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Habitat suitability modeling for mesophotic coral in the northeastern Gulf of Mexico

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ABSTRACT: The mesophotic coral ecosystem (MCE) of the eastern Gulf of Mexico hosts diverse invertebrate and fish fauna across an array of hard-ground features. However, the extent of the potential MCE habitat in the region is poorly constrained. Maximum entropy modeling was used to predict the spatial extent of mesophotic azooxanthellate octocorals and antipatharians within the mesophotic area located between Mississippi (Pinnacle Trend Area) and the mid-continental shelf and upper slope of Florida, eastern Gulf of Mexico. Habitat prediction models were generated using geo-referenced, coral-presence records obtained by classifying photographic samples with co-located geophysical data, oceanographic variables, and atmospheric variables. Resulting models were used to predict the extent of suitable habitat in the study area. An independent set of presence records was used to test the model performance. Results (general and by taxon) predict that suitable areas for MCE exceed 400 km^2 and occur along carbonate mounds and paleo-shoreline ridges (hard substrata and high surface rugosity). Reduced amounts of fine sediments, surrounding waters rich in chromophoric dissolved organic matter (CDOM), and downwelling currents also increased predicted suitability. The model significantly exceeded random performance and predicted that surface rugosity and CDOM are the most important variables contributing to coral habitat. Areas of hard substrate within the study area that were not identified as coral habitat by the model suggest that mesophotic sea fans and sea whips apparently depend as much on the chemical and physical conditions (e.g. currents that transport oxygen and food) as on hard substrata for settlement.

KEY WORDS: Habitat suitability · Mesophotic · Maximum entropy modeling · Corals · Octocorals · Antipatharian · Eastern Gulf of Mexico · Maxent

INTRODUCTION

In the Gulf of Mexico, there are 4 areas where mesophotic coral ecosystems (MCEs) extend from 30 to 100 m depths. They are characterized by the presence of light-dependent/independent corals and associated fauna (Kahng et al. 2010) and are designated as follows: the Pinnacles Reefs, the Flower Garden Banks and other hard-ground features offshore of Texas (Continental Shelf Associates & Texas A&M University 2001, Locker et al. 2010), the Florida Middle Ground reef system (Smith et al. 2006), and Pulley Ridge (Locker et al. 2010). However, these well-studied areas constitute a small fraction of the approximately 179 000 km^2 of substrata that could potentially support MCEs in the northern Gulf of Mexico (Locker et al. 2010).

The Pinnacles Reefs and the Florida Middle Ground mesophotic reefs comprise a broad array of carbonate features within the 30–100 m isobath, including flat-topped mounds measuring hundreds of meters across, fields of boulder-sized fragments, and intermediate aggregates, all of which are important habitat for commercial and recreational fish species (Dennis & Bright 1988, Weaver et al. 2002). The invertebrate fauna of the MCE is also diverse and abundant, with octocorals, hermatypic corals, sponges, and antipatharians numbering at least 40 taxa (Continental Shelf Associates and Texas A&M University 2001).

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In 2010, more than 4.1 million barrels of crude oil were discharged into the waters of the northeast Gulf of Mexico following loss of well control in the Macondo Prospect exploration site and the sinking of the *Deepwater Horizon* (DWH) drillship (McNutt et al. 2012). In addition, at least 500 000 t of hydrocarbon gas were released into the water column during the 87 d event (Joye et al. 2011). Potential exposure of the MCE in the Pinnacles Reefs and a portion of the Florida Middle Ground occurred via oil slicks that covered the region for approximately 35 d (Valentine et al. 2014, MacDonald et al. 2015). Response operations treated the floating oil with repeated aerial application of dispersants and by corralling the floating oil and burning it (Rufe et al. 2011; and see NOAA ERMA Deepwater Gulf Response: http://gomex.erma.noaa.gov/).

Concerns for injury to octocorals and other sessile organisms of the MCE arise from organismal exposure to surface oil, dispersant treatments, and soot from burning. DeLeo et al. (2016) demonstrated that the exposure of deep-sea corals to different combinations of oil and dispersant produce a decline in coral health. Several studies found frequent injuries in octocorals and antipatharians in mesophotic reefs within the impacted area (Etnoyer et al. 2016, Silva et al. 2016). The pathology of these injuries was similar to what has been described in corals from deep-sea habitats that were known to be impacted by oil from the DWH discharge (White et al. 2012, Hsing et al. 2013, Fisher et al. 2014). Thus, there is well-founded concern regarding the health of regionally significant portions of the Gulf of Mexico's MCE and a need to better define the extent of this resource.

While vulnerable marine ecosystems do occur at the scale of ocean basins, conservation efforts are generally undertaken within national jurisdictions where the national legal framework supports the establishment of marine protected areas (Elliott & Crowder 2005). Anthropogenic pressure on marine ecosystems, coastal areas, and the deep sea has been increasing (Davies et al. 2007). One of the biggest challenges in design and management of marine protected areas is estimating the spatial extent of habitats that can support taxa of concern (Rogers et al. 2007). This need increases in the case of corals because the composition of associated reef communities can change over relatively short distances (Rogers 1999). Determining the extent of ecosystem injury and verifying the efficacy of recovery strategies would benefit from a more comprehensive appraisal of the available habitat for mesophotic corals.

Habitat suitability models can be used to produce maps that predict continuous-coverage habitat in data-sparse areas, including the potential MCE area of the Gulf of Mexico. These models combine taxon presence/absence data with relevant environmental variables to statistically predict the distribution of species and to impart better understanding of which environmental factors are most important for the survival of species of interest (Guisan & Zimmermann 2000). Rengstorf et al. (2013) reviewed some of the approaches to this problem used by previous studies and cited the following methods: multidimensional envelopes of environmental factors (e.g. BIOCLIM), parametric regression and non-parametric smoothing procedures (Guisan et al. 2002), algorithms based on training sets, and hybrid combinations of these methods (Elith et al. 2006, 2011, Elith & Leathwick 2009). Data that verify the non-occurrence of modeled taxa in a region of interest, i.e. absence data, are problematic for museum collections and for surveys that could not comprehensively cover large regions; the alternative is to simulate absence through use of randomly selected background points (Pearce & Boyce 2006). The literature includes several studies where machine learning methods such as Maxent (Phillips et al. 2006) have performed well for presence-only datasets (Elith et al. 2006, Rengstorf et al. 2013, Georgian et al. 2014). Accordingly, this approach was used in the present study, which also provides a comparison with Maxent habitat models developed for deep-sea corals.

The aim of this study was to characterize and quantify the habitat suitability niche for the most conspicuous octocorals and antipatharian corals within the 30–100 m isobaths in relation to the available substrata, bottom topography, and oceanographic parameters situated between Mississippi and Florida. It builds upon a broad array of available data. Results can be used to formulate new strategies of restoration and conservation, and to inform management of mesophotic corals in the Gulf of Mexico.

METHODS

Study area

The present coral habitat suitability model was compiled within a region defined by the extent of a USGS bathymetric mapping program, which covers an area of 6228 km^2 and encompasses the following areas (Gardner et al. 2001b, 2002, 2003): (1) the Pinnacle Trend located between Mississippi and Alabama; (2) the Head of Desoto Canyon offshore of Panama City, Florida; and (3) The West Florida Shelf (Fig. 1). The MCE in this area comprises multiple

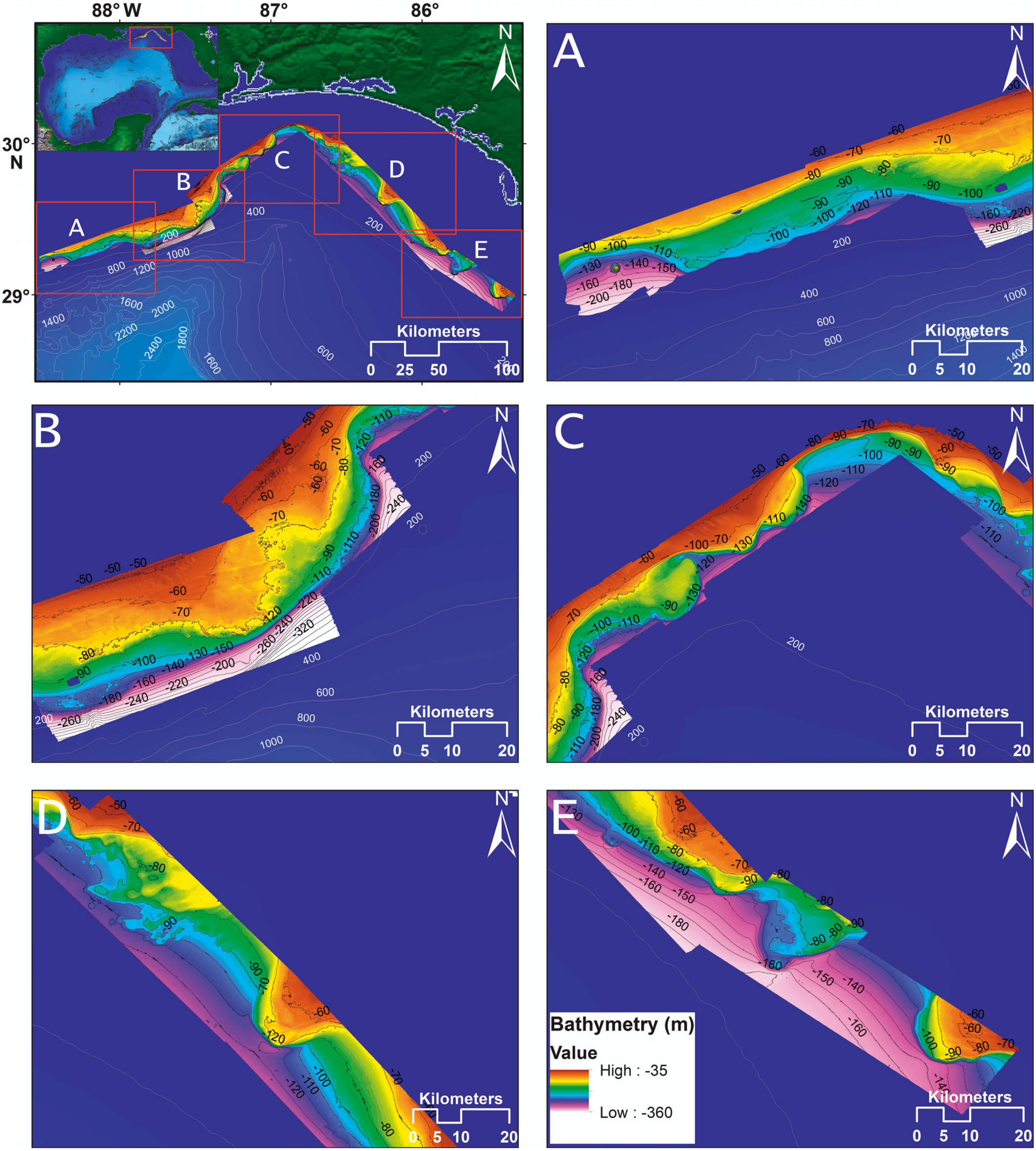

Fig. 1. Extent of the area mapped by the US Geological Survey (Gardner et al. 2001b, 2002, 2003), showing the region of potential mesophotic habitats between Mississippi and Florida analyzed in the coral habitat suitability model. (A) Alabama–Mississippi Pinnacle Trend Alabama Alps Reef area; (B) Alabama–Mississippi Pinnacle Trend Roughtongue Reef area; (C) Head of Desoto Canyon; (D) Florida Middle Grounds Coral Trees area; and (E) Florida Middle Grounds Madison Swanson Reef area

structures dating from Quaternary carbonates to Holocene sandstones (Locker et al. 2010). The area has been previously investigated during the multidisciplinary 'Mississippi-Alabama Pinnacle Trend Ecosystem Monitoring' (MAPTEM) program (Brooks & Giammona 1991, Continental Shelf Associates & Texas A&M University 2001).

Coral records

Photographic survey records of sea fans and sea whips were collected during 3 consecutive years (1997–1999) by the MAPTEM report (Continental Shelf Associates & Texas A&M University 2001) and Peccini & MacDonald (2008); they provide a baseline of the marine resources of the region, including the gross anatomical condition of mesophotic sea fans and sea whips in the Pinnacle Trend before the DWH oil spill. In the case of sites that were not visited during the MAPTEM program, the presence data were augmented with records from a survey expedition completed in 2014 (2014 Natural Resource Damage Assessment [NRDA] Mesophotic Expedition, see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m583p121_supp.pdf).

The MAPTEM survey efforts were accomplished using a SeaRover remotely operated vehicle (ROV) outfitted with a forward-facing still camera oriented at a 45° angle and illuminated by a 150 Ws strobe. The 2014 NRDA expedition utilized an ROV ('Global Explorer') equipped with a similarly oriented digital camera and LED lamps. The survey sites were located on several carbonate structures and the adjacent seabed within 2 main sites: Alabama Alps Reef (AAR) and Roughtongue Reef (RTR) (from the MAPTEM collection); and Coral Trees Reef (CTR) and Madison Swanson Reef (MSSR) (from the 2014 NRDA Mesophotic Expedition). Following the methodology described by Peccini & MacDonald (2008), each survey examined a circular region, nominally 200 m diameter, within which approximately 100 randomly chosen points were photographed in order to document the sessile community and local geomorphology. Although the camera systems differed, the survey methodology utilized in the 1997–1999 surveys was replicated in the 2014 survey. In total, 1975 photographic records of sea fans and sea whips were used to construct a presence database, from which the model was compiled. We developed morphological descriptions for 7 coral taxa (Fig. 2), which were known to be among the endemic taxa of the region (Etnoyer et al. 2016). This made it possible to classify potential habitat preferences by taxon.

Environmental data

We considered 32 environmental variables to build the model and test for factors that were significant in the observed patterns of coral presence. All variables were selected based on environmental factors thought to influence coral settlement, feeding, growth, and survival (Table 1). These variables include bottom current data because octocorals in the Pinnacle Reefs have been shown to grow so that their fans are oriented to maximize exposure to local currents (Peccini & MacDonald 2008). Bathymetric data were obtained from the USGS database (Gardner et al. 2001b, 2002, 2003) and gridded at their native resolution (8 m) using ArcGIS. Slope, curvature, and surface rugosity were calculated from the bathymetry layer using the Benthic Terrain Modeler Tool (Wright 2012) in ArcGIS. Slope was measured in degrees using the 8-cell method (3 × 3 cell neighborhood; Burrough & McDonell 1998). Surface rugosity, sometimes referred to as surface roughness (Hobson 1972), measures the topographical complexity of the seabed; areas with greater complexity often exhibit higher levels of diversity (Kostylev et al. 2001). Finally, we calculated the topographic position index (TPI) (Weiss 2001) using the ArcGIS Land Facet Corridor Designer Tool (Jenness 2006). TPI quantifies the elevation of points relative to surrounding features and is considered a measure of preference for exposure to topographically intensified currents (Wilson et al. 2007). TPI layers were calculated at increasing window sizes (10, 50, 100, 250, 500, and 750 m) in order to consider a range of potentially important geomorphologies within the study area. Seafloor locations containing hard substrata were derived from the backscatter raster and processed using the iso-cluster unsupervised classification from the Image Processing Toolbox, in ArcGIS. Four sediment classes were designated based on photograph records of the seafloor in the area: fine sediment areas, coarse-sand areas, gravel-sandy rocky areas, and exposed rock. The habitat classification layer was obtained using the Benthic Terrain Modeler Tool (Wright 2012), which classifies a given location as belonging to 1 of the following 7 categories: (1) high reef or ridge, (2) reef base, (3) low reef or ridge, (4) reef or ridge slope, (5) steep slope, (6) gentle slope, and (7) deep depression. In addition, dominant bottom sediment types and seabed sediment Folk code variables were obtained from the Gulf of Mexico Data Atlas (Jenkins 2011a,b) to further characterize potential habitat sites.

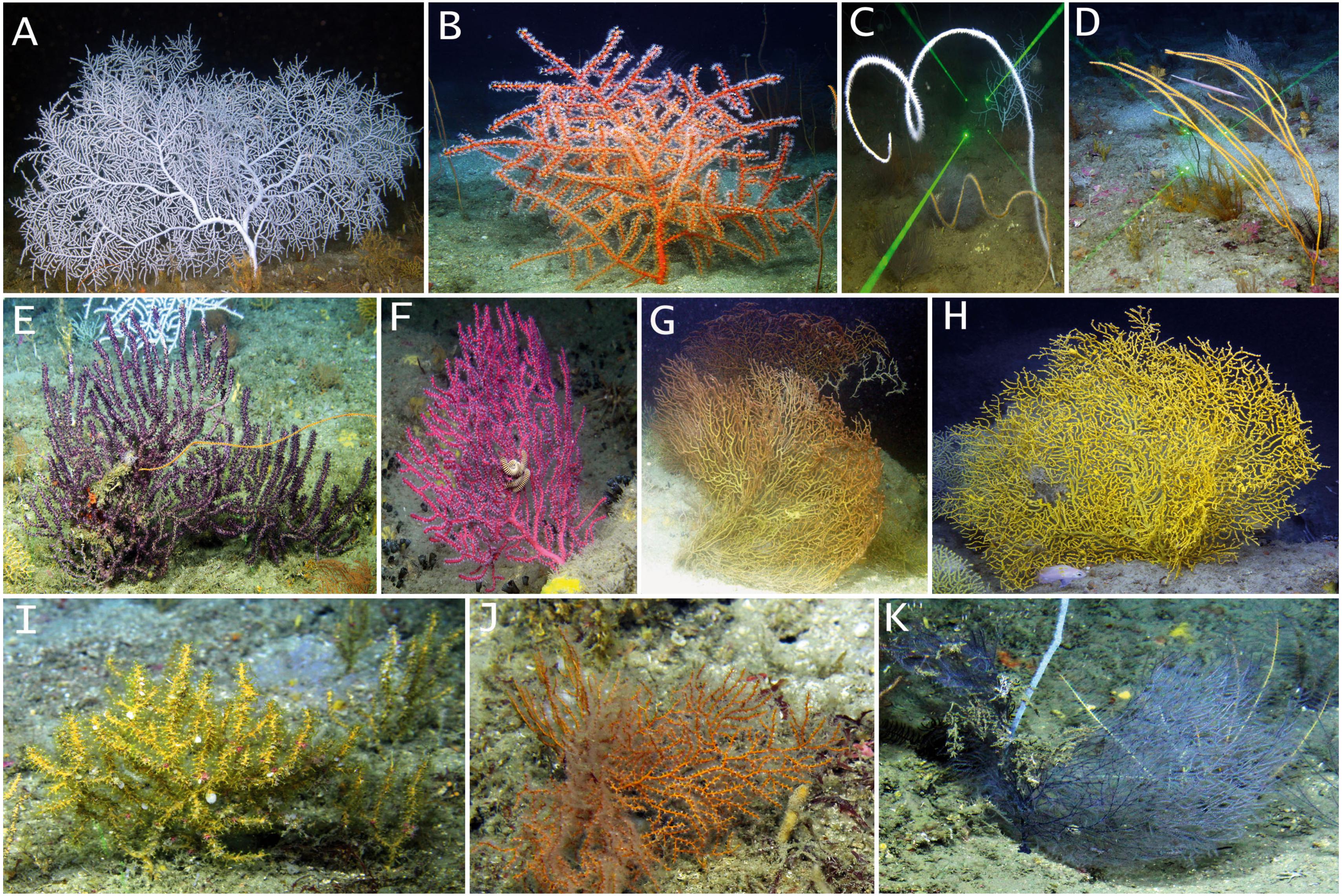

Fig. 2. Octocoral and antipatharian colonies found in the mesophotic coral ecosystem (MCE) of the study area: (A) *Hypnogorgia pendula*, (B) *Swiftia exserta*, (C) *Stichopathes* sp., (D) *Ellisella* sp., (E) *Thesea* cf. *nivea*, (F) *Thesea* cf. *rubra*, (G) *Placogorgia* sp., (H) *Placogorgia* cf. *tenuis*, (I) *Bebryce* sp., (J) *Nicella* sp., (K) *Antipathes* cf. *atlantica*

Table 1. Summary of the environmental variables used to develop the model. See Table S1 in the Supplement for statistics of each variable. Variables shown in **bold** were selected after Spearman correlation analysis (Table S2 in the Supplement) to perform a simplified model with selected variables. TPI: topographic position index (subscripts indicate grid cell size); SST: sea surface temperature; CDOM: chromophoric dissolved organic matter; PAR: photosynthetically active radiation; dV: digital value; na: not applicable

Environmental variables	Unit	Source	Method
Bathymetry & geomorphology			
Depth	m	USGS[a]	Multibeam echosounder
Slope	0–90°	Derived from bathymetry	Benthic Terrain Modeler (ArcGis)
Aspects	0–360°	Derived from bathymetry	Benthic Terrain Modeler (ArcGis)
Rugosity	dV	Derived from bathymetry	Benthic Terrain Modeler (ArcGis)
$TPI_{10\ m}$	na	Derived from bathymetry	Land Facet Corridor Designer (ArcGis)
$TPI_{50\ m}$	na	Derived from bathymetry	Land Facet Corridor Designer (ArcGis)
$TPI_{100\ m}$	na	Derived from bathymetry	Land Facet Corridor Designer (ArcGis)
$TPI_{250\ m}$	na	Derived from bathymetry	Land Facet Corridor Designer (ArcGis)
$\mathbf{TPI_{500\ m}}$	na	Derived from bathymetry	Land Facet Corridor Designer (ArcGis)
Backscatter	dB	USGS[a]	Multibeam echosounder
Backscatter isoclassification	na	Derived from backscatter	Image processing (ArcGis/Matlab)
Dominant sediment	φ	NOAA[b,c]	Folk
Loose sediment	φ	NOAA[b,c]	Folk
Oxygen variables			
Oxygen saturation	%	NOAA[c,d]	Winkler/photometric
Oxygen utilization	ml l^{-1}	NOAA[c,d]	Winkler/photometric
Dissolved oxygen	ml l^{-1}	NOAA[c,d]	Winkler/photometric
Nutrients variables			
Nitrate	µmol l^{-1}	NOAA[c,d]	Nitrate+Nitrite
Phosphate	µmol l^{-1}	NOAA[c,d]	Photometric analysis
Silicate	µmol l^{-1}	NOAA[c,d]	Photometric analysis
Model variables			
Bottom temperature	°C	Hycom[e]	Modeling
Bottom salinity	psu	Hycom[e]	Modeling
Bottom *u*	Eastward velocity (m s^{-1})	Hycom[e]	Modeling
Bottom *v*	Northward velocity (m s^{-1})	Hycom[e]	Modeling
Bottom *w*	Upward velocity (m s^{-1})	Hycom[e]	Modeling
Satellite data			
SST	°C	NOAA - Aqua MODIS[f]	Satellite
CDOM	na	NOAA - Aqua MODIS[f]	Satellite
Chlorophyll *a*	mg m^{-3}	NOAA - Aqua MODIS[f]	Satellite
Fluorescence	µW cm^{-2} s^{-2} nm^{-1} sr^{-1}	NOAA - Aqua MODIS[f]	Satellite
PAR	E m^{-2} d^{-1}	NOAA - Aqua MODIS[f]	Satellite
Attenuation coefficient	m^{-1}	NOAA - Aqua MODIS[f]	Satellite
Atmospheric variable			
Hurricane wind density[h]	na	NOAA[g]	Kernel density (ArcGis)

[a]Gardner et al. (2001b, 2002, 2003); [b]Jenkins (2011a,b); [c]https://gulfatlas.noaa.gov; [d]Garcia et al. (2010a,b); [e]https://hycom.org; [f]https://coastwatch.pfeg.noaa.gov; [g]https://nhc.noaa.gov; [h]derivired from frequency and average wind speed of hurricane passage through the model area

Dynamic environmental variables

All nutrients (phosphate, nitrate, silicate, dissolved oxygen, oxygen saturation, and apparent oxygen utilization) were obtained from the Gulf of Mexico Data Atlas, and normalized on a 5 × 5 km grid (Garcia et al. 2010a,b). These data were imported into ArcGIS; they were then scaled and re-projected to match the finer resolution and geographic projection of the bathymetry, but retained the source binning. Water column and atmospheric factors showed significant variations across the study area. To include model potential effects, synoptic datasets of sea surface temperature (SST day/night average), chlorophyll *a* (chl *a*), diffuse attenuation coefficient, fluorescence, photosynthetically active radiation (PAR), and chromatic dissolved organic material (CDOM) were acquired from the ERDDAP database (NOAA CoastWatch; http://coastwatch.noaa.gov). Water column temperature, salinity, and bottom currents (*u*, *v*, and *w* over the 30–60 m depth range) were obtained from the Hybrid Coordinate Ocean Model (HYCOM, https://hycom.org; Dukhovskoy et al. 2015). All oceanographic data were downloaded as monthly (satellite data) or daily

(HYCOM) files in NetCDF format (*.nc), which were standardized in MatLab. Historical hurricane data over the study area were obtained from NOAA (Knapp et al. 2010) and displayed in ArcGIS in order to create a hurricane wind intensity raster, weighting wind intensity as the primary factor. All atmospheric and oceanographic layers were scaled, resampled, and re-projected to match with the bathymetric data.

Modeling

Maximum entropy modeling routines of Maxent were used to evaluate the extent of habitat suitable for mesophotic sea fans and sea whips in the eastern Gulf of Mexico (Phillips et al. 2006). The method was chosen after consideration of the available occurrence data for MCE organisms. Some methods for modeling habitat suitability require both presence and absence data. When reliable absence data are available, presence/absence methods may perform better than presence-only models (Reiss et al. 2011, Rengstorf et al. 2013). However, reliable absence data are rarely available, or are poorly controlled. In such cases, presence-only models like Maxent have been shown to be more robust and consistent (Elith et al. 2006, Reiss et al. 2011, Yesson et al. 2012) because they utilize pseudo-absence (background) data rather than true absence data and have consistently outperformed other presence-only techniques (Elith et al. 2006, Elith & Leathwick 2009, Tittensor et al. 2009, Tong et al. 2013). Maxent assigns non-negative probability values to each background pixel of the study area such that their total sums to 1. Furthermore, presence-only modeling results have produced results consistent with traditional presence/absence methods in shallow corals (Bridge et al. 2012, Couce et al. 2013) and deep-water corals (Davies & Guinotte 2011, Howell et al. 2011, Tracey et al. 2011, Yesson et al. 2012, Rengstorf et al. 2013, Taylor et al. 2013).

Models were created using the default Maxent parameters that have been shown to optimize model performance (i.e. convergent threshold = 10–5, number of background points = 10 000, default prevalence = 0.50; see Phillips & Dudik 2008). In preliminary trials, the model was tested using different regularization multipliers (β= 1, 3, 5, 7, 11, and 13; default = 1), following procedures proposed by Georgian et al. (2014). However, after inspection, the best performance was obtained in default mode. The number of maximum iterations was increased to 5000 to ensure convergence. Pearson's rank correlation was calculated for all of the environmental layers following Yesson et al. (2012) This identified uncorrelated variables within each group and produced a simplified set of inputs, which avoided over-specification of the model (see Table S2 in the Supplement).

A jackknife procedure was employed to calculate the percent contribution of variables to each model. Because Maxent is robust regarding auto-correlated inputs (Phillips et al. 2006, Elith et al. 2011), 2 models were constructed. One model used all available variables, while an alternative model removed auto-correlated variables prior to analysis. This avoided biasing the results based on preconceived perceptions of variable importance.

A cross-validation routine was used to verify model performance. Data were randomly partitioned so that 75% of occurrences were used for calibrating and running the model, and 25% were used to evaluate model performance. As the model was constructed, the test gain, which is the improvement in the model performance compared with random, was used to assess the contribution of the individual variables and the entire variable set. The model was performed with 50 replications (number of runs), and averaged for the final result. The receiver operating characteristic measures performance of the model at any threshold using the area under the curve (AUC) value, which ranges from 0 (worse than random model) to 1 (ideal model), and includes a random prediction of 0.5 (Phillips et al. 2006). Target AUC values of 0.9 were surpassed by the final models. Sampling bias was not anticipated in the data due to the randomization of photo collection. To verify the habitat prediction, we evaluated results of the 2 models created using the online coral-presence dataset (NOAA National Database for Deep-Sea Corals and Sponges, https://deepseacoraldata.noaa.gov), which compiles various coral presence records from the study area (see Fig. S2 in the Supplement)

RESULTS

The single or 'general' model of sea fan and sea whip distribution of the potential mesophotic ecosystem encompassed the entire 6228 km^2 area mapped in the USGS bathymetric survey. A visual inspection of the suitable habitat of mesophotic corals revealed that most of the predictions of where coral may occur were located within well-known mesophotic reefs such as the AAR, RTR, CTR, and MSSR, but also extended to several tall (>7 m relief), intermediate (3–7 m relief), and, to a lesser degree, small (<3 m

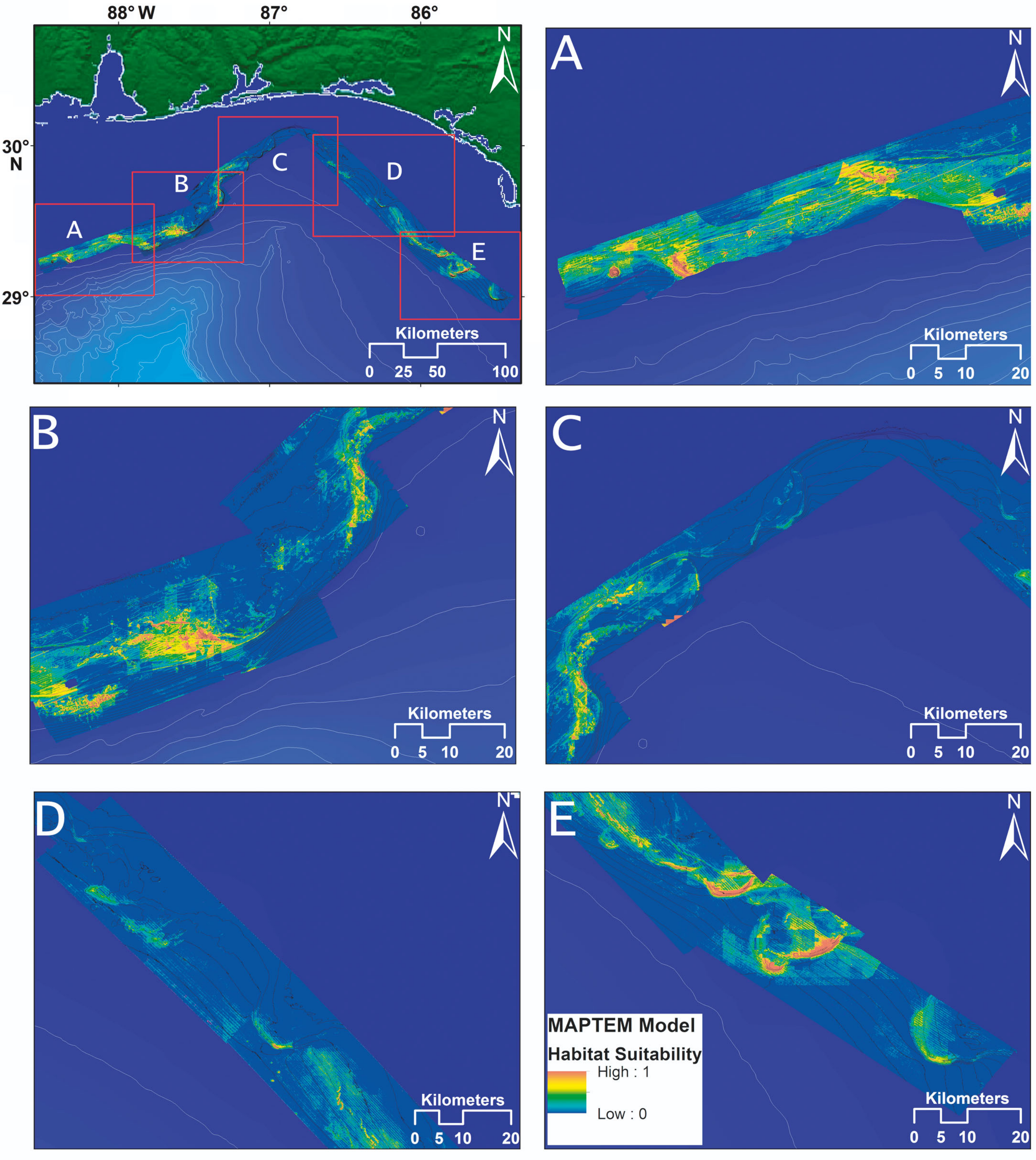

Fig. 3. General model of habitat suitability for all mesophotic corals in the study area using the selected variables and the MAPTEM data set. Warm colored areas (yellow to red) show the predicted locations where corals are likely to be found (high habitat suitability), while cold colored areas (dark green to blue) indicate a low probability of finding mesophotic corals (low habitat suitability). Habitat areas are listed in Fig. 1. See complementary Fig. S5 in the Supplement at www.int-res.com/articles/suppl/m583p121_supp.pdf for model build with the NOAA data set

Table 2. Summary statistics (mean ± SD) of training and test models for area under the curve (AUC) and gain, suitable area (% of the total, and total in km^2), and jackknife test of variables used in each model. Variable abbreviations are as follows: Rug: rugosity; B_u: bottom u (eastward velocity); Hurr: hurricane winds; CDOM: chromophoric dissolved organic matter; DoSed: dominant sediments; TPI 500: topographic position index at 500 m; OS: oxygen saturation; SST: sea surface temperature; LoSed: loose sediment; UnIso: backscatter unsupervised iso-classification; Var: variables; All: all variables; Sel: selected variables

Taxon/group	Var	Sample size	Training Gain	Training AUC	Test Gain	Test AUC	Suitable habitat %	Suitable habitat km^2	Jackknife test of importance (%) Variable 1	Variable 2	Variable 3
All corals MAPTEM	All	981	2.4 ± 0.003	0.978 ± 7 × 10^{-5}	2.5 ± 0.03	0.975 ± 8 × 10^{-5}	0.075	467.09	Rug. (19.9)	B_u (13.1)	Hurr. (11.1)
All corals MAPTEM	Sel	981	2.3 ± 0.005	0.960 ± 4 × 10^{-5}	2.4 ± 0.03	0.959 ± 0.002	0.079	492.00	Rug. (19.1)	CDOM (17.4)	DoSed (16.1)
All corals Test NOAA	All	185	3.1 ± 0.037	0.983 ± 0.001	3.1 ± 0.51	0.960 ± 0.018	0.018	112.10	Rug. (31.0)	TPI$_{500\ m}$ (28.6)	OS (6.6)
All corals Test NOAA	Sel	185	3.1 ± 0.027	0.981 ± 0.001	3.1 ± 0.38	0.958 ± 0.027	0.019	118.33	Rug. (32.2)	TPI$_{500\ m}$ (27.3)	OS (9.2)
Antipathes atlantica	All	230	3.2 ± 0.017	0.986 ± 0.001	3.2 ± 0.11	0.980 ± 0.005	0.021	130.78	B_u (14.3)	SST (13.7)	Depth (9.8)
Bebryce spp.	All	345	3.1 ± 0.015	0.982 ± 4 × 10^{-4}	3.2 ± 0.12	0.980 ± 0.005	0.030	186.83	B_u (25.7)	CDOM (14.6)	TPI$_{500\ m}$ (13.9)
Ellisella sp.	All	19	2.9 ± 0.346	0.974 ± 0.011	2.1 ± 1.85	0.876 ± 0.111	0.106	660.15	Rug. (34.3)	LoSed (16.8)	UnIso. (13.9)
Hypnogorgia pendula	All	144	3.7 ± 0.009	0.993 ± 1 × 10^{-16}	3.8 ± 0.25	0.992 ± 0.001	0.013	80.96	B_u (17.8)	Rug. (16.9)	CDOM (15.1)
Nicella sp.	All	8.8	2.9 ± 0.488	0.995 ± 0.002	3.7 ± 0.18	0.972 ± 0.037	0.023	143.24	LoSed (21.2)	DoSed (21.1)	Nitrate (15.8)
Placogorgia sp.	All	138	3.8 ± 0.017	0.993 ± 1 × 10^{-4}	4.0 ± 0.17	0.992 ± 0.001	0.012	74.73	B_u (20.2)	Rug. (13.5)	TPI$_{500\ m}$ (12.6)
Stichopathes sp.	All	206	3.4 ± 0.025	0.989 ± 4 × 10^{-4}	3.5 ± 3.22	0.987 ± 0.005	0.019	118.33	B_u (20.4)	CDOM (13.5)	Rug. (12.8)
Swiftia exserta	All	312	3.2 ± 0.007	0.984 ± 4 × 10^{-5}	3.3 ± 0.02	0.984 ± 7 × 10^{-4}	0.027	168.15	B_u (33.0)	CDOM (18.0)	Rug. (17.4)
Thesea nivea	All	64	3.8 ± 0.069	0.992 ± 0.002	4.1 ± 0.50	0.989 ± 0.014	0.007	43.59	LoSed (29.3)	Rug. (21.9)	CDOM (10.4)

relief) carbonate mounds, ridges, and paleo-shoreline structures adjacent to the main reefs. It also appears that suitable habitat for mesophotic corals occurs in some flat zones (Fig. 3)

Model performance

The general model performance significantly exceeded the random model prediction (AUC > 0.5). The performance of the model configured with all variables (test/training AUC): mean ± SD 0.978 ± 7 × 10^{-5}/0.975 ± 8 × 10^{-4}) was marginally better than the model configured with selected variables (AUC 0.963 ± 4 × 10^{-5}/0.960 ± 0.001) (Table 2). Overall, the jackknife test of importance indicated that surface rugosity was the best predictor to explain the distribution of mesophotic sea fans and sea whips in results for both models (Table 2), with 19.9 and 19.1% contribution to the all-variables models, versus selected-variables models, respectively. Bottom eastward currents (13.1%), hurricane winds (11.1%), CDOM (17.4%), and dominant sediments (16.1%) were secondary contributors to predict habitat suitability for both models (all and selected variables), respectively (Table 2, Fig. S3 in the Supplement). Within the general model for all variables, slightly positive values on the u component of bottom currents (0 to 0.25 m s^{-1}) provided favorable conditions for octocorals and antipatharians in the study area. Additionally, locations with CDOM values around 39.1 would host high densities of octocorals and antipatharians (Table 2). Other good contributors for both models were depth, bottom-upward currents (w), bottom salinity and temperature, slope, and nitrate concentrations.

Performance of each environmental variable is represented in the response curves (Fig. 4), which show the response of the suitability index plotted against change in the variable. Some variables showed a better response to the logistic prediction when the model takes advantage of all environmental variables available to build the habitat prediction with the model. This was the case for PAR, chl a, CDOM, SST, oxygen saturation, slope, curvature, and loose and dominant sediment fractions, all of which produced improved model performance when they interact with all variables. In contrast, bottom currents (u, v, and w), bottom salinity and temperature, backscatter (unsupervised iso-classification), and sediment type showed better individual performance in the marginal response curves (Fig. 4).

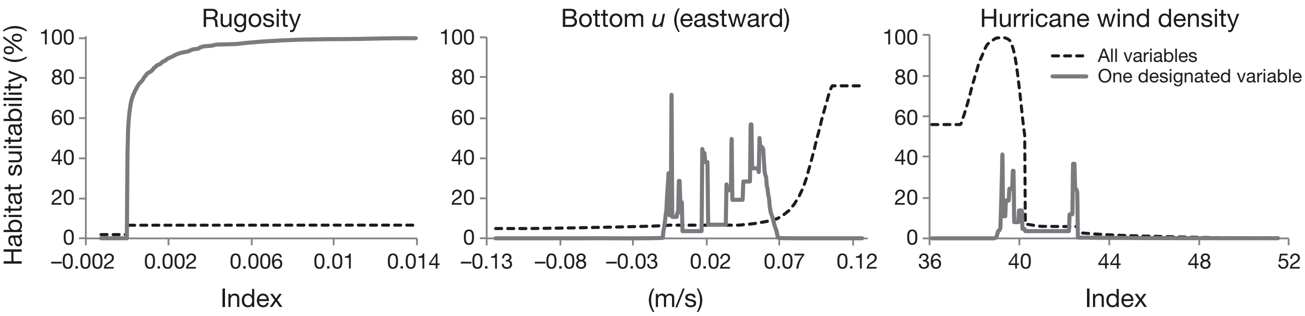

Fig. 4. Response curves of the most important variables showing the relationship between performance of predictors and the 'general' habitat suitability model for all mesophotic octocorals and black corals in the study area. Black dashed lines indicate how the model prediction changes as the environmental variable varies taking all other variables into consideration. Grey curves characterize the model's response using only that variable

Taxon-specific model results

Similar to the general model, suitability models that were independently evaluated for all coral taxa showed a good performance reflected in AUC values for training and test statistics. All test AUC values were >0.97 with the exception of *Ellisella* sp. (mean ± SD test AUC: 0.876 ± 0.111), and all test gain values were over 3.2, with the same exception for *Ellisella* sp. (test gain: 2.1). All by-taxon models significantly outperformed the random model (Table 2).

When the habitat suitability model was applied independently to all coral taxa, the same environmental factors played fundamental roles in affecting species or taxon distribution, but with a different order of contribution (Table 2). For the antipatharians *Antipathes atlantica* and *Stichopathes* sp., and the octocorals *Swiftia exserta*, *Bebryce* spp., *Hypnogorgia pendula*, and *Placogorgia* sp., bottom *u* was the most important environmental factor (>14.3%). For *Ellisella* sp., rugosity (34.3%) was the most relevant factor; for *Thesea nivea* and *Nicella* sp., loose sediment (29.3 and 21.2%) was the most important environmental variable in the model (Table 2; Fig. S3). Likewise, other environmental variables contributed to different degrees to the taxon's suitability model. These include bottom salinity, bathymetry, water temperature (surface and bottom), dominant and loose sediment fractions, current components (*u, v, w*), and TPI. Predictions of potential habitat area indicated that *Ellisella* sp. had the largest potential area (660 km^2) for the study area, followed by *Bebryce* sp. (186 km^2), and *S. exserta* (168 km^2). *H. pendula*, which is among the most conspicuous coral taxa in the MCE, was predicted to occur across only 80.9 km^2 within the study area (Table 2).

With regard to geomorphology of predicted habitat for mesophotic ocotocorals and antipatharians, the following preferences were indicated for all coral taxa and the general model: small and tall carbonate mounds, with high preference for reef tops and slopes, and adjacent hard substrata with small fractions of fine sediments. There was also high preference for areas with negative *w* current (down-welling) and moderate *u* (eastward) and *v* (northward) current, high CDOM, and relatively low bottom temperature for the area (18°C; Fig. 3; Fig. S4 in the Supplement).

Independent test models

The suitability model created using an independent set of mesophotic coral records (NOAA) performed similarly to the general models that used all-variable and selected-variable approaches. The AUC value for the test model based on all variables was 0.96, versus 0.95 for the test model generated with selected variables; both exceeded our target significance level of 0.90. The total extension of the suitable area for these models was less than the general models (>118 km^2). A jackknife test of importance of the variables showed that both test models were primarily driven by the same variables: rugosity (31.0 and 32.2%); $TPI_{500\ m}$ (28.6 and 27.3%), and oxygen saturation (6.6 and 9.2%) (Table 2; Fig. S5 in the Supplement).

DISCUSSION

The results obtained from suitability models for mesophotic corals in the Eastern Gulf of Mexico indicate that there are 405 km^2 of habitat suitable for mesophotic octocorals and antipatharians within that portion of the continental shelf between Mississippi and Florida for which detailed bathymetric mapping has been completed. Previous exploration efforts have focused on 2 well-known reefs: AAR and RTR, which are sites that have been explored over the past 2 decades (Peccini & MacDonald 2008, Etnoyer et al. 2016, Silva et al. 2016). We used a series of random photographic samples of those 2 locations from the MAPTEM program and expanded to 2 other well-known reefs in the Florida Middle Ground (MSSR and CTR) randomly sampled in 2014 to construct all-taxa and by-taxon suitability models for octocorals and antipatharians. For model validation, we used an independent set of coral records compiled by the NOAA Deep Coral Data Portal. Although the results confirm the suitable habitat for large and high carbonate structures (e.g. AAR and RTR), the results also suggest that mesophotic octocorals and antipatharians will also be found on many other medium-sized and small carbonate mounds, high reflectivity platforms, and paleo-shoreline structures like small ridges (Gardner et al. 2001a). The resulting suitable niche prediction for all models is located between 100 and 50 m depth. A similar depth range was used by Locker et al. (2010) and Bridge et al. (2012) to report areas with the potential to host MCEs in waters of the Gulf of Mexico and the mesophotic area in the Great Barrier Reef in Australia, respectively. Therefore, other factors besides depth range may play an important role in the formation of MCEs in the Gulf of Mexico.

High suitability indices from the general model, using all and selected variables, were driven primarily by geomorphological complexity of the terrain, expressed in several bathymetry-derived factors, principally surface rugosity and, to a lesser degree, TPI. In this case, high suitability indices are associated with high rugosity values, which are a measure of the complexity ('bumpiness') of the seafloor. This relationship between rugosity and coral diversity, especially hermatypic corals, has been well documented for shallow-water corals (Zainul Fuad 2010, Dustan et al. 2013) and deep reef assemblages (Howell et al. 2011, Rengstorf et al. 2013). High surface rugosity values in this area cannot be attributed to reef formation by corals in the present. Rather, these carbonate structures are evidence of relict shallow reef habitat, which provide hard substrata suitable for colonization by sessile organisms such as corals adapted to the 30–100 m depths (Locker et al. 2010, Donoghue 2011, Reich et al. 2013). Model results displayed some binning in areas where fine-scale variables, such as surface rugosity, were relatively monotonic (Fig. 3). Under these conditions, the climatic variables, which were gridded at a 5 × 5 km scale, tended to dominate. Setting higher display thresholds might reduce this apparent effect; however, it is not entirely an artifact because it might inform habitat potential for shipwrecks or other artificial structures located in such regions.

High suitability indices were further correlated with positive indices in $TPI_{500\ m}$, especially for the model formulated from the NOAA data set. High positive values of $TPI_{500\ m}$ represent topography elevated above surrounding areas. In the by-taxon models, $TPI_{500\ m}$ did make a relevant contribution to habitat suitability (third place), particularly for sea fans (e.g. *Bebryce* sp. and *Placogorgia* spp.). For other taxa, TPI played a less important role in each model. This was the case for *Hypnogorgia pendula*, which also prefers high negative and high positive values of $TPI_{50\ m}$ (fine TPI). A possible explanation is that fine-scale TPI detects smaller features, such as crests, depressions, small mounds, and reef-tops, which some taxa prefer. Large-scale TPI identifies larger features like ridges, mounds, flat areas, and slopes. Therefore, when suitability models predict potential habitat in areas characterized by positive values in a broad TPI raster, the models are predicting that suitable areas for corals will occur in larger structures that are elevated in comparison with their surroundings. In contrast, when suitable habitats are predicted in high or negative zones, this indicates that a specific taxon may prefer to settle in a particular zone (e.g. crest, depression) within a major structure (e.g. ridge). Among the taxa modeled individually, *Bebryce* were characterized by abundant, but small, colonies that were frequently observed among loose rubble and sediment. Taxon-specific preferences for TPI may be aliased with preference for additional variables as well.

In the general model, the large-scale TPI raster contributes more to the model because it includes all coral records in the model. However, when the model was constructed by taxon, some of the corals preferred flat tops or reef crests (e.g. *H. pendula*), while others would also be found in depressions and slopes within the reef (e.g. *Antipathes atlantica*). This situation is clearer in the habitat classification layer, which is derived from bathymetry, slope, surface rugosity, and fine and broad TPI layers. A possible explanation of coral preference for high grounds is that they can take advantage of currents, which transport nutrients, oxygen, and food (Thiem et al. 2006, Peccini & MacDonald 2008), while also reducing sediment deposition or re-suspension (C. Rogers 1990, A. Rogers 1999). For almost all individual suitability models (by taxon), currents, especially the eastward component (u), were the major contributor to suitable habitat in the study area (Table 2). In addition, coral-suitable areas were correlated with slightly negative values of vertical speed currents (w), and low values of northward current (v) for lateral transport. This situation has been documented by Peccini & MacDonald (2008), who demonstrated that octocorals in the Pinnacle Reefs area grow with their fans permanently oriented to local currents to maximize exposure to lateral transport and suspended material. Mesophotic octocorals and antipatharians are predominantly azooxanthellate corals and heterotrophic suspension feeders that depend on both plankton and detritus provided by local currents for nutrition (Bayer 1961, Fabricius & De'ath 2008).

Primary productivity in the water column, expressed as chl *a*, was mostly irrelevant in all models. This was also reported by Bridge et al. (2012), who identified high suitability areas for mesophotic corals in areas of the Australian Great Reef Barrier where chl *a* is low. In this study, seafloor chl *a* concentration or another measurement of food availability might be a better predictor of suitable areas for heterotrophic corals. However, Georgian et al. (2014) used 'export productivity' to predict a suitable niche for *Lophelia pertusa* in waters of the Gulf of Mexico. In the same vein, suitable areas for corals were characterized by fairly high values of CDOM, which corresponds to the dissolved organic carbon fraction that absorbs light (Rochelle-Newall & Fisher 2002). This applied especially to *Bebryce* sp., *H. pendula*, *Placogorgia* sp., and *Stichopathes* sp.

In the suitability model for the remainder of the coral taxa in this study, as well as in the general model, the CDOM variable was the second in importance. It was third in importance for the independent test model. Although CDOM cannot always be interpreted as an indication of particulate organic matter (POM), it could potentially be used as an indication of the food source for heterotrophic organisms. Evidence suggests that CDOM values are proportional to the POM concentration in highly productive waters due to the transformation in phase from particulate to dissolved fraction, which is mediated by physical, chemical, and biological processes (Stedmon & Markager 2001). In the northern Gulf of Mexico, particulate organic carbon supply to the seafloor is mediated by lateral currents and downwelling (vertical transportation) of detritus and marine snow, especially in areas close to the Mississippi Delta (Rowe et al. 2008), which could be a source of food for mesophotic corals.

Nevertheless, the proximity to the Mississippi River does not just provide a source of potential food; eutrophication and oxygen values can also be affected by runoff water, which potentially affects settlement and survival rates of mesophotic coral. All nutrient variables (nitrate, phosphate, and silicate) were highly correlated with each other, with oxygen (dissolved oxygen, oxygen saturation, and oxygen utilization), and with salinity (Table S1). However, the influence of the river and these variables is most pronounced in the area near the Mississippi Delta (west of AAR), while reduced towards Florida (Garcia et al. 2010b). High suitability areas are almost absent approaching the Mississippi River, where high nutrient concentrations (e.g. nitrate) values are found. Several studies have attributed high rates of coral diseases to highly eutrophic waters (Hallock & Schlager 1986, Bruno et al. 2003). High nutrient concentrations increase the rate of epizootics on octocorals, and may be associated with decreased autotrophic function in zooxanthellate hermatypic corals due to turbidity. Although the diffuse attenuation coefficient and fluorescence values increase with proximity to the Mississippi River, while PAR decreases, these variables do not seem to be major factors in either the general suitability model or the taxon-specific models.

While it is evident that sea fan and sea whip corals need reasonable oxygen concentrations for their survival, oxygen saturation contributed in a meaningful way only to the models generated from the independent set of coral records from NOAA. Although dissolved oxygen and oxygen saturation decrease in proximity to the Mississippi River (because oxygen consumption increases due to biological and chemical processes), the values are still sufficient to support MCEs to the east of the Mississippi River, despite the nutrient loading.

Two of the most important environmental variables were bottom reflectivity and sediment type. High values of bottom reflectivity are usually interpreted as hard substrate available for colonization by sessile organisms such as corals. However, sand and gravel deposits can also return high values in the backscatter image. Furthermore, high backscatter values can also be associated with biogeneous substrata (e.g. carbonates) or hard seabed covered by fine sediments, which are not always suitable for colonization due to biogeochemical process (methane release/oxidation). For example, Tseng et al. (2011) demonstrated that high concentrations of suspended sediments negatively affect feeding behavior, colony expansion, and mucus formation by octocorals. In our models, we used raw backscatter values and a backscatter-derived raster called unsupervised iso-classification. This technique separates pixel intensity values into classes, which subsequently can be associated with previously identified sediment types. This seems to be a better approach than binary interpretation (e.g. soft vs. hard) commonly used in this type of analysis. In our general model, suitable areas for mesophotic corals are correlated with gravel and exposed carbonate classes (see Fig. 4, response curves). If we look independently by taxa, some octocorals (e.g. *H. pendula*) will prefer areas of exposed rock as dominant substrate, whereas other taxa (e.g. *Stichopathes* sp. and *A. atlantica*) seem to prefer softer substrata (e.g. gravel with sandy fractions).

All models (general, by-taxon, and test) failed to identify numerous smaller reefs that we *a priori* expected would be part of the suitable habitat for mesophotic octocorals and antipatharians. However, when the predicted suitable area is compared with new data from an exploration conducted in 2014 (data under analysis), the new records within the Pinnacle Reef area are consistent with the habitat suitability prediction made by our model. A drawback of heavily weighting habitat suitability predictions on such widely used factors as substrate type can be a tendency to over-predict the area of habitat. By using a variety of environmental factors, the models developed for the present work incorporate more marginal differences that may favor individual taxa or influence development of a mesophotic coral community.

We acknowledge that habitat suitability models are highly dependent on the quantity and quality of taxon-presence records for robust habitat prediction, as well as the resolution of the environmental layers. The differences between the general and test models were not the result of the number of environmental variables used to construct the models. This is reflected in the stability of the model on the importance assigned to each variable (jackknife test) in the model. Surface rugosity was always the most important contributor to the models. Although there was some difference in the order of the following variables, the main difference was their contribution percentage, slightly changing the order of the variables; however, the same variables still played a relevant role in the model. This fact was more evident in the test model, where the order of the 3 most important contributors to the models built with all or with only selected variables, was always the same (rugosity, $TPI_{500\ m}$, and oxygen saturation), varying only by the respective percentage of their contribution to the model. Other statistics like AUC and Gain values were almost identical between models using selected or all environmental variables. The main difference between models is indicated by the predicted area (10th percentile) between the general and test models. The general model predicted a suitable habitat area of 405 km^2, while the suitable habitat predicted by the test model did not exceed 118 km^2 (Table 2). This difference can be attributed to source and number of records for each data set. While the MAPTEM/2014 dataset relies on a large number of samples (865 records) obtained from 4 well explored reefs (AAR, RTR, CTR, and MSSR), the NOAA dataset is composed of only 185 coral records distributed in the whole study area (6227.8 km^2). This reveals how the algorithm depends upon the number of samples.

Additionally, the number of records, distribution, and reliability of the presence data are relevant when we are trying to avoid over-prediction of suitable habitat in the model. It is important to use a set of records which has a high density of samples within similar values of the environmental variables rather than have presence records in a broader range of values within each variable. That approach could lead to over-estimation of the real extent of the suitable habitat for a given taxon. Therefore, it is imperative to continue to build habitat suitability models that include updated presence records and new and reliable environmental variables. This will allow us to increase the biogeographical extent of a given taxon or community in order to protect and eventually quantify the extent of corals susceptible to harm by natural or anthropogenic disasters.

CONCLUSIONS

We proposed 8 habitat suitability models (1 general and 7 by taxon) for mesophotic octocorals and antipatharians to predict their occurrence throughout a potential area located in the Northern Gulf of Mexico between Mississippi and Florida. All models significantly out-performed a randomized prediction of suitable areas, and also indicated that the distribution of octocorals and antipatharians is predominantly driven by surface rugosity of the substrata. Other variables like TPI, CDOM, currents, sediments, and hurricane wind density, among others, could influence the occurrence of these mesophotic corals. Our results differed from other coldwater coral suitability models with respect to which predictor factors played a more relevant role in the model, and, for instance, the extent of the suitable area. For reef-forming corals like *Lophelia pertusa*, bathymetry and substrate type are the most important predictive variables (Rengstorf et al. 2013, Georgian et al. 2014); in contrast, deep-sea octocoral suitability models are more sensitive to oxygen saturation and calcite concentration.

The habitat suitability maps provided in this study can be used as a baseline for future exploration in the area in order to verify the true extent of MCEs in the eastern Gulf of Mexico, and in turn, to provide an accurate estimation of MCEs that could be impacted by natural (heat stress, hurricanes) or anthropogenic (oil spills, eutrophication, ocean acidification) events for resource management planning and marine conservation strategies for MCEs in the Gulf of Mexico. In addition, this study improves the basis for evaluating the potential extent of injured octocorals and antipatharians resulting from the DWH oil discharge.

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