-time values	HYCOM summertime climatologic mean (June–August)
Bottom current direction	degrees (dir)		x	HYCOM real-time values	HYCOM summertime climatologic mean (June–August)

Sources: General Bathymetric Chart of the Oceans (GEBCO; <http://www.gebco.net/>); NOAA coast watch (<http://eastcoast.coastwatch.noaa.gov/>); Hybrid Coordinate Ocean Model (HYCOM; <http://code.nicholas.duke.edu/projects/mget/wiki/HYCOM>).

abiotic sites conditions on four separate assemblage attributes: species composition, species diversity, assemblage biomass, and economic value. In total, seven abiotic variables were considered (Table 2), including the substrate type, depth, and water mass strata of each sub-transect as well as the real-time daily average values at each sub-transect for bottom current direction, bottom current velocity, bottom temperature, and bottom salinity. The four water mass variables were acquired from hindcast HYCOM models through the Marine Geospatial Ecological Toolbox for ArcGIS (Table 2; Roberts et al. 2010; data *available online*).<sup>5</sup> Before running each model, we assessed the potential for multicollinearity among predictor variables using a variance inflation factor test (Naimi 2015) and then removed overly correlated variables. We also tested for spatial autocorrelation in the data using a Mantel test to confirm that assumptions of independent sampling were met (Wood 2006).

We modeled the effect of the seven abiotic variables on species assemblage composition (i.e., a matrix of relative population densities for all species) by fitting a canonical correlation analysis using the vegan package in R (Table 2; Oksanen et al. 2016). Through backward stepwise fitting, we retained only those abiotic variables that produced a significant improvement in model fit (i.e., a Pillai's permutation test) and explained variance (i.e., >1% improvement; e.g., Chen and Harvey 1995, Sherry and Henson 2005). Important abiotic variables and dominant recurring assemblages were determined by examining their correspondence to the new canonical variates.

We also modeled the effect of the seven abiotic variables on assemblage species diversity, assemblage biomass, and

economic value by fitting generalized additive models (GAM) with spline smoothers using the mgcv package in R (Table 2; Wood 2006). Through backward stepwise fitting, we retained only those abiotic variables that produced a significant improvement in model fit (i.e.,  $R^2$ , term alphas, etc.), explained variance (i.e., >1% improvement), and smoothness (i.e., minimization of GCV/UBRE and AIC; e.g., Wood 2006). The importance of each abiotic variable was determined through jackknifing, or the systematic removal and re-fitting of models. We evaluated the predictive capability of our best-fit models by examining the relationship between observed and predicted response values (i.e., Spearman correlation,  $R^2$ ).

### Scaling up benthic assemblages

We acquired the finest resolution abiotic GIS layers available in order to scale up our models for ecological attributes at the map pixel-by-pixel scale (i.e., 0.019° longitude by 0.019° latitude; Appendix S1: Fig. S1). All GIS layers were processed in ArcGIS 10.3 (ESRI, Redlands, California, USA) and clipped to the extent of the study area (i.e., Fig. 1B). By abiotic proxy, we derived a map of recurring summertime species assemblages by creating a composite GIS layer for all significant abiotic predictors from our best-fit CCorA model. Each pixel was colored to show the similarity of abiotic conditions and presumed species assemblages derived from the CCorA. We also created maps for summertime species diversity, assemblage biomass, and economic value using our best-fit GAMs, the predict function in the raster package, and the GIS layers for all significant abiotic predictors (Hijmans 2015).

A GIS layer from substrate type was derived from previous sidescan sonar and grab sample surveys aggregated

<sup>5</sup> <http://code.nicholas.duke.edu/projects/mget/wiki/HYCOM>

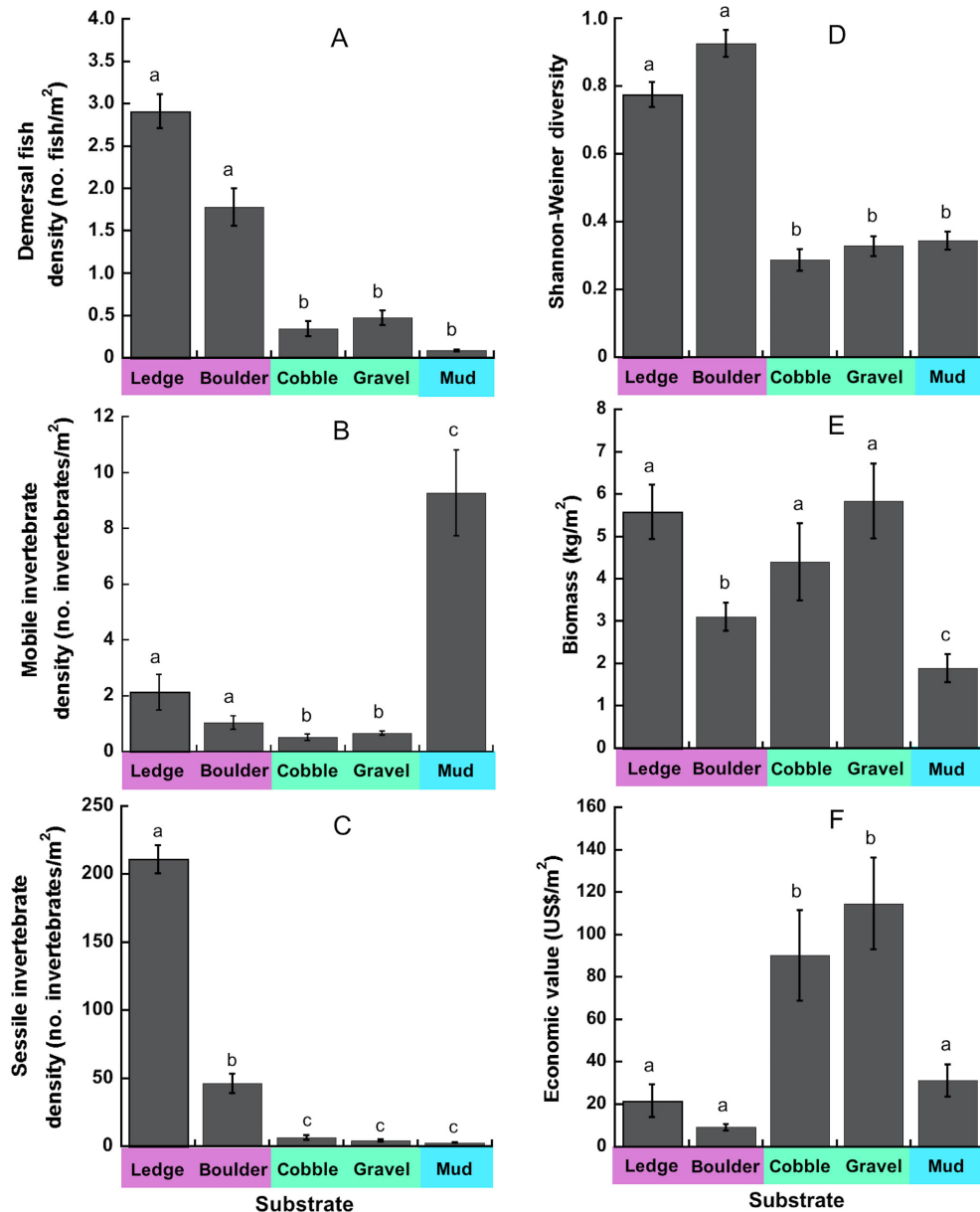


FIG. 2. The average (A) demersal fish density, (B) mobile benthic invertebrate density, (C) sessile invertebrate density, (D) species diversity,  $H'$ , (E) assemblage biomass, and (F) economic value of benthic megafaunal assemblages by substrate type along the Gulf of Maine coastal shelf. Error bars denote  $\pm 1$  SE. Small letters (a–d) mark significant pairwise differences ( $P < 0.05$ ) in ecological attributes by substrate type. Colored polygons over bar plots indicate how substrate strata were merged during model projection to accommodate the lower thematic resolution of the currently available GIS layer for substrate. [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

by Barnhardt et al. (1998). We acquired the bathymetric layer from the General Bathymetric Chart of the Oceans group (GEBCO; data available online).<sup>6</sup> Last, we acquired mean summertime water mass layers from hindcast HYCOM models via the Marine Geospatial Ecological Toolbox for ArcGIS (Roberts et al. 2010). Each water mass variable layer was first downloaded as monthly

<sup>6</sup> <http://www.gebco.net/>

climatologic layers and then averaged across months for long-term climatologic summertime conditions (June–August). Due to the thematic resolution of the substrate data, models had to be re-fit based on broader substrate categories for the purposes of map creation in this study (i.e., ledge and boulder classes were combined; cobble and gravel classes were combined, e.g., the symbology of Fig. 2). However, models could just as easily be re-projected at a finer thematic resolution as better

TABLE 3. Main effect of abiotic factors on ecological attributes of summertime benthic assemblages in the Maine coastal shelf using nonparametric one-way Kruskal-Wallis significance test.

Abiotic factors and ecological attributes	Demersal fish density	Mobile invertebrate density	Sessile invertebrate density	Assemblage density	Species diversity	Assemblage biomass	Economic value
Depth							
$P$	<0.0001	0.0001	0.0001	0.02	0.001	0.0001	0.0001
$\chi^2$ (df)	123.12	174.09	189.62	7.48	17.77	196.76	30.43
df	2	2	2	2	2	2	2
Substrate type							
$P$	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001
$\chi^2$ (df)	418.73	134.01	884.9	387.13	380.3	129.77	50.43
df	4	4	4	4	4	4	4
Water mass							
$P$	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.001
$\chi^2$ (df)	197.2	28.56	133.8	101.25	17	107.91	10.77
df	1	1	1	1	1	1	1

Notes: All comparisons were significant ( $P < 0.05$ ). All values except three were extremely highly significant ( $< 0.0001$ ).

substrate data becomes available. Below we present our results and predicted assemblage attribute maps.

## RESULTS

### Characterizing benthic assemblages

We conducted 1885 remotely operated video surveys across the Maine coastal shelf during the summer months from 2010 to 2013 (Fig. 1A). Over the course of the study, we observed a total of 90 species, including 29 demersal fishes and 58 benthic invertebrate taxa (Appendix S1: Table S1). While a few water-column dwelling species were observed, including harbor seals (*Phoca vitulina*), Atlantic herring (*Clupea harengus harengus*), and comb jellies (*Bolinopsis infundibulum*), only benthic macrofauna and megafauna living on or above the seabed were considered in this study.

### Identifying potential abiotic proxies

Substrate type, depth, and water mass each had highly significant univariate effects on the average densities, diversity, biomass, and economic value of assemblages along the Maine coastal shelf (Table 3). Ledge and boulder supported the highest average demersal fish densities, sessile invertebrate densities, species diversity, and assemblage biomass (Fig. 2A, C, E, respectively). Cobble and gravel also supported equally high biomass as well as the highest average economic value (Fig. 2E, F, respectively). And, sand-mud supported the lowest of all ecological attributes except mobile benthic invertebrate densities (Fig. 2B). The average density (for all organisms), diversity, biomass, and economic value of benthic assemblages significantly decreased with increasing depth (Fig. 3A, D, respectively). Last, assemblage composition significantly shifted from east to west, where the density of demersal fishes and sessile invertebrates increased (Fig. 4A, C, respectively) and the density of mobile benthic invertebrates decreased (Fig. 4B). Similarly, the average diversity

and biomass of assemblages significantly increased the EMCC to the WMCC (Fig. 4D, E, respectively), while the average economic value slightly decreased (Fig. 4F).

### Scaling up benthic assemblage attributes from known abiotic conditions

Abiotic variables effectively modeled patterns of species assemblage composition along the Maine coastal shelf. Substrate type, depth, current velocity, temperature, current direction, and salinity collectively explained a substantial portion of the variance in our best-fit CCorA model (37% explained, Pillai's Trace = 1.85;  $P < 0.001$ ), with the first two canonical variates accounting for the majority of the total explained variation (53.0%). The factor for water mass failed to contribute to model fitness and was therefore removed. The presence of ledge and/or mud corresponded with the primary significant canonical variate, meaning that substrate type had the strongest effect on species assemblage composition. The second significant canonical variate represented the effect of depth, and then current variables and temperature, meaning that these variables were secondarily important (Fig. 5A; Appendix S2: Table S1). Salinity had a small, but significant effect on species assemblages.

Examination of species abundance loadings along the primary and secondary canonical variates revealed five dominant recurring assemblages along gradients of substrate, depth, and water mass characteristics (Fig. 5B). Northern lampshells and cunner wrasse comprised Assemblage 1, dominating primarily shallow (i.e.,  $< 30$  m) ledge habitats (dark blue circle). Pollock, horse mussels, tunicates, and sponges comprised Assemblage 2, dominating intermediate (i.e.,  $\sim 60$  m) ledge and boulder habitats (light blue circle). Assemblage 3 consisted of American lobster, giant sea scallop, and common sand dollars, dominating intermediate to shallow habitats of gravel and cobble with persistent north and/or westward currents (green circle). Acadian redfish and jewel anemones comprised Assemblage 4, dominating

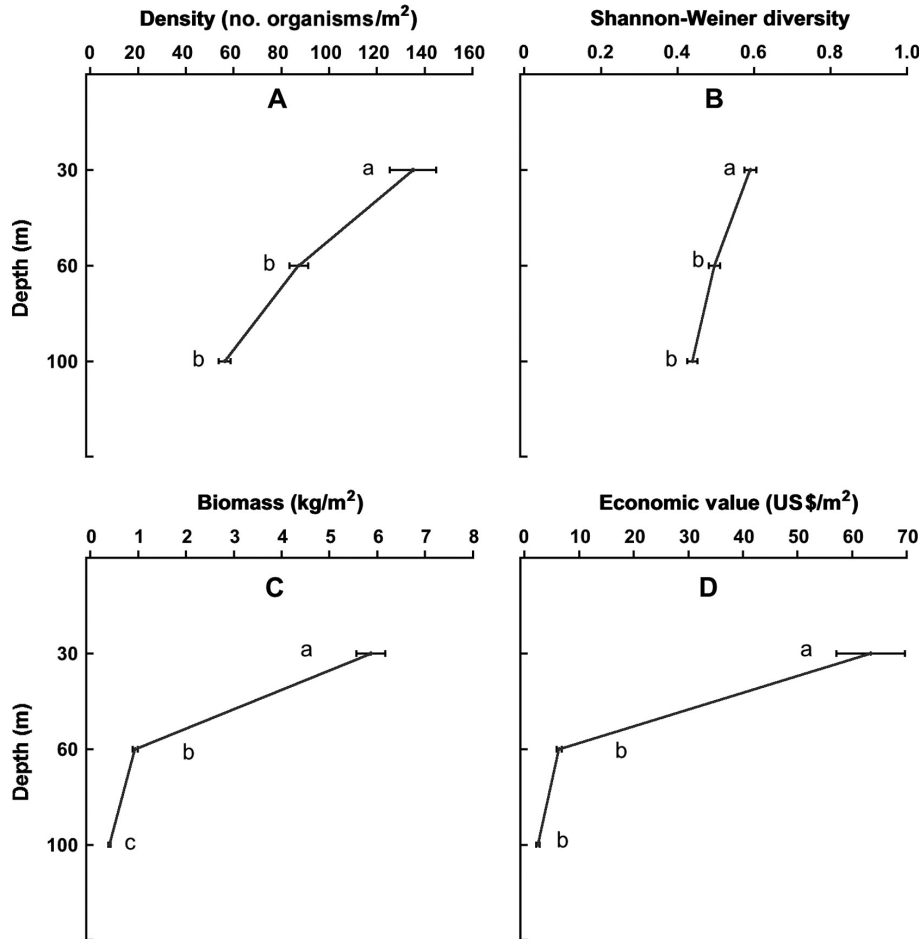


FIG. 3. The average (A) density of all organisms, (B) species diversity,  $H'$ , (C) assemblage biomass, and (D) economic value of benthic megafaunal assemblages with depth (m) in the Maine coastal shelf. Error bars denote  $\pm 1$  SE. Small letters (a–c) mark significant pairwise differences ( $P < 0.05$ ) in ecological attributes by depth.

deep (i.e., ~100 m) ledge and boulder habitats with persistently strong currents (light purple circle). Last, pandalid shrimp, cerianthid anemones, silver hake, American plaice, and other flatfishes comprised Assemblage 5, and dominated intermediate to deep sand-mud habitats (red circle). The composite GIS layer of significant abiotic predictors created a useful proxy map of these five recurring dominant assemblages for the Maine coastal shelf (Fig. 6A).

Abiotic variables also effectively modeled patterns of species diversity, assemblage biomass, and economic value along the Maine coastal shelf. Substrate type, depth, current direction, temperature, current velocity, and salinity collectively explained a substantial portion of the variance in our best-fit GAMs (42.4%, 40.0%, and 57.6%, respectively). Partial variance calculations revealed that substrate type, depth, current variables (i.e., direction and/or velocity) and temperature had the strongest collective effects (Table 4). Meanwhile, salinity had a small, but significant effect on each attribute (Table 4; Appendix S2: Figs. S1 and S3). Since the three

GAMs significantly predicted benthic species diversity, assemblage biomass, and economic value (Spearman's  $R^2 = 0.60, 0.57, 0.46$ , respectively), each produced a useful high-resolution prediction map for the Maine coastal shelf (Fig. 6B, D).

## DISCUSSION

Our study provides further evidence that abiotic variables affect the assembly of nearshore benthic communities. Substrate type, depth, and water mass characteristics captured significant spatial variation in summertime benthic assemblages and therefore serve as effective abiotic proxies for creating high-resolution maps of important ecological attributes (i.e., Fig. 6A, D). Our study provides useful tools for advancing ecosystem-based marine spatial planning along the Maine coastal shelf; however our approach relies largely on publicly available abiotic GIS layers that have predominantly global extents, meaning that the assessment method we describe could very easily be adapted for use in other



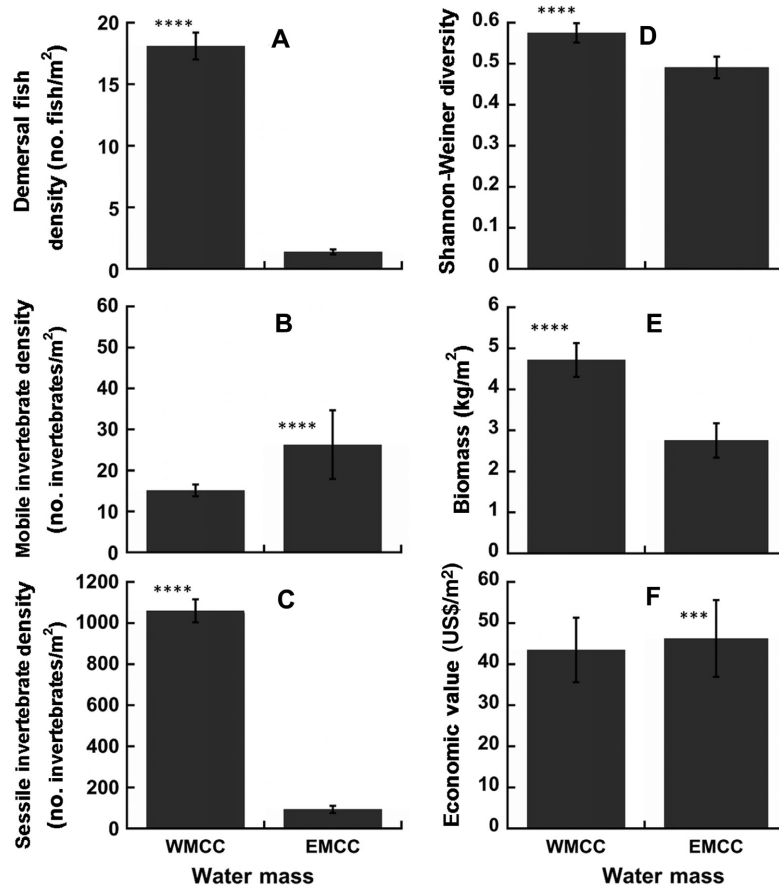


FIG. 4. The average (A) demersal fish density, (B) mobile benthic invertebrate density, (C) sessile invertebrate density, (D) species diversity,  $H'$ , (E) assemblage biomass, and (F) economic value of benthic megafaunal assemblages by Maine Coastal Current (MCC). Error bars denote  $\pm 1$  SE. Asterisks mark significant differences in ecological attributes by water mass (\*\*\*,  $P < 0.001$ ; \*\*\*\*,  $P < 0.0001$ ).

ecosystems. The individual abiotic proxies provide insight regarding the development of foundational ecological principles of MSP, while the high resolution maps reveal spatially explicit planning priorities. Here we describe why each of our abiotic proxies is important and discuss how they might be used for preserving important attributes of ecosystem structure and function (e.g., Foley et al. 2010) when designing effective MSPs.

#### *Importance of abiotic proxies*

Fine-scale spatial variation in substrate type corresponded to patterns of benthic community assembly along the Maine coastal shelf (Fig. 5A, Tables 3 and 4), where the most diverse, abundant, and economically valuable assemblages associated with complex substrates (i.e., ledge, boulder, cobble, gravel, etc.) and the least associated with homogenous substrates (i.e., sand-mud; Fig. 2D, F). Although differences in species composition among substrates (Fig. 2A, C) likely reflected the intrinsic morphological traits of species, i.e., a higher proportion of sessile suspension feeders have evolved to occupy hard

bottom areas than soft bottom (Gray 2002, Beaman and Harris 2007); higher assemblage densities, biomass, species diversity, and commercial fisheries value surrounding complex substrates (i.e., ledge, boulder, cobble, and gravel) reflects the quantity and variation in three-dimensional structural complexity provided by each substrate type. Compared to fine-grained sediment, larger amorphous rock formations create greater attachment area for sessile organisms, a greater variety of interstitial spaces for cryptic species (Gratwicke and Speight 2005), and more frequent exposure to food particles and larvae via structure-associated flow dynamics (Gili et al. 2001, Beaman and Harris 2007). As a result, many species selectively forage around (Auster et al. 1994, Hosack et al. 2006), shelter around (Auster et al. 1994), reproduce around (Ames 2004), and even recruit to complex substrates (Wahle and Steneck 1992, Auster et al. 2003, Diaz et al. 2003), meaning that substrate type can a useful abiotic proxy for a suite of ongoing ecological patterns and processes.

Benthic assemblages also structured according to depth (Fig. 5A, Tables 3 and 4), where the diversity, abundance,

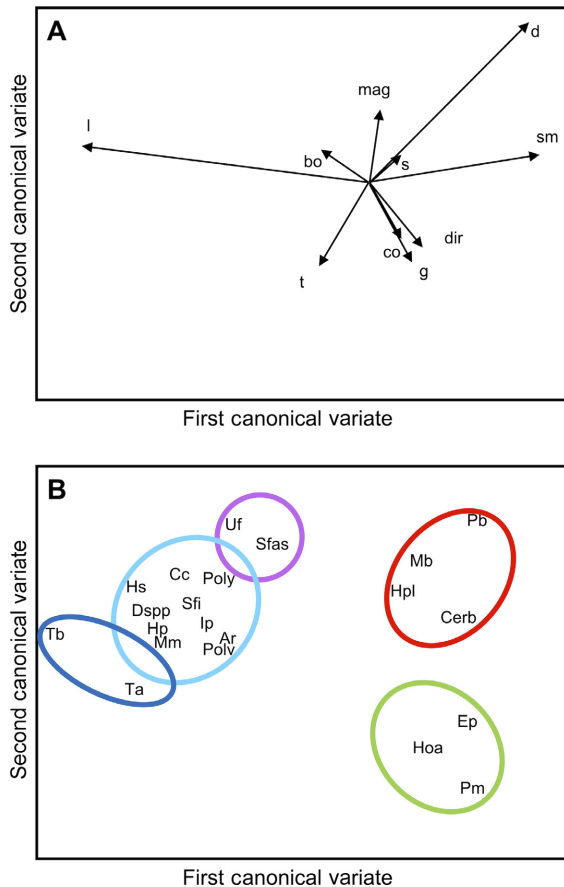


FIG. 5. Biplots depict the importance of (A) abiotic variables in (B) determining benthic species assemblage composition from canonical correlation analysis. Collectively, substrate type, depth, bottom current direction, bottom current velocity, bottom temperature, and bottom salinity accounted for 37% of the variance among sites, with the first two canonical functions accounting for 53% of the explained variation. The vector length and direction of biplot arrows indicate the importance of and correspondence between abiotic variables and new canonical variates (i.e., axes). This shows an overriding influence of substrate, then depth, and least important were water mass variables (i.e., bottom water velocity, bottom water direction, temperature, and salinity) in determining species composition. Multi-colored polygons surround recurring dominant assemblages along gradients of abiotic conditions, which are also depicted using similar symbology in Fig. 6A. Abiotic variables are abbreviated as l, ledge; bo, boulder; co, cobble; g, gravel; sm, sand-mud; mag, bottom current velocity; dir, bottom current direction; t, bottom temperature; s, bottom salinity. Species names can be found in Appendix S1: Table S1. [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

and value of assemblages declined significantly with increasing depth (Fig. 3A, D). While the depth associations of individual species for this region likely relate to a variety of factors (Overholtz and Tyler 1985, Gabriel 1992, Watling and Skinder 2007), e.g., species physiologies, life history traits (Methratta and Link 2007a), and summertime prey distributions (Lasley-Rasher et al. 2015), the observed assemblage-level decline reflects a widely occurring phenomenon (Langton et al. 1995,

Saiz-Salinas et al. 1998, Colloca et al. 2003, Thresher et al. 2014). In the shallows, benthic marine macrophytes such as kelp and seaweeds support traditional food webs by providing complex habitat structure and ample organic matter (i.e., POC and DOC) for herbivorous megafauna and their predators (Steneck et al. 2002). However, below the euphotic zone, food webs depend much more heavily on the delivery of organic matter from elsewhere. As organic matter is transferred to deeper depths, it is either progressively transferred through the food web or recycled (e.g., Brady et al. 2013, Testa et al. 2013), resulting in an incremental decrease in the available food resources with depth (Mann 1972, Stuart et al. 1981, Newell et al. 1982). Ultimately, this process lowers the carrying capacity of deeper areas, making seabed depth another effective abiotic proxy for assemblage function (Mann 1988, Tumbiolo and Downing 1994).

Finally, coastal water masses played a role in structuring benthic assemblages along the Maine coastal shelf (Fig. 5A, Tables 3 and 4). From east to west, there was a significant increase in average demersal fish densities, sessile invertebrate densities, species diversity, and assemblage biomass (Figs. 4A, C, E and 6B, C). Yet, the average economic value, and the density of mobile benthic invertebrates significantly decreased (Figs. 4B, F and 6D). Notably, this pattern corresponded to a shelf-wide transition from predominantly strong uniformly cool currents in the EMCC to warmer thermally stratified and spatially variable currents in the WMCC (Pettigrew et al. 2005, Appendix S1: Fig. S1). In part, species distributions along the shelf reflect individual species characteristics, e.g., intrinsic abilities to recruit and feed in high flow regimes (Eckman and Duggins 1993), thermal tolerances (Methratta and Link 2007a, b), and salinity tolerances. However, the shelf-wide shift in ecological attributes for this region largely reflects the overall contrast (and interconnectedness) between coastal currents regimes (Jordaan et al. 2010, Table 4; Appendix S2: Table S1, Figs. S1 and S3). Nearshore currents likely determine assemblage structure along the shelf by controlling the delivery of reproductive propagules, nutrients, and food particles (e.g., Palardy and Witman 2011, 2014). Meanwhile, ambient bottom temperatures likely regulate biomass accumulation by controlling the relative rates and phenology's of important ecological processes along the shelf, e.g., physiology (Pörtner 2001), primary productivity (Li and He 2014), spawning (Methratta and Link 2007a, b), development (Haynes and Wigley 1969), growth (Jordaan and Kling 2003), recruitment (Annis 2005), etc.

#### Implications for ecosystem-based MSP

Preservation of ecosystem function is implicit to the concept of marine spatial planning, but not guaranteed in practice—especially when multi-use interests are involved. Defining clear foundational principles that fit the ecological context of a study region will be critical to

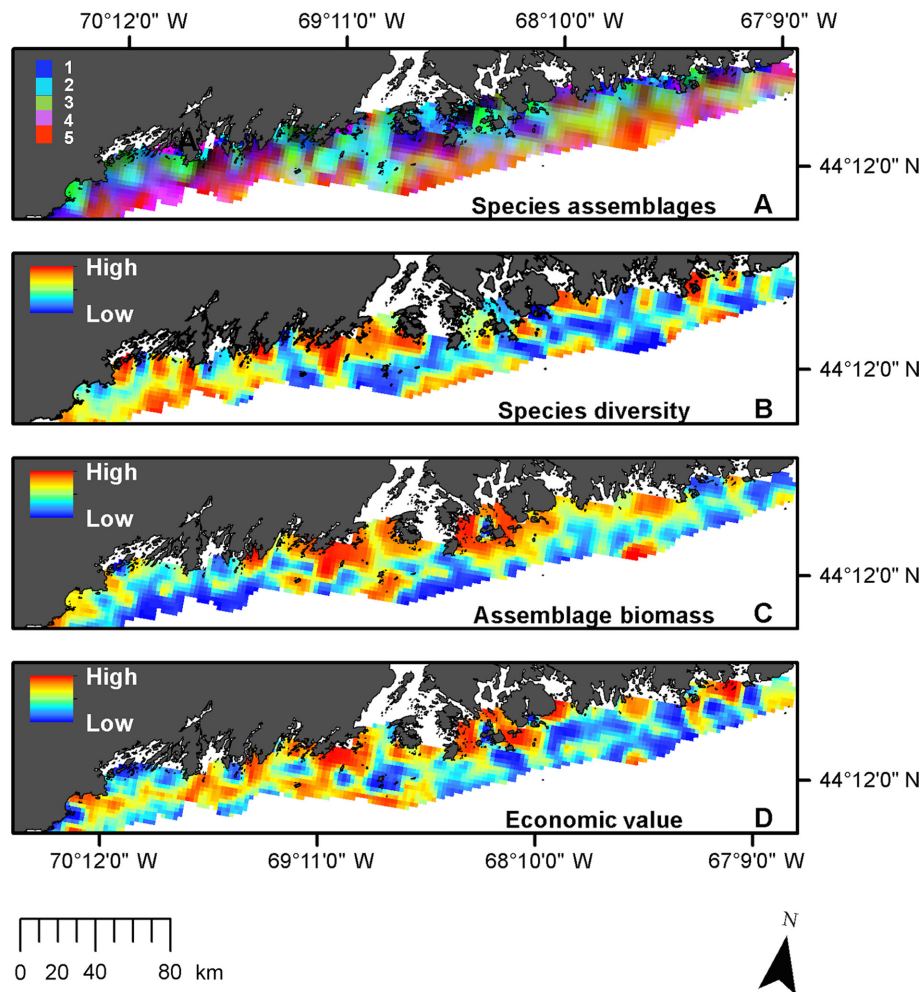


FIG. 6. Maps depicting shelf-wide predictions for (A) recurring species assemblages, (B) species diversity, (C) assemblage biomass, and (D) economic value from “abiotic proxy”-based models for the Maine coastal shelf. The recurring species assemblages map is a composite image showing pixels of similar abiotic conditions and species assemblages derived from the canonical correlation analysis; the color scale of pixels matches the color scale of polygons surrounding recurring species assemblages identified in Fig. 5B. The maps of species diversity, assemblage biomass, and economic value of benthic assemblages were predicted from the best-fit generalized additive models and GIS layers for significant abiotic variables. [Color figure can be viewed at [wileyonlinelibrary.com](#)]

building a solid conservation basis for MSP (Foley et al. 2010). Moreover, identifying and protecting priority areas that exhibit key ecological principles will ensure that important attributes of ecosystem function are maintained (Foley et al. 2010). In our study, we developed abiotic proxies for dominant recurring assemblages, species diversity, assemblage biomass, and economic value—each an important attribute for describing ecosystem function and services (although others are relevant also, e.g., Lester et al. 2013). The assessment method we describe provides critical tools that can allow resource managers to begin visualizing important ecological attributes, defining foundational ecological principles for a study region, and developing planning priorities to guide effective MSP.

First, the abiotic proxies help resource managers to develop clear foundational ecological principles by

highlighting where—within a broader spectrum of abiotic variation—ecological attributes might be maximal. This allows resource managers to begin a MSP exercise with clear expectations about what uses might be best suited across different areas. As an example, our study indicates that the most diverse, abundant, and valuable assemblages along the Maine coastal shelf generally concentrate on complex substrates, in shallow areas, and in warm east-west flowing waters, i.e., the WMCC (Figs. 2A, F, 3A, C, and 4A, C, F). Therefore, three notional foundational ecological principles might be to limit the effect of extractive uses in areas characterized by these abiotic attributes (Fig. 4A). By incorporating these foundational principles early on in the MSP process, resource managers will be more likely to build suitable protections for important ecological processes, to create spatial refugia from natural and anthropogenic

TABLE 4. Summary of best fit generalized additive models (GAMs) for summertime benthic species diversity, assemblage biomass, and economic value along the Maine coastal shelf.

Ecological attributes and abiotic variables	Partial explained variance	<i>P</i>	<i>R</i> <sup>2</sup> adjusted	Model explained variance (%)	Predictive <i>R</i> <sup>2</sup>
Species diversity			0.40	42.4	0.62
Bottom current direction	12.78	<0.0001			
Substrate type	9.70	<0.0001			
Depth	9.36	<0.0001			
Bottom current velocity	7.14	<0.0001			
Bottom temperature	6.49	<0.0001			
Bottom salinity	5.70	<0.0001			
Assemblage biomass			0.27	40.0	0.55
Depth	15.81	<0.0001			
Substrate type	4.41	<0.0001			
Bottom current direction	3.22	<0.0001			
Bottom temperature	3.14	<0.0001			
Bottom current velocity	2.03	<0.0001			
Bottom salinity	1.59	<0.0001			
Economic value			0.46	57.6	0.46
Substrate type	24.73	<0.0001			
Depth	8.49	<0.0001			
Bottom current direction	4.12	<0.0001			
Bottom salinity	1.88	<0.0001			
Bottom current velocity	0.96	<0.0001			
Bottom temperature	0.40	<0.0001			

Notes: Substrate type, depth, bottom current velocity, bottom current direction, bottom temperature, and bottom salinity explained a substantial portion of variance, with each making a significant contribution to model fit. All values of alpha were extremely highly significant ( $P < 0.0001$ ). Partial explained variances (i.e., systematic removal/model refitting) indicate that bottom current direction, substrate type, and depth had the strongest effect on species diversity; depth and substrate had the strongest effect on assemblage biomass; and substrate and depth had the strongest effect on economic value.

disturbances, and perhaps to better stabilize food-web dynamics in these ecologically and economically important areas (Foley et al. 2010).

Next, the abiotic maps provide insight regarding how foundational ecological principles might be applied within the spatial landscape of abiotic conditions (Appendix S1: Fig. S1). The abiotic maps allow models to be scaled up to describe important ecological attributes of assemblages at the pixel-by-pixel scale, thereby allowing resource managers to begin to prioritize the most valuable sites and to determine locations where extractive uses might be minimal. As an example from our study system, two notional candidates for special protection might be Penobscot Bay and/or the Mount Desert Island region, which support several areas of relatively high species diversity, biomass, and economic value (Fig. 6B, D). Conversely, several low-diversity and low-biomass areas with relatively low economic value persist in the midcoast of Maine, which may be suitable areas for certain emerging uses like offshore wind energy (Fig. 6B, D). Ultimately the planning process will need to be informed by other ecological and human dimensions (e.g., Gleason et al. 2010, Lester et al. 2013); however the assessment method, the abiotic proxies, and the assemblage attribute maps provide a useful starting point for advancing MSP.

#### *Broader application: incorporating seasonal dynamism*

For the purpose of demonstrating the abiotic proxy assessment method, we focused on just one season, i.e., the summer months. However, in reality, most temperate

assemblages exhibit some form of seasonal dynamism, e.g., seasonal movements, spawning, etc. (Apollonio et al. 1986, Methratta and Link 2007a, b, Ramenofsky and Wingfield 2007). In practice, therefore, resources managers will want to set ecological principles/priorities that account for such variation over the full annual cycle. Although seasonal variability was beyond the scope of the current study, our assessment method could easily be adapted to account for the temporal variability of marine assemblages. The limiting factor for the Maine coastal shelf (and likely in most other systems) will be the temporal resolution of abiotic GIS layers and species data. Geospatial platforms like the ArcGIS Marine Geospatial Ecology Toolbox for ESRI ArcGIS, which produces modeled and remote sensing GIS layers down to the daily and hourly time-scale, could supply the necessary abiotic layers (e.g., Roberts et al. 2010). However, an expanded ROV survey program would be required in order to characterize seasonal patterns of assemblages.

#### *Broader application: proxies for rapidly changing ecosystems*

Our study also solely focused on current spatial patterns of recurring species assemblages. Several recurring assemblages were consistent with past studies, e.g., cunner-dominated assemblages in shallow rocky areas (Witman and Sebens 1992, Stevenson et al. 2014) and Acadian-redfish-dominated assemblages in deeper rocky areas (Auster et al. 2003), while others indicate ongoing ecosystem changes, e.g., the current ecological absence of



Atlantic cod (Witman and Sebens 1992, Pershing et al. 2015) and the diffusion of American lobster and crabs into non-shelter-rich habitats (Fig. 5A, B, Steneck and Wahle 2013). The trajectory of these assemblages under increasingly warming conditions (e.g., Saba et al. 2016) is still largely unknown. Therefore it will be critical to consider climate-induced effects when developing foundational ecological principles and priorities for MSP. As species continue to shift their ranges in responses to warming conditions (e.g., Walsh et al. 2015), there could be cascading effects to the structure, function, and services provided by this ecosystem, which would nullify the value of our current ecological attribute maps. However, re-projecting the current models (i.e., for species assemblages, species diversity, biomass, and economic value) at decadal time steps might help to predict the extent and absolute magnitude of potential changes to the Maine coastal shelf. Projection of models onto real-time year-to-year abiotic forecasts could also serve as an early warning system for impending ecological shifts. In either case, our study provides an important baseline and assessment method for considering future changes to marine species assemblages.

#### *Broader application: beyond the Maine coastal shelf*

We focused on one component of one ecosystem: benthic assemblages along the Maine coastal shelf. However, our study is also widely applicable to mapping ecological attributes for marine spatial planning objectives all over the world (e.g., UNESCO 2016). The abiotic variables we explored are frequently cited as important determinants of marine assemblage structure (McArthur et al. 2010, Brown et al. 2011, Kovalenko et al. 2012, Thresher et al. 2014), meaning they could easily serve as useful abiotic proxies beyond our study area (although the effect and order of importance may vary due to ecological context; e.g., Foley et al. 2010, Lecours et al. 2015). We also rely heavily on public abiotic data layer sources with predominantly global extents (e.g., GEBCO, HYCOM, etc.), meaning that our assessment methods can be scaled up regardless of the system. For parts of the world that already support regional remote video surveys, e.g., the Mid-Atlantic USA (HabCam 2016) and Australia (AIMS BRUV 2016), our study is timely and could be expediently applied to support ongoing regional planning needs, e.g., the Mid-Atlantic Regional Planning Council on the Ocean; (UNESCO 2016) and the Australian Commonwealth Marine Reserve Review (CMR 2015). However, for some ecosystems, resource managers may need to rely temporarily on other regional data sets (e.g., trawl surveys, acoustic surveys, etc.) until an appropriate regional ROV survey program can be implemented.

#### CONCLUSIONS

The lack of relatively high-resolution maps that characterize the structure, function, and services of coastal marine ecosystems is a major limitation to developing useful MSPs.

Using the assessment method we lay out, resource managers can begin to develop fine-scale maps of assemblage attributes, clarify relevant system-specific principles, and define priorities within a given planning area, and then reconcile planning objectives with the current distribution and intensity of human activities (i.e., using cumulative impacts analysis; e.g., Micheli et al. 2013). Managers can also begin to identify any existing conservation gaps embedded in the current patchwork of spatial management schema (e.g., Crowder et al. 2006, Agardy et al. 2011), and then evaluate the potential trade-offs associated with various planning scenarios (e.g., Lester et al. 2013) in a spatial context. Through this process, managers may converge on a plan that better protects and maintains the many marine resources, species assemblages, and ecological processes on which humans rely.

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## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/eap.1469/full>

## DATA AVAILABILITY

Data associated with this paper have been deposited in Dryad: <http://datadryad.org/resource/doi:10.5061/dryad.cs17q>