1 **Predictive Modeling of Suitable Habitat for Deep-Sea Corals Offshore the Northeast**

2 **United States**

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25

26 **ABSTRACT**

27 Deep-sea corals (DSCs) are important living marine resources, forming both oases of biodiversity

28 and three-dimensional habitat structure for fishes and invertebrates. However, because of logistical

29 difficulties and expense of deep-sea exploration, much less is known about the distribution of

30 DSCs than is known for their shallow-water counterparts. Predictive modeling, therefore, is

31 essential for estimating the extent of DSC habitat in areas that are unexplored in order to support

32 conservation efforts, to provide information for effective management of offshore activities

33 affecting the seafloor, and for future exploration and research. In support of research and

34 management efforts in the U.S. Northeast (Cape Hatteras, NC north to the Canadian border), we

35 developed a comprehensive set of habitat suitability models covering this entire geographic region

36 for nine taxonomic groups of DSCs (Alcyonacea, gorgonian corals, non-gorgonian corals,

37 Scleractinia, Caryophylliidae, Flabellidae, Pennatulacea, Sessiliflorae, and Subselliflorae).

38 Maximum entropy (MaxEnt) models were fit to DSC presence records and spatially-explicit

39 environmental predictors depicting depth and seafloor topography, surficial sediment

40 characteristics, and oceanography. A stepwise model selection procedure was then implemented

41 to identify the set of predictor variables that maximized predictive performance for each taxonomic

42 group. To allow for comparisons across taxonomic groups, the standard MaxEnt logistic

43 predictions were converted into calibrated classes of habitat suitability. Overall, model

44 performance was high for all taxonomic groups. Model fit was best for Caryophylliidae,

45 Sessiliflorae, and Flabellidae, whereas model stability was greatest for the three taxonomic groups

46 of Alcyonacea. Model results reported here corroborate known distributions of corals in the region.

47 For example, large structure-forming taxa are predicted to occur mainly in canyon environments,

48 particularly in areas of steep slope ($> 30°$); sea pens in softer sediments of the continental shelf

49   and slope. Additionally, the models successfully predicted DSC locations during field testing.

50   Despite the limitations of presence-only data, several novel extensions to the traditional MaxEnt

51   analysis workflow improved model selection, accuracy assessment, and comparability of results

52   across taxonomic groups. This approach, when integrated with management processes, could be a

53   powerful tool for science-based conservation, management, and spatial planning for these marine

54   resources.

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58   **Keywords:** cold-water corals, species distribution models, statistical machine learning, MaxEnt,

59   marine spatial planning, biogeography

60 **1. INTRODUCTION**

61 Deep-sea corals (DSCs) are conspicuous components of deep-sea ecosystems. Their distribution

62 is cosmopolitan and most taxa (with the notable exception of Order Pennatulacea) are generally

63 found at approximately 50-3000 m depth on consolidated substrates of continental shelves, slopes,

64 submarine canyons, and seamounts (e.g., Spalding et al., 2001; Freiwald et al., 2004; Roberts et

65 al., 2006; Hourigan et al., 2007). A diverse assemblage of organisms, including many species of

66 fishes and other invertebrates, some of commercial or recreational importance, utilize the three-

67 dimensional habitat structure provided by DSCs (e.g., Roberts et al., 2009; Buhl-Mortensen et al.,

68 2010; Miller et al., 2012). DSCs are long-lived, slow-growing, sessile organisms that are

69 susceptible to a variety of anthropogenic impacts including fishing and ocean acidification (e.g.,

70 Guinotte et al., 2006; Turley et al., 2007; Roberts et al., 2009; Ragnarsson et al., 2017).

71

72 DSCs are the focus of significant spatial planning, conservation, and management efforts in the

73 United States (Hourigan et al., 2017), leading to a critical need for information on their spatial

74 distribution. This is particularly true for the Northwest Atlantic offshore of the northeastern U.S.

75 from North Carolina to Maine (hereafter U.S. Northeast). Recently, the Mid-Atlantic Fishery

76 Management Council protected DSC habitats utilizing the discretionary provisions of the

77 Magnuson-Stevens Reauthorization Act and, President Obama established the Northeast Canyons

78 and Seamounts Marine National Monument. Additionally, the New England Fishery Management

79 Council continues to work towards finalizing their recommendation to protect DSC habitats. Taxa

80 reported in the historical record for the U.S. Northeast include high diversities of species in the

81 orders Alcyonacea (soft corals and gorgonians) and Pennatulacea (sea pens), low diversity of

82   species in the Order Scleractinia (stony or hard corals), consisting almost entirely of solitary forms,

83   and few species in the Order Antipatharia (black corals) (Packer et al., 2007; 2017a).

84

85   While there has been considerable interest in protecting DSCs in this region, data describing the

86   locations of DSCs is limited because of the substantial costs and logistical challenges of surveying

87   the deep sea. Statistical modeling has proven to be a useful and cost-effective tool to predict the

88   distribution and extent of suitable habitat for DSCs and other benthic organisms at local scales

89   (Dolan et al., 2008; Huff et al., 2013; Georgian et al., 2014; Rooper et al., 2014; Rowden et al.,

90   2017), regional scales (Bryan and Metaxas, 2007; Rengstorf et al., 2013; Guinotte and Davies,

91   2014; Anderson et al., 2016), and globally (Davies et al., 2008; Tittensor et al., 2009; Davies and

92   Guinotte, 2011; Yesson et al., 2012). In general, habitat suitability modeling examines the

93   associations between the presence, absence, frequency and/or abundance of organisms and

94   relevant environmental or habitat variables to identify unexplored areas with similar conditions to

95   areas of known presence, high frequency and/or high abundance. Presence/absence or abundance

96   data are preferred because these types of data expand the range of statistical modeling approaches

97   that can be utilized and allow the prediction of absolute probabilities of occurrence (Elith et al.,

98   2011; Howard et al., 2014). However, initial syntheses of historical data for deep-sea taxa,

99   particularly at the relatively fine spatial scales demanded by regional planning efforts, often must

100 rely on presence-only data. Presence-only data contain potentially useful information, but must be

101 treated carefully and limitations must be recognized. Presence-only data can be used to predict the

102 relative likelihood that a given parcel of habitat is suitable compared to background environmental

103 variation. But this likelihood cannot be expressed as a probability of occurrence unless the true

104 global prevalence (fraction of potential habitat parcels occupied) is known *a priori* or sampling

105   was random and the true global prevalence can be estimated (Elith et al., 2011; Royle et al., 2012).

106   Practically speaking, presence-only data are seldom collected under a random design, and any

107   spatial sampling biases, unless known and corrected for, will be reflected in species distribution

108   predictions derived from these data (Varela et al., 2014). Because of limited DSC collections and

109   surveys, a tendency to report presence but not absence, and the inaccessibility of the deep ocean

110   environment, most historical DSC records or databases consist of presence-only data. Therefore,

111   methods to maximize the utility of presence-only data for regional DSC model syntheses are

112   essential to guide next steps in planning, conservation, and management efforts.

113

114   Maximum entropy modeling is a common method for estimating species distributions from

115   presence-only data (Elith et al., 2011; Merow et al., 2013) and is often implemented using the Java

116   software MaxEnt (Phillips et al., 2004, 2006). This method has been shown to perform as well or

117   better than other methods for presence-only data, both generally (Elith et al., 2006; Phillips et al.,

118   2006) and specifically for DSCs (Tittensor et al., 2009; Tong et al., 2013). MaxEnt uses a statistical

119   machine learning algorithm to estimate functional relationships between environmental variables

120   and habitat suitability, subject to constraints imposed by the values of environmental variables at

121   observed presence locations and a condition called maximum entropy (Phillips et al., 2004, 2006).

122   The maximum entropy condition guarantees, under certain assumptions, that the resulting habitat

123   suitability value will be the optimum value on which to base a decision about the suitability of a

124   parcel of habitat in question for a given organism (Ortega-Huerta and Peterson, 2008). However,

125   MaxEnt is not without pitfalls and controversy (Elith et al., 2011; Royle et al., 2012; Merow et al.,

126   2013; Yackulic et al., 2013). Here, we take advantage of advances in calculation of information

127   criteria and model selection for MaxEnt models (Warren et al., 2010; Warren and Seifort, 2011)

128   to develop a practical but cautious MaxEnt approach to predict locations of suitable habitat for

129   DSCs. This approach recognizes the utility of model-based syntheses of available data for

130   conservation and management planning in the deep sea, while addressing some of the key

131   limitations in the interpretation and presentation of models based on presence-only information.

132

133   Our goals in this work are threefold: 1) to develop models with sufficient spatial resolution and

134   accuracy to support regional conservation, management and exploration efforts; 2) to understand

135   better the distributions of DSCs in the U.S. Northeast and potential environmental drivers and

136   correlates of these distributions; and 3) to develop improved techniques for maximizing the value

137   of presence-only data in species distribution modeling, while recognizing and communicating the

138   associated limitations.

139

140   **2. METHODS**

141   **2.1 Study area**

142   The study area for this analysis (Figure 1) extended from North Carolina (36.031°N) northward

143   into the Gulf of Maine to the Canadian border (44.905°N) and offshore to the extent of the NOAA

144   Coastal Relief Model (CRM; National Geophysical Data Center 1999a, 1999b). The depth range

145   of the study area (~20–5000 m) was broad enough to cover most known DSC locations in the U.S.

146   Northeast (Packer et al., 2007).

147
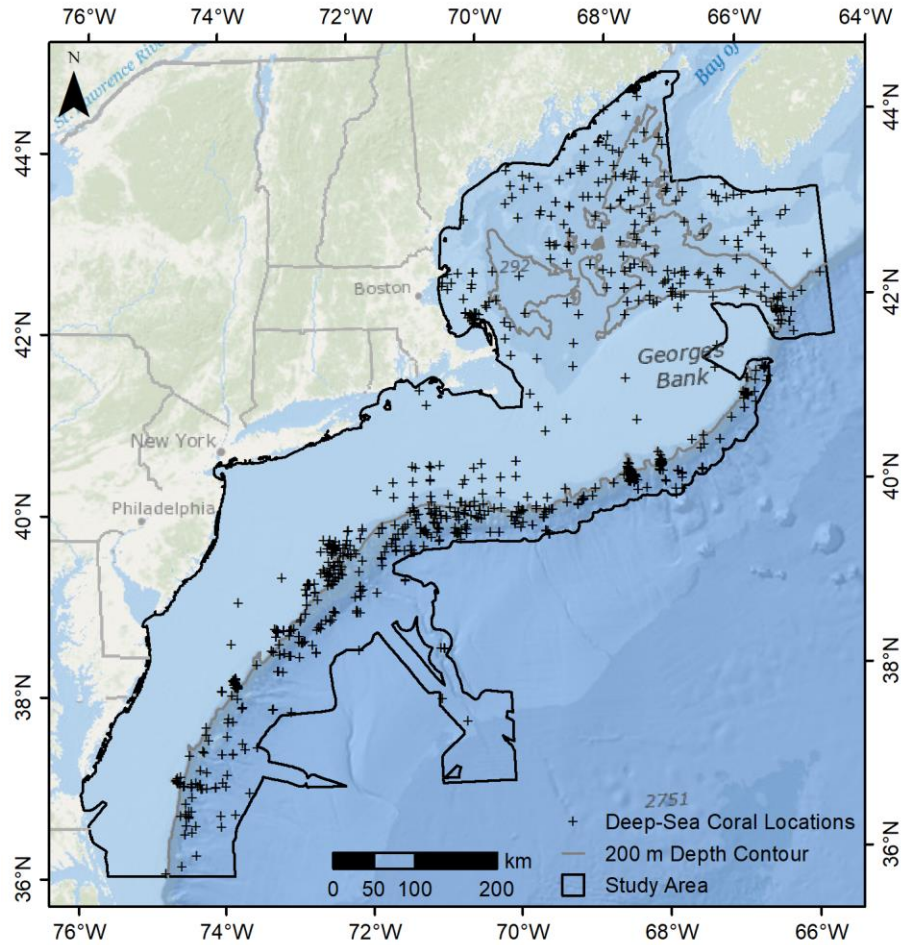
Figure 1. Map of the study area. Black crosses indicate locations of historical deep-sea coral presence records. The black line indicates the extent of the study area. The gray line denotes the 200 m depth contour.

2.2 Deep-sea coral data

2.2.1. Deep-sea coral presence database

We created a database of DSC presence records (>20 m depth) in the study area using the U.S. Geological Survey (USGS) Cold-Water Coral Geographic Database (CoWCoG; Scanlon et al., 2010) and additional records from museum collection databases (e.g., the Smithsonian Institution), the published literature, seamount expeditions conducted from 2003-2005, and recent data-mining

159   (sources described in Cairns, 2007; Packer et al., 2007; Packer and Dorfman, 2012; Packer and

160   Drohan, unpublished internal NOAA/NEFSC database. Data custodian email:

161   dave.packer@noaa.gov). When necessary we updated nomenclature and taxonomy to conform to

162   current classification (as in Packer et al., 2017a). We checked each record for grammatical errors,

163   incomplete fields, and incorrect taxonomy for the following fields: order, suborder, family, genus,

164   and species. We resolved incomplete fields, when possible, by cross checking with the World

165   Register of Marine Species (WoRMS; WoRMS Editorial Board, 2012) and the Integrated

166   Taxonomic Information System (ITIS, 2012) as well as obtaining expert taxonomic opinions. We

167   consulted taxonomic experts when generic and specific names were not assigned to higher

168   taxonomic categories in WoRMS or ITIS, or when classification schemes in WoRMS or ITIS

169   conflicted (S. Cairns, L. Watling, pers. comm.). Notwithstanding the likely biases in the database

170   related to the locations sampled, methods of sample collection, and variation in reporting and

171   observer expertise (Packer et al., 2007), this compilation represented the best available collection

172   of georeferenced DSC presence data for the region at the time the models were generated.

173

174   *2.2.2. Deep-sea coral taxonomic groups*

175   We organized DSC records into taxonomic groups for modeling (Table 1). These included three

176   orders, representing three of the four main DSC taxonomic groups: Order Alcyonacea (soft corals),

177   Order Scleractinia (hard corals), and Order Pennatulacea (sea pens). We did not model Order

178   Antipatharia (black corals) because there were insufficient records (n < 10) in the study area.

179   Within each order-level group, we included additional subgroups to highlight functional groups or

180   to capture higher taxonomic resolution. For example, within Alcyonacea we created separate

181   models for gorgonian and non-gorgonian corals. We considered these subgroups informative since

182   gorgonian corals include the major structure-forming families (those in suborders Calcaxonia,

183   Holaxonia, and Scleraxonia) of alcyonacean corals whereas non-gorgonian corals, in contrast,

184   include the true soft corals that are typically smaller in size, lack a rigid skeleton, and, therefore,

185   are of lesser importance as a structure-forming species. Within the orders Pennatulacea and

186   Scleractinia we included groups at the suborder level or family level, respectively, when the

187   number of records and taxonomic resolution were sufficient (Table 1). Others who have used

188   historical DSC databases to model DSC habitat suitability have noted difficulties with taxonomic

189   levels below suborder (Yesson et al., 2012; Guinotte and Davies, 2014). Family was the lowest

190   taxonomic level used in our analysis. Because of the nested arrangement of the taxonomic groups,

191   some DSC records were included in multiple groups (e.g., a record in the gorgonian coral group

192   was also included in the Alcyonacea group). Additionally, order-level groups used some records

193   not included in suborder- or family-level groups (e.g., an unidentified Alcyonacea record could

194   only be included in the order-level group). Totals for the number of DSC records in each group

195   reflect this overlap (Table 1). It is also important to remember that although we use order, suborder,

196   or family when referring to a group, each group represents only those taxa present in the database.

197   For example, our Scleractinia group does not represent all scleractinians that could potentially

198   occur in the region. Only solitary cup corals appear in the historical presence records for the U.S.

199   Northeast. Although Scleractinia is used as a proxy for all hard corals in the region, results should

200   be viewed with caution; colonial scleractinians could have different habitat requirements than

201   those of solitary cup corals.

202

203   Our database of DSC presence records contained 1,922 records in the orders Alcyonacea,

204   Scleractinia, and Pennatulacea (Table 1). Although spatial distributions of these records differed

205 among taxonomic groups (Figure 2), they were generally concentrated in or near submarine

206 canyons, on the continental shelf near the shelf break, and in the Gulf of Maine (Figure 2). The

207 principal exception was sea pens in the Suborder Subselliflorae, which were much more broadly

208 distributed on the shelf, extending into shallower areas (Figure 2). In general, records for all groups

209 spanned the geographic range of the study area, especially at depths >100-200 m.

210

211 Table 1. Taxonomic groups modeled, the order each group is within, description of deep-sea coral

212 records included in each group, total number of presence records for each group, and number of

213 model grid cells containing presence records for each group.

Group	Order	Description	Number of Presence Records	Number of Grid Cells containing Presence Records
Alcyonacea	Alcyonacea	All records in Order Alcyonacea	745	514
Gorgonian corals	Alcyonacea	All records in suborders Calcaxonia, Holaxonia, and Scleraxonia	529	361
Non-gorgonian corals	Alcyonacea	All records in suborders Alcyoniina and Stolonifera	151	123
Scleractinia	Scleractinia	All records in Order Scleractinia	262	176
Caryophylliidae	Scleractinia	All records in Family Caryophylliidae	157	91
Flabellidae	Scleractinia	All records in Family Flabellidae	105	88
Pennatulacea	Pennatulacea	All records in Order Pennatulacea	915	396
Sessiliflorae	Pennatulacea	All records in Suborder Sessiliflorae	150	77
Subselliflorae	Pennatulacea	All records in Suborder Subselliflorae	765	336

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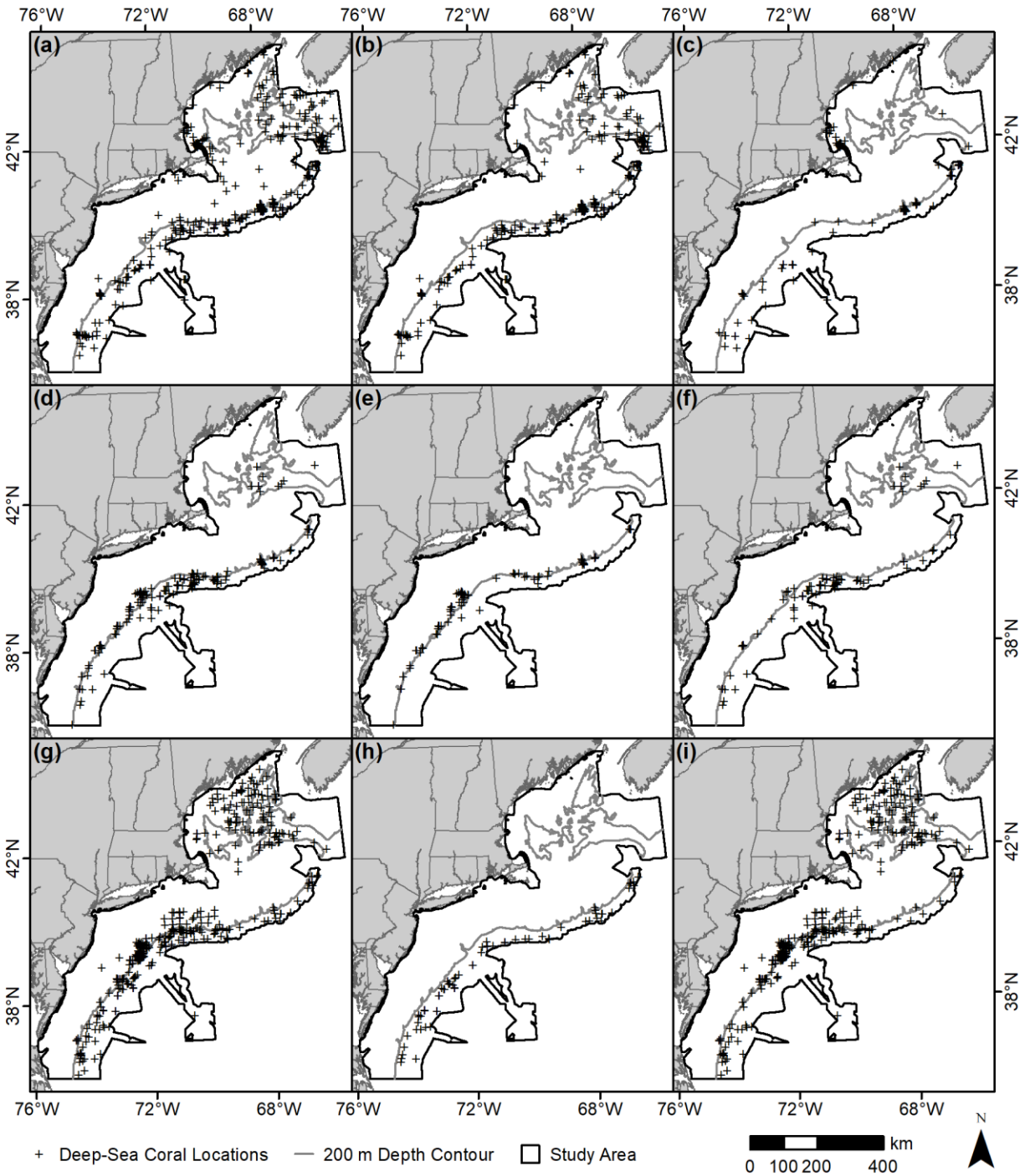
Figure 2. Maps of deep-sea coral presence records within the study area for (a) Alcyonacea, (b) gorgonian corals, (c) non-gorgonian corals, (d) Scleractinia, (e) Caryophylliidae, (f) Flabellidae, (g) Pennatulacea, (h) Sessiliflorae, (i) Subselliflorae. Black crosses indicate locations of deep-sea

219 coral presence records. The black lines indicate the extent of the study area. The gray lines denote

220 the 200 m depth contour.

221

222 *2.2.3. Spatial thinning of deep-sea coral data*

223 Because our database of DSC presences contains records compiled from numerous surveys with

224 various protocols and objectives, it is likely affected by both spatial and taxonomic sampling biases

225 (Varela et al., 2014). Sampling bias can result in models that are overfit (i.e., only predicting

226 suitable habitat in locations with existing occurrences) to the environmental conditions represented

227 in the training data (Boria et al., 2014; Varela et al., 2014). If sampling effort can be quantified,

228 this information can be used during model fitting to correct for sampling bias (Boria et al., 2014;

229 Varela et al., 2014; Aiello-Lammens et al., 2015). However, this information is not typically

230 available for databases such as ours that are compiled from many sources. A number of approaches

231 to thinning or filtering training data have been explored to reduce the effects of sampling bias on

232 model predictions (Boria et al., 2014; Varela et al., 2014; Aiello-Lammens et al., 2015). For each

233 taxonomic group, we thinned the sample of presence records by removing duplicate records within

234 each model grid cell, since only one presence is required to confirm that a given grid cell contains

235 suitable habitat (see Table 1 for number of grid cells containing presence records for each

236 taxonomic group). We performed this duplicate removal using ENMTools (Warren et al., 2010).

237 While removing duplicate records reduces sample size, it helps reduce the effect of sampling bias

238 in heavily sampled areas.

239

240 **2.3 Environmental predictor data**

241 We identified an initial set of environmental predictor variables (n = 108) for potential use in

242 predictive models of DSC habitat suitability based on previous studies of DSC habitats within the

243 U.S. Northeast. These variables included biological, chemical, and physical oceanographic

244 properties of deep-sea environments and physical characteristics of the seafloor (Mortensen and

245 Buhl-Mortensen, 2004; 2005; Lumsden et al., 2007; Packer et al., 2007; Roberts et al., 2009). We

246 generated all data layers depicting the environmental predictor variables on a 370.65 m (hereafter

247 370 m) resolution grid in a universal transverse Mercator projection (WGS 1984 UTM Zone 18N).

248 We selected this resolution because of the vertical and horizontal spatial uncertainty associated

249 with depth values from the CRM in deeper waters of the U.S. Northeast (Calder 2006; Poti et al.,

250 2012) and the horizontal uncertainty in the geographic positions of the DSC records. We excluded

251 many of the environmental predictor variables prior to modeling for a variety of reasons including

252 missing data, sparse data, artifacts in interpolated data and model products, low spatial resolution,

253 and high collinearity with other considered variables (see Appendix A for details of the screening

254 process). We performed a pairwise-correlation analysis on the environmental predictor data layers

255 using the ENMTools software (Warren et al., 2010). For each pair of highly correlated ($|r| > 0.9$)

256 environmental predictors, we excluded the predictor that was highly correlated with the most other

257 predictors. The final set of 22 environmental predictor variables included measures of seafloor

258 topography, seafloor substrate, and oceanography (Table 2).

259

260 Table 2. Environmental predictor variables in final set. All variables are on a 370 m resolution

261 grid. For seafloor topography variables, scale refers to the size of the Gaussian low-pass filter used

262 to smooth the bathymetry dataset or the size of the focal neighborhood (for BPI).

Variable	Category
Depth	Seafloor topography

Slope (370 m scale)	Seafloor topography
Slope (5 km scale)	Seafloor topography
Slope of slope (1500 m scale)	Seafloor topography
Slope of slope (5 km scale)	Seafloor topography
Aspect (1500 m scale)	Seafloor topography
Aspect (5 km scale)	Seafloor topography
Rugosity (370 m scale)	Seafloor topography
Rugosity (1500 m scale)	Seafloor topography
Plan curvature / slope index (1500 m scale)	Seafloor topography
Plan curvature / slope index (5 km scale)	Seafloor topography
Profile curvature / slope index (1500 m scale)	Seafloor topography
Profile curvature / slope index (5 km scale)	Seafloor topography
Bathymetry Position Index (BPI) / slope index (20 km scale)	Seafloor topography
Surficial sediment mean grain size	Seafloor substrate
Surficial sediment percent gravel	Seafloor substrate
Surficial sediment percent sand	Seafloor substrate
Annual mean bottom dissolved oxygen	Oceanography
Annual mean bottom salinity	Oceanography
Annual mean bottom temperature	Oceanography
Annual mean surface chlorophyll-*a* concentration	Oceanography
Annual mean surface reflectance	Oceanography

263

264 *2.3.1 Seafloor topography variables*

265 We acquired depth data for the study area from the 3 arc-second CRMs for the Northeast Atlantic

266 and Southeast Atlantic (National Geophysical Data Center, 1999a, 1999b; downloadable at

267 http://www.ngdc.noaa.gov/mgg/coastal/crm.html). We projected depth data from a geographic

268 coordinate system to WGS 1984 UTM Zone 18N and bilinearly resampled to a grid resolution of

269 92.6625 m (hereafter 92 m).

270

271 Measures of seafloor topography can serve as proxies for water flow and other oceanographic

272 patterns since flow interacts with seafloor geomorphology at various scales. From the 92 m

273 resolution depth layer we calculated slope, slope of slope, and aspect using ArcGIS 10.0 (ESRI,

274 2011) and rugosity, plan curvature, and profile curvature using DEM Surface Tools (Jenness,

275 2013). We also generated these seafloor topography variables at multiple spatial scales (370 m,

276 1500 m, 5 km, 10 km, 20 km) to depict fine-scale and broad-scale differences in these variables

277 (e.g., slope of fine-scale features like boulders vs. slope of broad-scale features like the continental

278 shelf break). We did this by using a Gaussian low-pass filter to smooth the 92 m depth layer using

279 focal neighborhoods at these scales and then calculating the seafloor topography variables from

280 the resulting smoothed depth layers. We also calculated bathymetric position index (BPI) for focal

281 neighborhoods with outer radii equal to each of these spatial scales using the Benthic Terrain

282 Modeler tool (Walbridge et al., 2018).

283

284 For each of the data layers depicting depth and seafloor topography at 92 m resolution, we derived

285 corresponding data layers at 370 m resolution by calculating the aggregate mean in 4 x 4 grid cell

286 non-overlapping blocks. At 370 m resolution, the impacts of spatial uncertainty of depth data on

287 average depth values are minimized. However, at this resolution some fine-scale bathymetric

288 features are lost. Because aspect (the direction the seafloor slope faces) is a circular variable, we

289 converted its continuous values to categories representing the 8 cardinal directions. Plan curvature,

290 profile curvature, and BPI were also classified into distinct categories using natural breaks and

291 were combined with a classified version of slope (slope index) to create categorical data layers

292 representing combinations of these variables and slope. This classification and combination with

293 slope were important because plan curvature, profile curvature, and BPI can all take on a value of

294 zero where the seafloor is either flat *or* at an inflection point where concavity and convexity in

295 perpendicular directions are balanced.

296

297 *2.3.2 Seafloor substrate variables*

298 We developed gridded data layers depicting predicted surficial sediment mean grain size and

299 sediment composition (percent mud, percent sand, percent gravel) at 370 m resolution using seabed

300 survey point data from the usSEABED Atlantic Coast Offshore Surficial Sediment Data Release,

301 version 1.0 parsed and extracted databases (Reid et al., 2005; downloadable at

302 http://pubs.usgs.gov/ds/2005/118/htmldocs/usseabed.htm). We filtered the survey point data to

303 remove duplicate points and points not related to surficial sediments. We then modeled each

304 variable as a linear combination of components representing a deterministic mean trend and a

305 spatially structured stochastic process (Cressie, 1993). We used local polynomial interpolation to

306 estimate the deterministic mean trend, and obtained the residual values by subtracting the trend

307 surface prediction at each survey point location from the observed value of the variable. We

308 quantified and modeled spatial autocorrelation in the residuals using semivariogram analysis and

309 used the fitted semivariogram model parameters to perform ordinary kriging of the residuals. We

310 summed the trend prediction and the kriging prediction to create the final gridded prediction. We

311 performed all geostatistical analyses using ArcGIS 10.0 Geostatistical Analyst (ESRI, 2011).

312

313 *2.3.3 Oceanographic variables*

314 We used geostatistics (see Section 2.3.2 for details of the approach) to create gridded data layers

315 depicting annual mean bottom dissolved oxygen, annual mean bottom temperature, and annual

316 mean bottom salinity at 370 m resolution from *in situ* ocean survey data. We downloaded dissolved

317 oxygen data from the World Ocean Database (WOD) Ocean Station Data (OSD) dataset (Boyer et

318 al., 2013; Johnson et al., 2013). We obtained temperature and salinity data from the NOAA NMFS

319 NEFSC Ecosystem Survey Branch bottom trawl survey database (accessed by S. Fromm on

320 December 20, 2011) and supplemented these records with data from the WOD OSD database

321 (Boyer et al., 2013; Johnson et al., 2013), the Woods Hole Oceanographic Institute (WHOI)

322 Hydrographic Database (accessed by D. Johnson on February 8, 2012), and the Marine Resources

323 Monitoring, Assessment, and Prediction (MARMAP) Program (database accessed by D. Johnson

324 on February 10, 2012). Prior to interpolation, we filtered point survey data to extract only those

325 measurements at depths within 5% of the 370 m depth data layer.

326

327 As a proxy for ocean surface primary productivity, we created a gridded data layer depicting annual

328 mean sea surface chlorophyll-*a* concentration. We extracted sea surface chlorophyll-*a*

329 concentration data for the period 1998-2006 from high-resolution (~1.1 km) SeaWiFS satellite

330 data, processed using standard OBPG reprocessing 5.1 algorithms

331 (https://oceancolor.gsfc.nasa.gov/reprocessing/r2005/seawifs). From the same SeaWiFS data we

332 created a gridded data layer depicting the annual sea surface reflectance, measured as the mean

333 normalized water-leaving radiance at 670 nm wavelength (nLw-670 nm), as a proxy for sea surface

334 turbidity. All SeaWiFS processing followed previously documented methods (Pirhalla et al.,

335 2009), except a de-speckling filter was also applied (Gonzalez and Woods, 1992). We projected

336 data layers depicting annual mean climatologies for sea surface chlorophyll-*a* concentration and

337 sea surface reflectance from a geographic coordinate system to WGS 1984 UTM Zone 18N and

338 bilinearly resampled to 370 m resolution.

339

340 **2.4 Model framework**

341 *2.4.1 Overview*

342 For each of the DSC taxonomic groups, we used a MaxEnt model framework to develop models

343 with high predictive performance and to create spatial predictions depicting the relative likelihood

344 of suitable habitat across the study area. Since the ability of models to predict habitat suitability or

345 to resolve the relationships between environmental predictors and habitat suitability can be

346 reduced when models are overly complex or overly simple (Yost et al., 2008; Warren and Seifort,

347 2011), we developed a stepwise model selection process to choose the set of predictor variables

348 for each taxonomic group that maximized predictive performance. To generate model predictions

349 in a format that could be directly compared across taxonomic groups, we classified predictions of

350 the relative likelihood of habitat suitability (i.e., the MaxEnt logistic output) into six classes of

351 habitat suitability: low, medium-low, high, very high, and robust very high.

352

353 *2.4.2 Model fitting*

354 For each iteration of the stepwise model selection process, we created ten replicate samples from

355 the DSC presence records. For each replicate, we split the DSC presence records into a model

356 training subset containing 70% of the records and a model testing subset containing the remaining

357 30% of the records. We fit models to each of the training subsets and evaluated model predictive

358 performance using the corresponding testing subsets. We evaluated model predictive performance

359 using the area under the receiver operating characteristic (ROC) curve (AUC; Fielding and Bell,

360 1997), which indicated how well the models predicted DSC presences at the test locations

361 compared to a random selection of locations (termed background points in MaxEnt). We calculated

362 test AUC for each of the ten replicate models and mean test AUC across the models. Akaike's

363 information criterion, with a correction for small sample size (AICc; Akaike, 1974; Burnham and

364 Anderson, 2002), provided a second measure of model predictive performance. We calculated

365 AICc using the ENMTools software (Warren et al., 2010) for each of the ten replicate models and

366 mean AICc across the models.

367

368 *2.4.3 MaxEnt parameter tuning*

369 As recommended by Elith et al. (2011), we fit preliminary models using a range of values for

370 several MaxEnt parameters - the regularization multiplier, number of background sample points,

371 maximum iterations, and convergence threshold (see Merow et al., 2013 for a description of each

372 parameter). Based on these preliminary models we chose settings for the regularization

373 multiplier and number of background points of 2.0 and 20,000, respectively, instead of using the

374 default values. These values consistently led to models with higher test AUC values.

375

376 *2.4.4 Stepwise model selection*

377 For each taxonomic group, we fit initial models with the full set of 22 potential environmental

378 predictors using the methods described in Section 2.4.2. We then identified the most redundant

379 environmental predictor in this initial model iteration as the predictor whose omission from model

380 fitting resulted in the smallest reduction in mean test AUC. For the next iteration of the stepwise

381 model selection procedure, we removed this environmental predictor and fit new models using the

382 updated set of environmental predictors. We repeated this process until a single environmental

383 predictor remained or the mean test AUC dropped below 95% of the mean test AUC for the initial

384 model iteration. We then ranked the model iterations from best to worst in terms of predictive

385 performance as measured by mean test AUC (highest mean test AUC = rank 1 to lowest = rank

386 22) and mean AICc (lowest mean AICc = rank 1 to highest = rank 22) and averaged the two ranks.

387   We selected the model iteration (i.e., subset of environmental predictors) with the lowest average

388   rank (1 = best, 22 = worst) as the best model iteration.

389

390   *2.4.5 Final model development*

391   For each taxonomic group, we fit a single, final MaxEnt model using all of the DSC presence

392   records (i.e., no data subsetting) and the set of environmental predictors from the best model

393   iteration identified through the model selection procedure. Using the final model, we predicted the

394   relative likelihood of habitat suitability for each grid cell in the study area. Although this prediction

395   (the MaxEnt logistic output) is an index scaled from 0 to 1, it should not be treated as a probability

396   of occurrence. To convert the MaxEnt logistic output to probability of occurrence requires an

397   estimate of prevalence. MaxEnt does not estimate prevalence and by default assigns it a value of

398   0.5 (Elith et al., 2011). Therefore, it is important to treat the MaxEnt logistic output value only as

399   a relative measure of habitat suitability among grid cells in the same model domain for the same

400   taxonomic group.

401

402   *2.4.6 Classified maps of habitat suitability*

403   To allow direct comparisons of predictions of relative habitat suitability between MaxEnt models

404   (e.g., across taxa), the MaxEnt logistic output is often converted into a binary map, where grid

405   cells with values above a selected breakpoint are defined as suitable habitat and grid cells with

406   values below the breakpoint are defined as unsuitable habitat (Elith et al., 2011; Merow et al.,

407   2013). However, choosing an appropriate breakpoint (e.g., one that is ecologically meaningful)

408   can be challenging (Merow et al., 2013). Rather than choosing a single breakpoint, we first

409   classified the MaxEnt logistic output (i.e., the relative likelihood of suitable habitat) into a map

410 with five habitat suitability classes (low, medium-low, medium, high, and very high), each defined

411 by the ratio of the cost of a false positive error to the cost of a false negative error. For example, a

412 2:1 ratio means that a false positive error (i.e., predicting suitable habitat in a location that is

413 actually unsuitable habitat) is twice as costly as a false negative error. We used ROC curve analysis

414 to identify the MaxEnt logistic output values that corresponded to ratios of 1:1, 2:1, 5:1, and 10:1

415 and used these values as the breakpoints between the five habitat suitability classes. We conducted

416 the ROC curve analysis using the 'ROCR' package in R (Sing et al., 2005). By increasing the cost

417 of false positive errors over the series of breakpoints, each successive breakpoint resulted in a

418 habitat suitability class with a more constrained prediction of the area likely to contain suitable

419 habitat, with the 'very high' class the least likely to overpredict suitable habitat. In addition, we

420 identified grid cells for which predictions from all ten of the replicate models created during the

421 best model iteration of model selection were classified in the 'very high' habitat suitability class.

422 We labeled these grid cells as a sixth 'robust very high' habitat suitability class.

423

424 *2.4.7 Assessment of model performance*

425 As described in Section 2.4.2, we evaluated model performance for each taxonomic group using

426 the mean test AUC for the ten replicate models from the best model iteration of model selection.

427 In addition, as a measure of how well predictions of relative habitat suitability from the final model

428 matched the data used to fit the model, we calculated the percentage of grid cells containing DSC

429 presence records that were predicted to be in the 'high' or 'very high' habitat suitability classes by

430 the final model. We also calculated the percentage of grid cells predicted by the final model to be

431 in the 'very high' habitat suitability class that were also predicted to be in the 'robust very high'

432 class by the best model iteration of model selection (i.e., all ten replicate models predicted the grid

433   cell to be in the 'very high' class). Since each of the replicate models used different subsets of the

434   DSC presence records for model fitting, this metric provided a measure of how sensitive the model

435   predictions were to variation in the location of the presence records. Finally, as a measure of the

436   relative uncertainty in model predictions, we calculated the coefficient of variation (CV) for

437   predictions of relative habitat suitability from the ten replicate models from the best model iteration

438   of model selection. Using the CV, the ratio of the standard deviation to the mean, to examine the

439   degree of variability in model predictions allows us to compare the variability in model predictions

440   among model grid cells with drastically different mean prediction values.

441

442   *2.4.8 Environmental predictor variable importance and response curves*

443   MaxEnt provided several measures to assess the relative importance of the environmental predictor

444   variables to model fitting (Phillips, 2009). We calculated these measures for each taxonomic group

445   using the best model iteration from the model selection procedure. First, MaxEnt provided a

446   measure of the relative contribution of each predictor variable to increasing the model gain over

447   the course of model fitting, where the gain is defined as the penalized likelihood function

448   maximized by MaxEnt during model fitting (Elith et al., 2011; Merow et al., 2013). Phillips (2009)

449   cautions that the relative contribution values must be interpreted carefully as the values are

450   dependent on the specific path used by the MaxEnt algorithm during model fitting and can be

451   influenced by the correlation structure among the predictor variables.

452

453   MaxEnt also provided a measure of predictor importance from a permutation test in which MaxEnt

454   randomly permuted the values of each predictor variable at the training data and background point

455   locations and determined the resulting decrease in the training AUC when evaluating the model

456   on the permuted data (Phillips, 2009). Models likely depend more heavily on predictors with

457   greater values of permutation importance. Unlike the relative contribution values, permutation

458   importance values are independent of the specific path used by the MaxEnt algorithm; however,

459   permutation importance can be influenced by the correlation structure among the predictor

460   variables. For both the relative contribution and permutation importance, we report the mean value

461   across the ten replicate models of the best model iteration.

462

463   At each iteration of model selection, MaxEnt fit a single-variable model for each individual

464   predictor variable using the methods described in Section 2.4.2. From these single-variable models

465   we calculated the mean test AUC for the ten replicate models fit for each environmental predictor

466   variable. A predictor variable with a relatively higher mean training gain in a single-variable model

467   is more useful for predicting suitable habitat. Similarly, a predictor with a relatively higher mean

468   test gain or test AUC value is more useful for creating a model that generalizes better to new data.

469   MaxEnt also performed predictor omission tests in which it fit a series of models omitting each

470   individual predictor variable in turn. From these models we calculated for each environmental

471   predictor variable the reduction in mean test AUC compared to the models fit with all the

472   predictors. If a predictor variable is highly correlated with other predictor variables, omitting it

473   will have little impact on model performance. However, if omitting a predictor variable resulted

474   in a significant decline in mean test AUC, then that would suggest the predictor variable contains

475   information not found in the other predictor variables that is useful for creating models that

476   generalize to new data.

477

478   For each measure of predictor variable importance, we created a bubble plot depicting the values

479   for each predictor variable and identified the three predictor variables with the highest values

480   (hereafter 'important' predictor variables) for each taxonomic group. We plotted marginal

481   response curves for each of these important predictor variables (Appendix B). It is important to

482   recognize that variables selected or identified as important are not necessarily direct causal drivers

483   of DSC distribution, but may simply serve as proxies for or correlates of direct mechanisms. Thus,

484   we suggest that the response curves be used to develop hypotheses about drivers of DSC

485   distribution that can be tested and validated with specific field surveys.

486

487   **3. RESULTS**

488   **3.1 Model performance**

489   Model performance as measured by mean test AUC was generally excellent for all taxonomic

490   groups, with values ranging from 0.84 to 0.97 (Table 3). Model fit, measured as the percentage of

491   grid cells containing DSC presence records that were predicted to be in the 'high' or 'very high'

492   habitat suitability classes by the final model, was best for Suborder Sessiliflorae and Family

493   Caryophylliidae, and was poorest for Order Scleractinia and Family Flabellidae (Table 3). Model

494   stability, measured as the percentage of grid cells predicted to be in the 'very high' habitat

495   suitability class by the final model that were also predicted to be in the 'robust very high' class by

496   the best model iteration of model selection, was greatest for the three taxonomic groups included

497   under the Order Alcyonacea umbrella (Table 3).

498

499   Table 3. Measures of model performance. Model fit was measured as the percentage of grid cells

500   containing DSC presence records that were predicted to be in the 'high' or 'very high' habitat

501   suitability classes by the final model. Model stability was measured as the percentage of grid cells

502   predicted in the 'very high' habitat suitability class by the final model that were also predicted to

503   be in the 'robust very high' class by the best model iteration of model selection.

Group	Mean Test AUC	Model Fit	Model Stability
Alcyonacea	0.87	44.6	62.3
Gorgonian corals	0.92	60.1	60.6
Non-gorgonian corals	0.92	55.3	67.2
Scleractinia	0.94	30.6	48.0
Caryophylliidae	0.97	76.6	43.2
Flabellidae	0.92	30.1	37.7
Pennatulacea	0.84	67.0	42.3
Sessiliflorae	0.96	81.3	47.2
Subselliflorae	0.85	72.7	47.1

504

505

506   **3.2 Spatial predictions**

507   Areas predicted as likely to contain suitable habitat for the Order Alcyonacea occurred in Mid-

508   Atlantic canyons that incise the continental shelf and Northeast canyons that do not incise the shelf

509   (Figure 3a). Gorgonian corals were predicted to be more tightly restricted to canyons (Figure 3b),

510   whereas predicted suitable habitat for non-gorgonian corals included more intercanyon areas

511   (Figure 3c). Models for all three taxonomic groups in the Order Alcyonacea showed a tendency

512   toward higher predicted habitat suitability in northern canyons.

513

514   Areas predicted as likely to contain suitable habitat for the Order Scleractinia were also

515   concentrated on the shelf and slope, but were more diffuse with highest concentrations near the

516   central portion of the study area, in the broad vicinity of Hudson Canyon (Figure 3d). Suitable

517   habitat for the Family Caryophyllidae was limited to the shallower areas of the shelf break and

518   upper slope in and near canyons (Figure 3e). Similar to predictions for the order-level model,

519   suitable habitat for the Family Flabellidae was also diffuse and covered a broader depth range than

520   that predicted for Family Caryophyllidae (Figure 3f).

521

522   Suitable habitat for the Order Pennatulacea was predicted to occur broadly across the outer

523   continental shelf, continental shelf-break, upper-middle slope and in basins of the Gulf of Maine

524   (Figure 3g). Suitable habitat for the Suborder Sessiliflorae was predicted to occur exclusively near

525   the shelf break and deeper on the continental slope at depths much deeper than those predicted as

526   suitable in the order-level model (Figure 3h). In contrast, areas of suitable habitat for the Suborder

527   Subselliflorae were similar to the areas predicted by the order-level model (Figure 3i).

528

529
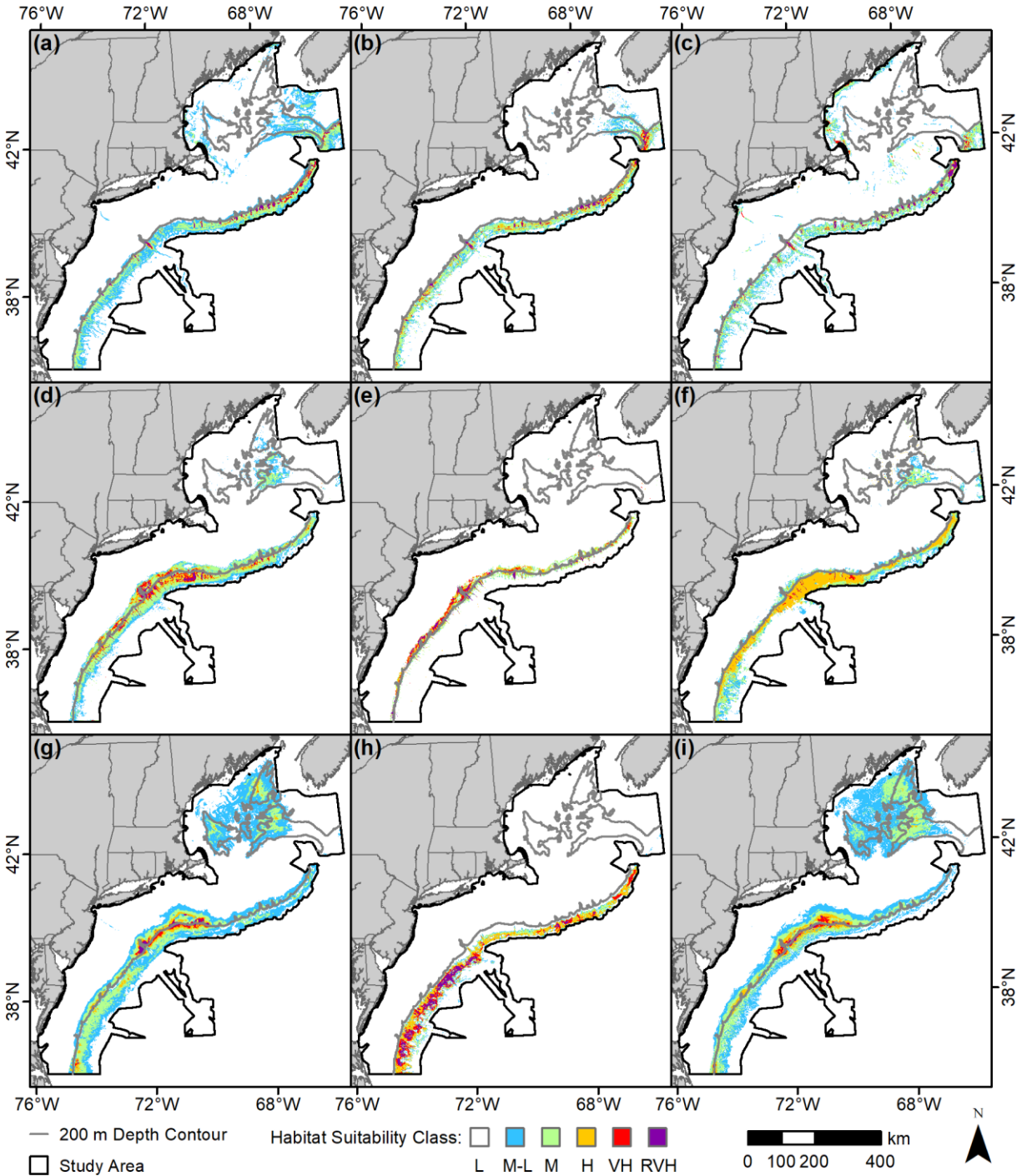
Figure 3. Maps of predicted habitat suitability for (a) Alcyonacea, (b) gorgonian corals, (c) non-

gorgonian corals, (d) Scleractinia, (e) Caryophylliidae, (f) Flabellidae, (g) Pennatulacea, (h)

Sessiliflorae, (i) Subselliflorae. The black lines indicate the extent of the study area. The gray lines

533   denote the 200 m depth contour. Habitat suitability classes: low (L), medium-low (M-L), medium

534   (M), high (H), very high (VH), robust very high (RVH).

535

536   **3.3 Environmental predictor variable importance**

537   For Order Alcyonacea, depth, slope of slope at 1500 m scale, rugosity at 1500 m scale, and annual

538   mean bottom salinity were identified as important environmental predictor variables by multiple

539   measures of importance (Figure 4). Slope at 5 km scale, BPI/slope index at 20 km scale, and

540   surficial sediment percent gravel were each important environmental predictors by one measure of

541   importance. Similar to the order-level model, multiple measures of predictor importance identified

542   depth and rugosity as important environmental predictor variables for gorgonian corals. However,

543   in this instance, rugosity was important at the 370 m scale. Additionally, surficial sediment mean

544   grain size, and surficial sediment percent sand were important environmental predictor variables

545   for gorgonian corals according to multiple measures of predictor importance. Slope at 370 m scale,

546   slope of slope at 5 km scale, and BPI/slope index at 20 km scale were important by one measure

547   of importance (Figure 4). For non-gorgonian corals, depth, slope of slope at 1500 m scale, rugosity

548   at 370 m scale, and annual mean sea surface chlorophyll-a concentration were identified as

549   important environmental predictor variables by multiple measures of importance (Figure 4). Plan

550   curvature/slope index at 1500 m scale and surficial sediment percent sand were important

551   according to one measure of importance.

552

553   Depth and annual mean bottom salinity were identified as important environmental predictor

554   variables for Order Scleractinia by all four measures of predictor importance (Figure 4). Surficial

555   sediment percent gravel was important according to two measures of importance, while slope at 5

556   km scale and annual mean bottom dissolved oxygen were each important by one measure. Depth,

557   slope at 5 km scale, slope of slope at 1500 m scale, annual mean bottom salinity, annual mean

558   bottom dissolved oxygen, and annual mean sea surface chlorophyll-*a* concentration were each

559   important environmental predictors by two measures of predictor importance for Family

560   Caryophyllidae (Figure 4). Like the order-level model, depth and annual mean bottom salinity

561   were identified as important environmental predictors for Family Flabellidae by all four measures

562   of importance (Figure 4). Rugosity at 370 m scale, surficial sediment percent gravel, annual mean

563   bottom temperature, and annual mean sea surface chlorophyll-*a* concentration were each important

564   environmental predictors according to one measure of importance.

565

566   For Order Pennatulacea, annual mean bottom dissolved oxygen was identified as an important

567   environmental predictor variable by all four measures of predictor importance, while depth and

568   annual mean bottom temperature were identified as important by three measures of importance

569   (Figure 4). Surficial sediment percent sand and annual mean sea surface reflectance were each

570   important environmental predictors by one measure of importance. Depth and slope of slope at

571   1500 m scale were recognized as important environmental predictors for Suborder Sessiliflorae by

572   all four measures of predictor importance (Figure 4). Surficial sediment mean grain size and

573   surficial sediment percent sand were each identified as important environmental predictors by two

574   measures of importance. Depth also was identified as an important environmental predictor by all

575   four measures of importance for Suborder Subselliflorae, while annual mean bottom dissolved

576   oxygen and annual mean bottom salinity were considered important environmental predictors

577   according to three measures of importance (Figure 4). Surficial sediment mean grain size and

578   annual mean sea surface reflectance were each identified as important environmental predictors

579   by one measure of importance.

580
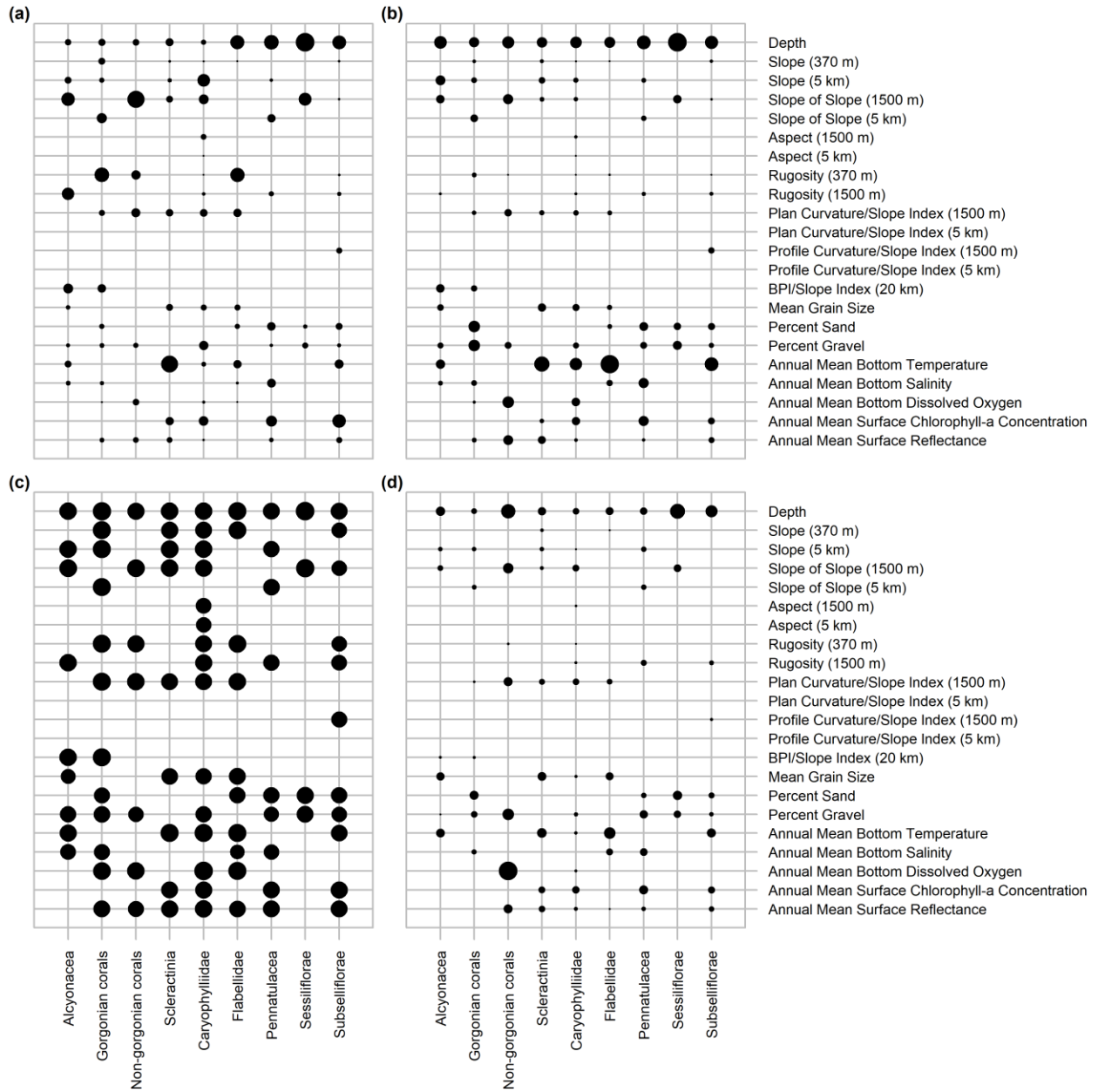
581

582   Figure 4. Bubble plots depicting environmental predictor variable importance for each taxonomic

583   group based on (a) relative contribution, where the area of a circle is proportional to the relative

584   contribution of each environmental predictor variable to increasing the model gain over the course

585   of model fitting, (b) permutation importance, where the area of a circle is proportional to the

586   decrease in training AUC when evaluating models on the permuted training and background data,

587   (c) single variable tests, where the area of a circle is proportional to the mean test AUC for models

588   built with each individual environmental predictor variable, and (d) omission tests, where the area

589   of a circle is proportional to the decline in mean test AUC when each environmental predictor

590   variable is omitted from models.

591

592   **4. DISCUSSION**

593   Prior to this study, regional-scale models predicting DSC habitat suitability for the entire U.S.

594   Northeast did not exist. Regional DSC habitat suitability models in the Northwest Atlantic covered

595   more northerly portions of the Atlantic continental margin including the U.S./Canada

596   transboundary region (Cape Breton, Nova Scotia to Cape Cod, MA; Bryan and Metaxas, 2006,

597   2007) and the Newfoundland and Labrador regions of Canada (Gullage et al., 2017), with little

598   overlap with our study area. Furthermore, global models of DSC habitat suitability have a

599   horizontal resolution on the order of 1000s of meters and did not use regional-scale datasets

600   depicting seafloor topography and substrate characteristics that are critical for constraining

601   predictions of DSC distributions (Davies et al., 2008; Tittensor et al., 2009; Davies and Guinotte,

602   2011; Yesson et al., 2012). Using the novel modeling approach outlined here, we have created

603   models of DSC habitat suitability that are of greater utility for regional conservation, management,

604   and exploration efforts in the U.S. Northeast. By including environmental predictor datasets

605   derived from regional data (e.g., bathymetry and seafloor topography measures from the NOAA

606   CRM, surficial sediment characteristics generated from a regional USGS database), we were able

607   to model habitat suitability at increased spatial resolution. In addition, we implemented a stepwise

608   model selection procedure to develop models with high predictive performance that were also

609   interpretable. The model predictions have been ground-truthed during numerous sampling surveys.

610   Initial review of imagery from these surveys has indicated that the models were successful in

611   predicting locations of suitable habitat for DSCs (Nizinski et al., unpublished data), thus providing

612   further evidence that the methodology described here has provided realistic predictions of where

613   suitable habitat is likely to occur in this region. Additional statistical analysis using this data to

614   ground-truth the models is forthcoming.

615

616   **4.1 Model performance**

617   Models for all taxonomic groups had mean test AUC scores greater than 0.8, generally indicative

618   of excellent model performance. However, there is considerable criticism of the use of AUC values

619   to assess model performance of species distribution models, particularly presence-only models

620   (Lobo et al., 2008; Jiménez-Valverde 2012; Yackulic et al., 2013). For example, while models for

621   rare species tend to have relatively higher AUC values (Franklin et al., 2009), AUC may

622   overestimate model performance for these models because they tend to be overfit to limited

623   occurrence data (Lobo et al., 2008; Breiner et al., 2015). We developed additional statistics to

624   assess model fit and model stability to avoid reliance on AUC as the only measure of model

625   performance. Model fit and model stability were generally greater for the suborder- and family-

626   level groups when compared to their respective order-level groups. Model performance may be

627   poorer for order-level groups because the records that comprise these groups represent species that

628   do not necessarily have the same habitat requirements (e.g., within the Order Alcyonacea,

629   members of the genus *Acanella* typically occur on soft substrates whereas members of the genus

630   *Paragorgia* occur on hard substrates). This suggests that, when possible, model groups based on

631 taxonomy should be at higher taxonomic resolution and/or be comprised of taxa whose

632 distributions can reasonably be expected to have similar relationships to the environmental

633 predictor variables used in the models.

634

635 **4.2 Implications for natural history and biogeography of DSCs in the U.S. Northeast**

636 A complete evaluation of the habitat suitability models developed here in light of previous work

637 on the natural history and biogeography of DSCs in the U.S. Northeast is beyond the scope of this

638 paper. However, we will highlight a few relevant comparisons of previous observations to our

639 model predictions.

640

641 Since the 1980s, the majority of *in situ* surveys for DSCs have occurred in submarine canyons,

642 particularly (from north to south) Heezen, Lydonia, Oceanographer, Hendrickson, Baltimore, and

643 Norfolk canyons (Packer et al., 2007; 2017b). The larger, northern canyons such as Lydonia and

644 Oceanographer have hard substrate along most of their axes and walls that support many DSCs.

645 The slope south of Georges Bank is covered mostly by soft substrates, supporting, with some

646 exceptions, mainly scleractinians on the upper slope and pennatulaceans deeper than ~1500 m.

647 Some harder substrate is found at depths greater than 1400 m on the mid-Atlantic slope off New

648 Jersey. Here, members of the orders Pennatulacea and Scleractinia are common but sparsely

649 distributed on the upper slope. Pennatulaceans and *Acanella arbuscula* (an alcyonacean, gorgonian

650 coral) occur on the lower continental slope. The larger, southern canyons such as Baltimore and

651 Norfolk canyons have less hard substrate, some of which occurs at depths much shallower than

652 that observed in the northern canyons. Thus, large coral assemblages, composed mainly of

653 alcyonaceans, occur in much shallower water than in the northern canyons. Additionally,

654 pennatulaceans occur on the upper slope whereas pennatulaceans and *A. arbuscula* are commonly

655 observed on the lower slope (Packer et al., 2017b). In general, the predicted distributions of

656 suitable DSC habitat from our models support these observations of the broad-scale distribution

657 patterns of DSC in the region (Figure 3).

658

659 Alcyonaceans are generally more densely distributed and diverse in the canyons than on the

660 adjacent slope. Some species, such as those restricted to hard substrates, are only found in the

661 canyons while other species that frequently occur on soft substrates, such as *Acanella arbuscula*,

662 are found both in canyons and on the slope (Hecker et al., 1980). The observation that many DSCs

663 in the Order Alcyonacea are restricted to the canyons is supported by our model predictions for

664 the three taxonomic groups in Order Alcyonacea (Figure 3). In particular, areas predicted to

665 contain suitable habitat for gorgonian corals, the most likely of all modeled taxonomic groups to

666 form complex, rigid, three-dimensional structure that can serve as important habitat for fishes and

667 invertebrates, were concentrated in canyons, particularly on steep canyon walls.

668

669 However, there appear to be two distinct distributional patterns for species in the Order Alcyonacea

670 (Watling and Auster, 2005). Most are deep-water species that occur at depths >500 m on the lower

671 continental slope and rise (e.g., species in the genera *Acanthogorgia*, *Acanella*, *Anthomastus*,

672 *Anthothela*, *Clavularia*, *Lepidisis*, *Radicipes* and *Swiftia*). Other species (e.g., *Paragorgia*

673 *arborea, Primnoa resedaeformis, Paramuricea spp.*) occur on the continental shelf to the upper

674 continental slope at depths of <500 m. Of the latter species, *Paragorgia arborea* and *Primnoa*

675 *resedaeformis* are frequently documented. These species are not only reported as being widespread

676 in the Northwest Atlantic (Tendal, 1992; Breeze et al., 1997; Bryan and Metaxas, 2006), but, more

677   specifically, are commonly observed on the Northeast Peak of Georges Bank (Theroux and

678   Grosslein, 1987), in the deep basins of the Gulf of Maine (e.g., Jordan Basin) and other areas where

679   fishing is limited due to rough topography (Auster 2005; Auster et al., 2013). Additionally, many

680   species represented in the Order Alcyonacea, several of which were recently discovered, are

681   dominant members of the epifaunal assemblage at the New England Seamounts (Packer et al.,

682   2007; Packer et al., 2017a, 2017b). Because the Alcyonacea groups were modeled at the order and

683   suborder level, these finer-scaled distributional patterns observed for specific genera or species

684   were not captured by our models.

685

686   Most representatives of Order Scleractinia in this region are small, solitary organisms (e.g.,

687   *Dasmosmilia lymani, Desmophyllum dianthus, Flabellum* spp.) found on the edge of the shelf as

688   well as in the canyons and on the New England Seamounts (Cairns, 1981; Cairns and Chapman,

689   2001; Packer et al., 2007; Packer et al., 2017a, 2017b). Colonial structure-forming scleractinians

690   such as *Solenosmilia variabilis* and *Lophelia pertusa*, may also occur on hard substrates in the

691   canyonized areas of the continental shelf-break and slope as well as on seamounts, but have not

692   been well-documented in the historical record (Hecker, 1980; Hecker et al., 1980; Hecker et al.,

693   1983; Moore et al., 2003, 2004) and, therefore, were not present in our DSC database. Predictions

694   of suitable DSC habitat from our models support the observation that species in the Order

695   Scleractinia occupy a wider range of habitats. Areas predicted to have 'high' or 'very high' habitat

696   suitability for taxonomic groups in Order Scleractinia occurred across the continental shelf and

697   slope and were not restricted to the canyons like predictions for Order Alcyonacea (Figure 3). This

698   pattern is likely driven by the fact that the only representatives of Order Scleractinia in our DSC

699   database for the U.S. Northeast were solitary cup corals, which can be found on both hard and soft

700   substrates. For example, species of the genus *Flabellum* can colonize both hard and soft substrates;

701   members of the genus *Desmophyllum* generally colonize hard substrates, *Dasmosmilia* species

702   colonize soft substrates, and members of the genus *Javania* generally colonize hard substrates

703   (Packer et al., 2007, 2017b). Order Scleractinia was represented overwhelmingly in our DSC

704   database by the two genera *Dasmosmilia* and *Flabellum*, with a large number of *Dasmosmilia*

705   records from the Hudson Canyon vicinity. This diffuse pattern is in contrast to what would be

706   expected for framework-forming scleractinians such as *L. pertusa* and *S. variabilis*. These colonial

707   scleractinians are usually restricted to consolidated substrates and often occur on steep slopes such

708   as canyon walls. However, the only records of *L. pertusa* in our database were of dead rubble and

709   were excluded from analysis.

710

711   Although the majority of species in Order Pennatulacea in this region are found on the continental

712   slope, in the canyons, and on the seamounts, two of the most common and widespread species are

713   found over wide swaths of the continental shelf. *Pennatula aculeata* (the common sea pen) is

714   common in the Gulf of Maine and occurs as far south as the Carolinas (Langton et al., 1990; Packer

715   et al., 2007), whereas *Stylatula elegans* (the white sea pen) is found on the outer shelf in the mid-

716   Atlantic region (Theroux and Wigley, 1998). From our models, areas with 'high' or 'very high'

717   habitat suitability for Order Pennatulacea were predicted across the continental shelf and slope as

718   well as basins of the Gulf of Maine (Figure 3). Looking at the nested suborder-level models, it is

719   clear that this pattern was driven primarily by records in our DSC database from Suborder

720   Subselliflorae, specifically representatives of the genera *Pennatula* and *Stylatula*, taxa known to

721   be widely distributed in soft sediment habitats of the continental shelf and slope (Packer et al.,

722   2007, 2017b). In contrast, predictions of suitable habitat for sea pens in Suborder Sessiliflorae

723   were generally more restricted to the continental slope, primarily in canyons but occurring in inter-

724   canyon areas as well. The largest patches of suitable habitat for the Suborder Sessiliflorae were

725   predicted to occur in the southern portion of the domain. These results illustrate that order-level

726   models may misrepresent the distributions of specific groups within the order. Numerically

727   dominant species can mask distributions of other taxa, particularly when taxa within the order have

728   disparate habitat requirements.

729

730   Overall, the predictions of DSC habitat suitability generated from our models generally support

731   the observations regarding broad-scale DSC distributions presented here. However, models

732   generated for individual species or genera would provide information about finer-scale distribution

733   patterns and would greatly expand our knowledge of DSC biogeography in the U.S. Northeast.

734

735   **4.3 Insights from environmental predictor variables**

736   Not surprisingly, depth, the dominant gradient over which fauna are distributed in this system,

737   was identified as important by at least two and sometimes all measures of environmental

738   predictor variable importance for each of the taxonomic groups. In addition to depth, measures of

739   seafloor topography were consistently important in models for the taxonomic groups within

740   Order Alcyonacea. Slope at a broader scale may be an important predictor for coral taxa, such as

741   gorgonian corals, that are predominantly found on the continental slope in the Northwest Atlantic

742   (Jones, 2008). Broad-scale slope and slope of slope (e.g., 1.5 and 5 km scales) may also be

743   proxies for features that accelerate and direct tidal currents in the region, and thereby deliver

744   food and nutrients to DSC ecosystems (Thiem et al., 2006). Slope may also be a proxy for

745   distribution of hard substrates (Metaxas and Bryan, 2007). In addition, measures of surficial

746   sediment characteristics were among the most important environmental predictors for the

747   gorgonian corals.

748

749   Bottom salinity was identified as important for the taxonomic groups within Order Scleractinia.

750   Given that salinity is fairly constant in deep waters (~34-35 psu), deep-sea scleractinian corals

751   occur within a relatively narrow salinity range. Thus, the importance of bottom salinity as a

752   useful predictor of suitable habitat for Scleractinia would be expected.

753

754   Of the taxonomic groups modeled, members of the Order Pennatulacea groups are the only taxa

755   most frequently found in soft sediments. Thus, surficial sediment mean grain size would be

756   expected to be an important predictor for sea pen habitat suitability. However, measures of

757   surficial sediment characteristics were far more important for Suborder Sessiliflorae than for the

758   other groups within Order Pennatulacea. For the other groups, measures of bottom salinity,

759   temperature, and dissolved oxygen were consistently more important.

760

761   Depth, slope and other aspects of geomorphology, sediment characteristics, and temperature have

762   all been recognized in previous studies as important correlates of DSC distribution (e.g., Davies

763   and Guinotte, 2011; Yesson et al., 2012). Although only identified as an important predictor

764   variable for a few of our taxonomic groups (non-gorgonian corals, Order Scleractinia, Family

765   Flabellidae), other studies of DSC distributions in the Northwest Atlantic (Bryan and Metaxas,

766   2007), North Atlantic (Knudby et al., 2013) and the southern California Bight (Huff et al., 2013)

767   have identified surface chlorophyll-*a* as an important predictor of DSC habitat. Thus, there may

768   be an important link between surface primary productivity and DSC habitat suitability. A statistical

769   interaction between surface turbidity and surface chlorophyll-*a* may represent a proxy for areas of

770   higher flux of particulate organic carbon (POC) and dissolved organic carbon (DOC) from the

771   mixed layer (Knudby et al., 2013).

772

773   Depth and bottom temperature are consistently recognized as important factors influencing

774   distributions of deep-sea corals. Predicted depth and temperature ranges for our modeled groups

775   (Appendix B) are within those reported in the literature (Packer et al., 2007; Tittensor et al., 2009;

776   Davies and Guinotte, 2011; Yesson et al., 2012; Guinotte and Davies, 2014). Dissolved oxygen,

777   salinity, and sediment characteristics may directly influence DSC distributions, but may also be

778   proxies for other oceanographic processes. For example, mean sediment grain size is highly

779   correlated with tidal current energy (Visher, 1969).

780

781   **4.4 Methodological advances to presence-only modeling**

782   Fusion of presence-only datasets with environmental predictor databases represents a powerful

783   tool in species distribution modeling, particularly for deep-sea biota for which absence data are

784   limited. Even in the presence of sampling bias (usually inevitable in presence-only datasets), the

785   resulting models synthesize all available information on the distribution of a taxonomic group with

786   knowledge of relevant environmental variables. Such models can inform conservation and

787   management planning while also providing a foundation for field survey and exploration efforts

788   to validate and improve models. However, it is important that results be carefully interpreted and

789   applied.

790

791   In developing habitat suitability models for the U.S. Northeast region, we were constrained

792   primarily by the type of available DSC records (presence-only with no confirmed absences).

793   Additionally, we were restricted by the number and quality of available environmental predictor

794   variable datasets. Given these constraints, we aimed to extract the maximum possible information

795   from the DSC records as well as any potential environmental predictor variables available from

796   oceanographic, geomorphological, and environmental data mining. Recognizing the limitations of

797   presence-only datasets, we introduced several innovations to mitigate potential pitfalls. We

798   developed a novel stepwise model selection algorithm for MaxEnt based on a weighted

799   combination of cross-validation AUC and training AICc statistics. Additionally, we presented a

800   method to classify MaxEnt logistic predictions to create comparable habitat suitability classes

801   across different models. We successfully used those methods to improve the predictive

802   performance, parsimony, and interpretability of the final selected models, and to facilitate

803   comparisons of habitat suitability across taxa. These techniques are broadly applicable to habitat

804   suitability modeling of presence-only data.

805

806

807

808   **4.5 Caveats and limitations**

809   Although we present some significant advances to presence-only models using MaxEnt, there are

810   several key caveats and limitations to keep in mind. First, care must be taken when making

811   comparisons within or between model/taxonomic groups. For example, the predicted habitat

812   suitability values are not probabilities of occurrence, and cannot be compared across models for

813   different groups. While our habitat suitability classes can be compared across taxonomic groups,

814   the choice of breakpoints (i.e., false positive error to false negative error cost ratios) defining

815   these classes involves some subjectivity not readily conveyed in map form.

816

817   Predictions of DSC habitat suitability are affected by sampling bias. Models generated from

818   presence-only data will only predict suitable habitat in areas similar to areas where DSCs were

819   found previously; the environmental envelope cannot be expanded. Therefore, future survey

820   efforts should always include some "risky" sampling in locations outside areas predicted to be

821   suitable habitat to expand the extent of the environmental space that has been sampled. Other

822   modeling techniques (e.g., presence-absence or abundance models) could use information

823   collected in less suitable habitat. Model predictions from this study do not necessarily correlate

824   with abundance, density, or diversity. Future field surveys are needed to assess such

825   relationships.

826

827   The spatial scale at which models can be applied is limited by the accuracy of the source data. In

828   this case, the 370 m model grid cell size was chosen with key environmental parameters (e.g.,

829   bathymetry) and the spatial precision of presence records in mind. The maps represent habitat

830   suitability at the resolution of the prediction grid. Predictions of habitat suitability, therefore, are

831   at the scale of a grid cell; no more specific location should be inferred.

832

833   The temporal scale of predictions must also be considered. Models presented in this study are

834   based on historical records collected from the 1800s to the present. Given the slow growth rates

835   of many DSC taxa, it is possible that predictions of suitable habitat will include areas in which

836   DSC existed previously, but have since been eliminated by disturbance. However, habitat

837   suitability models are also expected to overpredict actual occurrence for other reasons. For

838   example, the inherent stochasticity in distributions of sessile organisms with a biphasic life cycle

839   and the statistical realities of predicting a relatively rare habitat can lead to overpredictions of

840   coral occurrences. Even conservative thresholds can be shown to overpredict actual occurrence

841   unless false positive costs are weighted heavily. Moreover, our models do not account for habitat

842   dynamics. Bottom substrate is known to be dynamic at the scale of years to decades (Keller and

843   Shepard, 1978; Brothers et al., 2013). Additionally, changes in climatological factors may alter

844   relevant oceanographic conditions in DSC habitat, including bottom temperature and carbonate

845   system parameters, over long-time scales (Davies and Guinotte, 2011). Such issues deserve

846   further study.

847

848   We note that some of the environmental predictor variables we use are models themselves,

849   whether derived through interpolation, geostatistical modeling, or more complex hydrodynamic

850   modeling. These products have associated uncertainty for which we did not directly account. As

851   a result, caution should be used when applying the habitat suitability models on a pixel by pixel

852   basis. The underlying assumption that the environmental conditions at a pixel are well-

853   represented by the datasets we have compiled should be field tested and validated before

854   considering precise application of the models at the pixel level in any given area.

855

856   It is important to bear in mind that the taxonomic groups modeled were chosen on the basis of

857   the species occurring in the available DSC data. For example, our historical database for the U.S.

858   Northeast is strongly biased for solitary scleractinians. Solitary scleractinians and colonial

859   scleractinians such as *Lophelia pertusa* are sometimes found in different types of habitats (soft

860   sediments versus steep canyon walls). Thus, the Scleractinia model we produced is likely not

861   typical of deep-sea scleractinians as a whole. Our results reflect predictions only for taxa actually

862   included in the records used to fit the models.

863

864   Notwithstanding these caveats and limitations, we have shown that presence-only data can be

865   used to produce maps of predicted habitat suitability that, if carefully applied, can ensure that the

866   best available synthesis of scientific information is available for management, conservation and

867   planning efforts.

868

869   **4.6 Management and conservation implications**

870   As syntheses of available DSC presence and environmental predictor information in the region,

871   the models and maps described here have met important information needs for New England

872   (NEFMC; https://s3.amazonaws.com/nefmc.org/200102_Coral_Amendment-final-with-IRFA-edits.pdf,

873   https://s3.amazonaws.com/nefmc.org/Appendix-B-Coral-zone-boundary-development.pdf) and Mid-

874   Atlantic   (MAFMC;   http://www.mafmc.org/s/DeepSea-Corals-EA_Signed-FONSI.pdf)   Fishery

875   Management   councils,   regional   spatial   planning   processes   (e.g.,

876   https://portal.midatlanticocean.org/data-catalog/conservation/ Habitat for soft corals (modeled)), as

877   well as guided targeted field survey and exploration efforts to expand and confirm knowledge of

878   DSC distribution in the region. Additionally, a high correlation between recent coral observations

879   and locations predicted to be suitable coral habitat has increased confidence in using the regional

880   DSC habitat suitability models to inform current and future management decisions of the Councils.

881

882   Available global models of DSC distribution (e.g., Yesson et al., 2012) do not incorporate the

883   latest available regional data, and more importantly, do not provide the required spatial resolution

884   to assist regional spatial planning efforts in a meaningful way. Thus, in addition to the

885   methodological and ecological implications of the work presented here, results are expected to

886   advance scientific contributions to real-world applications at the U.S. state, regional and federal

887   scale.

888

889   **5.   CONCLUSIONS AND FUTURE DIRECTIONS**

890   This is the first comprehensive DSC habitat modeling study to be published for the U.S. Northeast.

891   Despite the limitations of presence-only data, we have demonstrated several novel extensions to

892   the traditional MaxEnt analysis workflow that improve model selection, accuracy assessment, and

893   comparability of results across disparate taxonomic groups. These approaches are applicable to all

894   other species distribution modeling efforts that utilize presence-only data, and could be used to

895   improve analysis and interpretation of results of species distribution models based on MaxEnt—a

896   critical tool for sparsely documented deep-sea taxa in particular.

897

898   In the interim between development and publication, these models have provided the basis for and

899   contributed to providing much needed information for spatial planning, management, conservation

900   and ocean exploration efforts in the region. An extensive amount of fieldwork, focused on

901   distributions, abundances, and diversity of DSC, has been conducted in the U.S. Northeast

902   recently. Multibeam sonar systems have collected high-resolution bathymetry and spatial

903   information at spatial scales below those resolved by this regional model (~370 m) throughout

904   much of the region. Remotely-operated vehicles and towed-camera systems collected high-

905 resolution imagery, documenting both coral presence and absence in areas surveyed. But most

906 importantly, these field surveys were planned in conjunction with the model predictions developed

907 here. Thus, we have had numerous opportunities to ground-truth the models and to gather new

908 data for subsequent improvements in the resolution and predictive accuracy of these models. This

909 iterative, integrated modeling and field survey process has proven to be an extremely successful

910 protocol.

911

912 The next generation of models for the U.S. Northeast are currently under development. We believe

913 that a systematic approach to DSC spatial ecology should be the standard operating procedure:

914 development of synthetic models based on all available knowledge, followed by model-driven

915 field surveys and validation, resulting in the production of improved and field validated spatial

916 models. This iterative approach, when integrated with management processes, is a powerful tool

917 for science-based conservation, management, and spatial planning (MacLean et al., 2017;

918 Georgian et al., 2019).

919

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921

927   marine spatial planning and conservation. He is sorely missed but his legacy lives on in his body

928   of published work.

929

AUTHOR CONTRIBUTIONS

- BPK conceived, designed, and conducted this work, analyzed and interpreted results, and prepared this manuscript.

- MP conducted work, analyzed and interpreted results, and assisted with manuscript preparation.

- AFD conducted work, analyzed results, and assisted with manuscript preparation.

- DBP obtained funding for, conceived, contributed data, analyzed data, interpreted results, and assisted with manuscript preparation.

- DSD contributed data, managed data, assisted with specific analyses, and reviewed the manuscript.

- MSN obtained funding for, conceived, and interpreted results from this work, assisted with manuscript preparation, reviewed and edited the manuscript.

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