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Distribution of deep-water corals along the North American continental margins: Relationships with environmental factors

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Abstract

Despite the increasing attention to assemblages of deep-water corals in the past decade, much of this research has been focused on documenting and enumerating associated fauna. However, an understanding of the distribution of most species of coral and the ecological processes associated with these assemblages is still lacking. In this study, we qualitatively and quantitatively described the habitats of two families of deep-water corals in relation to six oceanographic factors (depth, slope, temperature, current, chlorophyll *a* concentration and substrate) on the Pacific and Atlantic Continental Margins of North America (PCM and ACM study areas, respectively). This study focused primarily on the distributions of Primnoidae and Paragorgiidae because of the large number of documented occurrences. For each environmental factor, deep-water coral locations were compared to the surrounding environment using χ^2 tests. On both continental margins, coral locations were found to be not randomly distributed within the study areas, but were within specific ranges for most environmental factors. In the PCM study area, Paragorgiidae and Primnoidae locations were found in areas with slopes ranging from 0° to 10.0°, temperature from −2.0 to 11.0 °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 1.4°, temperature ranging from 0 to 11.0 °C and currents ranging from 0 to 207 cm s^{-1}. Although the patterns in habitat characteristics were similar, differences existed between families with respect to particular environmental factors. In both study areas, most environmental parameters in locations where corals occurred were significantly different from the average values of these parameters as determined with χ^2 tests ($p<0.05$) except for substrate in Paragorgiidae locations and depth in Primnoidae locations on the PCM. This is the first study to show coral distributional patterns at the continental shelf/slope scale.

Keywords: Abiotic factors; Abundance; Oceanographic data; Canada; United States of America; Paragorgiidae; Primnoidae

1. Introduction

The biological assemblages occupying most deep-water habitats are among the most poorly studied worldwide, with those at hydrothermal vents being the possible exception. Assemblages of deep-water coral were also mostly unknown until this decade when they have received increased attention both from the scientific community and the public. Despite this interest, information on the biology and ecology remain limited, mainly because of logistical difficulties in collecting specimens. Presently, most studies focus on documenting and

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enumerating associated fauna (e.g. Krieger and Wing, 2002; Buhl-Mortensen and Mortensen, 2004; Metaxas and Davis, 2005), while an understanding of the distribution, and the factors that influence it, is still lacking for most species of corals.

The high diversity of deep-water corals makes taxonomically based generalisations about habitat requirements difficult. However, there are several consistent patterns that emerge across all taxa. 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, but recorded abundance to date is maximal between 200 and 1000 m depth (Freiwald, 2002). 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 particulate loading (Moore and Bullis, 1960; Tendal, 1992). The deep sea is relatively homogeneous in salinity (Gage and Tyler, 1996) and most corals inhabit environments with salinities ranging between 34 and 37 (Mortensen et al., 2001; Freiwald, 2002). Although few studies have examined the relationships of coral distributions with temperature and salinity in detail, a recent study by Mortensen and Buhl-Mortensen (2004) indicated that the range of these variables in relation to coral habitat varies little among species. For example, most species of deep-water coral tend to occur in waters $>3.5\,^{\circ}$C and $<13\,^{\circ}$C (Freiwald, 2002), although some taxa such as *Gersemia* spp., have been found to occur in temperatures as low as $-1\,^{\circ}$C (Cimberg et al., 1981).

In this study, we described the distributional patterns of Paragorgiidae and Primnoidae along the Pacific continental margin (PCM) and the Atlantic continental margin (ACM) of North America in relation to six oceanographic factors: depth, slope, temperature, current, chlorophyll *a* concentration and substrate. These factors were selected based on available data in locations where corals had been recorded (MacIsaac et al., 2001; De Mol et al., 2002; Freiwald, 2002). Distributions were compared between the two study sites for each family, and between the two families for each site, to identify those factors with consistent influence on coral occurrence. By deriving first order relationships between the occurrence of corals and different environmental variables in their habitat, this study enhances our understanding of environmental factors limiting the distributions of these organisms. To our knowledge, this is the first study to describe the distribution of corals on spatial scales of 100–1000 s of kilometres and attempts to relate these to environmental factors at the continental shelf/slope spatial scale.

2. Materials and methods

2.1. Study areas

Study areas were selected along the PCM and ACM. The PCM study area encompassed an area approximately 2000 km wide and 3500 km long, from Alaska to California (Fig. 1). This region is defined by a continental shelf that ranges in width between ~10 and 100 km, and a narrow (~70 km wide), but steep continuous slope (Leier, 2001). This sharp gradient is the result of active subduction zones close to the continent. Near the continent, this study area also contains 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 (Fig. 2). This area is defined by a 200-km wide continental shelf and a 250-km wide continental slope (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 high density of coral locations.

2.2. Data collection

Sources of environmental data on depth, slope, temperature, current speed, surface chlorophyll *a* concentration and substrate type 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. Salinity was not included as an environmental variable because the variation within the study area was small (30–35, with 90% of the coral locations falling between 34.5 and 35.5) (Bryan, unpublished data), and most likely biologically meaningless.

For the PCM study area, data on coral locations were obtained from the Marine Conservation

Biology Institute (Etnoyer, 2003). 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 Institution of Oceanography, and the Santa Barbara Museum of Natural History, as well as by Cimberg et al. (1981). The data summarised in this report were obtained from recreational divers, fishers, historical records and scientific explorations. Metadata for these records, such as method of collection, are included in Etnoyer (2003).

Coral observations in the ACM study area were obtained from Breeze et al. (1997), Gass (2002) and L. Watling (University of Maine; and recently published in Watling and Auster (2005)). The data summarised in these reports were acquired mainly through interviews with fishers and historical reports. Metadata for these coral locations, such as type of collection and start and end coordinates for trawls/dredges, can be found within, or are referred to in, the individual publications.

As the taxonomic level of individual coral records within a database is determined by the level of scientific expertise present at the time of collection, not all records are identified to the species level (Cimberg et al., 1981; Heifetz, 2002). Thus, to ensure taxonomic accuracy and include as many location records as possible, coral observations were grouped to Family in both study areas. Since we expect differences in distributions to be greater between families than between species within families, we believe the broader grouping to be

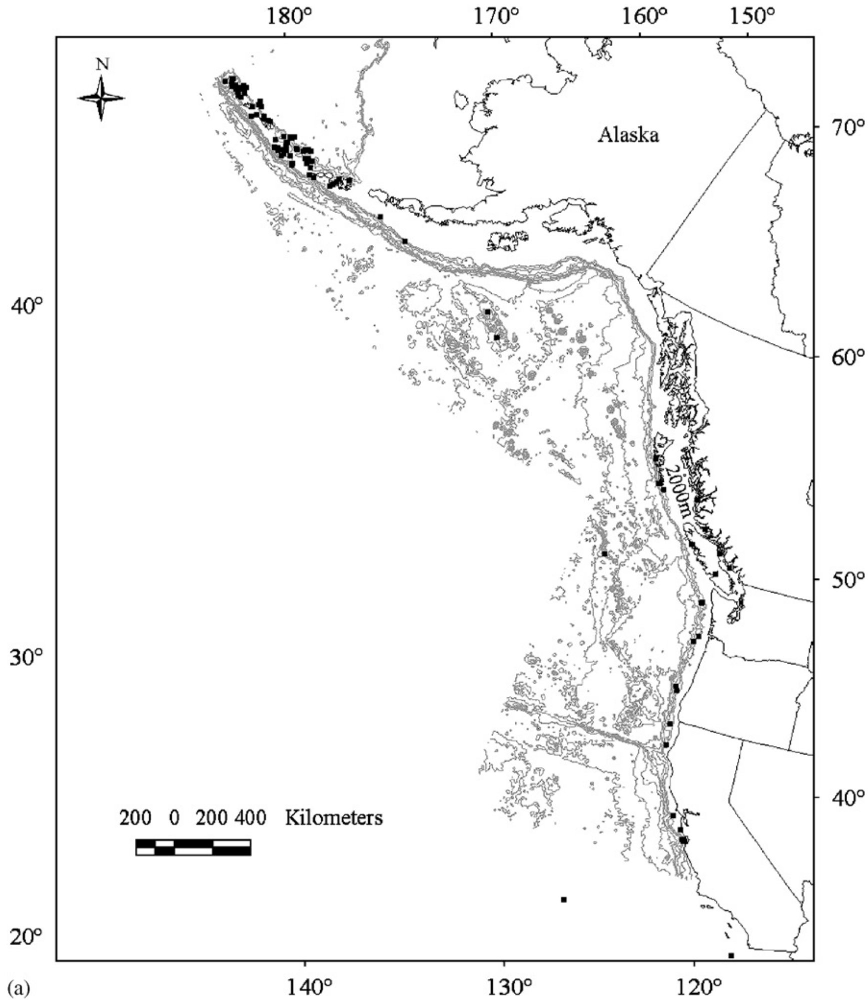

Fig. 1. Locations of (a) Paragorgiidae ($N = 184$) and (b) Primnoidae ($N = 1164$) along the Pacific continental margin (PCM) study area, Alaska to California. 500 m contours are shown.

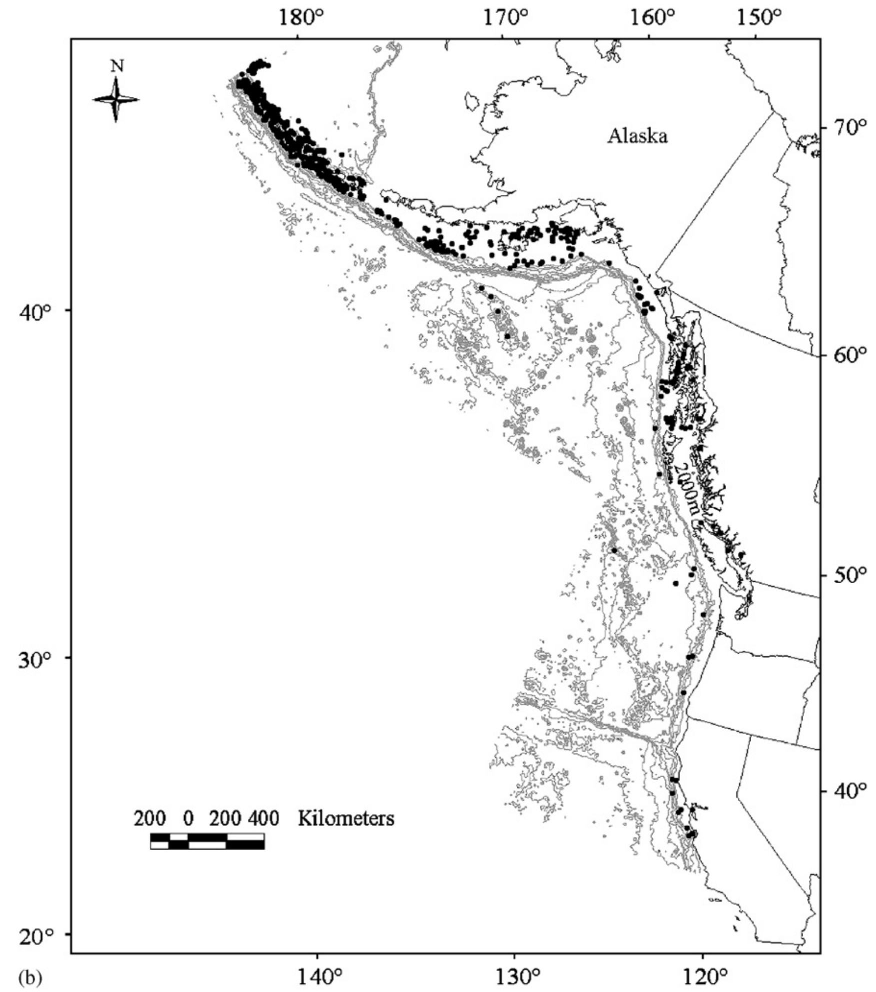

Fig. 1. (*Continued*)

more appropriate in this first step in identifying distributional patterns at shelf/slope scales. In the PCM study area, Paragorgiidae included two species (*Paragorgia arborea* and *Paragorgia pacifica*), while Primnoidae included 11 species in 9 genera (*Amphilaphis* sp., *Arthrogorgia* sp., *Callogorgia kinoshitae*, *Fanellia compressa*, *Fanellia fraseri*, *Narella bowersi*, *Parastenella doederleini*, *Plumarella longispina*, *Primnoa resedaeformis*, *Primnoa willeyi*, *Thouarella* sp.). In the ACM study area, Paragorgiidae consisted of *P. arborea,* and Primnoidae of *P. resedaeformis*. The smaller number of species present in the ACM study area may be due to many specimens being identified only to Family.

We used depth ranges of 0–2000 m for PCM and 0–500 m for ACM to ensure adequate representation of depth in coral observations. The frequency of coral observations in these ranges closely reflects the frequency of depth strata in the study area (Fig. 3), and there were $<17\%$ coral locations outside these depth ranges. In both study areas, coral location records were obtained primarily from fishers and scientific research cruises. In the PCM study area, these efforts were restricted mainly to depths above 2000 m and were focussed mostly on the continental shelf and on seamounts. In the ACM study area, most fishing and scientific studies have been focussed at depths between 200 and 500 m. In both study areas, depths >1000 m are under-sampled compared to shallower locations.

2.3. Chart generation and statistical analyses

Environmental data (depth, slope, temperature, current and chlorophyll *a* concentration), for both study areas were mapped as a raster-based grid file with a $5 \times 5\,km^2$ cell size using ArcView v.3.2 and Spatial Analyst v.2.1. This resolution was selected based on the resolution of the original environmental data. Substrate was imported as a $9 \times 9\,km^2$ cell size because of the limited spatial coverage of original point data estimates of average grain size. In the PCM study area, slope was originally plotted at 2′ resolution, temperature at ~5′ resolution, current using a 15 km uniform grid and chlorophyll *a* concentration using 9 km images. In the ACM study area, temperature and slope were plotted at 5′ resolution, current using a 15 km uniform grid, and chlorophyll *a* concentration at $1.5 \times 1.5\,km^2$ resolution. Although some of the original data were plotted in degrees, utilising a resolution based on kilometres enabled us to eliminate the variation caused by the convergence of longitude lines over the length of the study area. By interpolating using a higher power to place greater emphasis on nearby points, we were able to maintain the accuracy of the original data.

To obtain values for each environmental variable at each coral location, coral location data for Paragorgiidae and Primnoidae were overlaid on the map of each variable as point locations (latitude and longitude). However, the spatial coverage for the environmental variables depended on the available data points and did not overlap completely with that of coral locations. Consequently, we were only able to obtain values of environmental variables for a subset of coral locations.

For both study areas, the environmental characteristics in locations with Paragorgiidae and Primnoidae were compared to those across the

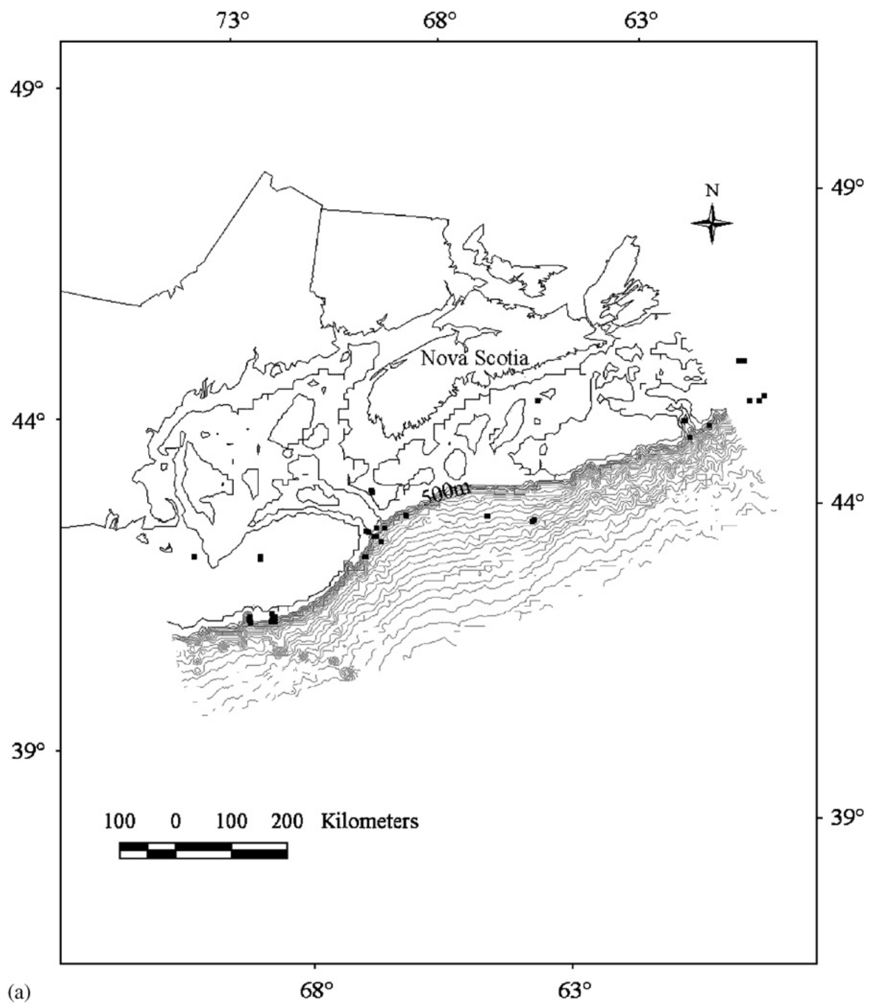

Fig. 2. Locations of (a) Paragorgiidae ($N = 62$) and (b) Primnoidae ($N = 82$) along the Atlantic continental margin (ACM) study area, Cape Breton to Cape Cod. 500 m contours are shown.

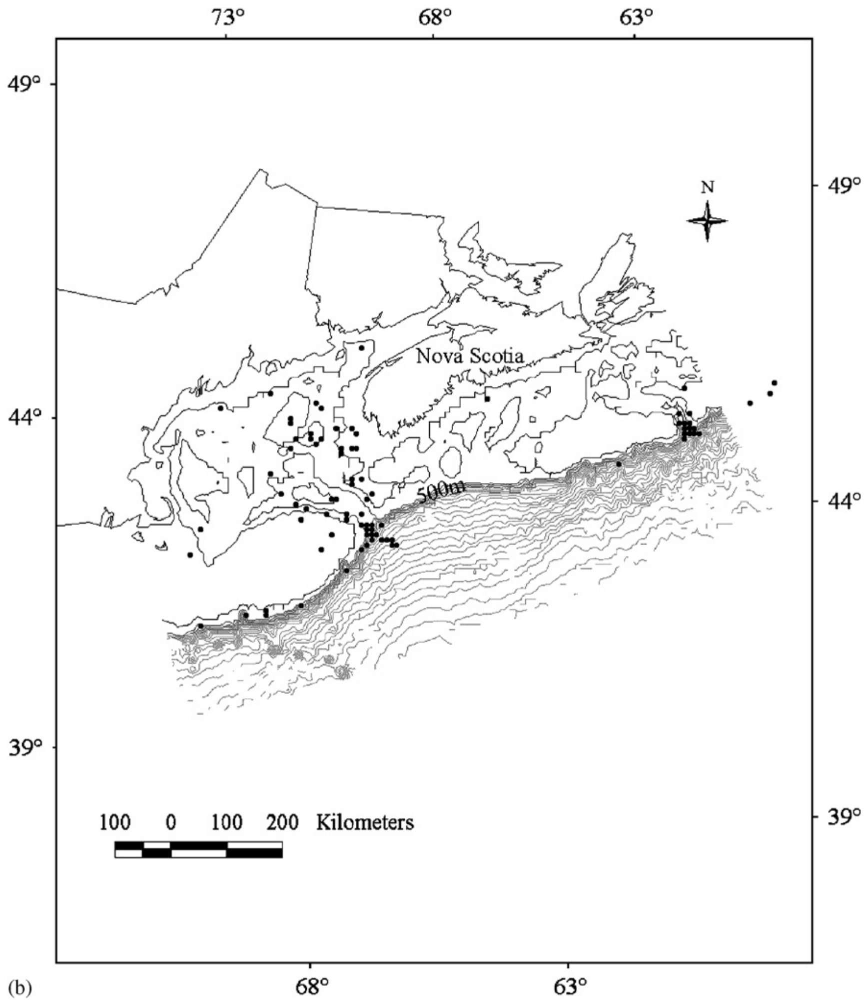

Fig. 2. (*Continued*)

entire study area using χ^2 tests to determine whether the corals occur under other-than-average conditions. For each environmental variable, firstly, the range of values was divided into classes of equal intervals (5 classes for all variables, except 8 for substrate). We then used the charts generated in ArcView to determine the relative frequency of locations within each class for the entire study area. For the χ^2 tests, we calculated expected frequencies in each class by multiplying the relative frequency in the entire study area by the number of coral locations with available data for that variable (see above). In 3 instances (temperature in the PCM; chlorophyll α and substrate in the ACM), some classes were combined to obtain an expected frequency of at least 1 (Zar, 1999). The expected frequencies were compared to the observed frequencies for each environmental variable in the coral locations. Additionally, the observed frequencies between locations of Paragorgiidae and Primnoidae were compared.

For each family and each study area, we used correlation analyses to determine whether any of the environmental parameters (except substrate because of its lower resolution) in the coral habitat, covary with depth, and thus assess their importance in distinguishing coral habitat from the surrounding environment.

3. Results

3.1. General description of PCM site

The PCM study area consisted of many subduction zones and a narrow continental shelf. Even beyond the edge of the shelf break, there were many

Table 1
Sources and types of environmental data used in this study

Study area	Environmental variable	Source	Type of data	*N*
PCM	Depth/slope	Marine Conservation Biology Institute, USA	Derived from bathymetry data composed of a 2′ resolution grid	327,427
	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	102,473
	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	51,328
	Surface chlorophyll *a* concentration	Marine Conservation Biology Institute, USA	Derived MODIS images, yearly average includes 1997–1999	265,732
	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 (−12–14) to decreasing grain size (boulder to clay) (Pettijohn et al., 1972)	11,900
ACM	Depth/slope	World Wildlife Fund Canada (Alidina and Roff, 2003)	Derived from bathymetry data composed of a 5′ resolution grid	183,709
	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	12,192
	Bottom current velocity	Charles Hannah, Bedford Institute of Oceanography, Canada (Hannah et al., 2001)	Modelled data, annual tidal velocities	19,125
	Surface chlorophyll *a* concentration	Moderate Resolution Imagining Spectroradiomters (MODIS)	Derived MODIS images, averaged from 1998–2001	5847
	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	2440

N = number of raw data records available to map each parameter.

rises in elevation on the seafloor, most likely because of the active geological nature of the area. Consequently, 7% of the total study area contained slopes greater than 3.0°, with 80% of the study area containing slopes between 0° and 1.0°, and the remaining 13% between 1.1° and 3.0° (Fig. 4a). Warm water was usually found in shallow areas along the coast and surrounding seamounts. Bottom temperature ranged from −2 to 11.0 °C, with a mean of 4.3 °C (Fig. 4b, Table 2). Extreme current velocities (>30.0 $cm\,s^{-1}$) were found only in isolated regions of the Aleutian Islands, and tidal current velocities between 10.1 and 30.0 $cm\,s^{-1}$ were more typical around islands. Although >53% of bottom current velocities were <5.0 $cm\,s^{-1}$ (Fig. 4c), the range was quite wide (0–143.0 $cm\,s^{-1}$). The mean chlorophyll *a* concentration in this study area was low (0.6 $mg\,m^{-3}$) (Table 2), but the range was wide (0–46.0 $mg\,m^{-3}$) (Fig. 4d). As with current velocity, areas with the highest chlorophyll *a* concentrations were found near the coast and in the vicinity of islands. However, concentrations >3.0 $mg\,m^{-3}$ were present only in 19% of the study area, and were mainly located on the continental shelf (Fig. 4d). Because of the presence of large rivers on the west coast of North America, sediment

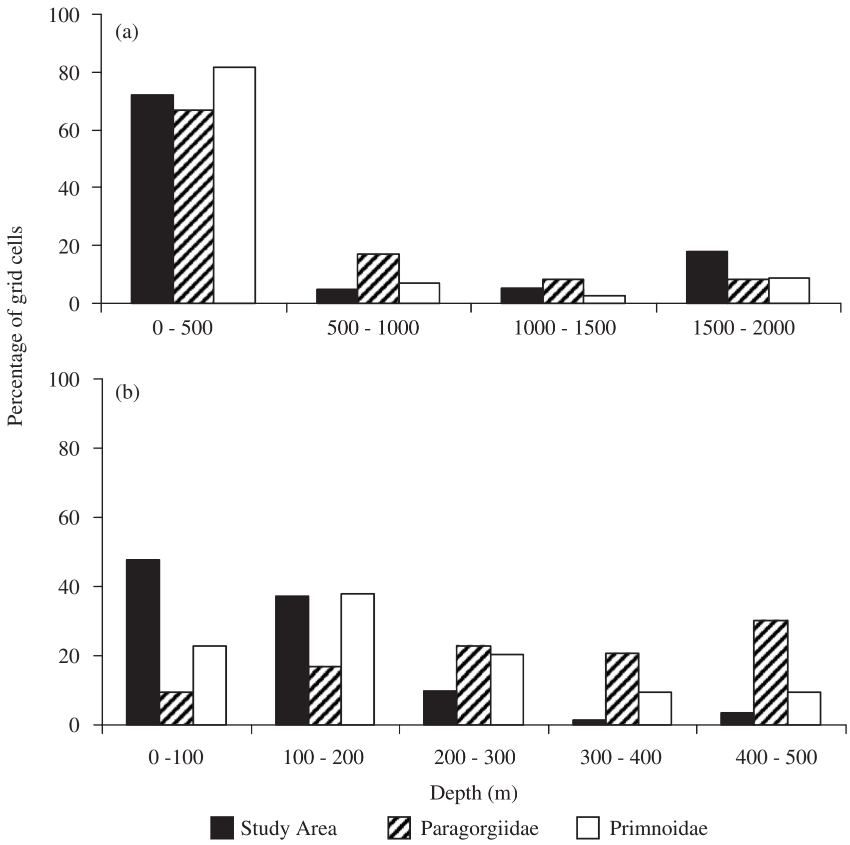

Fig. 3. Distribution of depths across the entire study area, as well as in locations of Paragorgiidae (PA) and Primnoidae (PR) in (a) the PCM study area (PA: $N = 159$, PR: $N = 958$) and (b) the ACM study area (PA: $N = 53$, PR: $N = 74$).

transport to offshore locations is enhanced. Consequently, much of the sediment present was silt (62%) (Fig. 4e).

3.2. Coral distribution at the PCM site

Most Paragorgiidae and Primnoidae locations were clustered along the continental shelf break and around seamounts (Figs. 1a, b). For both families, all environmental parameters were significantly different in coral locations than in the study area as a whole, except for substrate for Paragorgiidae and depth for Primnoidae (Table 3). Additionally, all characteristics varied between locations of the two families, except for substrate (Table 3). Most of the study area (72%), Paragorgiidae locations (67%) and Primnoidae locations (82%) fell within depths between 0 and 500 m (Fig. 3). Paragorgiidae were found at greater depths than Primnoidae. Many locations of Paragorgiidae (40%) and of Primnoidae (50%) were found in areas with slopes ranging from 0° to 3.0° (Fig. 4a). Most locations of Paragorgiidae (64%) were distributed between 7.1 and 9.0 °C, while 64% of Primnoidae locations were distributed in habitats with temperatures ranging between 3.1 and 5.0 °C. In 75% of the cells of the study area, bottom temperature ranged between 3.1 and 7.0 °C (Fig. 4b). Both Primnoidae and Paragorgiidae locations were found in a wide range of current velocities. Fewer than 76% of locations of Paragorgiidae and 33% of Primnoidae were found in areas with current velocity $<5.0\,\mathrm{cm\,s^{-1}}$, and in $<2\%$ of locations in the study area, current velocities ranged between 50 and $143\,\mathrm{cm\,s^{-1}}$ (Fig. 4c). Chlorophyll *a* concentrations were low throughout the study area ($<3.0\,\mathrm{mg\,m^{-3}}$), and 96% of Paragorgiidae and 92% of Primnoidae locations fell within this class of chlorophyll *a* concentration (Fig. 4d). Interestingly, 59% of locations of Paragorgiidae and 46% of Primnoidae were in areas with silt as the dominant substrate type (Fig. 4e). Primnoidae were located in habitats

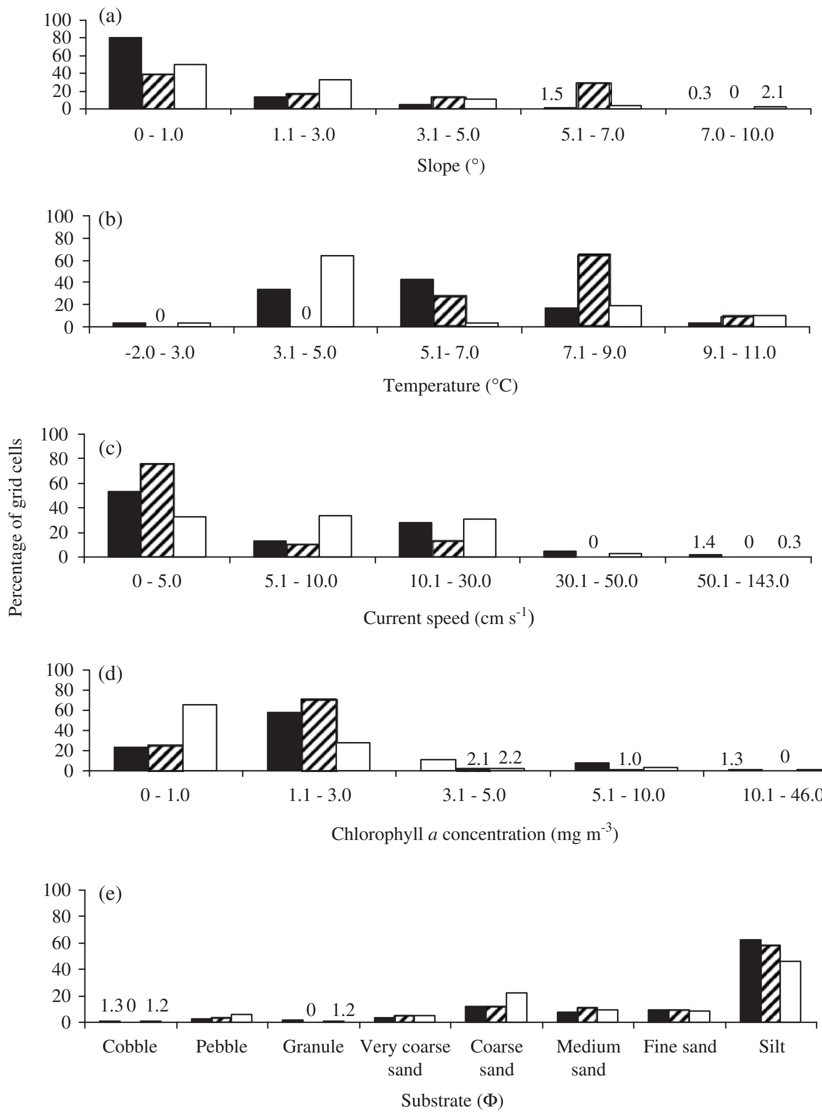

Fig. 4. Distribution of five oceanographic variables across the entire PCM study area as well as in locations of Paragorgiidae (PA) and Primnoidae (PR) for (a) slope (PA: $N = 159$, PR: $N = 958$), (b) bottom temperature (PA: $N = 11$, PR: $N = 59$), (c) bottom current (PA: $N = 96$, PR: $N = 318$), (d) surface chlorophyll *a* concentration (PA: $N = 96$, PR: $N = 318$) and (e) substrate (PA: $N = 82$, PR: $N = 84$).

Table 2
Mean and standard deviation values of six environmental variables (depth (m), slope (deg), temperature (°C), current (cm s^{-1}), chlorophyll *a* concentration (mg m^{-3}) and substrate (φ)) in the PCM study area for: the entire study area (Global), Paragorgiidae locations and Primnoidae locations

Environmental factor	Depth	Slope	Temperature	Current	Chlorophyll *a* concentration	Substrate
Global mean ± SD	596.0 ± 695 ($N = 69230$)	0.8 ± 1.3 ($N = 69230$)	4.3 ± 1.1 ($N = 111933$)	4.9 ± 8.9 ($N = 131319$)	0.6 ± 1.2 ($N = 586102$)	4.4 ± 3.0 ($N = 7133$)
Paragorgiidae mean ± SD	609.6 ± 1081.9 ($N = 159$)	2.1 ± 1.8 ($N = 159$)	5.2 ± 2.0 ($N = 11$)	10.0 ± 10.9 ($N = 96$)	1.2 ± 1.5 ($N = 96$)	4.6 ± 2.5 ($N = 82$)
Primnoidae mean ± SD	642.4 ± 1650.4 ($N = 958$)	1.8 ± 1.9 ($N = 958$)	4.6 ± 1.3 ($N = 59$)	12.3 ± 13.8($N = 318$)	1.3 ± 1.6 ($N = 318$)	4.1 ± 2.9 ($N = 84$)

N = sample size. Global mean and SD are calculated for the gridded data.

Table 3
Results of χ^2 tests comparing the observed distributions of six environmental factors (depth (m), slope (deg), temperature (°C), current (cm s^{-1}), chlorophyll *a* concentration (mg m^{-3}) and substrate (φ)) in locations with Paragorgiidae and Primnoidae to those expected based on the distributions of variables across the entire PCM study area

Environmental factor	Depth	Slope	Temperature	Current	Chlorophyll *a* concentration	Substrate
χ^2 critical (df)	9.8 (4)	9.8 (4)	6.0 (2)	9.8 (4)	9.8 (4)	14.1 (7)
Paragorgiidae	33.1	563.7	181.8	22.9	17.2	5.3
Primnoidae	3.1	63.5	763.3	44.3	102.9	19.1
Between corals	28.6	202.2	303.0	85.9	93.9	11.7

Also shown are comparisons of the distributions between locations of the two coral families.

Table 4
Mean and standard deviation values of six environmental variables (depth (m), slope (deg), temperature (°C), current (cm s^{-1}), chlorophyll *a* concentration (mg m^{-3}) and substrate (φ)) in the ACM study area for: the entire study area (Global), Paragorgiidae locations and Primnoidae locations

Environmental factor	Depth	Slope	Temperature	Current	Chlorophyll *a* concentration	Substrate
Global mean±SD	125.2±97.7 ($N = 13466$)	0.2±0.3 ($N = 13466$)	5.8±1.9 ($N = 16491$)	12.9±17.1 ($N = 37774$)	1.5±1.3 ($N = 20023$)	1.3±1.9
Paragorgiidae mean±SD	263.8±140.3 ($N = 53$)	0.9±0.5 ($N = 53$)	6.7±1.8 ($N = 55$)	19.1±17.9 ($N = 62$)	1.2±0.7 ($N = 57$)	0.3±1.3
Primnoidae mean±SD	199.6±111.3 ($N = 74$)	0.5±0.4 ($N = 74$)	6.5±1.5 ($N = 79$)	26.7±17.6 ($N = 81$)	1.3±0.4 ($N = 81$)	0.5±1.3

Global mean and SD are calculated for the gridded data.

in all categories of substrate, while Paragorgiidae were located in habitats with pebbles, very coarse sand, coarse sand, medium or fine sand and silt.

At the locations of Paragorgiidae, there were significant correlations between depth and temperature ($r = 0.141$) and chlorophyll *a* concentration ($r = 0.279$) (in both cases, $r_{crit} = 0.139$, $p < 0.05$, $N = 184$). Thus, while the distribution of these corals with respect temperature and chlorophyll *a* concentration may reflect their depth of occurrence, the distributions relative to slope and current do not. At the locations of Primnoidae, there were significant correlations between depth and slope ($r = 0.137$) and chlorophyll *a* concentration ($r = 0.155$) (in both cases, $r_{crit} = 0.062$, $p < 0.05$, $N = 1164$), and, thus, the coral distribution relative to these variables could be confounded by depth of occurrence. The distributions relative to all other environmental variables are independent of depth.

3.3. 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 0.2° (Table 4). Consequently, >80% of the study area had slopes between 0° and 0.3° (Fig. 5a). Mean bottom temperature for this study area was 5.8 °C (Table 4), with 35% between 5.1 and 7.0 °C (Fig. 5b). Bottom circulation was also influenced by the presence of deep channels, and currents ranged between 0 and 30 cm s^{-1} in 87% of the study area (Fig. 5c). Chlorophyll *a* concentration ranged from 0 to 13.0 mg m^{-3}, with concentrations between 0 and 3.0 mg m^{-3} in 90% of the area (Fig. 5d). The highest chlorophyll *a* concentrations were found along the coast in the Bay of Fundy and decreased towards the open ocean. Small pockets of higher concentrations occurred around Georges Bank, most likely resulting from local upwellings. Only 6% of the study area contained harder substrates, such as granules or pebbles (Fig. 5e). Although there are known bedrock outcrops, mainly along the walls of channels and gullies, these would not have been detected, because of the coarse resolution of the data.

3.4. Coral distribution at the ACM site

For both Paragorgiidae and Primnoidae, all environmental parameters in locations where coral occurred were significantly different from the values

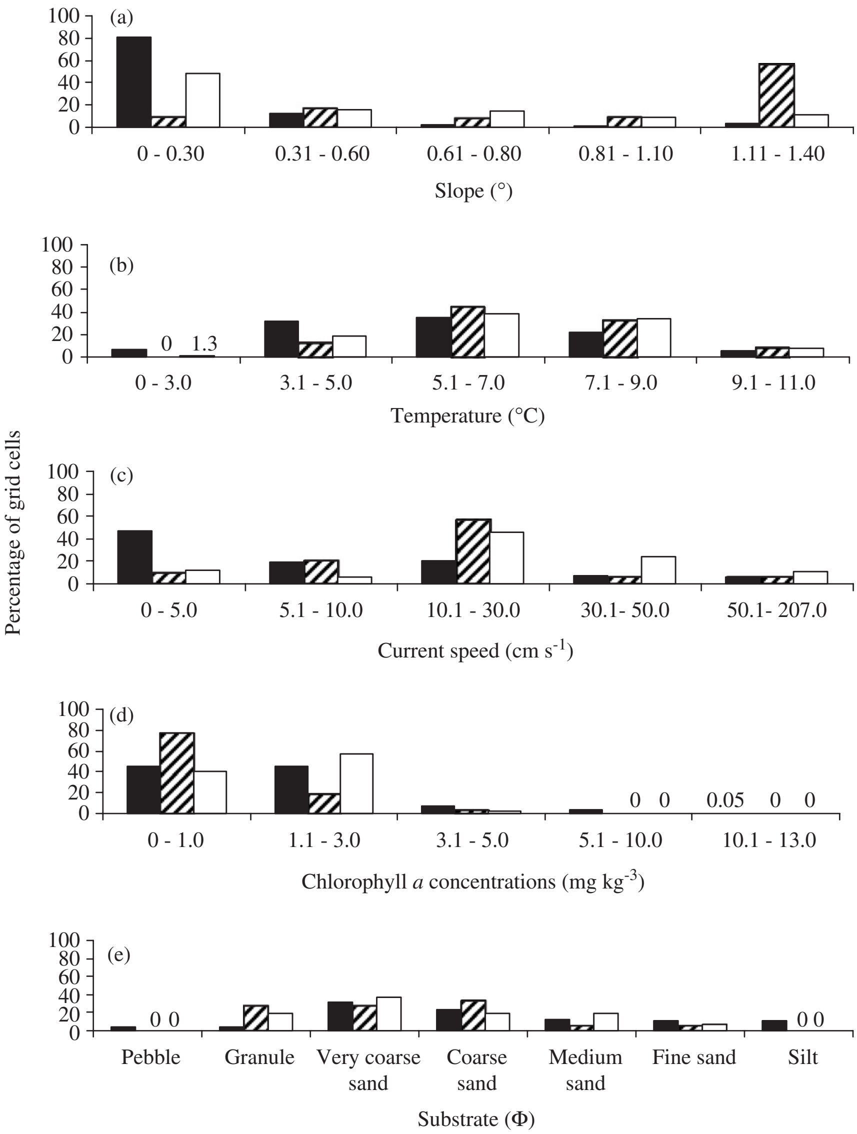

Fig. 5. Distribution of five oceanographic variables across the entire ACM study area as well as in locations of Paragorgiidae (PA) and Primnoidae (PR) for (a) slope (PA: $N = 62$, PR: $N = 82$), (b) bottom temperature (PA: $N = 55$, PR: $N = 79$), (c) bottom current (PA: $N = 62$, PR: $N = 81$), (d) surface chlorophyll *a* concentration (PA: $N = 57$, PR: $N = 81$) and (e) substrate (PA: $N = 23$, PR: $N = 57$).

of these parameters in the entire study area ($p < 0.05$) (Table 5). Also, all environmental parameters varied between locations of the two families, except temperature (Table 5). Most locations containing Paragorgiidae (51%) were found at depths between 300 and 500 m, while most Primnoidae locations (61%) were found in shallower waters, <200 m (Figs. 2a, b and 3). For Paragorgiidae, 57% of locations were in areas with slopes between 1.1° and 1.4°, and although Primnoidae were found in locations with a wide range of slopes, many (49%) were in locations with slopes ranging from 0° to 0.3° (Fig. 5a). As in the PCM study area, these two coral families were found mainly at temperatures >5 °C. While the mean temperature for the total study area was 5.8 °C, mean temperatures in Paragorgiidae and Primnoidae locations were 6.7 and 6.5 °C, respectively (Table 4). Fewer than 15% of Paragorgiidae and ~20% of Primnoidae locations had temperatures <5.0 °C (Fig. 5b). Both Paragorgiidae (56%) and Primnoidae (46%) were found primarily in regions

Table 5
χ^2 tests comparing the observed distributions of six environmental factors (depth (m), slope (deg), temperature (°C), current ($cm\,s^{-1}$), chlorophyll *a* concentration ($mg\,m^{-3}$) and substrate (φ)) in locations with Paragorgiidae and Primnoidae to those expected based on the distributions of variables across the entire ACM study area

Environmental factor	Depth	Slope	Temperature	Current	Chlorophyll *a* concentration	Substrate
χ^2 critical (df)	9.8 (4)	9.8 (4)	9.8 (4)	9.8 (4)	7.8 (3)	12.6 (6)
Paragorgiidae	525.5	1038.5	30.4	93.2	42.5	42.8
Primnoidae	80.8	163.4	18.5	112.5	9.2	46.6
Between corals	78.7	228.7	5.2	54.0	57.8	48.0

Also shown are comparisons of the distributions between locations of the two coral families.

with currents between 10 and 30 $cm\,s^{-1}$ (Fig. 5c). These coral families also tend to be present in areas of low chlorophyll *a* concentrations, with 77% of Paragorgiidae at 0–1 $mg\,m^{-3}$ and 57% of Primnoidae at 1.1–3.0 $mg\,m^{-3}$ chlorophyll *a* (Fig. 5d). Both Paragorgiidae and Primnoidae were found mainly in areas with coarse substrate, but also in fine sand or silt environments (Fig. 5e).

At the locations of Paragorgiidae, there were significant correlations between depth and slope ($r = 0.344$), temperature ($r = -0.211$), current speed ($r = -0.569$), and chlorophyll *a* concentration ($r = -0.511$) (in all cases, $r_{crit} = 0.139$, $p<0.05$, $N = 62$). The distribution of this coral family relative to slope and chlorophyll *a* concentration may reflect their depth of occurrence, as it changes monotonically with these two variables. However, the distribution relative to current and temperature is not confounded by depth. At the locations of Primnoidae, there were significant correlations between depth and all other variables: slope ($r = 0.310$), temperature ($r = -0.422$), current speed ($r = -0.594$) and chlorophyll *a* concentration ($r = -0.490$) (in all cases, $r_{crit} = 0.217$, $p<0.05$, $N = 82$). Since this family was most abundant at intermediate depths, its distribution relative to temperature and current could be confounded by depth. However, the distributions with respect to slope and chlorophyll *a* are not.

4. Discussion

On both the northeast Pacific and northwest Atlantic, 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 using point-source data have shown that deep-water corals occur 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 clear because of the coarse resolution of the available data, which would have obscured smaller areas of hard substrate. Unfortunately, current geological maps are of little use for studies such as ours, since substrate has been characterized patchily based on point estimates of average grain size. Presently, unpublished data sets collected by geological surveys (e.g. US Geological Survey) can be interpolated accurately only on scales of $9\times9\,km^2$, and are of limited spatial coverage (Institute of Arctic and Alpine Research, Boulder, CO, USA). Typically, gorgonian corals occur on isolated cobbles, boulders and rocky outcrops scattered within areas covered by sand or mud (e.g. Mortensen and Buhl-Mortensen, 2004) and would not be identified at these coarser resolutions.

Bottom topography (quantified as slope in our study) can be used as a proxy for locations with hard substrate, since areas of pronounced topographic relief will exhibit low sedimentation rates (Genin et al., 1986; Freiwald et al., 1999; Herring, 2002). In both study areas, Paragorgiidae were located primarily in areas with greater than average slopes, while Primnoidae were distributed more evenly throughout a wider range of slopes. Areas of pronounced vertical relief, such as seamounts and canyons, are often associated with the presence of low sediment deposition, hard substrate, and strong currents (Genin et al., 1986; Herring, 2002). Thus, primarily because of the availability of hard substrate, which is relatively rare in the deep sea, areas of high vertical relief harbour abundant communities of epibenthic, suspension-feeding organisms, including deep-water corals (Herring, 2002). For example, while the scleractinian *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, the strong currents associated with these locations would 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 torsion in the basal stem (Tunnicliffe, 1983; Reed, 2002). The resulting orientation of the corals may then modify the local current environment, thereby creating favourable habitat for associated species by providing protection from high currents (Etnoyer and Morgan, 2003).

This 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 $-1\,^{\circ}\mathrm{C}$ in Alaska (*Gersemia* spp.) to $12\,^{\circ}\mathrm{C}$ 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 primarily between 5.1 and $9.0\,^{\circ}\mathrm{C}$. The number of coral locations diminishes outside this range.

Coral locations are predominantly in areas of low concentrations ($<3.0\,\mathrm{mg\,m^{-3}}$) of chlorophyll *a*, as most deep-sea locations fall under oligotrophic areas. Isotopic studies of four 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-water coral (Griffin and Druffel, 1989; Druffel et al., 1995). According to Druffel et al. (1995), the main source of nutrition for many deep-water organisms is surface-derived organic-rich particles. Thus, if there were adequate lateral advection of POC these organisms, including corals, would not need to be located beneath areas of high primary productivity to receive adequate levels of nutrition (Smith and Kaufmann, 1999).

Habitat characteristics varied between Paragorgiidae and Primnoidae, except for substrate in the PCM and temperature in the ACM. In both study areas, Paragorgiidae were located more often in steeply sloping areas than Primnoidae. Paragorgiidae were also found in slower currents than Primnoidae. According to Tendal (1992), Paragorgiidae prefer current regimes with maximum velocities of $60\,\mathrm{cm\,s^{-1}}$. Although mostly present in areas with current speeds between 0 and $30.0\,\mathrm{cm\,s^{-1}}$, Primnoidae were also present in locations with higher currents more often than Paragorgiidae. Most previous studies measured current qualitatively (Frederiksen et al., 1992; Rogers, 1999; Freiwald et al., 2002), but dye-releases in Knight Inlet on the western Canadian coast, showed that Gorgonian fans experienced flows of $\sim 80\,\mathrm{cm\,s^{-1}}$ (Tunnicliffe, 1983). It is likely that the shape and larger size of Paragorgiidae make this family more vulnerable to being toppled over than Primnoidae, and at the same time more efficient at capturing particles in slower currents. 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 $11.0\,^{\circ}\mathrm{C}$, but, because of the lack of warm-water influence (Gulf Stream in the ACM), mean temperature was lower in the PCM study site. Warm water is found in shallow areas along the coast at both sites. Also similar to the ACM study area, bottom current velocities in $>45\%$ of the PCM study area were $<5\,\mathrm{cm\,s^{-1}}$. Mean chlorophyll *a* concentration in the PCM study area was lower than it was in the ACM study area, but the range was considerably larger.

Coral distribution patterns were similar between study areas with respect to all the environmental variables. In both areas, the slope in coral locations for both families was greater than the average within the study area. Both families were found mainly at low chlorophyll *a* concentrations in both study areas. In both study areas, both families were located in habitats with above-average temperatures and currents.

Several recent international fora (e.g., the NOAA funded Symposium on the Effects of Fishing Activities on Benthic Habitats (McDonough and Puglise, 2003) have recommended that mapping of coral locations is an immediate priority (see also Puglise et al., 2005). Presumably, such maps should provide the greatest spatial coverage possible. In this study, we attempted to map most of the collated data on coral location on sections of the North American continental margin. The geographic range of coral locations in our study, however, is by no means 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. We also have superimposed the synoptic oceanographic data with the greatest coverage possible to draw general patterns in the environmental characteristics of coral habitat. Unfortunately, the available data suffer by resolutions that may be too coarse to draw such patterns on these great spatial scales. This is particularly true for data on substrate. We suggest that greater coverage and higher resolution oceanographic data are needed to increase our understanding of deep-water coral habitat on finer spatial scales (metres vs. 100 s of kilometres).

Our study extends in several ways previous studies that have described distributions of deep-water corals on both the west and east coasts of North America (e.g. Cimberg et al. (1981), Tendal (1992), MacIsaac et al. (2001) and Mortensen and Buhl-Mortensen (2004)). We significantly expanded both the geographic range (from $<5^{\circ}$ latitude to 10's of degrees latitude and over two oceans) and the spatial scales (from km to 100–1000 km), and examined simultaneously a larger number of environmental variables than most previous studies. Additionally, we included both recently collected coral records, as well as historical locations. Consequently, our study described relationships between coral occurrence and habitat characteristics for the broadest distributional patterns of deep-water gorgonian corals currently known, using the most comprehensive data sets available. This comprehensive approach can provide the basis for further, and more detailed, examination of the limiting environmental factors to the occurrence of deep-water corals, and thus more accurately predict their potential habitats. Although we did not attempt to predict coral locations in this study, the large-scale patterns that we described can be used to erect hypotheses on the relative importance of different environmental factors in regulating the occurrence of deep-water coral on shelf/slope spatial scales. Such hypotheses can then be tested using predictive models, which in turn can be ground-truthed in future research explorations. To more effectively target such explorations, a method is needed to identify potential suitable habitat for these deep-water organisms.

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References

Alidina, H., Roff, J.C., 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.

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

Buhl-Mortensen, L., Mortensen, P.B., 2004. Crustaceans associated with the deep-water gorgonian corals *Paragorgia arborea* (L., 1758) and *Primnoa resedaeformis* (Gunn., 1763). Journal of Natural History 38 (10), 1233–1247.

Cimberg, R.L., Gerrodette, T., Muzik, K., 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, pp. 207–308.

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

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

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, Canada, unpublished.

Etnoyer, P., 2003. B2B 1.1: information for conservation planning—Baja California to the Bering Sea. Marine Conservation Biology Institute, CD-ROM.

Etnoyer, P., Morgan, L., 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, USA.

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

Freiwald, A., 2002. Reef-forming cold-water corals. In: Wefer, G., Billett, D., Hebbeln, D., Jorgensen, B.B., Schluter, M., Van Weering, T. (Eds.), Ocean Margin Systems. Springer, Berlin, Heidelberg, pp. 365–385.

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

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

Gage, J.D., Tyler, P.A., 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, unpublished.

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

Gordon Jr., D.C., Fenton, D.G., 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, Nova Scotia, Canada.

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

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

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

Herring, P., 2002. The Biology of the Deep Ocean. Oxford University Press, Toronto, Canada.

Krieger, K.J., Wing, B.L., 2002. Megafauna associations with deep-water 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., Bourbonnais, C., Kenchington, E., Gordon Jr., D., Gass, S., 2001. Observations on the occurrence and habitat preference of corals in Atlantic Canada. In: Willison, J.H.M., Hall, J., Gass, S.E., Kenchington, E.L.R., Butler, M., Doherty, P. (Eds.), Proceedings of the First International Symposium on Deep-Sea Corals. July 30–August 3, 2000. Ecology Action Center and the Nova Scotia Museum, Nova Scotia, Canada, pp. 58–75.

McDonough, J.J., Puglise, K.A., 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.

Metaxas, A., Davis, J.E., 2005. Megafauna associated with assemblages of deep-water corals on the Scotian Slope. Journal of the Marine Biological Association of the United Kingdom 85, 1381–1390.

Moore, D.H., Bullis, H.R., 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., Buhl-Mortensen, L., 2004. Distribution of deep-water gorgonian corals in relation to benthic habitat features in the Northeast Channel (Atlantic Canada). Marine Biology 144, 1223–1238.

Mortensen, P.B., Hovland, M.T., Fossa, J.H., Furevik, D.M., 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., Potter, P.E., Siever, R., 1972. Sand and sandstone. Springer, New York.

Puglise, K.A., Brock, R.J., McDonough, J.J., 2005. Identifying critical information needs and developing institutional partnerships to further the understanding of Atlantic deep-sea coral ecosystems. In: Freiwald, A., Roberts, J.M. (Eds.), Cold-water Corals and Ecosystems. Springer, Berlin, Heidelberg, pp. 1129–1140.

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

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.

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

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.

Watling, L., Auster, P.J., 2005. Distribution of deep-water Alcyonacea off the Northeast coast of the United States. In: Freiwald, A., Roberts, J.M. (Eds.), Cold-Water Corals and Ecosystems. Springer, Berlin, Heidelberg, pp. 279–296.

Zar, J.H., 1999. Biostatistical Analysis. Prentice-Hall, New Jersey.