Predicting suitable habitat for deep water corals in the Pacific and Atlantic Continental Margins of North America

by

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Submitted in partial fulfilment of the requirements
for the degree of Master of Science

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DEDICATION

To Carl and Ruth, without whom this would not have been possible.

To Aunt Duck, for the inspiration so long ago.

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ABSTRACT

Documentation of hundreds of locations for North American deep water corals, as well as relevant oceanographic data, has been obtained through scientific initiatives and local fishermen's knowledge. Historically, these corals have been a burden for the fishers because of loss of gear through entanglement. In some extreme cases, dragging of the bottom was used to dislodge the corals and prevent a further loss of gear. This thesis examined the quantitative relationships between physical seascape factors and biological data by developing an innovative habitat prediction model for deep water corals both in the Pacific and Atlantic Continental Margins of North America (PCM and ACM study areas). The study examined broad distributional patterns of several families of deep water coral, but focused mainly on the distribution of the families Primnoidae and Paragorgiidae due to the larger number of occurrences. The spatial suitability of deep water coral habitat on both continental margins was explored using Biomapper, a modeling program which can determine habitat suitability using presence-only data. Although there are many different techniques used to model habitats, few techniques using presence-only data are available. For both the PCM study site, the combination of temperature and current was the best at predicting habitat for all coral families combined ($\rho=0.7$); chlorophyll *a* concentration and substrate for Paragorgiidae ($\rho=0.87$); and temperature, substrate and chlorophyll *a* concentration for Primnoidae ($\rho=0.69$). In the ACM study area, the best combination for all coral families combined include all five environmental factors (temperature, slope, current, substrate and chlorophyll *a* concentration) ($\rho=0.58$); current, substrate and chlorophyll *a* concentration for Paragorgiidae ($\rho=0.82$) and temperature and substrate for Primnoidae ($\rho=0.65$). Using these models, I generated habitat suitability maps. Corals were primarily found in areas of complex topography, mainly along the continental shelf break. These maps are the first step in determining where coral may potentially be found. Results from the model suggested that slope, temperature, and current are important environmental factors in predicting suitable coral habitat. In the PCM study area, Paragorgiidae and Primnoidae locations were found in areas with slopes ranging from 0 to 10°, temperature from -2 to 11°C and currents from 0 to 143 cm s^{-1}. In the ACM study area, Paragorgiidae and Primnoidae locations were found in areas with slopes ranging from 0 to 6°, temperature ranging from 0 to 11°C and currents ranging from 2.67 to 74.51 cm s^{-1}. On both continental margins, coral locations were found to be not randomly distributed within the study areas, but were present within specific ranges of all environmental factors. Although the patterns in habitat characteristics were generally similar for most deep water corals, some differences existed between families with respect to particular environmental factors. In both study areas, for both Paragorgiidae and Primnoidae, all environmental parameters in locations where corals occurred were significantly different from the average values of these parameters as determined with χ^2 tests ($p<0.05$). To my knowledge, this is the first study to use Biomapper for marine species.

ACKNOWLEDGEMENTS

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For help with Biomapper, I am deeply indebted to Alexandre Hirzel and the many people on the Biomapper list serve. Without their help (and sometimes daily email contact), I never would have gained a thorough understanding of the program and what it can (and cannot) do. I need to also thank Jennifer Smith for her patience and understanding (both as she worked at the Killam Library and now at WWF) while we tried to figure out how ArcView and Biomapper meshed. Also, the folks at the Killam Library GIS Center were extremely helpful in sorting out some of my GIS challenges.

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CHAPTER 1

1.1. GENERAL INTRODUCTION

The oceans cover over 70% of the earth's surface, with 90% lying beyond the relatively shallow waters of the continental margins (Gage and Tyler, 1996). Yet, despite occupying almost two-thirds of the Earth's surface, these deep water habitats, particularly those on hard bottoms, are among the most poorly studied (excluding hydrothermal vents) (Messing et al., 1990). Our understanding of the deep sea environment has evolved greatly since the pioneering voyage of the Challenger expedition, from 1872-1876. Technology has since advanced to more accurately and less destructively sample the varied habitat and the associated flora and fauna. These advancements have confirmed the Challenger's initial findings: there are diverse communities of organisms below the photic zone, both pelagic and benthic, as well as variable oceanographic conditions at all depths and between oceans.

In 1965, Menzies published a review which described the conditions of life on the deep-sea floor. Recent studies have expanded upon some of the observations made in this study, although many of these observations made almost 40 years ago are still valid. On a coarse scale (100s km's), temperature is relatively stable near the seafloor, and is generally 4°C below the permanent thermocline (Tyler, 1995). Notable exceptions include semi-enclosed seas such as the Red Sea, where temperature is 21°C at 2000 m, and the Mediterranean with a bottom temperature of 13°C, as well as hydrothermal vents which can emit water at >350°C (Tyler, 1988). Salinity near the ocean bottom ranges between 34 to 38 (Herring, 2002). Most oceans have salinities between 34 to 35, except the Mediterranean and the Red Sea, with salinities as high as 39 (Mantyla and Reed, 1983; Tyler, 1995).

The topography of the seafloor is highly variable as a result of plate tectonics and glacial history, ranging from flat abyssal plains to steeply sloped seamounts. This variation in slope influences the distribution of sediments and the magnitude and direction of currents (Tyler, 1995). Currents vary depending on topography, as well as in response to tides, wind and baroclinicity. Current reversals due to tidal influences have been noted of depths up to 2000 m in the Bay of Biscay and may also vary due to unpredictable events, such as benthic storms and sediment slides (Tyler, 1988). Although the dominant substratum type in the deep sea is soft sediments, sloped areas frequently provide a source of hard substrate as accumulations of softer sediment is not possible (Gage and Tyler, 1996). Due to its rarity, patches of hard substrate often become “island” habitats, resulting in higher levels of diversity than in the surrounding soft sediments (Beaulieu, 2001). The organisms which colonize these islands may then become substratum themselves, supporting and providing refuge for a variety of encrusting and mobile organisms.

Deep water gorgonian corals typically occur on such islands of hard substrate and themselves provide biogenic habitat for associated organisms. These corals lack the symbiotic zooxanthellae normally present in shallow water corals. This lack of zooxanthellae results in a slower growth rate than most of their shallow water counterparts, as well as a slower metabolism (Cairns, 1977). Initially, recruits of these corals require hard substratum, such as a pebble or bedrock outcropping, on which to attach (Cimberg, 1981; Rogers, 1999). Once established, they provide the shelter and habitat for an abundance of associated fauna (Hecker, 1990; Mortensen, 2001; Heifetz, 2002; Krieger and Wing, 2002). Current research has mainly focused on documenting and enumerating associated species, without first establishing baseline knowledge regarding the ecology or distribution of most species of corals.

In this study, I examine the relative importance of different environmental factors in determining suitable habitat for several families of deep water gorgonian coral on the continental shelves and slopes off Eastern and Western Canada and the United States. In chapter 2, I qualitatively and quantitatively describe habitat in which corals are located in relation to five oceanographic factors: temperature, slope, current, chlorophyll *a* and substrate. For each environmental factor, deep water coral locations were compared to the surrounding environment using χ^2 tests.

Chapter 3 determines the spatial suitability of deep water coral habitat on both continental margins using Biomapper, a modeling program which predicted habitat suitability using presence-only data. This chapter also analysed the sensitivity of Biomapper to different input parameters, including varying the number of locations and environmental parameters.

This study was conducted to: (1) determine the distribution of each factor on the distribution of Paragorgiidae and Primnoidae; (2) generate a model which will predict suitable habitat for deep-sea corals using environmental factors; and (3) evaluate the performance of the model when the input parameters are varied. This thesis was written in the form of manuscripts, and sections of Materials and Methods are repeated in chapters 2 and 3.

CHAPTER 2

2.1. INTRODUCTION

Deep water corals have been receiving increased attention in the last five years both from the scientific community and the public in North America. However, information on their biology is sparse, mainly because of logistical difficulties in collecting specimens. In the last decade, *in situ* observations and collection of live specimens have become possible with the use of remotely operated vehicles (ROVs) and submersibles, allowing an increased understanding of the biology of these species. Deep water corals (Cnidaria, Anthozoa) include several Orders and Families, which represent solitary, reef-forming and colonial organisms. Much of our understanding of deep water corals is based on studies on *Lophelia pertusa*, a reef forming coral abundant in the northeast Atlantic. Found most commonly along shelf margins in the North Atlantic, Pacific and Indian Oceans, as well as in the Mediterranean Sea, the biology and distribution of this species have been studied extensively over the past ten years (Rogers, 1999; Mortensen, 2001; Freiwald, 2002). Although the highest abundance of this species has been recorded in the Atlantic Ocean, from Sweden to Africa and from Canada to Columbia, this pattern is most likely a combination of high surface productivity and availability of suitable substrate (Rogers, 1999). Corals have also been discovered along the Pacific coast of North America, from Alaska to California, as well as on seamounts near Tasmania (Figure 2.1; Rogers, 1999). However, these distributions are most likely biased by sampling effort and are presumably much wider.

Unlike shallow water corals, deep water corals lack zooxanthellae, and consequently their distribution can extend to depths below the photic zone (Jensen and Frederiksen, 1992). The high diversity of deep water corals makes generalizations about

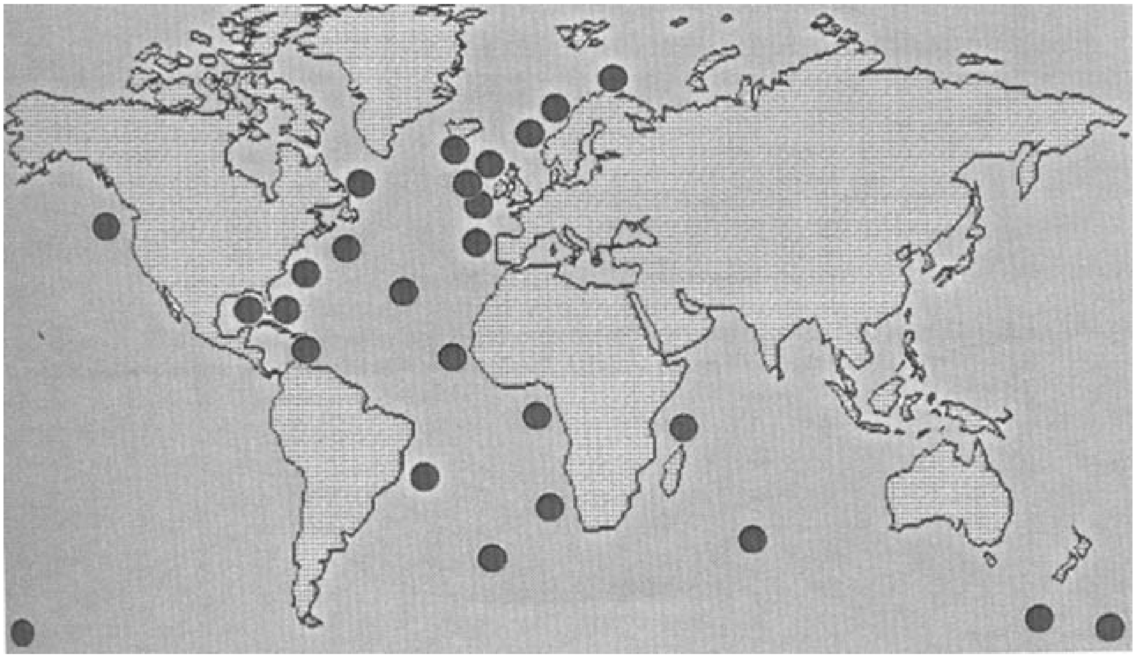

Figure 2.1. Global distribution of deep water coral assemblages (From: Hovland and Mortensen, 1999).

habitat requirements difficult. However, most deep water coral species require hard substrate, such as cobbles or pebbles, for attachment (Rogers, 1999). The depth range can vary between and within species. For example, *Primnoa resedaeformis* has been recorded from 10 m to 800 m (Cimberg et al., 1981; Andrews et al., 2002), while *Lophelia pertusa* has been found at depths between 39 and 3380 m (Mortensen et al., 2001). However, recorded abundance to date is maximal between 200 and 1000 m depth. Frederiksen et al. (1992) suggested that the shallow limit of distribution is mainly determined by temperature and salinity, and to a lesser extent, by wave action.

Deep water corals are found primarily in areas of pronounced topographic relief (Tendal, 1992; Mortensen et al., 2001), usually with strong current velocities or unique current patterns such as recirculation gyres, which in turn are indicative of increased concentrations of particles (Moore and Bullis, 1960; Tendal, 1992). It has been suggested that the presence of light hydrocarbon seepage may be an indication of suitable *Lophelia pertusa* habitat (Hovland et al., 1998), but this has yet to be confirmed. Although the relationships of coral distributions with temperature and salinity have yet to be studied in detail, the ranges of these variables in relation to coral habitat seem to vary between species. The deep sea is relatively homogeneous in salinity (Gage and Tyler, 1996), and most corals inhabit environments with salinities ranging mainly between 34 and 37 (Mortensen et al., 2001; Freiwald, 2002). In relation to temperature, most species tend to occur in waters warmer than 3.5ºC, although some, such as *Gersemia* spp., have been found to occur in temperatures as low as -1ºC (Cimberg et al., 1981).

Deep water corals are carnivorous, capturing food with their tentacles by nematocyst adhesion (Breeze, 1997). The type of captured food largely depends on the polyp size of the species. Species with larger polyps tend to feed more exclusively on zooplankton while those with smaller polyps feed more readily on bacteria, detritus, and dissolved substrates (Freiwald, 1998). The egested waste may serve as a source of nutrients for associated fauna (Freiwald, 1998; Ecology Action Centre, 1999; Freiwald et al., 2001). Similar to shallow water species, reproduction in deep water corals may occur sexually or asexually (Rogers, 1999). Asexual growth can occur through intertentacular budding, when an existing polyp forms new polyps, or through fragmentation, when a section of live coral is detached from the main colony and reattaches at a new location. This new section can continue to grow and form a new colony through budding (Rogers, 1999). Although specific information on sexual reproduction, larval development and dispersal is lacking for most species, a recent study by Brooke and Young (2003) found that the deep water coral *Oculina varicose* is a broadcaster spawner with high fecundity. During their planktonic stage, the larvae are active swimmers and able to regulate their position within the water column (Brooke and Young, 2003). Based on aquarium observations (Mortensen, 2001), stable isotope studies using skeletal cross-sections (Mikkelsen et al., 1982; Mortensen and Rapp, 1998) and estimates from broken deep-sea cables (Freiwald, 1998), growth rates of deep water coral colonies range from 2 to 25 mm yr $^{-1}$. It is unknown whether these rates are related to seasonal changes in temperature or variation in food availability (Mortensen, 2001).

My study examined distributional patterns of seven families of deep water coral in the Pacific Continental Margin (PCM) and eight families in the Atlantic Continental Margin (ACM) of North America in relation to five oceanographic factors: temperature, slope, current, chlorophyll *a* and substrate. These factors were selected based on available data in locations where coral had been recorded (MacIsaac et al. 2001; Del Mol et al. 2002; Freiwald, 2002). Distributions of three taxonomic groups (all coral families combined, Primnoidae, and Paragorgiidae) were compared between the two study sites. By deriving first order relationships between the occurrence of coral and different environmental variables in their habitat, this study will enhance our understanding of environmental factors limiting the distributions of these organisms. Through the use of geographic information systems and the presence of more complex oceanographic datasets, I examined the distribution of coral on spatial scales of 100s-1000s km's and multi-annual temporal scales for the first time.

2.2. MATERIALS AND METHODS

2.21. Study Area

Study sites were selected along the Pacific Continental Margin and Atlantic Continental Margin. The PCM study area encompassed an area approximately 2000 km wide and 3500 km long, from Alaska to California (Figure 2.2). This site was defined by a wide continental shelf (~100 km wide) and a narrow (~70 km wide) but steep continuous slope (from shelf break to ~5000 m deep) (Leier, 2001). This sharp gradient is the result of active subduction zones close to the continent. Near the continent, this study area also contained many islands which channel the water into high current locations.

The ACM study area included a band approximately 800 km long and 300 km wide from Cape Breton to Cape Cod (to ~500 m in average depth) (Figure 2.3). This area was defined by a 200 km wide continental shelf and a 250 km wide continental slope (sloping to 4000 m in depth) (Elsner, 1999; Gordon and Fenton, 2002). The continental shelf is composed of large, shallow banks surrounded by several basins and troughs along the inner shelf, as well as many canyons along the outer shelf. This topography influences throughflow and local recirculation of water masses (Hannah et al., 2001). Both study areas were chosen based on the observed high density of known coral sites.

3.22. Data Collection

Sources of environmental data on slope, temperature, chlorophyll *a* concentration, substrate type and current speed for both study areas are given in Table 1. Sources are mostly of empirical data, except for current velocity which was obtained through oceanographic circulation models. To obtain access to unpublished data on the variables included in my study, the sources listed in Table 1 can be contacted directly.

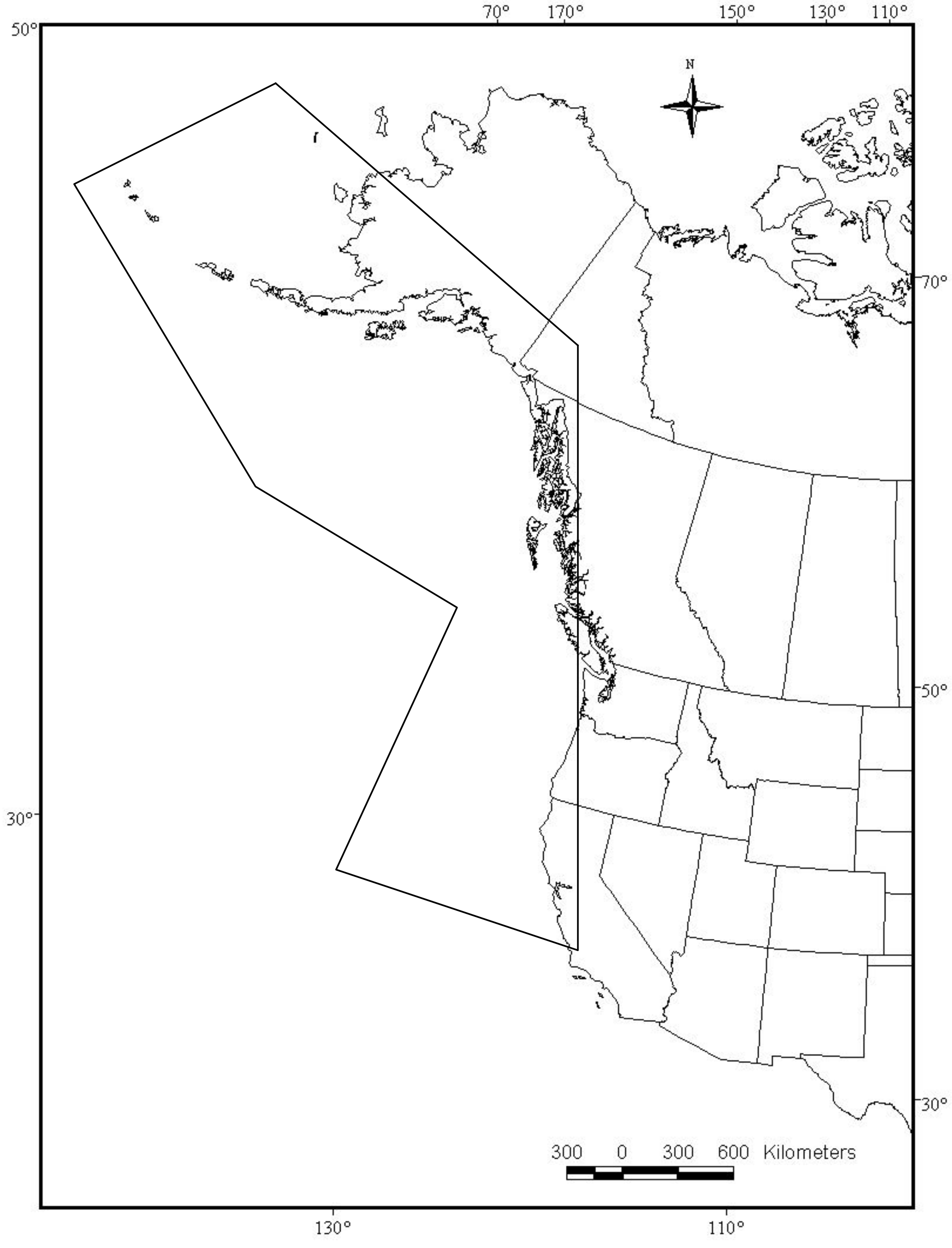

Figure 2.2. The Pacific Continental Margin (PCM) study area, from Alaska to California.

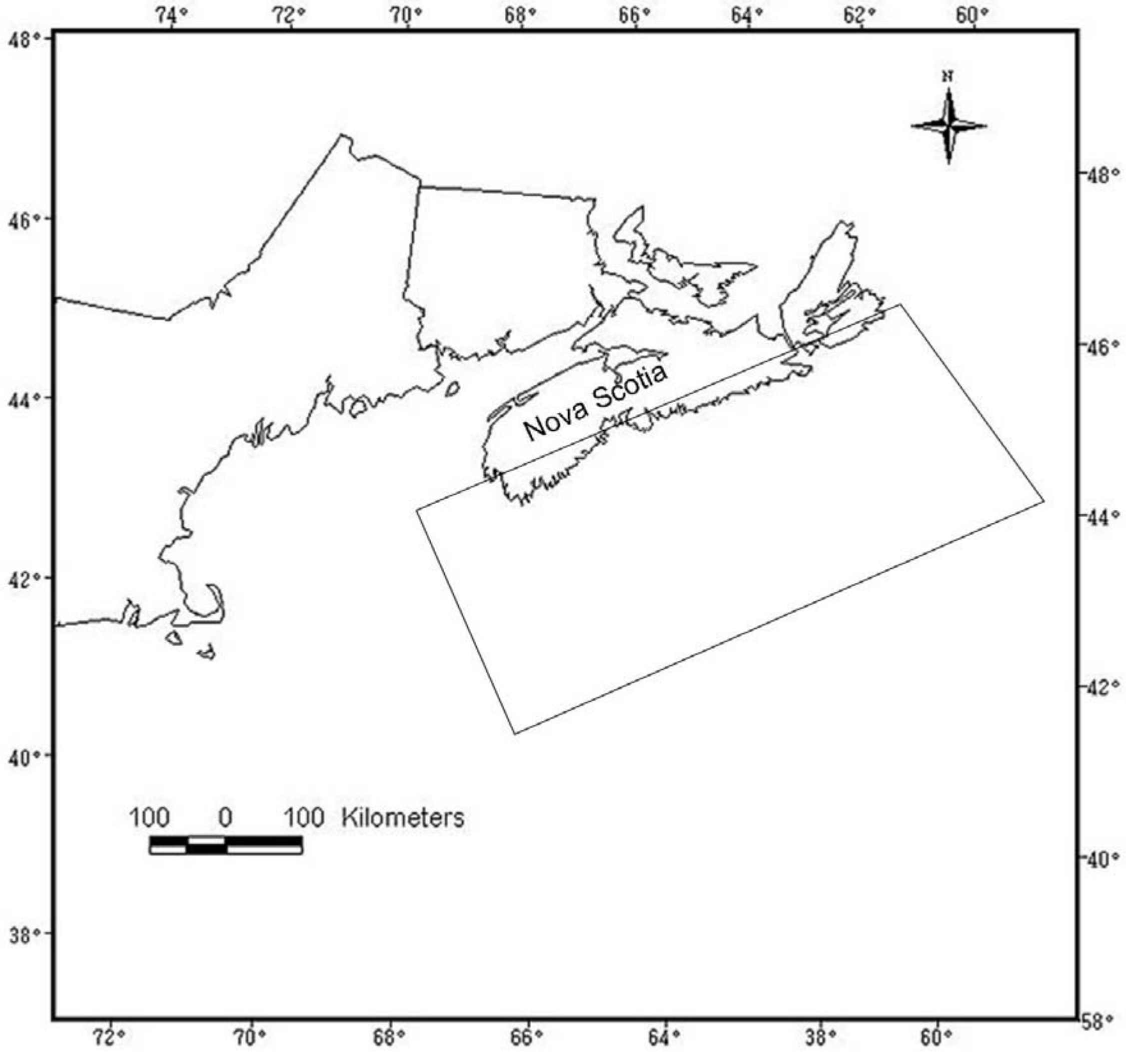

Figure 2.3. The Atlantic Continental Margin (ACM) study area, from Cape Breton to the Gulf of Maine.

Table 2.1. Sources and types of environmental data used.

Study Area	Environmental Variable	Source	Type of Data
PCM	Bottom current velocity	Mike Foreman, Institute of Ocean Science, Canada	Modelled data, tidal velocities modelled for winter, spring, summer, fall and then averaged for the year
	Slope	Marine Conservation Biology Institute, USA	Derived from bathymetry data composed of a 2' resolution grid
	Surface chlorophyll *a* concentration	Marine Conservation Biology Institute, USA	Derived MODIS images, yearly average includes 1997-1999
	Bottom temperature	Don Spears, Marine Environmental Data Services Branch (MEDS), Canada	Each point was averaged from seafloor to include a maximum of 50 m above the seafloor in the water column
	Substrate	Chris Jenkins, Institute of Arctic and Alpine Research (INSTAR), USA	Compiled from the USGS database, categorized into classes based on the Lidden-Wentworth size classification for sediment grains and assigned increasing phi (φ) values (-12 to +14) to decreasing grain size (boulder to clay) (Pettijohn et al., 1972)
ACM	Bottom current velocity	Charles Hannah, Bedford Institute of Oceanography, Canada (Hannah et al., 2001)	Modelled data, annual tidal velocities
	Slope	World Wildlife Fund Canada (Alidina and Roff, 2003)	Derived from bathymetry data composed of a 5' resolution grid
	Surface chlorophyll *a* concentration	Moderate Resolution Imagining Spectroradiomters (MODIS)	Derived MODIS images, averaged from 1998-2001
	Bottom temperature	World Wildlife Fund Canada (Alidina and Roff, 2003)	Each point was averaged from seafloor to included a maximum of 50 m above the seafloor in the water column
	Substrate	Vladimir Kostylev, Natural Resources Canada	Categorized into classes based on the Lidden-Wentworth size classification for sediment grains and assigned increasing phi (φ) values (-12 to +14) to decreasing grain size (boulder to clay) (Pettijohn et al., 1972); continous grid of mean grain size based on interpolation of existing grab and core samples

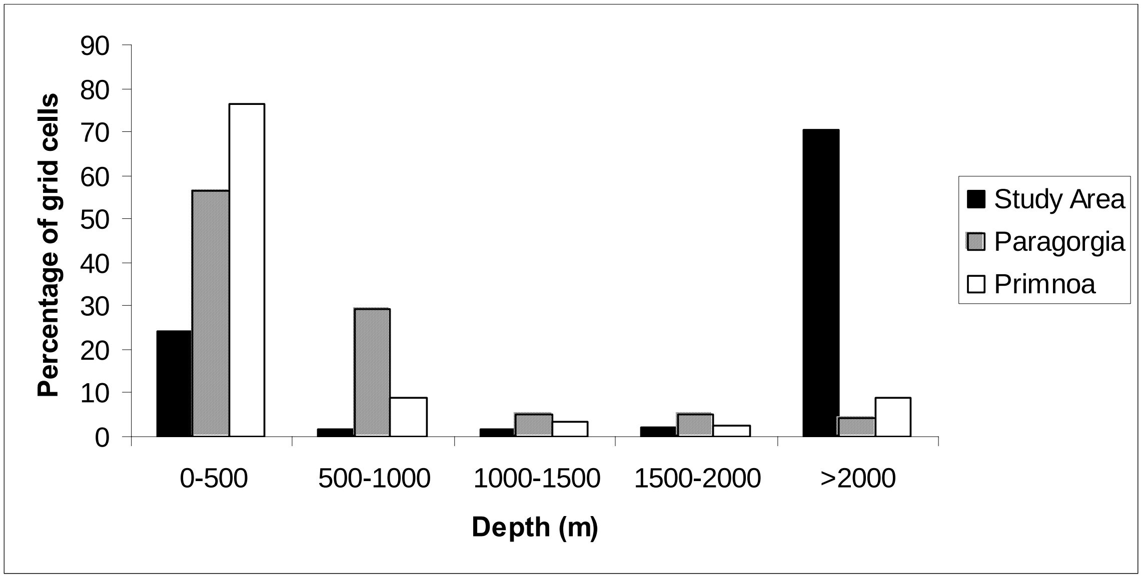

Figure 2.4. Depth (m) in the PCM study area and in locations with Paragorgiidae and Primnoiidae.

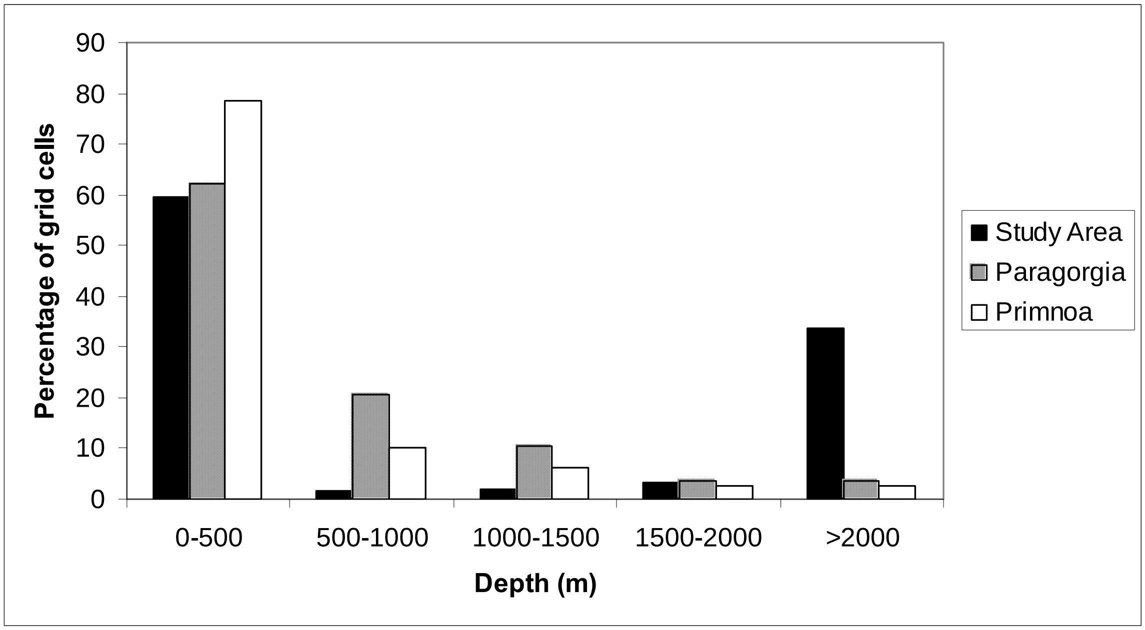

Figure 2.5. Depth (m) in the ACM study area and in locations with Paragorgiidae and Primnoiidae.

For the PCM study area, data on coral locations were obtained from the Marine Conservation Biology Institute (MCBI) (Etnoyer, 2003). This dataset included over 2000 coral locations from seven families (Antipathidae, Caryophyllidae, Corallidae, Isididae, Paragorgiidae, Primnoidae and Stylasteriidae). Data were provided by many institutions, including the California Academy of Sciences, the Smithsonian Institution National Museum of Natural History, NOAA Fisheries RACEBASE, Canadian Museum of Nature, the Monterey Bay Aquarium Research Institute, Scripps Institute of Oceanography, the REEF Foundation (Stylaster records) and the Santa Barbara Museum of Natural History, as well as by Cimberg et al. (1981).

Coral observations in the ACM study area included eight families: Acanthorgiidae, Caryophllidae, Flabellidae, Isididae, Keratoisidae, Paragorgiidae, Paramuriceida, and Primnoidae. They were obtained from Breeze (1997), Gass (2002) and Watling (unpublished data, University of Maine). The data summarized in these reports were acquired mainly through interviews with fishers and historical reports.

In both study areas, coral observations were grouped as Families as this was the lowest taxonomic designation that would allow the inclusion of all location data. In the PMC study area, the Paragorgiidae included approximately two species (*P. arborea*, *P. pacifica*), while Primnoidae include approximately 12 species in nine genera (*Amphilaphis* sp., *Arthrogorgia* sp., *Callogorgia kinoshitae*, *Fanellia compressa*, *Fanellia fraseri*, *Narella bowersi*, *Parastenella doederleini*, *Plumarella longispina*, *Primnoa reseda*, *Primnoa resedaeformis*, *Primnoa willeyi*, *Thouarella* sp.). In the ACM study area, Paragorgiidae mainly consisted of *Paragorgia arborea* and while Primnoidae consisted of *Primnoa resedaeformis*. Both families also contained observations which were only described to the family level.

Minimum, maximum, and average values were calculated for temperature and chlorophyll *a* concentrations in the ACM study area, but were not available for the PCM study area. Although data were available, salinity was not included as an environmental variable in the analysis because the variation within the study area was small (30-35, with 90% of the coral locations falling between 34.5 and 35.5) (Leverette, unpublished data) and most likely were biologically meaningless.

2.23. Chart Generation

Charts of each of the six environmental variables, as well as the coral observations, were generated in ArcView 3.2 with the Spatial Analyst extension. A grid with a 9 x 9 km cell size was created from each environmental factor. Because of their coarser spatial resolution, the current and temperature data in the PCM study area were initially interpolated using the Inverse Weighted Distance method with a 20-km fixed radius. Slope, substrate and chlorophyll *a* datasets were already in a grid format. None of ACM data required interpolation to create grids with a 9-km resolution.

2.24. Statistical Analysis

For both study areas, the environmental characteristics in locations of Paragorgiidae and Primnoidae were compared to those in the surrounding environment using χ^2 tests. For these tests, the range of values for each environmental variable was divided into classes of equal intervals. From the charts generated in ArcView, the frequency of locations within each class was calculated for the environmental variables in the entire study area, as well as for locations where the coral families, Paragorgiidae and Primnoidae were present.

2.3. RESULTS

2.31. General Description of PCM site

The PCM study area consisted of many subduction zones and a narrow continental shelf (Figure 2.4). Even beyond the edge of the shelf break, there were many rises in elevation on the seafloor, most likely because of the active geological nature of the area. As a result, 7% of the total study area contained slopes greater than 3°, with 80% of the study area containing slopes between 0 and 1° and the remaining 13% between 1 and 2° (Figure 2.5). Warm water was usually found in shallow areas, along the coast and surrounding seamounts (Figure 2.6) and bottom temperature ranged from 0 to 11°C (Figure 2.7), with a mean of 4.13°C (Table 2.2). Extreme current velocities (>20 cm s^{-1}) were only found in isolated regions of the Aleutian Islands, and tidal current velocities between 10 to 20 cm s^{-1} were more typical around islands (Figure 2.8). Although over 80% of the bottom current velocities were <5 cm s^{-1} (Figure 2.9), the range was quite wide (0-143 cm s^{-1}). As the terrestrial area surrounding the study area is steeply sloped and includes large rivers, there is a large amount of sediment being transported off shore from the continent (Figure 2.10). Consequently, much of the sediment present was silt (77%) (Figure 2.11). The mean chlorophyll *a* concentration in this study area was low (2.60 mg m^{-3}), but the range was wide (0 - 46 mg m^{-3}) (Table 2.2). As with current velocity, areas with the highest chlorophyll *a* concentrations were found near the coast and in the vicinity of islands (Figure 2.12). However, concentrations >3 mg m^{-3} were only present in 3% of the study area, which were mainly in the shelf regions (Figure 2.13).

2.32. Coral Distribution in the PCM site

The dominant coral families in this study area, based on number of locations, were Paragorgiidae and Primnoidae. For both Paragorgiidae and Primnoidae, all environmental parameters in locations where coral occurred were significantly different from the values of these parameters in the study area as determined with χ^2 tests ($p<0.05$) (Table 2.3). Most (~80%) Paragorgiidae and Primnoidae locations were found in areas with slopes ranging from 0-3° (Figure 2.5). Although slopes >5° are only present in 2% of the study area, over 7% for both coral families can be found in areas with this range of slope. For both families, 55% of coral locations were distributed in habitats with temperatures ranging between 3 and 5°C, reflecting the general bottom temperature for the study area (Table 2.2). Both Primnoidae and Paragorgiidae locations were found in a wide range of current velocities. Fewer than 40% of locations for Paragorgiidae and 20% for Primnoiidae were found in areas with current velocity <5 cm s^{-1}, and in >10% of locations current velocities ranged between 50 and 143 cm s^{-1} (Figure 2.9). Interestingly, 71% of Paragorgiidae and 55% of Primnoidae locations were in habitats with silt as the dominant substrate type (Figure 2.11). Primnoidae were located in habitats in all categories of substrate, except granule, while Paragorgiidae were located in habitats in all categories of substrate, except of granule and pebble. Although chlorophyll *a* concentrations were low throughout the study area (<1 mg m^{-3}), 67% of Paragorgiidae and 53% of Primnoidae locations were found within this class of chlorophyll *a* concentration (Figure 2.13).

Because there were too few locations for five of the families (Antipathidae, Caryophyllidae, Corallidae, Isididae, Stylasteriidae) present in this study to evaluate their individual distributions, most of my discussion focused on Paragorgiidae and Primnoidae.

Generally, these five coral families were found in areas with slopes ranging from 0 to 1°, bottom temperatures between 5 and 9°C, current velocity between 0 and 5 cm s^{-1} and chlorophyll a concentrations >3 mg m^{-3}. They were mostly found in areas with sand and silt.

2.33. General Description of the ACM site

The ACM study area was composed of several banks, which were interspersed with many channels, gullies and canyons along the shelf break, resulting in a mean slope of 0.57° (Figure 2.16, Table 2.4). Consequently, over 80% of the study area had slopes between 0 and 1.0° (Figure 2.17). The wide range in bottom temperature (0-11°C) is most likely the result of the close proximity to the Gulf Stream. This ocean current advects warm water to the deeper canyons and gullies, while the majority of the banks at shallower depths remain cooler (Figure 2.18). Mean bottom temperature for this study area was 6.0°C (Table 2.4), with 34% ranging between 5 and 7°C (Figure 2.19). Bottom circulation was also influenced by the presence of deep channels (Figure 2.20), and ranged between 0 and 30 cm s^{-1} in >87% of the study area (Figure 2.21). Most of the study area contained finer substrate (Figure 2.22) while only ~10% of the study area contained harder substrata such as granules or pebbles (Figure 2.23). Although there are known bedrock outcrops, mainly along the walls of channels and gullies, these would not be detected in this analysis, because of the coarse resolution of the data. The highest chlorophyll *a* concentrations were found along the coast in the Bay of Fundy and decreased towards the open ocean (Figure 2.24). Small pockets of higher concentrations occurred around Georges Bank, most likely resulting from local upwellings. Chlorophyll *a* concentration ranged from 0 to

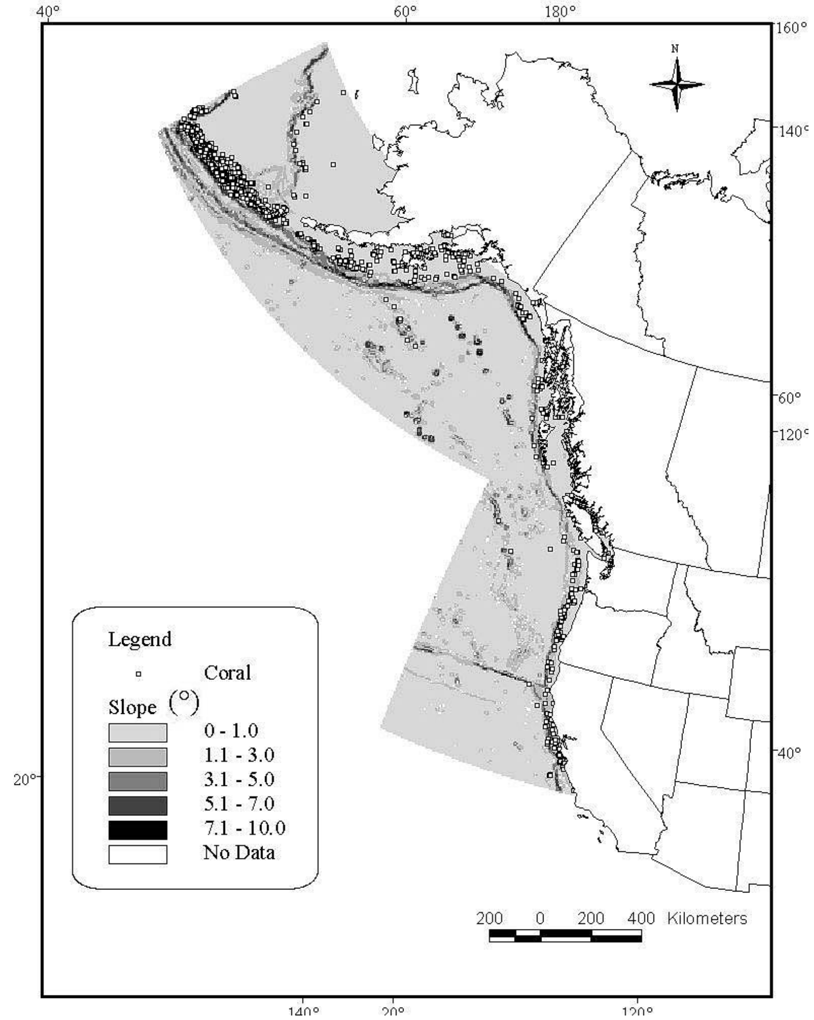

Figure 2.4. Chart of bottom slope angles (°) in the PCM study area overlaid with total coral locations.

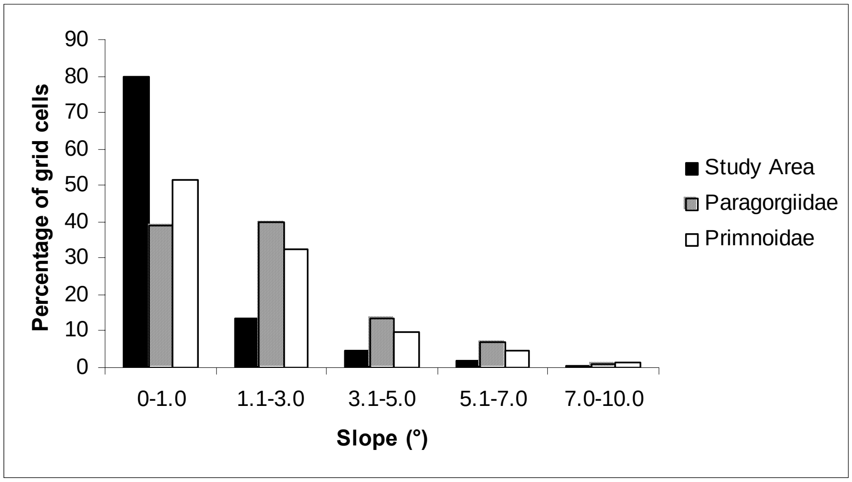

Figure 2.5. Bottom slope (°) angles in the PCM study area and in locations with Paragorgiidae and Primnoiidae.

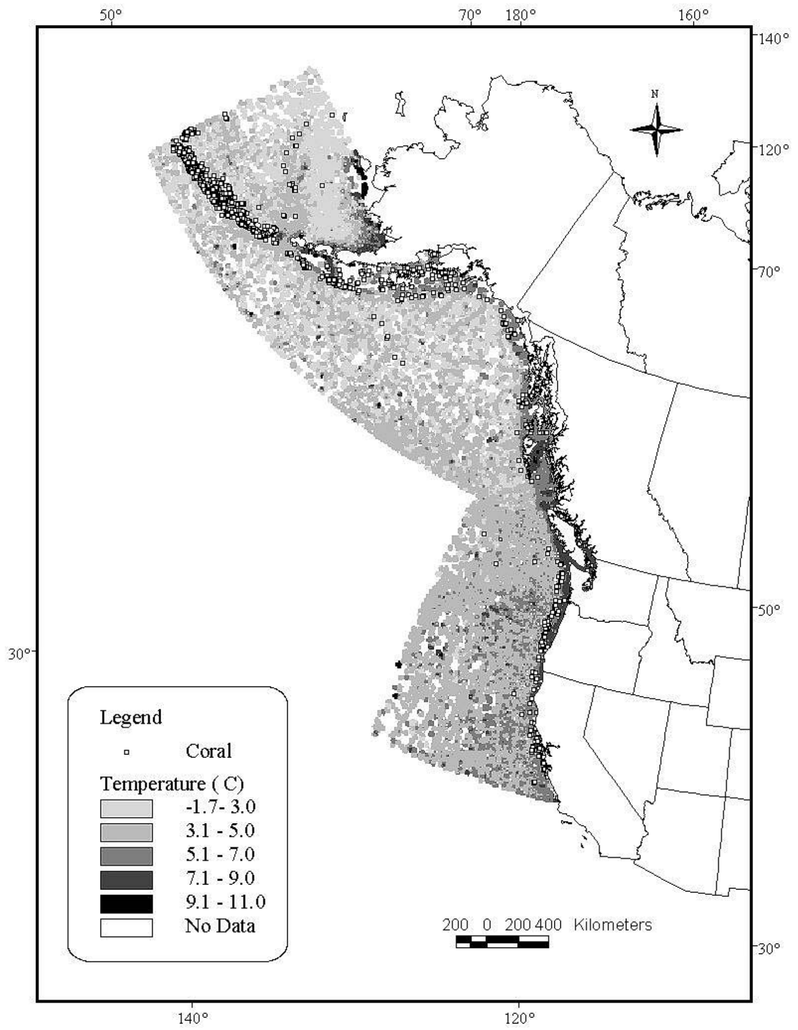

Figure 2.6. Chart of bottom temperature (°C) in the PCM study area overlaid with total coral locations.

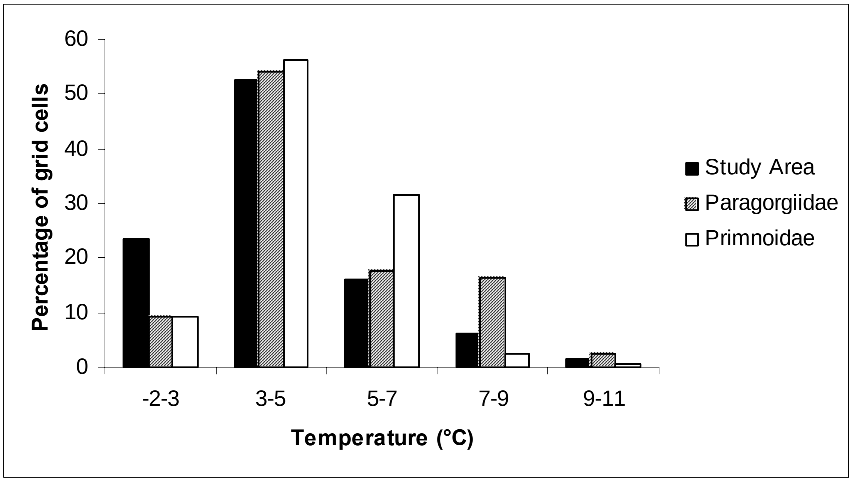

Figure 2.7. Distribution of Paragorgiidae and Primnoiidae locations based on bottom temperature (°C) in the PCM study area.

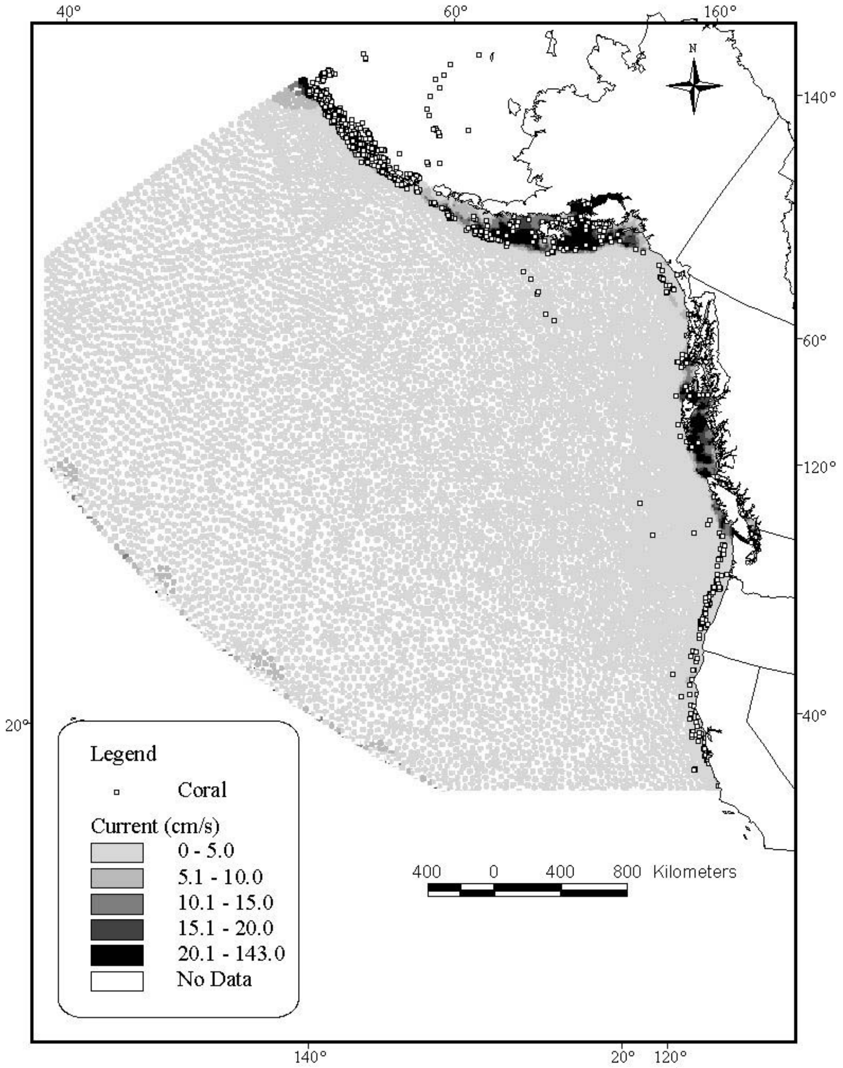

Figure 2.8. Chart of bottom tidal current speed (cm s^{-1}) in the PCM study area overlaid with total coral locations.

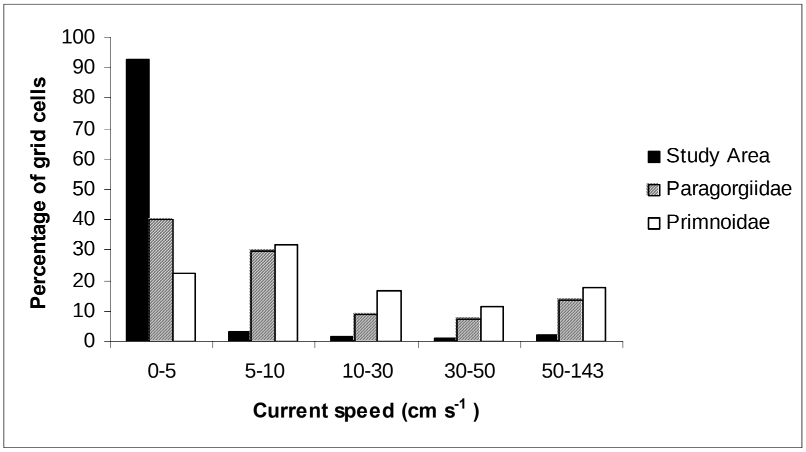

Figure 2.9. Distribution of Paragorgiidae and Primnoiidae locations based on bottom tidal current (cm s^{-1}) in the PCM study area.

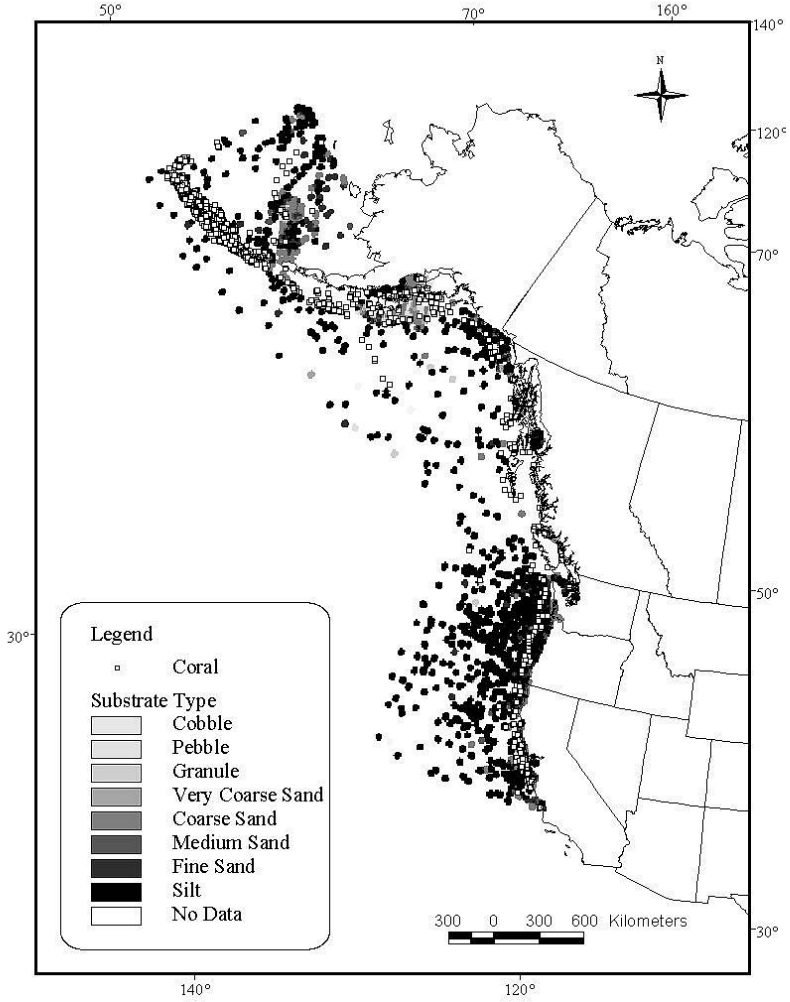

Figure 2.10. Chart of substrate types (φ) in the PCM study area overlaid with total coral locations.

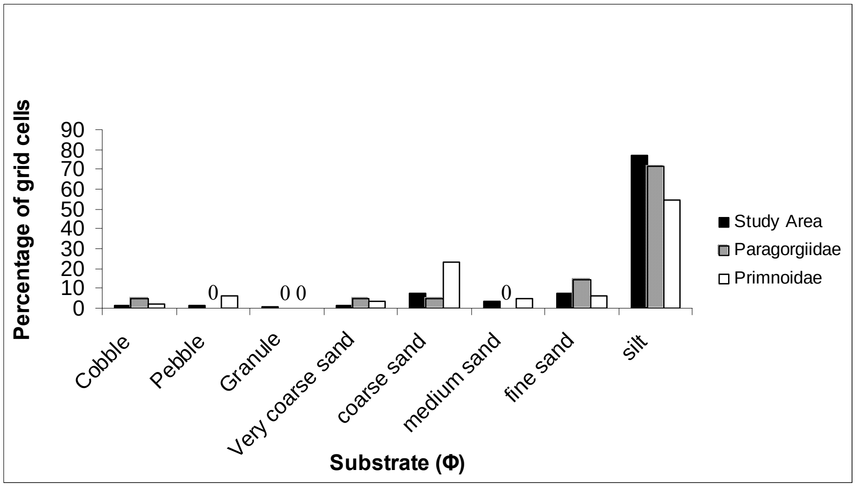

Figure 2.11. Distribution of Paragorgiidae and Primnoiidae locations based on substrate types (φ) in the PCM study area.

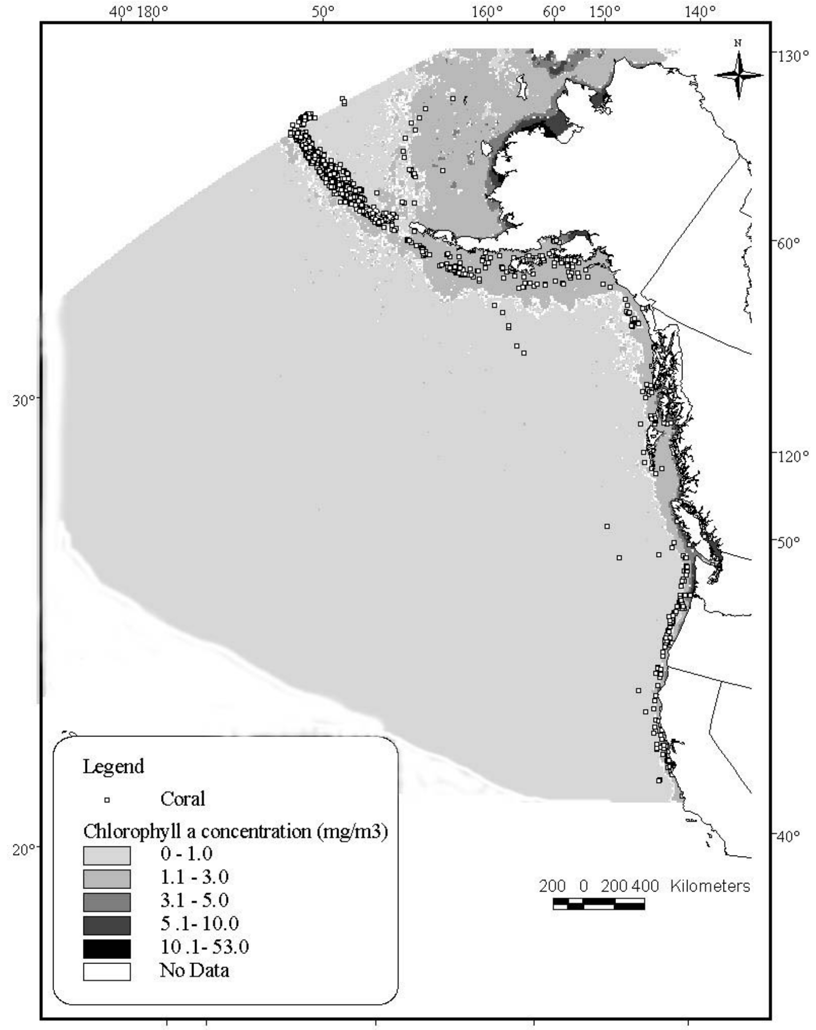

Figure 2.12. Chart of chlorophyll *a* concentrations (mg m^{-3}) in the PCM study area overlaid with total coral locations.

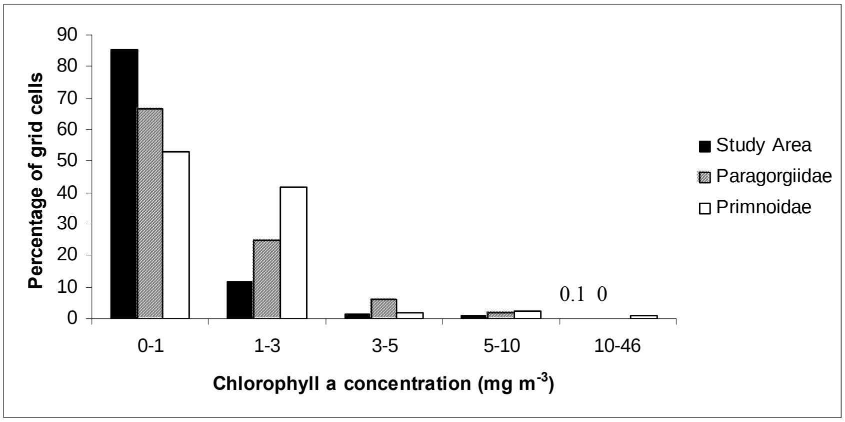

Figure 2.13. Distribution of Paragorgiidae and Primnoiidae locations based on chlorophyll *a* concentrations (mg m^{-3}) in the PCM study area.

Table 2.2. Values in the PCM study area, for the entire study area (Global) and in locations with all coral taxa combined (“all coral”), Paragorgiidae and Primnoidae of different environmental variables (slope (°), temperature (°C), current (cm s^{-1}), substrate (φ) and chlorophyll *a* concentration (mg m^{-3}).

Environmental Factor	Slope	Temperature	Current	Substrate	Chlorophyll *a* concentration
Global mean	0.80	4.13	3.27	5.39	0.66
Global Standard Deviation	1.24	1.74	5.82	2.68	1.38
AllCoral Mean (N=754)	2.37	4.86	7.02	4.38	1.47
AllCoral Standard Deviation	1.59	1.62	7.10	1.62	1.46
Paragorgiidae Mean (N=99)	1.95	4.79	11.67	4.79	1.21
Paragorgiidae Standard Deviation	1.72	1.90	15.25	1.90	1.18
Primnoidae Mean (N=406)	1.59	4.45	12.97	4.45	1.37
Primnoidae Standard Deviation	1.67	1.23	12.75	1.23	1.52

Table 2.3. χ^2 tests comparing the distribution of five environmental factors in Paragorgiidae and Primnoidae locations to those in the entire PCM study area.

Environmental Factor	Slope (°)	Chl *a* (mg m^{-3})	Substrate (φ)	Temperature (°C)	Current (cm s^{-1})
Degrees of Freedom	4	4	7	4	3
χ^2 Critical	9.84	9.84	14.07	9.84	7.82
Paragorgiidae	106.42	33.14	33.21	25.91	421.8
Primnoidae	49.25	93.17	65.86	26.4	729.24

13 mg m^{-3}, with 92% of the area having concentrations between 0 and 3 mg m^{-3} (Figure 2.25).

2.34. Coral Distribution in the ACM site

As in the PCM study site, the more common coral families for the ACM study area, based on number of locations, were Paragorgiidae and Primnoidae. In this study area, Paragorgiidae included approximately one species, while Primnoidae include approximately two species. Most observations though were only identified to the level of Family. For both Paragorgiidae and Primnoidae, the environmental parameters in locations where coral occurred were significantly different from the values of these parameters in the study area ($p<0.05$) (Table 2.5). While 36% of Paragorgiidae locations were in areas with slopes between 0 and 1°, 28% of locations were in areas with slopes ranging from 3 to 4° (Figure 2.17), indicating that this family can inhabit a wide range of sloping environments. In contrast, 83.0% of the study area contained slopes ranging between 0 to 1°. Although Primnoidae locations were also found in a wide range of slopes, most locations of this family were found in areas with slopes ranging from 0 to 1° (67%) (Figure 2.17). As in the PCM study area, these two coral families were mainly found in the ACM area in habitats with temperatures >5°C. While the mean temperature for the total study area was 6.06°C, the mean temperatures in Paragorgiidae and Primnoidae locations were 7.34°C and 6.52°C, respectively (Table 2.4). Fewer than 15% of Paragorgiidae and 20% of Primnoidae locations had temperatures <5°C (Figure 2.19). Both Paragorgiidae and Primnoidae were primarily found in regions containing currents between 10 and 30 cm s^{-1}. Primnoidae locations were found in areas with stronger currents than Paragorgiidae as 17% of Primnoidae locations were found in areas with currents >30 cm s^{-1}, while only < 8% of Paragorgiidae locations were found in this same current class. Both Paragorgiidae and Primnoidae locations were found mainly in areas with coarse substrate, but both families could also be found in fine sand or silt environments. More than 20% of the study area was comprised of fine sand and silt. These coral families also tend to be mainly distributed in areas of low chlorophyll *a* concentrations, with 87% of Paragorgiidae and 100% of Primnoidae in areas with <3 mg m^{-3} of chlorophyll *a* concentration.

As in the PCM study site, there were too few locations of six of the coral families (Acanthorgiidae, Caryophllidae, Flabellidae, Isididae, Keratoisidae, and Paramuriceida) in the ACM study area to evaluate their individual distributions. These coral families were found in areas with bottom temperatures ranging between 5 and 9°C, slope between 0 to 1°, current velocity between 0 to 10 cm s^{-1} and chlorophyll *a* concentration <3 mg m^{-3}. The range of substrate types was greater than in the PCM study area mainly because of the presence of Flabellidae, a solitary cup-coral inhabiting softer sediment areas.

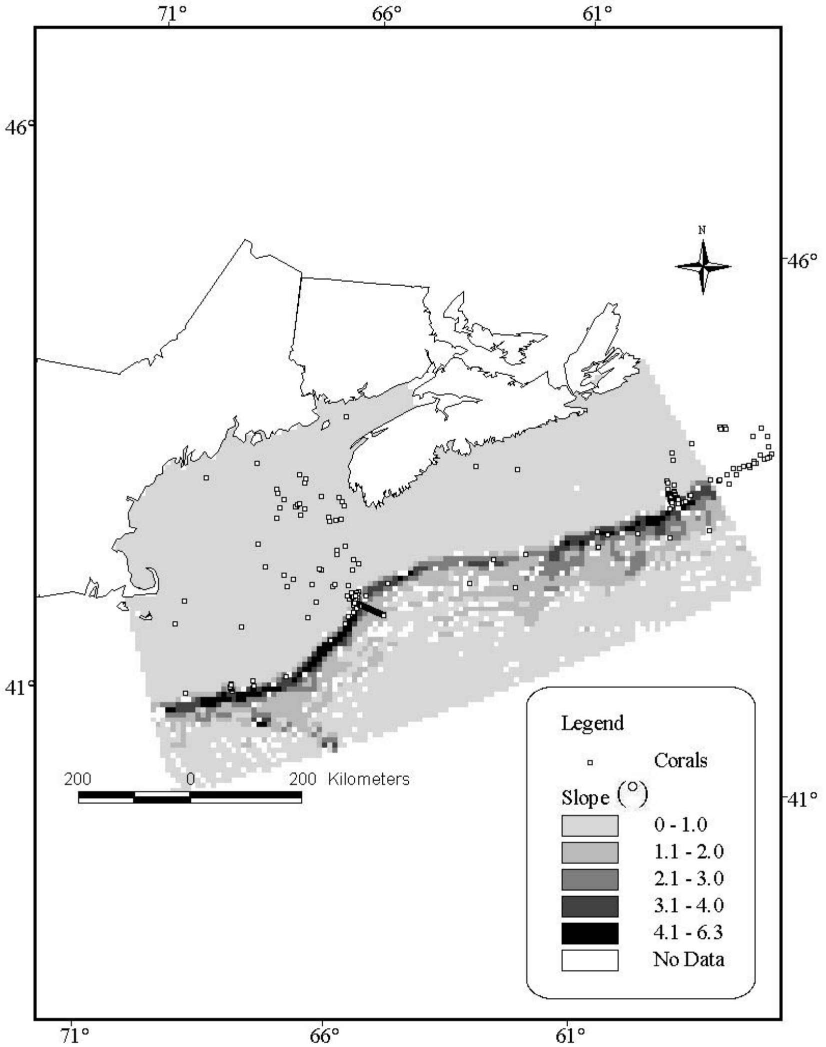

Figure 2.16. Chart of bottom slope angles (°)in the ACM study area overlaid with total coral locations.

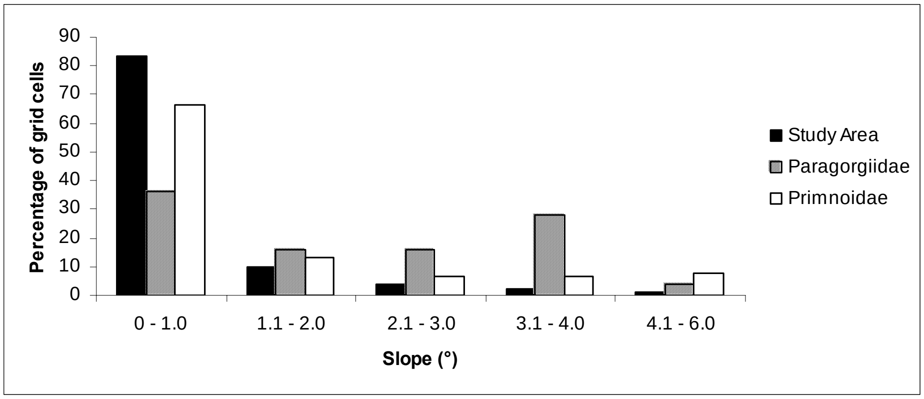

Figure 2.17. Distribution of Paragorgiidae and Primnoiidae locations based on Bottom slope angles (°) in the ACM study area.

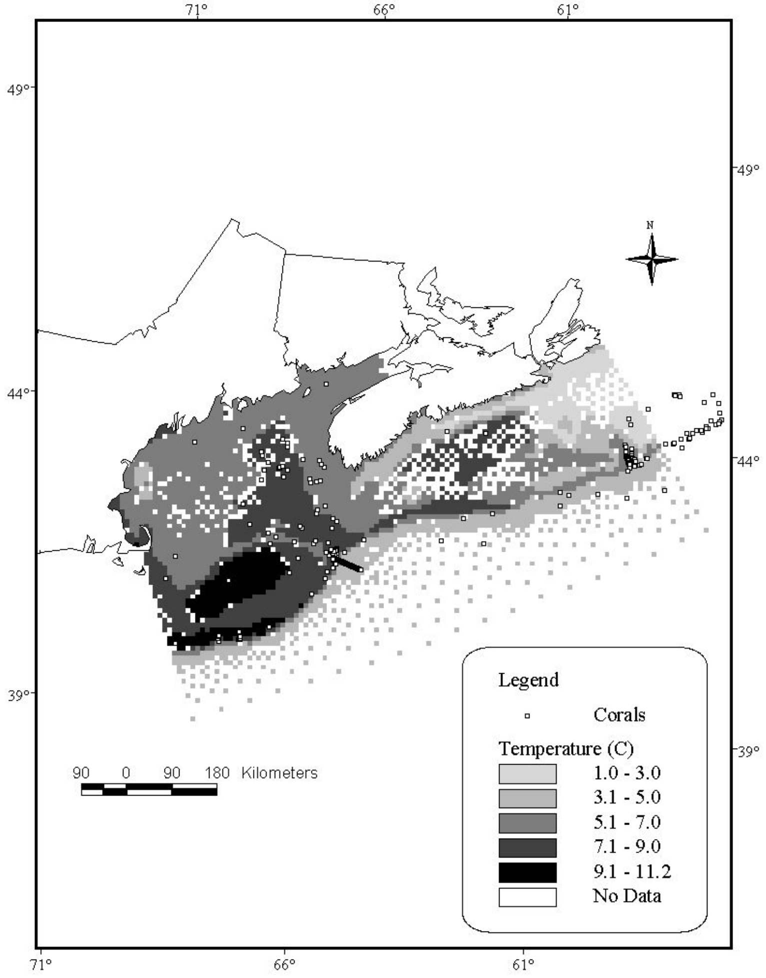

Figure 2.18. Chart of bottom temperature (°C) locations in the ACM study area overlaid with total coral locations.

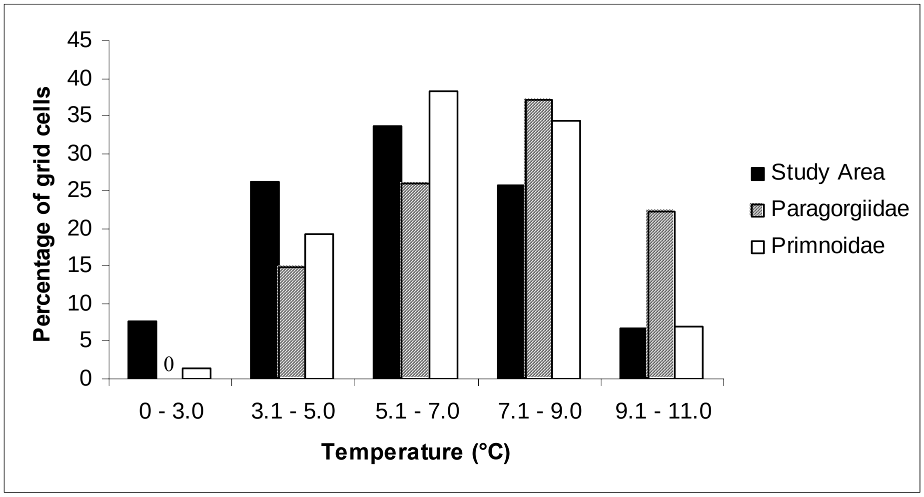

Figure 2.19. Distribution of Paragorgiidae and Primnoiidae locations based on bottom temperature (°C) in the ACM study area.

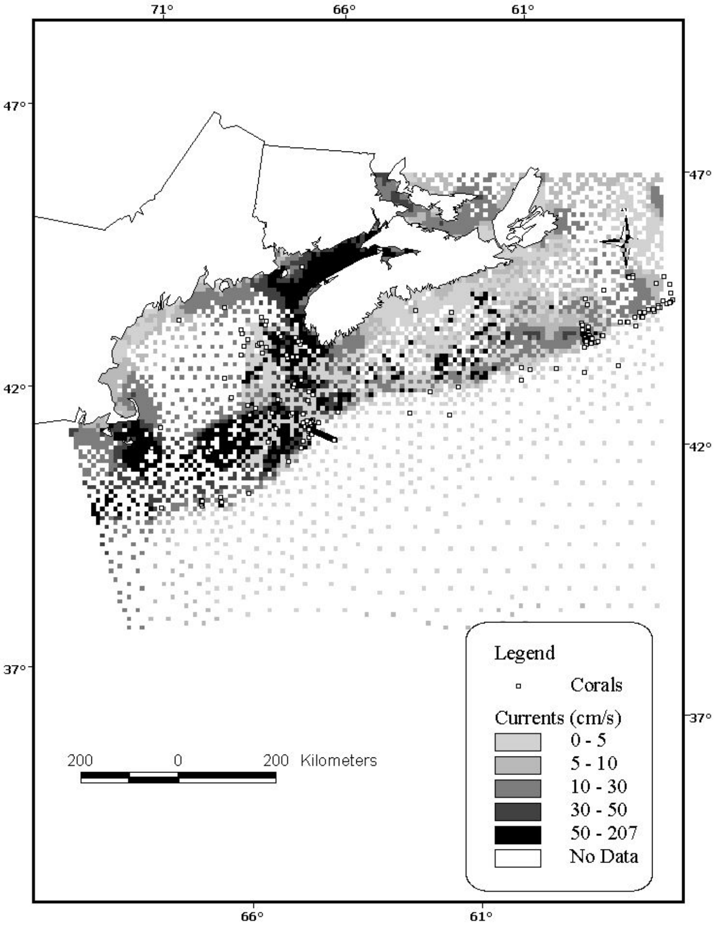

Figure 2.20. Chart of bottom tidal current speed (cm s^{-1}) in the ACM study area overlaid with total coral locations.

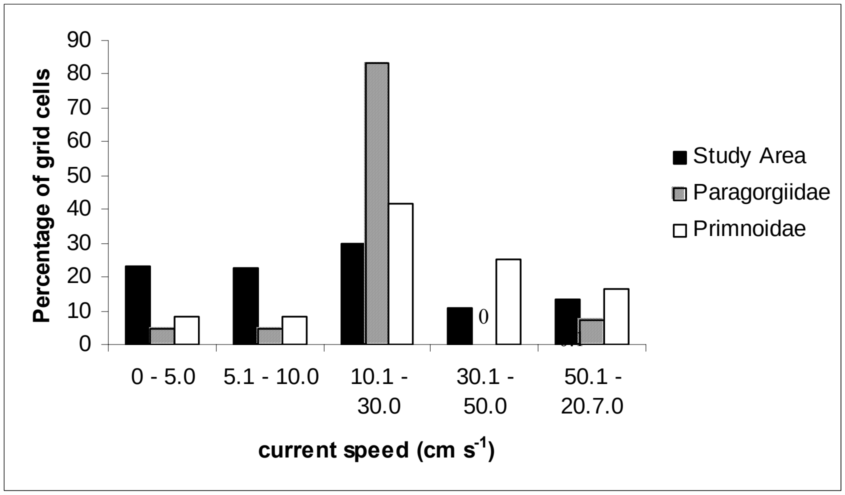

Figure 2.21. Distribution of Paragorgiidae and Primnoiidae locations based on bottom tidal current (cm s^{-1}) in the ACM study area.

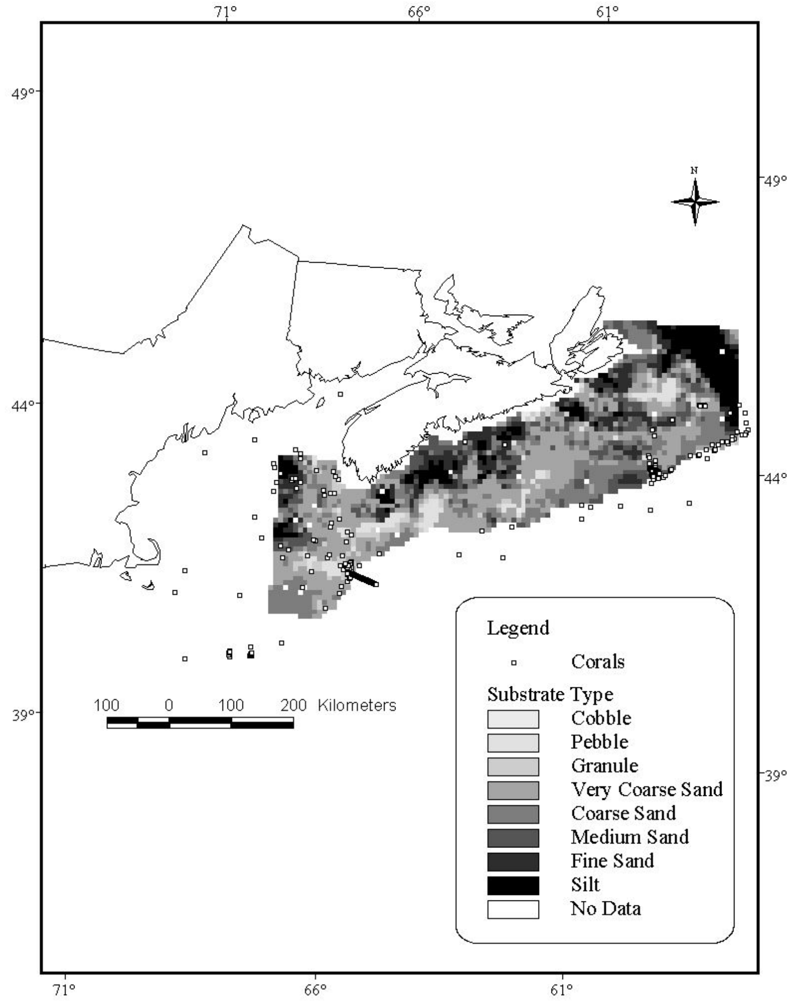

Figure 2.22. Chart of substrate types (φ) in the ACM study area overlaid with total coral locations.

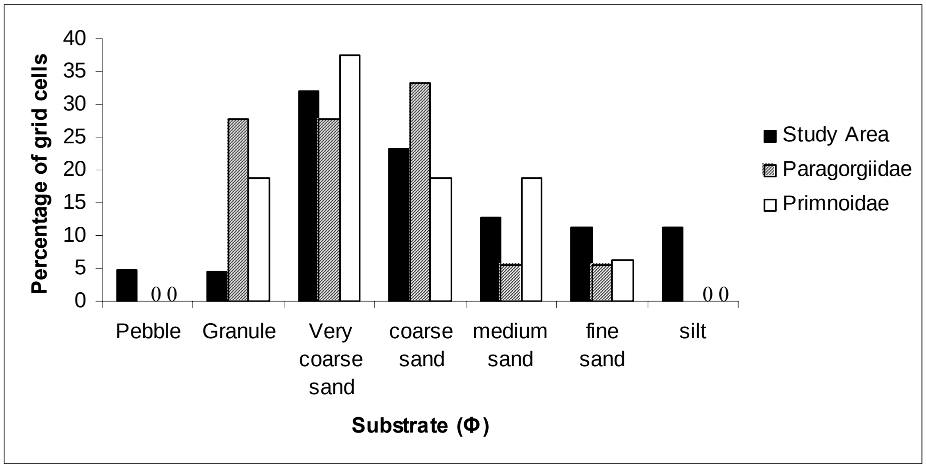

Figure 2.23. Distribution of Paragorgiidae and Primnoiidae locations based on substrate types (φ) in the ACM study area.

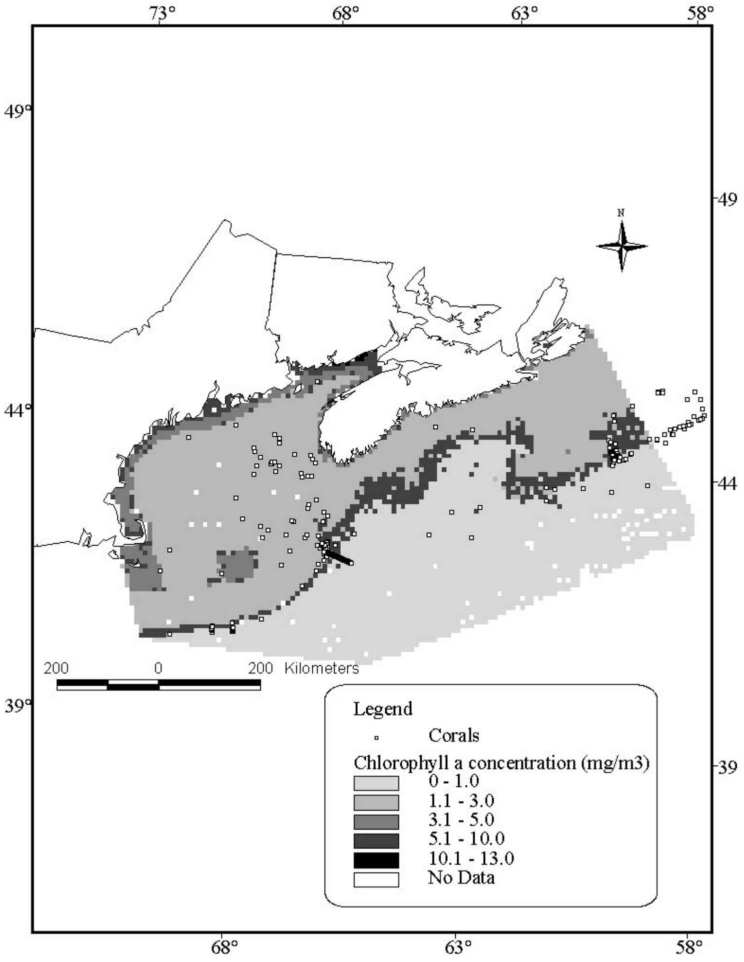

Figure 2.24. Chart of chlorophyll *a* concentration (mg m^{-3}) locations in the ACM study area overlaid with total coral locations.

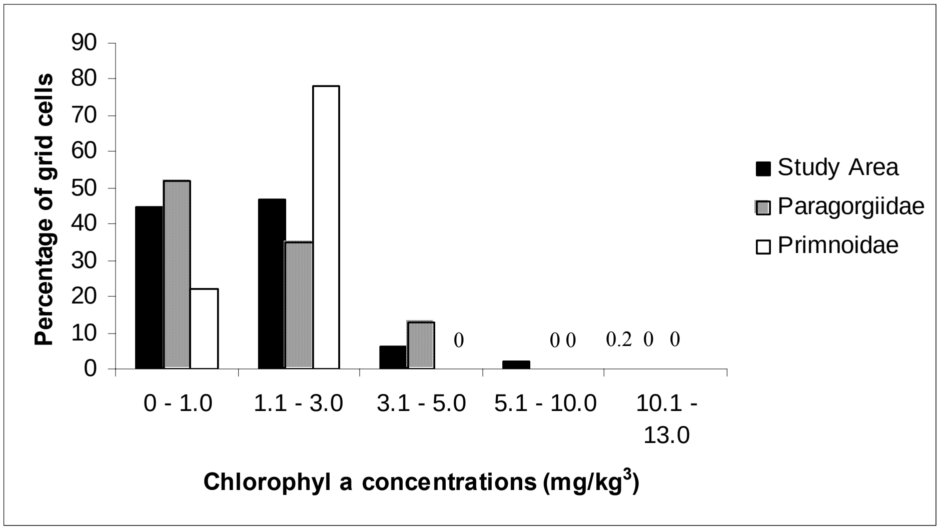

Figure 2.25. Distribution of Paragorgiidae and Primnoiidae locations based on chlorophyll *a* concentration (mg m^{-3}) in the ACM study area.

Table 2.4. Values in the ACM study area, for the entire study area (Global) and in locations with all coral taxa combined (Allcoral), Paragorgiidae (Parag.) and Primnoidae (Prim.) of different environmental variables (slope (°), temperature (°C), current (cm s^{-1}), substrate (φ) and chlorophyll *a* concentrations (mg m^{-3}). SD is standard deviation.

Environmental Factor	Slope	Temperature	Current	Substrate	Chlorophyll *a* concentration
Global mean	0.57	6.06	20.60	1.36	1.82
Global Standard Deviation	1.00	1.91	21.51	2.07	1.46
AllCoral Mean (N=754)	1.36	6.48	22.01	0.78	1.55
AllCoral Standard Deviation	1.50	1.64	18.01	1.62	0.65
Paragorgiidae Mean (N=99)	2.11	7.34	22.16	0.33	1.54
Paragorgiidae Standard Deviation	1.57	1.85	22.03	1.10	0.87
Primnoidae Mean (N=406)	1.18	6.52	30.06	0.60	1.59
Primnoidae Standard Deviation	1.52	1.61	19.30	1.27	0.61

Table 2.5. χ^2 tests comparing the distribution of five environmental factors in Paragorgiidae and Primnoidae locations to those in the entire ACM study area.

Environmental Factor	Slope (°)	Chla (mg m^{-3})	Substrate (φ)	Temperature (°C)	Current (cm s^{-1})
Degrees of Freedom	4	4	6	4	3
χ^2 Critical	9.84	9.84	12.59	9.84	7.82
Paragorgiidae	415.46	14.79	143.86	54.11	136.96
Primnoidae	53.69	40.56	66.1	10.52	42.47

2.4. DISCUSSION

On both the northeast Pacific and northwest Atlantic continental margins, coral locations were found not to be randomly distributed within the study areas, but to be present within specific ranges for all environmental factors examined. Previous studies have shown that deep water coral were recorded mainly in areas with hard substrate and high currents (Cimberg et al., 1981; Tendal, 1992; Rogers, 1999; De Mol et al., 2002; Freiwald, 2002). The patterns of distribution in relation to substrate in this study were not as clear as in previous studies most likely due to the coarse resolution of the substrate data, which generalized the data and obscured smaller areas of hard substrate. Areas of pronounced vertical relief, such as seamounts and canyons are often associated with hard substrate and strong current regimes (Genin et al, 1986; Herring, 2002). Deposition of softer sediments is prevented by large current velocities. Thus, primarily because of availability of hard substrate, which is relatively rare in the deep sea, areas of high vertical relief harbour abundant communities of benthic organisms, including deep water corals (Herring, 2002). Except for solitary cup corals, deep water corals require hard substrate for attachment. Although *Lophelia pertusa* has been recorded in coarse sand habitats, it is assumed that the coral initially settled on a hard substrate such as a pebble or a shell (Mortensen et al., 2001). Additionally, strong currents provide an adequate nutrient supply and remove resuspended sediment for these sessile filter feeders (Mortensen et al., 2001; Freiwald, 2002). The dominant current regime also regulates the physical structure of Gorgonian corals which may orient their fan into the prevailing current, thus reducing the torsion in the basal stem (Tunnicliffe, 1983; Reed, 2002). Corals may also modify the local current environment, thereby creating favourable habitat for associated species by providing protection from high currents (Etnoyer and Morgan, 2003). While <10% of both study areas contained slopes of >2°, almost half of Paragorgiidae locations in the PCM study area were found in these slopes.

My study found that corals were consistently located in a narrow range of temperatures. In their comprehensive examination of Alaskan deep water coral, Cimberg et al. (1981) were able to predict the distribution of *Primnoa* spp. using the annual minimum temperature and suitable substrate. Historically, deep water coral species have been recorded from -1°C in Alaska (*Gersemia* spp.) to 12°C in Europe (*L. pertusa*) (Cimberg et al., 1981; De Mol et al., 2002). Our findings indicate that while corals can survive in those temperature ranges, they are most abundant in temperatures between 3 and 9°C. The number of coral locations diminishes outside this range, indicating that distribution is related to temperature.

Coral locations are predominantly found in areas of low concentrations (<3 mg m^{-3}) of chlorophyll *a* as most deep sea locations fall under oligotrophic areas. Isotopic studies of five species of coral (*Lophelia* spp., *Gerardia* spp., *Paragorgia johnsoni* and *Corallium noibe*) revealed that surface derived particulate organic carbon (POC) is a major source of skeletal carbon for deep sea coral (Griffin and Druffel, 1989; Druffel et al., 1995). According to Druffel et al. (1995), the main source of nutrition for corals is surface-derived organic-rich particles. The corals would not need to be located beneath areas of high primary productivity to receive adequate levels of nutrition, if there was adequate lateral advection of POC (Smith and Kaufmann, 1999).

Although the general patterns in habitat characteristics were similar for most deep water corals examined, some differences exist between Paragorgiidae and Primnoidae. Habitat characteristics for Paragorgiidae included slower currents and steeper slopes than Primnoidae. I found that <8% of locations where Paragorgiidae were present had currents

>30 cm s^{-1} and most locations experienced average currents of 22 cm s^{-1}. Tendal (1992) stated that Paragorgiidae prefer current regimes with maximum velocities of 60 cm s^{-1}. This study found that Paragorgiidae were mainly located in areas with slower current velocities, but this may be the result of fewer locations overall having higher current velocities. Also, Paragorgiidae is a large Gorgonian species, reaching 2.5 to 3 m in height (Breeze, 1997), thus making it more susceptible to drag forces which could dislodge the coral. Although mostly present in areas with current speeds between 0 and 30 cm s^{-1}, Primnoidae also is present in locations with higher currents more often than Paragorgiidae. While most previous studies measured current qualitatively (Frederiksen et al., 1992; Rogers, 1999; Freiwald et al., 2002), dye-releases in Knight Inlet on the western Canadian coast, showed that Gorgonian fans experienced flows of ~80 cm s^{-1} (Tunnicliffe, 1983).

While the two study areas are geographically distinct, there are many similarities in oceanographic parameters. Bottom temperatures in both study areas ranged from 0 to 11°C, but, due to the lack of warm water influence (Gulf Stream in the ACM), mean temperatures are lower in the PCM study site. Warm water is found in shallow areas along the coast in both sites. Also similar to the ACM study area, bottom current velocities in >80% of the PCM study area are <5 cm s^{-1}. However, the range in current velocity is much larger for the PCM than the ACM study area. The mean chlorophyll *a* concentration in the PCM study area is lower than the ACM study area but the range is considerably larger.

Coral distribution patterns were also similar between study areas. In both study areas, coral locations for both families were mainly found in areas of shallow slopes. However, Paragorgiidae were located more often in steeply sloping areas than Primnoidae.

Deep water coral were mainly located in cooler temperatures in the PCM than the ACM, most likely because of the overall lower mean temperature in the study area. In both study areas, Primnoidae were found in areas of higher current velocities than Paragorgiidae. However, as the range within the PCM study area was considerably wider than in the ACM study area, it was difficult to accurately compare distributions at higher current velocities. Both families were found mainly in low concentrations in both study areas. However, more Primnoidae than Paragorgiidae locations were found in areas with concentrations between 1 to 3 mg m^{-3}.

The geographic range of coral locations in my study is not exhaustive. Although different types of data sources were used to assemble the locations, including research cruises, fishermen and recreational divers, the spatial extent of possible locations is enormous, making sampling at all areas with equal effort logistically unfeasible. More coverage and higher resolution oceanographic data are needed to facilitate future studies and to increase our understanding of deep water coral habitat on finer spatial scales (meters vs. 100s of kilometres).

This study has provided broad distributional patterns of deep water coral and indicated habitat characteristics for these organisms. A basic understanding of the biology of deep water corals would allow us to further understand limiting environmental factors and thus, more accurately predict their potential habitats. To more effectively target future research explorations, a method is needed to identify potential suitable habitat for these deep water organisms.

CHAPTER 3

3.1. INTRODUCTION

Mapping marine habitats and associated species distributions is a fundamental first step in determining locations of potential protected areas, aiding resource management, and assessing anthropogenic impacts on specific habitat types and associated organisms. Although advancements in surveying technologies have increased the accuracy of large-scale mapping projects in shallow water marine systems, data collection from deep water environments is considerably more difficult. Large scale marine datasets are becoming more common as organisations such as the International Oceanographic Data and Information Exchange (IODE) and its associated members synthesize data and make it available to a wide range of users. Many of these data are collected from ship tracks, and although still extremely valuable, their coverage is limited to mainly coastal areas. Consequently, data regarding the spatial distribution of most deep water benthic species are also sparse.

Deep water corals are benthic invertebrates which are primarily found in areas of pronounced topographic relief, at depths ranging from 10 to 3500 m (Cimberg et al., 1981; Mortensen et al., 2001). Unlike shallow water corals, deep water corals lack zooxanthellae, and consequently their distribution can extend to depths below the photic zone (Jensen and Frederiksen, 1992). Corals are abundant on slopes, in and around submarine canyons, gullies and on 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 them suitable for coral attachment (Freiwald et al., 1999). Primarily because of the rarity of hard substrate in the deep sea, areas of high vertical relief often harbour abundant communities of benthic organisms, including deep water corals

(Herring, 2002). Typically, these areas are also associated with strong current regimes (Genin et al, 1986; Herring, 2002). As they are sessile filter feeders, deep water corals rely on currents to remove resuspended sediments, as well as provide nutrition. Consequently, corals are usually associated with strong current velocities or unique current patterns such as recirculation gyres, which in turn are indicative of increased concentrations of particles (Moore and Bullis, 1960; Tendal, 1992). Historically, the distribution of deep water corals is known through fisher's records. Information on their general biology is sparse because of logistical difficulties in collecting and maintaining live specimens. In the last decade, *in situ* observations and collection of live specimens have become possible with the use of Remotely Operated Vehicles (ROVs) and submersibles, allowing an increased understanding of the biology of these species.

Habitat suitability 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 used to generate habitat maps, but they are frequently limited by the type of available data. Because of the remoteness and low accessibility of deep water marine environments, often only information on species presence is available, constraining the range of suitable habitat models. One modelling program is BioMapper, developed by Hirzel (2001). 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 variables to determine the species' niche (Hirzel et al., 2002). This program also incorporates descriptive statistics, as well as a Geographic Information System (GIS) for generating habitat suitability maps. ENFA has been utilized to generate HS maps for several terrestrial floral and fauna, such as ferns in New Zealand as well as ibex, bearded vultures and alpine mice in Switzerland (Hirzel, 2001; Sachot, 2002; Zaniewski et al., 2002; Reutter et al., 2003; Hirzel and Arlettaz, 2003). This modelling approach is highly recommended when absence data are not available (e.g. most deep water datasets), are unreliable (e.g. cryptic or rare species), or are ecologically meaningless (e.g. invading species) (Reutter et al. 2003). Several papers have compared the results of ENFA to more traditional statistical analyses, such as generalized linear models (GLM), by randomly generating pseudo-absences and indicated that ENFA outperformed GLM when the species were rare or cryptic (Hirzel et al., 2001; Guisan and Zimmerman, 2002; Hirzel and Arlettaz, 2003).

This study used ENFA to generate habitat suitability maps for seven families of deep water coral in the Pacific Continental Margin (PCM) and eight families in the Atlantic Continental Margin (ACM) of North America. The analysis focused mainly on two families, Primnoidae and Paragorgiidae, which had the largest number of presence locations. Data on remaining five families were limited, and thus were analysed as a larger group that included all five families. I also compared the relative importance of five environmental factors (temperature, slope, current, chlorophyll *a* and substrate) in determining suitable habitat for the three taxonomic groups (all corals combined, Paragorgiidae and Primnoidae). 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). This is the first study to use ENFA in the marine environment. By using this technique, I was able to process previously unusable or under-used data collections, as well as attempt to predict potential coral locations presently unknown, based on suitability of the habitat.

3.2. MATERIALS AND METHODS

3.21. Study Area and Data Collection

Study sites were selected along the Pacific Continental Margin and Atlantic Continental Margin. The PCM study area encompassed an area approximately 2000 km wide and 3500 km long, from Alaska to California (Figure 3.2). This site was defined by a wide continental shelf (~100 km wide) and a narrow (~70 km wide) but steep continuous slope (from shelf break to ~5000 m deep) (Leier, 2001). This sharp gradient is the result of active subduction zones close to the continent. Near the continent, this study area also contained many islands which channel the water into high current locations.

The ACM study area included a band approximately 800 km long and 300 km wide from Cape Breton to Cape Cod (to ~500 m in average depth) (Figure 3.3). This area was defined by a 200 km wide continental shelf and a 250 km wide continental slope (sloping to 4000 m in depth) (Elsner, 1999; Gordon and Fenton, 2002). The continental shelf is composed of large, shallow banks surrounded by several basins and troughs along the inner shelf, as well as many canyons along the outer shelf. This topography influences throughflow and local recirculation of water masses (Hannah et al., 2001). Both study areas were chosen based on the observed high density of known coral sites.

3.22. Data Collection

Sources of environmental data on slope, temperature, chlorophyll *a* concentration, substrate type and current speed for both study areas are given in Table 1. Sources are mostly of empirical data, except for current velocity which was obtained through oceanographic circulation models. Depth was not included in this analysis as it was correlated to slope in both study areas (PCM: 0.688; ACM: 0.655). Sampling effort was also not known, and therefore could not be assumed equal at all depths The frequencies distributions of coral observations and depth across the study area were similar for depth of 0 – 2000m for PCM and 0 – 500m for ACM (Figures 3.4, 3.5). Thus, I used these depth ranges for the prediction of suitable habitat. To obtain access to unpublished data on the variables included in my study, the sources listed in Table 1 can be contacted directly.

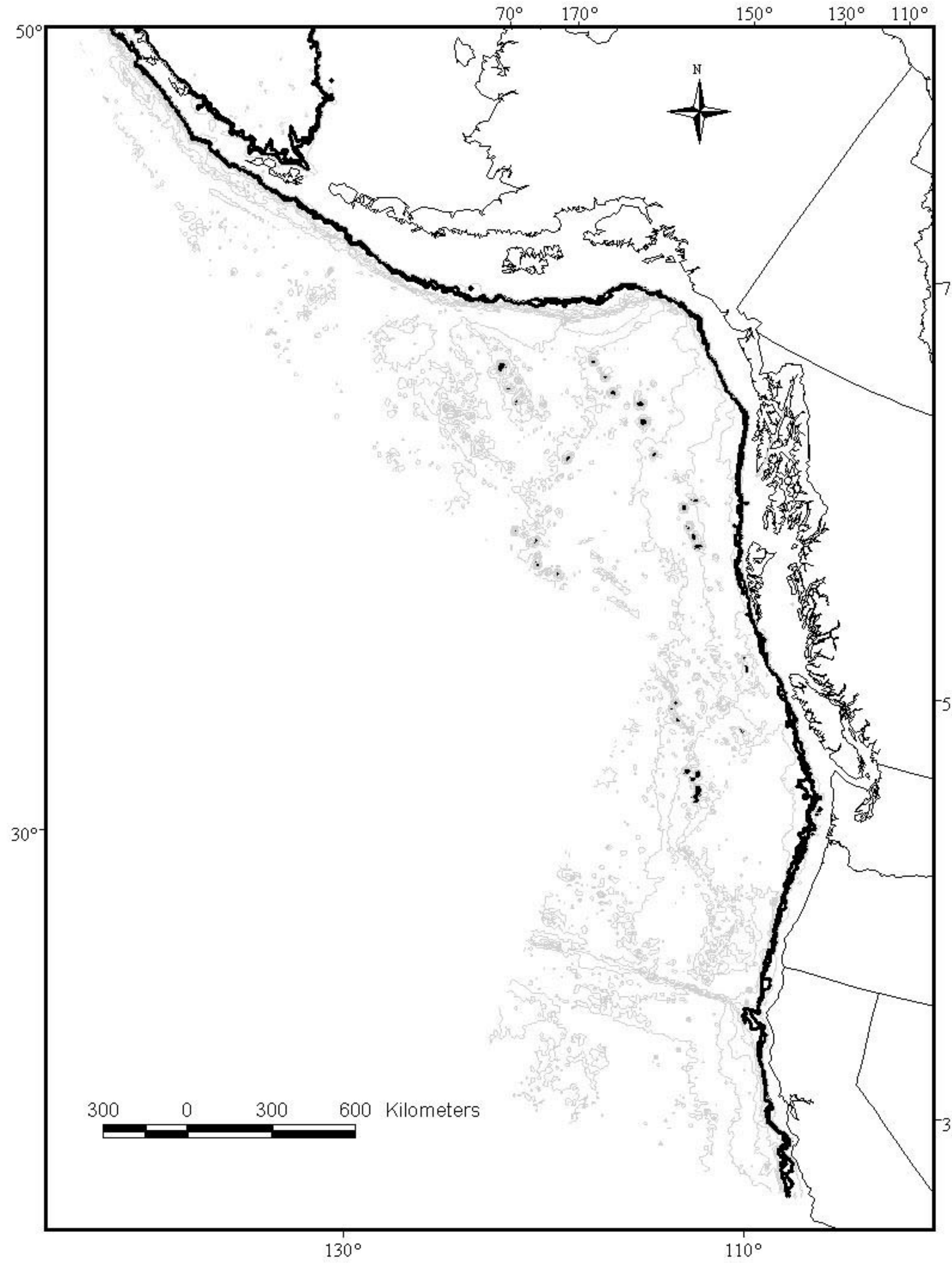

Figure 3.2. The Pacific Continental Margin (PCM) study area, from Alaska to California with 500m contours. The dark line represents the 2000m contour line.

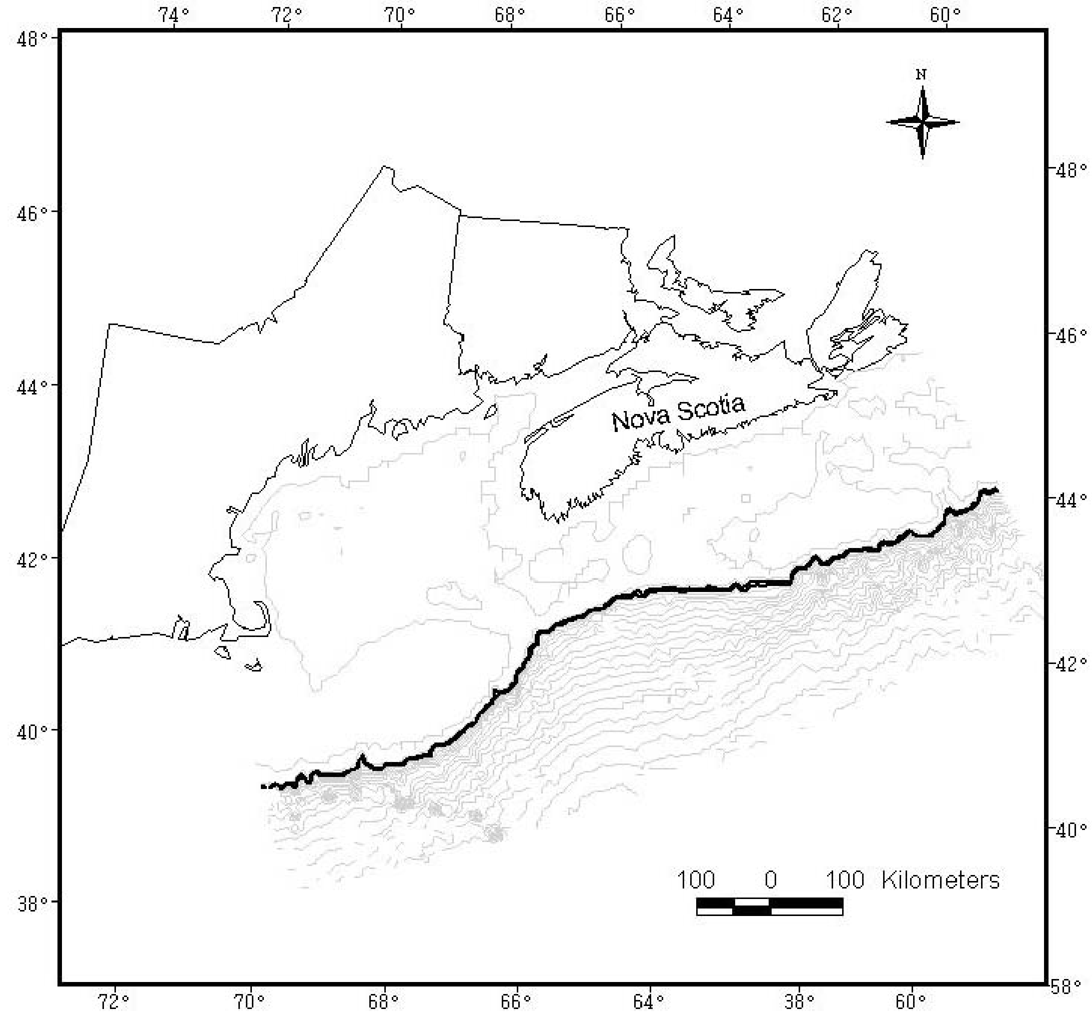

Figure 3.3. The Atlantic Continental Margin (ACM) study area, from Cape Breton to the Gulf of Maine with 200m contours. The dark line represents the 500m contour line.

Table 3.1. Sources and types of environmental data used.

Study Area	Environmental Variable	Source	Type of Data
PCM	Bottom current velocity	Mike Foreman, Institute of Ocean Science, Canada	Modelled data, tidal velocities modelled for winter, spring, summer, fall and then averaged for the year
	Slope	Marine Conservation Biology Institute, USA	Derived from bathymetry data composed of a 2’ resolution grid
	Surface chlorophyll *a* concentration	Marine Conservation Biology Institute, USA	Derived MODIS images, yearly average includes 1997-1999
	Bottom temperature	Don Spears, Marine Environmental Data Services Branch (MEDS), Canada	Each point was averaged from seafloor to include a maximum of 50 m above the seafloor in the water column
	Substrate	Chris Jenkins, Institute of Arctic and Alpine Research (INSTAR), USA	Compiled from the USGS database, categorized into classes based on the Lidden-Wentworth size classification for sediment grains and assigned increasing phi (φ) values (-12 to +14) to decreasing grain size (boulder to clay) (Pettijohn et al., 1972)
ACM	Bottom current velocity	Charles Hannah, Bedford Institute of Oceanography, Canada (Hannah et al., 2001)	Modelled data, annual tidal velocities
	Slope	World Wildlife Fund Canada (Alidina and Roff, 2003)	Derived from bathymetry data composed of a 5’ resolution grid
	Surface chlorophyll *a* concentration	Moderate Resolution Imagining Spectroradiomters (MODIS)	Derived MODIS images, averaged from 1998-2001
	Bottom temperature	World Wildlife Fund Canada (Alidina and Roff, 2003)	Each point was averaged from seafloor to included a maximum of 50 m above the seafloor in the water column
	Substrate	Vladimir Kostylev, Natural Resources Canada	Categorized into classes based on the Lidden-Wentworth size classification for sediment grains and assigned increasing phi (φ) values (-12 to +14) to decreasing grain size (boulder to clay) (Pettijohn et al., 1972); continous grid of mean grain size based on interpolation of existing grab and core samples

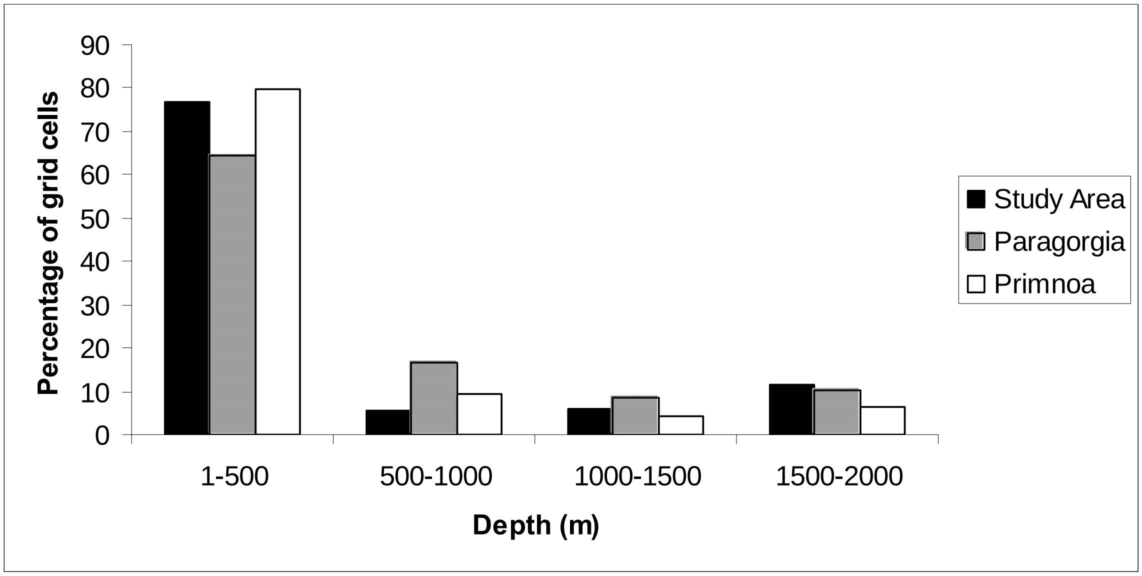

Figure 3.4. Depth (m) in the PCM study area and in locations with Paragorgiidae and Primnoiidae.

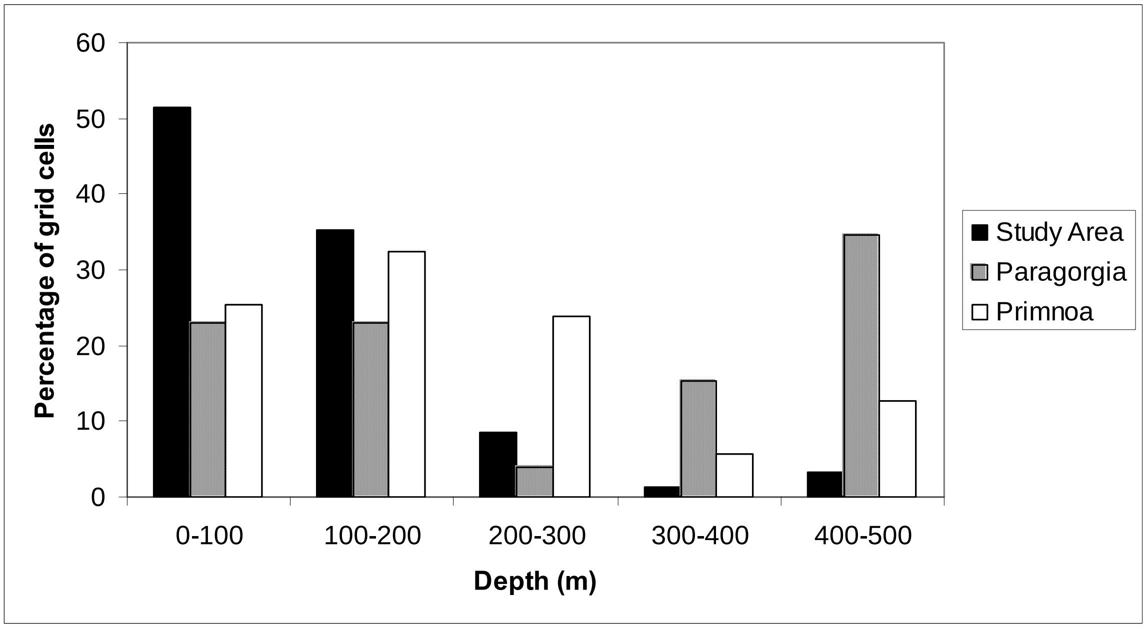

Figure 3.5. Depth (m) in the ACM study area and in locations with Paragorgiidae and Primnoiidae.

For the PCM study area, data on coral locations were obtained from the Marine Conservation Biology Institute (MCBI) (Etnoyer, 2003). This dataset included over 2000 coral locations from seven families (Antipathidae, Caryophyllidae, Corallidae, Isididae, Paragorgiidae, Primnoidae and Stylasteriidae). Data were provided by many institutions, including the California Academy of Sciences, the Smithsonian Institution National Museum of Natural History, NOAA Fisheries RACEBASE, Canadian Museum of Nature, the Monterey Bay Aquarium Research Institute, Scripps Institute of Oceanography, the REEF Foundation (Stylaster records) and the Santa Barbara Museum of Natural History, as well as by Cimberg et al. (1981).

Coral observations in the ACM study area included eight families: Acanthorgiidae, Caryophllidae, Flabellidae, Isididae, Keratoisidae, Paragorgiidae, Paramuriceida, and Primnoidae. They were obtained from Breeze (1997), Gass (2002) and Watling (unpublished data, University of Maine). The data summarized in these reports were acquired mainly through interviews with fishers and historical reports.

In both study areas, coral observations were grouped as Families as this was the lowest taxonomic designation that would allow the inclusion of all location data. In the PMC study area, the Paragorgiidae included two species (*P. arborea*, *P. pacifica*), while Primnoidae included 12 species in nine genera (*Amphilaphis* sp., *Arthrogorgia* sp., *Callogorgia kinoshitae*, *Fanellia compressa*, *Fanellia fraseri*, *Narella bowersi*, *Parastenella doederleini*, *Plumarella longispina*, *Primnoa reseda*, *Primnoa resedaeformis*, *Primnoa willeyi*, *Thouarella* sp.). In the ACM study area, Paragorgiidae included only *Paragorgia arborea* and while Primnoidae consisted of *Primnoa resedaeformis*. For both families, a number of observations were only described to the family level.

Minimum, maximum, and average values were calculated for temperature and chlorophyll *a*in the ACM study area, but were not available for the PCM study area. Although data were available, salinity was not included as an environmental variable in the analysis because the variation within the study area was small (30-35, with 90% of the coral locations falling between 34.5 and 35.5) (Leverette, unpublished data) and most likely were biologically meaningless.

3.23. Ecological Niche Factor Analysis

Ecological Niche Factor Analysis (ENFA) was used to generate habitat suitability maps for Paragorgiidae, Primnoidae and all families of coral combined with the software program BioMapper. 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 components (Manly, 1986). These components represent composite factors that explain variability. In ENFA, however, unlike PCA, the components have direct ecological meaning. The first component 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

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

where M is the marginality for a particular environmental variable, m_G is the global mean of the variable, m_S is the mean of the variable in species' range and σ_G is the standard deviation of the global distribution for the variable. The first component in ENFA is chosen to account for 100% of the marginality of the species, as well as some proportion of specialization, with the remaining components maximizing the remaining amount of specialization of the species (Hirzel, 2001).

The remaining components 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). It is calculated as:

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

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

Eigenvalues associated with specialization components can be larger than the values associated with the marginality values (Hirzel, 2001). In ENFA, coefficients for each environmental factor indicate the magnitude of variance in HS that they explain. Along the marginality component, the signs of the coefficients indicate whether the suitable habitat is represented by above average (positive coefficients) or below average (negative coefficients) values of the environmental variable. The signs of the coefficients are meaningless along the specialization components as the analysis uses absolute values in relation to the specialization components.

Combining the marginality of individual environmental variables, ENFA then computes an overall global marginality (Hirzel et al., 2002, Reutter et al., 2003) as:

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

where V is the number of environmental variables and m_i indicates the marginality value for each environmental variable. It also calculates a global specialization coefficient as

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

where λ_i indicates the specialization value for each environmental variable (Hirzel et al., 2002). The marginality coefficient, M, generally ranges between 0 and 1, with large values indicating that the species is not equally represented in all environments. The specialization coefficient S ranges from 1 to ∞, with the breadth of the niche decreasing as the specialization value increases. Tolerance, which is the inverse of specialization ranges from 0 to 1. The greater the tolerance coefficient, the wider the niche of a particular species (Reutter et al., 2003).

Coral location data for all available families of coral (hereafter referred to as "all coral"), Paragorgiidae and Primnoidae, as well as environmental data (temperature, slope, current, chlorophyll *a* and substrate) for both study areas were imported into Biomapper as a raster-based grid file with a 9-km cell size. Environmental variable maps were transformed using the Box-Cox transformation, which optimise normality of their distribution (Sokal and Rohlf, 1995). Using the median algorithm, 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 taxonomic group. This algorithm assumes that the median value for the environmental variable in the species distribution is approximately the same as in the study area and makes no assumptions based on the density of observation points (Hirzel et al., 2002; Hirzel and Arlettaz, 2003). These assumptions were met in the distribution patterns of this dataset.

3.24. Map Generation

Habitat Suitability (HS) maps were constructed from 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 was rescaled using the isopleth method, and ranged from 0 to 100, with zero being completely unsuitable (Hirzel, 2001). The isopleth method is preferable to a simple linear transformation as it uses the observations to scale the index. It determines class boundaries of the HS index to allow an equal number of observations in each HS class (e.g. 25% of the observations are found in HS classes of 75 or greater, 50% of observations are found in HS classes of 50 or greater). In doing so, this method does not assume that all observations are located in optimal habitat. As corals are sessile, all observations should theoretically be within highly suitable areas. But, because of the coarse resolution of the environmental maps, this assumption may not always be valid. Predicted locations were indicated only as being either suitable or unsuitable, and not assigned to within a range of suitability because of the low resolution.

3.25. Validation of HS Maps

Validation and confidence limits for the HS maps were calculated using a built-in jackknifing method in which coral location data were partitioned into ten equal-sized subsets. Nine of these subsets were used to generate the HS map and the remaining subset was used for validation (Fielding and Bell, 1997; Boyce et al., 2002). This procedure was repeated ten times, with a new subset being used for validation each time. HS were categorized into four equal sized bins (0-0.25, 0.26-0.50, 0.51-0.75, 0.76-1.00). For each subset, the area-adjusted frequency (F_{aa}) was calculated for each HS bin. F_{aa} is defined as the proportion of validation points in a HS bin, divided by the proportion of the study area covered by the bin, and was calculated as:

$$F_{aa} = \frac{\frac{N(i)}{N}}{\frac{S(i)}{S}}$$

where $N(_i)$ is the number of validation points in the i^{th} bin, N is the total number of validation points, $S(_i)$ is the map's total area covered by the i^{th} bin, S is the map's total area. The range of F_{aa} depended on the number of observations as well as the size of the study area. In an HS map generated based on a randomly distributed species, high HS values should be associated with high F_{aa} values (>1). The habitat is defined as unsuitable when F_{aa} is <1. For each validation subset, F_{aa} values were correlated with HS index (binned) using a Spearman's rank correlation. These rankings were averaged among subsets to produce a mean Spearman's rho (ρ), which indicated the relative accuracy of the particular combination of environmental variables at predicting coral locations.

3.26. Sensitivity Analysis

To test the sensitivity of map generation to changes in input parameters, two approaches were used. Firstly, coral locations were randomly removed to determine whether the number of observations significantly affected ρ values. Using the "all coral" dataset (N=757) from the PCM study area, the number of coral locations was reduced by 10%, 30%, 50%, and 90%. Ten randomly generated sets of locations were calculated for each percentage reduction. These sets were analysed in Biomapper using all five environment factors to obtain a maximum and minimum value for marginality, tolerance and ρ values. In the second approach, I used data from the ACM study area because minimum, maximum and average values for temperature and chlorophyll *a* were available. I used 9 possible environment combinations containing all five environmental variables to calculate HS maps. Each combination included the same values of slope, current and substrate. The remaining two environmental variables in each combination were all possible permutations of temperature (minimum, maximum, average), chlorophyll *a* concentration (minimum, maximum, average). Again, only the "all coral" dataset was used as it contained the highest number of locations.

3.3. RESULTS

3.31. Ecological Niche Factor Analysis and HS map generation

The combination of factors that most accurately predicted suitable habitat for coral was determined by running ENFA for each of all possible combinations of environmental variables. To compare accuracy between runs, I used Spearman's ρ values. In the PCM study area, Spearman's ρ for "all coral" ranged from 0.10 to 0.70 (Figure 3.3a). For Paragorgiidae, ρ values ranged from 0.093 to 1.00 (Figure 3.3b) and for Primnoidae, ρ ranged from 0.061 to 0.69 (Figure 3.3c).

For "all coral", the combination which included temperature and current was used to generate a habitat suitability map. This map indicated that suitable habitat was located mainly along the shelf break and throughout the Aleutian Islands (Figure 3.4). Many seamounts also arose as highly suitable habitats, as well as the Mendocino Fracture, extending seaward from the coast of California. The global marginality indicated conditions for "all corals" combined were similar to the average conditions in the study area (Table 3.2). The global tolerance indicated that these deep water coral are not very tolerant of a wide range of environmental conditions (Table 3.2). The marginality component generated in the ENFA indicated that suitable habitat for this taxonomic group was represented by below average current velocity and higher than average temperatures. The first component generated using ENFA explained 92% of the specialization with current and temperature also strongly influence specialization of this group (Table 3.2).

For Paragorgiidae, the combination with the highest ρ value included substrate and chlorophyll *a* concentration (Figure 3.3b). Similarly to "all coral", suitable habitat for Paragorgiidae was predicted to occur along the shelf break and throughout the Aleutian

Islands and on many seamounts (Figure 3.5). However, due to the patchy coverage of substrate data, it was difficult to accurately compare HS maps generated for Paragorgiidae to those maps for “all coral” and Primnoidae. Global marginality and global tolerance indicate that the conditions in the locations of occurrence of this coral were similar to the average conditions in the study area and that Paragorgiidae are tolerant of a relatively wide range of environmental conditions (Table 3.2). The marginality component indicated that suitable habitat is most strongly associated with below average substrate values (larger grain size). Within this component, 55% of the specialization was explained.

For Primnoidae, the combination including temperature, slope and chlorophyll *a* concentration was chosen to generate HS maps. Suitable habitat was predicted to be located mainly along the shelf break and throughout the Aleutian Islands and on many seamounts (Figure 3.6). Global marginality indicated that the conditions for Primnoiidae were as similar to the average conditions of the study area as were those of Paragorgiidae. Global tolerance was also similar to Paragorgiidae, indicating that this family is tolerant of variable environmental conditions. The first component indicated that 30% of the specialization for this species was most strongly associated with below average temperatures, while the remaining specialization was associated mainly with chlorophyll *a* concentration and, to a lesser degree, by slope (Table 3.2).

In the ACM study area, Spearman’s ρ values for “all coral” ranged from 0.1 to 0.58 (Figure 3.7a). For Paragorgiidae, ρ ranged from -0.061 to 0.82 (Figure 3.7b) and for Primnoidae, it ranged from 0.25 to 0.65 (Figure 3.7c). For “all coral”, the combination containing all five environmental factors (temperature, slope current, substrate and chlorophyll *a* concentration) was used to generate a habitat suitability map. The map located suitable habitat mainly along the shelf break, in the Gully, the Northeast Channel and the Gulf of Maine (Figure 3.8). The global marginality indicated the conditions of this group of corals were different than the average conditions in the study area. Additionally, these deep water corals are tolerant of variable environmental conditions (Table 3.2). The marginality component generated in the ENFA indicated strong, positive association with slope. The positive signs on the slope coefficient indicate that suitable habitat for this group was represented by steeper than average slopes. The first component explained 43% of the specialization. The remaining specialization is mainly explained by temperature (Table 3.2).

For Paragorgiidae, the combination of environmental variables which included current, chlorophyll *a* concentration and substrate provided the highest ρ value (Figure 3.7b) and was used to generate the HS map. This map identified fewer suitable habitat areas than for “all coral”. Those areas that were predicted as being suitable where found mainly along the shelf break. Common areas to “all coral” included the shelf break, the Gully and the Northeast Channel (Figure 3.9). Global marginality and global tolerance indicated that the conditions in the habitat were close to the average conditions in the study area and that Paragorgiidae are not tolerant of variable environmental conditions (Table 3.2). The marginality component indicated that suitable habitat is most strongly associated with lower than average current velocities and chlorophyll *a* concentrations. This first component explained 84% of the specialization for this family, with the remaining specialization strongly influenced again by chlorophyll *a* concentrations (Table 3.2). The F_{aa} curves of this combination were variable, indicating that this combination is not reliable in predicting suitable habitat. This is most likely the result of the small number of Paragorgiidae locations.

For Primnoidae, the combination which included temperature and substrate was chosen to generate the HS map. As for "all coral" and Paragorgiidae, the Gully, Northeast Channel and Gulf of Maine regions were still indicated as being highly suitable habitat, as they were in the "all coral" maps. Similarly to Paragorgiidae, global marginality indicated that the conditions in the habitat for Primnoiidae were different than the average conditions in the study area. Global tolerance indicated that this family is more tolerant to a wide range of environmental conditions than Paragorgiidae. The marginality component indicated a strong, positive association with both temperature and a negative association with substrate. Suitable habitat for this taxonomic group is represented by higher than average temperatures and lower than average substrate values (Table 3.2).

3.32. Sensitivity Analysis

In general, the higher percentage of locations removed, the more variable and thus, less accurate all parameters became. Overall, the maximum marginality value remained approximately constant (Table 3.3). The range between maximum and minimum values remained relatively constant and was the narrowest of the three statistics. The range in tolerance widened, with the maximum values increasing and the minimum values decreasing as progressively fewer locations were being included (Table 3.3). Tolerance had the highest percentage change between maximum and minimum values (78%).

Similarly to marginality, the range in ρ also remained relatively constant, but the actual minimum and maximum values decreased with decreasing number of locations.

Table 3.2. Results of ENFA for “all coral”, Paragorgiidae, Primnoidae in the PCM and ACM study areas, using five environmental variables (slope, temperature, chlorophyll *a* concentration, current and substrate).

Study Area	Taxonomic Group	Marginality	Tolerance	Component	Slope (°)	Temp. (°C)	Chl *a* ($mg\ m^{-3}$)	Current ($cm\ s^{-1}$)	Substrate (φ)	Proportion of variance explained
PCM	“all coral”	0.399	0.241	Marginality		0.760		-0.650		0.919
				Specialization		0.650		0.760		0.081
	Paragorgiidae	0.073	0.662	Marginality			-0.448		-0.894	0.547
				Specialization			-0.894		-0.448	0.453
	Primnoidae	0.071	0.737	Marginality	-0.494	-0.801	-0.338			0.30
				Specialization1	0.129	-0.452	0.883			0.404
				Specialization2	-0.866	0.488	0.109			0.297
ACM	“all coral”	0.860	0.630	Marginality	0.908	0.265	-0.195	0.214	-0.143	0.425
				Specialization1	-0.105	0.804	0.271	-0.463	-0.236	0.250
				Specialization2	-0.207	0.498	-0.760	-0.280	0.231	0.173
				Specialization3	-0.056	-0.031	-0.157	-0.452	-0.870	0.113
				Specialization4	0.256	0.141	0.451	-0.839	0.008	0.039
	Paragorgiidae	0.370	0.158	Marginality			-0.696	-0.695	-0.179	0.835
				Specialization			0.714	-0.647	-0.368	0.150
				Specialization2			0.025	0.226	-0.974	0.015
	Primnoidae	0.316	0.467	Marginality		0.770			-0.638	0.557
				Specialization1		0.638			0.770	0.443

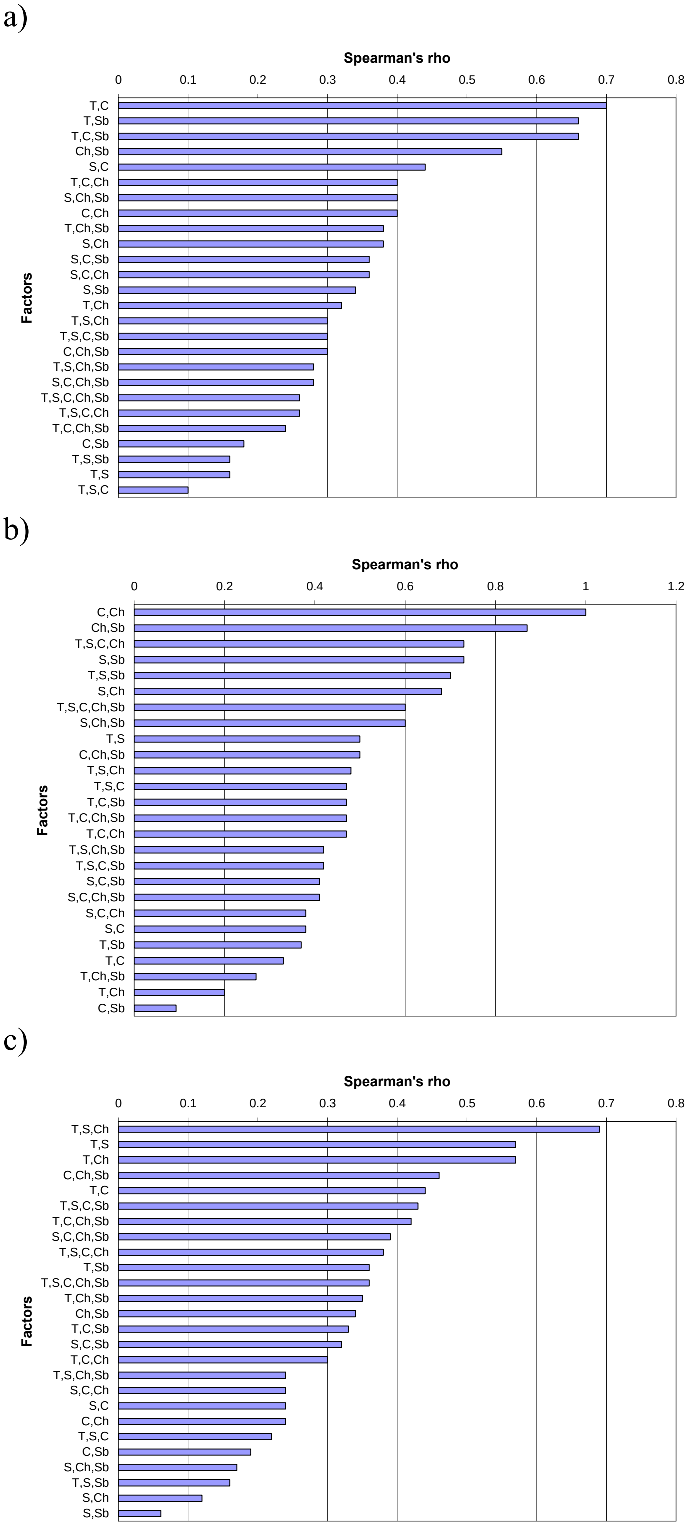

Figure 3.3. Spearman's ρ values generated using (a) "all coral", (b) Paragorgiidae, (c) Primnoidae and all possible combination of environmental variables to determine suitable habitat for the PCM study area. S – slope, T- temperature, C – current, Ch – chlorophyll *a* concentrations, Sb - substrate

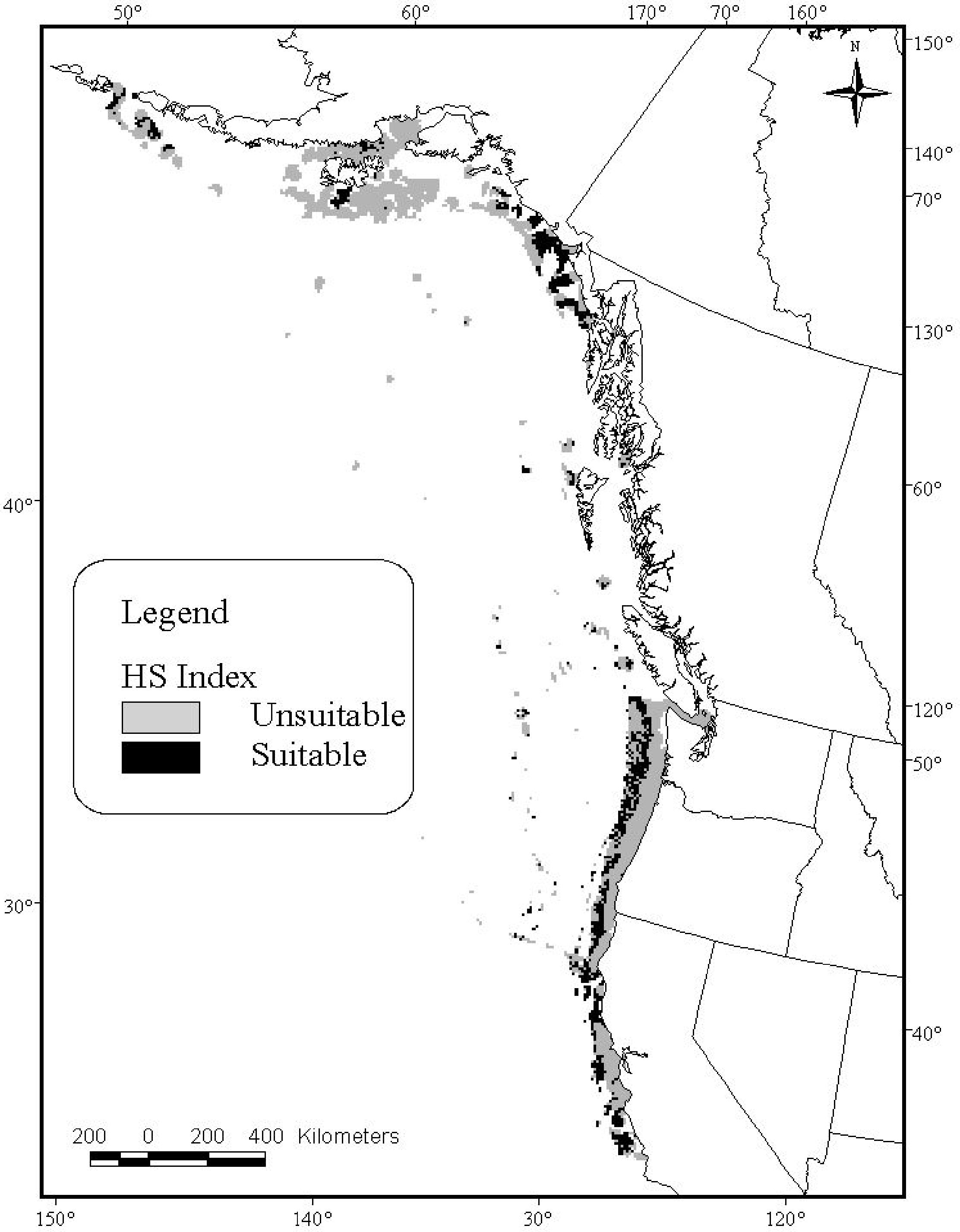

Figure 3.4. Habitat suitability map for "all coral" based on temperature (°C) and current (cm s^{-1}) in the PCM study area as computed by the Ecological Niche Factor Analysis.

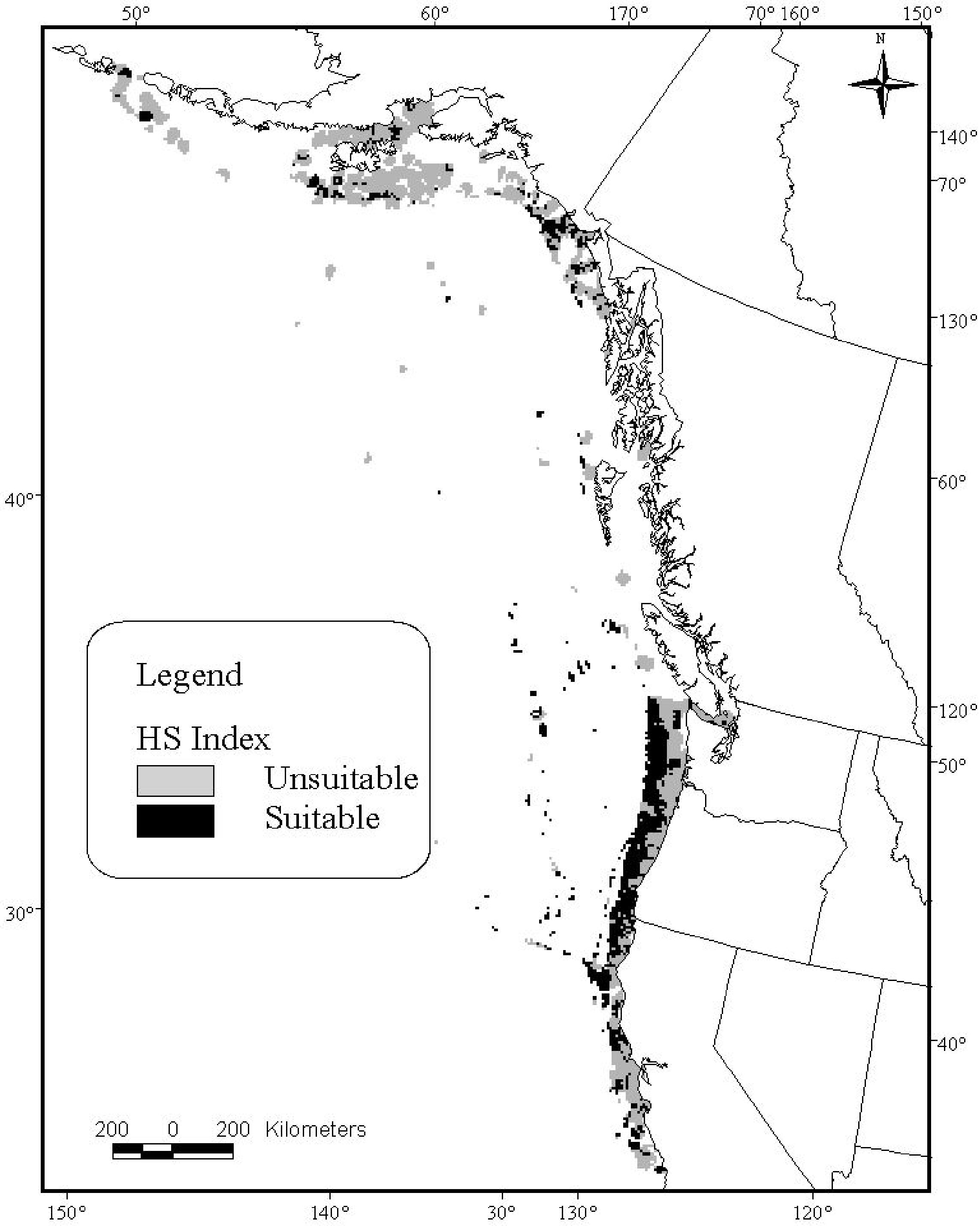

Figure 3.5. Habitat suitability map for Paragorgiidae based on chlorophyll *a* concentration (mg m^{-3}) and substrate (φ), in the PCM study area as computed by the Ecological Niche Factor Analysis.

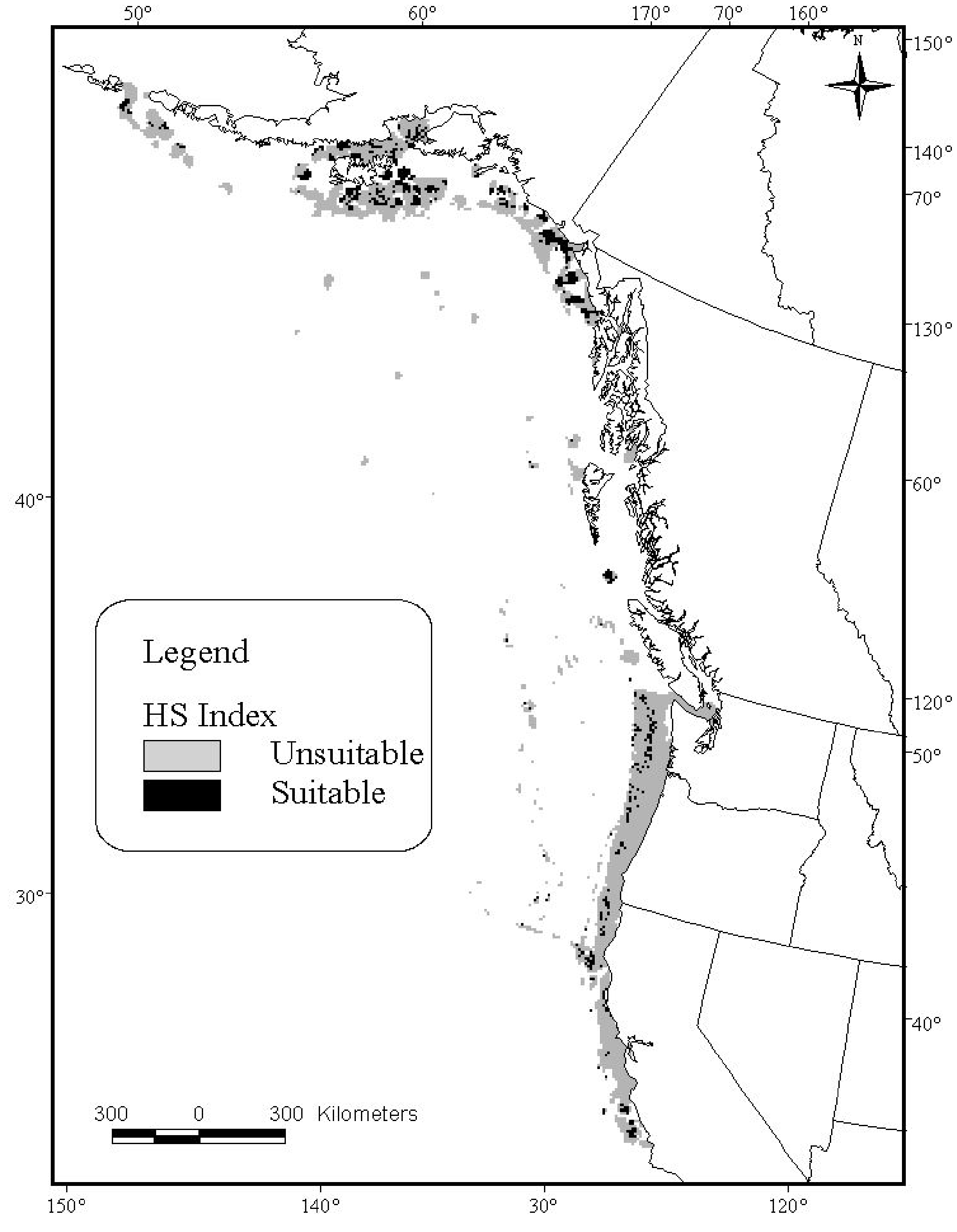

Figure 3.6. Habitat suitability map for Primnoidae based on temperature (°), slope (°) and chlorophyll *a* concentration (mg m^{-3}) in the PCM study area as computed by the Ecological Niche Factor Analysis.

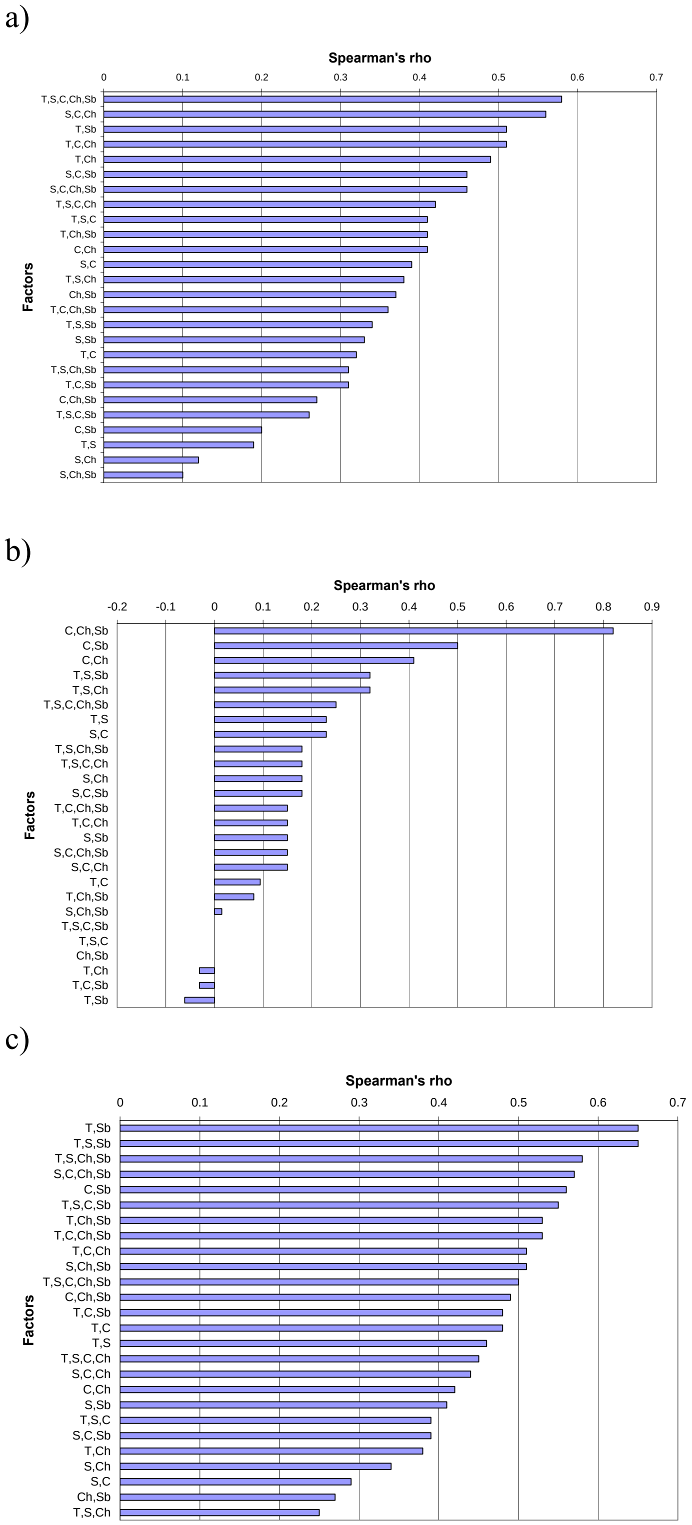

Figure 3.7. Spearman's ρ values generated using (a) "all coral", (b) Paragorgiidae, (c) Primnoidae and all possible combination of environmental variables to determine suitable habitat for the ACM study area. S – slope, T- temperature, C – current, Ch – chlorophyll *a* concentrations, Sb - substrate

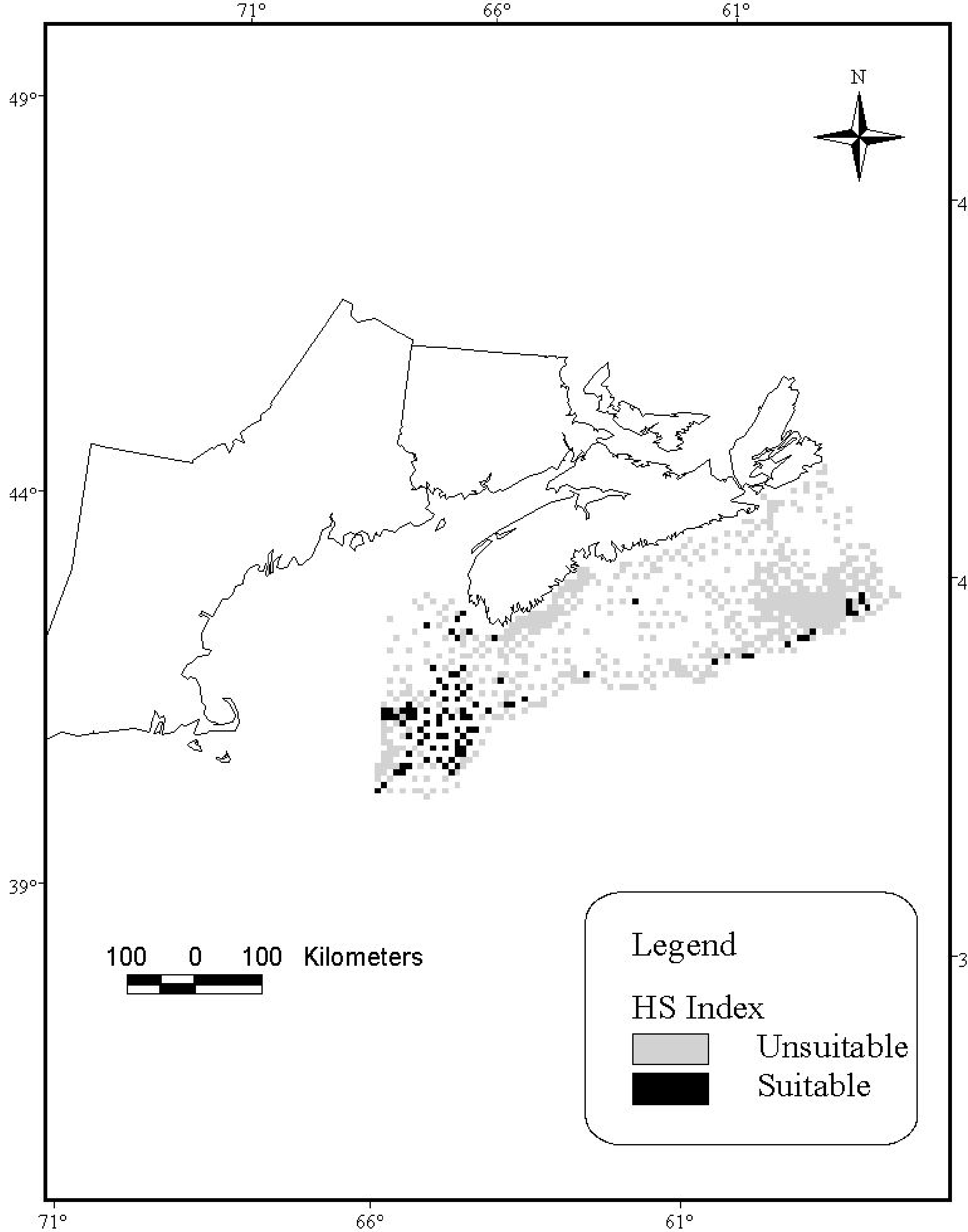

Figure 3.8. Habitat suitability map for "all coral" based on temperature (°C), slope (°), current (cm s^{-1}), substrate (φ) and chlorophyll *a* concentration (mg m^{-3}) in the ACM study area as computed by the Ecological Niche Factor Analysis.

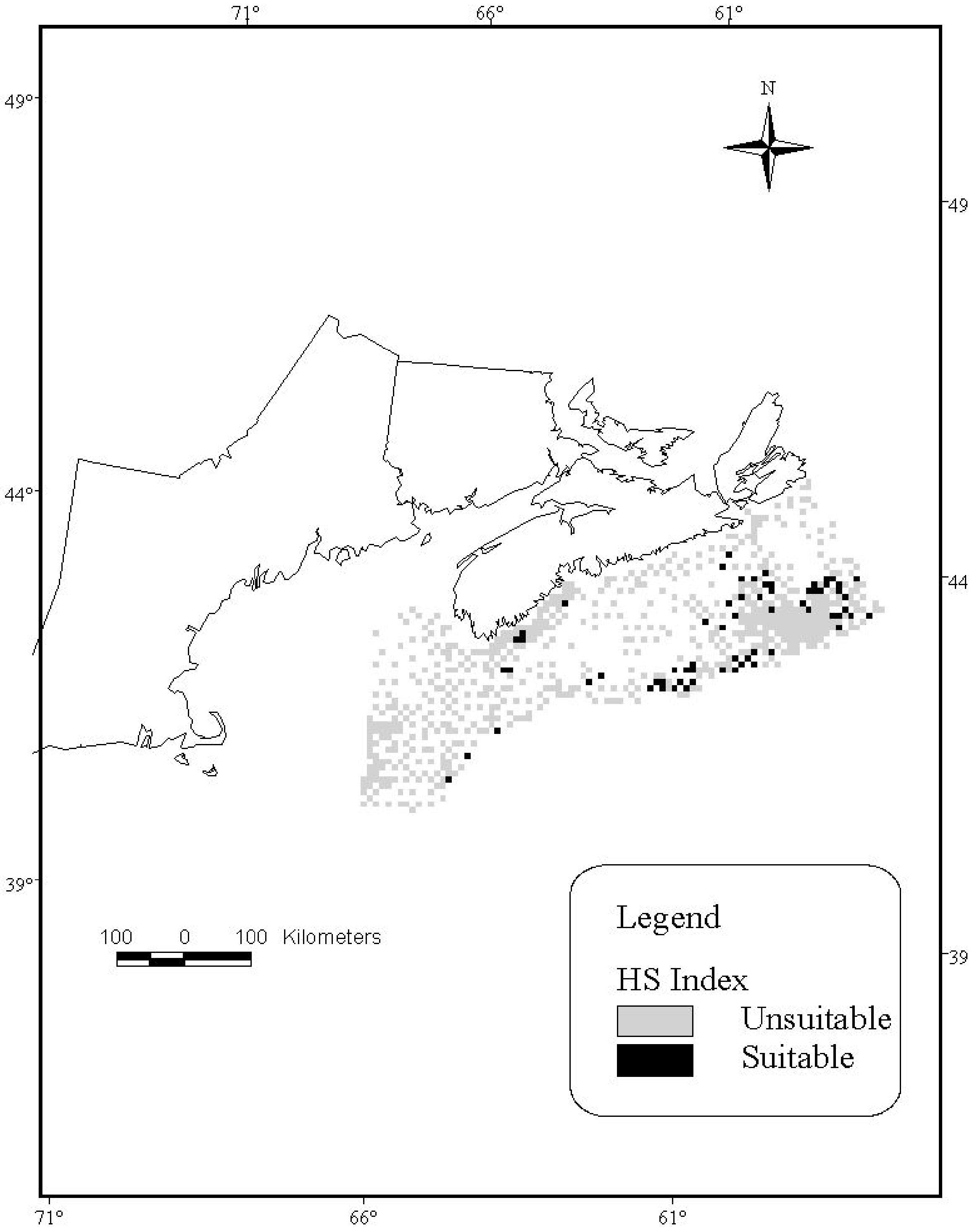

Figure 3.9. Habitat suitability map for Paragorgiidae based on current (cm s^{-1}), chlorophyll *a* concentration (mg m^{-3}) and substrate (φ) in the ACM study area as computed by the Ecological Niche Factor Analysis.

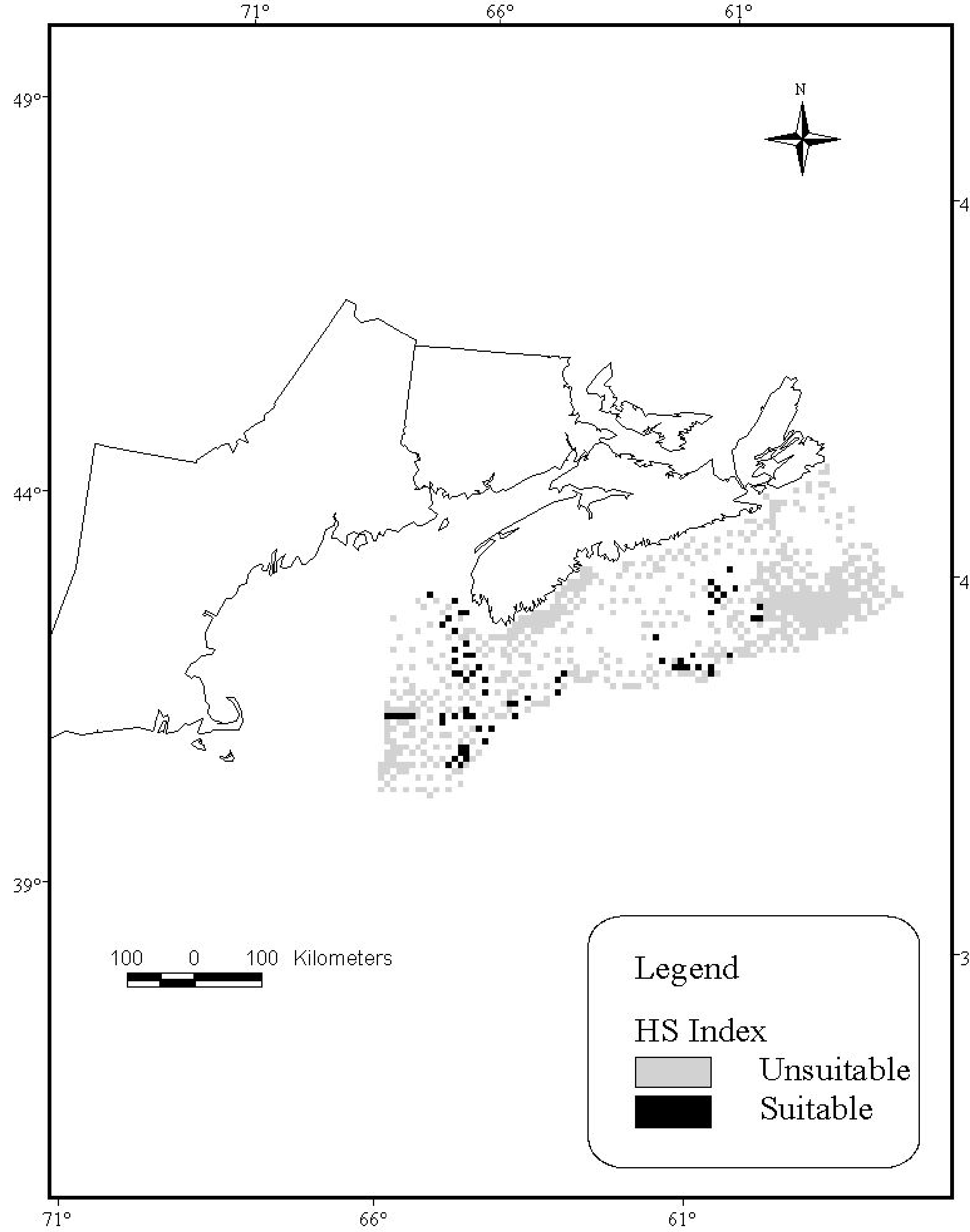

Figure 3.10. Habitat suitability map for Primnoidae based on temperature (°C), and substrate (φ) in the ACM study area as computed by the Ecological Niche Factor Analysis.

The accuracy of the prediction of suitable habitat for coral was also sensitive to the type of value (minimum, maximum, average) used for temperature and chlorophyll *a* concentration, while maintaining all 5 environmental variables in the combinations (Table 3.4). The range within all three statistics was narrow. Marginality, tolerance, and ρ were sensitive to the type of temperature values used. Both marginality and tolerance values were lower when minimum, rather than average or maximum, temperatures were used. The opposite was observed for ρ values. All three statistics remained relatively insensitive to the chlorophyll *a* measure used.

The HS maps generated indicate that for all three coral groups in the PCM study area, the majority of observed locations were found in areas of predicted suitable habitat. Observed locations which were not found in predicted areas of suitable habitat were mainly found in the deeper regions of the study area, indicating that these coral may be located on seamounts which were not identified in this analysis. More coral locations were found in areas of predicted unsuitable habitat in the ACM study area than in the PCM study area. These results are most likely due to the small number of observations, which affect the accuracy of the model.

Table 3.3. Results of sensitivity of ENFA to the number of locations included in the analysis for “all coral” in the PCM study area.

% removed	Marginality		Tolerance		ρ	
	Minimum	Maximum	Minimum	Maximum	Minimum	Maximum
0%	0.708	0.708	0.368	0.368	0.68	0.84
10%	0.661	0.910	0.235	0.257	0.46	0.92
30%	0.651	0.711	0.121	0.279	0.49	0.92
50%	0.642	0.705	0.175	0.309	0.33	0.84
90%	0.637	0.804	0.109	0.501	0.30	0.63

Table 3.4. Sensitivity analysis of the performance of ENFA in determining habitat suitability to different types of data. Marginality, tolerance and ρ values for “all coral” in the ACM study area in which slope (s), current (c), temperature maximum (tx), minimum (tn) or average (tv), chlorophyll a concentrations maximum (chx), minimum (chn) or average (chv), and substrate (sb) values were utilized.

Combination	Marginality	Tolerance	ρ
s,c,tn,chn,sb	0.910	0.647	0.37
s,c,tn,chv,sb	0.908	0.660	0.40
s,c,tn,,chx,sb	0.908	0.660	0.40
s,c,tv,chn,sb	0.852	0.625	0.34
s,c,tv,chv,sb	0.860	0.638	0.58
s,c,tv,chx,sb	0.860	0.638	0.58
s,c,tx,,chn,sb	0.824	0.590	0.48
s,c,tx,,chv,sb	0.832	0.619	0.51
s,c,tx,,chx,sb	0.832	0.619	0.51

3.4. DISCUSSION

On both continental margins, predicted areas of suitable coral habitat were located in distinct geographic regions. In the PCM study area, HS maps for all three coral taxonomic groups indicated that suitable habitat is predicted to occur throughout the Aleutian Islands, along the continental shelf break and in the many fjords and gullies formed near the coastline of British Columbia. Although suitable habitat was generally not predicted to exist beyond the shelf break and slope, seamounts tended to be the exception. These areas are already well known as locations of rich coral assemblages (Cimberg et al., 1981; Tuninifcliffe, 1983; Genin et al., 1986; Heifetz, 2002).

The commonality among the predicted sites of suitable habitat in the PCM study area is their complex topography. The intense geological activity has formed many steeply sloped areas, which are suitable habitat for all three taxonomic groups. Because of the coarse resolution of these maps and the limited amount of data coverage for environmental factors such as substrate, slope may be considered as a proxy for hard substrate and strong current velocities (Genin et al, 1986; Freiwald et al., 1999; Herring, 2002). Current may also be an important factor in suitable coral habitat. As deep water corals are sessile, suspension-feeding organisms that rely on near-bottom currents for nutrient supply, they must exist in habitats with strong currents (Mortensen, 2001).

The HS maps generated for the ACM study area also indicated several suitable locations which were common among all three coral groups. These areas included the Northeast Channel, the Gully, and the continental shelf break. As in the PCM study area, most of these predicted locations are already known to harbour coral assemblages through interviews with fishers and observations from several research cruises (Breeze, 1997, Gass, 2002). The research conducted in this region has mainly focused on the Northeast

Channel and the Gully (MacIsaac et al., 2001; Gordon and Fenton, 2002), both large submarine canyons along the edge of continental shelf. Their steeply sloping walls funnel water, creating strong currents. Although the ACM study area contains a wide continental shelf, it is riddled with many canyons, gullies and channels, making a large portion of the area potentially suitable to corals.

In general, along the PCM study area, more area was predicted as being suitable habitat for “all coral”, most likely due to the diverse range of families that this grouping represents. There were no pronounced differences in the mean habitats among the three coral taxonomic groups, each having similar global marginality coefficients indicating that the optimal habitat was similar to the average habitat in the study area. However, their tolerance coefficients did differ pronouncedly. Both Paragorgiidae and Primnoidae had higher global tolerance than “all coral”. Similar tolerance values substantiate the observations that Paragorgiidae and Primnoiidae often co-exist (Jensen and Frederiksen, 1992). The emerging most important factor in determining suitable habitat for all three taxonomic groups in this study area seemed to be temperature, as it was found in one or more of the top three ranked combinations for all three coral groups.

As in the PCM study area, the “all coral” group in the ACM study area had the most wide-spread predicted suitable habitat. This map had common suitable locations with these identified for Primnoidae and Paragorgiidae. The single environmental factor that was common between all three coral taxon was substrate and it is well documented in the literature that coral require hard substrate on which to attach (Jensen and Frederiksen, 1992; Rogers, 1999; Mortensen, 2001). As in the PCM study area, temperature was also included in the highest ranking combinations for both “all coral” and Primnoidae.

This is the first study to utilize Biomapper and ENFA to predict suitable habitat in the marine environment. All previous studies have focused on terrestrial flora and fauna, including ferns, ibex, mice, and vultures (Hirzel, 2001; Sachot, 2002; Zaniewski et al., 2002; Reutter et al., 2003; Hirzel and Arlettaz, 2003). One challenge in this study was the low numbers of occurrence locations, particularly in the ACM study area. Most previous studies included hundreds of locations, while in the ACM study area there were fewer than 100 observations for Primnoidae and Paragorgiidae combined. The sensitivity analysis indicated that while combinations of environmental parameters containing fewer locations produced less accurate predictions and more variable tolerance and rho values, while the range in marginality values was generally maintained. Thus, it is still possible to gain an overall understanding of the effects of different environmental factors in defining suitable habitat using relatively low numbers of locations, but with reduced accuracy.

The generated HS maps provide the first step in identifying suitable habitat for deep water coral. Biologically, substrate is the limiting factor for these organisms. Ideally, the locations indicated as being suitable would be validated with a more detailed geological chart. Unfortunately, this is also the environmental factor that has been sampled with the lowest fine-scale resolution. By immediately eliminating those areas with soft substrate, these maps would be more useful to future research cruises.

In addition to increasing our understanding of the relative importance of five common environmental factors in determining suitable habitat for deep water corals, this study provides one of the first attempts in developing a tool to predict suitable habitats in the marine environment. Many of the challenges faced in this study highlight the need for higher resolution oceanographic datasets, especially deep sea benthic data. These types of datasets would allow future studies to generate more accurate maps and to more effectively target specific 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, including the NOAA funded Symposium on the Effects of Fishing Activities on Benthic Habitats: Linking Geology, Biology, Socioeconomics, and Managements and the International Planning and Collaboration workshop for the Gulf of Mexico and the North Atlantic Ocean (McDonough and Pulise, 2003), as well as the marine conservation group Oceana, have recommended that mapping of coral locations is an immediate priority. I have used ENFA to extend these recommendations by attempting to predict potential coral locations, based on habitat suitability. Through an increased understanding of habitat requirements, this study was able to further our biological knowledge of species which have previously been inaccessible.

CHAPTER 4 GENERAL CONCLUSION

4.1. GENERAL DISCUSSION

My thesis has explored the quantitative relationships between physical factors and biological data by applying an innovative habitat prediction model for deep sea corals both on the Pacific and Atlantic Continental Margins of North America. On both continental margins, coral locations were found to be not randomly distributed within the study areas, but to be present within specific ranges for all environmental factors considered. Although the patterns in habitat characteristics were generally similar for most deep water coral, some differences existed between families relative to the ranges of particular environmental factors in which they occur. By qualitatively and quantitatively describing habitats in which corals are located in relation to oceanographic factors (chapter 2), I was able to more accurately interpret habitat suitability of deep water coral habitat generated in chapter 3.

Both chapters 2 and 3 individually included relationships between coral locations and environmental factors. In Chapter 2, the χ^2 tests indicated that coral locations are not randomly distributed within any of the five environmental factors examined. These results suggest that coral occupy habitat within particular ranges of these factors. The results from ENFA (chapter 3) expanded on the χ^2 analysis and not only was there a relationship between coral locations and environmental factors, but relationships were determined that can predict suitable habitat. This analysis allowed the determination of those factors which had the strongest influence in determining suitable habitat for the three coral taxonomic groups.

In both study areas, corals were primarily found in areas of complex topography, mainly along the continental shelf break and on seamounts. These HS maps are merely the first step in determining where coral may potentially be found. Because of the limited access to the deep sea and the huge costs associated with exploration, it is necessary to be able to effectively map target areas. Thus, more research is needed to increase the resolution of the maps as well as to ground-truth specific areas. The coarse resolution of the datasets makes it difficult to determine precise information on deep sea coral habitat. Additionally, the existing information needs to be assessed relative to known biological requirements. The quality of the data included in the analysis will determine the accuracy of the results. For example, data on substrate were least accurate in my analysis, yet this factor is known to limit suitable habitat for deep water coral. Thus, fine resolution geological maps should first be used to determine whether there is hard substrate present in the predicted areas.

This project benefited directly from the many conservation groups currently involved in protecting coral habitat. Groups such as the World Wildlife Fund Atlantic Region and the Ecology Action Centre in Nova Scotia, as well as American organizations such as the Marine Conservations Biology Institute and Oceana, have been spearheading projects that further our knowledge of deep sea corals, as well as educating the public. They have been active in lobbying for many critical habitat areas to be designated as marine protected areas. These efforts have lead to a coral-specific closure in the Northeast Channel to certain types of fishing gear which are known to be damaging to deep sea corals. Although no true marine protected areas have been designated yet, one area, the Sable Island Gully, has been set aside as a “pilot marine protected area”, which indicates that restriction on fishing and other activities are strictly voluntary (Willison et al., 2001).

The need to protect deep water coral from mechanical influences has become more obvious as recent observations in both northeast and northwest Atlantic have found evidence of sever trawling damage to deep water coral reefs (Fossä et al., 2002; Hall-Spencer et al., 2002). The most recent example was the discovery of a small *Lophelia* reef on the Scotian shelf. This reef represents the first evidence that this species of deep water coral occurs in the northwest Atlantic and efforts are currently underway to protect it from further damage by fishing gear.

Logistically, our ability to determine how various environmental parameters affect the growth and health of the corals is presently limited. Sampling of wide expanses of the deep ocean is financially prohibitive, while specimens brought back to laboratory environments often do not survive. By predicting target coral locations, this project helped bridge these knowledge gaps. In many areas, scientists often rely on fishers' local knowledge to determine coral locations. This knowledge may be not precise enough for sampling purposes or it may be flawed. Also, corals may be located in areas where fishers are unable to go either due to currents or other barriers. Without a predictive tool, these corals may remain unknown and unprotected. By developing a method that would increase the knowledge of coral locations, marine managers and legislators have the ability to more effectively protect specific areas, while still allowing users, such as industries and fisheries to have access to nearby areas. In doing so, critical habitats may be protected while allowing many people to benefit from the resources. As user groups increase, and more stress is placed on the margin's resources, science has become more involved in understanding the biology of margin habitats, to more effectively protect them.

LITERATURE CITED

Alidian, H. and J.C. Roff. 2003. Classifying and mapping physical habitat types (seascapes) in the Gulf of Maine and the Scotian Shelf: seascape version to May 2003. Report prepared by World Wildlife Fund – Canada and the Conservation Law Foundation, Halifax, Nova Scotia.

Andrews, A.H., E.E. Cordes, M.M. Mahony, K. Munk, K.H. Coale, G.M. Cailliet and J. Heifetz. 2002. Age, growth and radiometric age validation of a deep-sea, habitat-forming gorgonian (*Primnoa resedaeformis*) from the Gulf of Alaska. Hydrobiologia, 471:101-110.

Beaulieu, S.E. 2001. Colonization of habitat islands in the deep sea: recruitment to glass sponge stalks. Deep-sea Research, 48: 1121-1137.

Boyce, M.S., P.R. Vernier, S.E. Nielsen and F.K.A. Schmieglow. 2002. Evaluations resource selection functions. Ecological Modelling, 157:281-300.

Breeze, H., D.S. Davis, M. Butler and V. Kostylev. 1997. Distribution and status of deep sea corals off Nova Scotia. Marine Issues Committee Special Publication #1. Ecology Action Centre, Halifax, Nova Scotia.

Brooke, S. and C.M. Young. 2003. Reproductive ecology of a deep water scleractinina coral, *Oculina varicosa*, from the southeast Florida shelf. Continental Shelf Research, 23:847-858.

Cairns, S.D. 1977. Deep-water corals. Sea Frontiers, 23:84-89.

Cimberg, R.L., T. Gerrodette and K. Muzik. 1981. Habitat requirements and expected distribution of Alaska coral. Final Report, VTN Oregon, Inc. Report prepared for the Office of Marine Pollution Assessment, Alaska Office, US Department of Commerce, NOAA, OCSEAP Final Report 54:207-308.

De Mol, B., P. Van Rensbergen, S. Pillen, K. Van Herrewghe, D. Van Rooij, A. McDonnel, V. Huvenne, M. Ivanov, R. Swennen and J.P. Henriet. 2002. Large deep-water coral banks in the Porcupine Basin, southwest of Ireland. Marine Geology, 188:193-231.

Druffel, E.R.M., S. Griffin, A. Witter, E. Nelson, J. Southon, M. Kashgarian, and J. Vogel. *Gerardia*: bristlecone pine of the deep-sea? 1995. Geochimica et Cosmochimica Acta., 59(23):5031-5036.

Ecology Action Centre. 1999. Deep Sea Corals: Nova Scotia's secret forest. Ecology Action Centre, Halifax, Nova Scotia.

Elsner, P. 1999. The Scotian Shelf "seascape": using GIS for quantitative resource evaluation and management, a case study. Master of Marine Management thesis. Dalhousie University, Halifax, Nova Scotia.

Etnoyer, P. 2003. B2B 1.1: Information for Conservation Planning – Baja California to the Bering Sea. Marine Conservation Biology Institute, CD ROM.

Etnoyer, P. and L. Morgan. 2003. Occurrence of habitat-forming deep sea coral in the northeast Pacific Ocean: a report to NOAA's office of habitat conservation. Report prepared by Marine Conservation Biology Institute, Redmond, Washington.

Fielding, A.H. and J.F. Bell. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation, 24:38-49.

Fossä, J.H., P.B. Mortensen and D.M. Furevik. 2002. The deep-water coral *Lophelia pertusa* in Norwegian waters: distribution and fishery impacts. Hydrobiologia, 471:1-12.

Frederiksen, R., A. Jensen and H. Westerberg. 1992. The distribution of the scleractinian coral *Lophelia pertusa* around the Faroe Islands and the relation to internal mixing. Sarsia, 77:157-171.

Freiwald, A. 1998. Geobiology of *Lophelia pertusa* (Scleractinia) Reefs in the North Atlantic. University Bremen, Bremen Germany.

Freiwald, A. 2002. Reef-forming cold-water corals. *In* Ocean Margin Systems. Ed. G. Wefer, D. Billett, D. Hebbeln, B.B. Jorgensen, M. Schluter and T. Van Weering. Springer-Verlag, Berlin, Heidelberg, pp.365-385.

Freiwald, A., V. Huhnerbach, B. Lindberg, J.B. Wilson and J. Campbell. 2002. The Sula reef complex, Norwegian Shelf. Facies, 47:179-200.

Freiwald, A., A. Grehan, I. Mjolnerod and D. Jones. 2001. Conserving habitats that are poorly understood: deepwater corals and efforts to protect them. MPA News: International new and analysis on marine protected areas, 3(5):1-2.

Freiwald, A., J.B. Wilson and R. Henrich. 1999. Grounding Pleistocene iceberg shape recent deep-water coral reefs. Sedimentary Geology, 125:1-8.

Gage, J.D. and P.A. Tyler. 1996. Deep-sea biology. Cambridge University Press, New York.

Gass, S.E. 2002. An assessment of the distribution and status of deep sea corals in Atlantic Canada by using both scientific and local forms of knowledge. MES thesis, Dalhousie University, Halifax, Canada.

Genin, A., P.K. Dayton, P.F. Lonsdale and F.N. Spiess. 1986. Corals on seamount peaks provide evidence of current acceleration over deep-sea topography. Nature, 322(3):59-61.

Gordon, D.C. Jr. and D.G. Fenton. 2002. Advances in understanding the Gully ecosystem: a summary of research projects conducted at the Bedford Institute of Oceanography (1999-2001). Canadian Technical Report of Fisheries and Aquatic Science 2377, Dartmouth, Nova Scotia.

Griffin, S. and E.R.M. Druffel. 1989. Sources of carbon to deep-sea corals. Radiocarbon, 31(3):533-543.

Guisan, A. and N.E. Zimmermann. 2000. Predictive habitat distribution models in ecology. Ecological Modelling, 135:147-186.

Hall-Spencer, J., V. Allain and J.H. Fossä. 2002. Trawling damages to Northeast Atlantic ancient coral reefs. Proceedings of the Royal Society of London, series B: Biological Sciences, 269(1490):507-511.

Hannah, C.G., J.A. Shore and J.W. Loder. 2001. Seasonal circulation on the Western and Central Scotian Shelf. Journal of Physical Oceanography, 31(3):591-615.

Hecker, B. 1990. Variation in megafaunal assemblages on the continental margin south of New England. Deep-Sea Research, 37(1):37-57.

Heifetz, J. 2002. Corals in Alaska: distribution, abundance, and species associations. Hydrobiologia, 471:19-28.

Herring, P. 2002. The biology of the deep ocean. Ed. M.J. Crawley, C. Little, T.R.E. Southwood and S. Ulfstrand. Oxford University Press, Toronto.

Hirzel, A. and A. Guisan. 2002. Which is the optimal sampling strategy for habitat suitability modelling. Ecological Modelling, 157:331-341.

Hirzel, A., 2001. When GIS come to life. Linking landscape- and population ecology for large population management modelling: the case of Ibex (*Capra ibex*) in Switzerland. Doctoratal thesis. Institute of Ecology, Laboratory for Conservation Biology. University of Lausanne, Switzerland.

Hirzel, A.H. and R. Arlettaz. 2003. Modeling habitat suitability for complex species distributions by environmental-distance geometric mean. Environmental Management, 32:614-623.

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

Hirzel, A.H., V. Helfer and F. Métral. 2001. Assessing habitat-suitability models with a virtual species. Ecological Modelling, 145:111-121.

Hovland M. and P. Mortensen. 1999. Deep-water coral reefs and processes in the sea floor. Norway: John Grief Forlan, pp.153.

Hovland, M., P.B. Mortensen, T. Brattegard, P. Strass, K. Rokoengen. 1998. Ahermatypic coral banks off Mid-Norway: evidence for a link with seepage of light hydrocarbons. Palaios, 13:189:200.

Jensen, A. and R. Frederiksen. 1992. The fauna associated with the bank-forming deep-water coral *Lophelia pertusa* (Scleractinaria) on the Faroe Shelf. Sarsia, 77:53-69.

Krieger, K.J. and B.L. Wing. 2002. Megafauna associations with deepwater corals (*Primnoa* spp.) in the Gulf of Alaska. Hydrobiologia, 471:83-90.

Leier, M. 2001. World atlas of the oceans. Firefly Books, New York.

MacIsaac, K., C. Bourbonnais, E. Kenchington, D. Gordon Jr. and S. Gass. 2001. Observations on the occurrence and habitat preference of corals in Atlantic Canada. *In* Proceedings of the first international symposium on deep-sea corals. July 30 – August 3, 2000. Ed. J.H.M. Willison, J. Hall, S.E. Gass, E.L.R. Kenchington, M. Butler, P. Doherty. Ecology Action Center and the Nova Scotia Museum, Halifax, Nova Scotia, Canada, pp 58-75.

Manly, B.F.J. 1986. Multivariate statistical methods: a primer. Chapman and Hall, New York, pp.59-71.

Mantyla, A.W. and J.L. Reed. 1983. Abyssal characteristics of the world ocean waters. Deep sea research, 30:805-833.

McDonough, J.J and K.A. Puglise. 2003. Summary: deep-sea coral workshop, International Planning and Collaboration Workshop for the Gulf of Mexico and the North Atlantic, Galway, Ireland, January 16-17, 2003. NOAA Technical Memorandum NMFS-SPO-60.

Menzies, R.J. 1965. Conditions for the existence of life on the abyssal sea floor. Oceanography and marine biology: an annual review, 3:195-210.

Messing, C.G., A.C. Neumann, and J.C. Lang. 1990. Biozonation of deep-water Lithoherms and associated hardgrounds in the northeast straits of Florida. Palaios, 5:15-33.

Mikkelsen, N., H. Erlenkeuser, J.S. Killingley and W.H. Berger. 1982. Norwegian corals: radiocarbon and stable isotopes in *Lophelia pertusa*. Boreas, 11:163-171.

Moore, D.H. and H.R. Bullis. 1960. A deep-water coral reef in the Gulf of Mexico. Bulletin of Marine Science of the Gulf and the Caribbean, 10:125-128.

Mortensen, P.B. 2001. Aquarium observations on the deep-water coral *Lophelia pertusa* (L., 1758) (Scleractinia) and selected associated invertebrates. Ophelia, 54(2):83-104.

Mortensen, P.B. and H.T. Rapp. 1998. Oxygen and carbon isotope ratios related to growth line patterns in skeletons of *Lophelia pertusa* (L) (Anthozoa, Scleractinia): Implications for determination of linear extension rates. Sarsia, 83:433-446.

Mortensen, P.B., M.T. Hovland, J.H. Fossä and D.M. Furevik. 2001. Distribution, abundance and size of *Lophelia pertusa* coral-reefs in mid-Norway in relation to seabed characteristics. Journal of the Marine Biological Association of the UK, 81:581-597.

Pettijohn, F.J, P.E. Potter and R. Siever. 1972. Sand and sandstone. Springer-Verlag, New York.

Reed, J.K. 2002. Comparison of deep-water coral reefs and lithoherms off southeastern USA. Hydrobiologia, 471:57-69.

Reutter, B.A., V. Helfer, A.H. Hirzel, and P. Vogel. 2003. Modelling habitat-suitability on the base of museum collections: an example with three sympatric *Apodemus* species from the Alps. Journal of Biogeography, 30:581-590.

Rogers, A.D. 1999. The biology of *Lophelia pertusa* (Linnaeus 1758) and other deep-water reef-forming corals and impacts from human activities. International Review of Hydrobiologia, 84:315-406.

Sachot, S. 2002. Viability and management of an endangered capercaillie (*Tetrao urogallus*) metapopulation. Doctoratal thesis. Institute of Ecology, Laboratory for Conservation Biology. University of Lausanne, Switzerland.

Smith, K.L. Jr. and R.S. Kaufmann. 1999. Long-term discrepancy between food supply and demand in the deep eastern North Pacific. Science, 284:1174-1177.

Sokal, R.R. and F.J. Rohlf. 1981. Biometry: The principles and practices of statistics in biological research. W.H. Freeman & Co., New York.

Tendal, O.S. 1992. The North Atlantic distribution of the Octocoral *Paragorgia arborea* (L. 1758) (Cnidaria, Anthozoa). Sarsia, 77:213-217.

Tunnicliffe, V. 1983. Corals move boulders: an unusual mechanism of sediment transport. Limnology and Oceanography, 28(3):564-568

Tyler, P. A. 1988. Seasonality in the deep sea. Oceanography and Marine Biology: an Annual Review 26: 227-258.

Tyler, P.A. 1995. Conditions for the existence of life at the deep-sea floor: an update. Oceanography and Marine Biology: an Annual Review 33: 221-244.

Willison, J.H.M., D.K.P. Jones and S. Atwood. 2000. Deep sea corals and marine protected areas in Nova Scotia. *In* Managing Protected Areas in a Changing World. Proceedings of the Fourth International Conference on Science and Management of Protected Areas. 14-19 May 2000. Ed. S. Bondrup-Nielsen, N.W.P. Munro, G. Nelson, J.H.M. Willison, T.B. Herman, and P. Eagles. Science and Management of Protected Areas Association, Wolfville, Nova Scotia, Canada, pp 1157-1163.

Zaniewski A.E., A. Lehmann and J.McC. Overton. 2002. Predicting species spatial distributions using presence-only data: a case study of native New Zealand ferns. Ecological Modelling, 157:261-280.