

Deep-water corals and their habitats in The Gully, a submarine canyon off Atlantic Canada

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Abstract. Submarine canyons are structurally complex habitats known to support high densities and diversity of megafaunal organisms. This study describes deep-water corals and their habitats in The Gully, the largest submarine canyon in eastern North America, situated at the Canadian margin off Nova Scotia. Video recordings of the seabed were made along 49 transects, at depths between 110 and 544 m, using a tethered video camera system. The Gully has a high diversity of habitats with steep bedrock outcrops, high relief bottom with ledges of semi-consolidated mudstone, as well as level soft bottoms and areas with gravel. In total 95 megafaunal taxa were observed of which 16 species were corals. There was a strong, positive correlation between the total number of megafaunal taxa and number of coral species along transects, suggesting that coral diversity is a good indicator for overall megafaunal diversity. Corals were present in most parts of the canyon, and up to 11 species were observed along a single transect. The distribution patterns of corals were mainly related to distance along the axis from the canyon head and type of seabed substratum. The highest abundance of corals was found on the western side in the outer part of the canyon and is probably related to circulation patterns with a higher load of particulate matter in the out-flowing water. Nephtheid soft corals, mainly *Duva florida*, were most frequent and were found within the whole depth range. Gorgonian corals were observed only deeper than 340 m. Except for *Acanella arbuscula* and *Radicipes gracilis*, which are anchored in mud, the gorgonians were mainly confined to areas with cobble and boulder and in a few cases to semi-consolidated mudstone. Multivariate analyses were applied to identify groups of transects and species, and to indicate which environmental factors control the distribution of corals and other megafauna in The Gully.

Keywords. Deep-water corals, submarine canyon, Atlantic Canada, habitat

Introduction

Submarine canyons are a major feature along the edge of the continental shelf and slope along the northeastern USA and Atlantic Canada. In general, they contain a high diversity of habitats within a relatively small area, and have been recognised as rich coral habitats (Hecker et al. 1980; Breeze and Davis 1998). The Gully, the largest submarine canyon in eastern North America, is located off Nova Scotia just east of Sable Island. The Gully was formally declared as a Marine Protected Area in 2004 (DFO 2004). This designation is largely based on the residency of a small population of the Northern Bottlenose whale (*Hyperoodon ampullatus*) found there (Gowans et al. 2000) but considers other special attributes as well.

Deep-water corals are found around the world at depths most commonly on the order of 200–1500 m (Broch 1912, 1935, 1957; Jungersen 1917; Madsen 1944; Carlgren 1945; Hecker et al. 1980; Zibrowius 1980; Genin et al. 1986; Tendal 1992; Cairns 1994; Rogers 1999), and may be important components of deep-sea ecosystems. They occur off Atlantic Canada, mainly in channels between fishing banks and in submarine canyons (Breeze et al. 1997; MacIsaac et al. 2001; Gass and Willison 2005; Mortensen et al. in press). Until recently, most of the limited information available on the distribution of deep-sea corals in Atlantic Canada was anecdotal, based primarily on observations made by the fishing industry (Breeze et al. 1997). Since 1997 DFO has been collecting video and photographic information of epibenthic communities on an opportunistic basis at prime coral habitat sites in Atlantic Canada including the Northeast Channel, Stone Fence and The Gully. Some of the results have been published by MacIsaac et al. (2001), Buhl-Mortensen and Mortensen (2004), Gass and Willison (2005) and by Mortensen et al. (in press). These studies have improved the understanding of the distribution of corals and controlling environmental factors in Atlantic Canada, and have also documented that bottom fishing can impact corals (Mortensen et al. in press). However, the knowledge of how the presence of corals influences the faunal associations and the general megafauna composition remains rudimentary.

Awareness of deep-sea corals and their ecological importance is growing rapidly. Concern has been expressed about the potential effects of human activities on deep-water coral ecosystems, especially fishing and oil and gas activities (Rogers 1999). While there is considerable debate over the extent of past damage, it is clear that certain fishing activities can affect deep-sea coral ecosystems (Fosså et al. 2002; Mortensen et al. in press). The first offshore hydrocarbon developments in Atlantic Canada have been in shallow water, where only the soft corals (Alcyonacea) *Alcyonium digitatum* and *Gersemia rubiformis* have been recorded. However, exploration activity is now moving into deeper water where black (Antipatharia), horny (Gorgonacea), stony (Scleractinia) and soft corals can occur. Available information indicates that these corals provide important habitat and could play a critical role in the life history of many marine species, including some of commercial interest (Rogers 1999; Buhl-Mortensen and Mortensen 2005; Mortensen et al. in press). The conservation community is calling for the establishment of marine protected

areas (MPAs) to protect important coral habitats (Hall-Spencer et al. 2002). More information about the distribution of deep-sea corals is needed to define relevant coral protection areas.

The main goal of DFO coral studies in recent years has been to expand the knowledge of the distribution and ecology of deep-sea corals and their habitats in Atlantic Canada. The objectives of this paper are to describe the distribution of corals in The Gully and to relate their abundance to environmental factors and megafaunal composition.

The study area

The Gully is a deep and large submarine canyon approximately 40 km east of Sable Island on the edge of the Scotian Shelf (Fig. 1A). It is the largest submarine canyon off Atlantic Canada and eastern North America, being more than 70 km long and 20 km wide (Harrison and Fenton 1998). It consists of a deep (up to 2700 m) main canyon with several side-canyons (termed feeder canyons or channels) branching into the continental shelf. Reviews of the environment and processes of The Gully are provided by Harrison and Fenton (1998) and Gordon and Fenton (2002). It is thought to be an area of high productivity and important marine mammal habitat. Fifteen species of whales and dolphins have been identified in the area.

The Gully was formed from a combination of fluvial, glacial ice and glacial meltwater erosion occurring mainly 150–450 kyrs ago. It is cut into Tertiary bedrock in the deeper sections, and covered with thick quaternary glaciomarine sediments, mainly the Sambro Sand unit (sand and silty mud) in the shallower parts (200–600 m) (Fader et al. 1998). The steep-walled “ridge and valley” core area of The Gully widens seaward until the shelf break (Fig. 1B). Further down the continental slope it narrows again. At depths of about 600 to 3000 m sequences of mud and silts predominate, with sandier channels interspersed. The thalweg (deepest channel floor profile) of The Gully presents a remarkably uniform, sand-covered surface, sloping at approximately 2 degrees seaward from its head (Fader et al. 1998). At 2700 m depth the slope of the thalweg begins to decrease slightly. Nine major feeder canyons and many other smaller associated channels occur on the western flank of The Gully (Fig. 1A).

The physical oceanography of The Gully is described by Petrie et al. (1998). The main current pattern, as indicated by numerical modelling, is a strong south-westward flow along the shelf edge with greatest strength in fall and winter (Han et al. 2002). Some of that flow is steered into The Gully along its eastern side and out along its western side, forming a partial cyclonic gyre. There is an enhanced vertical mixing in The Gully in summer and fall as a result of tidally generated internal waves. This indicates that there is vertical transport of nutrients from below the pycnocline during periods of stratification, and that one might expect to find enhanced phytoplankton production (Mann 2002).

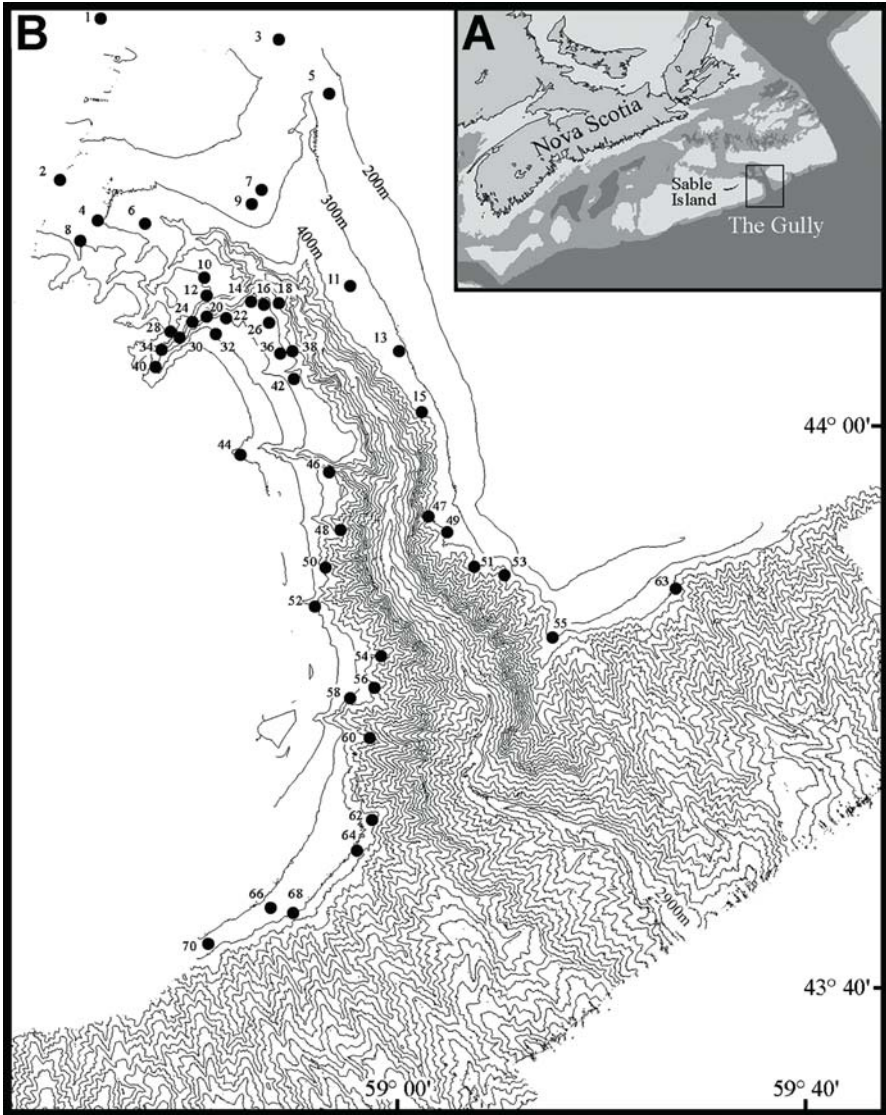


Fig. 1 A Map showing the location of The Gully. **B** The topography of The Gully, based on multibeam bathymetry, and the location of survey sites

Material and methods

Video imagery

The seabed was investigated with the video and still photo camera system Campod. Campod is an observation platform, without propulsion, equipped with a high-resolution video camera for viewing the seabed directly below and an oblique

video camera providing an overview of the seabed ahead. It can also land on the seabed and take photographs. Working depth is limited to ~500 m by cable length. Gordon et al. (2000) provides a more detailed description of this system. Campod was deployed while the ship was slowly (<1 knot) drifting and was kept close (1–2 m) to the seabed for at least 5 min on each transect. Campod was equipped with an Ultra Short Baseline navigation system (ORE Trackpoint II) providing detailed records of the tracks along the seabed. The geographical positions provided by the navigation system were quite noisy with an error in the order of ± 5 m. However, after post-processing and filtering of the data, the navigation error was reduced to ± 2 m.

Study sites

Video footage was recorded during one cruise on the C.C.G.S. *Parizeau* (8 transects in October 1997) and three cruises on the C.C.G.S. *Hudson* (12 transects in May 1999, 7 transects in June 2000, and 22 transects in September 2001). In total, 49 sites at depths between 110 and 544 m (Fig. 1B; Table 1) were selected for deployment of Campod. The sites were selected based on two criteria: high likelihood of finding coral, and good spatial coverage of the area. The site selection process made use of multibeam bathymetry collected in The Gully by the Canadian Hydrographic Service, the Geological Survey of Canada (Atlantic) and the oil and gas industry (Fader and Strang 2002). Twenty-two sites were selected within areas with rugged seabed topography most likely to support corals (i.e. at noses and ridges along the canyon edge at depths in the range of 300 to 500 m). The rest of the sites were selected to fill in areas poorly represented in order to describe the geographical distribution and the upper depth limits for corals in The Gully. As a reference for later discussions, The Gully was divided into an inner and an outer part, which in turn were divided into a western and an eastern part. Five transects were located outside The Gully just below the shelf break. The maximum depth of the investigated transects increased seaward along the axis of the canyon. The inner transects (<20 km from the innermost transect) covered depths between 110 and 370 m while middle and outer transects were located at depths from 140 to 544 m.

Estimates of megafaunal abundance

Transects varied between 19 and 1327 m in length covering a total distance of 16.6 km along the seabed (Table 1) and an area of approximately 43,940 m². The total duration of the video records was 18 h and 34 min. Transects covering a depth range >100 m were divided into two parts at the site of the middle depth. These parts are denoted as 'a' and 'b' in Table 1. The abundance of coral colonies was estimated from subsamples (sequences) of the video transects. These sequences were mainly of 30 s duration but were made shorter when abrupt changes in the habitat occurred. Geographical positions and depth were registered at the start and end of each sequence. In total 1879 video sequences were analysed each covering a distance of between 5 and 100 m (average = 9 m) as estimated from the navigation data. Unfortunately, there was no practical way to continuously estimate the width of the visual field, which varied with the height above bottom and the pitch angle

Table 1 Brief description of video transects in The Gully. Depth range, number of video sequences (Seq), length of transects (Dist), percentage cover of different bottom substrates: M-st = semi-consolidated mudstone, Bo = boulder, Co = cobble, Pe = pebble, Sa = sand, M = mud. Diversity is given as Shannon-Wiener index (H') and abundance is given as individuals or colonies per 100 m²

Tr. #	Depth	Seq	Dist	M-st	Bo	Co	Pe	Sa	M	H'	No of taxa		Abundance	
											All	Coral	All	Coral
Inner canyon														
Eastern side														
1	110-111	14	42	0	0	13.2	55	31.8	0	1.3	7	0	22.9	0
3	254-258	18	151	0	0	0.1	0	0	99.9	1.49	7	0	11.5	0
5	223-232	14	26	0	0	0	0.6	99.4	0	1.21	5	0	40.7	0
7	275-276	20	47	0	0	0	0	100	0	0.18	6	1	272.4	0.8
9	274-276	13	176	0	0	0.1	1	0	99	0.47	8	1	119.7	0.4
11	323-325	8	43	0	3.1	5.5	1	90.4	0	1.15	4	1	34.4	10.9
13	321-345	24	398	0	0.4	0.3	0	0	99.3	1.71	11	0	3.2	0
15	374-466	118	1041	2.2	0.3	0.3	0	0	97.2	1.21	29	3	181.1	37.1
Western side														
2	287-290	16	76	0	0	0.3	1.5	98.2	0	1.1	3	0	2.6	0
4	298-300	25	123	0	0.2	1	10.6	88.2	0	1.06	3	0	1.2	0
6	364-367	52	309	0.3	0.1	0.3	3.6	95.7	0	0.96	3	0	0.6	0
8	271-274	13	88	0	0	0	1	99	0	0	1	0	0.8	0
10	322-323	12	31	0	0	0	0.1	99.9	0	0.64	2	0	4.2	0
12	306-308	11	57	0	0	0.1	0	99.9	0	1.33	4	0	4.4	0
14	387-411	34	319	0	1.4	10.6	20.9	67.1	0	2.35	25	6	26.6	13.4

Table 1 continued

Tr. #	Depth	Seq	Dist	M-st	Bo	Co	Pe	Sa	M	H'	No of taxa		Abundance	
											All	Coral	All	Coral
Inner canyon														
Western side														
16	406-411	26	161	0.2	5.2	12.4	10.7	0	71.5	2	19	6	50.9	8.9
18	277-316	6	68	0	0.2	43.3	43.3	0	13.2	2.05	10	1	17.4	0.8
20	400-436	51	393	7.2	0	0	0	0	92.8	1.62	12	2	13.1	2.3
22	316-369	44	556	34.6	0.3	0.2	0	64.9	0	1.24	25	5	126.9	24.9
24	439-460	13	151	0	0	0	0	100	0	1.77	7	0	4.3	0
26	397-446	49	597	9.8	2	15.9	14.4	57.9	0	2.19	30	7	47	6.6
28	274-331	26	136	4.9	0.1	0	1	94	0	1.81	8	1	7.6	0.8
30	396-399	12	72	0	0	0	0	100	100	1.23	6	0	17.5	0
32	233-306	92	1007	3.7	0.4	0.6	0.2	95.1	0	2.73	28	1	6.7	0.1
34	302-306	6	19	0	0	0	0	100	0	0.69	2	0	7	0
36	403-416	15	79	4.4	1.8	10.4	12.1	0	71.3	0.95	11	2	164.8	5
38	441-466	14	202	0	0.2	0.1	0.1	0	99.6	0.33	5	0	19.1	0
40	246-290	10	72	0	0.3	0	0.3	0	99.4	1.06	9	0	29.9	0
42	387-404	22	184	9.9	0.7	1.5	1.5	0	86.5	0.77	12	3	49.1	1.3
44	139-148	40	235	0	0	0	0	0	100	0.7	11	0	202.7	0
46a	368-444	40	440	23	0.02	0	0	0	77		16	2	38.7	12.1
46b	445-519	50	366	72	0	0	0	0	28		23	6	52	40

Table 1 continued

Tr. #	Depth	Seq	Dist	M-st	Bo	Co	Pe	Sa	M	H'	No of taxa		Abundance	
											All	Coral	All	Coral
Outer canyon														
Eastern side														
47	473-527	18	149	31.1	0.6	5.1	0.6	0	62.6	2.52	19	1	22.5	3.2
49	421-433	25	124	0	1.4	16.1	20.2	0	62.3	1.56	8	0	14	0
51	432-506	83	690	10.6	1.2	2.6	2.4	0	83.2	2.43	41	8	32.8	10.1
53	470-541	11	159	0	0	0	0	0	100	0.75	11	1	146.8	14.6
55	395-436	54	415	0	1.7	8.4	12.2	0	77.7	2.77	35	9	50.6	22.1
Western side														
48a	364-434	51	495	0.4	0	0.1	0	0	99.5		18	2	46.4	0.7
48b	439-509	13	117	47.2	0	0	0	0	52.8		16	4	24.7	8.2
50	424-490	14	37	0	0	0	0.1	0	99.9	0.08	2	0	63.8	0
52a	247-339	30	331	31.7	0.4	0.6	0.7	0	66.7		21	3	70.8	9.1
52b	152-244	30	267	29.8	0.6	1.1	0.7	0	67.8		19	2	92.2	13.7
54	395-443	71	604	0	0.6	1	1	0	97.4	2.6	34	6	46.8	8.2
56	399-487	70	1327	0	1.1	5.1	0.2	92.1	0	0.77	30	5	99.8	85.7
58	357-364	54	324	23.6	1.5	1.3	0.2	0	73.4	1.57	23	2	72.1	9.4
60	479-518	58	390	15.5	0.3	0.7	0	0	83.5	2.17	24	3	30.2	8
62a	424-484	32	239	0	0.03	0.1	0	0	99.9		27	6	45.5	7
62b	486-544	40	375	0.2	0.9	3	2.9	0	93		40	9	43.5	5.3

Table 1 continued

Tr. #	Depth	Seq	Dist	M-st	Bo	Co	Pe	Sa	M	H'	No of taxa		Abundance	
											All	Coral	All	Coral
Slope														
63	404-409	41	237	0	0	0	0.2	0	98.5	1.21	25	6	438.1	303.6
64a	389-440	73	553	0.3	1.9	3	28.8	0	66		37	6	56.1	0.9
64b	441-493	20	245	0	2.8	5.1	7.2	0	85		20	2	35.7	1.3
66	433-487	55	553	0	1.1	1.8	5.7	0	91.4	1.87	25	3	28.1	0.8
68	338-350	101	998	1.3	1.2	4.3	4.9	0	87.4	2.49	37	5	70.3	9.3
70	337-368	27	305	0	0.3	0.9	1.7	0	97.1	2.01	23	2	40.4	9.7
Sum	110-544	1879	16599								95	17		
Average				6.7	0.6	3.3	5.0	29.1	55.2	1.47	16.4	2.5	58.4	12.9

of the video camera lens. Most of the time the Campod was kept c. 1.5 m above the bottom, giving a visual field width of 2 and 4 m for the vertical and oblique camera respectively. These values were used for calculation of the approximate area covered by each of the investigated video sequences. Organisms were identified and counted within the sequences and abundances of observed species were calculated by applying the approximate area of the sequences.

Estimates of seabed substratum coverage

The percentage cover of six classes of bottom substrates (mud, sand, pebbles, cobbles, boulders and outcrops including bedrock and semi-consolidated mudstone, following the size classes as defined by the Wentworth scale (Wentworth 1922), was estimated subjectively at a scale of 5 % intervals in the same video sequences. In cases where the substrate composition showed clear variation within a video sequence, average values of two or more estimates were used.

Estimates of seabed topography

An index of seabed relief was estimated for each video transect as the actual length of the bottom profile along the transect divided by the horizontal distance. The angle of the seabed inclination was measured as the average and maximum inclination along each transect.

Temperature and salinity

Data on temperature and salinity for the study area were extracted from the hydrographic database assembled at the Bedford Institute of Oceanography, Fisheries and Ocean Canada (Petrie and Dean-Moore 1996; also accessible at <http://www.mar.dfo-mpo.gc.ca/science/ocean/home.html>). These data, from 1933 to the present, represent 843 unevenly distributed records (single measurements or vertical profiles) from different times of the year. The data set did not have sufficient resolution in time and space to enable detailed maps of the distribution of near-bottom temperature and salinity. To gain information on these variables for the video transects, all temperature and salinity records from the five divisions of the study area were plotted against depth. These plots were used to determine minimum, average and maximum values for temperature and salinity for the depths of each of the video transects.

Statistical analyses

Diversity indices - The Shannon-Wiener index (H') was used as a measure of the diversity of megafaunal taxa using the formula:

$$H' = - \sum_{i=1}^S (N_i/N) \cdot \log_2 (N_i/N) \quad (\text{Shannon and Weaver 1949})$$

where S = total number of taxa, N = total number of individuals, and N_i = number of individuals of the i^{th} taxa.

Canonical Correspondence Analysis - CCA was applied to group transects and species, based on species composition and environmental conditions, using the software PC-Ord. In total 17 environmental variables were used for this analysis: axis distance (distance from the head of the canyon measured along the thalweg), depth (average, minimum and maximum for the transects), temperature (average, minimum and maximum), salinity (average, minimum and maximum), angle (average and maximum), topographic index (relief), and the percentage cover of the six types of seabed substrates. CCA was performed on two sets of the transect data (all video sequences in a transect pooled): 1) all megafaunal species, and 2) only coral species. Only species occurring on >5 % of the transects (occurrence at >2 transects) were included. These criteria left 72 species and 42 transects for the analysis of the first data set, and 14 species and 36 transects for the second data set. Transect 44, situated on the shelf on the western side of The Gully (Fig. 1B) was omitted from the CCA because it differed markedly in species composition and occurred as an extreme outlier in an initial analysis of all transects. This anomaly resulted from an extreme high abundance of sculpins (Cottidae).

Results

General habitat description

Five types of seabed substrate types were identified: 1) bedrock walls, 2) terraced ledges of semi-consolidated mudstone, 3) gravel (with boulder), 4) sand, and 5) mud. The highest topographic relief was associated with the bedrock walls, and semi-consolidated mudstone. More level or gently sloping bottoms were found in areas with soft bottoms and gravel. Sand and mud were the dominant bottom types covering 29 and 55 % on average, respectively (Table 1). The composition of the seabed changed along the axis of the canyon, and with increasing depth. Sand dominated in the inner part of the canyon while mud dominated the outer part. Boulders occurred on 30 transects with an average cover of only 0.6 % (Table 1). The highest cover of 5.2 % was recorded at Transect 16 (values for transects are average of estimates of video sequences). Smaller stones (cobbles and pebbles) were more common (occurring on 33 and 34 transects respectively) and had higher average % cover than boulder (3.5 and 5.2 % respectively). Semi-consolidated mudstone was observed below 150 m depth, but was most common and abundant below 250 m. On average this bottom type covered 6.7 % of the seabed. Sudden changes in bottom type composition were often related to changes in bottom inclination. The mean bottom inclination for whole transects varied between 0.6 and 26.6°, while the maximum value for video sequences was 74.6°. Even though the steepest transect was found within the inner west division, on average the transects in the outer part of The Gully (average inclination = 11.5°) were about twice as steep as those in the inner part.

Analysis of temperature and salinity data revealed some slight differences between the five divisions of the study area. The estimated bottom temperature varies between 1.9 and 10.3°C, with a mean value of 5.3°C. Largest difference in

mean temperatures was found on the eastern side between the inner (6.2°C) and outer (5.0°C) divisions. The highest mean salinity was found for the outer eastern division (34.86 ‰), and the lowest was found for the inner western division (34.55 ‰).

We were not able to detect any consistent pattern of bathymetric distribution for the megafauna. The general picture of the distribution of coral habitats along the transects can be summarised as follows: The shallower parts inside the shelf break consisted mainly of sandy mud in the inner parts of The Gully. Here, the only corals observed were alcyonarians attached to scattered cobbles. The most common organisms in this habitat were cerianthid anemones. In the other parts of The Gully, the seabed inside the shelf break could be characterised more as clayey mud. In this habitat *Flabellum* spp. were abundant. Below the shelf break the seabed became suddenly coarser with gravelly patches supporting a great diversity of suspension feeders. Of corals, the gorgonian *Acanthogorgia armata* and the alcyonarian *Anthomastus grandiflorus* were observed on cobbles and boulders. On transects in areas with small side canyons a rugged terrain was observed with dense cover of semi-consolidated mudstone. The nephtheid soft corals were situated on the crests of these structures, and along Transect 46 *Paragorgia* and *Primnoa* were observed on the top of ridges where this semi-hard bottom substratum was exposed. Elsewhere, *P. resedaeformis* and *P. arborea* were more commonly found on boulders. The gorgonian *Keratoisis ornata* was often observed on cobbles and boulders in the bottom of small channels.

Distribution and abundance of corals

Colonial corals (Alcyonacea, Gorgonacea and Scleractinia) were represented by 1067 colonies, belonging to 16 taxa (Table 2), whereas solitary scleractinians accounted for 4206 individuals and three species (*Flabellum* cf. *angulare*, *F. alabastrum* and *F. macandrewi*). *Flabellum* specimens that could not be identified to species were recorded as *Flabellum* spp. but were most likely represented by both *F. angulare* and *F. macandrewi*. The three orders of deep-sea corals were quite evenly represented in terms of number of species (Alcyonacea: 5 spp., Gorgonacea: 6 spp. and Scleractinia: 4 spp.; Table 2). Up to 11 species were observed along a single transect (Transect 62). The corals showed distribution patterns both with depth, and along the axis of the canyon. Corals were present in most parts of the canyon, except for the shallower locations near the canyon head (Figs. 2A-D). The gorgonians *Paragorgia arborea* and *Primnoa resedaeformis* were observed in inner and outer divisions along five and four transects respectively (Fig. 2A). They occurred together on three transects. *Acanella arbuscula* and *Acanthogorgia armata* were observed only on the outer transects on the slope close to the canyon mouth (Fig. 2B). *Flabellum* species were observed along transects mainly in the outer divisions (Fig. 2D). A small fragment or colony of *Lophelia* was spotted on Transect 46b at a depth of 451 m but it was not possible to determine whether this coral was alive. The depth distribution of corals is summarized in Table 2, Figs. 3 and 4. Gorgonians and scleractinians were observed only deeper than about 340 m while some of the alcyonarians (the nephtheids) occurred as shallow as 170 m.

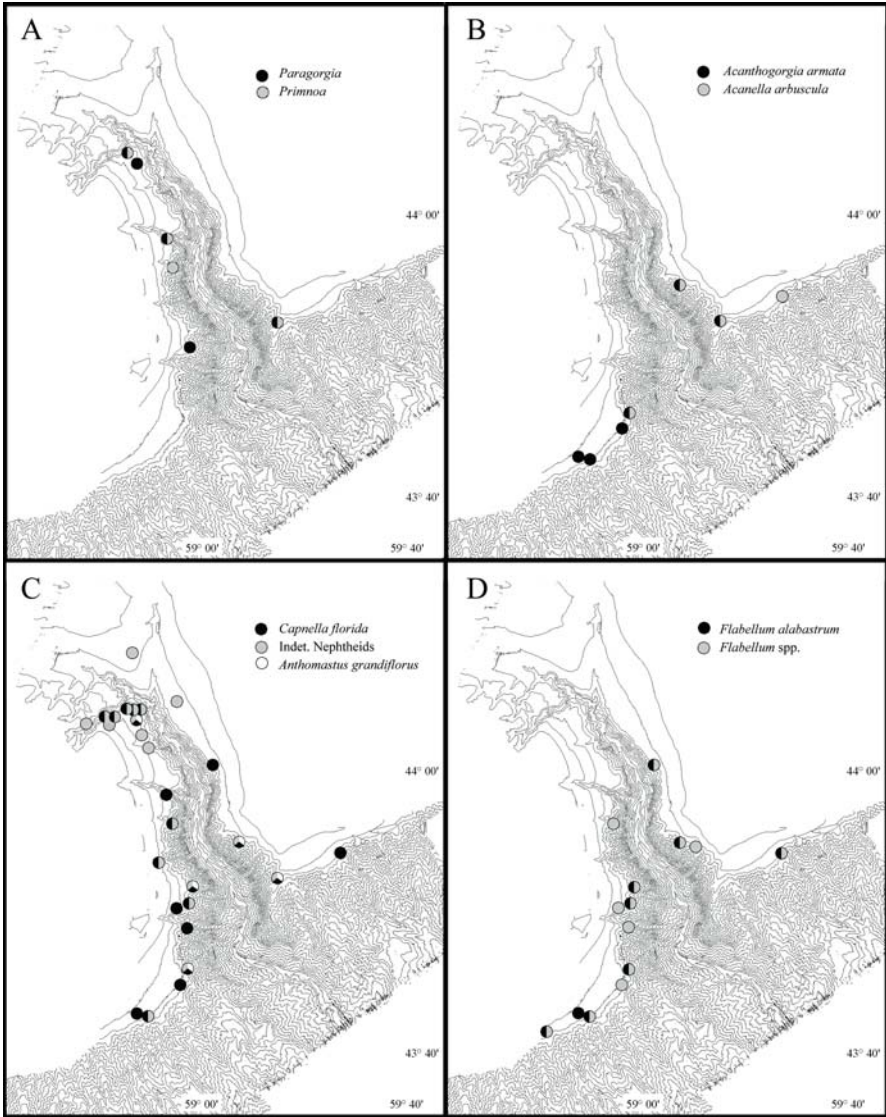


Fig. 2 The distribution of corals in The Gully. **A** *Paragorgia arborea* and *Primnoa resedaeformis*, **B** *Acanthogorgia armata* and *Acanella arbuscula*, **C** *Duva florida*, unidentified Nephtheidae and *Anthomastus grandiflorus*, **D** *Flabellum alabastrum* and *Flabellum* spp.

Maximum abundance tended to occur between about 350 and 450 m. These data do not identify the full depth range of corals since observations were limited to about 500 m because of cable length.

A summary of the abundance of corals is given in Tables 2 and 3. In general, the larger corals were less abundant than smaller corals. The nephtheid soft coral *Duva*

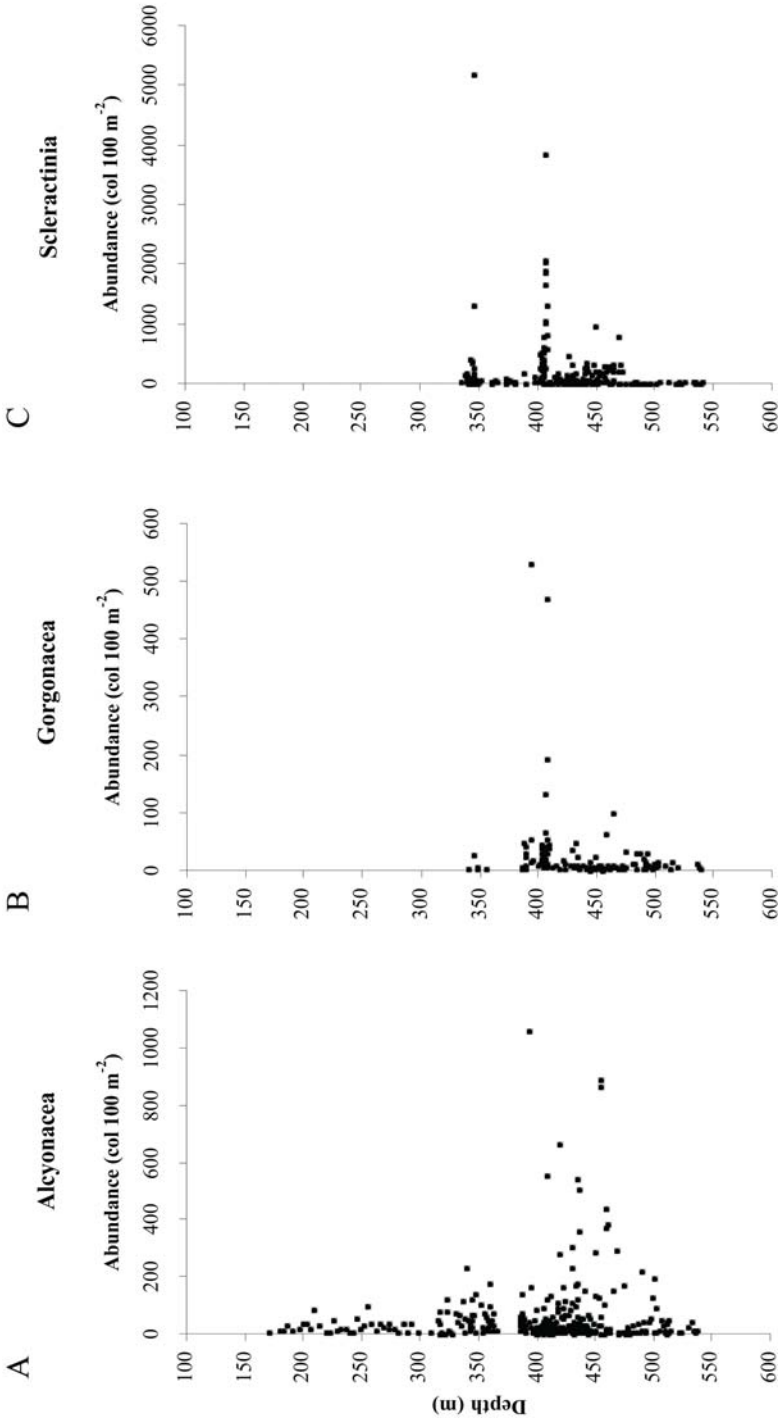


Fig. 3 Abundance of corals *versus* depth. **A** Alcyonacea, **B** Gorgonacea and **C** Scleractinia

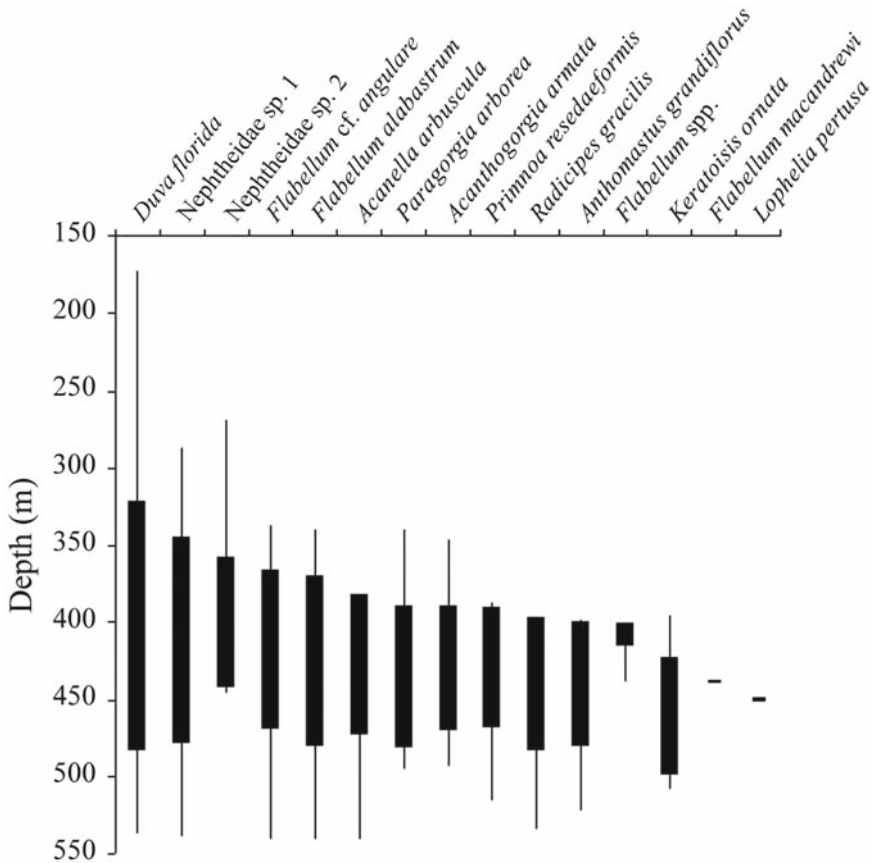


Fig. 4 Bathymetrical distribution of corals. Bars indicate standard depth range expressed as \pm standard deviation of depth records. Vertical lines indicate maximum and minimum depth of occurrence

florida was the most abundant coral with a total of 1498 specimens and an average abundance of $3.4 \text{ col} \cdot 100 \text{ m}^{-2}$. *Flabellum cf. angulare* was the most abundant coral locally with an average abundance of $706 \text{ ind} \cdot 100 \text{ m}^{-2}$ within patches (video sequences with presence of the coral; Table 2). The most abundant gorgonians were *Acanella arbuscula*, *Primnoa resedaeformis* and *Radicipes gracilis* which occurred with average patch abundance between 40.1 and $43.2 \text{ col} \cdot 100 \text{ m}^{-2}$. The abundance of corals was higher in the outer divisions than the inner (Table 3). The highest abundance was found for the transects on the slope with an average abundance of $64.9 \text{ specimens} \cdot 100 \text{ m}^{-2}$. This was mainly due to high numbers of *Flabellum* spp. Within the canyon, the highest abundance of corals was found for the western outer division with an average abundance of $16.4 \text{ col} \cdot 100 \text{ m}^{-2}$. The lowest coral abundance was found for the western inner division with $3.9 \text{ col} \cdot 100 \text{ m}^{-2}$.

Table 3 Diversity (H'), average number of species per transect, and average abundance of individuals and colonies (col·100 m⁻²) for all megafauna and corals only within the different divisions of the study area in The Gully

	H'	Average no of species/transect		Average abundance (col·100 m ⁻²)	
		All	Coral	All	Coral
Inner					
East	1.1	9.6	0.8	85.7	6.2
West	1.3	11.6	1.7	37.0	3.9
Outer					
East	2.0	22.8	3.8	53.3	10.0
West	1.6	25.5	4.4	59.9	16.4
Slope	2.1	29.6	4.4	125.2	64.9
Average	1.5	16.5	2.5	59.3	13.2

Composition and diversity of megafauna

In total 95 megafaunal taxa were recorded, of which 16 species were corals (Table 4). The number of taxa per transect varied between 1 and 41, and the diversity index (H') varied between 0 and 2.77 (Table 1). The highest numbers of taxa (both for all megafauna and for corals only) were found below 400 m depth. The number of taxa was positively correlated with maximum transect depth ($r = 0.52$, $p < 0.001$), distance along the canyon axis ($r = 0.71$, $p < 0.001$), and maximum salinity ($r = 0.47$, $p < 0.001$). There was a strong and positive correlation between the total number of megafaunal taxa and number of coral species along transects ($r = 0.87$, $p < 0.001$) suggesting that coral diversity is a good indicator for overall species diversity. The most species rich groups were fish (Teleostei, 19 taxa), and octocorals (18 taxa). Fifteen species level taxa occurred on more than 35 % of the transects. The agglutinated foraminifer *Bathysiphon cf. filiformis* occurred on 57 % of the transects.

The most common fish species was redbfish (*Sebastes* sp.) which occurred on 68 % of the transects. The second most common fish was long-finned hake (*Urophycis chesteri*), which occurred on 51 % of the transects. Fish abundance was strongly correlated with maximum temperature ($r = 0.57$, $p < 0.05$, $N = 54$). The correlation between abundance of fish and corals, collectively or as single species, was weak and not significant ($p < 0.05$).

Relationship between species composition and the environment

In total, the 17 environmental variables (listed in Table 5) explained 18.3 % of the variance represented by the three first CCA axes in the analysis of all megafauna. The percentage explained was much higher for the CCA of the coral species alone (43.4 %). Some of the environmental factors were strongly inter-correlated (Table 5): for example depth/maximum temperature ($r = -0.87$), average temperature/

Table 4 Megafaunal taxa observed along the 54 video transects in The Gully, and the number of transects they were observed on

Taxon name	Descriptive name	No of transects
Foraminifera		
<i>Bathysiphon cf. filiformis</i>		32
Porifera		
cf. <i>Hymedesmia</i> spp.		11
Clathrididae indet.		1
<i>Farrea occa</i>		5
<i>Geodia</i> sp.		1
<i>Phakellia</i> sp.		6
<i>Polymastia cf. mammillaris</i>		24
Porifera indet.		34
Porifera sp. 1	Small white round	34
Porifera sp. 2	Branched	1
Porifera sp. 3	Stalked	13
<i>Vazella pourtalesi</i>		4
Cnidaria		
Hydrozoa		
Hydroidea Thecaphora		10
Actinaria		
Actinaria indet.		14
Actinaria sp. 1	Red-orange	17
Actinaria sp. 2	Small red	19
Actinaria sp. 3	Small dark	9
Actinaria sp. 4	Small orange	14
<i>Actinauge</i> sp.		14
Cerianthidae indet.		18
Cerianthidae sp. 1	White	2
Cerianthidae sp. 2	Small	10
Cerianthidae sp. 3	Pink	9
Cerianthidae sp. 4	Small violet	5
cf. <i>Bolocera tuediae</i>		3
Pennatulacea		
<i>Halipterus cf. finmarchica</i>		18
<i>Pennatula</i> sp.		5
Pennatulidae indet.		8
<i>Virgularia mirabilis</i>		18
Alcyonacea		
<i>Anthomastus grandiflorus</i>		6
<i>Duva florida</i>		21
Nephteidae sp. 1	White	15
Nephteidae sp. 2	Blue	10
Nephteidae indet.		12
Gorgonacea		
<i>Acanella arbuscula</i>		5

Table 4 continued

Taxon name	Descriptive name	No of transects
<i>Acanthogorgia armata</i>		4
Gorgonacea		6
<i>Keratoisis ornata</i>		8
<i>Paragorgia arborea</i>		8
<i>Primnoa resedaeformis</i>		5
<i>Radicipes gracilis</i>		8
Scleractinia		
<i>Flabellum alabastrum</i>		11
<i>Flabellum macandrewi</i>		1
<i>Flabellum</i> cf. <i>angulare</i>		3
<i>Flabellum</i> spp.		12
<i>Lophelia pertusa</i>		1
Polychaeta		
<i>Hyalinoecia tubicola</i>		5
Polychaeta indet.		2
Sabellidae indet.		10
Serpulida indet.		7
Mollusca		
cf. <i>Bathypolypus</i> sp.		2
cf. <i>Buccinum</i> sp.		3
Decapoda indet.		6
Octopoda indet.		1
Echinodermata		
Crinoidea		
Crinoidea indet.		10
Ophiuroidea		
<i>Novodinia</i> sp.		3
Ophiuroidea indet.		11
Asteroidea		
Asteroidae indet.		22
Asteroidae sp. 1	<i>Porania</i> -like	1
<i>Astropecten irregularis</i>		2
<i>Ceramaster</i> sp.		4
<i>Henricia</i> sp.		22
<i>Hippasterias</i> cf. <i>phrygiana</i>		8
<i>Porania</i> cf. <i>pulvillus</i>		4
<i>Solaster endeca</i>		2
<i>Tremaster mirabilis</i>		2
Echinoidea		
<i>Echinarachnius parma</i>		3
Echinoidea indet.		1

Table 4 continued

Taxon name	Descriptive name	No of transects
Pycnogonidae		1
Crustacea		
Brachyura indet.		10
Brachyura sp.1	<i>Hyas-like</i>	1
<i>Chionoecetes opilio</i>		20
<i>Chaceon quinquedens</i>		1
<i>Lithodes maja</i>		12
Natantia indet.		1
Aanomura indet.		1
Paguridae indet.		10
Pandalidae indet.		2
Agnatha		
<i>Myxine glutinosa</i>		5
Condriichthyes		
<i>Chimaera</i> sp.		2
<i>Raja</i> sp. 1		10
<i>Raja</i> sp. 2	Small pink	4
<i>Squalus acanthias</i>		5
Teleostei		
Cottidae indet.		3
Gadeidae indet.		3
<i>Gadus morhua</i>		1
<i>Hippoglossus hippoglossus</i>		4
<i>Lophius americanus</i>		15
Macrouridae indet.		28
<i>Molva molva</i>		3
Pleuronectidae indet.		29
<i>Sebastes</i> sp.		37
Teleostei indet.		28
Teleostei sp. 1	Eel-like	17
<i>Urophycis chesteri</i>		27

maximum temperature and ($r = 0.85$), average salinity/maximum salinity ($r = 0.86$), average angle/maximum angle ($r = 0.84$), and sand/clay ($r = -0.89$). In Figures 5 and 6 only variables with a relatively strong correlation ($r > 0.34$) with axes are shown. CCA identified four environmental factors (% boulder, axis distance, % sand and maximum salinity) that explained most of the variation in the total species data. For the coral-only data the combination of the following variables explained most of the variation: axis distance, average salinity, % sand, % clay, % cobbles, % mudstone and average seabed angle. The percentage of boulder substrate was strongly negatively correlated with Axis 1 in Figures 5A and 5B (Table 6) and the species (Fig. 5B) were distributed widely along this axis. Most coral species occurred to the left in this diagram, reflecting their substratum needs. Much of the

Table 5 Correlation coefficients (r) for the relationship between environmental variables for the video transects. T = temperature, S = salinity, Ang. = seabed angle, Topo = topographic relief, Bo = % boulder, M-st = % mudstone, Co = % cobble, Pe = % pebble, Sa = % sand, M = % mud. Values >0.36 are significant (p <0.01)

	Axis dist.	Depth	T ave	T min	T max	S ave	S min	S max	Angle ave	Angle max	Topo	Bo	M-st	Co	Pe	Sa	M
Axis dist.	1.00																
Depth	0.60	1.00															
T ave	-0.34	-0.70	1.00														
T min	0.18	0.42	-0.01	1.00													
T max	-0.36	-0.87	0.85	-0.45	1.00												
S ave	0.62	0.73	-0.16	0.63	-0.49	1.00											
S min	-0.10	0.09	-0.06	0.08	-0.03	0.03	1.00										
S max	0.63	0.53	-0.02	0.22	-0.17	0.86	0.03	1.00									
Ang. Ave	0.36	0.49	-0.35	0.09	-0.33	0.29	0.25	0.33	1.00								
Ang. Max	0.23	0.37	-0.36	0.13	-0.32	0.16	0.33	0.15	0.84	1.00							
Topo	0.00	0.26	-0.23	0.09	-0.22	0.13	0.30	0.13	0.61	0.77	1.00						
Bo	0.28	0.28	-0.15	0.09	-0.22	0.20	-0.09	0.16	-0.14	-0.21	-0.19	1.00					
M-st	0.11	0.16	-0.07	0.00	-0.06	0.19	0.00	0.28	0.65	0.40	0.47	-0.12	1.00				
Co	-0.09	-0.07	-0.12	-0.20	-0.02	-0.17	-0.07	-0.16	-0.11	-0.16	-0.17	0.31	-0.13	1.00			
Pe	-0.14	-0.25	-0.16	-0.62	0.16	-0.44	-0.07	-0.25	-0.22	-0.23	-0.16	0.20	-0.19	0.77	1.00		
Sa	-0.56	-0.40	0.16	0.02	0.15	-0.41	-0.10	-0.50	-0.39	-0.18	-0.04	-0.17	-0.22	-0.12	-0.09	1.00	
M	0.57	0.42	-0.07	0.17	-0.16	0.48	0.13	0.50	0.25	0.14	-0.04	0.09	-0.04	-0.20	-0.23	-0.89	1.00

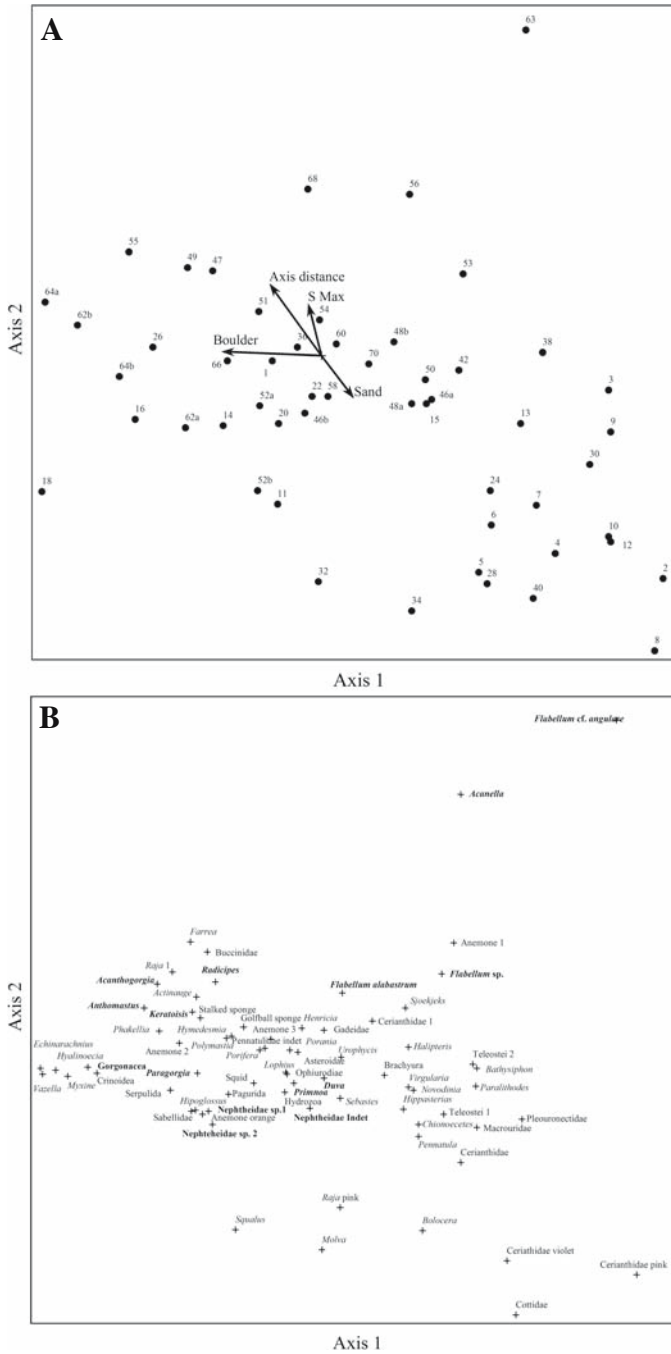


Fig. 5 Ordination plots from Canonical Correspondence Analysis of all species. **A** Plot of transects and environmental vectors. **B** Plot of species

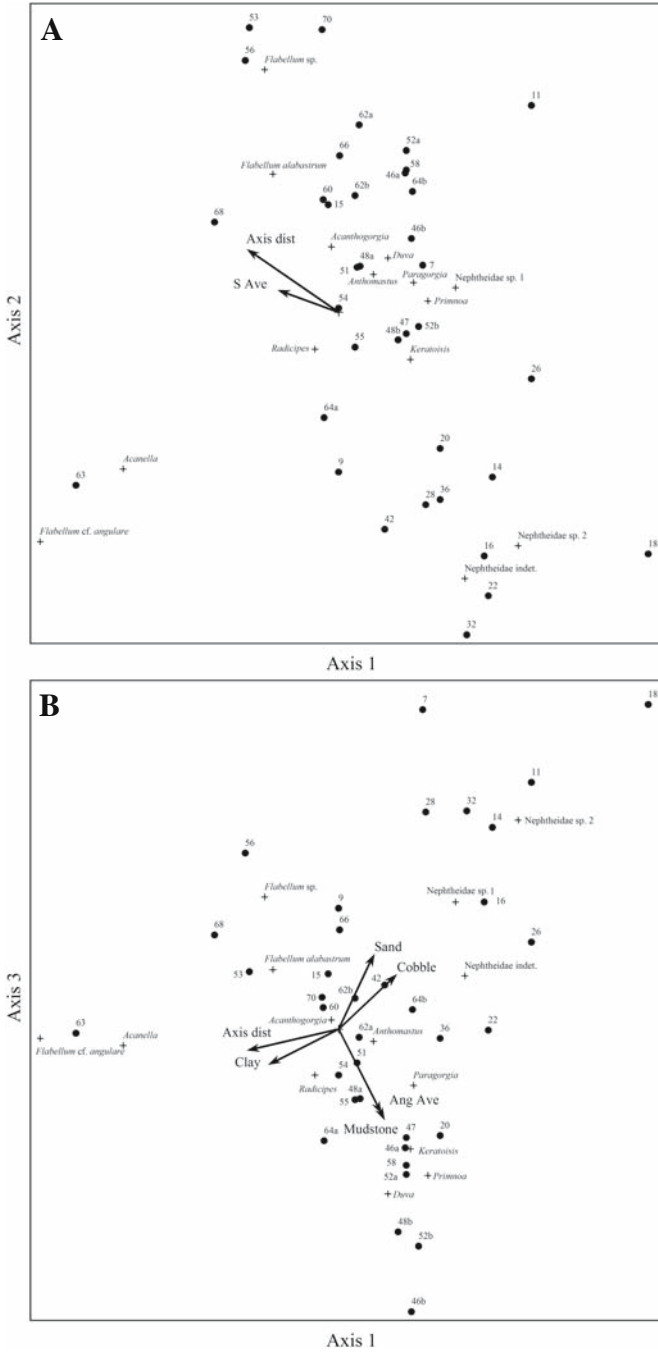


Fig. 6 Ordination plots from Canonical Correspondence Analysis of only the corals. **A** Plot of transects, species and environmental vectors on first and second axis. **B** Plot of transects, species and environmental vectors on first and third axis

Table 6 Correlation coefficients (R^2) for the relationship between environmental variables and CCA axis (inter-set correlation) in analyses of all species and for corals only

Variables	All megafauna			Corals only		
	Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3
Axis dist	-0.31	0.53	-0.36	-0.67	0.34	-0.14
Depth	-0.26	0.39	-0.08	-0.17	0.24	-0.05
T Ave	0.34	-0.34	0.04	0.13	0.07	0.06
T Min	0.10	-0.06	-0.03	0.29	0.14	0.25
T Max	0.24	-0.32	0.07	0.10	0.11	-0.05
S Ave	-0.04	0.45	0.03	-0.44	0.12	-0.09
S Min	-0.03	-0.05	0.04	0.08	-0.08	-0.08
S max	-0.08	0.38	0.07	-0.26	0.26	-0.27
Ang Ave	-0.22	-0.18	-0.03	0.32	0.34	-0.56
Ang Max	-0.22	-0.25	-0.18	0.30	0.31	-0.51
Topo	-0.02	-0.18	0.03	0.22	0.16	-0.51
Boulders	-0.61	0.03	-0.01	0.39	-0.07	0.31
Mudstone	-0.05	-0.13	0.38	0.34	0.00	-0.60
Cobbles	-0.46	-0.03	0.30	0.43	-0.19	0.37
Pebbles	-0.50	0.01	0.13	0.38	-0.29	0.25
Sand	0.20	-0.32	-0.07	0.26	0.03	0.51
Clay	0.06	0.33	-0.17	-0.52	0.05	-0.24

variation in the coral-only data was not explained by the environmental variables. This was demonstrated by the few environmental variables selected for the second axis (Fig. 6A).

Except for *Acanella arbuscula* and *Radicipes gracilis*, which occurred on clay bottoms, the gorgonians were confined to areas with cobble and boulder. The nephtheid corals utilised a wider range of substrates including semi-consolidated mudstone. Figure 6b indicated that the nephtheid corals, except *Duva florida*, occurred in areas with a relatively dense cover of sand and cobble close to the head of the canyon. On the other side of the plot *Flabellum cf. angulare* and *Acanella arbuscula* was associated with dense cover of clay in the outer part of the canyon (high value of "axis distance"). The figure also demonstrated that *Keratoisis ornata*, *P. resedaeformis*, and *D. florida* were associated with steep transects and dense cover of semi-consolidated mudstone. All *Flabellum* species were associated with low values for average angle, indicating that they are associated with level seabed. The position of *R. gracilis* in the centre of the plot indicated that this species occurred in areas with mixed seabed.

Discussion

Methods

It is difficult to standardise video recording of habitats in deep-water to enable quantitative data with minimal error. As video-records and photos are not well suited for identification of small epibenthic organisms (<5 cm), only larger forms were taxonomically identified (i.e. megafauna). The diversity and abundance of epibenthos reported here are therefore minimum estimates. The inaccuracy of the estimates of investigated areas leads to errors in abundance estimates for megafauna. There were two sources of error in estimating the area of video sequences: inaccurate geographical positions, and variable width of the visual field. The navigation error of ± 2 m induced an error of ~ 17 % in the abundance of corals. Unfortunately, there was no practical way available to estimate the width of the visual field continuously. However, the height above bottom was quite stable most of the time and the error resulting from this factor is estimated to be <10 %.

The method used for estimating the relative abundance of different bottom types is not as precise as a point-count method. However, the latter method would have been very time-consuming applied to the large amount of video records used in this study. Previously Mortensen and Buhl-Mortensen (2004) compared estimates gained by the visual “subjective” method with estimates made by counting points overlying the different substrate classes in a grid of 20 point. This comparison was based on parallel estimates using the two techniques at three transects with a total of 72 video sequences. Since the correlation between the two estimation techniques was good ($R^2 = 0.86$, $p < 0.001$) the simple and fast visual “subjective” method was chosen for this study.

The seabed below 500 m has been poorly investigated in The Gully, and little is known about the distribution and abundance of corals below this depth. Based on the results from a study of megafauna in canyons off northeastern USA (Hecker et al. 1980) larger gorgonians such as *Paragorgia* and *Primnoa* may occur with higher abundance deeper.

The abundance of corals compared to other regions

The average abundance of corals found in this study was lower than what has been reported from deep-sea coral reefs off Norway (Mortensen et al. 1995) and from gorgonian “forests” in the Northeast Channel off Atlantic Canada (Mortensen and Buhl-Mortensen 2004), but comparable to what Hecker et al. (1980) found for Canyons off the northeast coast of USA. Hecker et al. (1980) provided an early quantitative study of the distribution of corals and megafauna from photographs and submersible observations in three canyons. Averaged for 100-m depth intervals, they estimated a highest abundance for *Acanthogorgia armata* of 3.2 colonies $\cdot 100$ m⁻² and for *Paragorgia arborea* of 0.3 colonies $\cdot 100$ m⁻² between 400 and 800 m depth in Oceanographers Canyon. The average abundance of *Primnoa resedaeformis* is 4.8 and 4.3 colonies $\cdot 100$ m⁻² in the Northeast Channel and on the Sula Reef respectively, compared to 2.0 colonies $\cdot 100$ m⁻² for transects with presence in The

Gully (Table 2). The same pattern applies for *P. arborea* with 0.6 and 3.1 colonies ·100 m⁻² in the Northeast Channel and on the Sula Reef respectively, whereas only 0.3 colonies ·100 m⁻² were observed in The Gully, identical to the value reported from Oceanographers Canyon (Hecker et al. 1980). Unfortunately, there are no similar data to provide a similar comparison for the other corals. However, *Keratoisis ornata* seems to be more common in The Gully than other sites in Atlantic Canada.

Distribution of corals and environmental controls

In general, the distribution of deep-water corals is uneven and the importance of different environmental factors may differ between regions. Of physical factors, suitable seabed substratum, water temperature and salinity are obvious requirements that must be met to enable the colonisation and growth of corals. Mortensen and Buhl-Mortensen (2004) found that the distribution of deep-water gorgonians in the Northeast Channel was patchy even within areas with high percentage of cobble and boulder, and within the depth range were the highest abundance was found. This indicated that other factors varying over small spatial scales are also important.

Geographic location

The number of species was significantly ($p < 0.005$) correlated with the distance along the canyon axis, and different species were more common or abundant in certain divisions than others. This is explained by the strong correlation of axis distance with other variables such as depth, substratum types and salinity (Table 5). The two sides of The Gully have some differences in oceanographic conditions (currents, temperature, and salinity). The possible effects of these factors will be discussed below.

Substratum and topography

With the exception of a few species having anchorage structures for soft sediments, deep-water gorgonians are found on hard substrata such as cobbles, boulders or bedrock. In The Gully, the distribution of the gorgonians appears to be controlled by the availability of hard substrata. The average percentage cover of cobble and boulder in The Gully (3.9 % combined) is lower than in the Northeast Channel (25 %) (Mortensen and Buhl-Mortensen 2004) where the abundance of gorgonian corals is higher. The semi-consolidated mudstone was a suitable substrate for nephtheid corals but is probably too loose to serve as a solid substrate for the larger gorgonians.

The topographic index was poorly correlated with diversity and abundance of megafauna. The angle of the seabed was relatively strongly correlated with the fauna patterns revealed by CCA (Figs. 5 and 6). This variable is also a collective variable correlated with the topographic index and the cover of semi-consolidated mudstone. Topography also influences to the strength and pattern of near-bottom currents, and has been suggested as factor modifying the environment to the benefit of corals (Genin et al. 1986; Mortensen et al. 2001). Previous studies have demonstrated that the inclination of the seabed is related to re-suspension of

particulate matter and increased productivity (Rice et al. 1990; Frederiksen et al. 1992).

Depth and hydrography

Many factors that co-vary with depth can be expected to determine vertical distribution patterns. In the Northeast Atlantic different regional maximum depths of deep-water corals in offshore areas generally reflect different maximum depths of water masses with suitable temperatures (Frederiksen et al. 1992; Tendal 1992; Freiwald 1998; Mortensen et al. 2001). Unfortunately, this investigation was limited to depths above 544 m, which prevents discussion of the local maximum depths of corals in The Gully. There are few attempts to study corals below this depth off Nova Scotia. These studies, using dredges or trawls, have found *Paragorgia* and *Primnoa* as deep as 1097 and 457 m, respectively (Verrill 1922; Deichman 1936; Breeze et al. 1997). During previous habitat mapping in The Gully using a deep-sea drop camera *Keratois ornata*, *Anthomastus grandiflorus*, and *Radicipes gracilis* were observed at depths between 800 and 1300 m (Kostylev 2000). On the northeast coast of USA, Hecker et al. (1980) found *Paragorgia* down to 800 m depth, and *Primnoa* down to 560 m. These observations indicate that peak abundance for these corals may occur deeper than indicated by our study (Fig. 3).

Depth was not selected as a variable explaining much of the variation in the species data by CCA. This is probably explained by inter-correlation with temperature, which was strongly correlated with the variance in species data. Diversity and abundance of corals was negatively correlated with maximum temperature and positively correlated with maximum salinity. Tendal (1992) and Madsen (1944) describe the distribution of *Paragorgia* and *Primnoa* in the North Atlantic and suggest it is connected to the North Atlantic Current characterised by temperatures generally between 4 and 8°C, and stable salinity around 35 ‰. Our study indicated a shallower upper limit for alcyonacean corals (170 m) than for the rest (340 m; Fig. 3), suggesting that these taxa have different environmental requirements.

The lower abundance and diversity of corals on the eastern side of the canyon (Table 3) may be explained by the hydrographical conditions and currents, but it is hard to draw conclusions because the conditions are not known in a sufficient detail. These differences may also relate to differences in food supply. Food supply is an important biological factor, which may control the distribution of sessile invertebrates at both large and small scales. Unfortunately, the food requirement of deep-water gorgonians is generally unknown.

The significance of canyons as coral habitats

Similar to other submarine canyons, The Gully houses a diverse coral fauna. Nine coral species (one alcyonacean, seven gorgonians and one scleractinian) have previously been reported from The Gully (Breeze et al. 1997; MacIsaac et al. 2001). The new records for the area include *Anthomastus grandiflorus*, *Duva florida*, all three *Flabellum* species, and *Radicipes gracilis*. *Paramuricea placomus* has

previously been recorded from The Gully (Breeze et al. 1997), but was not observed during this study. Other canyons off Nova Scotia, such as Shortland and Halidimand Canyons, have been identified by fishermen as sites where large, colonial corals are found at depths greater than 300 m (Breeze et al. 1997). The reason why canyons are diverse coral habitats is probably primarily due to their great variety of habitats (depth, topography, bottom substrates and hydrographic conditions). Previous studies have shown that the benthic communities are more diverse and have greater abundance in canyons than in nearby slope areas (Hecker et al. 1980; Harrison and Fenton 1998; Vetter and Dayton 1998).

Hargrave et al. (2004) found the highest diversity of epifauna in The Gully on hard substrates of glacial origin along the edges of the channels, where alcyonaceans and gorgonians were common. In contrast with our findings Hargrave et al. (2004) found the maximum species richness of epifauna to be relatively shallow, around 180 m. Within the depth range of our study the species richness was higher below 300 m than above. This difference may occur because of the different scales of imagery processed in these two studies, which could mean that different components of the fauna were studied (photographs *vs.* sequences of video records).

Canyons influence local water properties and zooplankton distribution (Allen et al. 2001). It has been suggested that submarine canyons accumulate organic debris (Vetter 1994), and it is possible that deep-ocean currents, such as the south-westward flowing deep-water in the North Atlantic (Dickson et al. 1990) may bring particulate organic matter (POM) into The Gully. Harding (1998) suggests that there is a greater availability of POM in submarine canyons because of deposition of organic matter on continental slopes and patterns of water circulation in canyons. Storm activity may be an important factor for the high input of benthic detritus from shelf (Harding 1998). High concentration of POM may be important as food for the corals. The high coral abundance on the western outer division fits with an outflow of water that has been trapped from the current following the slope from northeast. Hargrave et al. (2004) conclude that organic matter is transported down the axis of the canyon. This transport is likely to be stronger on the western side because of the general current direction to the west.

There are very few species known to be obligate symbionts on deep-sea corals. The associated fauna of corals generally consists of generalistic commensal species that are able to survive without corals in other habitats. The frequency and abundance of larger corals in The Gully is low, which indicates that these corals play a limited role as habitat for other megafaunal species. The abundance of fish in The Gully was not significantly correlated with abundance of corals. Probably a coral habitat needs to have certain minimum abundance before it serves the function of shelter, and enhanced food availability.

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