



Distributional patterns of deep-sea coral assemblages in three submarine canyons off Newfoundland, Canada

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ABSTRACT: Deep-sea corals are fragile and long-lived species that provide important habitat for a variety of taxa. The rarity of *in situ* observations in deep waters off Newfoundland, Canada, motivated the first extensive deep-sea research cruise to that region in 2007. We conducted 7 dives in 3 canyons (Haddock Channel, Halibut Channel, and Desbarres Canyon) with ROPOS (Remotely Operated Platform for Ocean Science). Over 160 000 coral colonies were enumerated and, of the 28 species found, *Acanella arbuscula*, *Pennatula* spp., and *Flabellum* spp. were most frequently observed. The largest coral observed was *Keratoisis grayi* at over 2 m in height. Corals spanned the entire depth range sampled (351 to 2245 m) and inhabited all bottom types surveyed, but boulder and cobble habitats were most species-rich. Assemblages differed significantly with depth class and bottom type. The unique assemblage at outcrops was strongly driven by the presence of *Desmophyllum dianthus*. *Keratoisis grayi*, *D. dianthus*, and *Anthomastus* spp. were largely absent in mud-sand habitats. Sea pen meadows covered large tracts of muddy seafloor spanning >1 km. *Acanella arbuscula* and *Flabellum* spp. characterised large coral fields with abundant corals but relatively low species richness. These results highlight not only the importance of hard structure in determining patterns of coral distributions, abundances, and assemblages, but also the need to focus conservation efforts on a variety of habitats to ensure protection for the full suite of deep-sea coral species.

KEY WORDS: Deep-sea corals · Assemblage patterns · Abundance · Conservation

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INTRODUCTION

Deep-sea corals are long lived, slow growing, and highly vulnerable to fishing gear damage (Roberts et al. 2006, 2009, Edinger et al. 2007a, Althaus et al. 2009, Roark et al. 2009, Sherwood & Edinger 2009), climate change, and ocean acidification (Turley et al. 2007, Guinotte & Fabry 2008, Hall-Spencer et al. 2008). Corals create feeding habitats, shelter, surfaces for attachment, and simple structural complex-

ity for other organisms including fish (Husebo et al. 2002, Ross & Quattrini 2007, Buhl-Mortensen et al. 2010), echinoderms (Krieger & Wing 2002), polychaetes (Schembri et al. 2007, Fiege & Barnich 2009), crustaceans (Krieger & Wing 2002), and other invertebrates (Krieger & Wing 2002, Roberts & Hirshfield 2004). Deep-sea coral habitats often have greater species diversity than surrounding areas and host unique assemblages (Henry & Roberts 2007, Ross & Quattrini 2007). These characteristics underscore the

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importance of understanding distribution patterns of deep-sea corals for planning appropriate ocean conservation measures.

The rapid growth of knowledge on deep-sea coral distributions has focused largely on specific regions or sites (Roberts et al. 2005) and associated research tends to concentrate on scleractinian coral reefs (Fossa et al. 2002, Cordes et al. 2008). Coral research in the deep waters off Newfoundland and Labrador is still in its infancy, but substantial knowledge and data began to accumulate from these previously unknown deep waters when dedicated deep-sea coral research began in this region in 2003 (e.g. Edinger et al. 2007a,b, Wareham & Edinger 2007, Gilkinson & Edinger 2009, Murillo et al. 2010). These biogeographic and ecological studies concentrated on results from broad-scale trawl surveys and/or bycatch from fisheries observer programs. Video studies in 2002 examined deep-sea corals on the slope of the Southwest Grand Banks, but covered only a few km of bottom to a maximum depth of 500 m (Mortensen et al. 2006a,b). Therefore, little information is available on deep-sea coral distributions and patterns on small spatial scales for this region and *in situ* observations of deep-sea corals are rare. Fine-scale, *in situ* observations would allow better understanding of local patterns of distribution, changes in abundance, assemblages, associations with other taxa, and impacts of deep-sea fishing.

Like most marine organisms, deep-sea corals have preferred depth distributions and habitat characteristics. Temperature, salinity, substrate, currents, and slope all contribute to distributional trends and levels of abundance (Roberts et al. 2009). For example, in Atlantic Canada, Mortensen et al. (2006b) found *Flabellum* spp. on primarily muddy substratum and most coral species occurred between 4.5 and 6.0°C. In a submarine canyon off Nova Scotia, *Keratoisis grayi* and *Duva florida* were associated with steep topography and semi-consolidated mudstone (Mortensen & Buhl-Mortensen 2005).

Most previous deep-sea coral studies focused on individual distributions of species and few examined patterns in composition among and between coral communities and species' co-occurrences. Understanding these facets of coral ecology would allow development of more appropriate conservation actions that recognize the importance of unique and/or

diverse communities above and beyond individual species.

We present here the results of the first extensive, *in situ* study of deep-sea corals on the Newfoundland continental slope, and describe the distributions and abundances of the observed species, assemblages, and species diversity with respect to bottom type, depth, and study area. We increase the known distribution, depth range, and abundance concentrations for multiple species and genera, and conclude by describing how this new knowledge may facilitate deep-sea conservation planning.

MATERIALS AND METHODS

Video surveys

We focused on 3 submarine canyons on the slopes of the Grand Banks south of Newfoundland: Halibut Channel, Haddock Channel, and Desbarres Canyon (Fig. 1). A small bank separates Halibut Channel and Haddock Channel, which are situated ~110 and 175 km east of Laurentian Channel, and ~150 and 200 km northwest of Desbarres Canyon, respectively. The cold Labrador Current from the north and the warm Gulf Stream from the south both influence the study area. Temperature regimes were similar in the 3 canyons, with an average bottom temperature of ~5°C during relatively shallow dives (<1100 m) and ~4.4°C during relatively deep dives (>1100 m). Bottom current measurements taken in Haddock Chan-

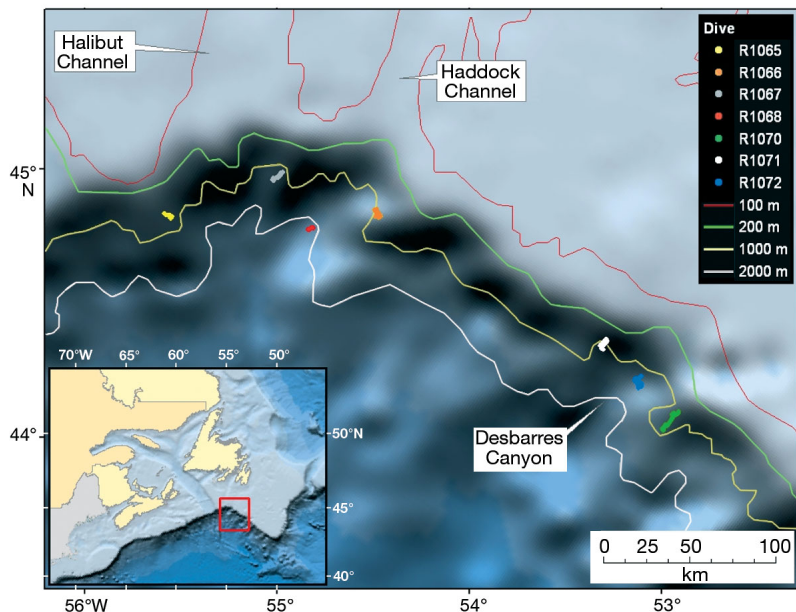


Fig. 1. Location of ROV dive sites during a 2007 cruise off Newfoundland, Canada

nel (~700 m) indicated relatively slow current speeds (5 to 10 cm s⁻¹), compared to previously studied coral habitats on the slope of the Scotian Shelf (e.g. Northeast Channel, The Gully, Stone Fence) (Zedel & Fowler 2009). Data from Fisheries and Oceans Canada surveys and bycatch records suggested species-rich and abundant corals at these 3 sites.

The remotely operated vehicle (ROV), ROPOS (Remotely Operated Platform for Ocean Science) (CSSF 2010), performed video surveys from CCGS 'Hudson' during 7 dives between 16 and 24 July 2007 (Table 1). Lasers on the ROV placed 10 cm apart indicated scale. Depth, date, time, altitude (distance above bottom), temperature, and position were logged at 1-s intervals, though sporadic problems with the logger resulted in several long periods with no temperature data.

Based on known distributions of corals and bathymetry from previous work, we planned 1-km transects every 200 m of depth along depth contours between 2200 and 500 m and along contours every 100 m in waters shallower than 500 m (Fig. 1). We standardized transects by keeping the ROV as close to the bottom as possible, maintaining a constant slow speed (~0.2 to 0.3 m s⁻¹) while tilting the camera down slightly on a wide-angle view in order to image the seafloor and water column directly above. Between pre-selected transects, we explored the area with ROPOS, capturing still images and video of interesting features, and collecting physical specimens to validate visual identification.

Video processing

Using the program ClassAct Mapper (Benjamin 2007), we continuously recorded geo-referenced data describing bottom type, ROV behaviour, and corals. All corals were identified to the lowest possible taxonomic level and the colony height and diameter of

Table 1. ROV cruise dives off Newfoundland in 2007, associated depths, time on bottom, and distance covered

Dive	Date	Depth range (m)	Time on bottom (h)	Distance (km)
R1065	16–17 July	606–1015	12.6	10.7
R1066	17–18 July	493–1020	16.0	15.8
R1067	18–19 July	395–996	10.2	13.4
R1068	19 July	1990–2245	4.5	5.9
R1070	21 July	351–940	15.5	23.6
R1071	22–23 July	353–1174	12.8	16.9
R1072	23–24 July	1116–1900	18.8	19.0
Total			90.4	105.3

relatively large corals (antipatharians, Isididae, *Paramuricea* spp., and other gorgonians) were measured to the nearest 5 cm using the lasers for scale.

We characterized bottom type every second by primary (most abundant) substrate and secondary (next most abundant) substrate, with optional additional comments. We categorized bottom type as (1) outcrop (vertically exposed bedrock and consolidated Quaternary sediment), (2) boulder (>25 cm), (3) cobble (5–25 cm), (4) gravel (0.2–5 cm), or (5) mud-sand (fine-grain) sediments (Thrush et al. 2001). For example, a bottom type description might consist of mud-sand as the primary bottom type and gravel as the secondary bottom type, with 'scattered boulders' as an additional comment.

ROV behaviour was categorized at 1 s intervals as transect-mode, benthic-mode, sampling, too high, stationary viewing, panning, or view obstruction. 'Transect-mode' was defined as any portion of the video when the ROV followed the prescribed methodology for transects (described above), regardless of whether the transect was planned. 'Benthic-mode' described periods when the ROV moved forward with a clear view of the seafloor and the camera pointed directly toward the sediment. 'Sampling' denoted any sections of the video during which sampling occurred and 'stationary-viewing' denoted periods when we stopped the ROV to view a feature of interest. 'Panning' described situations when the ROV moved forward, but with the camera at an inconsistent angle or position. 'View obstruction' occurred when other sampling gear (e.g. pushcore handles) obstructed part of the camera view.

Data analysis

We characterized survey sites according to depth, duration, and distance surveyed and used transect segments to describe bottom type. We illustrated the overall characteristics of the habitats surveyed by plotting bottom type versus depth for each second of data when the ROV moved forward with a clear view of the seafloor (i.e. transect-mode, benthic-mode, and panning). All dead corals in the video were noted, but because live coral communities were the focus of this study, we removed dead corals from the analyses.

Species composition and occurrence

We described the overall distribution and composition of corals by calculating the number of colonies

and their sizes for each species (or species group) and by examining occurrence of each species in relation to depth.

For more detailed analyses of patterns, we focused on those species identified to the lowest possible taxonomic level. For example, we excluded gorgonians that could not be identified to a unique genus from further analysis. We could easily distinguish one species of *Pennatula* (*Pennatula* sp. 1) during video processing, but combined all other *Pennatula* into *Pennatula* spp., so that the abundant 'unknown *Pennatula*' could be included in analyses. For the same reason, we combined all *Flabellum* into the single category *Flabellum* spp.

We assigned a single bottom type to each 1-s observation based on the premise that hard structure can influence the coral assemblage regardless of its prevalence. Therefore, bottom type was categorized as the largest sediment structure for each 1-s observation. For example, if a given observation included the bottom type categories of cobble (primary), boulders (secondary), and scattered gravel (comments), we assigned it the bottom type 'boulders'. We found one large fishing net in an otherwise muddy habitat that created attachment structure for several coral species, so we removed this portion of the data from analyses involving bottom type. We then examined coral occurrence in relation to bottom type and depth.

We split video data collected in transect mode into a series of 10-m segments (samples). For each sample, we defined bottom type as the largest structure encountered during the 10-m segment and depth as the mean depth recorded within the segment. Coral

abundance was calculated as the number of colonies per sample and this value was used to investigate maximum abundance for each species (or species group).

We used the 10-m segments to examine patterns in coral richness by calculating species richness for each sample and comparing among dive locations, depth categories, and bottom types. We defined depth categories based on the distribution of corals and the number of samples in each category: (1) 300–800 m, (2) 800–1300 m, and (3) 1300–2300 m. Patterns in richness among bottom types were compared graphically using box-plots.

Assemblages

We determined patterns in assemblages within the samples using Primer 6.0 (Clarke & Gorley 2006) analyses of square-root transformed data to reduce the influence of abundant species. A Bray-Curtis similarity matrix was used to conduct a 2-way analysis of similarities (ANOSIM) test for differences in assemblages between and within samples. We examined species similarities (and dissimilarities) within and between depth classes and bottom types in SIMPER (similarity percentages).

We examined similarities between species by creating a Bray-Curtis species similarity matrix of standardized samples and species that contributed at least 50% to a sample. We then produced a multi-dimensional scaling (MDS) plot and dendrogram (using group average clustering) based on these similarities.

Table 2. Number of 10-m transect segments in each dive, in relation to depth categories and bottom types

Depth (m)	Bottom type	ROPOS dive number						Total	
		R1065	R1066	R1067	R1068	R1070	R1071		R1072
300–800	Mud–sand	159	192	14	–	490	371	–	1226
	Gravel	–	35	8	–	56	9	–	108
	Cobble	98	345	320	–	223	54	–	1040
	Boulders	30	75	124	–	7	17	–	253
	Outcrop	–	–	1	–	–	–	–	1
800–1300	Mud–sand	200	203	103	–	507	289	246	1548
	Gravel	2	–	–	–	–	–	–	2
	Cobble	14	–	1	–	–	–	–	15
	Boulders	4	–	–	–	–	–	3	7
	Outcrop	–	–	2	–	–	–	–	2
1300–2300	Mud–sand	–	–	–	101	–	–	640	741
	Gravel	–	–	–	69	–	–	6	75
	Cobble	–	–	–	7	–	–	–	7
	Outcrop	–	–	–	–	–	–	6	6
Total		507	850	573	177	1283	740	901	5031

RESULTS

In total, we recorded 90 h of bottom video footage over the 7 dives, covering a distance of ~105 km (Table 1) and a depth range of 351 to 2245 m. We recorded 5031 samples (10-m transect segments) over a variety of habitats and depth categories (Table 2). Most transect segments were over mud-sand habitats (Fig. 2) within the 300–800 m depth category. Boulders were rare in deep waters and outcrops were rare over the entire depth range. Dive R1070 produced the most samples (n = 901).

Species composition and occurrence

We recorded over 160 000 coral colonies, comprising at least 28 distinct species (Table 3). Although we identified *Flabellum macandrewi*, *F. alabastrum*, and *F. angulare* from specimens collected during the cruise, these species were usually grouped as *Flabellum* spp. in the video analysis. The most abundant species were *Pennatula* sp. 2 (possibly *P. aculata*), *Acanella arbuscula*, *Flabellum* spp. and *Acanthogorgia armata*. The maximum number of a single species observed in a 10-m segment was *Pennatula* spp. (622 colonies), followed by *Flabellum* spp. (300 individuals), and *Heteropolypus cf. insolitus* (123 colonies) (Table 4). Rare species included anti-patharians, *Lepidisis* sp., and *Paragorgia arborea*.

The tallest coral colony observed was a *Keratoisis grayi* colony measuring 215 cm in height. Although rare, anti-patharians were fairly large, one exceeding 60 cm in height. Of the 3 *Paragorgia arborea* observed, 2 were only ~5 cm in height, whereas the largest colony was only ~20 cm. The abundant corals *Acanella arbuscula* and *Acanthogorgia armata* both averaged almost 10 cm in height.

Many species spanned a wide depth range and appeared unrestricted by depth (Fig. 3). This pattern was especially true for many of the sea pens (e.g. *Protoptilum carpenteri*, *Anthoptilum grandiflorum*, and *Halipteris finmarch-*

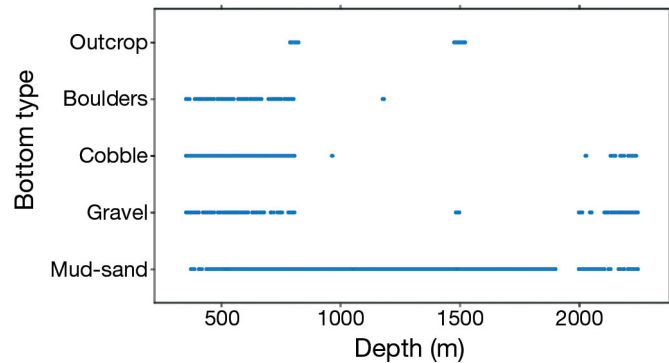


Fig. 2. Depth and sediment type surveyed off the Grand Banks, Newfoundland during the 2007 *in situ* survey. Each point: 1 s of video footage while the remotely operated vehicle moved forward with an unobstructed view of the seafloor

Table 3. Taxonomic composition, abundance, and heights of coral colonies found off the Grand Banks, Newfoundland during the 2007 *in situ* survey

Coral group	Species	Number observed	Max. / Av. height (cm)
Antipatharians	<i>Bathypathes patula</i>	1	15
	Schizopathidae n. gen. et n. sp.	2	>60 / 58
	Antipatharian (unknown)	1	50
Scleractinians	<i>Vaughanella</i> sp.	7	
	<i>Desmophyllum dianthus</i>	143	
	<i>Flabellum alabastrum</i>	6965	
	<i>Flabellum macandrewi</i>	320	
	<i>Flabellum</i> spp.	7894	
	<i>Javania cailleti</i>	4	
Gorgonians	Scleractinian (unknown)	5	
	<i>Keratoisis grayi</i>	5116	215 / 37
	<i>Lepidisis</i> sp.	1	30
	<i>Acanella arbuscula</i>	24334	30 / 9
	Isididae (unknown)	3	30 / 30
	<i>Paramuricea</i> spp.	32	45 / 15
	<i>Paragorgia arborea</i>	3	20 / 12
	<i>Radicipes gracilis</i>	212	
	<i>Chrysogorgia agassizii</i>	80	30 / 13
	<i>Acanthogorgia armata</i>	7688	51 / 8
Alcyonaceans	Gorgonian (unknown)	2	50 / 38
	<i>Anthomastus</i> spp.	3239	
	<i>Heteropolypus cf. insolitus</i>	4869	
	<i>Duva florida</i>	232	
	Neptheidae (unknown)	417	
Pennatulaceans	<i>Anthoptilum grandiflorum</i>	355	
	<i>Funiculina quadrangularis</i>	4694	
	<i>Halipteris finmarchica</i>	1681	
	<i>Kophobelemnon stelliferum</i>	1812	
	<i>Pennatula grandis</i>	6032	
	<i>Pennatula</i> sp. 1	152	
	<i>Pennatula</i> sp. 2	67752	
	<i>Pennatula</i> (unknown)	11350	
	<i>Protoptilum carpenteri</i>	3086	
	<i>Distichoptilum gracile</i>	665	
	<i>Umbellula</i> spp.	20	
	Pennatulacea (unknown)	2220	
Unknown	Coral (unknown)	11	

ica). The distribution of *Flabellum alabastrum* spanned nearly 1900 m (355 to 2244 m), resulting in the widest depth range of all coral species observed;

however *H. finmarchica* also spanned a considerable depth range (353 to 2217 m). Very few species were restricted to deep water, although *Chrysogorgia agassizii* was limited to depths >1997 m and the single colony of *Bathypathes patula* was found at 2242 m. In comparison, many more species were limited to the upper and middle slope, including all *Pennatula* spp. (<1204 m), *Keratoisis grayi* (<967 m), *Duva florida* (<906 m), and *Paragorgia arborea* (<800 m).

Table 4. Maximum abundance of corals, its depth and dive number in 10-m transect segments. Abundances with a maximum of 1 are not included

Coral group	Species	Maximum abundance	Depth (m)	Dive
Scleractinians	<i>Desmophyllum dianthus</i>	61	1506	R1072
	<i>Flabellum</i> spp.	300	380	R1070
Gorgonians	<i>Keratoisis grayi</i>	43	573	R1067
	<i>Acanella arbuscula</i>	77	639	R1065
	<i>Paramuricea</i> spp.	3	664	R1065
	<i>Radicipes gracilis</i>	31	1427	R1072
	<i>Chrysogorgia agassizii</i>	3	2243	R1068
	<i>Acanthogorgia armata</i>	36	540	R1066
Alcyonaceans	<i>Anthomastus</i> spp.	54	573	R1067
	<i>Heteropolypus cf. insolitus</i>	123	611	R1070
	<i>Duva florida</i>	35	406	R1070
Pennatulaceans	<i>Anthoptilum grandiflorum</i>	3	843	R1070
	<i>Funiculina quadrangularis</i>	17	930	R1070
	<i>Halipteris finmarchica</i>	12	437	R1071
	<i>Kophobelemnion stelliferum</i>	13	585	R1071
	<i>Pennatula</i> sp. 1	7	912	R1071
	<i>Pennatula</i> spp.	622	835	R1071
	<i>Protoptilum carpenteri</i>	9	993	R1071
	<i>Distichoptilum gracile</i>	4	1323	R1072
	<i>Distichoptilum gracile</i>	4	1294	R1072

Most corals occurred in a variety of bottom types, but several appeared to be restricted in relation to bottom type (Fig. 4). *Javania cailleti*, *Desmophyllum dianthus*, *Paragorgia arborea*, and Schizopathidae n. gen. et n. sp. occurred only in areas with large, hard substratum. *Paramuricea* spp., *Keratoisis grayi*, and *Anthomastus* spp. were mostly limited to areas with hard substratum, but that bottom type ranged in size and included small substrate, such as gravel. In comparison, *Distichoptilum gracile*, *Umbellula* spp., *Bathypathes patula*, and *Kophobelemnion*

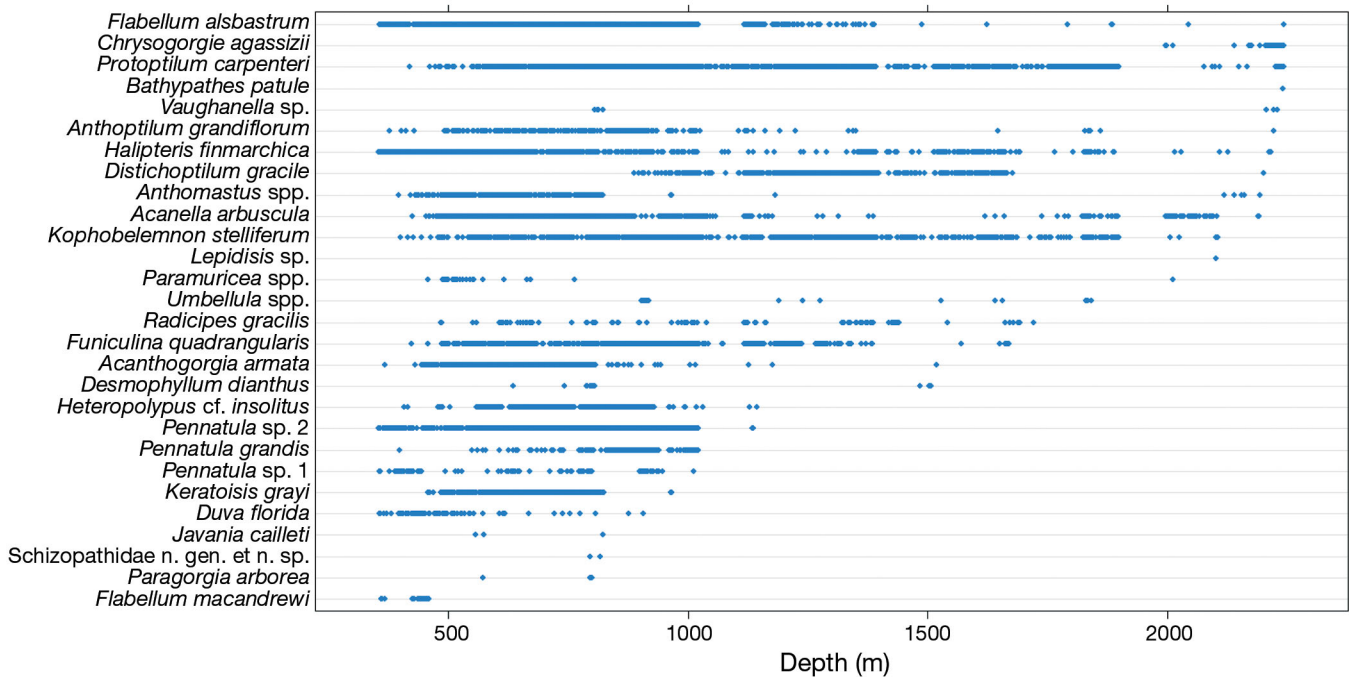


Fig. 3. Depth distributions of coral species observed off the Grand Banks of Newfoundland during the 2007 *in situ* survey. Each point: single coral observation

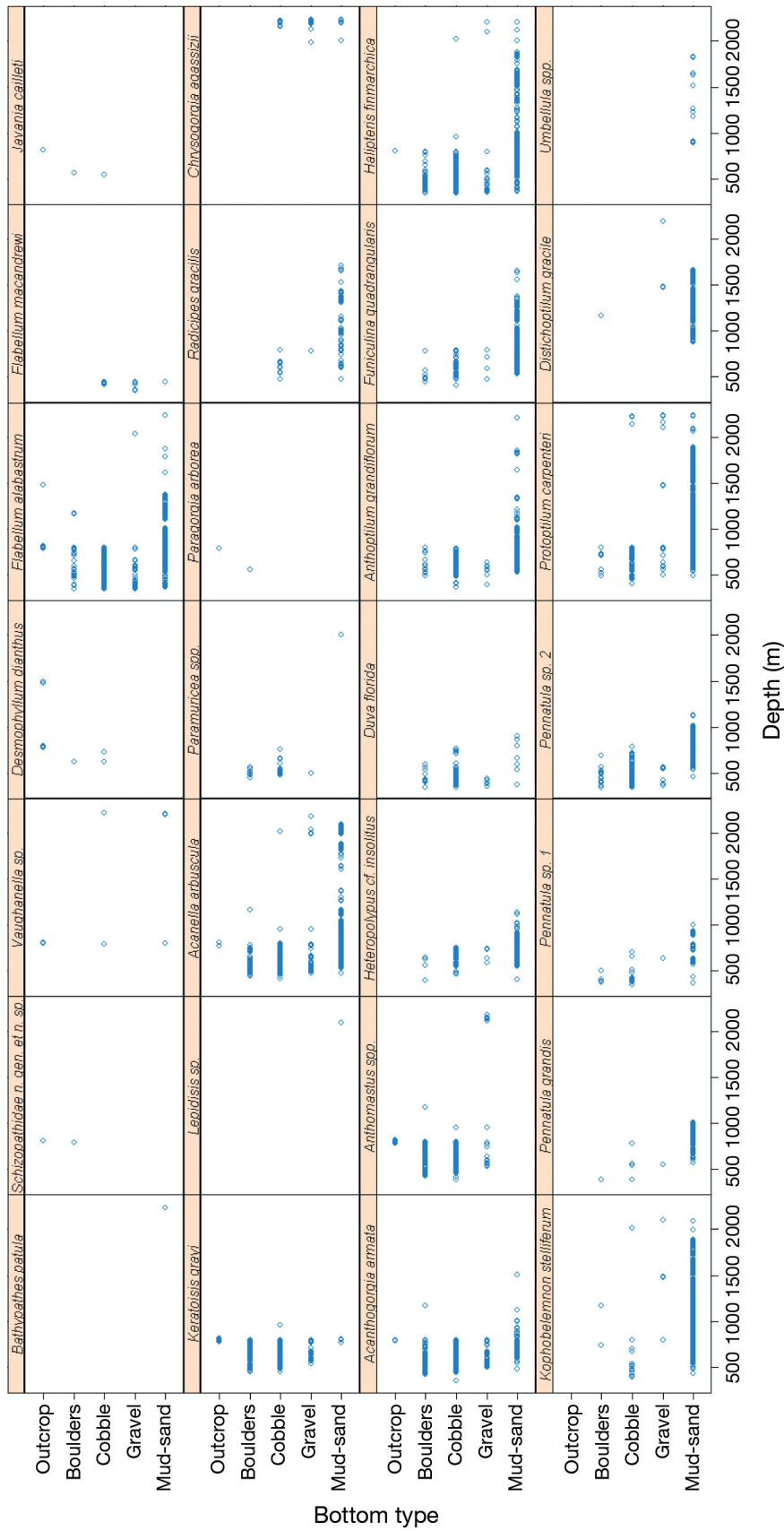


Fig. 4. Depth and sediment type of habitats where corals were observed off the Grand Banks of Newfoundland during the 2007 *in situ* survey. Each point: single coral observation

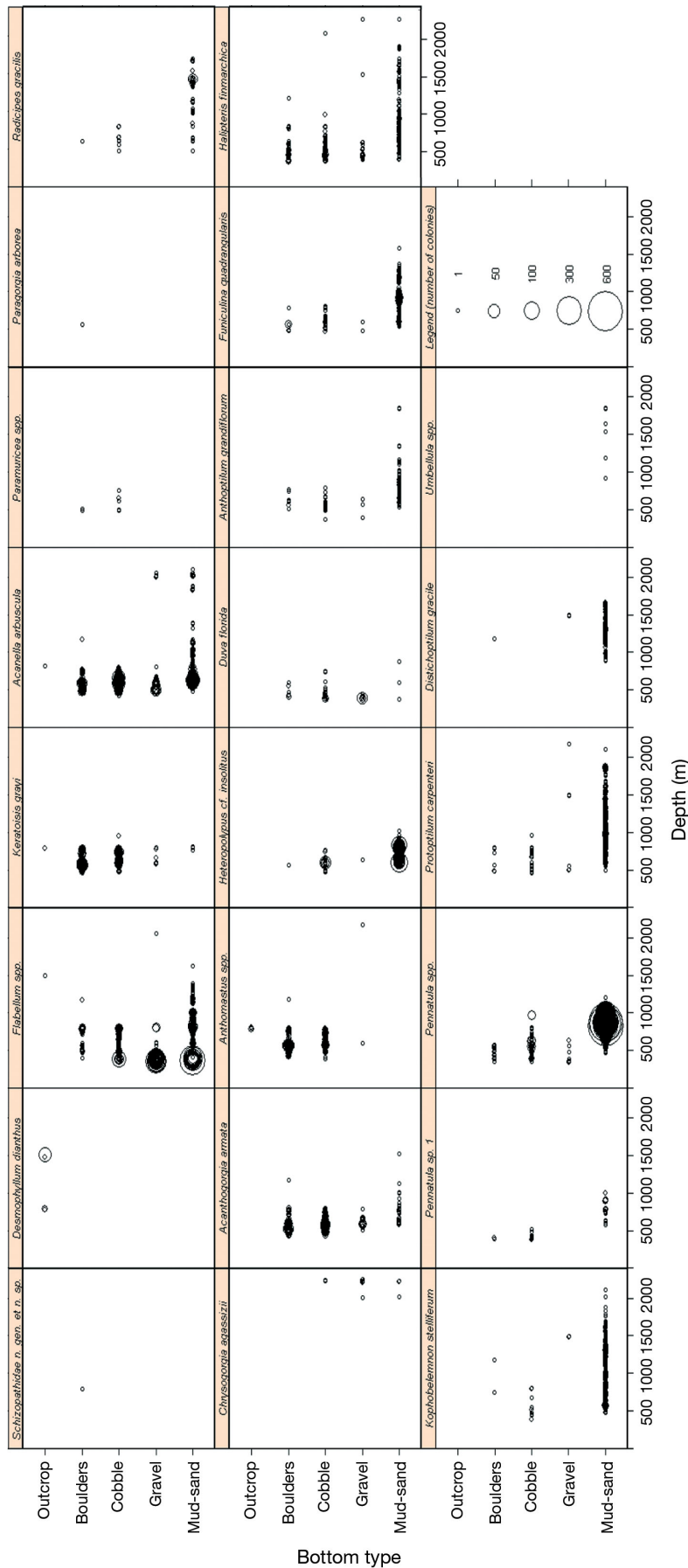


Fig. 5. Number of coral colonies found in 10-m transect segments plotted in relation to depth and sediment type. Sizes of circles are directly proportional to the square root of number of colonies

stelliferum occurred primarily in soft sediments. Species that spanned a wide variety of bottom types included *Flabellum alabastrum*, *Acanella arbuscula*, *Acanthogorgia armata* and others.

Although many species spanned a variety of bottom types and depths, when we plotted their abundances within 10-m transect segments against bottom type and depth, several patterns emerged (Fig. 5). For example, *Flabellum* spp. spanned a large depth range, but were most dense in waters <500 m. Although *Heteropolypus cf. insolitus* and *Pennatula* spp. spanned a variety of bottom types, they were much more abundant in mud-sand sediments than in bottom types categorized by hard substratum.

In general, species richness was highest in boulder areas (Fig. 6). The maximum species richness within any sample (7 species) occurred twice in boulders (489 and 470 m, Halibut Channel) and once in cobble (600 m, Haddock Channel) (Table 5). The maximum number of coral colonies was associated with mud-sand sediments (835 m) in Desbarres Canyon (Table 5), but only 3 of these were colonies other than *Pennatula* spp.

Assemblages

The global ANOSIM showed assemblages that differed significantly among depth classes ($p < 0.001$) and pairwise comparisons showed significant differences between each depth class ($p < 0.001$) (Table 6). However, the R-statistic indicated that assemblage composition differed most between depth ranges 300–800 and 1300–2300 m ($R = 0.471$). This dissimilarity (average dissimilarity = 92.6%) was largely driven by higher abundances of *Acanella arbuscula* and *Pennatula* spp. in shallower waters. *Pennatula*

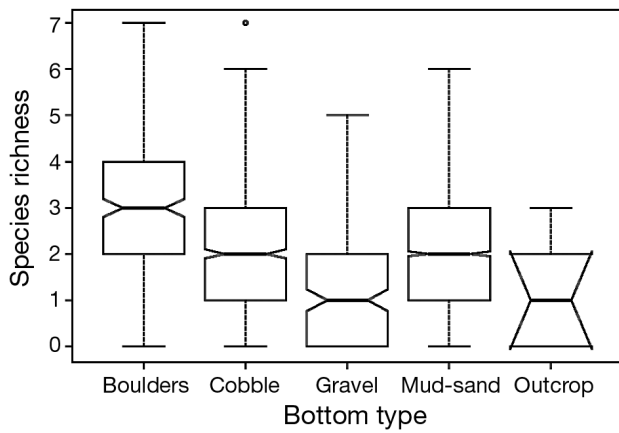


Fig. 6. Species richness in relation to sediment type from 10-m transect segments recorded by an ROV off Newfoundland, Canada in 2007. Median, upper/ lower quartiles, minimum/maximum values, and an outlier are shown

Table 5. Maximum species richness and number of coral colonies in 10-m transect segments in a variety of habitat categories

	Habitat category	Maximum species richness	Maximum number of colonies
Sediment type	Outcrop	3	61
	Boulders	7	99
	Cobble	7	82
	Gravel	5	200
	Mud-sand	6	625
Depth category (m)	300–800	7	301
	800–1300	6	625
	1300–2300	4	61
Dive	R1065	6	79
	R1066	7	183
	R1067	7	99
	R1068	2	4
	R1070	6	301
	R1071	6	625
	R1072	5	61

spp. and *A. arbuscula* also drove differences between the 300–800 and 800–1300 m assemblages (average dissimilarity = 85%); *Pennatula* spp. was most abundant in the 800–1300 m depth class, whereas *A. arbuscula* was more abundant in the 300–800 m depth class. The assemblage differences between the 800–1300 and 1300–2300 m depth classes (average dissimilarity = 88%) were largely driven by *Pennatula* spp. and *Protoptilum carpenteri*. *Pennatula* spp. occurred in the shallower depth range but not in deeper waters and *P. carpenteri* was more abundant in the deeper depth class compared to the shallower depth range.

Table 6. Results from 2-way analysis of similarity (ANOSIM) to compare coral assemblages between depths and sediment types from an ROV survey off the Grand Banks in 2007

Comparison group	R statistic	Level of significance (p)	Permutations > R
Depth, global test	0.302	0.001	0
300–800, 800–1300 m	0.239	0.001	0
300–800, 1300–2300 m	0.471	0.001	0
800–1300, 1300–2300 m	0.292	0.001	0
Sediment type, global test	0.224	0.001	0
Mud-sand, Boulders	0.316	0.001	0
Mud-sand, Cobble	0.171	0.001	0
Mud-sand, Gravel	0.222	0.001	0
Mud-sand, Outcrop	0.552	0.001	0
Boulders, Cobble	0.073	0.001	0
Boulders, Gravel	0.440	0.001	0
Boulders, Outcrop	0.560	0.069	68
Cobble, Gravel	0.191	0.001	0
Cobble, Outcrop	0.585	0.020	19
Gravel, Outcrop	0.466	0.001	0

The ANOSIM analysis showed significant differences in composition among bottom types ($p < 0.001$) (Table 6). Mud-sand sediment assemblages differed from those associated with boulders ($R = 0.316$, $p < 0.001$) and outcrops ($R = 0.552$, $p < 0.001$). Assemblages in boulder habitats also differed from those in gravel ($R = 0.440$, $p < 0.001$) and outcrops ($R = 0.56$, $p = 0.069$), but not from assemblages associated with cobble ($R = 0.073$). Coral assemblages on outcrops also differed from those in cobble ($R = 0.585$, $p = 0.02$) and gravel ($R = 0.466$, $p < 0.001$) habitats.

Generally, the paucity of species in mud-sand habitats had the greatest influence on assemblage dissimilarities. For example, fine sediments lacked *Keratois grayi*, *Desmophyllum dianthus*, and *Anthomastus* spp., and abundances of *Flabellum* spp. and *Acanella arbuscula* were lower than in areas with hard substrate like boulders (average dissimilarity = 86.9%) and outcrops (99.31%). The high dissimilarity of coral assemblages between boulders and outcrops (87.3%) was largely driven by low abundances of *K. grayi* on outcrops and the absence of *D. dianthus* from boulder habitats. The higher abundance of *Flabellum* spp. contributed most to the dissimilarities between boulders and gravel (84.2%). The low abundance of *A. arbuscula* and high abundance of *D. dianthus* associated with outcrops drove dissimilarities with cobble (95.0%). Unlike outcrops, gravel had abundant *Flabellum* spp., but lacked *D. dianthus* (99.2%).

Species similarity analyses grouped *Keratois grayi*, *Acanthogorgia armata*, and *Anthomastus*

spp. in the dendrogram (Fig. 7) and MDS plot (Fig. 8), indicating regular co-occurrence. *Acanella arbuscula* and *Flabellum* spp. also grouped closely in the MDS plot. *Desmophyllum dianthus*, *Chrysogorgia agassizii*, *Pennatula* sp. 1, *Umbellula* spp., and *Radicipes gracilis* were generally not associated

with other species in the plot. The dendrogram showed the same species as outliers and illustrated groupings (albeit with relatively weak similarity of ~20%) of *Kophobelemnnon stelliferum* and *Protoptilum carpenteri*, and *Funiculina quadrangularis* and *Pennatula* spp.

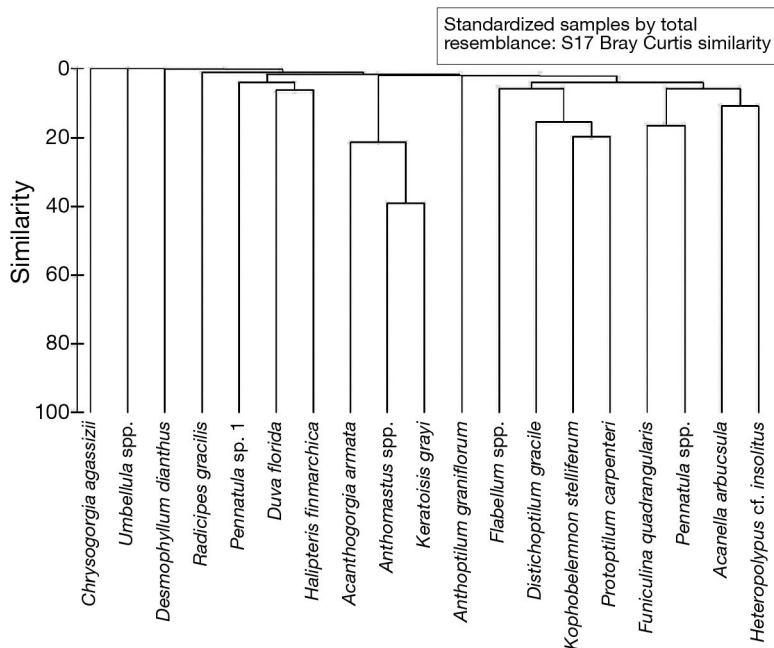


Fig. 7. Dendrogram of species, using group-average clustering from Bray-Curtis similarities on standardized samples. Data collected using an ROV off Newfoundland in 2007

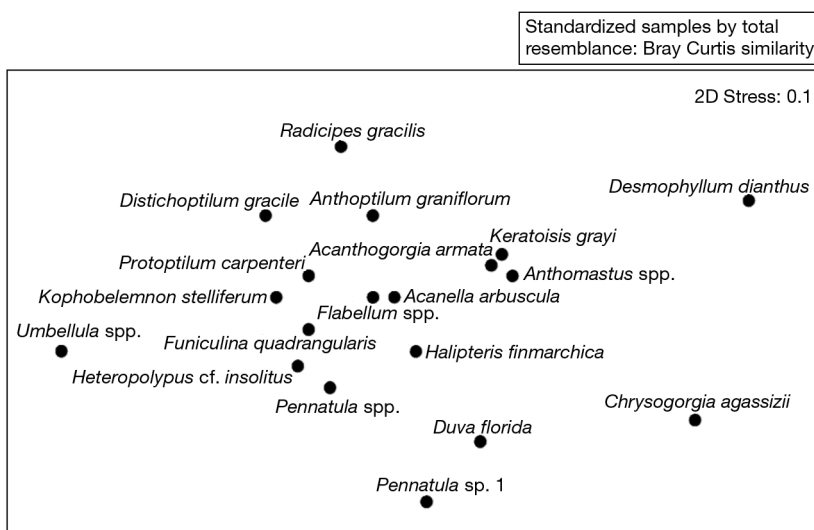


Fig. 8. MDS plot of Bray-Curtis similarity matrix based on standardized samples and species that contribute at least 50% to a sample. Data collected using an ROV off Newfoundland in 2007

DISCUSSION

Patterns in species occurrences and abundances

Bottom type and depth clearly influenced species occurrences and abundance. Physical characteristics of some species explain how bottom type influences their distributions. Peduncles anchor sea pens in sediments, thus largely restricting them to muddy habitats (Williams 2011). Some species can retract into the sediment when disturbed (Packer et al. 2007), elevating their requirement for muddy substrate. We often observed rapid retraction of entire colonies of *Protoptilum carpenteri* into the sediment, complicating sampling of this species. Although we found sea pens occupied a variety of bottom types, they were almost always anchored in the mud/sand portions of the substratum. The one exception was *Halipteris finmarchica*, which sometimes anchored in gravelly habitat with little mud or sand. As reported by Mortensen et al. (2006b) and Hecker & Blechschmidt (1980), holdfast structures anchored *Radicipes gracilis* and *Acanella arbuscula* in the soft substratum. Other species, such as *Keratoisis grayi*, *Anthomastus* spp., Schizopathidae n. gen. et n. sp. and *Duva florida*, require hard substrate for attachment (Roberts et al. 2009), and their distributions are therefore limited by hard structure availability.

As reported elsewhere (Packer et al. 2007), *Desmophyllum dianthus* typically occurred in high abundances on outcrops (Fig. 5). A strong base attaches this cup coral to hard substrate where it can benefit from high currents associated with local topo-

graphic features (Dolan et al. 2008). Försterra et al. (2005) also recorded *D. dianthus* on vertical walls and the undersides of rock ledges, and they hypothesized the coral's downward facing polyps were caused by sensitivity to sedimentation. Laboratory experiments demonstrate physiological thresholds in corals beyond which they cannot compensate for sedimentation (Brooke et al. 2009). *Desmophyllum dianthus* strongly influenced the unique assemblage associated with outcrops and thus could be considered an indicator species for vertical cliff-like structures in the study region (i.e. large quantities of *D. dianthus* likely indicate outcrop-type substrate).

Many species spanned wide depth ranges, including *Flabellum alabastrum*, *Protoptilum carpenteri*, and *Halipterus finmarchica*. This pattern parallels findings of exceptionally wide depth ranges in corals from the Northeast Pacific Ocean; Antipathidae, Primnoidae, and Paragorgiidae spanned minimum depths shallower than 30 m to depths >1900 m (Etnoyer & Morgan 2005). The especially wide depth ranges of Pennatulaceans are thought, in part, to reflect their ability to inhabit soft sediments (such as those found in the abyssal plains) (Williams 2011). In contrast to the wide depth ranges of some species, several species in our study, such as *Duva florida* and *Paragorgia arborea*, were restricted to shallow depths. The influence of depth on coral distributions likely reflects associated changes in

environmental characteristics, such as temperature (Roberts et al. 2009), available bottom type (Fig. 2), and currents.

Temperature is thought to restrict deep-sea coral distributions (Mortensen et al. 2006b, Bryan & Metaxas 2007, Roberts et al. 2009, Davies & Guinotte 2011, Waller et al. 2011). For example, high temperatures (>10°C) may restrict the upper depth limit of *Paragorgia arborea* off Atlantic Canada (Mortensen et al. 2006b). Given that our study focused on relatively deep waters, the maximum temperatures for each species were well within the temperature ranges recorded by Mortensen et al. (2006b). In comparison to other surveys off Canada that recorded temperature (Mortensen et al. 2006b, Beazley 2011), we extended the known minimum temperature limit in this region for *Radicipes gracilis* (4.4°C), *Anthomastus* spp. (4.3°C), *Acanella arbuscula* (3.5°C), and *Flabellum alabastrum* (3.7°C). Nevertheless, because these species are known to occur in higher latitudes and in deeper waters off Atlantic Canada (Fisheries and Oceans Canada [DFO] and K. Baker, unpubl. data), these values likely do not represent their lower temperature limit.

Patterns in community composition and diversity

Keratoisis grayi, *Anthomastus* spp., and *Acanthogorgia armata* co-occurred (Fig. 9a) at relatively

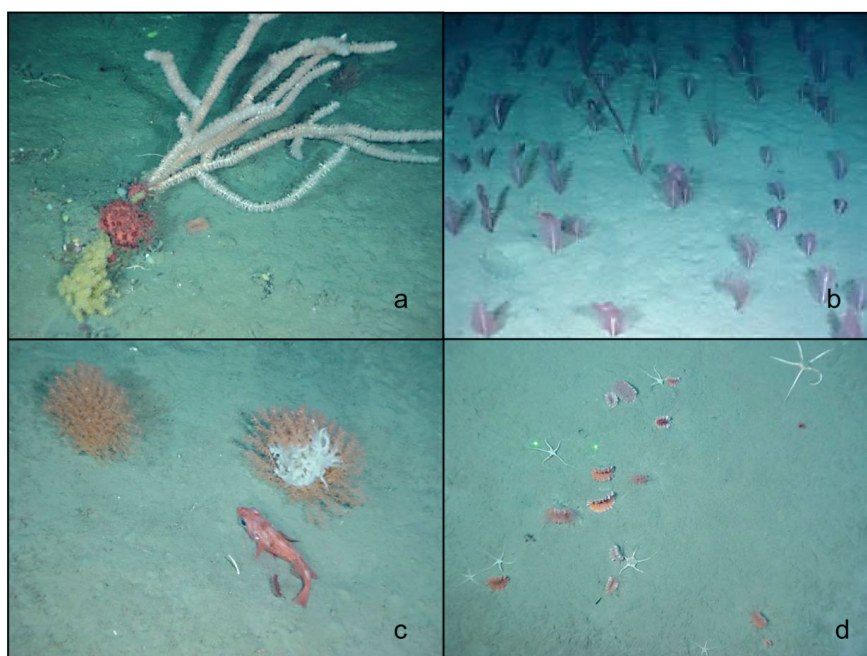


Fig. 9. Photos of coral in ROPOS transects off Newfoundland in 2007. (a) Assemblage of *Keratoisis grayi*, *Anthomastus* sp., and *Acanthogorgia armata* on a small boulder (dive R1065 at 671 m) (*Flabellum* sp. can also be seen), (b) sea pen field (mostly *Pennatula* spp.) in fine-sediment habitat (R1071, 835 m), (c) close up view of 2 *Acanella arbuscula* in fine sediments with *Sebastes* sp. (R1071, 594 m), (d) view of *Flabellum* spp. in fine sediments (R1065, 946 m)

shallow depths with boulders and cobbles throughout Halibut and Haddock Channels. The most species-rich and diverse transects were similar in species composition, comprising of *A. armata*, *Anthomastus* spp., *K. grayi*, *Acanella arbuscula*, and *Halipterus finmarchica* among others. The associated bottom types were boulders or cobble, but closer examination of the bottom classification indicated that these assemblages occurred in specific segments of transects with mixed substrate. For example, we recorded sand (primary), boulders (secondary), and scattered cobble/gravel (comments) for one of the most species rich segments. These features created a small-scale habitat mosaic in which a variety of species could co-occur.

The most numerous species occurred within a variety of bottom types and with a variety of other species, but these dominant corals also created unique assemblages in relatively uniform sediments. *Pennatula* spp. sometimes occurred in large sea pen meadows >1 km in length (Fig. 9b), and reached maximum numbers of 622 colonies per 10-m segment. Many colonies oriented in a similar direction (presumably to maximize use of currents) (Roberts et al. 2009). *Halipterus finmarchica*, *Protoptilum carpenteri*, *Kophobelemnion stelliferum*, and other sea pens were scattered throughout these meadows. Although it is unclear what role these meadows play in the wider ecosystem context, their large extent, large number of colonies, and added structure in an otherwise low-structure habitat suggest their presence may be important for other taxa (Tissot et al. 2006). Tissot et al. (2006) hypothesized that aggregations of sea pens may create important refugia for small invertebrates, alter current regimes, and influence prey availability. The sea pen meadows did not appear to host noticeably more abundant or diverse megafauna, but this does not preclude their potential importance for macrofauna or small life stages of mobile megafauna.

Acanella arbuscula (Fig. 9c) or *Flabellum* spp. (Fig. 9d) also dominated large tracts of seafloor. We observed both types of coral fields in fine sediments, sometimes with scattered gravel. In general, species richness in *A. arbuscula* fields was low with only a few species in any 10-m segment. Sea pens and *Flabellum* spp. (Fig. 8) were also present in *A. arbuscula* fields. Low coral species richness (≤ 2 species) also characterized fields with an abundance of *Flabellum* spp. Although few species were present in these fields, numbers of corals were considerable and appeared to represent unique ecosystems in this area.

Large scale patterns in species distributions and diversity

We observed at least 28 coral species during the 7 dives. Murillo et al. (2010) found only 17 species on the Grand Banks during their bottom trawl surveys, Mortensen et al. (2006b) identified 12 species on the Grand Banks using a variety of techniques, and Wareham & Edinger (2007) recorded 30 species throughout all Newfoundland and Labrador waters. In a towed camera survey of more southerly canyons, Hecker et al. (1980) found at least 12 species of corals in Baltimore Canyon, 13 species in Lydonia Canyon, and 16 species in Oceanographer Canyon.

Our study represents the first observations for many deep-sea coral species in Newfoundland waters: *Heteropolypus cf. insolitu*, *Lepidisis* sp., *Bathypathes patula*, Schizopathidae n. gen. et n. sp., *Protoptilum carpenteri*, *Umbellula* sp. (likely *encrinus*), *Flabellum macandrewi*, and *Javania cailleti*. Other species found in this study confirm those recorded in extensive fishery and trawl surveys of the Grand Banks and surrounding areas, though several studies did not report *Chrysogorgia agassizi* (Gass & Willison 2005, Wareham & Edinger 2007, Murillo et al. 2010). Our cruise identified at least 3 species of *Flabellum*, compared to the one (*F. alabastrum*) recorded by the other survey methods (Wareham & Edinger 2007, Murillo et al. 2010). Mortensen et al. (2006b) found *F. macandrewi* along the Scotian Shelf and within The Gully off Nova Scotia, but not off Newfoundland and Labrador. *Pennatula aculeata* and *P. grandis* were commonly found in surveys by Murillo et al. (2010), but at least 3 species of *Pennatula* could be distinguished from our video and require additional taxonomic and genetic work.

Coral size

Although the tallest *Keratoisis grayi* was 215 cm, many colonies were greater in width than height (e.g. 160 × 250 cm and 200 × 230 cm). The ages and growth rates of corals sampled suggest that the 215 cm tall *K. grayi* is likely over 200 yr old (Sherwood & Edinger 2009). The tallest Schizopathidae n. gen. et n. sp. (incorrectly identified as *Stauropathes arctica* in Sherwood & Edinger 2009) was over 50 yr old, and the tallest *Acanella arbuscula* (30 cm) was ~30 yr old. These large sizes and slow growth rates highlight the slow recovery times for disturbed coral assemblages and the need for strong conservation measures in the deep sea.

Conservation implications

Scientists recognize the importance of protecting deep-sea corals (Roberts & Hirshfield 2004), which is often achieved through protected areas (Brock et al. 2009). But despite the growing international push for coral protection, no official marine protected areas currently exist off Newfoundland and Labrador to protect deep-sea corals within Canadian waters. Conservation objectives should guide selection of which areas to protect. Many conservation efforts prioritize protection of high concentrations/abundances of corals, high species richness, or unique corals. Our high-resolution video surveys provide *in situ* observations and highlight patterns that can be used to help guide future conservation initiatives.

If the objective is to protect rare, unique assemblages of corals, our results indicate that known deep-sea outcrops off Newfoundland would be an appropriate starting point, given the relatively rare species for this region present at outcrops, such as *Paragorgia arborea*, antipatharians, and several species of cup corals. Protection of high coral species richness should concentrate on upper to middle slope areas with a variety of substratum including boulders, cobble, and fine sediments. Selection of areas to protect high abundances of corals varies with species. The middle to upper slope with large areas of relatively hard substrate should be targeted if the goal is to protect large, fragile corals (such as gorgonians and antipatharians). Although conservation priorities should not shift from rarer species, conservation efforts should at least consider common species as well (Gaston 2010). More common species (such as sea pens and *Flabellum* spp.) tend to be overlooked in conservation initiatives (for example Edinger et al. 2007a, Brock et al. 2009), to the benefit of large, spectacular corals or deep-water coral reefs. The fine sediment habitats where these common species occur contain unique coral assemblages and often have abundant corals.

Nevertheless, we believe the most successful conservation initiative for deep-sea corals off Atlantic Canada would take a holistic approach to conservation planning and use a representative network of protected areas to help conserve a variety of species, assemblages.

In 2008, the Northwest Atlantic Fisheries Organization (NAFO) created a closed area for corals off the slope of the Grand Banks to protect corals from bottom fishing (NAFO 2011). The protection zone runs roughly along the 800–1000 m isobath crossing into Canada's exclusive economic zone (Rogers & Gianni

2010). In general, our results show the highest abundance of fragile corals and highest species richness occur on the upper to middle slope, adding to the growing research that indicates this zone is too deep for its intended purpose (Rogers & Gianni 2010). Therefore, this zone should be extended into shallower waters where corals currently remain at risk to fishing activities.

Future work

Although this study illuminates general patterns of deep-sea coral occurrence off Newfoundland, the unique sampling problems associated with deep-sea corals necessitates much more *in situ* research in this region. Studies should aim to collect detailed multi-beam bathymetry data (Dolan et al. 2008), geological samples, sedimentation rates, current speed and direction (Mortensen & Buhl-Mortensen 2004), and temporal and spatial trends in primary productivity to understand better the processes driving coral distributions. Many sites thought to be important for corals based on fishing or trawl survey data (Edinger et al. 2007a) remain unexplored with other methods, constraining any comprehensive understanding of coral abundances, assemblages, and diversity. Meanwhile, deep-water fishing (especially bottom trawling) activities continue to threaten corals, and as long these activities remain our primary data source, destruction will outpace our understanding of coral distributions and assemblage patterns.

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LITERATURE CITED

- Althaus F, Williams A, Schlacher TA, Kloser RJ and others (2009) Impacts of bottom trawling on deep-coral ecosystems of seamounts are long-lasting. *Mar Ecol Prog Ser* 397:279–294
- Beazley L (2011) Reproductive biology of the deep-water gorgonian coral *Acanella arbuscula* from the Northwest Atlantic. MSc thesis, Dalhousie University, Halifax
- Benjamin R (2007) ClassAct Mapper. Fisheries and Oceans Canada
- Brock R, English E, Kenchington E, Tasker M (2009) The

- alphabet soup that protects cold-water corals in the North Atlantic. *Mar Ecol Prog Ser* 397:355–360
- Brooke SD, Holmes MW, Young CM (2009) Sediment tolerance of two different morphotypes of the deep-sea coral *Lophelia pertusa* from the Gulf of Mexico. *Mar Ecol Prog Ser* 390:137–144
- Bryan TL, Metaxas A (2007) Predicting suitable habitat for deep-water gorgonian corals on the Atlantic and Pacific Continental Margins of North America. *Mar Ecol Prog Ser* 330:113–126
- Buhl-Mortensen L, Vanreusel A, Gooday AJ, Levin LA and others (2010) Biological structures as a source of habitat heterogeneity and biodiversity on the deep ocean margins. *Mar Ecol* 31:21–50
- Clarke KR, Gorley RN (2006) PRIMER v6: user manual/tutorial. PRIMER-E, Plymouth
- Cordes EE, McGinley MP, Podowski EL, Becker EL and others (2008) Coral communities of the deep Gulf of Mexico. *Deep-Sea Res I* 55:777–787
- CSSF (2010) Canadian Scientific Submersible Facility, available at: www.ropos.com (accessed November)
- Davies AJ, Guinotte JM (2011) Global habitat suitability for framework-forming cold-water corals. *PLoS One* 6(4): e18483
- Dolan MFJ, Grehan AJ, Guinan JC, Brown C (2008) Modelling the local distribution of cold-water corals in relation to bathymetric variables: adding spatial context to deep-sea video data. *Deep-Sea Res I* 55:1564–1579
- Edinger EN, Baker KD, Devillers R, Wareham V (2007a) Coldwater corals off Newfoundland and Labrador: distribution and fisheries impacts. World Wildlife Fund (WWF), Toronto
- Edinger EN, Wareham VE, Haedrich RL (2007b) Patterns of groundfish diversity and abundance in relation to deep-sea coral distributions in Newfoundland and Labrador waters. In: George RY, Cairns SD (eds) Conservation and adaptive management of seamount and deep-sea coral ecosystems. Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, FL
- Etnoyer P, Morgan LE (2005) Habitat-forming deep-sea corals in the Northeast Pacific Ocean. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer-Verlag, Berlin, p 331–343
- Fiege D, Barnich R (2009) Polynoidae (Annelida: Polychaeta) associated with cold-water coral reefs of the northeast Atlantic and the Mediterranean Sea. In: Maciulek NJ, Blake JA (eds) Proc 9th Int Polychaete Conf. Zoosymposia 2:149–164
- Försterra G, Beuck L, Haussermann V, Freiwald A (2005) Shallow-water *Desmophyllum dianthus* (Scleractinia) from Chile: characteristics of the biocoenoses, the bioeroding community, heterotrophic interactions and (paleo)-bathymetric implications. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer-Verlag, Berlin, p 937–977
- Fossa JH, Mortensen PB, Furevik DM (2002) The deep-water coral *Lophelia pertusa* in Norwegian waters: distribution and fishery impacts. *Hydrobiologia* 471:1–12
- Gass SE, Willison JHM (2005) An assessment of the distribution of deep-sea corals in Atlantic Canada by using both scientific and local forms of knowledge. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer-Verlag, Berlin, p 223–245
- Gaston KJ (2010) Valuing common species. *Science* 327: 154–155
- Gilkinson K, Edinger EN (2009) The ecology of deep-sea corals of Newfoundland and Labrador waters: biogeography, life history, biogeochemistry and relation to fishes. Can Tech Rep Fish Aquat Sci 2830
- Guinotte JM, Fabry VJ (2008) Ocean acidification and its potential effects on marine ecosystems. *Ann NY Acad Sci* 1134:320–342
- Hall-Spencer JM, Rodolfo-Metalpa R, Martin S, Ransome E and others (2008) Volcanic carbon dioxide vents show ecosystem effects of ocean acidification. *Nature* 454: 96–99
- Hecker B, Blechschmidt G (1980) Appendix A: Epifauna of the Northeastern US Continental Margin. Final historical coral report for the Canyon Assessment Study in the Mid- and North Atlantic areas of the US outer continental shelf. In: Hecker B, Blechschmidt G, Gibson P (eds) Canyon Assessment Study. US Department of Interior Bureau of Land Management, Washington, DC
- Hecker B, Blechschmidt G, Gibson P (1980) Epifaunal zonation and community structure in three Mid- and North Atlantic canyons. In: Hecker B, Blechschmidt G, Gibson P (eds) Canyon Assessment Study. US Department of Interior Bureau of Land Management, Washington, DC
- Henry LA, Roberts JM (2007) Biodiversity and ecological composition of macrobenthos on cold-water coral mounds and adjacent off-mound habitat in the bathyal Porcupine Seabight, NE Atlantic. *Deep-Sea Res I* 54: 654–672
- Husebo A, Nottestad L, Fossa JH, Furevik DM, Jorgensen SB (2002) Distribution and abundance of fish in deep-sea coral habitats. *Hydrobiologia* 471:91–99
- Krieger KJ, Wing BL (2002) Megafauna associations with deepwater corals (*Primnoa* spp.) in the Gulf of Alaska. *Hydrobiologia* 471:83–90
- Mortensen PB, Buhl-Mortensen L (2004) Distribution of deep-water gorgonian corals in relation to benthic habitat features in the Northeast Channel (Atlantic Canada). *Mar Biol* 144:1223–1238
- Mortensen PB, Buhl-Mortensen L (2005) Deep-water corals and their habitats in The Gully, a submarine canyon off Atlantic Canada. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer-Verlag, Berlin, p 247–277
- Mortensen PB, Buhl-Mortensen L, Gass SE, Gordon DC, Kenchington E, Bourbonnais C, MacIsaac KG (2006a) Deep-water corals in Atlantic Canada: a summary of ESRF-funded Research (2001–2003). Environmental Studies Research Funds Report Vol. 143
- Mortensen PB, Buhl-Mortensen L, Gordon DC (2006b) Distribution of deep-water corals in Atlantic Canada. Proc 10th Int Coral Reef Symp, Okinawa 1:1832–1848
- Murillo FJ, Durán Muñoz P, Altuna A, Serrano A (2010) Distribution of deep-water corals of the Flemish Cap, Flemish Pass, and the Grand Banks of Newfoundland (Northwest Atlantic Ocean): interaction with fishing activities. *ICES J Mar Sci* 68:319
- NAFO (2011) Northwest Atlantic Fisheries Organization, available at www.nafo.int (accessed 30 September)
- Packer D, Boelke D, Guida V, McGee L (2007) State of deep coral ecosystems in the Northeastern US region: Maine to Cape Hatteras. In: Lumsden SE, Hourigan TF, Bruckner A, Dorr G (eds) The state of deep coral ecosystems of the United States. NOAA, Silver Spring, MD
- Roark EB, Guilderson TP, Dunbar RB, Fallon SJ, Mucciarone DA (2009) Extreme longevity in proteinaceous deep-sea

- corals. *Proc Natl Acad Sci USA* 106:5204–5208
- Roberts S, Hirshfield M (2004) Deep-sea corals: out of sight, but no longer out of mind. *Front Ecol Environ* 2:123–130
- Roberts JM, Brown CJ, Long D, Bates CR (2005) Acoustic mapping using a multibeam echosounder reveals cold-water coral reefs and surrounding habitats. *Coral Reefs* 24:654–669
- Roberts JM, Wheeler AJ, Freiwald A (2006) Reefs of the deep: the biology and geology of cold-water coral ecosystems. *Science* 312:543–547
- Roberts JM, Wheeler AJ, Freiwald A, Cairns S (2009) Cold-water corals: the biology and geology of deep-sea coral habitats. Cambridge University Press, New York, NY
- Rogers A, Gianni M (2010) The implementation of UNGA Resolutions 61/105 and 64/72 in the management of deep-sea fisheries on the high seas. International Programme of the State of the Ocean, London
- Ross SW, Quattrini AM (2007) The fish fauna associated with deep coral banks off the southeastern United States. *Deep-Sea Res I* 54:975–1007
- Schembri PJ, Dimech M, Camilleri M, Page R (2007) Living deep-water *Lophelia* and *Madrepora* corals in Maltese waters (Strait of Sicily, Mediterranean Sea). *Cah Biol Mar* 48:77–83
- Sherwood OA, Edinger EN (2009) Ages and growth rates of some deep-sea gorgonian and antipatharian corals of Newfoundland and Labrador. *Can J Fish Aquat Sci* 66: 142–152
- Thrush SF, Hewitt JE, Funnell GA, Cummings VJ and others (2001) Fishing disturbance and marine biodiversity: the role of habitat structure in simple soft-sediment systems. *Mar Ecol Prog Ser* 223:277–286
- Tissot BN, Yoklavich MM, Love MS, York K, Amend M (2006) Benthic invertebrates that form habitat on deep banks off southern California, with special reference to deep sea coral. *Fish Bull* 104:167–181
- Turley CM, Roberts JM, Guinotte JM (2007) Corals in deep-water: Will the unseen hand of ocean acidification destroy cold-water ecosystems? *Coral Reefs* 26:445–448
- Waller RG, Scanlon KM, Robinson LF (2011) Cold-water coral distributions in the Drake Passage area from towed camera observations: initial interpretations. *PLoS One* 6(1):e16153
- Wareham VE, Edinger EN (2007) Distribution of deep-sea corals in the Newfoundland and Labrador region, Northwest Atlantic Ocean. *Bull Mar Sci* 81:289–313
- Williams GC (2011) The global diversity of sea pens (Cnidaria: Octocorallia: Pennatulacea). *PLoS One* 6(7): e22747
- Zedel L, Fowler WA (2009) Comparison of boundary layer current profiles in locations with and without corals in Haddock Channel, southwest Grand Banks. In: Gilkinson K, Edinger EN (eds) *The ecology of deep-sea corals of Newfoundland and Labrador waters: biogeography, life history, biogeochemistry, and relation to fish*. Can Tech Rep Fish Aquat Sci 2830

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