Predicting habitat for two species of deep-water coral on the Canadian Atlantic continental shelf and slope

Tanya L. Leverette, Anna Metaxas

Department of Oceanography, Dalhousie University, Halifax, Nova Scotia, B3H 4J1, Canada
(tleveret@dal.ca)

Abstract. Documentation of hundreds of locations for Canadian deep-water corals has been obtained through scientific initiatives and local fishermen's knowledge. Using these locations, as well as relevant oceanographic data, this study determined areas of suitable habitat for *Paragorgia arborea* and *Primnoa resedaeformis* along the Canadian Atlantic continental shelf and shelf break using predictive models. The study area included a band approximately 800 km long x 200 km wide from Cape Breton to the Gulf of Maine, and was chosen based on density of coral sites. Several environmental factors including slope, temperature, chlorophyll *a*, current speed and substrate may be important in determining suitable coral habitat and were included in the analysis. There are many different techniques used to model habitats, but frequently they are limited by the type of data available. Comparatively, few techniques using presence-only data are available. We utilized BioMapper, a program which uses Ecological Niche Factor Analysis (ENFA), to generate habitat suitability maps by relating data on species presence with background environmental data to determine the species' niche. We found that habitat requirements differed between the two species of coral. For *Paragorgia arborea*, the niche was highly specialized, and characterized by steeply sloped environments and rocky substrate. In contrast, for *Primnoa resedaeformis*, suitable habitat was more broadly distributed in the study area, and located in areas with high current speed, rocky substrates and an approximate temperature range between 5 and 10°C. This is the first study to use predictive modelling to identify suitable habitat for deep-water coral, which may prove an important tool for the conservation of these organisms.

Keywords. Deep-water corals, mapping, *Paragorgia arborea*, *Primnoa resedaeformis*, predictive modelling, BioMapper

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Introduction

Over the past decade, research on deep-water corals has intensified globally. In the Canadian northwest Atlantic continental margin, *Paragorgia arborea* (Linnaeus, 1758) and *Primnoa resedaeformis* (Gunnerus, 1763), both Order Gorgonacea, are the most abundant corals (Willison et al. 2000). *Paragorgia* occurs in the northeast and northwest Atlantic Ocean, off the Norwegian coast and from Newfoundland to Maine (Tendal 1992). Also termed "bubble gum" coral, this species is often bright pink in colour with a spongy outer layer and colonies that can grow to 2.5-3 m tall (Breeze et al. 1997). *Primnoa*, also called "popcorn coral", is smaller, lighter in colour and more densely branched than *Paragorgia*. The two species occupy similar habitats and often, but not always, co-occur. Most often found along shelf edges and in deeper channels, these corals colonize areas with hard substrate and strong bottom currents (~60 cm s^{-1}) (Tendal 1992). Local fishermen have reported that corals are found at water depths from 200 m to 650 m, although this may reflect gear restrictions rather than an accurate measurement of the range of the species. Specimens have also been reported in much shallower water (128 m) off the coast of Maine (Breeze et al. 1997). Estimated temperature range for both species is between 4°C and 8vC (Tendal 1992). Recent research on the ecology of deep-water corals in Atlantic Canada has mainly focused on the Northeast Channel, because of high abundance, and on the Sable Island Gully, because of high species diversity.

Although advancements in surveying technologies have increased the number and accuracy of large-scale mapping projects in shallow-water marine systems, data collection from deep-water environments is considerably more difficult. Consequently, data on the spatial distribution of most deep-water species, including deep-water corals, are also sparse. Species distribution maps can be generated by habitat modelling, a method which examines relationships between the presence and/or absence of species and relevant environmental parameters. There are many different techniques to generate habitat maps, but frequently they are limited by the type of available data. Because of the remoteness and low accessibility of deep-water marine environments, only information on species presence is most frequently available, constraining the range of suitable habitat models. One suitable modelling program is BioMapper. This program uses the statistical technique Ecological Niche Factor Analysis (ENFA), which generates habitat suitability (HS) maps by relating species presence data with background environmental data (ecogeographical variables (EGVs)) to determine the species' niche (Hirzel et al. 2001). BioMapper has been utilized to generate HS maps for several terrestrial floral and fauna, such as ferns in New Zealand and ibex and alpine mice in Switzerland (Hirzel 2001; Sachot 2002; Zaniewski et al. 2002; Reutter et al. 2003). This type of modelling approach is highly recommended when absence data are not available (e.g., most deep-water data sets), unreliable (e.g., cryptic or rare species), or ecologically meaningless (e.g., invading species) (Reutter et al. 2003). Ours is the first study to use ENFA in the marine environment.

We used ENFA to generate habitat suitability maps for the two species, belonging to two different families (Paragorgiidae and Primnoidae), of deep-water coral that are most abundant in the NW Atlantic, *Paragorgia arborea* and *Primnoa resedaeformis*. We also compared the relative importance of several environmental factors (temperature, slope, current, chlorophyll *a* and substrate) in determining suitable habitat for each species. These factors were selected based on available data in locations where coral have been recorded (MacIsaac et al. 2001; Del Mol et al. 2002; Freiwald 2002).

Methods

Study area

The study area encompassed approximately a band 800 km long x 200 km wide along the continental shelf and shelf break, from Cape Breton to the Gulf of Maine (58°N to 67°N and 42°W to 46°W) (Fig. 1). This is an area of current active research on deep-water corals.

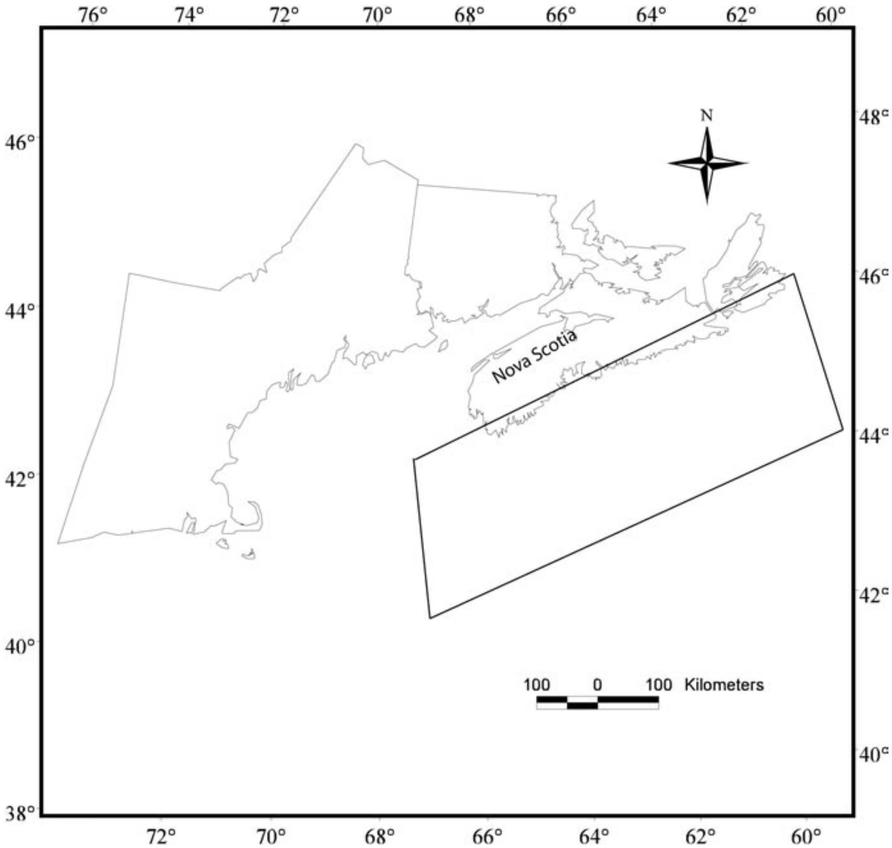

Fig. 1 The study area from Cape Breton to the Gulf of Maine (see box)

Data collection

Locations of *Paragorgia arborea* (n = 72) and *Primnoa resedaeformis* (n = 270) were obtained from scientific cruise reports and literature sources, including Breeze et al. (1997), Gass (2002) and Watling (unpublished data, University of Maine). The literature sources included data mainly acquired from interviews with local fishermen. Environmental data on bathymetry, bottom temperature, surface chlorophyll *a*, substrate and bottom current speed were obtained from several oceanographic sources. Minimum, maximum, and average values were calculated from the temperature, chlorophyll *a*, and current speed datasets. Slope was calculated from the bathymetry data, using ARCView 3.2. Although data were available, salinity was not included as an environmental variable in the analysis because the variation within the study area was small. Sources of empirical data were used whenever possible, although current velocity was obtained through oceanographic models representing 3D seasonal circulation (Hannah et al. 2001). There is little temporal variation in temperature at depths >100 m (typical of coral occurrence), and thus bottom temperature data were averaged over one-year periods (Alidina and Roff 2003). Chlorophyll *a* data were obtained from SeaWIFS data and averaged over 5-year periods, as corals are sessile. Substrate was categorized into classes based on the Lidden-Wentworth size classification for sediment grains and assigned increasing phi values (-12 to +14) to decreasing grain size (boulder to clay) (Pettijohn et al. 1972). This classification produces continuous data for substrate (Kostylev pers. comm). Current data were annual averages calculated from the seasonal (winter, spring, summer, fall) model outputs.

Model generation

ENFA was used to generate habitat suitability maps for *Paragorgia arborea* and *Primnoa resedaeformis* with the software program BioMapper 2.1. ENFA is similar to principal component analysis (PCA) in that it determines relationships between variables and finds combinations of these variables to produce uncorrelated indices or axes (Manly 1986). These axes represent composite factors that explain variability in the data, with the first axis displaying the largest amount of variation. Unlike PCA, however, in ENFA, the axes have direct ecological meaning. The first axis is defined as the “marginality” of the species’ niche, which describes the mean of the species distribution in relation to the mean of the global (study) distribution. It is defined as “the absolute difference between the global mean and the species mean” for each environmental variable (Hirzel et al. 2002) and is calculated as:

$$M = \frac{|m_G - m_S|}{1.96 \cdot \sigma_G}$$

where M is the marginality for a particular environmental variable, m_G is the global mean of the variable, m_S is the species mean of the variable and σ_G is the standard deviation of the global distribution for the variable. Unlike PCA, the first axis in ENFA is chosen to account for 100 % of the marginality of the species as well as some proportion of specialization, with the remaining axes maximizing the remaining amount of specialization of the species. Thus, eigenvalues associated with specialization axes can be larger than the values associated with the marginality values (Hirzel 2001).

The remaining axes explain progressively decreasing amounts of the “niche specialization” of the species. Specialization indicates how restricted the species’ niche is in relation to the study area and is defined as “the ratio of variance in the global distribution to that in the species distribution” of the environmental variable (Hirzel et al. 2002; Reutter et al. 2003):

$$S = \frac{\sigma_G}{\sigma_S}$$

where S is the specialization for a particular environmental variable and σ_S is the standard deviation of the species distribution for the variable.

Combining the marginality and specialization of individual environmental factors, ENFA then computes an overall global marginality (Hirzel et al. 2002; Reutter et al. 2003):

$$M = \frac{\sqrt{\sum_{i=1}^{V} m_i^2}}{1.96}$$

where V is the number of EGVs and m_i indicates the marginality value for each EGV, and a global specialization coefficient:

$$S = \frac{\sqrt{\sum_{i=1}^{V} \lambda_i^2}}{1.96}$$

where σ indicates the specialization value for each EGV (Hirzel et al. 2002). The marginality coefficient M generally ranges between 0 and 1, with large values indicating that the species inhabits a narrow range of the globally available environment. The specialization coefficient S ranges from 1 to ∞, and tolerance, which is the inverse of specialization, from 0 to 1. The greater the tolerance coefficient, the wider the niche of a particular species (Reutter et al. 2003).

An HS map was constructed to visually represent the ENFA results. Firstly, for each environmental factor, the values at each location of species occurrence were determined. A frequency histogram was generated with these values, and scores were assigned to each class in the histogram. Assuming a normal distribution, these scores are maximal at the median of the distribution and decrease towards either tail (Hirzel et al. 2002). Secondly, the class of each cell in the study area was determined and a suitability value ("partial suitability") assigned based on the score of that class in the histogram. The further the class of the cell is from the median, the lower the habitat suitability of the cell. A global suitability map was then generated by computing a weighted mean of the partial suitabilities, producing a habitat suitability (HS) index which ranged from 0 to 100, with zero being completely unsuitable (Hirzel et al. 2004). Model validation and confidence limits for the HS maps were calculated using a built-in jackknifing method in which the presence data were partitioned into ten subsets of equal size. Nine of these subsets were used to calibrate the HS map and the remaining subset was used for validation (Boyce et al. 2002). This procedure was repeated ten times, with a new subset being used for validation each time. Two statistics generated from the jackknifing procedure are useful for evaluating model validity. The Absolute Validation Index (AVI) provides an overall assessment of the model and is determined by calculating the number of validation points which have an HS index greater than 50 %. Higher values indicate a more accurate model. The Contrast Validation Index (CVI) is the difference between the AVI of the model and an AVI generated for a completely randomly-distributed species. This number should also be large if the data fit the model well. In BioMapper 2.1, the most accurate model is one that maximizes both the AVI and CVI.

Coral location data for the species and environmental data were imported into BioMapper as a raster-based grid file with a 9-km cell size. ENFA was used to obtain marginality and specialization values, which indicated those environmental parameters with the greatest influence (weight) on the distribution of each coral species. A total of 11 ecogeographical variables (EGVs) (Table 1) were used to generate 27 possible model combinations (which contained all five environmental factors: temperature, slope, current speed, chlorophyll *a* and substrate).

Table 1 List of the eleven ecogeographical variables (EGV) used to generate the 27 models included in the Ecological Niche Factor Analysis (ENFA) for *Primnoa resedaeformis* and *Paragorgia arborea* in the NW Atlantic Ocean

Code	EGV
Sl	Slope
Tn	Temperature (minimum)
Tv	Temperature (average)
Tx	Temperature (maximum)
Cn	Current (minimum)
Cv	Current (average)
Cx	Current (maximum)
Chn	Chlorophyll *a* (minimum)
Chv	Chlorophyll *a* (average)
Chx	Chlorophyll *a* (maximum)
Sb	Substrate

Results

Paragorgia arborea

For this species, the model that included slope, average temperature (1.2-10.2°C), average current speed (0.02-0.21 m s^{-1}), maximum chlorophyll *a* concentration (0.9-6.9 mg m^{-3}) and substrate, resulted in the best combination of AVI (82.7 %, SD = 18 %) and CVI (0.63, SD = 0.19) (Table 2). Global marginality was 0.61 and global tolerance was 0.16, indicating that the conditions in the preferred habitat of this coral species are notably different from average for the study area. The three retained factors (of the five computed) accounted for 100 % of marginality and 98 % of total specialization. Marginality coefficients showed that suitable habitat for this species is most strongly associated with steep slope (0.72) and rocky substrate (-0.40) (Table 3). Current speed, chlorophyll *a* concentration and average temperature are less important in determining suitable habitat (Table 3). As the first factor accounts for 100 % of the marginality, the large eigenvalue (40 %) associated with this indicates that a large portion of the specialization of *Paragorgia arborea* is strongly influenced by changes in topography. The next two factors account for the remaining specialization in response to chlorophyll *a* concentration (factor 2) and

Table 2 Validation indices for the three best models (those with the highest AVI and CVI) run to evaluate habitat suitability for each coral species

Species	Factors included in the model	AVI %	CVI
P. arborea	Sl,Tv,Cv,Chx,Sb	83	0.63
	Sl,Tv,Cn,Chn,Sb	77	0.58
	Sl,Tx,Cn,Chn,Sb	75	0.40
P. resedaeformis	Sl,Tv,Cn,Chn,Sb	82	0.33
	Sl,Tn,Cv,Chv,Sb	81	0.25
	Sl,Tn,Cv,Chx,Sb	80	0.19

Table 3 Coefficients of each ecogeographical variables (EGV) in the best model generated by ENFA for *Paragorgia arborea*. The first axis explains 100 % of the marginality, as well as a proportion of the specialization. The specialization explained by the first three (of five) factors is shown in brackets. Positive values on the marginality factor indicate that the species prefers locations with higher values on the corresponding EGV than the global (study area) average

EGV	Marginality (40 %)	Specialization1 (55 %)	Specialization2 (4 %)
Sl	0.72	0.33	0.14
Tv	0.26	0.07	0.89
Cv	0.38	0.07	0.16
Chx	-0.31	0.91	0.14
Sb	-0.40	0.23	0.38

average temperature (factor 3). A habitat suitability map illustrated that relatively suitable habitat for this species occupies a very narrow band along the shelf break (Fig. 2).

Primnoa resedaeformis

For this species, the model that included slope, average temperature (0-8.6°C), minimum current speed (0-0.16 m s^{-1}), minimum chlorophyll *a* concentration (0.5-5.7 mg m^{-3}), and substrate resulted in the best combination of AVI (75.5 %, SD = 23 %) and CVI (0.34, SD = 0.21) (Table 2). Global marginality was 0.50 and global tolerance was 0.53, indicating that the preferred habitat of *P. resedaeformis* is more similar to the average conditions in the study area than that of *P. arborea*. The three retained factors (of the five computed) accounted for 100 % of marginality and 90 % of total specialization. Marginality coefficients show that suitable habitat for this species is most strongly associated with average temperature (0.53), minimum

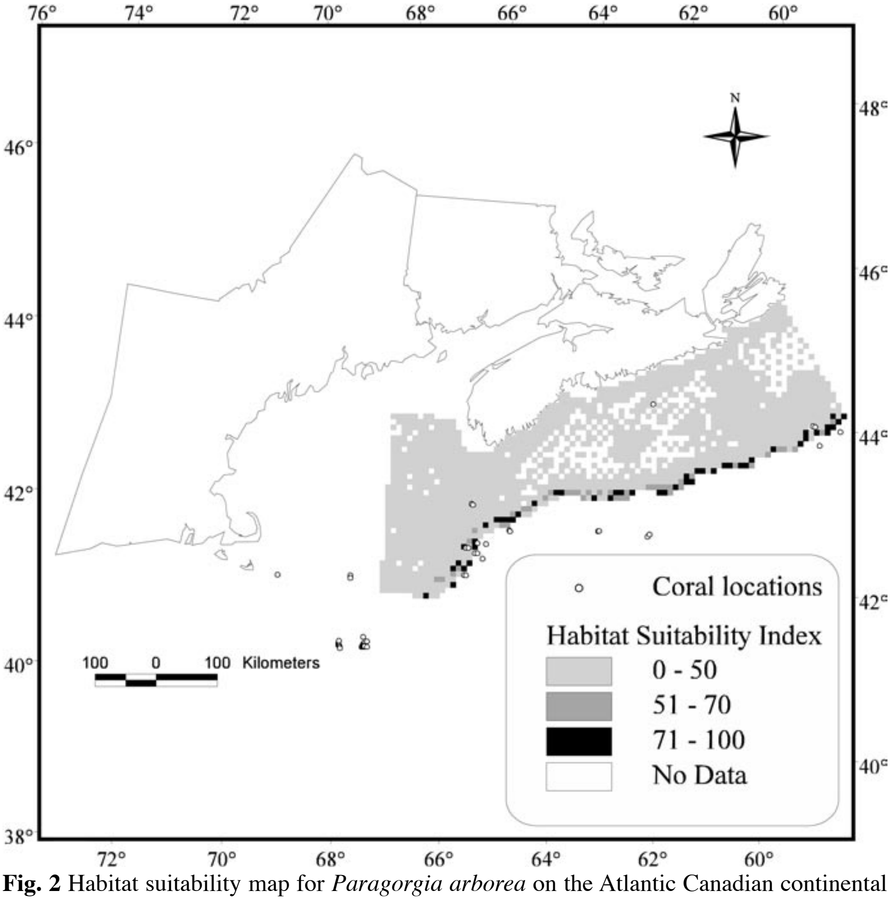

Fig. 2 Habitat suitability map for *Paragorgia arborea* on the Atlantic Canadian continental shelf and shelf break, as computed by the Ecological Niche Factor Analysis. The scale indicates habitat suitability values

current speed (0.54) and rocky substrates (-0.56) (Table 4). Slope and chlorophyll *a* concentrations are less important in determining suitable habitat (Table 4). A small eigenvalue (15 %) associated with the first factor, indicates that *P. resedaeformis* is not particularly sensitive to changes in the environmental factors included in this axis. The next two factors account for more specialization, mainly in response to chlorophyll *a* concentration (factor 2) and substrate (factor 3). The eigenvalues for the specialization factors are relatively large, indicating that they have a strong effect in restricting the range of *P. resedaeformis*. A habitat suitability map generated from these variables illustrates areas with suitable habitat for this species are scattered throughout the continental shelf and shelf break (Fig. 3).

Table 4 Coefficients of each ecogeographical variables (EGV) in the best model generated by ENFA for *Primnoa resedaeformis*. The first axis explains 100 % of the marginality, as well as a proportion of the specialization. The specialization explained by the first three (of five) factors is shown in brackets. Positive values on the marginality factor indicate that the species prefers locations with higher values on the corresponding EGV than the global (study area) average

EGV	Marginality (15 %)	Specialization1 (64 %)	Specialization2 (11 %)
Sl	0.30	0.25	0.08
Tv	0.53	0.02	0.63
Cn	0.54	0.10	0.15
Chn	-0.16	0.93	0.13
Sb	-0.56	0.25	0.75

Discussion

Fisheries and Oceans Canada have been collecting qualitative and quantitative data on deep-water coral habitat on the Scotian Margin since 1997. These observations have revealed that, in general, the highest densities of corals are found in elevated areas, such as iceberg scours, with strong currents (MacIsaac et al. 2001). Our results also indicated a strong relationship between habitat suitability and current speed, particularly for *P. resedaeformis*. As deep-water corals are sessile, filter-feeding organisms that rely on near-bottom currents for nutrient supply in order to obtain adequate nutrients, they must exist in habitats with strong currents (Mortensen 2001).

The results of our study also indicate that distributions for both species were strongly influenced by temperature. Previous observations indicated that most deep-water corals inhabit areas with minimum temperatures >3°C, with some species present in locations with temperatures as low as -1°C (Cimberg et al. 1981). Our study showed that although these species can tolerate colder waters, the majority of the locations were found in warmer waters, ranging between 4-8°C (Tendal 1992; Krieger 2001).

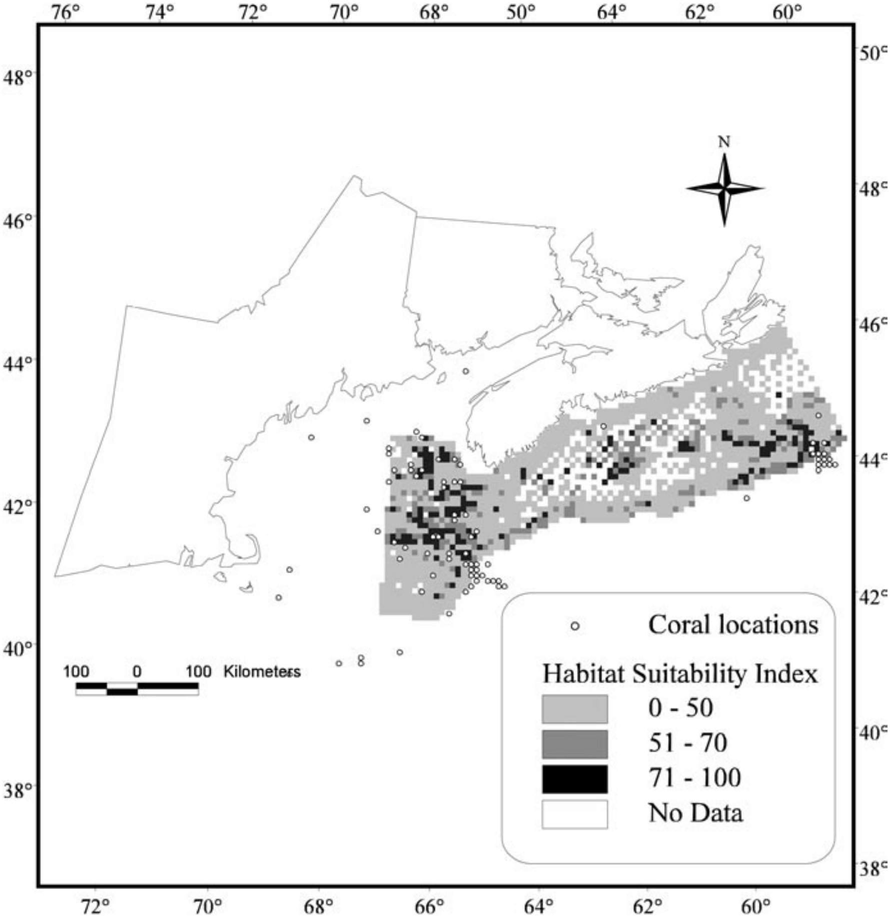

Fig. 3 Habitat suitability map for *Primnoa resedaeformis* on the Atlantic Canadian continental shelf and shelf break, as computed by the Ecological Niche Factor Analysis. The scale indicates habitat suitability values

Corals are abundant on slopes, in and around submarine canyons, gullies and the edge of the continental shelf (MacIsaac et al. 2001). These sloping areas are normally associated with hard substrate, such as cobble and boulders, making then ideal for coral attachment (Freiwald et al. 1999). Suitable habitats for *P. arborea* were associated most strongly with slope values that were above average for the study area. Steeply sloping areas can be a highly suitable habitat for these large corals, as current velocities are often high there. *P. arborea* is a large gorgonian species, reaching 2.5-3 m in height (Breeze et al. 1997), and their branches form large fan-like structures, often convex and facing into the main direction of current (Reed 2002). This adaptation likely maximizes the surface area exposed to the current flow and, thus, the filter feeding effectiveness of the organism, as well as reducing torsion in the basal stem (Tunnicliffe 1983). In contrast, suitable habitat for *P. resedaeformis* was defined by a combination of ranges for substrate, current speed and temperature. The differences in niche breadth between the two coral species were clearly illustrated in the ENFA results. Although *P. resedaeformis* and *P. arborea* have similar global marginality coefficients (0.5 and 0.6 respectively), their tolerance coefficients differ markedly (0.53 and 0.15 respectively). These values indicate that although these two species of coral are expected to co-exist often, *P. resedaeformis* is considerably more tolerant of inhabiting a wider range of habitats.

This study increased our understanding of the relative importance of different environmental factors in determining suitable habitat for deep-water corals. In turn, the habitat suitability maps generated from the results of ENFA can allow for clear identification of target areas for exploration. Data collected as presence-only, and previously unusable data, such as those from museum collections, can be successfully processed with ENFA. Several recent international fora (e.g., the NOAA funded Symposium on the Effects of Fishing Activities on Benthic Habitats (McDonough and Puglise 2003)), have recommended that mapping of coral locations is an immediate priority (see also Puglise et al. 2005). We have used ENFA to extend these recommendations by attempting to predict potential coral locations presently unknown, based on suitability of the habitat. To our knowledge, this is the first study that attempts to predict deep-water coral habitat. Our study is also the first to use ENFA for marine species. This analysis may prove particularly useful for the remote and relatively inaccessible deep-water environment.

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