Modeling the habitat suitability for deep-water gorgonian corals based on terrain variables

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A B S T R A C T

The coral species Paragorgia arborea and Primnoa resedaeformis are abundant and widely distributed gorgonians in North Atlantic waters. Both species add significant habitat complexity to the benthic environment, and support a host of invertebrate species. Mapping their distribution is an essential step in conservation and resource management, but challenging as a result of their remoteness. In this study, three predictive models—Ecological Niche Factor Analysis, Genetic Algorithm for Rule-set Production and Maximum Entropy modeling (MaxEnt)—were applied to predict the distribution of species’ suitable habitat across a region of Røst Reef (Norwegian margin) based on multiscale terrain variables.

All three models were successful in predicting the habitat suitability for both gorgonian species across the study area, and the MaxEnt predictions were shown to outperform other predictions. All three models predicted the most suitable habitats for both species to mainly occur along the ridges and on the upper section of the large slide, suggesting both species preferentially colonize topographic highs. Jackknife tests for MaxEnt predictions highlighted the seabed aspect in relation to P. arborea distribution, and the seabed relative position (curvature) in relation to the distribution of both species. Given the vulnerability of deep-water corals to anthropogenic impacts, further comparative study over a wider study area would be particularly beneficial for the management of the species.

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1. Introduction

Paragorgia arborea and Primnoa resedaeformis are abundant and widely distributed gorgonian coral species observed in North Atlantic waters (Mortensen and Buhl-Mortensen, 2004; Tendal, 1992). The two species are among the largest deep-sea gorgonians, with P. arborea colonies reaching heights above the seafloor of 0.5–2.5 m and P. resedaeformis colony lengths of 0.5–1 m, with both providing complex biotic habitats for numerous invertebrate species (Buhl-Mortensen et al., 2010; Mortensen et al., 2008; Roberts et al., 2009). The deep-water gorgonians are long lived and slow growing species, and are fragile and vulnerable to damage which may result from anthropogenic activity such as bottom trawling and oil exploration (Mortensen and Buhl-Mortensen, 2005). Mapping the distribution of deep-water coral species is fundamental in assessing the potential risks to these ecosystems posed by these activities, and for developing management plans, particularly as species protection legislation such as the EC Habitats Directive stipulates protection of these habitats for all member states. However, such distribution mapping is challenging given the remoteness of these habitats, and predictive modeling techniques address this challenge as a way of understanding the distribution of suitable habitat for a species by quantifying the species–environment relationship (Guisan and Thuiller, 2005).

For the majority of deep-water coral species, prime habitats are typically observed on topographic relief structures, such as along continental shelf edges, on seamounts (Huvenne et al., 2005; Leverette and Metaxas, 2005), in canyons or on carbonate mounds (Huvenne et al., 2011), on sills (Lavaleye et al., 2009), and are associated with strong bottom current velocities and hard substrates (Bryan and Metaxas, 2007; Freiwald et al., 1999; Genin et al., 1986; Tendal, 1992). On the Norwegian margin, many of these structures were formed since the last glaciation, such as the ridges and moraine structures (Fosså et al., 2005). It has been suggested that the seabed topography controls the coral distribution indirectly by governing the local current regimes, thus regulating food particle delivery and larval concentrations (Bryan and Metaxas, 2007; Dolan et al., 2008; Guinan et al., 2009a, 2009b; Mortensen and Buhl-Mortensen, 2004; Thiem et al., 2006; Thiem et al., 2008). In terms of terrain parameters, seabed slope has often been adopted as representative of topography, and together with other environmental variables used to model the habitat suitability for deep-water corals at large scales, such as for the scleractinian coral Lophelia pertusa (Davies et al., 2008; Guinan et al., 2009a), and deep-water gorgonians (Bryan and Metaxas, 2007; Leverette and Metaxas, 2005).

A number of terrain parameters, including slope, aspect, terrain complexity (rugosity and terrain ruggedness index (TRI)), curvature (plan curvature, profile curvature and mean curvature) and bathymetric...
position index (BPI) can be derived from multibeam bathymetry data to characterize the seabed topography (Dolan et al., 2008; Wilson et al., 2007). The seabed topography in terms of these terrain parameters is likely to represent proxies for bottom current flow regimes and substrate types at local and regional scales (Dolan et al., 2008; Guinan et al., 2009a, 2009b; Howell et al., 2011), which may well be ecologically relevant to deep-water coral distribution.

Multiscale terrain analysis is a valuable tool for describing seabed terrain features across a range of scales (Wilson et al., 2007). Such analysis has been used to predict habitat suitability for scleractinian deep-water corals, with key terrain parameters determined at a selection of study sites (Dolan et al., 2008; Guinan et al., 2009a). Guinan et al. (2009b) suggest that the relationship between percent cover of the scleractinian coral *L. pertusa* and terrain parameters is scale-dependent.

Various predictive models have been developed for modeling habitat suitability for species, such as the well-established models Ecological Niche Factor Analysis (ENFA) and Genetic Algorithm for Rule-set Production (GARP), and the novel machine-learning methods Maximum Entropy modeling (MaxEnt), Artificial Neural Networks and Support Vector Machine (Elith et al., 2006; Huang et al., 2011; Li et al., 2009; Phillips et al., 2006; Segurado and Araújo, 2004; Tittensor et al., 2009). ENFA, GARP and MaxEnt have been applied to predict the habitat suitability for deep-water coral species successfully in previous studies.

ENFA is an ecological niche based, presence-only method. The technique was first applied to predict the habitat suitability for deep-water gorgonians (*P. arborea* and *P. resedaeformis*) on the Canadian Atlantic continental margin (Leverette and Metaxas, 2005). Subsequently, ENFA has been applied to model the habitat suitability for scleractinian corals on global seamounts (Clark et al., 2006); for deep-water gorgonians (Families Paragorgiidae and Primnoidae) on the Atlantic and Pacific Continental margins of North America (Bryan and Metaxas, 2007); for *L. pertusa* in the Northeast Atlantic and global oceans (Davies et al., 2008); and for scleractinian corals (*L. pertusa* and *Madrepora oculata*) on the mound BEL 47 in the Belgica Mound province of SW Ireland (Dolan et al., 2008). GARP is a machine-learning method based on a genetic algorithm (Stockwell and Noble, 1991). GARP has been applied to predict the habitat suitability for *L. pertusa* on the Irish margin at regional and local scales, respectively (Guinan et al., 2009a). Most recently, MaxEnt, a general-purpose machine-learning technique (Phillips et al., 2006), has been used to model the habitat suitability for scleractinians on global seamounts (Tittensor et al., 2009) and in global oceans (Davies and Guinotte, 2011). By comparing the performance using cross-validation, Tittensor et al. (2009) found that both ENFA and MaxEnt models performed well, and that the MaxEnt method consistently outperformed ENFA. To date, few studies have modeled the habitat suitability for deep-water gorgonians (particularly using these newly-developed techniques), and it is considered that such predictions are beneficial to developing conservation and management strategies.

In this study, the three methods ENFA, GARP and MaxEnt were applied to predict the habitat suitability for gorgonians *P. arborea* and *P. resedaeformis* at Røst Reef. This paper focuses on the following research questions: (1) Can ENFA, GARP and MaxEnt models predict the habitat suitability for deep-water gorgonians at local scales using terrain parameters derived from bathymetry data, and if so how accurate are these predictions? (2) Do the methods predict similar or different habitat suitability for each species? (3) In what way does local topography at a Norwegian reef complex appear to influence the distribution of the two gorgonian species?

2. Material and methods

2.1. Study area and data acquisition

The Røst Reef complex is located to the NE of the Vøring Plateau on the mid-Norwegian continental shelf break (Fig. 1). The Røst Reef complex was surveyed as part of the Norwegian seabed mapping program MAREANO (Dolan et al., 2009), and has been the focus of a number of scientific studies in the last 5–10 years (Dullo et al., 2008; Fossà et al., 2004; Fossà et al., 2005; Wehrmann et al., 2009).

As the largest *L. pertusa* reef complex located to date, the Røst Reef complex is 35–40 km long and up to 3 km wide, characterized by steep and rugged ridges elongated in SW–NE direction along the shelf break mainly at water depths 300–400 m (Fig. 2). These ridges originate from the Traenadjupet slide with individual ridges being up to 1 km long and tens of meters high (Fossà et al., 2004; Laberg et al., 2002; Wehrmann et al., 2009). The North Atlantic currents flow approximately parallel to the Røst Reef in a NE direction (Dullo et al., 2008).

Underwater investigations during the Polarstern ARK XXII/1a expedition in 2007, with the manned submersible JAGO (IFM-Geomar), conducted a number of survey dives. Aside from the abundant occurrence of *L. pertusa* reefs within the complex, both *P. arborea* and *P. resedaeformis* were often observed along the JAGO dive transects. In this study, the ship-borne multibeam bathymetry (acquired by a Hydrosweep DS–3), JAGO dive videos and the corresponding positioning data from the Polarstern ARK XXII/1a expedition were used to model the habitat suitability for the two gorgonian species (*P. arborea* and *P. resedaeformis*) at Røst Reef.

The multibeam bathymetry data was further processed employing the open source program MB-system, subsequently projected into WGS 1984 UTM Zone 32N and gridded to 10 m cell size raster data using ArcGIS 9.2. The JAGO dive positioning data was cleaned by deleting the gross-error points, and Gaussian smoothing (Adelie-GIS v1.8) was further employed to decrease the random error. Occurrences of colonies of both gorgonian species were logged along these three JAGO dive transects (Fig. 2) using the software Ocean Floor Observation Protocol (OFOP v3.2.0).

2.2. Multiscale terrain variables

In this study, 30 m, 90 m and 170 m were adopted as analysis scales to calculate multiscale terrain variables, which corresponded to moving window sizes $3 \times 3$, $9 \times 9$ and $17 \times 17$. The multiple scales were chosen
ENFA (Biomapper v4.0) is based on Hutchinson’s concept (Hutchinson, 1957) of the ecological niche, which transforms a selection of possibly correlated environmental variables into the same number of uncorrelated factors (Hirzel et al., 2002). The first of these factors is defined as the ecological distance between the species optimum and the mean available habitat, which maximizes the species marginality. The higher the absolute coefficient of the marginality factor, the further the species distribution departs from the mean available habitat for that particular variable. Positive coefficients indicate preference for higher-than-mean values, and vice versa. The remaining factors (the species specialization) are defined by the ratio of the ecological variance of the available habitat with that of the localities where the species observed. The higher the absolute coefficient of specialization factor, the more dependent the species distribution is on a particular range of the corresponding variable, whether this be a negative or positive coefficient (Hirzel et al., 2002).

In this study, the Box–Cox algorithm (Hirzel et al., 2002) was applied to normalize the depth and 20 terrain variables. Following this normalization, ENFA was performed based on species occurrence data logged from the JAGO dive videos and the 21 normalized variables. A certain number of factors were retained to produce the habitat suitability map based on a comparison with MacArthur’s broken stick distribution (Hirzel et al., 2002). The three algorithms, including median, harmonic mean and geometric mean, were applied to calculate the habitat suitability maps for both gorgonian species.

2.4. Genetic Algorithm for Rule-set Production

GARP (Desktop GARP v1.1.6) is a non-parametric, machine-learning modeling method, which develops rule sets and predicts species potential distribution based on a genetic algorithm (Stockwell and Noble, 1991; Stockwell and Peters, 1999). GARP starts with an initial set of four types of rules (atomic, bioclimatic envelope, negated bioclimatic envelope and logistic regression), then further modifies the rules by employing an iterative learning process of rule selection, testing, evaluation and incorporation or rejection (Anderson et al., 2003). Whether a particular rule should be incorporated into the model or rejected is judged by comparing the predictive accuracy from one iteration with that of the next. The predictive accuracy of a particular iteration is evaluated based on a randomly chosen 1250 pixels from pixels holding training points as presence data, and 1250 pixels from the remainder of the pixels as pseudo-absence data (Anderson et al., 2003). GARP randomly applies these rules and chooses pseudo-absence data each time; therefore, GARP provides non-deterministic predictions with considerable random variability.

In this study, the default specification in Desktop GARP v1.1.6 was employed, with the exceptions of 100 runs and using 100% calibration data for training. The 10 best-subset models were chosen by referring to the method of previous studies (Anderson et al., 2003; Peterson and Shaw, 2003; Phillips et al., 2006). The predictions with intrinsic omission rate larger than 0.05 were deleted. The 10 models with the commission rate closest to the median commission rate among the retained models were determined as the best performing models and combined to form the composite GARP prediction.

2.5. Maximum Entropy modeling

MaxEnt (MaxEnt v3.3.3e) is a general-purpose machine-learning method based on maximum entropy theory for species distribution modeling (Phillips et al., 2006). MaxEnt predicts a species’ potential distribution by seeking the probability distribution of maximum entropy, subject to a set of constraints (linear, quadratic, product, threshold, hinge and categorical features) representing the known constraints of all environmental variables on species distribution (Elith et al., 2011; Phillips and Dudík, 2008). The hinge features are used to model arbitrary piecewise linear responses to the environmental variables, which can effectively replace the linear, quadratic, product and threshold features together whilst hardly impacting on predictive performance (Phillips and Dudík, 2008). Given a minimum of 15 observations, hinge features can be used in prediction, whilst a minimum of 80 are required for use of threshold or product features (Phillips and Dudík, 2008). The ‘target-group’ background sampling method has been applied to avoid the influence of sampling bias, which has been shown to be preferable than using random background sampling (Phillips and Dudík, 2008). MaxEnt can evaluate the importance of environmental variables by using Jackknife tests (Elith et al., 2011).

In this study, the default settings of MaxEnt v3.3.3e were applied, with the exceptions that only hinge features and the ‘target-group’ background data were used in predictions. The ‘target-group’ background pixels were composed of all pixels associated with the three dive routes with usable JAGO dive videos.

2.6. Model assessment methods

In order to assess the average behavior of the models, 10 random partitions were used in the modeling following Phillips et al. (2006) and Tittensor et al. (2009). Each partition was generated by randomly
choosing 75% species occurrence (logged from the dive videos) as calibration data, and the remaining 25% species occurrence as evaluation data.

No one single method is best in assessing the accuracy of predictive models (Ben-David, 2007; Jiménez-Valverde et al., 2008; Lobo et al., 2007). The area under the curve (AUC) of the receiver operating characteristic (ROC) and Cohen’s Kappa are two of the major statistics methods for measuring model accuracy, with very closely related concepts behind these two methods (Ben-David, 2008). As the most widely used statistical method in assessing the accuracy of predictive models (Jiménez-Valverde, 2012; Lobo et al., 2007), AUC statistics was applied to evaluate the model performance in this study. An AUC value of 0.5 indicates random prediction, whilst 1—significantly better than another, and the ENFA models based on a harmonic mean algorithm were found to perform averagely better than models based on algorithms of median or geometric mean, with outperformance (higher AUC values) in eight out of 10 partitions for each species. (2) By comparing the AUC values and P (ENFA (HM) and CARP) values, Enfa (HM) were found to perform better than composite CARP in each of the 10 partitions for both species, and significantly better in four partitions. For P. resedaeformis, MaxEnt were found to perform better than ENFA (HM) in each of the 10 partitions for P. arborea, and significantly better in four partitions. For P. resedaeformis, MaxEnt were found to perform significantly better than CARP in nine of the 10 partitions for both species.

3. Results

3.1. Model evaluation

In this study, all habitat suitability predictions of ENFA, composite CARP and MaxEnt for both species were found to perform significantly better than the random performance (P<0.0001, Mann–Whitney U test, 95% confidence level). Table 1 provides the modeling evaluation results, which can be summarized in four points. (1) By comparing the mean AUC values and AUC values, the ENFA models based on a harmonic mean algorithm were found to perform averagely better than models based on algorithms of median or geometric mean, with outperformance (higher AUC values) in eight out of 10 partitions for each species. (2) By comparing the AUC values and P (ENFA (HM) and CARP) values, Enfa (HM) were found to perform better than composite CARP in each of the 10 partitions for both species, and significantly better in four partitions. For P. resedaeformis, MaxEnt were found to perform better than ENFA (HM) in each of the 10 partitions for P. arborea, and significantly better in four partitions. For P. resedaeformis, MaxEnt were found to perform significantly better than CARP in nine of the 10 partitions for both species.

![Table 1](https://example.com/table1.png)

<table>
<thead>
<tr>
<th>Data partition</th>
<th>AUC</th>
<th>P</th>
<th>ENFA(HM) and CARP</th>
<th>ENFA(HM) and MaxEnt</th>
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<tr>
<td>P. arborea-1</td>
<td>0.825</td>
<td>0.866</td>
<td>0.793</td>
<td>0.75</td>
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<tr>
<td>P. arborea-2</td>
<td>0.911</td>
<td>0.858</td>
<td>0.842</td>
<td>0.745</td>
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<tr>
<td>P. arborea-3</td>
<td>0.823</td>
<td>0.849</td>
<td>0.792</td>
<td>0.746</td>
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<tr>
<td>P. arborea-4</td>
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<td>0.722</td>
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<td>0.858</td>
<td>0.813</td>
<td>0.737</td>
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<td>0.815</td>
<td>0.735</td>
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<td>0.771</td>
<td>0.751</td>
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<tr>
<td>P. arborea-8</td>
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<td>0.857</td>
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<td>0.741</td>
</tr>
<tr>
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<td>0.776</td>
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<td>0.81</td>
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<td>0.767</td>
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<tr>
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<td>0.836</td>
<td>0.796</td>
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<td>0.027</td>
<td>0.033</td>
<td>0.008</td>
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<td>0.713</td>
<td>0.778</td>
<td>0.683</td>
<td>0.723</td>
</tr>
</tbody>
</table>

M — median algorithm. HM — harmonic mean algorithm. GM — geometric mean algorithm. CARP — composite CARP. The highest AUC values of ENFA (HM), composite CARP and MaxEnt models were highlighted in bold. The mean and standard deviation of the AUC values of the 10 partitions were given for each algorithm and species. The statistical analysis on differences was performed between ROC curves of ENFA (HM), composite CARP and MaxEnt with P values shown in the table.
sensitivity thresholds (maximizing the sensitivity) (Pearson et al., 2004; Thuiller et al., 2003). For the GARP predictions, thresholds were identified by visual inspection (Table 2). The habitat suitability of predictions was classified into four levels by the three thresholds, where with the lowest level 1 referred to an unsuitable habitat, and the highest level 4 referred to a core suitable habitat and the two remaining levels 2 and 3 referred to a marginal suitable habitat (Figs. 4 and 5).

Around the NW facing slide in the northern part of the study area (Fig. 2), all six predictions for both species indicated the upper-slide as suitable habitat for both species (Fig. 4 and 5). The composite GARP and MaxEnt predictions indicated the extensive area around the slide as suitable habitat for both species, with particularly suitable habitat for *P. resedaeformis* indicated by GARP prediction extending down to the lower-slide area. Some suitable habitat regions for both species were predicted on the small relief structures in the lower-slide area by ENFA, whereas this was barely indicated by GARP and MaxEnt predictions for *P. arborea*, and not indicated by MaxEnt prediction for *P. resedaeformis* at all.

In the middle and south sections of the study area, all six predictions for both species showed the trend for suitable habitat to occur predominantly along the ridges, and on the west-facing slope of the large relief structure (Figs. 4 and 5).

In ENFA predictions, the suitable habitat for *P. arborea* was predicted to occur predominantly on top of the narrow ridges, and narrowly along both sides of the wider ridges (Fig. 4b). The core suitable habitat for *P. resedaeformis* was mainly situated in a thin band on top of narrow ridges and in approximately the middle regions on each side of wide ridge structures (Fig. 5b). The marginal suitable habitat for *P. resedaeformis* was predicted mainly on the crest of the wide ridges and the large relief structure. Table 3 provides information on the ENFA transformation. The first five factors were retained based on a comparison with the broken-stick distribution for *P. arborea* prediction, whilst the first six factors were retained for *P. resedaeformis* prediction. The retained first five factors accounted for 84% specialization variance of *P. arborea* distribution, whereas the retained first six factors accounted for 83% specialization variance of *P. resedaeformis* distribution (Table 3). The first factor explained 100% marginality of each species distribution.

The composite GARP predictions were more extensive, with predicted suitable habitat for both species throughout the ridges. *P. arborea* was generally predicted as being absent from the bathymetric depressions between ridges (Fig. 4c). Fig. 5c indicates *P. resedaeformis* had a more extensive suitable habitat than *P. arborea* with few regions between the ridges considered as unsuitable habitat. Table 4 provides the high commission (false positive) rate and low intrinsic omission rate of the 10 best-subset predictions, which were combined as the composite GARP predictions with best performance — ninth partition for *P. arborea* and fourth partition for *P. resedaeformis*.

MaxEnt prediction indicated that the suitable habitat for *P. arborea* occurred mainly on the crest of narrow ridges and along both sides of the large ridges, with the core suitable habitat predominantly on the eastern side of the large ridges (Fig. 4d). Fig. 5d indicates that the predicted suitable habitat for *P. resedaeformis* occurred predominantly on the crest of
3.3. Key terrain variables

Among these terrain variables used in this study, some were highly correlated with each other, such as BPI with mean curvature and profile curvature. MaxEnt is robust to the strong correlation between these terrain variables (Phillips et al., 2006). The jackknife tests, which are used to evaluate the variable importance in MaxEnt prediction, may be confused by these strong correlations (Huang et al., 2011; Tittensor et al., 2009). However, the jackknife tests can still provide some information on variable importance.

Jackknife tests in this study indicated that no one terrain variable represented a substantial amount of useful information that was not already contained in other variables in the habitat suitability predictions of MaxEnt for P. arborea and P. resedaeformis. The tests suggested that Aspect9, ProfileCurvature17 and Aspect3 contained the most useful information in MaxEnt prediction for P. arborea when used in isolation, whereas for P. resedaeformis, depth, ProfileCurvature17, and PlanCurvature17 contained the most useful information in MaxEnt prediction when used in isolation.

4. Discussion

4.1. Performances of the three models

In this study, all habitat suitability predictions for both species based on the three modeling methods (ENFA, GARP and MaxEnt) performed significantly better than random, which is consistent with former studies (Phillips et al., 2006; Sérgio et al., 2007; Tittensor et al., 2009). The MaxEnt outperformed ENFA and GARP, again consistent with previous studies (Elith et al., 2006; Li et al., 2009; Phillips et al., 2006; Tittensor et al., 2009). This suggests that the MaxEnt technique predicted more successfully than both ENFA and GARP in discriminating the suitable habitat versus unsuitable habitat for both gorgonian species.

ENFA addresses linear relationships by extracting the linear combinations of environmental variables on which the species shows its
marginality and specialization, unless nonlinearly transformed or combined variables are included (Hirzel et al., 2002; Tittensor et al., 2009). However, since the relationship between species distribution and environmental variables tend to be complex, nonlinear functions may also be important in predictive modeling (Austin, 2002).

GARP is largely successful in avoiding overfitting or overly specializing rules by maximizing both significance and predictive accuracy (Anderson et al., 2003; Peterson and Cohoon, 1999). Additionally, the 10 best-subset predictions (combined to form the composite GARP prediction) were chosen as the predictions with median commission rate (false positive rate) among these predictions with low intrinsic omission rates (<0.05). The commission rate of the 10 best-subset predictions was overestimated as high as 65.02% and 73.13% (mean), for P. arborea and P. resedaeformis, respectively (Table 4). Therefore, the results for the composite GARP technique did not differentiate the terrain quality until a high true positive rate was reached, corresponding to a relatively high commission rate with a relatively low resultant AUC value (Fig. 3).

MaxEnt has been found to perform with a high success rate and statistical significance with sample sizes as low as five (Pearson et al., 2007). The hinge features of MaxEnt fit nonlinear functions of varying complexity (Elith et al., 2011) and form a relatively smooth model, rather like a generalized additive model (Elith et al., 2010; Elith et al., 2011). The ‘target-group’ background sampling method was applied to decrease the influence of species sampling bias. Therefore, the MaxEnt has advantages over the other techniques in both the algorithm and input data used, with these two factors possibly contributing to its outperformance of the other models.

4.2. Predicted habitat suitability

High abundant P. arborea (0.043 colonies/m²) and P. resedaeformis (0.069 colonies/m²) have been reported at L. pertusa reefs on the Norwegian shelf (Mortensen et al., 1995). At the Røst Reef, all six predictions in this study indicated similar spatial patterns of habitat suitability with suitable habitat predicted to occur mainly on the upper-slide, along the complex ridges and on the west-facing slope of the large relief structure, suggesting that both species preferentially colonize topographic highs. Deep-water corals have been observed primarily on or close to such
pronounced topographic highs previously (Dolan et al., 2008; Howell et al., 2011; Huvenne et al., 2011; Mortensen et al., 2001; Tendal, 1992). Such regions are elevated from the surrounding seafloor and therefore tend to receive exposure to currents of greater magnitude, thus the encounter rate of food particles for sessile animals on such structures is enhanced. Additionally, these topographic highs may enhance bottom current velocities, or create current patterns beneficial for food or larvae retention, such as recirculation gyres (Bryan and Metaxas, 2006; Mortensen and Buhl-Mortensen, 2004). The lower-slide area appears to be smoother and lower in relief than the surrounding area, as indicated by the hill-shaded bathymetry data in Fig. 2. Therefore, the lower-slide area is likely unsuitable for utilization by either coral species. Additionally, some suitable habitat was predicted to occur in bathymetric depressions between the ridges (Figs. 4 and 5). Although the highest abundances of a species are commonly found in regions where environmental conditions are most favorable, individual gorgonian colonies have been reported to occupy less than ideal regions of the seabed (Sebens, 1984). In this study, a large number of the colonies of both gorgonian corals were observed in the topographic low-lying areas in relation to seabed relative position and Aspect3 in relation to the bottom current and enhance the nutrient resuspension (Mortensen and Buhl-Mortensen, 2004).

### 4.3. Important terrain variables in predictions

Jackknife tests (MaxEnt) highlighted Aspect9, ProfileCurvature17 (seabed relative position) and Aspect3 in relation to P. arborea distribution, and variables depth, ProfileCurvature17 and PlanCurvature17 (seabed relative position) in relation to P. resedaeformis distribution. Locations with suitable seabed aspect and flow velocity regime combined with elevated topographic height are important for successful prey capture and feeding for deep-water corals (Purser et al., 2010).

The aspect variables provide information on the extent to which the seabed terrain faces into the prevailing bottom currents. Locations facing into the current tend to be more suitable for coral (as filter-feeders) than locations sheltered from bottom currents (Dolan et al., 2008). The fan-shaped morphology of P. arborea is particularly well adapted for the capture of suspended food transported by the prevalent seabed currents (Mortensen and Buhl-Mortensen, 2005). The core suitable habitat for P. arborea was predicted to occur predominantly on SE-facing edges of the wider ridges by MaxEnt (Fig. 4d), which is consistent with the direction (northwestward-flowing) of the prevalent bottom current (Moje et al., 2011). The more reclined and bushy growth morphology of P. resedaeformis indicates that it utilizes a diet that is likely made up of resuspended material from turbulent currents (Mortensen and Buhl-Mortensen, 2005). Given the effects of the irregular seabed terrain of coral reefs, an increase in resuspended material and turbidity can be expected in the reef benthic boundary layer (Wagner et al., 2011). This may partly caused by the local rugged seafloor topography that effectively influence the bottom current and enhance the nutrient resuspension (Mortensen and Buhl-Mortensen, 2004).

### Table 3

<table>
<thead>
<tr>
<th>% specialization</th>
<th>(a) ENFA (HM) P. arborea</th>
<th>(b) ENFA (HM) P. resedaeformis</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>F1</td>
<td>F2</td>
</tr>
<tr>
<td>Depth</td>
<td>24%</td>
<td>30%</td>
</tr>
<tr>
<td>Slope3</td>
<td>0.045</td>
<td>−0.05</td>
</tr>
<tr>
<td>Slope9</td>
<td>0.046</td>
<td>0.255</td>
</tr>
<tr>
<td>Slope17</td>
<td>0.159</td>
<td>−0.13</td>
</tr>
<tr>
<td>Aspect3</td>
<td>−0.19</td>
<td>−0.07</td>
</tr>
<tr>
<td>Aspect9</td>
<td>−0.42</td>
<td>−0.01</td>
</tr>
<tr>
<td>Aspect17</td>
<td>−0.07</td>
<td>0.008</td>
</tr>
<tr>
<td>BP3</td>
<td>0.043</td>
<td>0.001</td>
</tr>
<tr>
<td>BP9</td>
<td>0.191</td>
<td>0.23</td>
</tr>
<tr>
<td>BP17</td>
<td>0.325</td>
<td>−0.18</td>
</tr>
<tr>
<td>MeanCurvature3</td>
<td>0.052</td>
<td>−0.02</td>
</tr>
<tr>
<td>MeanCurvature9</td>
<td>0.244</td>
<td>−0.67</td>
</tr>
<tr>
<td>MeanCurvature17</td>
<td>0.437</td>
<td>0.094</td>
</tr>
<tr>
<td>PlanCurvature3</td>
<td>−0.19</td>
<td>0.015</td>
</tr>
<tr>
<td>PlanCurvature9</td>
<td>0.27</td>
<td>−0.39</td>
</tr>
<tr>
<td>PlanCurvature17</td>
<td>−0.38</td>
<td>−0.03</td>
</tr>
<tr>
<td>ProfileCurvature3</td>
<td>−0.05</td>
<td>0.03</td>
</tr>
<tr>
<td>ProfileCurvature9</td>
<td>0.069</td>
<td>0.009</td>
</tr>
<tr>
<td>ProfileCurvature17</td>
<td>0.243</td>
<td>0.002</td>
</tr>
<tr>
<td>Rugosity3</td>
<td>−0.13</td>
<td>0.118</td>
</tr>
<tr>
<td>TR5</td>
<td>−0.07</td>
<td>0.031</td>
</tr>
</tbody>
</table>

Marginality: 1.003, specialization: 3.722

The median commission rates were highlighted in bold.
was predicted to occur in the SE shallower region of the study area by MaxEnt, which may be more the result of the relatively small surveyed area covered by this study than a reflection of a depth preference by *P. resedaeformis*.

Additionally, other environmental factors such as substrate type may influence coral distribution and are likely to play an important role in habitat suitability predictions (Howell et al., 2011). Both gorgonian species require a hard substrate, such as cobbles or boulders, on which to attach (Mortensen and Buhl-Mortensen, 2005). *P. arborea* abundance has been found to be significantly correlated with *L. pertusa* structure and hard ground substrate availability, whilst *P. resedaeformis* has shown a clustered distribution across coral rubble and structural substrate (Purser et al., unpublished results). The seabed substrate information can be investigated using multibeam backscatter (Howell et al., 2011), or directly using multibeam backscatter data acting as a proxy (Dartnell and Gardiner, 2004).

5. Conclusions

In this study, we predicted the habitat suitability for both gorgonian species across a local area at the Røst Reef. The outputs based on the modeling techniques used are encouraging and all three algorithms performed significantly better than random with MaxEnt predictions outperforming ENFA and GARP predictions, indicating the suitability of the MaxEnt approach for further development.

Suitable habitat was predicted to mainly occur on the upper-slope, along the ridges, and on the west-facing slope of the large relief structure for both species, suggesting a tendency for both species to occupy topographic highs. Jackknife tests (MaxEnt) highlighted the seabed aspect (90 m, 30 m) in relation to *P. arborea* distribution, and curvature (170 m) in relation to the distribution of both species.

Forthcoming data soon to be available from MAREANO would allow a comparative study to be conducted over a wider study area, and to include other environmental controls on coral distribution such as substrate type. Such information would be beneficial to the conservation management of the species.

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Primnoa resedaeformis

Paragorgia arborea

Paragorgia arborea

Nephthya eirei

Paragorgia arborea

Primnoa resedaeformis

Ceratitis capitata, Ceratitis cosyra, and Ceratitis rosai in China.

Ceratitis capitata, Ceratitis cousia, and Ceratitis rosai in China.

Ceratitis cousia, and Ceratitis rosai in China.

Ceratitis capitata, Ceratitis cosyra, and Ceratitis rosai in China.

Ceratitis capitata, Ceratitis cousia, and Ceratitis rosai in China.

Ceratitis capitata, Ceratitis cosia, and Ceratitis rosai in China.

Ceratitis cousia, and Ceratitis rosai in China.

Ceratitis capitata, Ceratitis cosia, and Ceratitis rosai in China.

Ceratitis cousia, and Ceratitis rosai in China.

Ceratitis capita, Ceratitis cousia, and Ceratitis rosai in China.

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