PREDICTIVE MODELING OF MESOPHOTIC HABITATS IN THE NORTHWESTERN GULF OF MEXICO

by

Travis Keenan Sterne [a, 1, *], David Retchless [a], Rebecca Allee [b], Wesley Highfield [a]

[a] Texas A&M University Galveston, Department of Marine Sciences, 200 Seawolf Parkway, Galveston, TX 77554, U.S.A.

[b] NOAA Office for Coastal Management - Gulf Region, 1021 Balch Boulevard, Suite 1003, Stennis Space Center, MS 39529, U.S.A.

*Corresponding Author: Travis Sterne
Phone Number: +1 (512) 228-1695
Email Address: travis.sterne17@gmail.com

[1] Corresponding Author Permanent Mailing Address: 3837 FM 1685, Victoria, TX 77905, U.S.A.

This is the author manuscript accepted for publication and has undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1002/aqc.3281

ABSTRACT

1. Effective management of marine resources requires an understanding of the spatial distribution of biologically important communities.

2. The north-western Gulf of Mexico contains diverse marine ecosystems at a large range of depths and geographic settings. To better understand the distribution of these marine habitats across large geographic areas under consideration for marine sanctuary status, presence-only predictive modelling was used.

3. Results confirmed that local geographic characteristics can accurately predict the probability of occurrence for marine habitat types, and include a novel technique for assigning a single, most likely habitat in areas where multiple habitats are predicted.

4. The highest resolution bathymetric data (10m) available for the region was used to develop raster layers that represent characteristics that have been shown to influence species occurrence in other settings.

5. A georeferenced historical photo record collected via Remotely Operated Vehicle (ROV) was classified according to six commonly found mesophotic habitats across the 18 reefs and banks under consideration for Flower Garden Banks National Marine Sanctuary (FGBNMS) boundary expansion.

6. Using maximum entropy (Maxent) modelling, the influence of local geographic characteristics on the presence of these habitats was measured and a spatial probability distribution was developed for each habitat type across the study area.

KEYWORDS
benthos, coral, fishing, habitat mapping, modeling, ocean, trawling

I. INTRODUCTION

Resource management is becoming increasingly urgent as humans continue to place heavier pressure on the finite stocks of living and non-living resources. Mostly due to the limitations of common research methods, coral reef distribution known to the scientific community is primarily limited to the dense assemblages of shallow reef-building corals. However, diverse coral ecosystems exist in deep waters of continental shelves, slopes, seamounts, and ridges. These habitats contain fragile and slow-growing species of lesser-known invertebrates, some of which serve as proxies for environmental conditions over millennia (Etnoyer et al., 2018; Roberts, Wheeler, & Freiwald, 2006).

Marine Protected Areas (MPAs) are established to allow marine species and their habitats to exist and reproduce without human interaction, reducing their vulnerability to exploitation and climate change (National Oceanic and Atmospheric Administration [NOAA], 2015). To aid in the identification of potentially sensitive biological communities or expansion of MPAs, resource managers need to know the spatial distribution of conservation priorities. It is not economically efficient to survey every environment with great detail, particularly those that exist in the deepest waters of the ocean.

By combining information on the observed habitat locations with spatial predictors, the spatial association between the presence of biota and local geographic characteristics can be modelled across space (Baker & Weber, 1975; Guisan & Zimmerman, 2000; Pittman, Costa, & Battista, 2009; Stolt et al., 2011). Founded on ecological niche theory, predictive habitat and species distribution modelling of mesophotic communities provides a rapid and cost effective tool for predicting large-scale distribution, the effects of human use, and environmental change (Guisan & Zimmerman, 2000; Hirzel, Helfer, & Metral, 2001; Phillips, Anderson, & Schapire, 2006; Pittman & Brown, 2011). Data for predictive modelling of biological communities may come from several sources, including imagery from exploratory Remotely Operated Vehicle (ROV) operations conducted in marine environments by various governments, private companies, and academic institutions.

This project developed an ROV-based approach to predictive habitat modelling in ocean-floor environments and evaluated its suitability and effectiveness for mesophotic environments in the Northwestern Gulf of Mexico. Specifically, the project addressed: 1) how well local geographic characteristics predict the presence of marine habitats in the north-western Gulf of Mexico; 2) given this, where are habitats predicted to occur in the region, and 3) important policy and planning implications of the results.

1.1 Hypothesized Relationships between Geographic Characteristics and Habitat Types

With the exception of soft bottom environments, the habitats in this study are largely characterized by the benthic taxa they contain. Recent studies have shown geographic characteristics to be statistically significant predictors of coral and algae species; it is therefore inferred that they can be used to predict occurrence of the habitats in which they thrive. For example, in applying this surrogate approach to coral habitats, scleractinian coral presence indicates coral reef or coral community habitat (depending on density), dense crustose coralline algae (CCA) cover indicates algal nodule or CCA reef (depending on morphology), and substrate inhabited by antipatharian and octocoral species indicates Deep Coral habitat (Schmahl, Hickerson, & Precht, 2008). It is also inferred that local geographic characteristics capable of influencing probability of occurrence for species (scleractinians, crustose coralline algae, antipatharians, octocorals) within one habitat (Coral Reef, Algal Nodule, Algal Reef, or Deep Coral) have a high potential to affect the probability in others.

Prior research suggests likely relationships between geographic characteristics and benthic ecology in environments characterized by coral and algae species. Depth is well known to influence the growth rate of coral and algae species (Adey, 1966, 1970; Adey & Macintyre, 1973; Baker & Weber, 1975; Bosellini & Ginsberg, 1971; Minnery, Rezak, & Bright, 1985; Minnery, 1990; Rezak, Bright, & McGrail, 1985). In general, habitats that are characterized by photosynthesizing organisms such as hermatypic corals and CCA are expected to share an inverse relationship with depth, given that it limits the amount of available light needed for their progression due to refraction and turbidity caused by suspended sediments (Adey, 1966, 1970; Adey & Macintyre, 1973; Baker & Weber, 1975; Bosellini & Ginsberg, 1971; Minnery et al., 1985; Minnery, 1990; Rezak et al., 1985). Antipatharians and octocorals that characterize deep coral habitats benefit from the lack of competing, faster-growing benthic species such as CCA and need much lesser amounts of light to grow. Thus, these habitats would likely share a positive correlation with depth.

Bottom slope, rugosity, and plan curvature capture the geographic complexity of a specific area. Prior research has shown a strong correlation between these three metrics and the occurrence of hard coral species and associated fish communities (Pittman, Costa, & Battista, 2009; Wedding & Friedlander, 2008); these metrics have also been examined as predictors of species richness and abundance (Anderson et al., 2016; Lecours, Lucieer, Dolan, & Micallef, 2018; Pittman & Brown, 2011; Pittman et al., 2009; Wedding & Friedlander, 2008; Young & Carr, 2015). Thus, it was expected that all habitats characterized by high morphometric complexity would share a positive correlation with the presence of coral habitats.

Aspect represents the compass direction in which a given sloping area faces. This parameter has not been well-documented to have substantial influence on the occurrence of species found within these habitats, and the results of this model were not expected to be greatly influenced by it. However, past research has shown that current velocity, a parameter that is often determined by aspect, has a direct influence on some species included in the modelled habitats (Adey, 1966, 1970; Adey & Macintyre, 1973; Minnery, 1990).

Soft Bottom habitats are known to occur primarily on low-lying, level geographic features in the north-western Gulf of Mexico. The sediments that make up the sea floor in these habitats are primarily terrigenous and calcareous in nature, resulting from coastal river outflows and skeletal remains of planktonic organisms (Schmahl, Hickerson, & Precht, 2008). Given the relatively featureless characteristics of these habitats, they were expected to be found in areas with minimal local relief (rugosity), slope of slope, slope, and plan curvature. Areas with high values for these co-variables were expected to decrease the probability of Soft Bottom habitat occurrence.

In line with this literature, hypotheses were made about each geographic characteristic-habitat type relationship. **Table 1** defines the relationships expected to be found between each habitat and associated geographic characteristics. The relationships between these geographic characteristics and the presence of specific FGBNMS habitat types are discussed in **Appendix 1.1** in more detail.

II. MATERIALS AND METHODS

2.1 Background: Study Site and Associated Habitat Types

At present, FGBNMS protects only three of the many reefs and banks located on the edge of the continental shelf in the Gulf of Mexico: East and West Flower Garden Bank, and Stetson Bank. NOAA has proposed adding 15 underwater areas located 70-100 miles from the coastlines of Texas and Louisiana to the existing sanctuary. Should the proposed expansion into these areas be adopted, the total area would increase from 56 to 383 square miles (**Figure 1**). These underwater features include: Horseshoe, 28 Fathom, MacNeil, Rankin, Bright, Geyer, Elvers McGrail, Bouma, Bryant Rezak, Sidner, Sonnier, Alderdice, and Parker Bank. According to the Gulf of Mexico Ecosystem Restoration Task Force, these areas are listed as ecologically significant sites that should be protected and managed to maintain overall biological productivity and resilience (Office of National Marine Sanctuaries [ONMS], 2016). All of these areas have been the focus of exploratory ROV expeditions, which have recorded data used not only to measure species richness and abundance but also to describe bottom types via in-situ annotations.

Over the course of this research, ROV-based habitat observations have been recorded under a localized FGBNMS classification scheme. The habitat categories under this scheme include: Coral Reef, Coral Community, Algal Nodule, Algal Reef, Deep Coral, and Soft Bottom habitat – all of which refer to commonly-found ecosystems in the north-western Gulf of Mexico. These habitat descriptions are useful in communicating observations internally as well as to the general public and affiliated stakeholders in the region. Accordingly, this research primarily used this localized FGBNMS classification scheme. National-level classification schemes such as the Coastal and Marine Ecological Classification Standard (CMECS) may also be applied to FGBNMS habitats (Carollo, Allee, & Yoskowitz, 2013; Federal Geographic Data Committee, 2012; Ruby, 2017); an explanation of how the FGBNMS and CMECS scheme are inter-related can be found in the Appendix (Table A-1).

2.2 Data Collection and Photo Analysis

A probability distribution predicting the likelihood of occurrence for six commonly observed habitat types in the north-western Gulf of Mexico was generated using: 1) photographic ROV data collected by the National Oceanic and Atmospheric Administration's (NOAA) Flower Garden Banks National Marine Sanctuary (FGBNMS); and 2) local geographic characteristics extracted from high-definition bathymetry data using Environmental Systems Research Institute (ESRI) ArcMap mapping software. Field data collection for this project included 16 years (2001-2016) of collaboration between FGBNMS and the University of North Carolina Wilmington - Undersea Vehicles Program (UNCW-UVP). Two different models of ROV were used to collect data utilized for this model. A description of each model can be found in the Appendix **(Table A-2).** Approximately 7,150 geo-referenced photographs analysed by FGBNMS scientists during previous habitat classification research (Sammarco et al., 2016) were combined with the entire mesophotic photo record from FGBNMS expeditions in the Northwestern Gulf, totalling 19,514 photos. These photos were geo-referenced using post-processing procedures that use the photos' timestamps and information about the ROV's speed to correct for gaps in location data from the ROV Hypack GPS (approximately 10% of photos were so corrected, introducing an additional horizontal error of up to 1.03 m) (**Appendix 2.2.1**).

Still images from each dive were reviewed to determine their usability for qualitative analysis. If at least 50% (approximate) of the photo could be analysed for benthos, it was used in the primary data analysis for the project. Usable photos were classified according to the regional FGBNMS habitat scheme based on the qualitative analysis to detect the presence of any definitive species, as well as substrate type that characterize the habitats of interest, using Windows Photo Viewer. The defining characteristics of each habitat type were found in the guidance documents for each respective classification category (Federal Geographic Data Committee, 2012; Schmahl et al., 2008). Under the FGBNMS scheme, a photo has a classification for Biological Zone and Major Habitat (**Table A-1**). Each usable photo was assigned to one of the six FGBNMS habitats considered in this study; this habitat code was stored along with its latitude and longitude in a Comma Separated Value (.csv) file. These data points served as the occurrence records that Maxent used to construct the spatial probability distribution across the study area. Data points used to develop the probability distribution include 238 Coral Reef, 203 Coral Community, 1,431 Algal Nodule, 4,178 Algal Reef, 4,746 Deep Coral, and 8,718 Soft Bottom classifications.

2.3 Bathymetric Data

Digital terrain models derived from high-definition multibeam acoustic sensor data were used to quantify spatial predictors representing a range of variables of seafloor morphology. Since 2002, these bathymetric data have been collected by a coalition of FGBNMS, Bureau of Ocean Energy Management (BOEM) (formerly known as Minerals Management Service), and USGS.

Raster surfaces derived from the bathymetric data obtained for this project were projected in WGS 1984 UTM Zone 15N coordinate system. The original resolution of the bathymetry data being used for this research ranges from approximately one to eight metres. In order to account for the coarsest resolution of the original data (8m) and the error in the ROVs' horizontal position during data collection, ESRI's Resampling tool for ArcMap was used with a bilinear resampling technique (ESRI, 2017) to standardize the resolution of each raster dataset to a 10m x 10m cell size. The 18 multibeam datasets were compiled into one single-band raster layer with 32-bit floating point pixel type using ArcMap's Mosaic to New Raster Tool.

Based on a review of the literature, depth, bottom slope, slope of slope, rugosity, plan curvature, and aspect are the characteristics most likely to predict presence of FGBNMS habitat types. These were therefore the characteristics that were used as environmental covariates to estimate habitat distribution in this study. The raster mosaic served as both the depth raster and the base raster surface from which all remaining environmental parameters for this project were calculated. Five morphometric transformations of the depth surface layer were generated in ArcMap software:

- slope (maximum rate of change in the three-by-three cell neighbourhood; Slope tool with depth as input),
- slope of slope (maximum rate of slope change in the three-by-three cell neighbourhood; Slope tool with slope as input),
- rugosity (the secant of slope in radians, equivalent to 3D to 2D area ratio, for each grid cell; Raster Calculator tool, as described in Berry, 2007),
- plan curvature (the horizontal convexity or concavity of a sloping pixel; Curvature tool),
- and aspect variation (direction each grid cell faces; Aspect tool output vectorized on 0-1 scales to westerly and southerly components, each evaluated independently).

Following their creation, each file was converted into an ASCII grid layer, as is required by Maxent.

2.4 Maximum Entropy Modelling

Habitat suitability modelling has been widely used to predict the distribution of number of deep-sea and cold-water scleratinians, octocorals, and antipatharians in order to more comprehensively understand shelf habitats and aid resource management decisions regarding their protection (Krigsman, Yoklavich, Dick, & Cochrane, 2012; Rengstorf, Yesson, Brown, Grehan, & Crame, 2013; Tazioli, Bo, Boyer, Rotinsulu, & Bravestrello, 2007; Woodby, 2009). For this project, habitat suitability was predicted using the maximum entropy estimation method, which was developed for modelling species' geographic distributions (Elith et al., 2010; Phillips, Anderson, & Schapire, 2006; Phillips & Dudik, 2008). Specifically, this modelling approach offers the most random distribution of each habitat type across the full extent of the study area consistent with the covariate values (depth, slope, slope of slope, plan curvature, rugosity, and aspect) observed at each ROV-observed sample point. This results in the least-biased estimate given the region(s) of phase space included in the available information (Jaynes, 1957). Maxent uses independent variables, or covariates, from a sample record for each habitat, along with a sample of background points from an ASCII raster grid that represents a geographic region, to independently estimate a spatial probability distribution for each habitat occurrence (Elith et al., 2010; Phillips et al., 2006).

2.5 Maxent Outputs

2.5.1 Receiver Operating Characteristic (ROC)

A major concern of ecological modelling is the accuracy of a model in predicting the presence and/or absence of some organism or habitat. Maxent allows a subset of data to be set aside for an independent accuracy assessment called the Receiver Operating Characteristic (ROC). This test refers to a measure of model accuracy in terms of its ability to correctly predict the occurrence of a given habitat type; it is a function of the proportion of error in testing the model with a random subset of data

(Deleo, 1993; Fielding & Bell, 1997). In the case of maximum entropy modelling, the ratio represents the ability of the model to identify presence relative to a completely random distribution (Phillips et al., 2006). This ratio is also known as *sensitivity.* The area underneath this ROC curve (AUC score) is equal to the probability that a randomly chosen positive instance and a randomly chosen locality with probability equal to zero are correctly predicted by the model.

2.5.2 Response Curves

Maxent response curves illustrate the probability response for each habitat type as predictor values vary. Each plot is developed by creating a model using only the corresponding environmental predictor (Phillips, 2017). The patterns represented by the curves are useful for comparative analysis between habitat types and their relative response to increasing/decreasing values of each predictor.

2.5.3 Percent Contribution and Permutation Importance

These metrics present the relative estimates of model contribution by each environmental predictor. The second estimate (permutation importance) is calculated by taking the presence data used for training and background samples and running a random permutation using each variable in turn. The software then records the successive drop in AUC during each permutation to determine importance as a percentage. The jackknife test of variable importance gives further insight by evaluating the relative influence of each environmental predictor independently.

The value of variable contribution or permutation importance is indicative of the degree to which the presence of each respective habitat is dependent upon each variable; a high value indicates high dependability, and vice-versa. In some cases, the relative contribution to model performance is increased or decreased substantially between variable contribution and permutation importance. A shift from a high contribution score to a substantially lower permutation score may be the result of multi-collinearity among covariates (Baldwin, 2009). The permutation process of Maxent highlights these relationships and the regularization of the model algorithm protects overall model performance from this effect (Bradie & Leung, 2016; Cruz-Cardenas, López-Mata, Villaseñor, & Ortiz, 2014).

2.5.4 Spatial Probability Distributions

In the final step of the modelling process, Maxent produces a spatial probability distribution for each habitat type across the study area. It builds a raster grid (.ASC) for each habitat in which each pixel represents the probability (0-1.0) for it to occur.

2.6 Mapping Maxent Probabilities Using Multinomial Logit Regression

For habitat prediction and management applications of the Maxent model output, it is important to illustrate the spatial distribution of each habitat type in relation to others. To do this, the probability distributions for all habitat types were combined using ArcMap raster calculator. A major challenge in combining habitat types was presented by areas where Maxent predicts more than one type of habitat to occur with probability greater than 50%; in this project, these areas were termed "transitional zones." In order to maximize the statistical accuracy of the model, a multinomial logistic regression (MLR) analysis using both the Maxent probability distributions for each habitat (independent variables) and sample observation point data (dependent variable) was used to find which Maxent habitat type probabilities were more predictive of the habitats actually observed at the sample points (classified ROV imagery) within each transitional zone.

This allowed the development of a rule set for breaking ties in transitional zones, with the goal of assigning grid cells in these areas to a single habitat type from among the two or more habitat types predicted with high probability at that location. **Table 2** contains the MLR-based guidelines on which decisions were made to assign categorical values to pixels of overlapping habitats with high probability. These distributions were combined so as to qualitatively and quantitatively realize the relative spatial relationships between the mesophotic habitats across the study area. A more comprehensive description of the methods used to process transitional areas can be found in the **Appendix 3.1.2**.

III. RESULTS

3.1 AUC and Overall Model Performance

The AUC scores for Coral Reef Coral Community, Algal Nodule, Algal Reef, Deep Coral, and Soft Bottom habitat were 0.988, 0.995, 0.944, 0.901, 0.876, and 0.798, respectively. These results showed that, relative to the other models, the Coral Community model performed best according to the random test sample (25%) set aside from the observation data. That is, this model correctly identified Coral Community presence 99.5% of the time.

3.2 Percentage Contribution and Permutation Importance

Depth showed the strongest contribution to model gain, especially for Coral Reef habitats (Table 3). It also showed the highest permutation importance across all habitats. It is important to note that its permutation importance increased relative to variable contribution across all habitats, indicating that depth was minimally or unaffected by multicollinearity between variables in this model (Baldwin, 2009). Slope of slope substantially contributed to the model, primarily for Algal Reef and Deep Coral habitats, though its importance decreased when used as the only predictor. Slope was also a relatively important contributor to overall model performance, especially for deeper habitats, however, model gain decreased substantially in permutations using this variable alone. While rugosity appears to have had little relative influence on overall model performance, AUC scores recorded during permutations indicated an interesting shift from very low to moderate importance in model gain for Algal Reef, Deep

Coral, and Soft Bottom habitats. Using this metric for variable contribution to the model, all other variables showed minimal influence.

3.3 Response Curves

For depth, response curves showed that probabilities for habitats characterized by dense assemblages of light-dependent species (such as hermatypic corals and photosynthesizing algae) were higher in shallower areas, while Algal Nodule, Algal Reef, and particularly Deep Coral habitats showed peaks in probability in deeper water (Figure 2). Slope appeared to have high initial influence as it increased from zero at the low end, though its effect gradually decreased for high slope values, having either a slight negative (Coral Reef, Coral Community, and Algal Nodule) or slightly positive (Algal Reef, Deep Coral, Soft Bottom) effect on occurrence probability in this range. The curves for slope of slope and rugosity showed similar response patterns. For planform curvature, Coral Community showed lower probabilities for convex features (negative values) and higher probabilities for concave features (positive values). The probability response for planform curvature for the remaining habitats in the model all presented a relatively constant probability greater than 0.70 for convex features, with a slightly higher probability prediction for concave features, and a dip in probability to 0.40 or lower for flat features. For aspect, probabilities appeared to be slightly higher for northerly and easterly facing areas.

3.4 Maps of Likely Habitat Locations

As one would expect to find, Coral Reef and Coral Community habitats were estimated to occur primarily around the shallowest features of the study area; the general patterns of Algal Nodule, Algal Reef, Deep Coral, and Soft Bottom distributions appear less definitive (**Figure 3**). In an initial assessment of these raster surfaces, substantial overlap in the spatial distribution of high-probability (>.50) for occurrence of each habitat type were observed, with many instances in which Maxent assigned a high probability for two, three, four and occasionally five types of habitats to occur in the same location. **Table A-4** identifies all combinations of overlapping habitat types, the total area they cover, and the outcome of applying MLR-based guidelines (Table 2) for each case. **Figure 3** illustrates the distribution of these overlapping areas, as well as areas in which only one habitat was predicted to occur with high confidence, throughout East Flower Garden Bank. The final map**, (Figure 3c)**, was rendered by combining the categorical raster grid of habitat types with their respective probabilities as assigned by Maxent; the opacity of each grid cell represents the probability that said habitat occurs. **Table 4** quantifies total area covered by each habitat in the study area after addressing high probability discrepancies using MLR.

IV. DISCUSSION

In general, the results showed that local geographic characteristics provided accurate metrics for predicting the occurrence of the habitats of interest; the 18 reefs and banks included in the FGBNMS Expansion Proposal were predicted to contain networks of biologically important habitats (ONMS, 2016), and the results support this prediction. For each habitat, environmental predictors' influence in the Maxent model (as measured by variable contribution, permutation importance, and jackknife tests of variable importance) was compared to that set forth in the hypotheses and the findings of existing empirical studies. The implications of the results for the hypothesized influence of each environmental variable on FGBNMS habitat classifications are summarized in **Table 1**. Consistent with the hypotheses, the majority of predictive environmental variables included in the model were shown to have influence on the presence of Coral Reef, Coral Community, Algal Nodule, Algal Reef, Deep Coral, and Soft Bottom habitats in the study area (**Table 1 & Figure 2**).

4.1 Effects of Environmental Predictors on Habitat Probability

4.1.1 Coral Reef and Coral Community

For Coral Reef and Coral Community habitats, the results supported the hypothesized decrease in probability with increasing depth. This was supported by the jackknife plots, which showed a large decline in model performance when depth was removed as an environmental predictor for these habitats. This observation is consistent with the relationship predicted to occur (**Table 1**) and conclusions of Baker and Weber (1975). Coral Reef and Coral Community are both characterized by the presence of photosynthesizing hard corals and other benthos and thus one would logically expect to find this relationship to hold true. According to the jackknife test data, the second most influential parameter for Coral Reef was slope of slope. For Coral Community, rugosity appeared to have high relative influence on habitat occurrence; however, when the permutations were performed, its relative influence decreased (**Table 1**). This indicated that, in the absence of other variables (primarily depth), rugosity did not have much predictive power for this habitat. The results for planform curvature also indicated that Coral Community habitat was more likely to occur on laterally convex bottom features.

4.1.2 Algal Nodule and Algal Reef (CCA)

In the case of running the model without depth as a predictor, a substantial decrease in model performance was observed for both these habitats. This observation is consistent with the hypothesis and findings of Adey (1966, 1970) and Minnery (1990). These studies indicate that the presence of CCA is largely controlled by available light, temperature, and grazing herbivores (parrot fish) whose distribution is limited by depth and competing organisms such as hermatypic corals. Algal Nodule habitat was also shown be significantly influenced by degree of Slope. This is speculated to be a result of the general distribution of this habitat around prominent features where sunlight still penetrates the entire water column and waves and currents still influence the sea floor to a degree that allows the formation of nodules (Bosellini & Ginsburg, 1971; McMaster & Conover, 1966; Minnery, 1990; Rezaket al., 1985; Scoffin, Stoddart, Tudhope, & Woodroffe, 1985). For Algal Reef, slope of slope performed as the strongest environmental predictor when including all covariates in the model, while the omission of depth caused the largest decline in model performance; slope also showed substantial relative importance in predicting presence of this habitat (**Table 1**).

4.1.3 Deep Coral

Performance of the predictive model for Deep Coral declined when depth was excluded, indicating that it is a strong predictor of Deep Coral habitat. In line with this result, past research has indicated that the density of scleractinian and algal species decrease with depth, reducing competition and enabling gorgonian and antipatharian species characteristic of Deep Coral habitats to proliferate (Tazioli et al., 2007; Wagner et al., 2012). Comparatively, however, slope of slope provided the best predictive performance for this habitat in the overall model. This may be a result of reaching a minimum threshold of available light required by photosynthesizing benthos, at which point those species can no longer compete with deep coral species. Upon reaching this depth, slope of slope, a metric reflective of available hard bottom substrate and shelter, becomes the strongest predictor for the presence of characteristic benthic fauna (Pittman, Costa, & Battista, 2009). Slope was also indicated to be a strong predictor in the model, though its performance decreased substantially when used by itself. These results indicated that, in the absence of ample sunlight, bottom complexity has significant influence on the presence of deep coral habitat and the species that characterize them. This is consistent with the reported sensitivity of antipatharian (black coral) species to prevailing currents and surrounding seafloor composition as well as depth (Tazioli et al., 2007; Wagner, Luck, & Toonen, 2012) and previously observed associations between slope of slope, plan curvature, and rugosity on octocoral abundance (Pittman et al. 2009, Sammarco 2016, Woodby 2006, and Wedding, Jorgenson, Lepcyzk, & Friedlander 2019) and the relationships predicted in **Table 1**.

4.1.4 Soft Bottom

Slope of slope, slope, and depth showed substantial influence on the presence of Soft Bottom habitat. According to the test of permutation importance, model performance decreased by 25.8% (**Table 1**) when slope of slope was omitted from the model. Furthermore, slope and depth appeared to have substantial predictive influence on the model for Soft Bottom habitat. In the model developed using all environmental predictors, slope of slope had the highest relative influence, although depth was a stronger predictor on its own.

4.2 Conclusions

This project utilized the entirety of the ROV-derived dataset from NOAA's 16-year-long endeavour to explore and document seafloor features of the north-western Gulf of Mexico. The results suggest that Maxent modelling (as supplemented by MLR to resolve conflicting habitat predictions) is an accurate and useful tool for environmental management bodies interested in preserving the biological integrity of natural marine ecosystems. Specifically, the results of this predictive model show that depth, slope, slope of slope, rugosity, and planform curvature have significant influence on the presence of Coral Reef, Coral Community, Algal Nodule, Algal Reef, Deep Coral, and Soft Bottom habitats described by Schmahl et al. (2008).

By applying this modelling approach and using logistical regression techniques to combine independent models, a series of maps for informing management decisions was created. In the context of this study, these results are particularly relevant to decisions regarding which areas of the north-western Gulf of Mexico should be included in a proposed expansion of the FGBNMS. NOAA researchers have previously confirmed the presence of biologically important habitats and benthic species within the preferred alternative of the FGBNMS boundary expansion proposal (ONMS, 2016); the results of this empirical study suggest that these biologically important habitats are highly likely to be widespread throughout the preferred alternative region (ONMS, 2016). To best inform policy decisions related to FGBNMS boundary expansion, these habitat distribution maps should be subject to future research to refine and validate their depiction of the spatial extent of mesophotic habitats in the northwest Gulf of Mexico. Specifically, to further refine estimates of the extent of biologically important habitats on the reefs and banks in the FGBNMS preferred alternative, the results of this research should be used to target new areas for exploratory work using ROVs, which could be used to ground truth the predicted habitats' extents.

The inclusion of other critical environmental variables and verification of this and forthcoming predictive models will enhance the success of resource management efforts by NOAA and other responsible authorities. It is important to consider that the real distribution of habitats predicted by this model are not explicitly bound by the mathematically derived geographical attributes included in this model. Additionally, the environmental predictors used to develop this model are vulnerable to the inherent error of instruments used to collect data in the marine environment. To address these limitations, future research related to the predictive modelling of these and similar habitats in the north-west Gulf of Mexico should consider incorporating other biological, chemical, and physical properties of the water column that have been empirically shown to influence the growth rate and survival of the benthic species that characterize them. Among these attributes are temperature, salinity, prevalent current direction and speed, nutrients (nitrogen and phosphorous), and turbidity. Built on the observations of unique mesophotic habitats and their associated local geographic characteristics, this model serves as a valid base on which to develop further predictive models with enhanced accuracy by the addition of other contributing variables.

Future studies should also test the methods employed by this research for transferability by applying them to other regions in the Gulf of Mexico and Outer Continental Shelf (OCS) areas. The results suggest that the methods may be broadly suitable for identifying areas which may contain vital benthic communities that require careful consideration in resource management decisions. The geographic features identified in this study may serve as a useful starting point in developing Maxent models for predicting occurrences of benthic habitats across other regions. Similarly, the MLR technique developed here for resolving classification conflicts in "transitional zones" (areas where multiple habitats are predicted to occur with high probability) may also be transferable to classification conflicts identified in Maxent output for other regions.

When management plans for marine protected areas are based on inaccurate or incomplete assessments of benthic habitats, unforeseen environmental consequences may result, potentially contributing to the degradation of habitats and communities beyond recoverable levels. The risk of this occurring can be minimized by incorporating predictive models when developing natural resource policy. Maxent models like that developed here may serve as a cost-effective means of informing management decisions that prioritize the longevity of natural systems. They are a statistically accurate means of finding specific geographic locations where sensitive biological features are likely to occur. Accordingly, these locations and features may be spared from direct and unintended detrimental effects of resource extraction, or other similarly disruptive activities.

ACKNOWLEDGMENTS

Many thanks to the experienced faculty at Texas A&M Galveston who provided the base of knowledge to carry out this research, especially to those who provided support throughout this project. Thank you to the boat crew and staff at FGBNMS for carrying out over a decade of data collection, maintaining organized data sets, and painstakingly analysing thousands of photographs. Sincerest gratitude goes out to the ROV technicians and pilots at UNCW's Underwater Vehicle Program; without your expertise, patience, and hard work, none of this would have been possible.

REFERENCES

Adey, W. H. (1966). Distribution of saxicolous crustose corallines in the northwestern North Atlantic. *Journal of Phycology*, *2*, 49–54.

Adey, W. H. (1970). The effects of light and temperature on growth rates in boreal-subarctic crustose corallines. *Journal of Phycology*, *6*, 269–276.

Adey, W. H., & Macintyre, I. G. (1973). Crustose coralline algae: A re-evaluation in the geological sciences. *GSA Bulletin*, *84*, 883–904.

Anderson, O.F., Guinotte, J.M., Rowden, A.A., Tracey, D.M., Mackay, K.A. and Clark, M.R., 2016. Habitat suitability models for predicting the occurrence of vulnerable marine ecosystems in the seas around New Zealand. *Deep Sea Research Part I: Oceanographic Research Papers*, 115, 265-292.

Baker, P. A., & Weber, J. N. (1975). Coral growth rate: Variation with depth. *Earth and Planetary Science Letters*, *27*, 57–61.

Baldwin, A. R. (2009). Use of maximum entropy modeling in wildlife research. *Entropy*, *11*, 854-866.

Bosellini, A., & Ginsburg, R. N. (1971). Form and internal structure of recent algal nodules (Rhodolites) from Bermuda. *The Journal of Geology*, *79*, 669–682.

Bradie J., & Leung, B. (2016). A quantitative synthesis of the importance of variables used in Maxent species distribution models. *Journal of Biogeography*, *44*, 1344–1361.

Brooke, S., & Schroeder, W.W. (2007). State of deep coral ecosystems in the Gulf of Mexico region: Texas to the Florida Straits. In *State of Deep Coral Ecosystems in the Gulf of Mexico Region* pp. 217-306.

Carollo, C., Allee, R. J., & Yoskowitz, D. W. (2013). Linking the Coastal and Marine Ecological Classification Standard (CMECS) to ecosystem services: An application to the US Gulf of Mexico. *International Journal of Biodiversity Science, Ecosystem Services & Management*, *9*, 249–256.

Cruz-Cárdenas, G., López-Mata, L., Villaseñor, J. L., & Ortiz, E. (2014). Potential species distribution modeling and the use of principal component analysis as predictor variables. *Revista Mexicana de Biodiversidad*, *85*, 189–199.

Deleo, J. (1993). Receiver operating characteristic laboratory (ROCLAB): Software for developing decision strategies that account for uncertainty.

Elith J., Phillips S. J., Hastie, T., Dudík M., Chee Yung E., & Yates C. J. (2010). A statistical explanation of Maxent for ecologists. *Diversity and Distributions*, *17*, 43–57.

Etnoyer, P. J., Wagner, D., Fowle, H. A., Poti, M., Kinlan, B., Georgian, S. E., & Cordes, E. E. (2018). Models of habitat suitability, size, and age-class structure for the deep-sea black coral *Leiopathes glaberrima* in the Gulf of Mexico. *Results of Telepresence-Enabled Oceanographic Exploration*, *150*, 218–228.

Federal Geographic Data Committee. (2012). Coastal and Marine Ecological Classification Standard. Marine and Coastal Spatial Data Subcommittee, Federal Geographic Data Committee.

Fielding, A. H., & Bell, J. F. (1997). A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation*, *24*, 38–49.

Guisan, A., & Zimmermann, N. E. (2000). Predictive habitat distribution models in ecology. *Ecological Modelling*, *135*, 147–186.

Hirzel, A. H., Helfer, V., & Metral, F. (2001). Assessing habitat-suitability models with a virtual species. *Ecological Modelling*, *145*, 111–121.

Jaynes, E. T. (1957). Information theory and statistical mechanics. *The Physical Review*, *106*, 620–630.

Krigsman L. M., Yoklavich M. M., Dick E. J., & Cochrane G. R. (2012). Models and maps: predicting the distribution of corals and other benthic macro-invertebrates in shelf habitats. *Ecosphere*, *3, Art. 3*.

McMaster, R. L., & Conover, J. T. (1966). Recent algal stromatolites from the Canary Islands. *The Journal of Geology*, *74*, 647–652.

Minnery, G. A., Rezak, R., & Bright, T. J. (1985). Depth zonation and growth form of crustose coralline algae: Flower Garden Banks, Northwestern Gulf of Mexico.

Minnery, G. A. (1990). Crustose Coralline Algae from the Flower Garden Banks, Northwestern Gulf of Mexico: Controls on distribution and growth morphology. *SEPM Journal of Sedimentary Research*, *Vol. 60*.

Office of National Marine Sanctuaries [ONMS]. (2016). Flower Garden Banks National Marine Sanctuary Expansion draft environmental impact statement. U.S. Department of Commerce, National Oceanic and Atmospheric Administration, Office of National Marine Sanctuaries, Silver Spring, MD.

Phillips, S. J. (2017). A brief tutorial on Maxent. AT&T Research.

Phillips, S. J., Anderson, R. P., & Schapire, R. E. (2006). Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, *190*, 231–259.

Phillips S. J., & Dudík, M. (2008). Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography*, *31*, 161–175.

Pittman, S. J., & Brown, K. A. (2011). Multi-scale approach for predicting fish species distributions across coral reef seascapes. *PLoS ONE*, *6*, e20583.

Pittman, S. J., Costa, B. M., & Battista, T. A. (2009). Using lidar bathymetry and boosted regression trees to predict the diversity and abundance of fish and corals. *Journal of Coastal Research*, Special Issue 53, 27–38.

Rengstorf A. M., Yesson C., Brown C., Grehan A. J., & Crame A. (2013). High-resolution habitat suitability modelling can improve conservation of vulnerable marine ecosystems in the deep sea. *Journal of Biogeography*, *40*, 1702–1714.

Rezak, R., Bright, T., & McGrail, D. (1985). Reefs and banks of the northwestern Gulf of Mexico: Their geological, biological, and physical dynamics. *Northern Gulf of Mexico Topographic Features Monitoring and Data Synthesis*, *Contract No. AA851-CT1-55*.

Roberts, J. M., Wheeler, A. J., & Freiwald, A. (2006). Reefs of the deep: The biology and geology of cold-water coral ecosystems. *Science*, *312*, 543.

Ruby, C. (2017). Application of coastal and marine ecological classification standard (CMECS) to remotely operated vehicle (ROV) video data for enhanced geospatial analysis of deep sea environments. Mississippi State University, Mississippi.

Sammarco, P. W., Nuttall, M. F., Beltz, D., Horn, L., Taylor, G., Hickerson, E. L., & Schmahl, G. P. (2016). The positive relationship between relief and species richness in mesophotic communities on offshore banks, including geographic patterns. *Environmental Geosciences*, *23*, 195–207.

Schmahl, G. P., Hickerson, E. L., & Precht, W. F. (2008). Biology and ecology of coral reefs and coral communities in the flower garden banks region, northwestern Gulf of Mexico. In B. M. Riegl & R. E. Dodge (Eds.), *Coral Reefs of the USA* (pp. 221–261). Dordrecht: Springer Netherlands.

Scoffin, T. P., Stoddart, D. R., Tudhope, A. W., & Woodroffe, C. (1985). Rhodoliths and coralliths of Muri Lagoon, Rarotonga, Cook Islands. *Coral Reefs*, *4*, 71–80.

Stolt, M., Bradley, M., Turenne, J., Payne, M., Scherer, E., & Cicchetti, G., Shumchenia, E. (2011). Mapping shallow coastal ecosystems: A case study of a Rhode Island lagoon. *Journal of Coastal Research*, 27, 1–15.

Tazioli, S., Bo, M., Boyer, M., Rotinsulu, H., & Bavestrello, G. (2007). Ecological observations of some common antipatharian corals in the marine park of Bunaken (North Sulawesi, Indonesia*)*. (Vol. 46).

Villas Bôas, A. B., Figueiredo, M. A. de O., & Villaça, R. C. (2005). Colonization and growth of crustose coralline algae (Corallinales, Rhodophyta) on the Rocas Atoll. *Brazilian Journal of Oceanography*, *53*, 147–156.

Wagner, D., Luck, D. G., & Toonen, R. J. (2012). Chapter two - The biology and ecology of black corals (Cnidaria: Anthozoa: Hexacorallia: Antipatharia). In M. Lesser (Ed.), *Advances in Marine Biology* , 63, 67–132

Wedding, L. M., & Friedlander, A. M. (2008). Determining the influence of seascape structure on coral reef fishes in Hawaii using a geospatial approach. *Marine Geodesy*, *31*, 246–266.

Wedding, L. M., Jorgensen, S., Lepczyk, C. A., & Friedlander, A. M. (2019). Remote sensing of three-dimensional coral reef structure enhances predictive modeling of fish assemblages. *Remote Sensing in Ecology and Conservation*, *5*, 150–159.

Woodby, D., Carlile, D., & Hulbert, L. (2009). Predictive modeling of coral distribution in the Central Aleutian Islands*, USA*. *Marine Ecology Progress Series, 397*, 227-240.

Young, M., & Carr, M.H., 2015. Application of species distribution models to explain and predict the distribution, abundance and assemblage structure of nearshore temperate reef fishes. *Diversity and Distributions*, 21, 1428-1440.

TABLES

Table 1: Predicted and Observed Influence of Covariates on Probability. This table represents the predicted relationship (+/-) and expected strength of co-variate influence (•) for each habitat within the model. This does not represent specific quantitative significance levels; "•" to "•••" represents the strength of the expected relationship. Predicted levels of influence for each covariate represent qualitative assessments of likely relationships based on cited literature results and the researchers' *in situ* observations, and should not be confused with statistical significance levels.

	Predicted /Observed	**Depth**	**Slope**	**Slope of Slope**	**Rugosity**	**Plan Curvature**	**Aspect (S→N)** †	**Aspect (W→E)** †
Coral Reef	Predicted	- (•••)	+ (••)	+ (•••)	+ (•••)	+ (•••)	•	•
	Observed	- (•••)	+ (••)	+ (••)	+ (••)	+ (•)	•	•
Coral Community	Predicted	- (•••)	+ (••)	+ (•••)	+ (•••)	+ (•••)	•	•
	Observed	- (•••)	+ (•••)	+ (•••)	+ (•••)	+ (•••)	•	•
Algal Nodule	Predicted	+ (•••)	- (••)	- (••)	- (••)	- (••)	••	••
	Observed	- (•••)	+ (•••)	+ (•••)	+ (•••)	+ (••)	•	•
Algal Reef	Predicted	+ (•••)	+ (••)	+ (•••)	+ (•••)	+ (•••)	••	••
	Observed	- (•••)	+ (•••)	+ (•••)	+ (•••)	+ (••)	•	•
Deep Coral	Predicted	+ (•••)	+ (••)	+ (•••)	+ (•••)	+ (•••)	•	•
	Observed	+ (••)	+ (•••)	+ (•••)	+ (•••)	+ (•••)	•	•
Soft Bottom	Predicted	+ (•••)	- (••)	- (••)	- (••)	- (••)	•	•
	Observed	+ (••)	N/A (•••)	+ (•••)	N/A (•••)	N/A (••)	•	•

† Specific relationships (+/-) for this variable are not included in this study.

Table 2: Scenario Description for Outcome Decisions.

Scenario	**Coefficient of var *a* ((log of the odds of observing *a* relative the the odds of observing *b*)**	**Coefficient of var *b* ((log of the odds of observing *b* relative the the odds of observing *a*)**	**Result**
1	*Positive; p ≤ 0.05*	*Positive; p ≤ 0.05*	Location assigned to habitat with highest MaxEnt probability.
2	*p ≤ 0.05; positive*	*p ≥ 0.05 and/or negative*	Location assigned to var *a*. (Inverse situation = *b)*
3	*p ≥ 0.05 and/or negative*	*p ≥ 0.05 and/or negative*	Habitat type considered transitional.

Table 3: Variable Contribution and Permutation Importance.

Variable Contribution (%)							
Habitat	**Depth**	**Slope**	**Slope of Slope**	**Rugosity**	**Plan Curvature**	**Aspect (S-N)**	**Aspect (W-E)**
Coral Reef	96.4	2.3	0.3	0.4	0.0	0.5	0.0
Coral Community	76.0	2.3	3.6	16.9	0.1	0.2	0.3
Algal Nodule	49.4	33.6	6.6	10.1	0.0	0.3	0.1
Algal Reef	33.6	26.9	38.1	0.6	0.6	0.1	0.0
Deep Coral	11.8	17.0	67.0	0.2	4.0	0.0	0.0
Soft Bottom	28.5	30.0	38.4	0.9	0.7	0.0	0.1
Average Contribution	49.3	18.7	25.7	4.9	0.9	0.2	0.1
Permutation Importance							
Habitat	**Depth**	**Slope**	**Slope of Slope**	**Rugosity**	**Plan Curvature**	**Aspect (S-N)**	**Aspect (W-E)**
Coral Reef	98.5	0.0	0.0	0.8	0.0	0.6	0.0
Coral Community	99.0	0.0	0.1	0.8	0.0	0.0	0.0
Algal Nodule	76.1	14.8	1.5	7.3	0.0	0.1	0.1
Algal Reef	73.8	0.5	12.6	12.5	0.5	0.1	0.0
Deep Coral	32.2	1.8	52.2	9.5	3.2	0.1	0.1
Soft Bottom	54.5	3.2	20.9	15.5	0.9	0.0	0.1
Average Importance	72.4	3.4	14.5	7.7	0.8	0.2	0.1

Table 4: Total Area of Habitat Coverage. Prior Area refers to total area prior to statistical transformation via MLR analysis (Prior Area) and Final Area represents high confidence habitat coverage by type following this transformation.

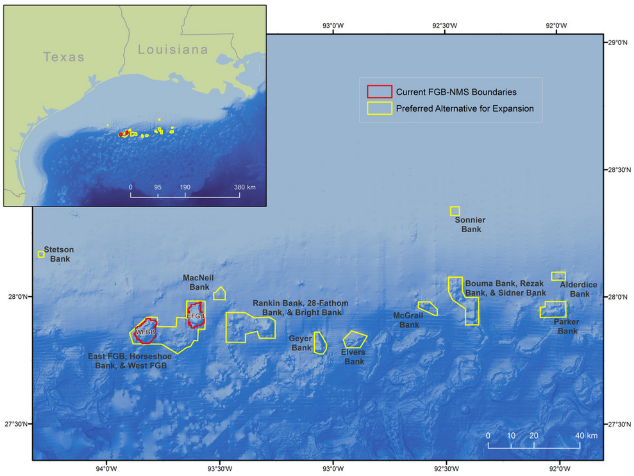
Habitat Type	**Prior Area (km^2)**	**Final Area (km^2)**
Coral Reef	5.53	5.93
Coral Community	0.24	0.48
Algal Nodule	3.93	9.31
Algal Reef	0.26	32.76
Deep Coral	3.36	59.12
Soft Bottom	53.93	53.93
Transitional	102.81	6.71

FIGURE LEGENDS

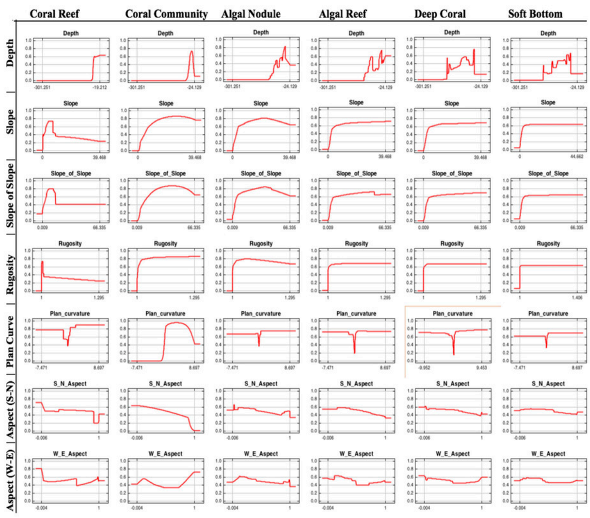
Figure 1: Flower Garden Banks National Marine Sanctuary and the preferred alternative boundary expansion alternative as per the Draft of the Environmental Impact Statement (DEIS) prepared by NOAA.

Figure 2: Response curves. The curve represents a model using only the corresponding variable.

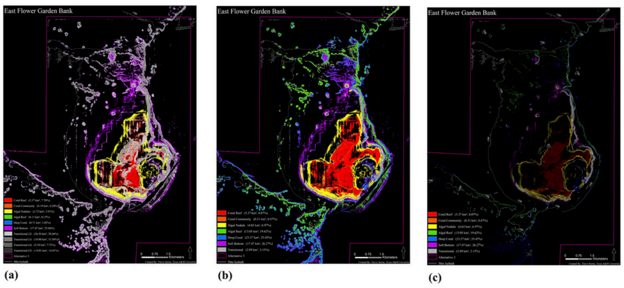
Figure 3: Sequence of probability distributions**: (a)** represents the distribution of habitats across East Flower Garden Bank including four degrees of overlapping area predicted with high probability; **(b)** represents the resulting distribution of habitats following selection of primary habitat type via MLR, as outlined in Section 3.4; and **(c)** represents the final distribution of habitats with the highest probability of occurrence, mapped with opacity indicating the degree of confidence that the model has in predicting occurrence.



AQC_3281_figure 1.jpg



AQC_3281_figure 2.jpg



AQC_3281_figure 3.jpg