Prepublication Edition

Predictive Habitat Modeling for Deep-Sea Corals in U.S. Waters

Chapter 8 in The Deep-Sea Coral and Sponge Ecosystems of the United States: 2015 Report

Recommended citation: Guinotte JM, Georgian S, Kinlan BP, Poti M, Davies AJ. (2016) Predictive Habitat Modeling for Deep-Sea Corals in U.S. Waters. In: Hourigan TF, Etnoyer PJ, Cairns SD (eds) The State of Deep-Sea Coral and Sponge Ecosystems of the United States: 2015. NOAA Technical Memorandum X. NOAA, Silver Spring, p 8-1 – 8-XX.

PREDICTIVE HABITAT MODELING FOR DEEP-SEA CORALS IN U.S. WATERS

John M. Guinotte[1], Sam Georgian[1], Brian P. Kinlan[2], Matthew Poti, and Andrew J. Davies[3]*

[1]Marine Conservation Institute

*Corresponding Author: sam.georgian@marineconservation.org

[2]NOAA National Centers for Coastal Ocean Science

[3]School of Ocean Sciences, Bangor University, U.K.

Introduction

Predictive habitat modeling (PHM) is a cost-effective method for extending the range and utility of expensive and time consuming field efforts to identify deep-sea coral habitat in locations that have not been sampled. PHM is not intended and should not be used as a substitute for field surveys via remotely operated vehicles (ROVs), submersibles, and similar instruments. Instead, modeling is one component of a highly integrated process that includes biological surveys, oceanographic data gathering efforts, management and conservation actions, and new exploration and scientific efforts. New data collection and verification of model results generates feedback that allows for the creation of better models (as illustrated by the conceptual model in Figure 1). Recognition of the utility of regional-scale habitat suitability models for deep-sea corals is increasing both in domestic and international waters and the models have become accepted as a useful indicator of vulnerable marine ecosystems.

PHM complements field efforts by facilitating habitat predictions across large regions, and this method can be used to help focus limited resources in areas that have the highest probability of supporting deep-sea coral ecosystems. Predictive habitat models also provide important insights into the environmental conditions controlling deep-sea coral distribution (feedbacks in Figure 1). Threats to deep-sea coral habitats such as climate change and the looming threat of ocean acidification reinforce the need to gain a better understanding of the physical, chemical, and oceanographic conditions that influence deep-sea coral survival.

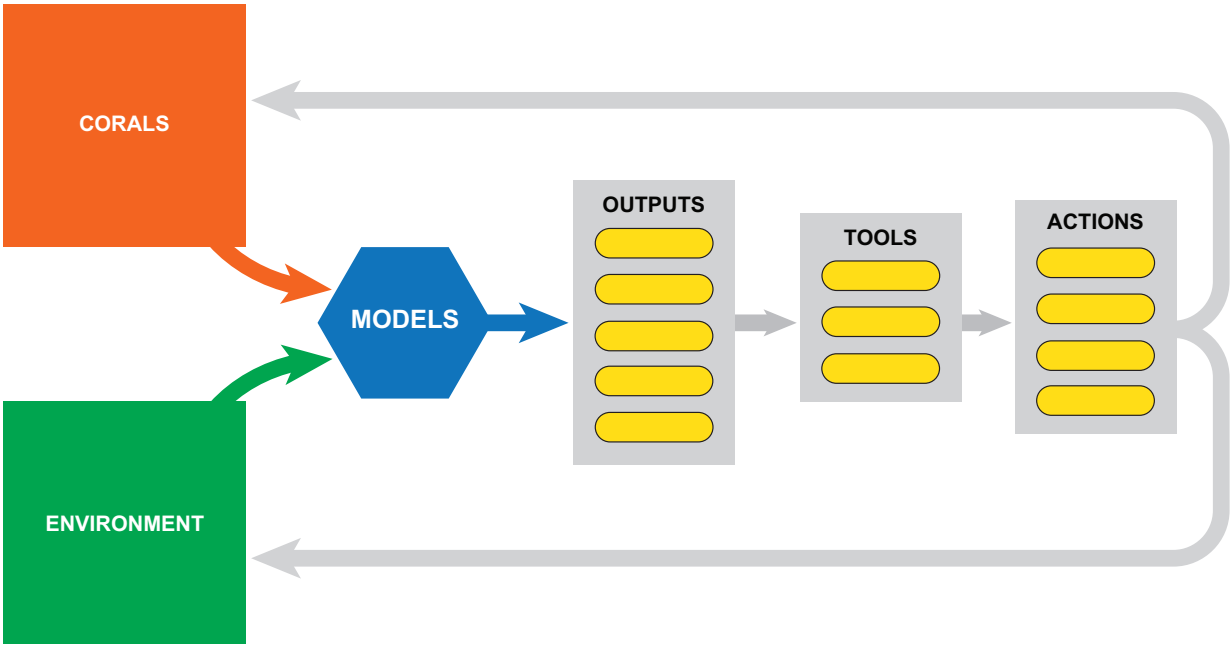

Figure 1. *Conceptual process diagram showing the inputs and outputs of predictive habitat models for deep-sea corals, including feedbacks from model outputs to exploration and scientific efforts that lead to continual improvement in model quality, as well as informed management, conservation, and spatial planning actions.*

In this spotlight we provide an overview of regional-scale modeling efforts in U.S. waters, some of the methods used to determine predicted habitat for deep-sea corals, the utility of these efforts for researchers and resource managers, and the limitations of such models.

Model Methodology

Predictive habitat modeling (often called habitat suitability modeling, ecological niche modeling, or species distribution modeling) integrates the spatial distribution of coral colonies with environmental data (including geomorphology of the seafloor and physical, biological, and chemical variables) to estimate the potential niche and distribution of deep-sea corals.

Most deep-sea coral PHM studies to-date have used "presence-only" approaches, as the vast majority of data on coral distribution consists only of records of presence (occurrence). The range of environmental conditions for known coral locations is used to determine an "environmental envelope" which is then mapped across the entire region, including areas where no sampling has taken place. This process results in an index of relative habitat suitability, typically ranging from 0-1 or 0-100, that predicts the relative likelihood that a given area harbors deep-sea coral habitat. Presence-only modeling approaches that have been commonly used have included maximum entropy modeling (Maxent; e.g., Davies and Guinotte 2011, Rengstorf et al. 2012, Yesson et al. 2012, Rengstorf et al. 2013,

Recent trends in deep-sea coral modeling

1. Predictive habitat modeling for deep-sea corals has increased in the last ten years due to: a) improved resolution and availability of environmental data, b) increased quality and quantity of coral data, c) increased recognition that modeling is a useful and cost-effective means to identify vulnerable benthic habitats and d) increased computational power and the availability of appropriate algorithms and software for predictive habitat modeling.

2. For the first time, global and regional modeling efforts can predict habitat at scales that are biologically relevant as well as practical for resource management (10s of meters to 10s of kilometers).

3. Presence-only modeling approaches (e.g., Maxent, ENFA) have been the most frequently used method to model deep-sea coral habitat at regional scales, but they do not show probability of occurrence. Improved sampling and analysis methods are required to allow for presence/absence models in the deep-sea. The next generation of models should incorporate measures of abundance (e.g., biomass, number of colonies, percent cover), and move beyond presence-absence approaches.

4. Modeling has helped identify important environmental correlates of deep-sea coral distribution, which is useful for forecasting areas where corals are most at risk from climate change and ocean acidification.

Georgian et al. 2014), Ecological-Niche Factor Analysis (ENFA; eg., Leverette and Metaxas 2005, Bryan and Metaxas 2007, Davies et al. 2008, Dolan et al. 2008, Tittensor et al. 2009, Taylor et al. 2013), and Genetic Algorithm for Rule Set Production modeling (GARP; e.g., Guinan et al. 2009, Tong et al. 2013). Of these, Maxent is becoming increasingly common, as it has consistently outperformed other presence-only techniques (Elith et al. 2006, Tittensor et al. 2009, Tong et al. 2013).

Models that incorporate known absences in addition to known presences are being increasingly used to predict deep-sea coral habitats. These "presence/absence" approaches have included Boosted Regression Trees (BRT; Tracey et al. 2011), Generalized Linear Models (GLM; e.g., Woodby et al. 2009), Generalized Additive Models (GAM; e.g., Ross and Howell 2013, Rooper et al. 2014), and logistic regression and Generalized Estimating Equation models (GEE; e.g., Woodby et al. 2009). When both presences and absences are recorded with reasonable certainty, presence/absence models can produce more accurate and therefore, more useful habitat predictions. It is important to note however, that absence data can be misleading in models with coarse spatial resolutions (> 200 m), as it cannot be assumed that coral is absent from a large area unless the entire area has been surveyed. Current sampling methods in the deep-sea often give us confirmation of coral absence in only a small portion of each modeled cell. In addition, absence data may be misleading if the species' distribution is not in equilibrium, if dispersal is limiting, or due to historical artifacts including population losses due to human activities (Hirzel et al. 2002).

Difficulties in determining 'true' absences have led researchers to generate ensemble

models produced by using a combination of presence-only and presence/absence approaches (e.g., GAMs and Maxent; Ross and Howell 2013) to identify potential habitat. In the future, as databases improve, more data on deep-sea coral presence/absence and abundance (e.g., biomass, number of colonies, percent cover) will facilitate more sophisticated models (e.g., Guinan et al. 2009). Models that can predict areas of high abundance or biodiversity hotspots are of particular importance to conservation and resource managers, who must weigh the biological and ecological value of different areas against economic costs associated with their protection (Ardron et al. 2014).

Field survey efforts offer critical support to these improved datasets and help to avoid one of the primary pitfalls of presence-only models: important, undiscovered coral habitats can easily be missed because the presence locations are unlikely to fully represent the range of possible deep coral habitats. Verified absence data should always be preferred over a model prediction of "unsuitable habitat." The collection of georeferenced, verified absence data with broad spatial coverage would greatly reduce sampling bias and help to improve the next generation of models. Yet, due to the time and expense involved, deep-sea field surveys are rarely randomly distributed spatially, introducing sampling bias that will always be an important consideration in the interpretation of model results. The adage by Carl Sagan that "absence of evidence is not the evidence of absence" is especially critical in interpretation of deep-sea field survey data and model outputs (discussed in Etnoyer and Morgan 2007). Habitat suitability models can influence spatial management decisions, so they should be tested for their validity, updated, and improved periodically.

Models also differ in the types of environmental data they use to make predictions. At a minimum, environmental data usually include bathymetry (depth) and statistics derived from bathymetry that characterize the topography of the seafloor, generally referred to as terrain metrics. Other types of environmental variables often included in models are substrate (benthic sediment types and the distribution of hard bottom) and oceanographic data. Oceanographic data encompasses physical variables (e.g., temperature, salinity, and currents), biological variables (e.g., surface productivity and particulate organic carbon flux to the seafloor), and chemical variables (e.g., pH, dissolved oxygen, and carbonate chemistry). The importance of individual environmental variables in determining the distribution of deep-sea corals appears to vary considerably both among taxa and among regions (Table 1).

Seven environmental variables that are consistently strong predictors across regions and taxa include: depth, seafloor geomorphology (slope, curvature, roughness, changes in slope), sediment/substrate type, carbonate chemistry, temperature, salinity, indices of near-bottom current velocity, and food flux to benthic environments. The regional variation in approach and data priority in modeling efforts often depends in part on the types of data are available. For example, carbonate chemistry has been found to be among the most important predictor variables for the global occurrence of both scleractinian reef-forming corals and octocorals (Davies and Guinotte 2011, Yesson et al. 2012), but deep-water carbonate chemistry data are limited or non-existent in many regions. Other variables are proxies for the actual processes driving coral distribution; for example, near-bottom currents are thought

Table 1. *Summary of key features of the regional and global-scale deep-sea coral predictive habitat models discussed in this article, including the taxa modeled, the modeling approach used, the spatial resolution, and the environmental variables used as predictors. Environmental variables that were significant in models are highlighted in bold and italicized. Abbreviations: ENFA=Environmental Niche Factor Analysis, Maxent=Maximum Entropy, GAM=Generalized Additive Models. Variable abbreviations: Chl. a=chlorophyll a, CPI=Chlorophyll Persistence Index, BPI=bathymetric position index, POC=particulate organic carbon, ΩA=aragonite saturation state, ΩC=calcite saturation state TPI=topographic position index, AOU=apparent oxygen utilization, TA=total alkalinity, [CO_3^{2-}]=carbonate ion concentration, DIC=dissolved inorganic carbon, lat./long.=latitude/longitude, TRI=terrain ruggedness index, DO=dissolved oxygen, SL=slope, SL-of-SL=slope of slope, PLC=plan curvature, PRC=profile curvature, LonC=longitudinal curvature, LatC=latitudinal curvature, GC=general curvature, FF=Framework Forming. Variables are at-depth unless otherwise indicated (i.e., surface chlorophyll a, surface primary production, surface turbidity).*

Study	Model	Taxa	Resolution	Terrain	Substrate	Chemical	Physical	Biological
Northeast and Mid-Atlantic U.S.								
Kinlan et al. in press	Maxent	Alcyonacea, Gorgonacea, Pennatulacea, Sessiliflorae, Scleractinia, Caryophylliidae, Flabellidae	370 m	Aspect, ***depth, SL, SL-of-SL, rugosity, PLC***, PRC, BPI	*Mean grain size*, % sand, %mud, %gravel	–	Temperature, *salinity, surface turbidity*, DO	*Surface chl. a*
Bryan and Metaxas 2007	ENFA	Paragorgiidae, Primnoidae	5 km	Depth, *SL*	–	–	*Current velocity, temperature*	*Surface chl. a*
Southeast U.S.								
Davies (unpublished), Mienis et al. 2014	Maxent	*Lophelia pertusa, Madrepora oculata, Enallopsammia profunda, Solenosmillia variabilis, Oculina varicosa*	90 m, 1 km	Depth, SL, rugosity SL-of-SL, PLC, PRC, BPI	–	ΩA, *nitrates*	*Temperature, salinity, DO*	POC
Kinlan et al. 2012a	Maxent	*Lophelia pertusa, Madrepora oculata, Enallopsammia profunda*, FF Scleractinia (exc. *Oculina* spp.), Non-FF Scleractinia, Antipatharia, Stylasteridae, Pennatulacea, Alcyonacea, Gorgonacea, Holaxonia, Calcaxonia	370 m	*Depth*, SL, *SL-of-SL*, aspect, rugosity, *PLC, PRC*, BPI	Mean grain size, % sand, %mud, %gravel	–	*Temperature*, salinity, surface turbidity	*Surface chl. a*
Gulf of Mexico								
Guinotte and Davies (in prep)	Maxent	*Lophelia pertusa, Madrepora oculata, Enallopsammia profunda, Solenosmillia variabilis, Oculina varicosa*	~90 m	*Depth, SL*, rugosity	To be determined	ΩA, ΩC	*Temperature*, salinity, *DO*, surface turbidity	Export POC
Georgian et al. 2014	Maxent	*Lophelia pertusa*	5 m, 25 m	*Depth, SL, roughness, TPI*, LonC, LatC, GC, eastness, northness	*Potential hard-bottom locations from 3D seismic data*	ΩA	–	Export POC
Kinlan et al. 2012b	Maxent	*Lophelia pertusa, Madracis, Madrepora, Bebryce, Callogorgia, Hypnogorgia*, Paramuriceidae, Plexauridae, Isididae, Ellisellidae, Chrysogorgiidae, Antipatharia, Alcyonacea, Gorgonacea, Scleractinia, FF Scleractinia, Non-FF Scleractinia, All FF taxa	370 m	*Depth, SL, SL-of-SL*, aspect, rugosity, PLC, PRC, *BPI*	Mean grain size, % sand, % mud, % gravel, potential hard-bottom locations interpreted from 3D seismic data	–	*Temperature, salinity*, surface turbidity, DO	Surface chl. a
West Coast U.S.								
Guinotte and Davies 2012, 2014	Maxent	Antipatharia, Scleractinia, Alcyoniina, Calcaxonia, Holaxonia, Scleraxonia	500 m	*Depth, SL*	–	ΩA, ΩC, nitrate, phosphate, silicate	*Temperature, salinity*, DO	Export POC
Huff et al. 2013	GAM, GLM	*Antipathes dendrochristos*	90 m	*Depth, SL*, PRC	–	–	*Temperature*, salinity, DO, *current velocity, current direction*	*Surface primary productivity (CPI)*
Bryan and Metaxas 2007	ENFA	Paragorgiidae, Primnoidae	5 km	*Depth, SL*	–	–	Current velocity, temperature	*Surface chl. a*

Study	Model	Taxa	Resolution	Terrain	Substrate	Chemical	Physical	Biological
Alaska								
Guinotte and Davies 2013	Maxent	Alcyoniina, Antipatharia, Calcaxonia, Filifera, Holaxonia, Scleractinia, Scleraxonia, Stolonifera	700 m	*Depth, SL*, rugosity, BPI, PLC, PRC, tangential curvature, aspect, northness, eastness, TRI, TPI, roughness	–	ΩA, ΩC, nitrate, phosphate, silicate	*Temperature, salinity*, DO	Export POC
Bryan and Metaxas 2007	ENFA	Paragorgiidae, Primnoidae	5 km	*Depth, SL*	–	–	*Current velocity, temperature*	*Surface chl. a*
Rooper et al. 2016	GAM	Primnoidae, Stylasteridae, all corals combined, Porifera	100 m (Aleutian Islands), 1km (Bering Sea)	*Depth, SL, rugosity, lat./long.*, aspect	Sediment type	–	Temperature, mean ocean current, *maximum tidal current*	Surface primary productivity
Sigler et al. 2015	GAM	Plexauridae,Primnoidae, Isididae, Paragorgiidae, Antipatharia, Pennatulacea, Porifera	1 km	*Depth, SL, lat./long.*	*Grain size, sediment sorting*	–	*Temperature, current velocity*	*Surface primary productivity*
Hawaii and U.S. Pacific Territories								
Bauer et al. 2016	Maxent	Calcaxonia, Holaxonia, Scleraxonia, gold corals, red and pink corals, black corals, bamboo corals, bubblegum corals, FF and non-FF stony corals, gorgonian and non-gorgonian soft corals	360 m	Depth , SL, SL-of-SL , aspect, rugosity, total curvature , PLC, PRC, BPI, distance to shore , distance to seamounts	–	–	*Temperature* , salinity, turbidity, current velocity, current direction, mixed layer depth	*Surface chl. a*
Global								
Davies and Guinotte 2011	Maxent	FF deep-sea corals (*Enallopsammia rotrata, Goniocorella dumosa, Lophelia pertusa, Madrepora oculata, Solenosmillia variabilis*)	~1 km	***Depth***, SL, rugosity	–	TA, [CO23-], pH, ΩA, ΩC, nitrate, phosphate, silicate, DIC	Regional current flow, vertical flow, ***salinity, temperature***, DO, % oxygen saturation	AOU, surface POC, surface primary productivity, POC export
Yesson et al. in press	Maxent	Antipatharia (Antipathidae, Aphanipathidae, Cladopathidae, Leiopathidae, Myriopathidae, Schizopathidae, Stylopathidae)	1 km	***Curvature, SL***	–	TA	***Temperature***, % oxygen saturation	***Surface chl. a***
Yesson et al. 2012	Maxent	Alcyoniina, Calcaxonia, Holaxonia, Scleraxonia, Sessiliflorae, Stolonifera, Subselliflorae	~1 km	Depth, ***SL***, rugosity	–	TA, [CO23-], pH, ΩA, ***ΩC***, nitrate, phosphate, silicate, DIC	***Temperature***, regional current flow, vertical flow, DO, % ***oxygen saturation, salinity***	POC, ***surface primary productivity***, POC export, AOU
Tittensor et al. 2009	Maxent, ENFA	Scleractinia corals on seamounts	~130 km	Depth	–	TA, ***ΩA, nitrate, phosphate, silicate, total DIC***	Temperature, salinity, ***DO***, regional current velocity, **% oxygen saturation**	***Surface primary productivity***, export POC
Davies et al. 2008	ENFA	*Lophelia pertusa*	0.25°, 1°	***Depth***, aspect, ***SL***	Hydrocarbon seeps and pockmarks, iceberg ploughmarks	TA, ΩA, DIC, ***nitrate, phosphate, silicate***	***Current velocity, temperature, salinity, DO***	***Surface primary productivity***

to be very important determinants of particle flux, coral distribution and abundance (White et al. 2007, Mienis et al. 2012), but data on bottom currents are limited. Terrain metrics may therefore serve as proxies for currents. Moreover, the importance of geomorphological variables such as slope and curvature appears to be highly scale-dependent, with high-resolution multibeam bathymetry often required to reveal fine-scale seafloor features associated with suitable coral habitat. More in situ observation and experimentation, more consistent collection and integration of high-resolution bathymetric and seafloor characterization products, and better data-assimilating deep ocean biophysical and chemical models are necessary to better resolve questions about the primary drivers of deep-sea coral distribution and abundance.

Finally, models vary in the level of spatial and taxonomic detail, or resolution, they convey. The spatial resolution of predictive habitat modeling is often limited by the availability of fine-grained spatial data for environmental variables. For example, the spatial scales of environmental data may be coarse (1,000-10,000 meters resolution) compared to the resolution of multibeam bathymetry available in the same study area (2-40 m resolution, depending on depth). This issue, combined with the reality that high-resolution multibeam does not exist across entire study areas, often leads modelers to predict habitat at coarser resolutions than the multibeam bathymetry. Regional fisheries management councils, conservation organizations, and habitat suitability modelers seek to manage areas larger than the extent of fine-scale data that are available, so such a compromise is necessary. There is a need for more extensive spatial coverage of fine-scale resolution environmental data, and conversely, a need for more habitat suitability studies that operate over smaller extents. Local-scale studies with fine-resolution data allow researchers to incorporate locally important drivers of species distributions, like bottom hardness and local relief. One large boulder, or one meter of vertical relief can make a considerable difference in habitat quality for deep-sea corals and sponges.

Difficulties with species identification can inhibit taxonomic resolution: it is not always possible to model habitat for a single coral species because the observations are recorded at the genus or family level. In many cases, useful models are created by grouping coral species at higher taxonomic levels, ranging from genus to family, suborder, or order. Grouping to high taxonomic levels is often necessary from a practical resource management perspective when managers cannot deal with hundreds of species models. However, careful interpretation and assessment of predictions should be exercised when members of those taxa occupy very different environmental niches (e.g., Quattrini et al. 2013). In other cases, corals may be grouped for modeling by their functional similarity, for example, branching stony corals that form a rigid framework and thus form habitat for fishes and invertebrates (e.g., Dolan et al. 2008).

Below, we review the recent and ongoing predictive habitat modeling efforts in different regions of the U.S.[1], providing a brief overview of the approaches, data, taxa modeled, resolution, results, and management/conservation applications in each region.

[1]There are many fine-scale PHM efforts underway or completed for deep-sea coral habitat for specific sites in U.S. waters. These efforts are not reviewed here.

Predictive Habitat Modeling in U.S. Regions

Northeast and Mid-Atlantic

Over the past 5 years, NOAA's Deep-sea Coral Research and Technology Program has supported development of a geospatial database of known coral presence locations in the Northeast and Mid-Atlantic regions (e.g., Packer et al. 2007, Scanlon et al. 2010, Packer and Dorfman 2012, Packer and Drohan 2012, NOAA 2015). The New England Fishery Management Council has used these locations, in conjunction with primary literature, expert opinion, and geomorphological characteristics of canyons, to help identify and prioritize known and potential areas of deep-sea coral habitat (NEFMC 2012). This constitutes a first step toward predictive modeling and has helped the Council as they consider various alternatives for coral habitat protection.

NOAA scientists also produced a suite of moderate resolution (~370 m) models for multiple deep-sea coral taxonomic groupings in the northeast and Mid-Atlantic region (Kinlan et al. in press; Figures 2 and 3). The inclusion of multiple spatial scales was designed to capture biologically-relevant features ranging from relatively fine-scale topography, the presence of deep-water canyons, and the continental shelf break. Maxent models were constructed using presence-only data and environmental variables including depth, terrain metrics calculated at multiple spatial scales (slope, slope-of-slope, rugosity, plan curvature, profile curvature, and bathymetric position index), substrate (mean grain size and percent sand/mud/gravel of benthic sediments), and physical (bottom temperature, salinity, and surface turbidity), biological (surface chlorophyll-*a*), and chemical (dissolved oxygen) oceanographic variables.

In order to improve model parsimony while maintaining predictive power, a stepwise model selection process was employed to reduce the final number of environmental variables included in the models by removing the most redundant variable remaining at each step. The model runs from the model selection process were ranked from best to worst by model performance and by model complexity, and the model run with the best average rank was selected as the final model. To generate model predictions in a format that can be directly compared across taxonomic groups and regions, Maxent outputs were classified into habitat suitability likelihood classes using breakpoints corresponding to ratios of the cost for false positive errors versus the cost for false negative errors.

Three major taxonomic groups were modeled: stony corals (order Scleractinia), sea pens (order Pennatulacea), and other octocorals (orders Alcyonacea and Gorgonacea combined). For each major taxonomic group, two subgroups were also considered based on suborder or family-level taxonomy. The Gorgonacea subgroup incorporates most of the potential habitat-forming species in this region (Packer et al., Chapter 9 in this volume, see Figure 1).

The models predicted extensive areas of potential habitat on the continental slope for all major taxonomic groups and subgroups modeled. Highest suitability values were concentrated in submarine canyon areas at depths of 300-2000 m. Results were used to identify several unexplored potential hotspots of deep coral habitat suitability in the Mid-Atlantic and New England canyons, and subsequent ground-truthing cruises from 2012-2015 aboard the NOAA Ship Henry B. Bigelow and the NOAA Ship Okeanos Explorer (Nizinski and Shank 2012, NOAA OER, 2013, 2014, NRDC 2014, Quattrini et

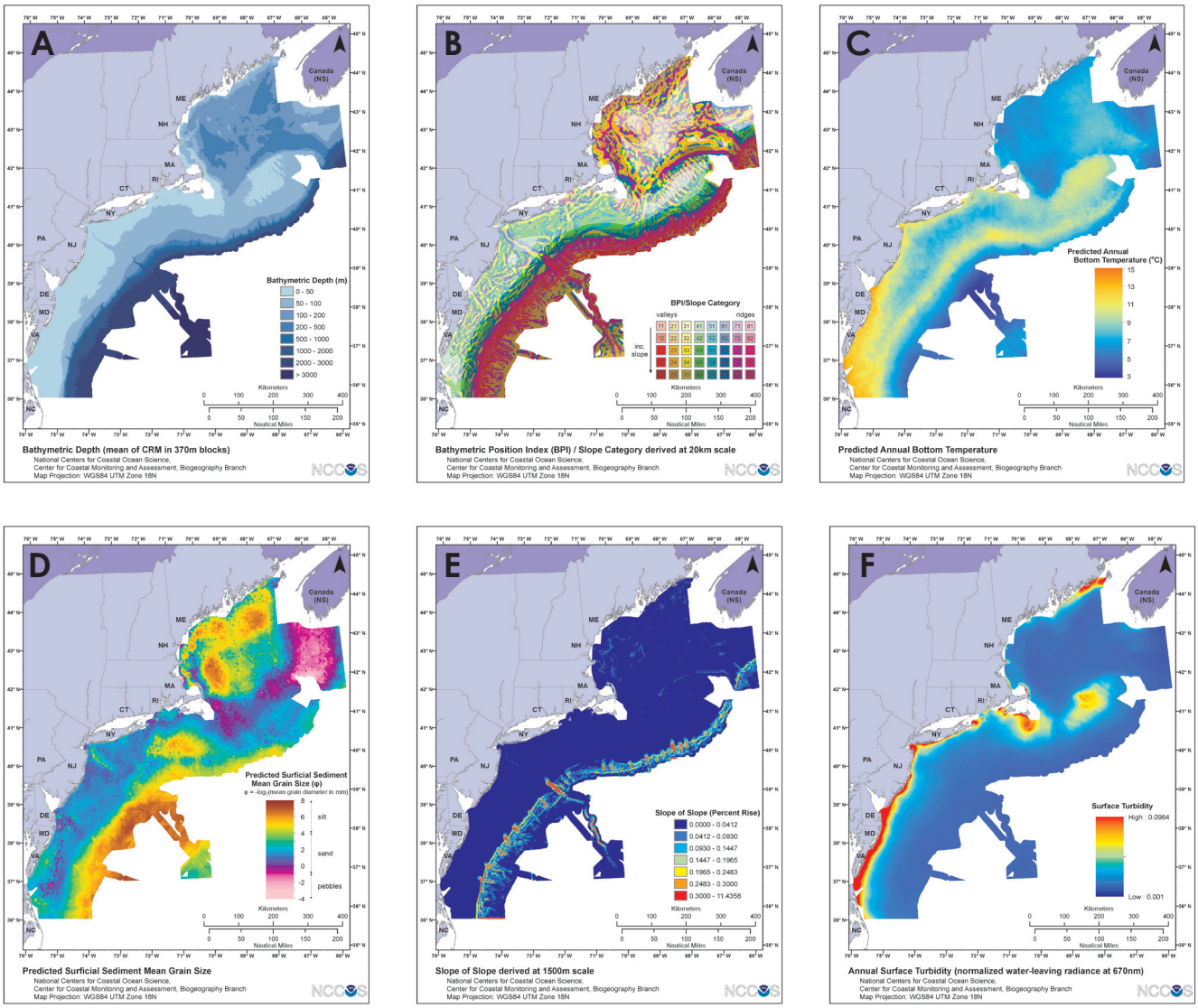

Figure 2. *Environmental layers used in the creation of Maxent deep-sea coral predictive habitat models for the Northeast U.S. region. A) bathymetric depth, B) bathymetric position index (BPI) calculated at a 20 km scale, C) predicted annual bottom temperature, D) predicted surficial sediment mean grain size, E) slope, F) surface turbidity.*

al. 2015) confirmed the existence of these hotspots (e.g., Figure 3). Efforts are underway to improve the resolution and accuracy of this model using coral data collected during these field efforts and multibeam bathymetry collected as part of the Atlantic Canyons Undersea Mapping Expeditions (ACUMEN) project (NOAA OER 2012), in a direct application of the process model illustrated in Figure 1.

Predictive habitat modeling helped guide BOEM-funded field surveys of canyons in the Mid-Atlantic region in 2012 (Ross and Brooke 2012). Using archived historical observations from surveys in the 1980s in conjunction with modern state-of-the-art multibeam, areas of potential hard ground and coral habitat were modeled from a suite of terrain and environmental variables within Mid-Atlantic canyons using the Maxent approach. This

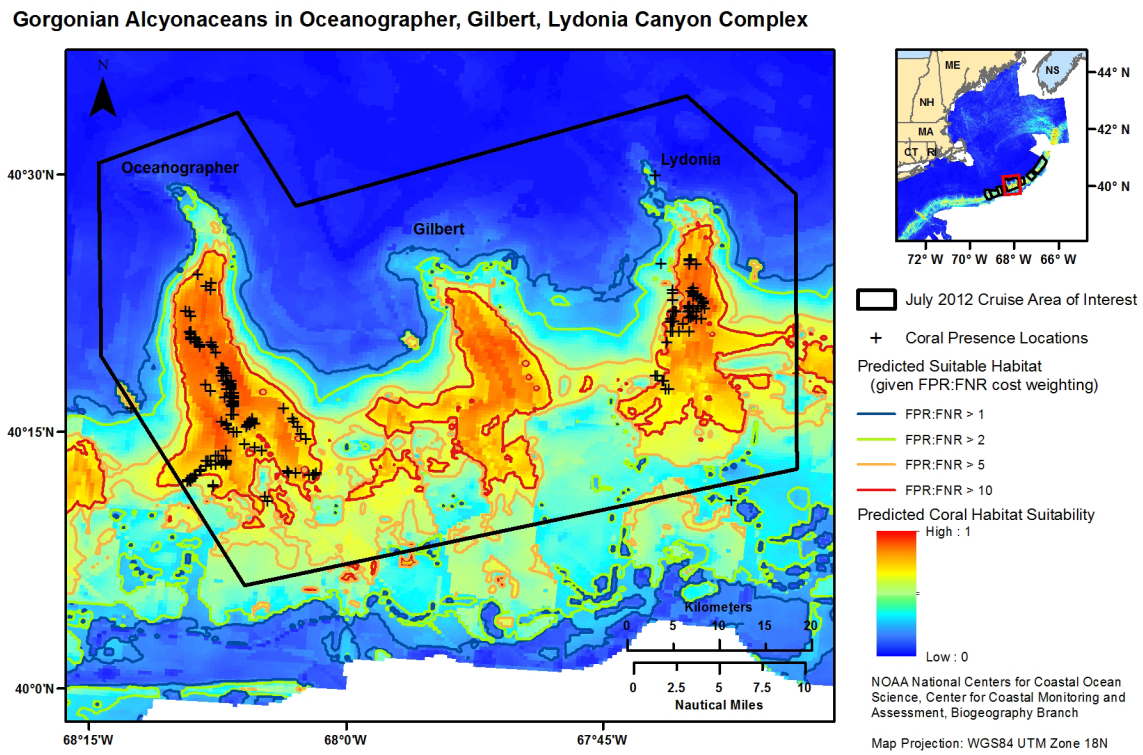

Figure 3 *Maxent predictive habitat model for Gorgonian Alcyonaceans in the Oceanographer, Gilbert, and Lydonia Canyon Complex in the Northeast U.S. region. Black crosses indicate locations of known coral locations discovered during a 2012 ground-truthing cruise aboard the NOAA Ship Henry B. Bigelow (Nizinski and Shank 2012). FPR=False positive rate. FNR=false negative rate.*

approach highlighted the value of local-scale, high-resolution models in guiding and focusing research effort within a clearly defined area whilst utilizing past observations. The models have been validated in the field and visual observations collected during 2012 cruises will be used to enhance the local-scale model.

All of the models described will continue to be developed and refined, however they have already played a seminal role in regional fishery management. In 2015, the Mid-Atlantic Fishery Management Council (MAFMC 2015) recommended establishment of "deep-sea coral zones" to protect deep-sea corals from the impacts of bottom-tending fishing gear. This fishery management plan amendment was recently approved by the National Marine Fisheries Service, and will protect over 98,000 km^2 of habitat in canyons and deep-water areas where corals have been observed or where they were predicted to occur based on NOAA Maxent models. This was among the first explicit examples of deep-sea coral predictive habitat models playing a major role in U.S. fishery management conservation decisions, confirming the utility of PHM for future conservation and management efforts. The New England Fishery Management Council is expected to use similar approaches in a planned deep-sea coral amendment.

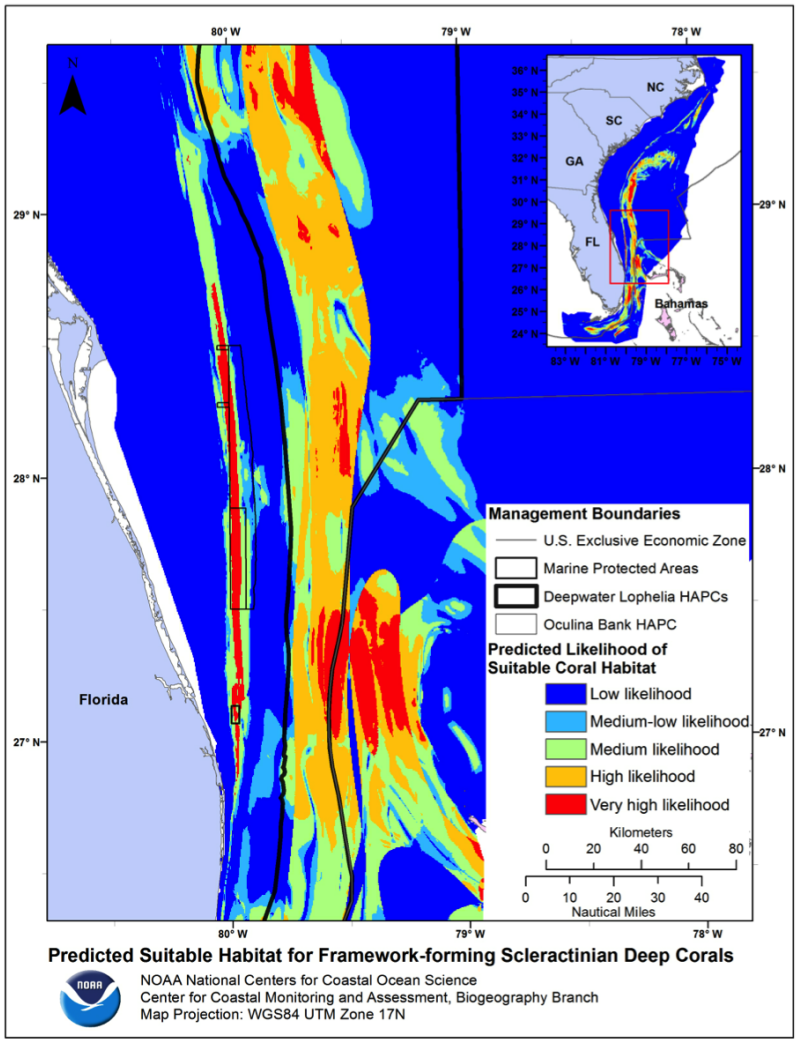

Figure 4. *Maxent predictive habitat model for all framework-forming Scleractinian deep-sea corals in a subset of the U.S. Southeast Atlantic. Warmer colors indicate greater likelihood of suitable habitat, determined by a cross-validation method that determined likelihood thresholds using the ratio of false positive to false negative classification results when the model was tested on data left out of the fitting process (see Kinlan et al. 2012b and David et al., this volume for details).*

Southeast

In 2009, Davies (unpublished) created the first Maxent predictive habitat model in the Southeast U.S. Atlantic region for framework-forming scleractinian corals (including records for *Lophelia pertusa*, *Madrepora oculata*, *Enallopsammia profunda*, *Solenosmilia variabilis* and *Oculina varicosa)*. Environmental variables were created following procedures later described in Davies and Guinotte (2011) using the highest resolution bathymetry available including the National Geophysical Data Center's Coastal Relief Model at 3 arc second (~90 meter) resolution and global bathymetry available at 30 arc second (~1 km) resolution (Becker et al. 2009). Relevant environmental layers were selected for the model, including omega aragonite (Orr et al. 2005), depth (Becker et al. 2009), dissolved oxygen (Garcia et al. 2006), salinity (Boyer et al. 2009), nitrate concentrations (Garcia et al. 2006), temperature (Boyer et al. 2009) and rugosity (Wilson et al. 2007). Model results from this effort were overlaid with existing fishery closures to identify areas with high habitat suitability that remain at risk from destructive fishing practices.

In 2012, NOAA produced a set of 370 meter resolution regional predictive habitat models for deep-sea coral taxonomic groups in the

Southeast U.S. (Kinlan et al. 2012a). Example outputs from this model are shown in Figure 4 and in Hourigan et al. (Chapter 13 in this volume, see Figure 3). Using a similar approach to that employed in the Northeast region, Maxent models were constructed using presence-only data and environmental variables selected from a set of candidate predictors. A total of 14 taxonomic groups were modeled, including three important species of framework-forming stony corals (*Lophelia pertusa*, *Madrepora oculata*, and *Enallopsammia profunda*), an important framework-forming genus (*Oculina* spp.), all framework-forming stony corals as a group (Figure 4), non-framework-forming stony corals, black corals, lace corals, sea pens, gorgonian and non-gorgonian soft corals, and two suborders of gorgonian soft corals (Holaxonia, Calcaxonia). The models predicted extensive areas of potential framework-forming deep coral habitat, concentrated at depths of 100-1000 m. Results confirmed that existing coral protection areas covered the majority of likely framework-forming deep coral habitat (Figure 4). The models were provided to the South Atlantic Fishery Management Council to support discussions of Ecosystem Based Management measures including a recent amendment to the Fishery Management Plan for Coral, Coral Reef, and Live/Hardbottom Habitats in the South Atlantic Region (SAFMC 2013).

The two Southeast models highlight the issue that model results can vary considerably in both the extent of highly suitable habitat and in the suitability scores of individual grid cells, even when similar modeling methods are used (i.e., Maxent). Predictor variables used as input in the models are likely responsible for these differences (e.g., seafloor substrate type), but the coral records used to determine the environmental niche also play an important role in determining final model results. Multiple independent modeling efforts are useful because they can highlight areas of high certainty (where multiple models agree), reveal sensitivity of model predictions to different assumptions, methods, and input data, and improve future model iterations. Determination of which model(s) more accurately predicts reality can only be accomplished through field validation efforts.

Gulf of Mexico

Marine Conservation Institute and Bangor University are currently developing Maxent models for both deep-sea and mesophotic coral habitat in the Gulf of Mexico. The spatial resolution of model results is based on the National Geophysical Data Center's Coastal Relief Model at 3 arc second (~90 meter) resolution. Modeling methods are similar to the approach used in the Southeast U.S, U.S. West Coast, and Alaska. The objectives of this work are to identify both deep-sea and mesophotic reef habitat that are not currently under protection from human activity including oil and gas production/accidents, bottom trawling, and climate change.

The Gulf of Mexico presents unique challenges and opportunities for predictive coral habitat modeling. High-resolution seismic data that can be used to detect potential hard-bottom patches are lacking in most of the U.S. Exclusive Economic Zone (EEZ), but this is not the case in the Gulf of Mexico due to a long history of oil and gas exploration in the region. Extensive 3D seismic surveys conducted over several decades in large areas of the Gulf have recently been interpreted to provide high-resolution information on potential hardground areas that are helping to improve predictions of coral habitat suitability (Boland et al., this volume).

In 2012, scientists at NOAA applied the Maxent modeling approach used in the Northeast and Southeast regions to develop moderate spatial resolution (370 meter) regional models for deep-sea coral taxonomic groups in the northern Gulf of Mexico (Kinlan et al. 2012b). Maxent models were constructed using presence-only data and environmental variables selected from a suite of terrain, substrate (including potential hardground locations), and physical and biological oceanographic variables. Taxonomic groups similar to those used in the Southeast region were used for modeling, with an emphasis on predictions of key framework-forming species. This work has already been used in targeting exploration surveys and is expected to contribute to efforts at habitat protection, spatial planning, and fishery management in the Gulf of Mexico.

In 2014, Georgian et al. developed high-resolution (25 m) Maxent models predicting the distribution of *Lophelia pertusa* across a large region of the northern Gulf of Mexico. The authors used a suite of 11 environmental variables including depth, a number of terrain metrics, omega aragonite, substrate type, and export productivity. Substrate type consisted of potential hardground areas developed by the Bureau of Ocean Energy Management (Boland et al., this volume) and was highly predictive of *L. pertusa* distribution, demonstrating the utility of these type of data for future PHM efforts. The model was tested during a field survey aboard EV Nautilus by Ocean Exploration Trust in 2013 and successfully predicted the location of two large *L. pertusa* mounds.

U.S. Caribbean

There have been no predictive habitat models for deep-sea corals in the U.S. Caribbean (Puerto Rico, U.S. Virgin Islands, and Navassa Island), despite their relatively high diversity in the region (Cairns 1979, 2007). While several global-scale modeling efforts have included parts of the Caribbean (e.g., Tittensor et al. 2009, Davies and Guinotte 2011), there is an urgent need to better characterize the distribution of cold-water corals throughout the region.

West Coast (Washington, Oregon, California)

Bryan and Metaxas (2007) published the first predictive habitat models for deep-sea corals (Families Paragorgiidae and Primnoidae) for the West Coast and Alaska. Four years later, in 2011, predictive habitat models were developed for six taxonomic groups of deep-sea corals (Orders Antipatharia and Scleractinia, Suborders Alcyoniina, Calcaxonia, Holaxonia and Scleraxonia) in the waters of Washington, Oregon and California (Guinotte and Davies 2012, 2014). The objectives of this effort were to: 1) aid future research and mapping efforts for deep-sea coral habitats, 2) Assess potential coral habitat suitability both within and outside existing bottom trawl closures (e.g., to inform designation and protection of essential fish habitat – EFH), and 3) identify suitable habitat in and around the region's six National Marine Sanctuaries. Maxent was used to model deep-sea coral habitat at a 500 m spatial resolution using coral records collected from a variety of sources and a regional database of 30 physical, chemical and environmental variables. Figure 5 shows

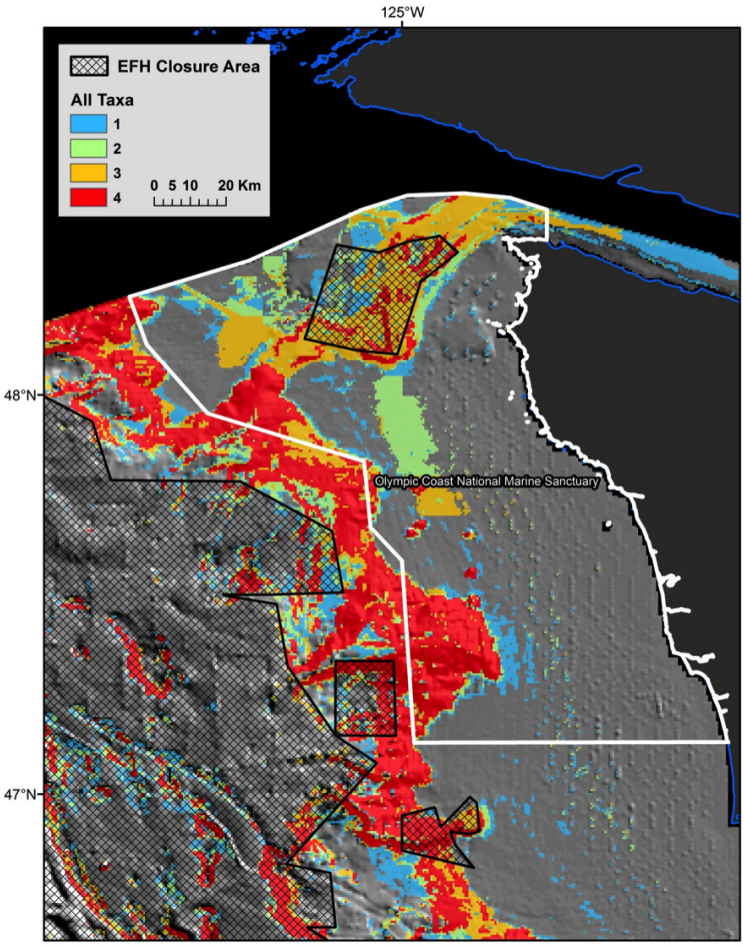

Figure 5. *Maxent predictive habitat model for all taxa (Orders: Antipatharia and Scleractinia; Suborders: Alcyoniina, Calcaxonia, Holaxonia, and Scleraxonia) for the Olympic Coast National Marine Sanctuary. Warmer colors indicate greater likelihood of suitable habitat across all taxa modeled (see Guinotte and Davies 2012 for details on likelihood). Hatched areas are existing trawl closures (EFH).*

the model results for Washington waters with overlays of existing fishing closures and the Olympic Coast National Marine Sanctuary. These modeling results will be used to assess gaps in protection afforded by existing fishery management closures through the Pacific Fishery Management Council's periodic review of essential fish habitat (Huff et al. 2013; Guinotte and Davies, 2014).

Alaska

Several regional-scale predictive habitat-modeling efforts have been conducted or are currently underway for deep-sea coral and sponge habitats in Alaskan waters. Guinotte and Davies (2013) developed Maxent models for the Alaska EEZ at a spatial resolution of ~700 m using 30 environmental, physical, and chemical predictor variables. Models at the Suborder and Order levels revealed that the majority of predicted suitable habitat for gorgonians and lace corals (Suborder Filifera) occurs in the Aleutian Islands, and to a lesser extent the eastern Bering Slope, Gulf of Alaska seamounts, and the Fjord region and shelf break of Southeast Alaska. Soft corals (Suborders Alcyoniina and Stolonifera) additionally had predicted suitable habitat on the eastern Bering Sea Shelf. Guinotte and Davies (2013) also modeled a complex habitat type, coral and sponge "gardens" (Stone and Shotwell 2007) in the Aleutian Islands. While some coral and sponge gardens are currently protected from bottom-contact fishing, other areas of predicted suitable habitat remain open to such fishing. Results from

this modeling effort will be combined with new information on the skeletal mineralogy of Alaska's deep-sea corals (Stone et al. in prep.) and predicted changes in carbonate chemistry through 2100 to produce a spatially explicit ocean acidification risk assessment for Alaska's coral resources.

NOAA's Alaska Fisheries Science Center has also developed generalized additive models (GAMs) for coral and sponge habitat in Alaska that utilizes data from bottom trawl surveys. Rooper et al. (2014) presented models that predicted presence or absence, abundance, and family diversity of corals and sponges (as opposed to presence-only models) for the Aleutian Islands. The predictor variables included remotely-sensed data, predictions from oceanographic models, and location-specific data collected during trawl surveys. The PHM objective is to develop and parameterize a spatially explicit model to predict coral and sponge presence, abundance, and diversity at 100 m spatial resolution for the Aleutian Islands. Field validation surveys using towed camera systems and a stratified-random station selection were conducted in 2012-2014 and data are in the process of being analyzed. Similar models based on bottom trawl survey data have also been produced for corals and sponges in the Gulf of Alaska (Rooper et al. in prep.). These models will be ground truthed using available underwater image data.

Using catches from trawl surveys and similar GAM techniques, Sigler et al. (2015) developed models of coral (excluding Pennatulacea), sea whip (Pennatulacea), and sponge distribution for the outer shelf and slope of the eastern Bering Sea. In 2014, randomized camera surveys were conducted to verify these distribution models (Rooper et al. 2016). Coral densities were low, but the model based on trawl survey data was generally reliable for predicting coral presence or absence in the camera survey. The bottom trawl survey models were also successfully predicted sponge and sea whip presence or absence, but to a lesser degree than for coral. Presence or absence models of corals, sponges and sea whips were also constructed from the camera survey data. Combining these models with the distribution models constructed from bottom trawl survey data predicted the distribution of corals, sponges, and sea whips with better accuracy than the individual models did during cross-validation. These models and associated data are being used by the North Pacific Fishery Management Council in deliberations on potential additional habitat protections in the Eastern Bering Sea.

Hawaii and U.S. Pacific Territories

In 2015, scientists at NOAA National Centers for Coastal Ocean Science applied the same Maxent modeling approach used in the Northeast, Southeast, and Gulf of Mexico to develop moderate resolution (360 meter) regional models for deep-sea coral taxonomic groups in the Main Hawaiian Islands (Bauer et al. 2016). Maxent models were constructed using presence-only data and a suite of environmental variables including depth, terrain metrics calculated at multiple spatial scales, proximity to seamounts, and physical and biological oceanography. A total of 16 taxonomic groups were modeled, including gold corals, red and pink corals, black corals (separated into distinct groups by depth), bamboo corals, bubblegum corals, framework-forming and non-framework-forming stony corals, gorgonian and non-gorgonian soft corals, three suborders of gorgonian soft corals (Calcaxonia, Holaxonia, Scleraxonia), and sea pens (separated into distinct groups by substrate). In addition, models were

constructed to predict high diversity areas likely to support ≥4 and ≥7 genera of deep-sea corals. For many of the taxonomic groups, predictions of potential habitat were driven by depth. These models were part of a comprehensive marine biogeographic assessment to provide data products to inform the Bureau of Ocean Energy Management's renewable energy policy decisions in Hawaii.

While there are many records of coral occurrence in the Hawaiian archipelago, information from other U.S. Pacific Territories is sparse (Parrish et al. Chapter 7, this volume). The only modeling results for these areas are from global-scale efforts for 6 species of scleractinian reef formers (Davies and Guinotte 2011) and octocorals (suborders Alcyoniina, Calcaxonia, Holaxonia, Scleraxonia, Sessiliflorae, Stolonifera, and Subselliflorae (Yesson et al. 2012). Both efforts modeled deep-sea coral habitat at a ~1 km spatial resolution using Maxent, global databases for coral locations, and 30 environmental, physical and chemical predictor variables.

Application of Predictive Habitat Models to Fishery Management

In addition to helping researchers identify areas where coral habitat is most likely to be found, modeling results can be used in conjunction with existing fisheries management boundaries to help resource managers identify areas where potential deep-sea coral habitat remains at risk from human activity. Figure 5 shows the predicted distribution of several taxa of deep-sea corals and existing areas closed to bottom trawls to protect essential fish habitat for groundfish off Washington (Guinotte and Davies 2012, 2014).

Commercial fishing using bottom-contact gear is a common practice in most U.S. regions, but field surveys for deep-sea corals are limited by the expense and extent of area that can be surveyed. Predictive habitat modeling represents a potential cost-effective means to fill these gaps.

Modeling results can also be overlaid with coral bycatch maps to test the accuracy of model results. However, this type of comparison can give conflicting results when commercial fishers actively avoid high-relief areas (most likely to harbor most deep-sea corals) in order to minimize gear damage and/or loss. Modeling results can and should be incorporated into U.S. regional Fishery Management Councils' fisheries review processes to help determine areas where additional management measures may be warranted or where existing boundaries need to be amended.

For example, regional PHM results in the Southeast U.S. Atlantic contributed to discussions of alternatives in the development of the SAFMC's Coral Amendment 8 to the Fishery Management Plan for Coral, Coral Reef, and Live/Hardbottom Habitats in the South Atlantic Region, which resulted in both the expansion of some Habitat Area of Particular Concern (HAPC) boundaries (Figure 4) to capture more high-likelihood coral habitat and opening up some flat bottom areas of low likelihood to support coral habitat (SAFMC 2013). In 2015, the Mid-Atlantic Fishery Management Council approved the closure of 15 submarine canyon and slope areas to almost all bottom-contact fishing gear specifically to protect deep-sea coral habitats (MAFMC 2015). The results of the NOAA deep-sea coral PHM were included in the closure proposal and specifically used in the identification of boundaries for these discrete

areas. Decisions like these are difficult to make based on spatially limited field sampling efforts alone; comprehensive regional maps of habitat suitability produced by PHM can greatly assist in developing and prioritizing spatial boundaries. Similar discussions are underway to varying degrees in other Fishery Management Councils, including the New England, Pacific and North Pacific Councils, and PHM results are likely to be a useful tool for shaping and evaluating alternative spatial management and conservation measures in these regions.

Limitations of Predictive Habitat Modeling Results

There are several limitations to predictive habitat modeling. Many of the variables that are important for coral settlement, growth and survival cannot be incorporated into the models because data on these variables do not exist at sufficient resolutions or are limited in geographic extent. This is particularly true for data on high-resolution current direction/velocity, water-column data (e.g., turbidity, temperature, salinity, saturation state), and benthic substrate type (Davies and Guinotte 2011). These variables, particularly hard substrata, can be patchy at small scales, and these alone may determine whether or not deep-sea corals inhabit a given location. In addition to predictor variables, there are limitations with the coral records used in models. The taxonomy of deep-sea coral records can be highly uncertain. This is particularly true for deep-sea coral records obtained from video and/or images when no specimens were collected for expert examination. Coral records obtained from trawl/bycatch surveys have inherent spatial errors associated with them as trawls can be several kilometers in length and precise georeferencing can be difficult depending on the technology used.

Perhaps the most important question that arises pertains to the accuracy of these models for deep-sea corals. The preferred method to assess model accuracy is to perform robust field validation surveys to assess model performance. Field validation efforts must be conducted to assess the accuracy of the models, enable model refinement, and gauge the utility of these methods for determining deep-sea coral habitat in unsurveyed areas, as illustrated in Figure 1. Rooper et al. (2016) demonstrated a systematic field validation for a U.S. deep-sea coral predictive habitat model for the Eastern Bering Sea, and similar efforts are currently underway in the Aleutian Islands, Gulf of Mexico and Northeast U.S. Field validation of models should be integrated into the cruise plans of existing/future NOAA deep-sea exploration and research. These surveys should record both georeferenced locations of coral presence (identified to the best taxonomic resolution possible) as well as locations of areas where corals have been confirmed to be absent. They should also be appropriately stratified so that areas predicted to have low, intermediate, and high habitat suitability are sampled adequately to support model calibration and validation. These accuracy assessments will guide refinement of future deep-sea coral predictive habitat modeling efforts, and also shape the appropriate use of such models for conservation and management purposes. If field validation is not possible, cross-validation methods can be used to aid in the assessment of predictive model results (e.g., Huff et al. 2013)

Conclusions and Recommendations

Predictive habitat modeling is increasingly used to help identify areas that are most likely to harbor deep-sea coral taxa. The growth and adoption of these techniques in most U.S. regions are primarily due to improvements in input data quality/quantity, the low cost of producing the models, and the need to identify habitat across large spatial extents for management. The spatial resolution of model results has improved in the last five years to the point where model outputs can be used to aid management decisions, and this is also spurring an increase in their development and subsequent use. Some of the regional examples reviewed here have been used to help target areas for field sampling efforts and others have been used to help inform U.S. regional Fishery Management Councils' EFH/HAPC review processes. High-resolution substrate data (e.g. backscatter, side scan sonar) can be used in conjunction with model results to identify areas with the highest probability of finding deep-sea corals, but the limited availability of substrate data at regional scales continues to hinder the accuracy of predictive habitat models. Model results tend to over predict suitable deep-sea coral habitat in many regions due to the absence of high-quality substrate data and this issue will likely persist as the distribution substrate is highly variable over small spatial scales.

Acknowledgments

Marine Conservation Institute and Bangor University would like to thank the Ittleson Foundation, Oak Foundation, NOAA's Deep-Sea Coral Research & Technology Program, and ESRI's Conservation Program for providing funding and software support for

Recommendations to NOAA Deep-Sea Coral Research & Technology Program:

1. Encourage all Program funded cruises to provide presence *and* absence data at relevant spatial scales to help validate and improve predictive habitat models.
2. Develop and improve the publicly available national database of coral occurrences and absences for the U.S. EEZ, including in situ environmental data where possible.
3. Support the development of a publicly available database for high-resolution substrate data for the U.S. EEZ.
4. Ensure that the modeling results funded by the Program are incorporated into U.S. regional Fishery Management Councils' EFH/HAPC reviews and other relevant Council processes.
5. Provide support to make the best regional predictive habitat model maps broadly available to the public and federal agencies for marine spatial planning purposes.
6. Convene regular working groups to compare and synthesize the results of modeling efforts in each region. Multiple modeling efforts lead to more robust understanding, but require expert review, comparison, and synthesis to identify strengths and weaknesses of different approaches as well as areas of consensus and disagreement among models.
7. Ensure that field surveys, habitat modeling, and management efforts are efficiently integrated to take advantage of the feedback loops illustrated in Figure 1.
8. Improve mapping and modeling of real and potential human impacts and integrate these maps with deep-sea coral PHM to identify and prioritize high risk areas.

modeling efforts. We also would like to thank Bob Stone and Chris Rooper for their input on Alaskan modeling efforts. BPK would like to thank Matt Poti, Chris Caldow, Dave Packer, Martha Nizinski, Amy Drohan, Richard Langton, Vincent Guida, Peter Etnoyer, Andrew David, Thomas Hourigan, Gregory Boland, William Shedd, James Sinclair, Christopher Jenkins, and Laughlin Siceloff for helpful discussions, data and technical assistance. BPK was supported under NOAA Contract No. DG133C07NC0616 with Consolidated Safety Services, Inc.

References

Ardron JA, Clark MR, Penney AJ, Hourigan TF, Rowden AA, Dunstan PK, Watling L, Shank TM, Tracey DM, Dunn MR, Parker SJ (2014) A systematic approach towards the identification and protection of vulnerable marine ecosystems. Marine Policy 49:146–154

Bauer L, Poti M, Costa B, Wagner D, Parrish F, Donovan M, Kinlan B (2016) Chapter 3: Benthic Habitats and Corals. In: Costa B, Kendall MS (eds.). Marine Biogeographic Assessment of the Main Hawaiian Islands. OCS Study BOEM XXXX-XX and NOAA Technical Memorandum NOS NCCOS, p XXX–XXX

Becker JJ, Sandwell DT, Smith WHF, Braud J, Binder B, Depner J, Fabre D, Factor J, Ingalls S, Kim SH (2009) Global Bathymetry and Elevation Data at 30 Arc Seconds Resolution: SRTM30_PLUS. Marine Geodesy 32:355–371

Boyer TP, Antonov JI, Baranova OK, HE, Johnson DR, Locarnini RA, Mishonov AV, O'Brien TD, Seidov D, Smolyar IV, Zweng MM (2009) World Ocean Database 2009. In: Levitus S (ed) NOAA Atlas NESDIS 66, U.S. Government Printing Office, Washington, D.C., 216 pp., DVDs.

Bryan TL, Metaxas A (2007) Predicting suitable habitat for deep-water coral in the families Paragorgiidae and Primnoidae on the Atlantic and Pacific continental margins of North America. Marine Ecology Progress Series 330:113–126

Cairns SD (1979) The deep-water Scleractinia of the Caribbean and adjacent waters. Studies on the fauna of Curaçao and other Caribbean Islands 57:1–341

Cairns SD (2007) Deep-water corals: an overview with special reference to diversity and distribution of deep-water scleractinian corals. Bulletin of Marine Science 81(3):311–22

Davies A, Guinotte JM (2011) Global habitat suitability for framework-forming cold-water corals. PLoS ONE 6(4):e18483

Davies AJ, Wisshak M, Orr JC, Roberts JM (2008) Predicting suitable habitat for the cold-water reef framework-forming coral *Lophelia pertusa* (Scleractinia). Deep-Sea Res Part I 55:1048–1062

Dolan MFJ, Grehan AJ, Guinan JC, Brown C (2008) Modelling the local distribution of cold-water corals in relation to bathymetric variables: adding spatial context to deep-sea video data. Deep-Sea Res Part I 55:1564–1579

Elith J, Graham CH, Anderson RP and others (2006) Novel methods improve prediction of species' distributions from occurrence data. Ecography 29:129–151

Etnoyer P, Morgan LE. (2007) Predictive habitat model for deep gorgonians needs better resolution: comment on Bryan & Metaxas (2007). Mar Ecol Prog Ser 339:311–2

Garcia HE, Locarnini RA, Boyer TP, Antonov JI (2006) World Ocean Atlas 2005, Volume 3: Dissolved Oxygen, Apparent Oxygen Utilization, and Oxygen Saturation. In: Levitus S (ed) NOAA Atlas NESDIS 63, U.S. Government Printing Office, Washington, D.C., 342 pp.

Garcia HE, Locarnini RA, Boyer TP, Antonov JI (2006) World Ocean Atlas 2005, Volume 4: Nutrients (phosphate, nitrate, silicate). In: Levitus S (ed) NOAA Atlas NESDIS 64, U.S. Government Printing Office, Washington, D.C., 396 pp.

Georgian SE, Shedd W, Cordes EE (2014) High-resolution ecological niche modelling of the cold-water coral *Lophelia pertusa* in the Gulf of Mexico. Mar Ecol Prog Ser 506:145–161

Guinan J, Grehan AJ, Dolan MFJ, Brown C (2009) Quantifying relationships between video observations of cold-water coral cover and seafloor features in Rockall Trough, west of Ireland. Mar Ecol Prog Ser 375: 125–138

Guinotte, JM, Davies AJ (2012) Predicted deep-sea coral habitat suitability for the U.S. West Coast. Report to NOAA/NMFS. 85 pp.

Guinotte JM, Davies AJ (2013) Predicted deep-sea coral habitat suitability for Alaskan waters. Report to NOAA/NMFS. 22 pp. Available at: http://docs.lib.noaa.gov/noaa_documents/CoRIS/deep-sea_coral-habitat-Alaska_2013.pdf

Guinotte JM, Davies AJ (2014) Predicted deep-sea coral habitat suitability for the U.S. West Coast. PLoS One. 9(4):e93918, doi:10.1371/journal.pone.0093918

Hirzel H, Hausser J, Chessel D, Perrin N (2002) Ecological-niche factor analysis: how to compute habitat-suitability maps without absence data? Ecology 83: 2027–2036.

Huff DD, Yoklavich MM, Love MS, Watters DL, Chai F, Lindley ST (2013) Environmental factors that influence the distribution, size, and biotic relationships of the Christmas tree coral *Antipathes dendrochristos* in the Southern California Bight. Mar Ecol Prog Ser 494:159–17

Kinlan BP, Poti M, Drohan A, Packer DB, Nizinski M, Dorfman D, Langton R (in press) Predictive model of deep-sea coral habitat suitability in the U.S. Northeast and Mid-Atlantic regions. Deep-Sea Res Part I

Kinlan BP, Poti M, Hourigan T, Dorfman D (2012a) Predictive model of deep-sea coral habitat suitability in the U.S. Southeast region. Presented at NOAA Deep-Sea Coral Research & Technology Program Southeast Deep-Sea Coral Fieldwork Wrap-Up Workshop, 18-19 September 2012, Charleston, SC. Author email: Brian.Kinlan@NOAA.gov

Kinlan BP, Poti M, Etnoyer P, Siceloff L, Jenkins C (2012b) Predictive model of deep-sea coral habitat suitability in the northern Gulf of Mexico. NOAA National Centers for Coastal Ocean Science. Project in progress. Information available at: http://coastalscience.noaa.gov/

Leverette TL, Metaxas A (2005) Predicting habitat for two species of deep-water coral on the Canadian Atlantic continental shelf and slope. In: Freiwald A, Roberts JM (eds) Cold-water Corals and Ecosystems. Berlin Heidelberg: Springer-Verlag, p 467–479

Mid-Atlantic Fishery Management Council (MAFMC) (2015) Deep-Sea Corals Amendment to the Atlantic Mackerel, Squid, and Butterfish Fishery Management Plan: Measures to Protect Deep-Sea Corals from Impacts of Fishing Gear. 114 pp. Available at: http://www.mafmc.org/actions/msb/am16

Mienis F, Duineveld GCA, Davies AJ, Ross SW, Seim H, Bane J, Van Weering TCE (2012) The influence of near-bed hydrodynamic conditions on cold-water corals in the Viosca Knoll area, Gulf of Mexico. Deep-Sea Reseach I 60:32–45.

Mienis F, Duineveld GCA, Davies AJ, Lavaleye MSS, Ross SW, Seim H, Bane JM, Van Haren H, Bergman M, De Haas H, Brooke S, Van Weering TCE (2014) Cold-water coral growth under extreme environmental conditions, the Cape Lookout area, NW Atlantic. Biogeosciences 11: 2543-2560.

New England Fishery Management Council (NEFMC) (2012) Deep-sea coral management alternatives (June 2012 Draft). 56 pp. Available at: http://www.nefmc.org/library/omnibus-deep-sea-coral-amendment

Nizinski MS, Shank TM (2012). Research cruise, NOAA Ship Henry Bigelow, Cruise No. HB 12-04, Deep-sea corals and benthic habitat: ground-truthing and exploration in deepwater canyons off the Northeast. 2-18 July 2012. NOAA and Woods Hole Oceanographic Institution. Additional information available at: http://www.nefsc.noaa.gov/press_release/2012/SciSpot/SS1210/

NOAA (2015) National Database for Deep-Sea Corals and Sponges (version 20150814-1). Available at: https://deepseacoraldata.noaa.gov/

NOAA OER (2012) Atlantic canyons undersea mapping expeditions (ACUMEN) mission plan. National Oceanic and Atmospheric Administration, Office of Ocean Exploration and Research, Silver Spring, MD. Available at: http://oceanexplorer.noaa.gov/okeanos/explorations/acumen12/background/plan/welcome.html

NRDC (2014) The Atlantic's deep-sea treasures: Discoveries from a new frontier of ocean exploration. IB: 14-11-C, 12 pp. Additional information available at: https://www.nrdc.org/sites/default/files/atlantic-deep-sea-treasures-IB.pdf

Orr JC, Fabry VJ, Aumont O, and others (2005) Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. Nature 437:681–686

Packer DB, Drohan AF (2012) Database of recorded deep-sea coral presences in the U.S. Northeast/Mid-Atlantic region. Unpublished data product. Available by contacting author. Email: dave.packer@noaa.gov; Phone: 732-872-3044.

Packer DB, Boelke D, Guida V, McGee L-A (2007) State of deep coral ecosystems in the northeastern US region: Maine to Cape Hatteras. In: Lumsden SE, Hourigan TF, Bruckner AW, Dorr G (eds) The state of deep coral ecosystems of the United States. NOAA Tech. Memo. CRCP-3. National Oceanic and Atmospheric Administration, Silver Spring, MD, p 195–232

Packer DB, Dorfman DS (2012) Deep-Sea corals. In: Menza C, Kinlan BP, Dorfman DS, Poti M, Caldow C (eds) A biogeographic assessment of seabirds, deep-sea corals and ocean habitats of the New York Bight: science to support offshore spatial planning. NOAA Tech. Memo. NOS NCCOS 141. National Oceanic and Atmospheric Administration, Silver Spring, MD, p 69–86

Quattrini AM, Georgian SE, Byrnes L, Falco R, Stevens A, Cordes EE (2013) Niche divergence by deep-sea octocorals in the genus *Callogorgia* across the upper continental slope of the Gulf of Mexico. Mol Ecol 22:4123–4140

Quattrini AM, Nizinski MS, Chaytor JD, and others (2015) Exploration of the canyon-incised continental margin of the Northeastern United States reveals dynamic habitats and diverse communities. Plos One 10:e0139904 doi:10.1371/journal. pone.0139904

Rengstorf AM, Grehan A, Yesson C, Brown C (2012) Towards high-resolution habitat suitability modeling of vulnerable marine ecosystems in the deep-sea: Resolving terrain attribute dependencies. Marine Geodesy 35:343–361

Rengstorf AM, Yesson C, Brown C, Grehan AJ (2013) High-resolution habitat suitability modelling can improve conservation of vulnerable marine ecosystems in the deep-sea. Journal of Biogeography 40:1702–1714

Rooper CN, Sigler M, Goddard P, Malecha PW, Towler R, Williams K, Wilborn R, Zimmermann M (2016) Validation and improvement of species distribution models for structure forming invertebrates in the eastern Bering Sea with an independent survey. Mar Ecol Prog Ser 551: 117-130.

Rooper CN, Zimmermann M, Prescott MM, Hermann AJ (2014) Predictive models of coral and sponge distribution, abundance and diversity in bottom trawl surveys of the Aleutian Islands, Alaska. Mar Ecol Prog Ser 503:157–176

Rooper CN, Zimmermann M, Prescott MM (in prep) Comparison of modeling methods to predict the spatial distribution of deep-sea coral and sponge in the Gulf of Alaska.

Ross RE, Howell KL (2013) Use of predictive habitat modeling to assess the distribution and extent of the current protection of 'listed' deep-sea habitats. Diversity and Distributions 19:433–445

Ross SW, Brooke S (2012) Research cruises. Deepwater canyons 2012: pathways to the abyss. Legs I and II. NOAA Office of Exploration and Research, Bureau of Ocean Energy Management, and US Geological Survey. Additional information available at: http://oceanexplorer.noaa.gov/explorations/12midatlantic/background/habitats/habitats.html and http://deepwatercanyons.wordpress.com

SAFMC (2013) Decision Document for Coral Amendment 8 to the Fishery Management Plan for Coral, Coral Reef, and Live/Hardbottom Habitats in the South Atlantic Region. Available at: http://www.safmc.net/LinkClick.aspx?fileticket=1z62Aojkbnc%3d&tabid=797

Scanlon KM, Waller RG, Sirotek AR, Knisel JM, O'Malley JJ, Alesandrini S (2010) USGS cold-water coral geographic database - Gulf of Mexico and Western North Atlantic Ocean, Version 1.0. USGS Open File Report 2008-1351. US Geological Survey, Reston, VA. Available at http://pubs.usgs.gov/of/2008/1351/

Sigler MS, Rooper CN, Hoff GR, Stone RP, McConnaughey RA, Wilderbeur TK (2015) Faunal features of submarine canyons on the eastern Bering Sea slope. Mar Ecol Prog Ser 526: 21–40

Stone RP, Guinotte JM, Cohen AL, A. H, Cairns SD (in prep.) Carbonate mineralogy of Alaskan Corals.

Stone RP, Shotwell SK (2007) State of Deep Coral Ecosystems in the Alaska Region: Gulf of Alaska, Bering Sea and the Aleutian Islands. In: Lumsden SE, Hourigan TF, Bruckner AW, Dorr G (eds) The State of Deep Coral Ecosystems of the United States. Department of Commerce, Silver Spring, MD, p 65–108

Taylor MT, Yesson C, Agnew DJ, Mitchell RE, Rogers AD (2013) Using fisheries by-catch data to predict octocoral habitat suitability around South Georgia. Journal of Biogeography 40:1688–1701

Tittensor DP, Baco AR, Brewin PE, Clark MR, Consalvey M and others (2009) Predicting global habitat suitability for stony corals on seamounts. Journal of Biogeography 36:1111–1128

Tong R, Purser A, Guinan J, Unnithan V (2013) Modeling the habitat suitability for deep-water gorgonian corals based on terrain variables. Ecological Informatics 13:123–132

Tracey DM, Rowden AA, Mackay KA, Compton T (2011) Habitat-forming cold-water corals show affinity for seamounts in the New Zealand region. Mar Ecol Prog Ser 430:1–22

White M, Mohn C, Orren MJ (2007) Physical processes and seamount productivity. In: Pitcher TJ, Morato T, Hart PJB (eds) Seamounts: Ecology, Fisheries and Conservation. Blackwell Publishing, Oxford, p 65–84

Wilson MFJ, O'Connell B, Brown C, Guinan JC, Grehan AJ (2007) Multiscale terrain analysis of multibeam bathymetry data for habitat mapping on the Continental Slope. Marine Geodesy 30:3–35

Woodby D, Carlile D, Hulbert L (2009) Predictive modeling of coral distribution in the Central Aleutian Islands, USA. Mar Ecol Prog Ser 397:227–240

Yesson, C, Bedford F, Rogers AD, and Taylor ML (2015). The global distribution of deep-water Antipatharia habitat. Deep-Sea Research Part II: Topical Studies in Oceanography.

Yesson C, Taylor M, Tittensor D, Davies A, Guinotte J, Baco-Taylor A, Black J, Hall-Spencer J, and A Rogers (2012) Global habitat suitability of cold water octocorals. Journal of Biogeography 39(7):1278–92