

Predictive distribution modelling of cold-water corals in the Newfoundland and Labrador region

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ABSTRACT: Information on the distribution of cold-water corals in Newfoundland and Labrador (NL) waters largely comes from scientific multi-species trawl surveys and commercial fisheries observer programs. As a result, knowledge of coral distribution has been influenced by the type of gear used and by fishing effort distribution, leaving large knowledge gaps beyond the fishing footprint along the edge of the continental shelf. In support of international efforts to preserve marine biodiversity, maximum entropy (Maxent) species distribution models (SDMs) were generated for cold-water coral functional groups and individual species to predict their distributions throughout the NL region. Although functional group models have also been produced using a random forest (RF) approach in the past, the species level models provided here are thought to be the first of their kind in the NL region. Models generated for this study were found to be statistically robust, even for species with limited observation data, with average area under the receiver operating curve and true skill statistic values of 0.914 and 0.684, respectively. Findings indicated that models for functional groups typically overgeneralized habitat suitability and did not always reflect the distribution of the individual species they were based on. Furthermore, suitable habitats delineated by Maxent fit closely to *in situ* observations. In general, the highest suitability was found along the continental shelf break and within canyons on the upper continental shelf, with Maxent models capturing variations in habitat suitability not previously described in the region.

KEY WORDS: Cold-water corals · Species distribution modelling · Maxent · Atlantic Canada · Conservation

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INTRODUCTION

Coral ecosystems have been extensively studied in shallow tropical water, but knowledge of cold-water corals is more recent, as a result of the difficulties in sampling or observing them *in situ*. Recent advances in underwater technologies, coupled with rising pressures to support marine conservation, have led to an increased understanding of these species and a better appreciation of their ecological significance in deep-sea environments (Roberts et al. 2006, 2009, Cairns et al. 2007, Roberts & Cairns 2014).

Cold-water corals are a multi-taxonomic assemblage of azooxanthellate skeletal cnidarians (Cairns et al. 2007), capable of surviving below the photic zone (Roberts et al. 2009), whose distribution is thought to be largely driven by depth, substrate type, food availability, and currents (Bryan & Metaxas 2007, Buhl-Mortensen et al. 2014). Typically found between 50 and several thousand metres depth, cold-water corals are often concentrated along shelf edges or other areas where the flow of water rich in particulate organic matter provides a continuous supply of food and prevents the accumulation of fine

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sediments, exposing hard substrates suitable for settlement (Mortensen et al. 2006, Wareham & Edinger 2007, Turley et al. 2007, Edinger et al. 2011, Buhl-Mortensen et al. 2014).

Gorgonian coral forests in the Newfoundland and Labrador (NL) region can form locally dense aggregations with densities of up to 5 ind. 100 m⁻² (Mortensen & Buhl-Mortensen 2004, Baker et al. 2012), with individual colonies reaching 1 to 2.5 m in height, depending on the species. Most gorgonian corals are dependent on hard substrates, with the exception of some of the bamboo corals (e.g. *Acanella*) (Wareham & Edinger 2007, Baker et al. 2012), and sometimes *Keratoisis* (Neves et al. 2015a). Sea pen meadows in the region can have densities as high as 31 ind. m⁻² although most sea pens are broadly distributed in multi-species assemblages on muddy bottoms (Wareham & Edinger 2007, Baker et al. 2012).

Similar to coral–fish associations in other regions, cold-water coral habitats in NL can be important habitats for sustaining fish and diversity, and for abundance of some commercially important fish and invertebrate species (Edinger et al. 2007b, Baillon et al. 2012). Unfortunately, due to their slow growth rates and sensitivity, cold-water corals are extremely vulnerable to physical disturbances, particularly those resulting from anthropogenic activities (Roberts et al. 2006).

Bottom trawling represents one of the most damaging practices in marine environments, leading to the destruction of corals or to smothering as a result of sediment resuspension (Thrush & Dayton 2002, Watling 2005, Clark et al. 2016). Studies indicate that many known coral habitats in the North Atlantic, including Atlantic Canada, have already been damaged or destroyed as a result of deep-sea fishing activities (Hall-Spencer et al. 2002, Gass & Willison 2005, Edinger et al. 2007a), and the growing interest in offshore oil and gas in the region only amplifies these threats. As a result, the identification of areas that are likely to host coral habitat, but have not already been impacted by fishing or other human activities, has become an important marine conservation goal, which is aided by species distribution modelling (Bryan & Metaxas 2007, Davies & Guinotte 2011, Yesson et al. 2012, 2015).

In Canada and adjacent waters, efforts are underway to identify and protect important areas of vulnerable marine ecosystems (VMEs), including cold-water coral and sponge habitats, in response to the United Nations General Assembly (UNGA) 2006 Resolution 61/105 (Kenchington et al. 2009, 2014). VMEs are defined by the Food and Agriculture Organiza-

tion (FAO) as ecosystems which are functionally significant, rare, fragile, structurally complex, and slow to recover after disturbance (UNGA 2006, FAO 2009). This definition encompasses cold-water corals and sponges, species that have since been identified as VME indicators by the Northwest Atlantic Fisheries Organization (NAFO) (Kenchington et al. 2015). In 2010, Canada also committed to meeting the Aichi conservation targets set by the Convention on Biological Diversity (CBD), including Target 11 that aims to protect 10% of coastal and marine areas by 2020 (CBD 2010). In support of these conservation goals, NAFO has made considerable progress mapping the distribution of many species in the NL region, including cold-water corals. As a result of this work, the region has implemented closures in 13 areas containing VMEs, only one of them being located within Canadian waters (NAFO 2015).

To support these closures, information on the distribution of cold-water corals was largely collected using bottom trawls, as *in situ* surveys, for example using remotely operated vehicles (ROV), are limited by their high costs and inability to investigate large areas efficiently. In the NL region, this research was concentrated along the continental shelf, where fishing pressure puts cold-water coral species at greatest risk. However, significant portions of the continental slope and abyssal plains within Canada's exclusive economic zone (EEZ) have been left unsampled and unprotected.

In areas that have not yet been sampled directly, species distribution models (SDMs) are increasingly used by conservation ecologists to better understand the habitat ranges of species that are rare, endangered, or difficult to access, due to the ability of these models to identify suitable habitats using existing environmental data (Blank & Blaustein 2012, Clements et al. 2012, Stirling et al. 2016). As such, SDMs have become particularly useful for assessing the distribution of cold-water corals and sponges regionally (Bryan & Metaxas 2007, Knudby et al. 2013, Rengstorf et al. 2013, Tong et al. 2015, Howell et al. 2016) and globally (Davies & Guinotte 2011, Yesson et al. 2012, 2015). SDMs can be generated using a variety of methods including, but not limited to, generalized linear regression and non-parametric smoothing (Guisan & Zimmerman 2000), environmental envelopes (Busby 1991), and machine learning algorithms (Elith et al. 2006). When properly derived, these methods represent a cost-effective and non-destructive means of generating habitat suitability maps in areas with limited data (Busby 1991).

The goal of our study was to predict the distribution of cold-water corals in the NL region, at both the functional group and species level using a maximum entropy (Maxent) approach; a method that has been successfully used for cold-water coral modelling in other regions (Georgian et al. 2014, Tong et al. 2015). This contrasts previous work done in the region using random forest (RF) modelling (Guijarro et al. 2016) and supports ongoing conservation research in an effort to meet Aichi Target 11 and preserve marine biodiversity in Canadian waters.

MATERIALS AND METHODS

Study area

The study area is located on the east coast of Canada and includes most of the NL waters, covering a large region of 1 109 139 km² (Fig. 1). Due to the modelling approach used, the boundaries of the study area were delineated to ensure the presence of all environmental variables at all locations. As a consequence, the study area did not include portions of the abyssal plain located off the coast of Labrador as well as a small region of the Flemish Cap, but extended at several places beyond the EEZ into deeper waters. Coastal waters for which most coral distribution and environmental data do not exist as continuous layers were also excluded from the analysis.

Data

Data used for the generation of SDMs originated from a range of sources (Table 1). As a result they varied in terms of resolution, extent, and quality. To account for this, individual datasets were reviewed prior to use in Maxent in order to remove erroneous data.

Coral data

Presence-only coral data (2004 to 2011) (Table 1 and Fig. S1 in Supplement 1 at www.int-res.com/articles/suppl/m582p057_supp.pdf) were obtained from the Department of Fisheries and Oceans Canada

(DFO) for NAFO Zones 2HJ and 3KLMNOPnPs (Fig. 1). Data were collected as part of scientific multi-species trawl surveys using a random sampling design, stratified by depth (McCallum & Walsh 1996). More recent data that had not been assessed by DFO as of 2016 were not included in the analyses. Additionally, data off the northeastern coast of Labrador (NAFO Zone 2G), which is sampled by the fishing industry rather than by DFO, were not included. To provide a basis for comparison with RF models generated by Guijarro et al. (2016), data were organized by functional group, and positional information was extracted for all large gorgonian, small gorgonian, and sea pen coral species described in Table 2. However, because RF models have not been performed on cup corals, soft corals or antipatharians, models for these groups were generated at the species level

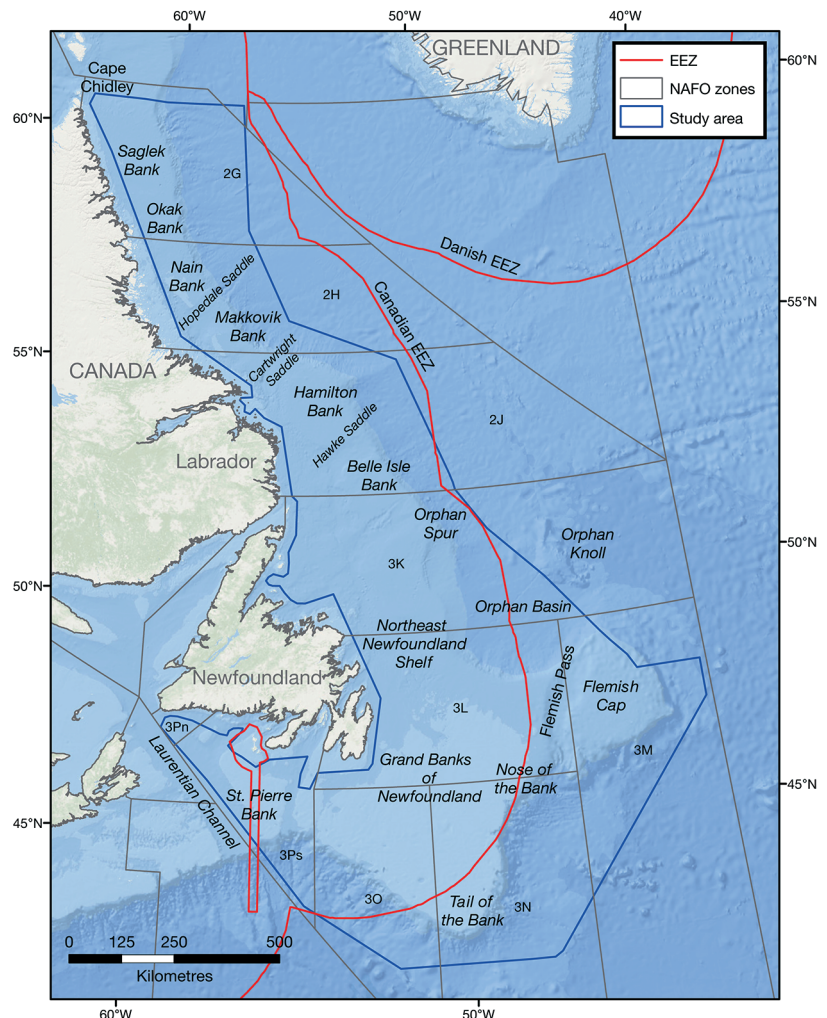


Fig. 1. Study area showing the Canadian exclusive economic zone (EEZ), the Northwest Atlantic Fisheries Organization (NAFO) fisheries management zones (e.g. 3K, 3L), and key oceanographic features

Table 1. Datasets used to generate species distribution models. DFO: Department of Fisheries and Oceans; GEBCO: General Bathymetric Chart of the Oceans; NOAA: National Oceanic and Atmospheric Administration; MODIS: moderate resolution imaging spectroradiometer

| Dataset | Source | Temporal extent | Description |
|---------------------|-------------------------------------|--------------------|---|
| Coral species | DFO | 2004–2011 | Coral species observations made during scientific survey trawls |
| Bathymetry | GEBCO | Published in 2014 | 30 arc-second gridded bathymetric data |
| Temperature | DFO | 1910–2016 | Point temperature data taken near bottom |
| Salinity | DFO | 1910–2016 | Point salinity data taken near bottom |
| Surface chl a | NOAA | 2016 | Annual average of chl a concentrations recorded by the MODIS sensor at 0.5° resolution |
| Terrain derivatives | Derived from bathymetry | Same as bathymetry | TASSE Toolbox v. 1.0 (Lecours 2015) was used to derive standard deviation, slope, easternness, northernness, and relative deviation from mean value (RDMV) surfaces from the GEBCO bathymetry |
| Bias file | Derived from coral species datasets | 2004–2011 | Heat map depicting sampling effort throughout the study area generated using positional information of coral observations supplied by DFO |

only. Coral observations for species present in 20 or more trawls as outlined in Table S1 in Supplement 1, were modelled individually for comparison with functional group models. With the exception of models for large gorgonian species, which are presented here, models at the species level are available in Section I in Supplement 1. To ensure the generation of robust models, species present in fewer than 20 trawls were excluded from further analysis. Remaining data were imported into ArcGIS 10.3 (ESRI 2014) where duplicate points sharing exact coordinates were reduced to single observations, and data points falling outside the boundaries of the study area were removed.

Data layer resolution and extent

The average length of the scientific trawls used for recording coral presences was 1.4 km (McCallum &

Walsh 1996, Wareham & Edinger 2007). To account for spatial uncertainty and ensure the validity of the final SDMs, all environmental layers (observed and derived) were generated at a 1.6 km resolution. These layers, as well as the coral observations, were then transformed into the World Geodetic System 1984 (WGS 1984) geographic datum and clipped to the extent of the environmental layer encompassing the smallest area of the seabed.

Environmental data layers

Four environmental datasets were obtained on the basis of ecological significance for generating cold-water coral SDMs. Bathymetric data were retrieved from the General Bathymetric Chart of the Oceans (GEBCO, www.gebco.net) database in the form of an ASCII file containing gridded bathymetric data at 30 arc-second resolution.

Table 2. Functional groups of cold-water corals considered in this study (adapted from Edinger et al. 2007a)

| Functional group | Species |
|------------------------|--|
| Large gorgonian corals | <i>Primnoa resedaeformis</i> , <i>Paragorgia arborea</i> , <i>Keratoisis grayi</i> , <i>Acanthogorgia armata</i> , <i>Paramuricea</i> spp. (<i>P. placomus</i> or <i>P. grandis</i>) |
| Small gorgonian corals | <i>Acanella arbuscula</i> , <i>Radicipes gracilis</i> , <i>Anthothela grandiflora</i> |
| Cup corals | <i>Flabellum alabastrum</i> , <i>Vaughanella margaritata</i> , <i>Desmophyllum dianthus</i> , <i>Dasmosmilia lymani</i> |
| Sea pens | <i>Distichophyllum gracile</i> , <i>Funiculina quadrangularis</i> , <i>Halipteris finmarchica</i> , <i>Pennatula grandis</i> , <i>Pennatula aculeata</i> , <i>Pennatula</i> sp., <i>Umbellula lindahli</i> , <i>Anthoptilum grandiflorum</i> |
| Soft corals | <i>Gersemia rubiformis</i> , <i>Gersemia</i> spp., <i>Duva florida</i> , <i>Anthomastus grandifloras</i> , <i>Anthomastus agarigus</i> , <i>Anthomastus</i> spp., <i>Drifa glomerata</i> , <i>Drifa</i> spp. |

Bottom temperature and bottom salinity data collected between 1910 and 2016 were provided by DFO. These data consisted of 146 114 temperature points and 88 521 salinity points, collected by either conductivity temperature depth instruments (CTDs) deployed at varying depths throughout the study area, or sensors mounted directly on equipment during trawls. To ensure that these data represented near-bottom conditions, additional quality checks were performed to exclude data points for which recorded bottom depths were >20% different from GEBCO bathymetry in that location. The remaining points were interpolated using inverse distance weighting (IDW) in ArcGIS 10.3 (ESRI 2014) to construct raster surfaces.

Mean monthly chlorophyll *a* (chl *a*) concentration (mg m^{-3}) data at 0.5° resolution were retrieved from the NASA Earth Observations website (<http://neo.sci.gsfc.nasa.gov>). Based on known correlations between the presence of cold-water corals and levels of primary productivity (Leverette & Metaxas 2005, Bryan & Metaxas 2007), raw surface chl *a* concentrations measured by the moderate resolution imaging spectroradiometer (MODIS) sensor aboard the Terra and Aqua satellites were incorporated into the models. In order to capture the largest intra-annual variation in chl *a* concentrations, data from February 2016 and August 2016 were combined in ArcGIS 10.3 (ESRI 2014) to produce a mean annual chl *a* concentration surface for the study area.

Terrain derivatives

Terrain derivative layers were chosen based on work by Lecours et al. (2016) which found local mean, standard deviation, slope, easternness, northernness, and relative deviation from mean value (RDMV) to be a useful combination of variables for species distribution modelling, reducing collinearity and maximizing the information extracted from terrain data. Often recognized as proxies for current and substrate type, these attributes are considered to be particularly important components for the generation of SDMs for cold-water corals (Genin et al. 1986, Bryan & Metaxas 2007, Dunn & Halpin 2009). For the purpose of this study, the terrain attribute selection (TASSE) toolbox v. 1.0 (Lecours 2015) was used to derive the 6 terrain attributes described above from the GEBCO bathymetric surface for the NL region. Local mean was excluded from further analyses as the GEBCO surface was considered to be an adequate bathymetric surface for modelling purposes.

Once computed, these attributes were then assessed for collinearity prior to use in Maxent.

Correlation of environmental layers

Collinearity amongst input variables has not been found to affect Maxent performance (Kuemmerle et al. 2010); however, the inclusion of such variables may result in overfit models and thus risk underpredicting the range of suitable habitats (Heikkinen et al. 2006, Cao et al. 2013). Following the parsimony principle (Seasholtz & Kowalski 1993), and in an effort to reduce the likelihood of generating an overly complex model (Dormann et al. 2013, Merow et al. 2013), a correlation matrix was produced to measure correlation amongst the 9 selected environmental variables. The resulting matrix was subsequently analyzed and, in the event that 2 variables were highly correlated ($r > 0.7$), only 1 variable was retained for use in Maxent (Davies & Guinotte 2011, Dormann et al. 2013).

Bias file generation

To account for sampling bias in the study area, latitudinal and longitudinal information identifying the centre of each trawl performed between 2004 and 2011 were imported as point data into ArcGIS 10.3 (ESRI 2014) and a heat map was generated using a Gaussian kernel density function to represent sampling effort throughout the study area (Phillips et al. 2009, Elith et al. 2010, Merow et al. 2013). The raster values were then rescaled from 1 to 20 to minimize extreme values and ensure compatibility with Maxent (Elith et al. 2010, Fourcade et al. 2014).

Setting Maxent parameters

Once the coral functional groups and individual species presence-only datasets, uncorrelated environmental layers, and sampling bias file had been processed, they were imported into Maxent. Following the methodology developed by Phillips et al. (2006), 70% of the observations were used to train the model, while 30% of the observations were reserved for testing. Feature types were set to 'auto-select' based on the sample size (e.g. number of species observations), with larger samples supporting more complex combinations of features (Phillips et al. 2006). As suggested by Barbet-Massin et al. (2012), a

random background sample of 10 000 cells was used throughout the modelling process, and the program was set to run jackknife tests, create response curves, and write background predictions to be used for model assessment and validation.

Regularization multiplier values (β) are user-specified coefficients within Maxent which alter a model's level of regularization (Radosavljevic & Anderson 2014). By default, this parameter is set to 1 in Maxent (Phillips & Dudik 2008, Elith et al. 2010, Anderson & Gonzalez 2011); however, to ensure model fit was optimized, raw model outputs were generated over a range of β -values (0.5 to 4.0) (Moreno-Amat et al. 2015). Statistical evaluation of these raw outputs were performed using Akaike information criterion corrected for small sample size (AICc), which informed on the robustness of individual models by comparing model accuracy, while penalizing the use of excess parameters which often leads to overfitting (Warren & Seifert 2011). The ENMTools 1.4.4 software was used to determine the AICc values associated with each of the raw model outputs (Warren et al. 2010). Once computed, the β -value for the model with the lowest AICc was reintroduced into Maxent and run to generate a logistic output of the model. Habitat suitability scores ranged from 0 to 1, where 0 indicated unsuitable habitat and 1 indicated highly suitable habitat. The 4 most significant variables used in model generation were determined from jackknife plots and ranked based on test gain.

Model validation

To provide a basis for validating the models, the 10th percentile training presence threshold was applied to SDM outputs (Phillips & Dudik 2008). This approach identified a threshold for the habitat suitability scores, below which 10% of the training dataset fell. This threshold was used to define suitable (above the threshold) and unsuitable (below the threshold) habitats for each of the modelled species. Unlike cases where threshold values are arbitrarily assigned, validations based on this process have been found to generate more refined models which can accurately describe continuous prediction surfaces as binary ones (Liu et al. 2005, Radosavljevic & Anderson 2014).

For each SDM, area under the receiver operating curve (AUC) values of the test data were assessed to determine whether models were able to define suitable habitats better than random (AUC > 0.5) (Phillips & Dudik 2008, Davies & Guinotte 2011, Georgian et

al. 2014). However, because studies have criticized the sole use of AUC as a measurement of model accuracy, due to its sensitivity to spatial extent (Lobo et al. 2007, Peterson et al. 2008), true skill statistics (TSS) were also computed as supplementary validation tests (Allouche et al. 2006). Through the use of confusion matrices, TSS detects misclassification resulting from the generation of false presences by SDMs, and is increasingly used to assess model accuracy (Barbet-Massin et al. 2012, Fortini et al. 2015). In this approach, model performance is scored between -1 and $+1$, with values below zero indicating performance no better than random (Allouche et al. 2006).

In addition, models constructed at the species level were further validated using presence-only independent commercial fishery observer datasets. These were compiled by DFO and contained observations of coral species in the region from 2004 to 2007. For species with 10 or more independent observations, habitat suitability scores were extracted. Scores were also extracted for 80 points that had been randomly generated within the study area using the 'create random points' tool in ArcGIS 10.3 (ESRI 2014). Habitat suitability data for the fishery observer and randomly generated data were then exported by species for analysis in R version 3.3.2 (R Core Team 2013). A non-parametric, 1-tailed, Wilcoxon rank-sum test was used to assess whether or not the habitat suitability values associated with fishery observer data points were significantly larger than those associated with the randomly selected points. If this was true, it indicated Maxent models were predicting suitable habitats where species observations had not been made, better than random.

Functional group variability

To assess variability in the environmental niches occupied by each of the functional groups and individual species, the 'repeating shapes' tool for ArcGIS (Jenness 2012) was used to superimpose a regular grid of points (every 2 km) over the study area. Data were extracted from each of the gridded points for the habitat suitability surfaces for each functional group and each species, as well as the raster surfaces of the 4 most important environmental variables; determined from the Maxent jackknife outputs. Within R 3.3.2 (R Core Team 2013), scatterplots were produced to illustrate how changes in each of the 4 environmental variables affected the habitat suitability output for each SDM. These were used in place of the species–response curves output by Maxent as

they more clearly illustrated variability in habitat suitability. Habitat suitability scores corresponding with the 10th percentile training presence threshold of each model were used to define ranges of highly suitable habitat for each species.

Niche overlap

The *I* statistic was also computed for the Maxent ASCII outputs within ENMTools 1.4.4 software (Warren et al. 2010) to determine the niche overlap of species within and between functional groups, as well as the similarities of the functional group models to those of the species they were derived from. This statistic, developed by Warren et al. (2010), uses cell-by-cell comparisons of habitat suitability to determine niche differences and assess their statistical significance.

Identifying areas of conservation priority

Effective areas for conservation were identified by overlaying the suitable habitats of species by functional group. For the purpose of this exercise, only functional groups of corals which contained more than 1 model at the species level were assessed. Suitable habitat was identified and extracted within ArcGIS (ESRI 2014) based on the 10th percentile training presence threshold output by Maxent. Suitability rasters were then converted to polygons and intersecting areas were identified.

Comparison to *in situ* data

Ranges of depth and temperature associated with suitable habitat for corals were compared against *in situ* observations, where possible. For the purpose of this comparison, slope and salinity were not assessed due to a lack of *in situ* observations detailing specific requirements for large gorgonian, small gorgonian, and sea pen corals. Because the *in situ* data used for these comparisons were obtained from studies performed in the Northwest Atlantic, data was limited and did not always reflect the total environmental niche that the species' may occupy.

RESULTS

Environmental variable correlation

The correlation matrix for the 9 environmental variables showed a strong positive relationship between slope and standard deviation of the bathymetric surface ($r = 0.995$). (Table 3). Therefore, standard deviation was excluded from further analyses. Salinity and depth surfaces ($r = -0.687$), as well as salinity and temperature surfaces ($r = 0.599$), still correlated with depth; however, correlations were below the threshold identified by Dormann et al. (2013) as the point at which collinearity between variables will begin to affect model estimation and prediction ($r = 0.7$). Combined with Maxent's ability to overcome low levels of collinearity through the use of weighted variable selection and regularization procedures (Merow et al. 2013), and previous research highlighting the ecological significance of salinity and temperature with respect to cold-water corals (Mortensen & Buhl-Mortensen 2005), both of these variables were retained for use in Maxent.

Functional group distribution models

All 3 functional group models were found to perform well (Table 4); however, the model for sea pens was determined to be the best based on the computed AUC, omission rate, and TSS. Depth was the most significant variable for predicting suitable habitat for large and small gorgonians, while sea pens were found to be more dependent on bottom temperature.

Table 3. Correlation coefficients (r) of environmental variables as functions of aspect: chl *a* (mg m^{-3}), salinity, bottom temperature (temp, $^{\circ}\text{C}$), slope (degrees), standard deviation (SD), relative deviation from mean value (RDMV), northernness (north, 0 to 90°), easternness (east, 0 to 90°) and depth (m)

| | Chl <i>a</i> | Salinity | Temp | Slope | SD | RDMV | North | East |
|--------------|--------------|----------|--------|--------|--------|--------|-------|--------|
| Chl <i>a</i> | – | – | – | – | – | – | – | – |
| Salinity | 0.233 | – | – | – | – | – | – | – |
| Temp | 0.073 | 0.599 | – | – | – | – | – | – |
| Slope | –0.010 | 0.345 | 0.358 | – | – | – | – | – |
| SD | –0.010 | 0.337 | 0.349 | 0.995 | – | – | – | – |
| RDMV | 0.003 | 0.010 | 0.006 | 0.001 | 0.002 | – | – | – |
| North | 0.148 | –0.013 | –0.053 | –0.072 | –0.073 | 0.023 | – | – |
| East | 0.167 | 0.188 | 0.070 | 0.027 | 0.023 | –0.003 | 0.033 | – |
| Depth | –0.300 | –0.687 | –0.326 | –0.235 | –0.230 | –0.021 | 0.079 | –0.194 |

Table 4. (a) Validation statistics and presence threshold, and (b) jackknife analysis of environmental variables for species distribution models of large gorgonian, small gorgonian, and sea pen corals. In (a), values in brackets for the test AUC indicate standard deviation. In (b), values in **bold** indicate the variables contributing most significantly to model generation for each functional group. AUC: area under the receiver operating curve; TSS: true skill statistic

| Variable | Large gorgonians | Small gorgonians | Sea pens |
|--|------------------|------------------|---------------|
| (a) Validation statistics | | | |
| Test AUC | 0.886 (0.022) | 0.925 (0.012) | 0.922 (0.002) |
| Test gain | 1.199 | 1.573 | 1.535 |
| 10th percentile training presence | 0.250 | 0.283 | 0.416 |
| Omission rate (%) | 17.20 | 11.70 | 11.70 |
| TSS | 0.688 | 0.720 | 0.768 |
| (b) Gain for top 4 jackknife variables | | | |
| Depth | 1.207 | 0.573 | 1.025 |
| Bottom temperature | 0.833 | 0.459 | 1.230 |
| Slope | 0.557 | 0.471 | 0.180 |
| Bottom salinity | 0.538 | 0.374 | 0.670 |

Large gorgonians. The model of the large gorgonian coral functional group ($n = 227$) (Fig. 2) identified areas of highly suitable habitat along the edge of the Labrador shelf extending from Orphan Spur to Cape Chidley. Less extensive habitat was also located on the eastern edge and southwest point of the Flemish Cap, as well as along the southwest edge of the Grand Banks of Newfoundland beyond the Laurentian Channel.

Small gorgonians. Small gorgonian coral samples ($n = 298$) helped identify highly suitable habitat along the southwest edge of the Grand Banks, beyond the Laurentian Channel, as well as extending north along the Labrador shelf edge from the Orphan Spur to Cape Chidley (Fig. 3). In addition to these areas, relatively suitable habitats were also located on the edge of the continental shelf surrounding the Orphan Basin, as well as along the Flemish Cap, particularly along the eastern and southern edges.

Sea pens. The most suitable habitats for sea pen corals ($n = 711$) were identified along the southwest edge of the Grand Banks, extending from the Tail of the Bank along the Laurentian Channel. Additional areas of suitable habitat were identified along broad portions of the Flemish Cap, throughout the Flemish Pass, and extending north along the edge

of the Labrador shelf to Okak Bank (Fig. 4).

Individual species distribution models

Large gorgonians. Observations of 4 large gorgonian corals were also used to generate SDMs at the species level. These included: *Acanthogorgia armata*, *Paramuricea* spp., *Paragorgia arborea*, and *Keratoisis grayi*. As documented in Table 5, the AUC and TSS values computed for each of the SDMs were high, indicating all

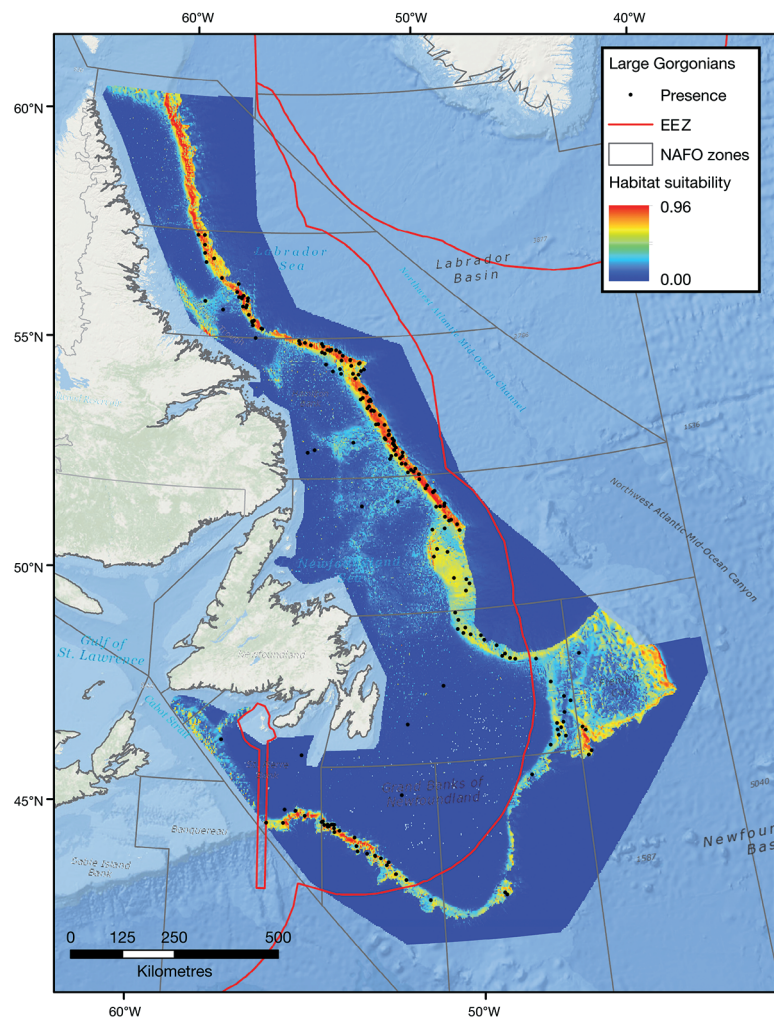


Fig. 2. Habitat suitability model for large gorgonian corals ($n = 227$) in the study area. Habitat suitability scores ranged from 0 (blue) to 1 (red), where 0 indicates unsuitable habitat and 1 indicates highly suitable habitat. EEZ: exclusive economic zone; NAFO: Northwest Atlantic Fisheries Organization

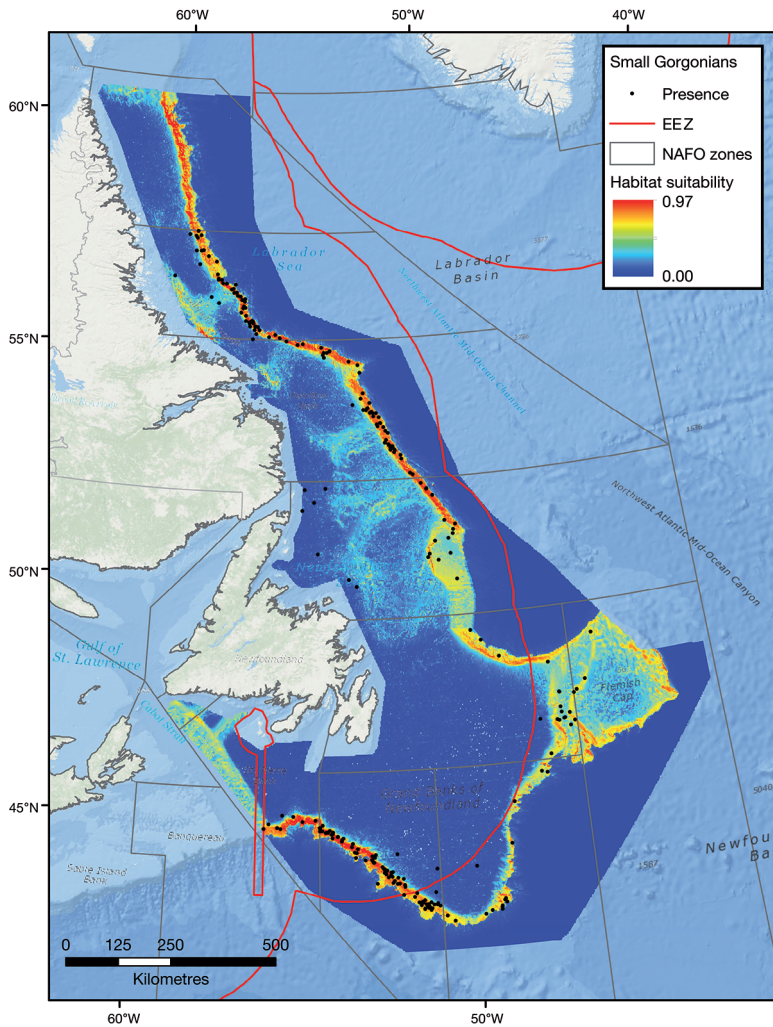


Fig. 3. Habitat suitability model for small gorgonian corals ($n = 298$) in the study area. For key to colours, symbols and abbreviations see Fig. 2 legend

models performed well. Furthermore, Wilcoxon rank-sum tests of *A. armata*, *Paramuricea* spp., and *P. arborea*, indicated that each of the models were better than random (the test could not be performed for *K. grayi* due to an insufficient number of independent observations). These findings, as well as the low omission rates, suggest that the models for *A. armata* and *K. grayi* performed the best. In contrast, reduced AUC and TSS values, as well as a 50% omission rate, indicate that the model for *P. arborea* was the least accurate. In general, the most significant factor contributing to model output was depth, with the exception of *K. grayi* which was most dependent on bottom temperature.

A. armata. Highly suitable habitat for *A. armata* ($n = 113$) was identified along the edge of the Labrador shelf and upper slope extending from Funk

Island Bank as far north as Cape Chidley, eastern and southern portions of the Flemish Cap boundary, as well as a narrow portion of the southwestern Grand Banks (Fig. 5).

Paramuricea spp. Habitat suitability for *Paramuricea* spp. ($n = 57$) was highest along the edge and upper slope of the Labrador shelf between Orphan Spur and Cape Chidley, as well as along a small portion of the southern Flemish Cap (Fig. 6).

P. arborea. Fig. 7 illustrates areas of high suitability for *P. arborea* ($n = 27$), ranging along the eastern and southern boundaries of the Flemish Cap, the continental shelf edge and upper slope west of Orphan Basin, as well as along narrow portions of the continental shelf edge from Orphan Spur to Hamilton Bank, and north of Makkovik Bank to Cape Chidley.

K. grayi. Compared to other large gorgonian species, suitable habitat for *K. grayi* ($n = 27$) was found to be quite limited. It included the southwest edge of the Grand Banks, as well as a small portion of the western Flemish Cap (Fig. 8).

Small gorgonians, sea pens, cup corals, antipatharian, and soft coral. With an average AUC of 0.908 and TSS of 0.703, models for the remaining species were highly accurate (see Tables S2–S16 in Supplement 1). Major findings indicate that the distributions of coral species are largely concentrated along the continental shelf edge and upper slope (see Figs. S2–S16 in Supplement 1), with the exception of some soft

corals that were largely concentrated on the continental shelf (Figs. S11, S12, S14 & S15). However, the distribution of species along the continental shelf, edge, and upper slope, varied on a species-by-species basis, and was rarely found to be consistent for species within each functional group (Figs. S2–S16).

In general, jackknife outputs for species-based models indicated that the 4 most significant variables controlling species distributions were depth, bottom temperature, bottom salinity, and slope (Tables S2–S16). However, chl *a* was among the top 4 significant variables for 2 sea pen species (*Funiculina quadrangularis* and *Pennatulula aculeata*) and 3 soft corals (*Duva florida*, *Gersemia* spp., and *Drifa* spp.), suggesting the importance of this variable for defining habitat suitability of some cold-water coral species (Tables S4, S7, S11, S12 & S14).

Functional group variability

Large gorgonians. As illustrated in Fig. 9, suitable habitat for large gorgonian corals is defined by a depth range of 100 to 1900 m, temperatures from 2.5 to 5.8°C, and salinities from 34 to 34.9 PSU, while the range of suitable slopes for sea pen corals are found at slopes between 1 and 13°.

Small gorgonians. Fig. 10 illustrates that suitable habitats for small gorgonians are defined by depth ranges of 100 and 1600 m, temperatures of 0.8 to 6°C, salinities of 33.8 to 34.9 PSU, and slopes ranging from 0 to 22°.

Sea pens. Fig. 11 highlights suitable habitat for sea pen corals at depths between 100 and 1500 m, temperatures from 1.8 to 6°C, salinities above 32.8 PSU, and slopes ranging from 0 to 26°.

Species-specific variability

Large gorgonians. Habitat suitability for large gorgonian corals varied at the species level, with some tolerating broader environmental conditions than others (Figs. 5–8). Suitable habitats for *A. armata* were concentrated between depths of 100 and 2100 m (Fig. 12A), while *K. grayi* was found between 25 and 2500 m (Fig. 12B). *P. arborea* presented at a range of depths from 200 to 1300 m (Fig. 12C) and *Paramuricea* spp. between 200 and 1900 m (Fig. 12D).

Bottom temperatures associated with high habitat suitability for *A. armata* were between 0.8 and 6°C (Fig. 13A), while *K. grayi* were concentrated at temperatures above -1°C (Fig. 13B). *P. arborea* was most common between 1.1 and 5.8°C (Fig. 13C), and *Paramuricea* spp. between 1.1 and 6°C (Fig. 13D). Ranges of bottom salinity were less variable, with all 4 species most commonly found between 32.9 and 34.9 PSU (Fig. 14A–D).

The range of slopes delineating suitable habitat for large gorgonians was also found to vary at the species level, with *A. armata* concentrated between 0 and 22° (Fig. 15A), and *K. grayi* concentrated

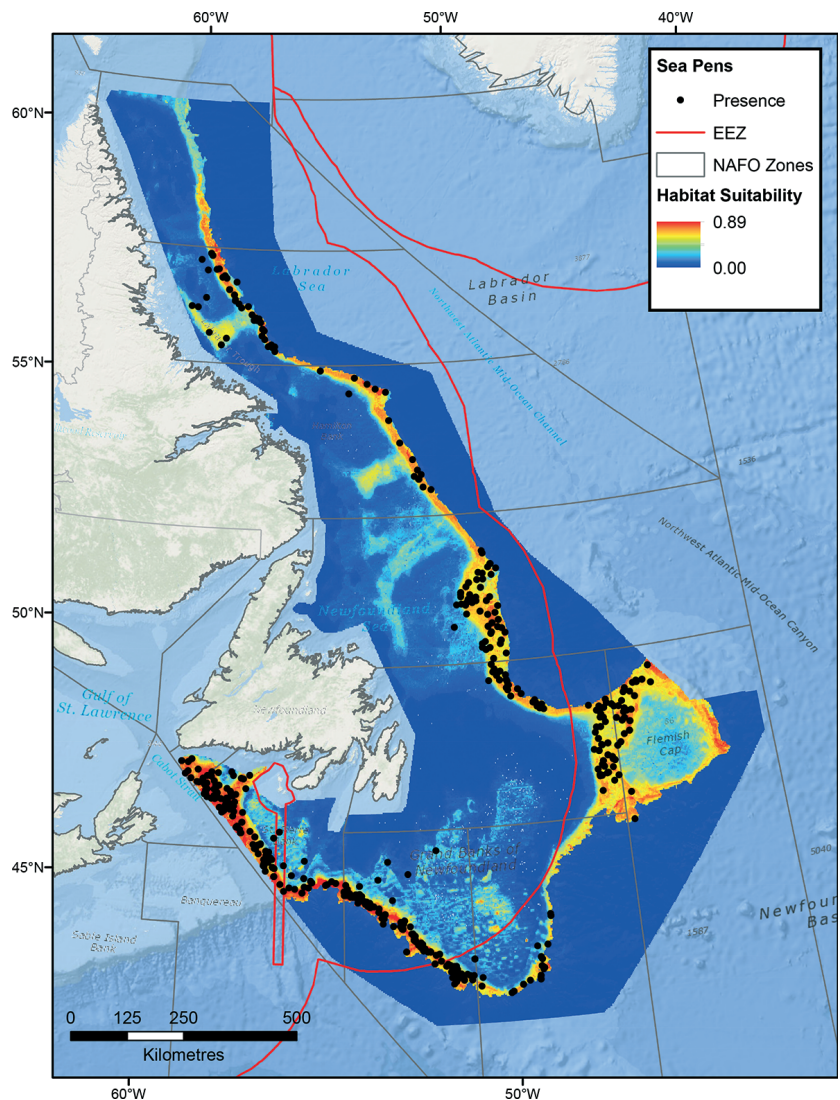


Fig. 4. Habitat suitability model for sea pen corals ($n = 711$) in the study area. For key to colours, symbols and abbreviations see Fig. 2 legend

between 0 and 26° (Fig. 15B). Meanwhile, *P. arborea* and *Paramuricea* spp. were most common at slopes between 1 and 14° (Fig. 15C,D).

Sea pens and soft corals. Similar findings were also produced for species-specific SDMs generated for sea pen and soft coral species, confirming that different species belonging to the same functional group can have different associations with environmental variables, ultimately leading to different predicted distributions (see Figs. S17–S24 in Supplement 2 at www.int-res.com/articles/suppl/m582p057_supp.pdf). This was particularly true for the suitable habitats of soft coral species, where some were found to be restricted to small ranges of depth, bottom temperature, bottom salinity, and slope, while others were observed across

Table 5. (a) Validation statistics and presence threshold, and (b) jackknife analysis of environmental variables for species distribution models (SDMs) of *Acanthogorgia armata*, *Paramuricea* spp., *Paragorgia arborea*, and *Keratoisis grayi*. In (a), values in brackets indicate standard deviation. The Wilcoxon rank-sum test could not be performed for *K. grayi* due to the small number of independent observations. In (b), values in **bold** indicate the variables contributing most significantly to model generation for each functional group. AUC: area under the receiver operating curve; TSS: true skill statistic

| Variable | <i>A. armata</i> | <i>Paramuricea</i> spp. | <i>P. arborea</i> | <i>K. grayi</i> |
|---|------------------|-------------------------|-------------------|-----------------|
| (a) Validation statistics | | | | |
| Test AUC | 0.936 (0.011) | 0.916 (0.026) | 0.864 (0.073) | 0.951 (0.044) |
| Test gain | 1.512 | 1.488 | 1.042 | 3.493 |
| 10th percentile training presence | 0.354 | 0.271 | 0.325 | 0.085 |
| Omission rate (%) | 12.10 | 17.60 | 50.00 | 14.30 |
| Wilcoxon rank-sum (<i>W</i> , <i>p</i>) | 3557, <0.001 | 2207, <0.001 | 2088, <0.001 | – |
| TSS | 0.721 | 0.709 | 0.449 | 0.725 |
| (b) Gain for top 4 jackknife variables | | | | |
| Depth | 1.211 | 1.137 | 1.720 | 1.285 |
| Bottom temperature | 0.791 | 0.570 | 1.009 | 2.344 |
| Slope | 0.642 | 0.623 | 0.819 | 1.309 |
| Bottom salinity | 0.555 | 0.560 | 1.051 | 0.365 |
| Chl <i>a</i> | 0.232 | 0.324 | 0.026 | 0.536 |

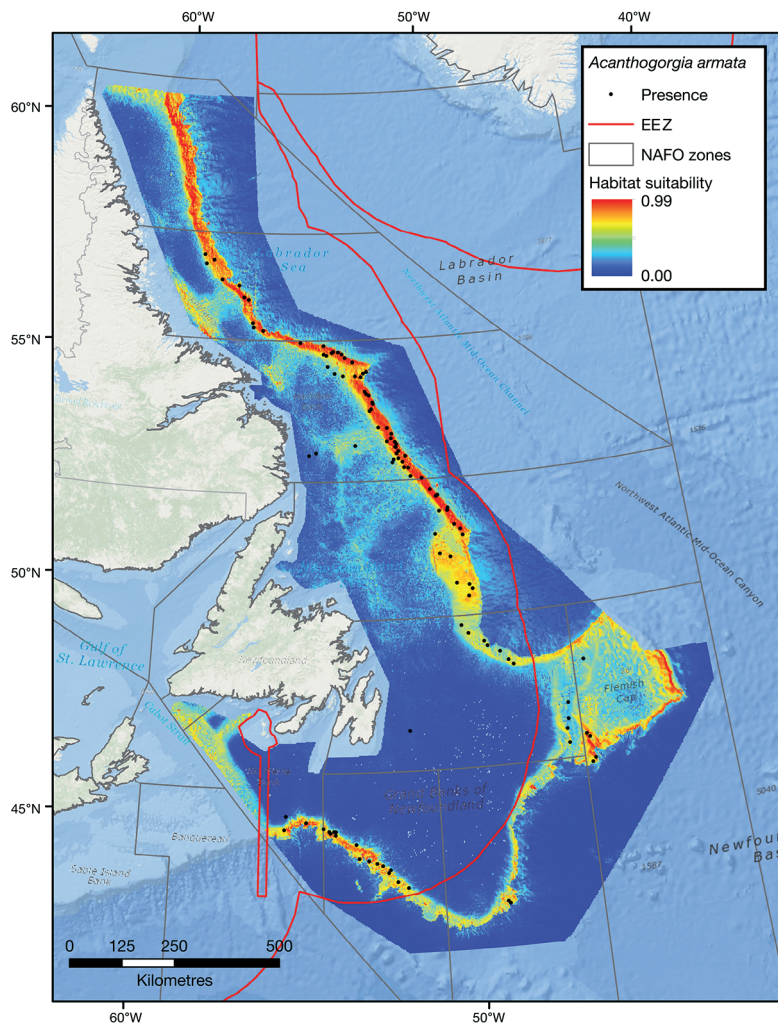


Fig. 5. Habitat suitability model for *Acanthogorgia armata* ($n = 113$) in the study area. For key to colours, symbols and abbreviations see Fig. 2 legend

much broader ranges (Figs. S21–S24). Similar, although more subtle trends were also found for sea pens (Figs. S17–S20). Comparisons between species of small gorgonians, antipatharians, and cup corals were not possible as only 1 species per functional group was observed frequently enough (≥ 20 observations) to support model generation.

Niche overlap

At the species level, niche overlap (I) was found to be lowest for *Gersemia* spp. when compared to other models (Table S17 in Supplement 3 at www.int-res.com/articles/suppl/m582p057_supp.pdf), likely due to the concentration of this species on the continental shelf. Comparisons between all other models indicate niche overlap was more significant ($I > 0.5$), illustrating overarching similarities in habitat requirements. Within functional groups, niche overlap was higher, with species of large gorgonians (Table S18 in Supplement 3) and sea pens (Table S19 in Supplement 3) consistently having an $I > 0.7$. However, some variations were observed in comparing the individual species models to that of their functional group, where niche overlap was higher for the most abundant species (e.g. *A. armata* and *Anthoptilum grandiflorum*), suggesting that functional group models are less effective conservation tools for rarer species.

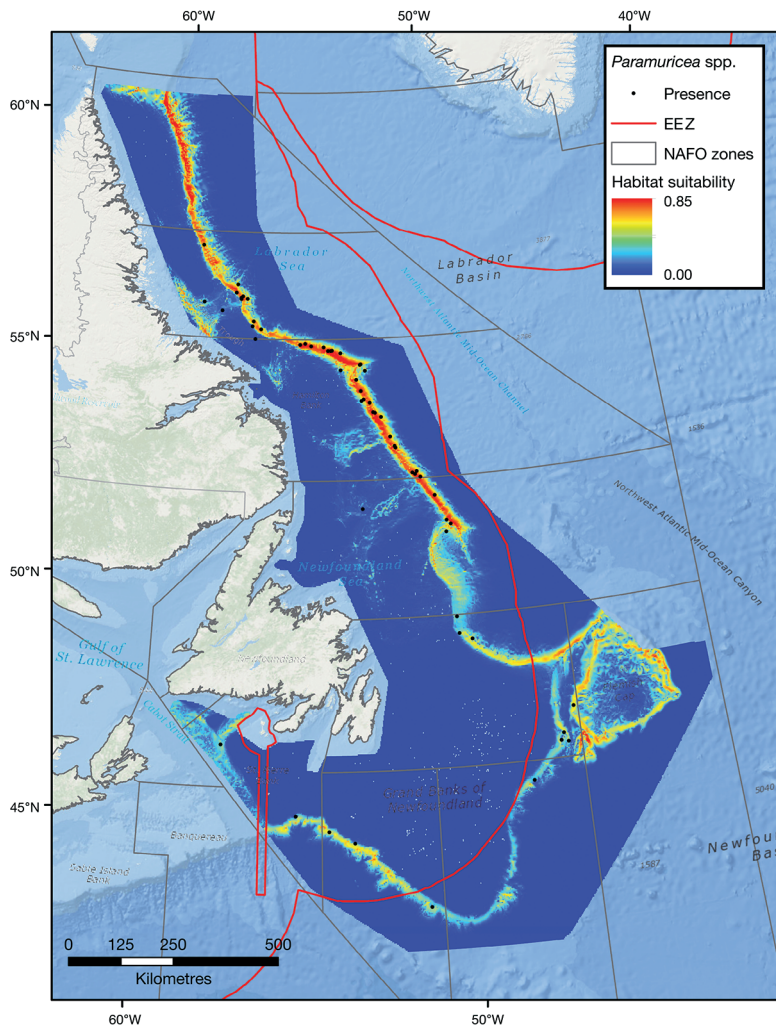


Fig. 6. Habitat suitability model for *Paramuricea* spp. ($n = 57$) in the study area. For key to colours, symbols and abbreviations see Fig. 2 legend

Areas of conservation priority

Large gorgonians. As illustrated in Fig. 16, overlapping areas of suitable habitat for large gorgonian coral species existed along the southwest Grand Banks, the edges of the Flemish Pass and Flemish Cap, and continued, somewhat discontinuously, along the shelf edge from Orphan basin north to Cape Chidley.

Sea pens and soft corals. Based on the areas of intersecting suitable habitat for individual species of sea pen corals (Fig. S25 in Supplement 3), conservation applications would be most effective for a broad range of species along the northern boundary of the Laurentian Channel, along the southwest Grand Banks, on either side of the Flemish Pass, on the edge of the Flemish Cap, as well as along the

eastern edge of the Orphan Basin. In contrast, variation between SDMs for species of soft corals meant that very little overlap was observed, likely due to the variation which exists within this functional group (Fig. S26 in Supplement 3).

DISCUSSION

Cold-water coral distributions and factors controlling them

Our analyses indicate that the most suitable habitat for cold-water corals is generally found along the continental shelf break and within canyons on the upper continental shelf, with locations including the edge of the southwest Grand Banks, outer edges of the Flemish cap, along the continental shelf surrounding Orphan Basin, and along the sections of the edge of the continental shelf extending from Orphan Spur, in some cases, as far north as Cape Chidley. The Laurentian Channel was found to be highly suitable habitat for sea pen corals, while relatively suitable habitat extended onto the continental shelf within deep channels off the coast of Labrador for each of the functional groups. These findings support existing research within the NL region (Mortensen et al. 2006, Wareham & Edinger 2007, Gilkinson & Edinger 2009) and elsewhere (Bryan & Metaxas 2007, Davies & Guinotte, 2011, Yesson et al. 2012), which suggest that conservation efforts for cold-water corals should be concentrated along the shelf edge, upper slope, and incised portions of the continental shelf.

The factors most strongly indicative of coral functional group distributions were depth, bottom temperature, salinity, and slope, as observed in previous species distribution modeling efforts for octocorals (Bryan & Metaxas 2007, Yesson et al. 2012). Slope has often been interpreted as a proxy for bottom type, specifically linking high slope environments with coarser substrates. The importance of depth and bottom type for affecting distributions of cold-water corals has long been recognized (Mortensen et al. 2006, Watanabe et al. 2009, Edinger et al. 2011, Baker et al. 2012). Temperature is also often a strong determinant of marine species distributions including cold-water corals, both geographically and bathymetrically (Davies & Guinotte 2011, Yesson et

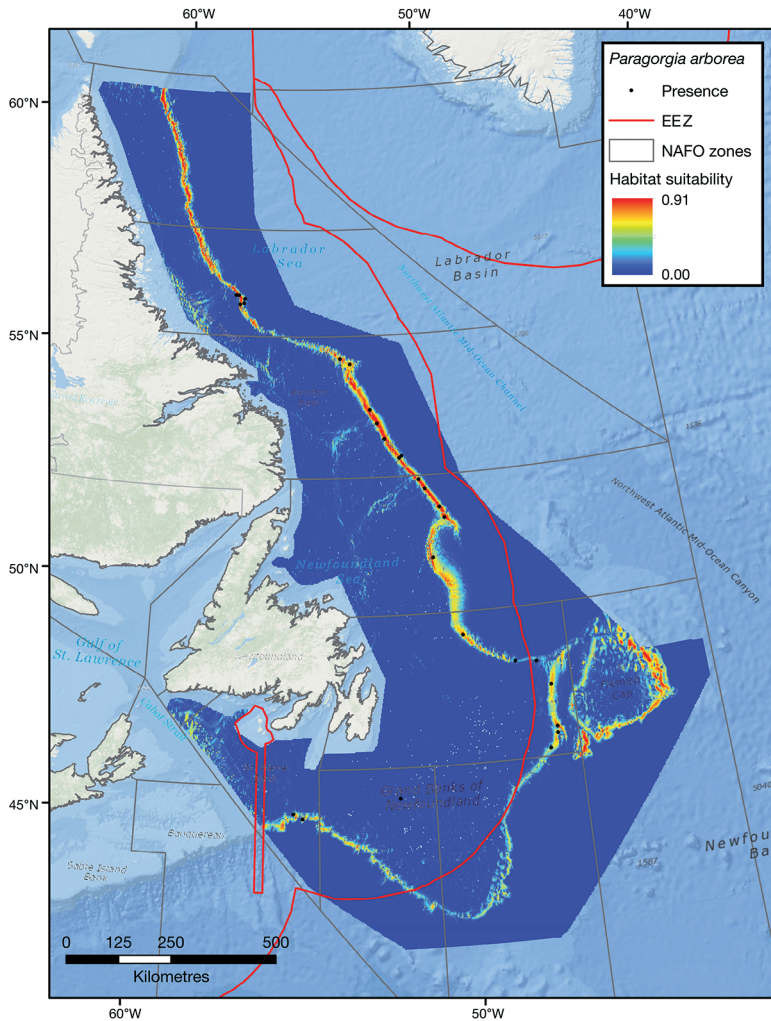


Fig. 7. Habitat suitability model for *Paragorgia arborea* ($n = 27$) in the study area. For key to colours, symbols and abbreviations see Fig. 2 legend

al. 2012, Buhl-Mortensen et al. 2014). The importance of salinity may relate more to specific water masses (cf. Yesson et al. 2012). With the exception of the nephtheid soft corals, most of the coral species in the NL region are concentrated along the continental shelf edge and upper continental slope, most often in Labrador Slope Water (LSW), warmer and deeper than the cold and relatively low salinity Labrador Current (Wareham & Etinger 2007, Buhl-Mortensen et al. 2014). Unlike examples from *Lophelia pertusa* reefs in the Northeast Atlantic, distributions are not apparently tied to a specific seawater density (Dullo et al. 2008), nor to water mass boundaries along which food may be concentrated and resuspended by internal waves.

When assessed on the basis of individual species, suitable habitats were found to vary within and

between functional groups (see Figs. 5–8, Figs. S2–S16 in Supplement 1, Tables S17–S19 in Supplement 3). Specifically, the suitable habitats highlighted by functional group models (Figs. 2–4) did not consistently reflect the habitats occupied by each of the species they included. Instead, the functional group models were found to over-generalize the distribution of suitable habitat, reducing the applicability of functional group models. Similar findings were also reported by Yesson et al. (2012), whose global SDMs of octocorals, generated at the sub-order level, did not accurately illustrate the distribution of suitable habitat for individual taxa. The combination of species level SDMs (Fig. 16, Figs. S25 & S26 in Supplement 3) supports this point, illustrating, particularly for soft corals, that individual species within a functional group may in fact occupy very different niches in the environment (Fig. S26). From a conservation perspective, these findings highlight the importance of developing models for individual cold-water coral species, rather than for broader taxonomic categories.

Modelling method comparison

Jackknife plots output by Maxent identified depth, bottom temperature, bottom salinity, and slope as the 4 variables contributing most significantly to model performance (Table 4). This was consistent with RF SDMs for the NL region (Guijarro et al. 2016), as well as those generated for cold-water corals in other regions (Finney 2010, Guinotte & Davies 2014). However, these variables were not always ranked with the same order of importance, and in some cases contributed less to modelled habitat suitability than chl *a* concentrations (see Tables S5, S8, S11, S15, S16 & S18). To assess the accuracy of these findings, and compare the models produced in this study with those existing for the NL region, suitable depth and temperature ranges identified by Maxent were compared with *in situ* observations (Table 6). In addition, visual comparisons were made between the extrapolation of suitable habitat in species distribution maps produced by Maxent and RF.

As outlined in Table 6, the majority of Maxent SDMs were able to identify suitable habitats within the range of *in situ* observations for depth. However,

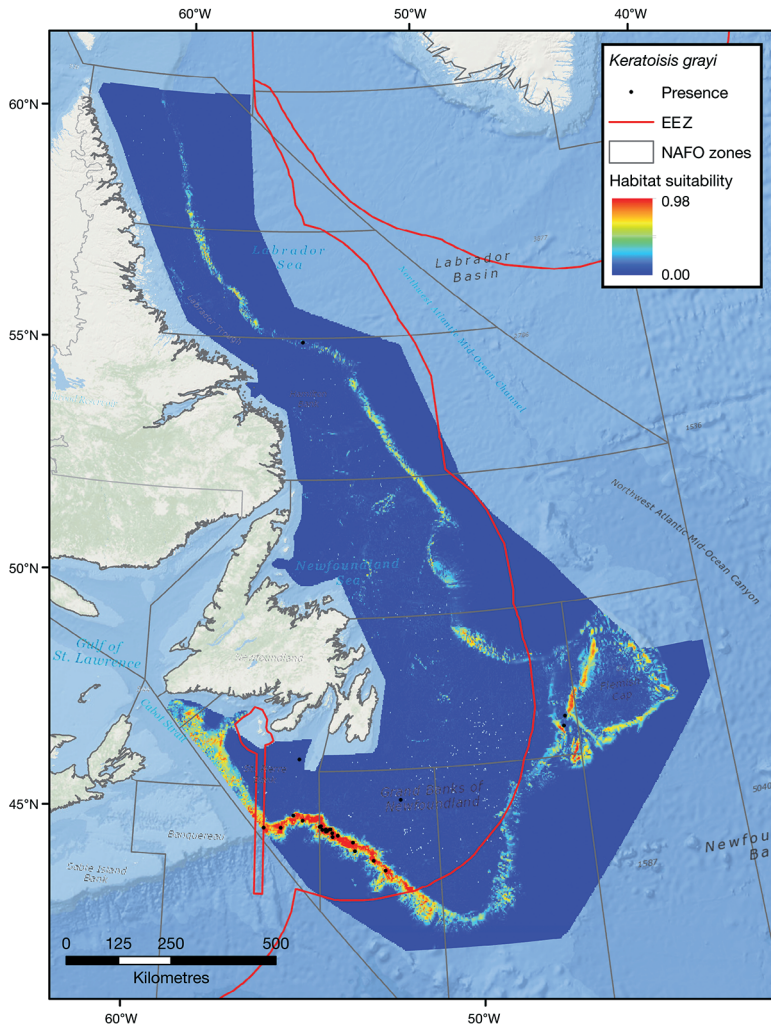


Fig. 8. Habitat suitability model for *Keratoisis grayi* ($n = 27$) in the study area. For key to colours, symbols and abbreviations see Fig. 2 legend

in some cases (e.g. sea pens), the RF predictions were closer to *in situ* observations (Guijarro et al. 2016), with Maxent generally predicting shallower suitable habitats. In particular, the lower depth for *P. aculeata* predict suitable habitat to 0 m. Suitable temperature ranges defined by Maxent also corresponded closely with *in situ* observations for all functional groups.

The extrapolations of suitable habitat by Maxent and RF models were also found to vary throughout the study area. Regionally, the distribution of gorgonian corals is largely related to the availability of hard substrate for settlement (Mortensen & Buhl-Mortensen 2005, Wareham & Edinger 2007, Murillo et al. 2011). Therefore, at depths greater than 1500 m, generally defined by muddy sand (Litvin & Rvachev 1963), the presence of these corals is considered to be rare. At these depths, the species will most often be associated with bathymetric anomalies

such as seamounts, outcrops, submarine canyons, or cliff faces where hard substrate is available for settlement (Edinger et al. 2011, Baker et al. 2012). For the NL region, SDM outputs by Maxent were consistent with these observations, with extrapolations classifying areas along the abyssal plain as unsuitable habitat for each of the functional group and species-specific models (Figs. 2–8, Figs. S2–S16 in Supplement 2). RF models classified much of the same area as suitable habitat, with the authors recognizing such extrapolation as a limitation of the RF modelling technique used (Guijarro et al. 2016). Along the continental shelf there was more consistency, with Maxent and RF models identifying suitable habitats for respective functional groups in similar locations. However, in all cases Maxent models extrapolated larger areas of the continental shelf and slope edge as suitable habitat (Figs. 2–4).

Based on these findings, Maxent proved to be a useful alternative to RF based on its ability to integrate bias information and extrapolate beyond the range of environmental data used to train the model. However, observational data of coral distributions at depths beyond these are needed for validating the contrasting results of the Maxent and RF models in deep water, and will have important consequences for conservation planning in the region. As such, it is anticipated that the Maxent modelling approach that considers terrain variable

predictors would also be well-suited for research outside of the NL region, where cold-water coral observations also experience sparseness and spatial/temporal biases (Bryan & Metaxas 2007, Yesson et al. 2012).

Model limitations

Although gear restrictions would have biased the collection of coral observations to unobstructed bottom types, Maxent models for functional groups and species were found to perform very well (average AUC and TSS values of 0.910 and 0.710, respectively). However, as seen with existing regional and global coral distribution models, the low resolution of bathymetric data and possibly other environmental data may have prevented the identification of fine-

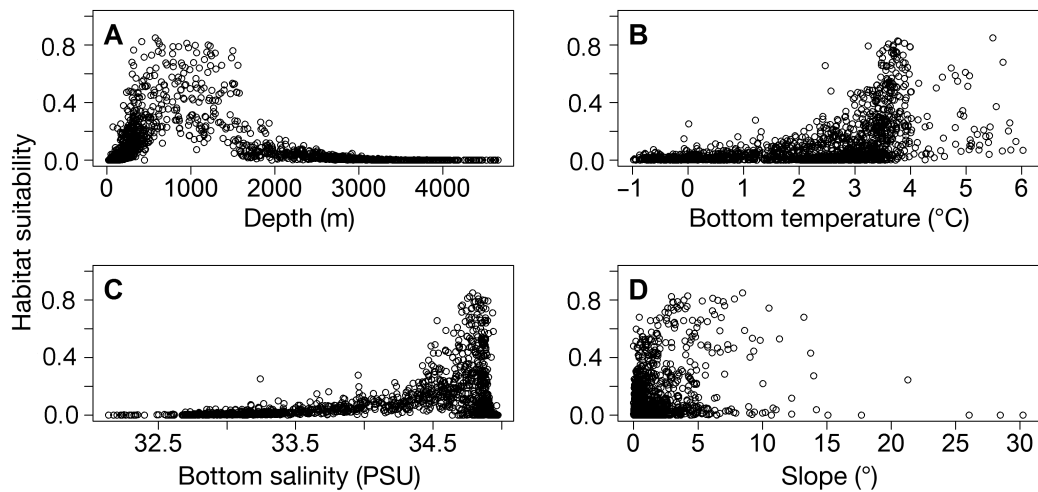


Fig. 9. Habitat suitability of large gorgonian corals with respect to (A) depth, (B) bottom temperature, (C) bottom salinity, and (D) slope

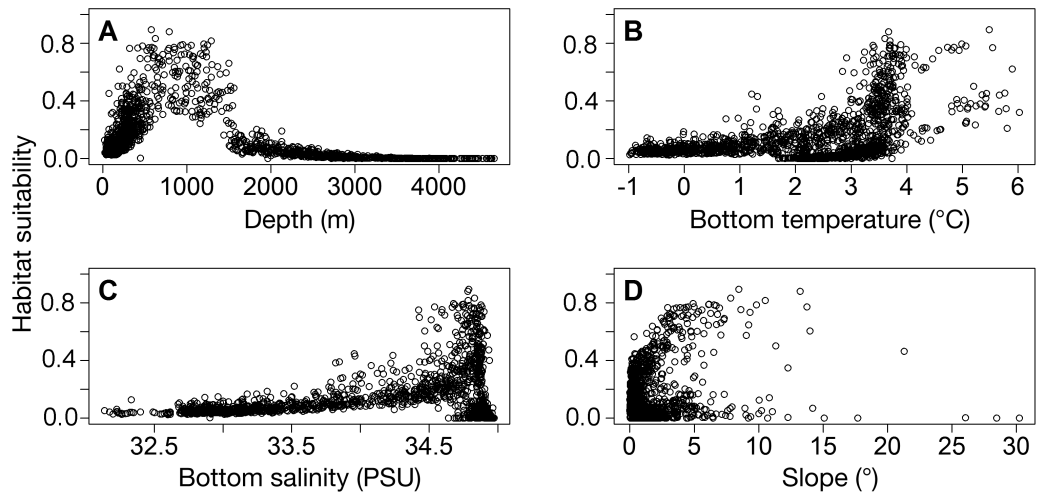


Fig. 10. Habitat suitability of small gorgonian corals with respect (A) depth, (B) bottom temperature, (C) bottom salinity, and (D) slope

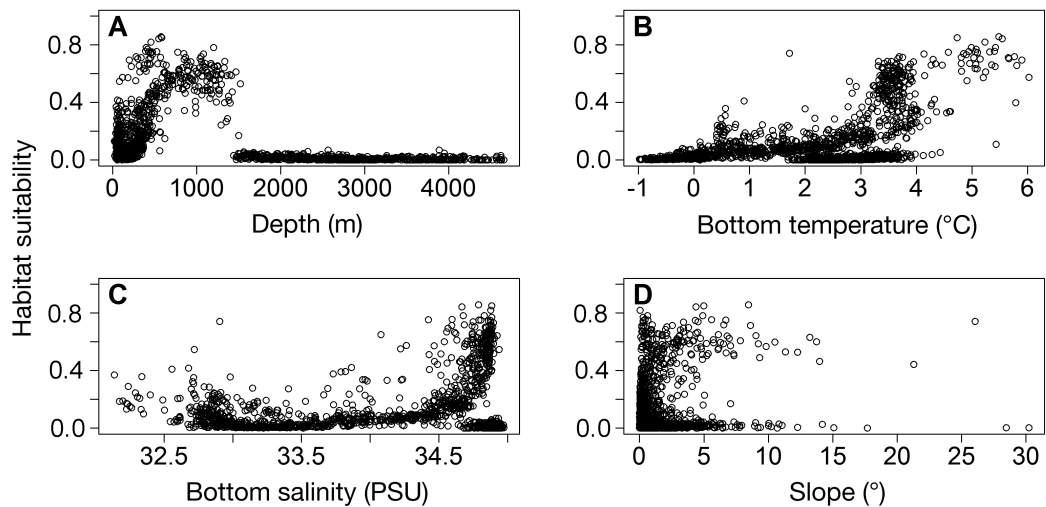


Fig. 11. Habitat suitability of sea pen corals with respect to (A) depth, (B) bottom temperature, (C) bottom salinity, and (D) slope

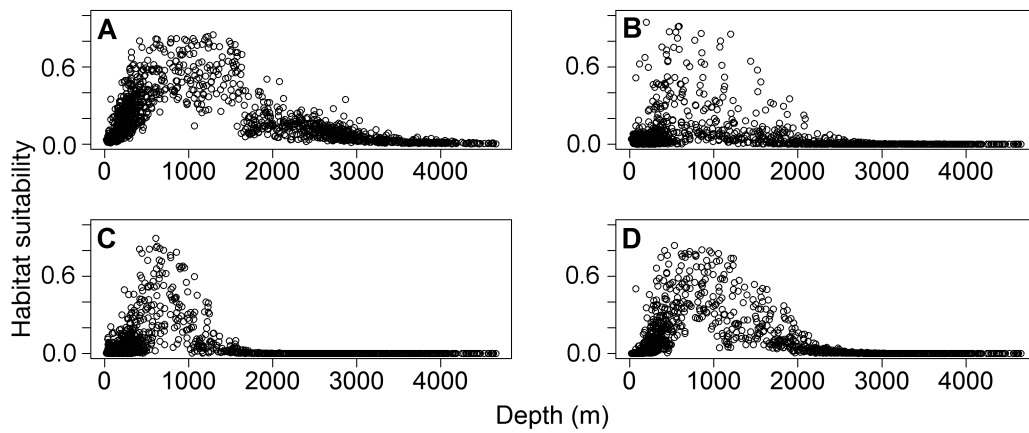


Fig. 12. Comparisons of habitat suitability scores for large gorgonian coral species with respect to depth for (A) *Acanthogorgia armata*, (B) *Keratoisis grayi*, (C) *Paragorgia arborea*, and (D) *Paramuricea* spp.

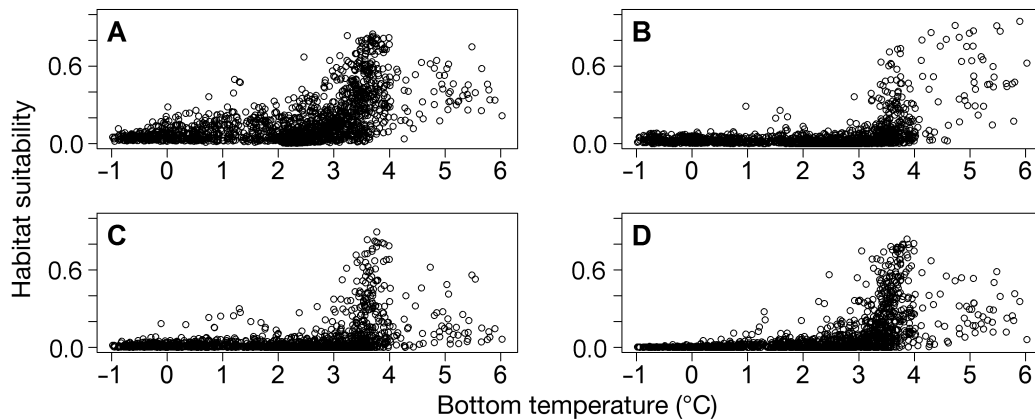


Fig. 13. Comparisons of habitat suitability scores of large gorgonian coral species with respect to bottom temperature for (A) *Acanthogorgia armata*, (B) *Keratoisis grayi*, (C) *Paragorgia arborea*, and (D) *Paramuricea* spp.

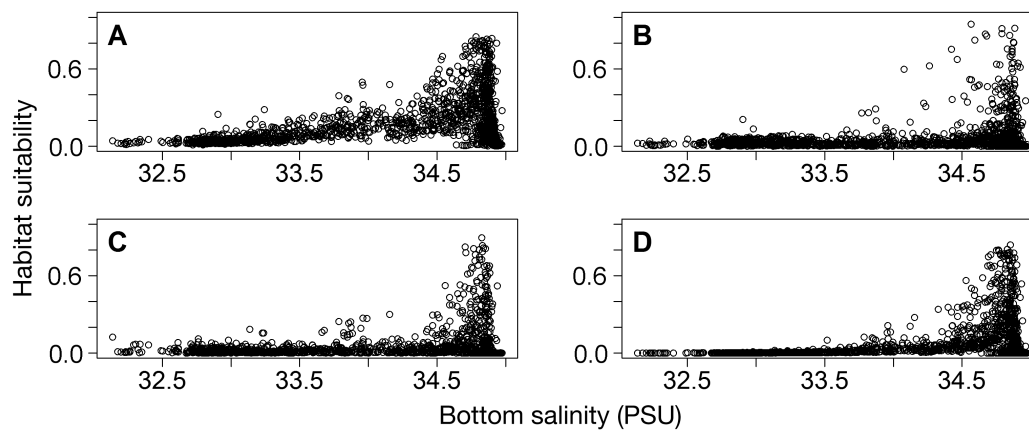


Fig. 14. Comparisons of habitat suitability scores of large gorgonian coral species with respect to bottom salinity for (A) *Acanthogorgia armata*, (B) *Keratoisis grayi*, (C) *Paragorgia arborea*, and (D) *Paramuricea* spp.

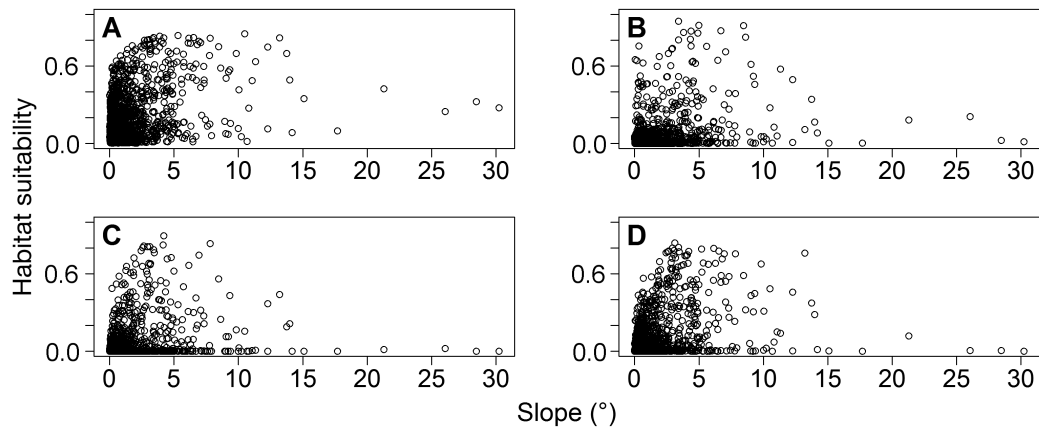


Fig. 15. Comparisons of habitat suitability scores for species of large gorgonian corals with respect to slope for (A) *Acanthogorgia armata*, (B) *Keratoisis grayi*, (C) *Paragorgia arborea*, and (D) *Paramuricea* spp.

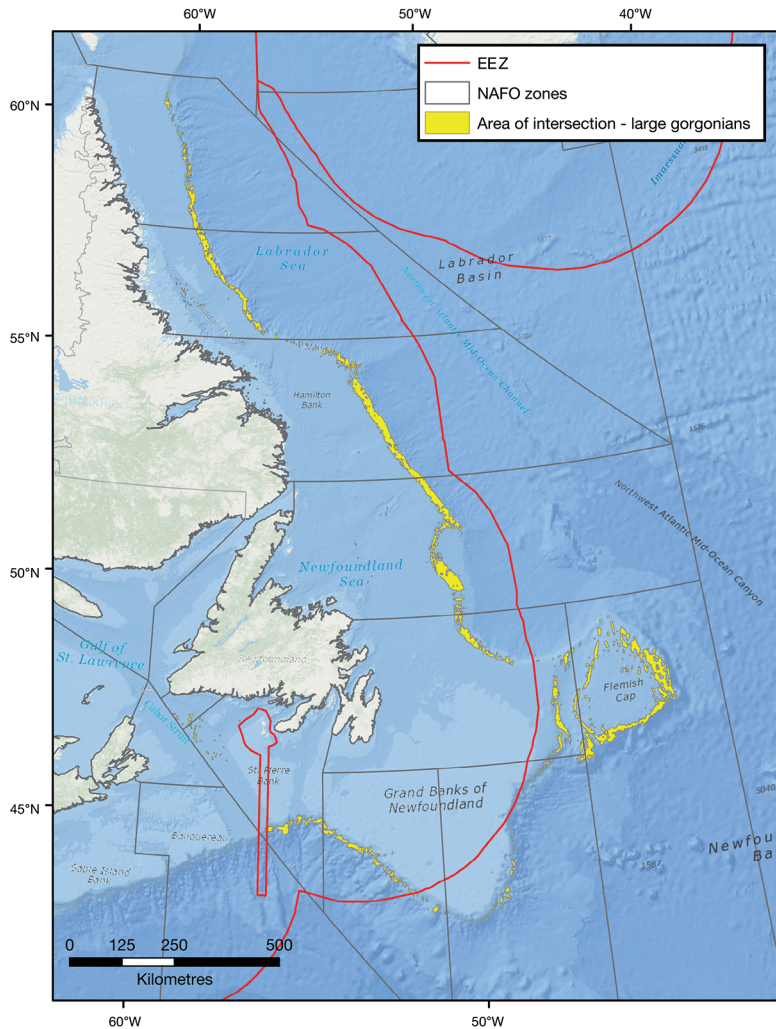


Fig. 16. Areas where suitable habitat for large gorgonian species ($n = 4$) intersected

scale features, such as rocky outcrops, boulders, vertical walls, or small troughs and ridges in the seafloor, which are known to provide suitable habitats for unique assemblages of coral species (Baker et al. 2012). In the past, coarse resolution data such as this has been known to lead to over-prediction of habitat suitability (Yesson et al. 2015). Additionally, due to insufficient spatial coverage or very low spatial resolution, information on currents and substrates were not incorporated into Maxent models. This is not uncommon for SDMs of cold-water corals, particularly for sediment, where interpolation of *in situ* data is often unable to provide an accurate delineation of surficial geology across the study area (Guijarro et al. 2016). However, because these variables are known to influence the distribution of some coral species, future modelling work would likely benefit from the addition of such data (Mortensen et al. 2006, Roberts et al. 2009, Davies & Guinotte 2011).

CONCLUSION

Cold-water coral species represent an ecologically significant group of organisms supporting biodiversity in the deep sea; however, these corals have historically received very little protection from the destructive activities associated with fish-

Table 6. Depth and temperature ranges delineating suitable habitat for coral species and functional groups, as defined by maximum entropy (Maxent) and *in situ* observations. –: no data. Superscript letters indicate data sources. See Table S1 in Supplement 1 for full species names

| Functional group/ Species | Depth (m) | | | Temperature (°C) | | |
|------------------------------|---------------------|--------------------------|-----------------------------|---------------------|---------------------------|-----------------------------|
| | Maxent (species) | Maxent (funct. group) | <i>In situ</i> (species) | Maxent (species) | Maxent (funct. group.) | <i>In situ</i> (species) |
| Sea pen | | | | | | |
| <i>A. grandiflorum</i> | 100 to 1400 | 100 to 1500 | 400 to 2200 ^a | 2.9 to 6 | –1.8 to 6 | 3.6 to 4.8 ^d |
| <i>F. quadrangularis</i> | 200 to 1800 | 100 to 1500 | 400 to 1700 ^a | 3.3 to 6 | –1.8 to 6 | – |
| <i>H. finmarchica</i> | 100 to 1800 | 100 to 1500 | 250 to 2400 ^a | >2.5 | –1.8 to 6 | 3.5 to 6 ^e |
| <i>P. aculeata</i> | 0 to 2200 | 100 to 1500 | 150 to 2400 ^a | >1.8 | –1.8 to 6 | – |
| <i>P. grandis</i> | 300 to 1500 | 100 to 1500 | 400 to 1050 ^a | 2.8 to 5.8 | –1.8 to 6 | – |
| <i>Pennatula</i> sp. | 100 to 1800 | 100 to 1500 | 250 to 1200 ^a | >2.4 | –1.8 to 6 | – |
| Large gorgonian | | | | | | |
| <i>A. armata</i> | 100 to 2100 | 100 to 1900 | 250 to 1200 ^a | –0.8 to 6 | 2.5 to 5.8 | 3.5 to 10 ^{a,f} |
| <i>K. grayi</i> | 25 to 2500 | 100 to 1900 | 450 to 950 ^a | >–1 | 2.5 to 5.8 | 3.5 to 10 ^{a,f} |
| <i>P. arborea</i> | 200 to 1300 | 100 to 1900 | 200 to 1300 ^b | 1.1 to 5.8 | 2.5 to 5.8 | 3.5 to 10 ^{a,f} |
| <i>Paramuricea</i> spp. | 200 to 1900 | 100 to 1900 | 150 to 2200 ^b | 1.1 to 6 | 2.5 to 5.8 | 3.5 to 10 ^{a,f} |
| Small gorgonian | | | | | | |
| <i>A. arbuscula</i> | 100 to 1500 | 100 to 1600 | 150 to 2300 ^b | 1.8 to 5.8 | 0.8 to 6 | 3.5 to 10 ^{a,f} |
| Soft coral | | | | | | |
| <i>A. agaricus</i> | 100 to 2300 | – | 170 to 1400 ^b | –0.5 to 5.9 | – | – |
| <i>Anthomastus</i> spp. | 300 to 1500 | – | 400 to 2200 ^a | –2.8 to 5.5 | – | – |
| <i>D. florida</i> | 50 to 1600 | – | 200 to 900 ^a | –1 to 6 | – | – |
| <i>D. glomerata</i> | 0 to 1600 | – | 350 to 1240 ^c | –1 to 3.8 | – | – |
| <i>Drifa</i> spp. | 0 to 1000 | – | 350 to 1240 ^c | –1 to 4.2 | – | – |
| <i>Gersemia</i> spp. | 0 to 500 | – | 35 to 700 ^b | –1 to 3.8 | – | – |
| Cup coral | | | | | | |
| <i>F. alabastrum</i> | 100 to 1700 | – | 250 to 2500 ^a | 1.8 to 6 | – | 4 to 14 ^g |
| Antipatharian | | | | | | |
| <i>S. arctica</i> | 500 to 1800 | – | 700 to 1850 ^b | –2.4 to 4.9 | – | – |

^aBaker et al. (2012), ^bKenchington et al. (2009), ^cSun et al. (2010b), ^dBaillon et al. (2014), ^eNeves et al. (2015b), ^fLeverette & Metaxas (2005), ^gSun et al. (2010a)

ing. SDMs represent a powerful tool to better understand the distribution of these corals, but the successful application of conservation measures depends on the accurate delineation of suitable habitats.

This study provided predicted distributions of cold-water coral species in NL waters, using the presence-only modelling approach Maxent. Based on this work, it was determined that depth, bottom temperature, bottom salinity, and slope are, in general, the most significant contributors to model production. Species-specific models produced using Maxent were found to be accurate, even for species containing relatively few observations. They were also found to illustrate different ranges of suitable habitats for species within and between functional groups, suggesting that individual coral species likely occupy different habitats. Results from the study do not support the generation of SDMs at the functional group level, due to the overgeneralization of suitable habitat for species that have vastly differ-

ent environmental preferences. Instead, models of single coral species should be implemented when predicted distributions are intended for conservation planning applications. However, it is possible that, in some cases, species level models could be combined to identify overlaps in suitable habitat, allowing conservation applications to continue at the functional group level. Overall, ranges of depth and temperature defining the most suitable habitats corresponded well with *in situ* observations; however, in most cases, models were unable to depict exact minimum and maximum limits described for the species. When compared with RF models, Maxent models derived from functional group classifications were found to identify habitat on the abyssal plain as unsuitable for coral species, while extrapolating larger portions of the continental shelf as suitable habitat. These findings illustrate that Maxent can effectively predict species habitat suitability in unsampled areas. From a conservation perspective,

this work was able to identify areas of suitable habitat for 19 species and 3 functional groups modelled within the study area. In addition, models were performed without the implementation of additional destructive or financially burdensome research techniques. Although it is impossible to surpass the quality of directly observing species distributions, applications of Maxent could be helpful in refining where scientific research trawls are performed, and supporting the implementation and management of future marine protected areas.

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