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Distribution of cold-water corals in the Whittard Canyon, NE Atlantic Ocean



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ABSTRACT

The deep-sea floor occupies about 60% of the surface of the planet and is covered mainly by fine sediments. Most studies of deep-sea benthic fauna therefore have concentrated on soft sediments with little sampling of hard substrata, such as rocky outcrops in submarine canyons. Here we assess the distribution and abundance of cold-water corals within the Whittard Canyon (NE Atlantic) using video footage from the ROV *Isis*. Abundances per 100 m of video transect were calculated and mapped using ArcGIS. The data were separated into five substratum types, 'Sediment', 'Mixed Sediment and Rock', 'Sediment Slope', '*Lophelia* reef' and '*Lophelia* and rock'. Abundance and community structure were compared. A maximum abundance of 855 coral colonies per 100 m of ROV transect were observed with 31 coral types identified. Highest taxon richness was observed along a '*Lophelia* reef' area, although a larger richness of Octocorallia was observed away from the '*Lophelia* reef' areas. '*Lophelia* reef' and '*Lophelia* and rock' areas were found to have a different coral community structure from the other substratum types. We suggest this is the result of *Lophelia* outcompeting other coral types because there is increased coral taxon richness in areas without *Lophelia*. We also hypothesise that the hydrodynamic regime within the Whittard Canyon results in differences in organic matter input including higher quality food, in comparison with other deep-water environments, leading to changes in the coral communities.

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1. Introduction

Corals are best known from shallow tropical seas, despite > 65% of recorded coral species occurring below 50 m depth (Cairns, 2007; Lindner et al., 2008; Roberts et al., 2009). In contrast to their shallow-water counterparts, cold-water corals do not require light or high temperatures to survive in deep-waters because they do not have a symbiotic relationship with zooxanthellae (algae). They are exclusively filter feeders. The morphology of many cold-water corals allows them to contribute structural complexity to deep-sea ecosystems (Watanabe et al., 2009) and to provide a habitat for a wide variety of different taxa (Buhl-Mortensen and Mortensen, 2005; Clark et al., 2006). Recognition that these ecosystems make a potentially significant contribution to deep-sea biodiversity means there is a requirement for better understanding of the distribution of coral habitats in the deep ocean, including in submarine canyons, in order to improve the management of these ecosystems.

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Submarine canyons are steep-sided valleys that cut across continental margins. They are common on many continental shelf edges and slopes (de Stigter et al., 2007; de Leo et al., 2010; Harris and Whiteway, 2011). Canyons exhibit a range of morphologies from relatively shallow systems with many gullies to deeply incised sinuous valleys (Harris and Whiteway, 2011). The flow of water in canyons is governed by the surrounding topography and the physical environment, which differs from the continental slope (Genin et al., 1986; Davies et al., 2008). Current velocities increase when flow comes into contact with steep topography (Genin et al., 1986, 1989). In a canyon this can be coupled with the creation of higher intensity internal waves than the surrounding slopes (Quaresma et al., 2007). This can result in increased turbulence and sediment resuspension, leading to the creation of nepheloid layers and turbidity flows within the canyon (de Stigter et al., 2007; Arzola et al., 2008). The combination of these phenomena make canyons significant for shelf-slope particulate exchange (Oliveria et al., 2002; Quaresma et al., 2007; Arzola et al., 2008; Garcia et al., 2008). Consequently, canyons are highly heterogeneous environments leading to the creation of a wide variety of niches for biological communities. The amalgamation of these

factors means canyons are often thought of as areas of enhanced biodiversity (de Leo et al., 2010; Vetter et al., 2010). However, very little work has occurred on the biological assemblages and their community structure within canyons, especially cold-water coral assemblages (Huvenne et al., 2011). The present study seeks to increase knowledge on the distribution of deep-sea corals within submarine canyons, focussing on the Whittard Canyon system on the continental margin in the NE Atlantic.

The Whittard Canyon is located to the south east of the Goban Spur (NE Atlantic), along the continental margin in the northern Bay of Biscay around 300 km south of Ireland (Fig. 1). Water masses in the North Eastern Atlantic have been described by Vangrieshem (1985) and Arhan et al. (1994). Aminot and Kerouel (2004) summarised the water masses as North Atlantic Surface Water (max 100 m depth) overlying Eastern North Atlantic Central Water (ENACW) (< 700 m). A steep pycnocline separates the ENACW from Mediterranean Outflow Water (MOW). The MOW extends down to about 1200 m, mixing with the underlying Labrador Sea Water marked by a salinity minimum at around 1800 m. There is some influence of Norwegian Sea Water at around 2000 m. Below this depth North Atlantic Deep Water (NADW) derived from Greenland appears, and is heavily influenced by the pervading Atlantic Antarctic Bottom Water at greater depths (Matthias and Godfrey, 2003; Aminot and Kerouel, 2004; De Mol et al., 2011).

The Whittard Canyon extends from the upper slope to abyssal depths, varying in depth between 200 and 4000 m (Duineveld et al., 2001), with two main branches (Fig. 1). These run from the shelf edge down into the canyon and at approximately 3700 m depth merge into one large channel which opens out onto the Porcupine Abyssal Plain. The canyon floor is sediment-covered with very little exposed rock, other than on the extreme walls (Reid and Hamilton, 1990). Duineveld et al. (2001) found that the POC concentrations were higher in the canyon than in the surrounding open slope areas, indicating organic enrichment

within the canyon. The surface waters of the upper reaches of the canyon have relatively high biological productivity because of nutrient upwelling along the Celtic Shelf edge (Wall et al., 2010), resulting in increased nutrient transport through the canyon via mechanisms such as internal wave formation and turbidity flows.

The main aim of our research was to describe the abundance, distribution and community composition of cold-water corals in the Whittard Canyon in relation to substratum type. The study was based on video and photographic observations taken from the Remotely Operated Vehicle (ROV) *Isis*.

2. Materials and methods

2.1. Data collection

Observations of the seabed were taken with video and stills imagery using the ROV *Isis* during RRS *James Cook* cruises 10 and 36 (JC10 and JC36) to the Whittard Canyon (Weaver and Masson, 2007; Masson, 2009). A total of 13 dives with extensive video transects were completed resulting in over 80 hours of video. Transects were obtained mainly in the major branches of the canyon, the easternmost and westernmost tributaries (Fig. 2). The flanks of the canyon were studied over a range of depths between 520 and 4073 m (Table 1).

Isis was fitted with multiple cameras, which were used for piloting the vehicle and for scientific observations. The scientific cameras were a fixed Atlas 3-chip camera with a 14× optical zoom and a Pegasus pan and tilt camera, which both record onto DVCAM tapes and DVD, and a Scorpio 3.34 mega-pixel digital still colour camera. In order to obtain video footage, the sea floor was illuminated by two 600 J strobe lamps, five 250 W incandescent lamps and three HMI 1200 W lamps.

2.2. Video analysis

The video footage was analysed using the computer package U-lead Video, version 10. Each video was analysed in its entirety with the occurrence of individual coral colonies being noted along the transect with the time, depth and substratum type. The seabed observed within the video footage indicates the Whittard Canyon is dominated by sediment (mud and sand) and sediment-draped rocks. Two dives provided footage of *Lophelia* reefs on steep overhangs. In some cases, the *Lophelia* had been covered in sediment and subsequently had perished. However, this led to a novel substratum colonised by octocorals, the focus of this study. A distinction was made therefore between live 'Lophelia reef' and 'Lophelia and rock' where reefs were not created (Fig. 3). Five different substratum types were identified in the Whittard Canyon; 'Sediment', 'Sediment Slope', 'Mixed Sediment and Rock', 'Lophelia reef' and 'Lophelia and rock' (Fig. 3).

Although laser scales are used in conjunction with video on *Isis*, it was not always possible to view where they mark the seabed, due to changes in ROV altitude, making the area of the field of view hard to determine. Therefore it was decided to analyse the images in terms of time rather than area, making the assumption that during transects *Isis* travelled at a speed of ~0.1 knots (5 cm s⁻¹). For each dive a 50 min concatenated segment of the parameter being analysed i.e. depth or substratum type (Supplementary Tables 1 and 2) was used to allow a consistent method for comparison between dives of differing lengths as well as ensuring a manageable data set was achieved. These 50-minute concatenated segments consisted of ten continuous 5 min segments randomly chosen per dive. Where it was not possible to obtain these data the dive was not included in the analysis. This resulted

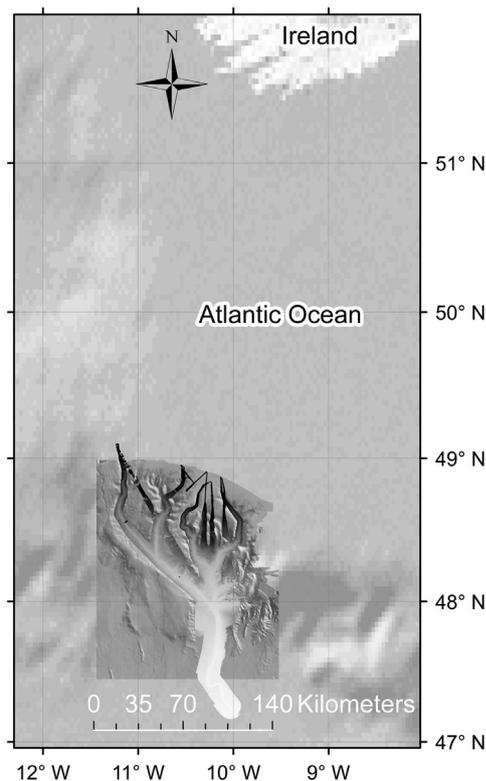


Fig. 1. Location of Whittard Canyon on the Celtic margin, Bay of Biscay.

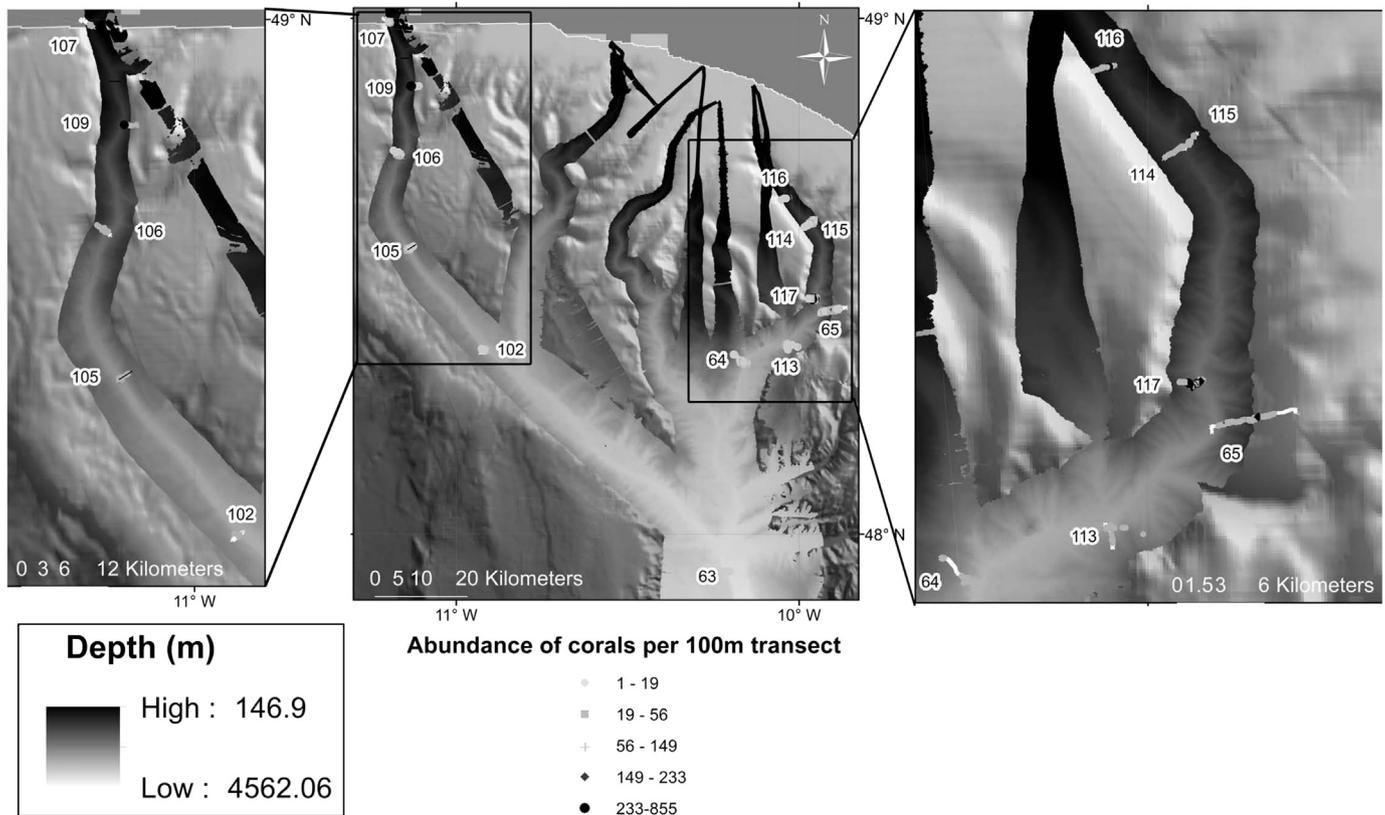


Fig. 2. Distribution of cold-water corals identified and ROV transects in the Whittard Canyon. Symbols indicate the number of corals found per 100 m transect. Bathymetry generated from a multibeam survey. White dots indicate the extent of the dive where no corals are found. No contours were included as they are too close together and mask the coral occurrence. For finer scale along track data on coral distributions see Supplementary Figs. 1–4.

Table 1
Dates, positions, depths hours of video and transect length recorded by ROV *Isis* during Whittard Canyon video dives on cruises JC10 (dives 63–65) and JC36 (dives 102–117).

<i>Isis</i> (dive no)	Date	Start longitude (W)	Start latitude (N)	End longitude (W)	End latitude (N)	Depth range (m)	Hours video	Length transect (m)
63	03/07/2007	10° 12.09'	48° 55.75'	10° 13.31'	47° 55.45'	3706–4073	6.5	1810
64	04/07/2007	10° 9.200'	48° 19.94'	10° 11.48'	48° 21.04'	2157–3455	9.5	3822
65	04/07/2007	10° 11.49'	48° 21.04'	09° 51.62'	48° 26.39'	520–2641	14.5	6875
102	25/06/2010	10° 54.48'	48° 21.87'	10° 55.64'	48° 21.18'	2578–3163	7.5	2485
105	28/06/2010	11° 08.44'	48° 33.26'	11° 07.40'	48° 33.67'	2840–3085	7	1905
106	29/06/2010	11° 09.48'	48° 44.01'	11° 11.04'	48° 44.77'	1640–2300	7	2501
107	30/06/2010	11° 11.36'	48° 59.38'	11° 12.14'	48° 59.80'	600–1062	12	2751
109	01/07/2010	11° 08.16'	48° 52.22'	11° 08.22'	48° 52.31'	958–1727	8.5	2539
113	13/07/2010	10° 02.37'	48° 22.29'	10° 01.95'	48° 21.47'	2395–3202	9	2010
114	18/07/2010	09° 58.00'	48° 36.19'	09° 57.28'	48° 36.75'	1102–1640	11.5	1704
115	19/07/2010	09° 58.07'	48° 36.28'	09° 59.08'	48° 35.85'	1378–1677	6	1876
116	19/07/2010	10° 01.85'	48° 39.29'	10° 03.05'	48° 39.04'	892–1370	9	1707
117	20/07/2010	09° 56.97'	48° 27.65'	09° 58.20'	48° 27.60'	1672–2448	11	1999

in 28 samples for 200 m depth bands, 17 samples for 500 m depth bands, and 17 samples for substratum type, to be used for time-normalised statistical analyses.

2.3. Data analyses

2.3.1. Map creation

All data were collated and formatted for compatibility with ESRI ArcGIS. A single bathymetric chart was created using EM120 swath mapping data collected during a previous cruise (JC35). Once video analysis was complete, latitudes and longitudes were assigned to each observation by identifying the time of observation in the *Isis* data string. Depth was also obtained in this manner. A map showing abundance of corals per 100 m along a transect was created by calculating the distances between observations. This ensured that all observation of corals could be visualised and

overall occurrence patterns assessed, which would not have been possible with the time-normalised data.

A graduated colour scheme was applied to allow the difference in coral density to be visualised with five categories being chosen from 1–855 with high density of corals (233–855) being binned into one grade (Fig. 3). Substratum type was also plotted as a layer on this map for Dive 65, Dive 106, Dive 114 and Dive 116 to allow an in-depth view of the relationship between substratum and the genera *Acanella*, *Anthomastus* and *Lophelia* (Supplementary Figs. 1–4). Again a graduated colour scheme was applied for the substratum type and individual genera per dive diving each genera into 5 categories.

2.3.2. Multivariate analysis

Multivariate analyses were carried out with PRIMER v6 to assess if coral assemblages change dependent on depth or substratum type. A

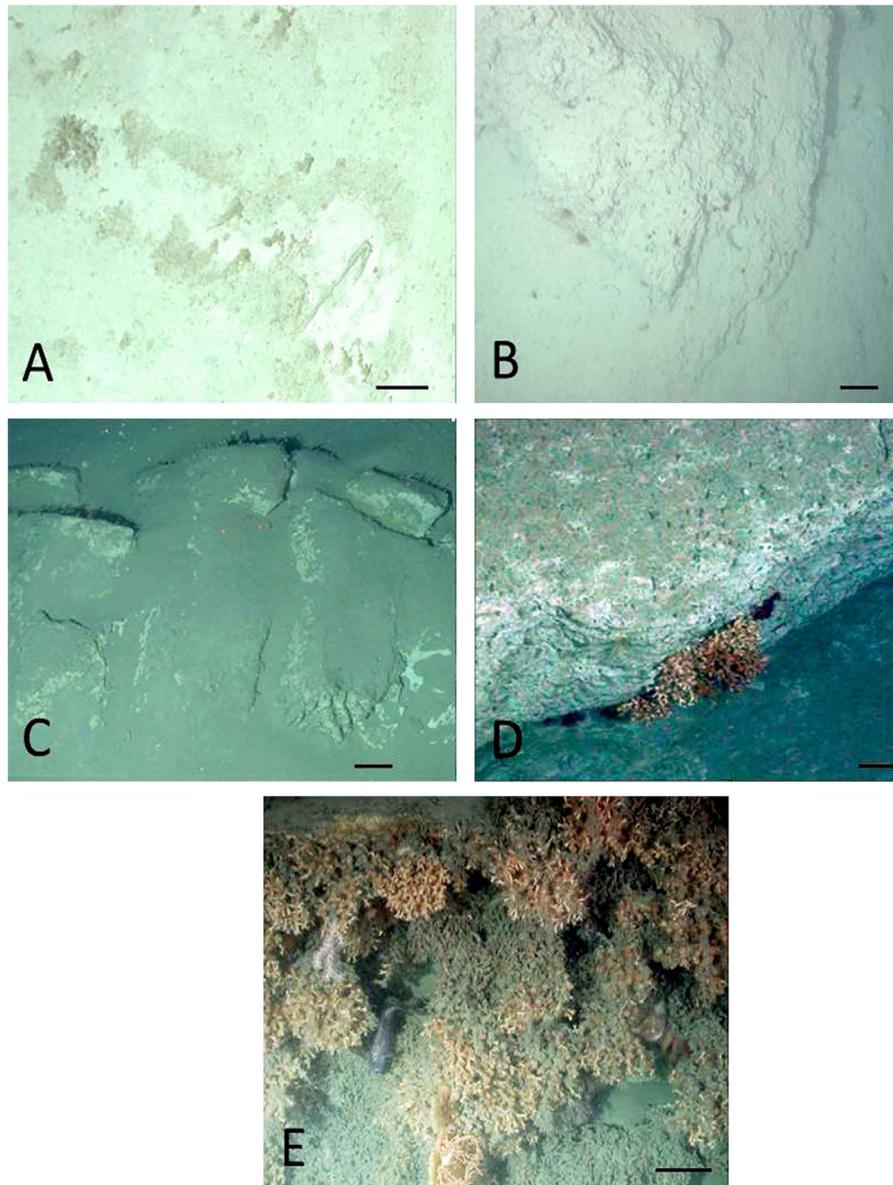


Fig. 3. Picture plate of substratum types used throughout the study. A = 'sediment', B = 'sloped sediment', C = 'mixed rock and sediment', D = '*Lophelia* and rock', E = '*Lophelia* reef'. Scale bar represent 10 cm.

fourth-root transformation was used to reduce the effect of the dominant coral types on the faunal abundance data analyses (Clarke and Warwick, 1994) allowing SIMPER (Similarity Percentage analysis) to be employed to investigate which coral types were responsible for the changes in assemblage structure between variables. A Bray–Curtis coefficients were calculated allowing the use of ANOSIM (Analysis of Similarity) to analyse both depth and substratum type using the time-normalised data. Multi-dimensional scaling (MDS) was used to provide a visual representation of the data. MDS ordinates were plotted against substratum type.

3. Results

3.1. Distribution and abundances of coral

Thirteen usable dives were completed within the Whittard Canyon during the two RRS *James Cook* cruises JC10 and JC36 in 2007 and 2009, respectively (Table 1). Thirty-one putative types of coral (Table 2, Fig. 4) were recognised among 10,353 individuals. It

was not always possible to distinguish either whip coral species or some pennatulid species in the videos and thus individuals within these taxa were grouped under the headings 'whip coral', 'pink whip coral' and 'Pennatulacea'. Of the 31 assigned coral types, three were responsible for 74.4% of all individuals: *Acanella*, *Anthomastus* and *Lophelia*. The greatest number per 100 m transect length (855 individuals) occurred during Dive JC36-116 along a '*Lophelia* reef' wall, where there was a steep overhang (Fig. 3). The areas with the greatest number of individuals occurred in the upper canyon where the slopes were at their steepest. Most areas were either devoid of coral or had only between 1 and 56 individuals per 100 m transect (Fig. 3).

Maps were created to compare the distributions of the dominant taxa with the occurrence of the different substratum types along four different dive tracks (Dive 65, Dive 106, Dive 114 and Dive 116). These dives included all the substratum types encountered in the study (Supplementary Figs. 1–4). The maps illustrate that the greatest numbers of *Acanella* coincided with areas of 'Mixed Sediment and Rock' and 'Sediment Slope' substratum types. *Anthomastus* was mainly associated with 'Sediment Slope'.

Table 2
Presence/absence data of coral taxa observed within the Whittard Canyon during thirteen dives by the ROV Isis. Numbers correspond to ROV Isis dive numbers on JC10 (Dives 63–65) and JC36 (Dives 102–117). Each + sign indicates the presence of a taxon within a given dive.

	63	64	65	102	105	106	107	109	113	114	115	116	117
Subclass: Hexacorallia													
Order Antipatharia													
Family Schizopathidae													
<i>Bathypathes</i> sp.	+		+										
Order Scleractinia													
Family Caryophylliidae													
<i>Lophelia</i> sp.			+					+		+	+	+	+
<i>Madrepora</i> sp.			+							+			
<i>Desmophyllum</i> sp.								+		+		+	+
Subclass: Hydroidolina													
Order Anthoathecatae													
Family Stylasteridae													
Stylasterid sp			+										
Subclass: Octocorallia													
Order Gorgonacea													
Red gorgonian												+	
Whip coral													
Whip	+		+			+	+		+	+			
Pink whip		+							+	+			+
Sub-Order Alcyoniina													
Family Alcyoniidae													
<i>Anthomastus</i> sp.		+	+	+	+	+		+	+	+	+	+	+
Sub-Order Scleraxonia													
Family Paragorgiidae													
Orange Paragorgia										+			
Pink Paragorgia								+					
Sub-Order Calcaxonia													
Family Chrysogorgiidae													
<i>Radicipes</i>			+		+	+			+	+			+
Family Isididae													
<i>Acanella cf arbuscula</i>	+	+	+	+	+	+	+	+	+	+	+	+	+
Brush Isididae (Sp A)										+			
Bamboo bush coral (Sp B)				+									
Candelabra Isididae (Sp C)												+	+
Pink Isididae (Sp D)	+		+									+	
Skeleton Isididae (Sp E)			+							+			
Whip Isididae (Sp F)		+	+	+									
Pink fan Isididae (Sp G)			+									+	
Slender Pink Isididae (Sp H)												+	
Family Acanthogorgiidae													
<i>Acanthogorgia</i> sp.			+			+		+	+	+	+	+	+
Family Primnoidae													
<i>Priminoa</i> sp.								+					
Order Pennatulacea													
Sub-Order Sessiliflorae													
Family Kophoblemnidae													
<i>Kophoblemnon</i> sp.			+										
Family Umbellulidae													
<i>Umbellula</i> sp.	+		+		+	+	+		+	+	+	+	
Family Anthoptilidae													
<i>Anthoptilum</i> sp.			+			+	+	+		+	+		+
Family Protoptillidae													
<i>Distichoptilum gracile</i>			+			+				+			+
Family Pennatulidae													
<i>Pennatula aculeata</i>			+				+			+	+	+	+
Pennatulacea	+		+				+		+	+			
Unknown family													
Purple coral										+			
Peach single polyp											+	+	

Lophelia formed reef structures and occurred in small patches in the 'Lophelia and rock' substratum. *Acanella* and *Lophelia* were not seen in the same region on any dive.

3.2. Depth and distributions

Multivariate analyses of coral community differences using time-normalised data binned into 200 and 500 m depth intervals revealed no obvious depth segregation (Supplementary Figs. 5 and 6). ANOSIM tests also indicated no significant differences in community

composition (200 m bands $N=28$, $R=0.411$, $P=0.01$; 500 m bands $N=17$, $R=0.033$, $P=0.36$). As a result, depth was not considered as a co-variant in subsequent analyses.

3.3. Overall distributions and substrata type

Time-normalised data resulted in 17 samples where there was sufficient footage to allow analysis across the different substratum types (Supplementary Table 1). Within each 50 min observation period, the highest mean number of individuals occurred on

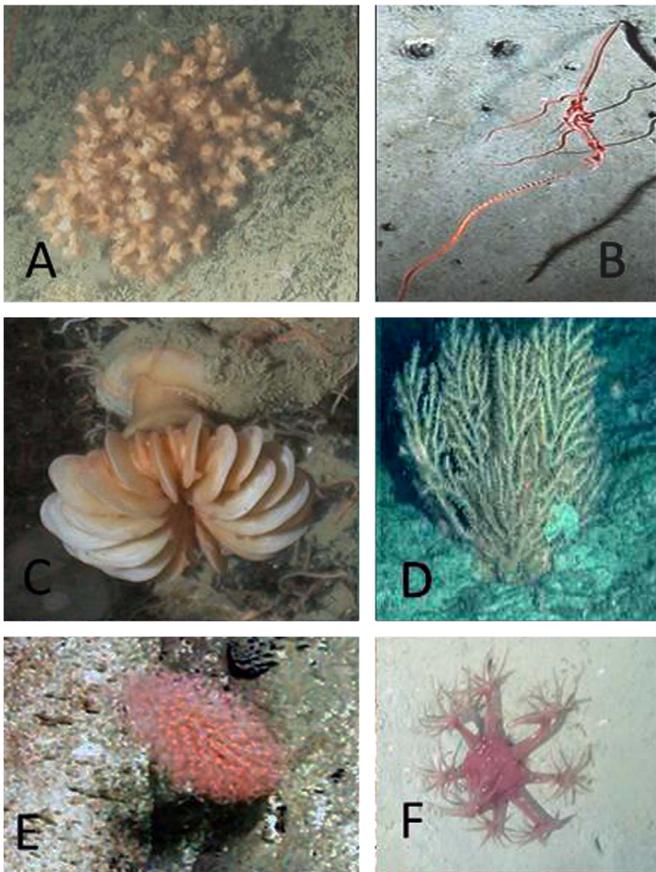


Fig. 4. Picture plate 1 of coral observed on video footage of the Whittard Canyon. (A) *Lophelia pertusa* (~30 cm), (B) *Distichoptilum gracile* (~45 cm), (C) *Desmophyllum* sp. (~10 cm), (D) *Primnoa* sp. (~60 cm), (E) *Acanella* sp. (~20 cm), (F) *Anthomastus* sp. (~15 cm). Scale could not be included as a result of a lack of laser points within the pictures therefore rough estimations of size are given.

'*Lophelia* reef' with the lowest occurring on sediment (Fig. 5). This difference was not significant (Kruskal–Wallis, $DF=4$, $N=17$, $P=0.054$). This is likely to be the result of the large standard errors indicating a large variation in the numbers observed within each substrata types on each dive (Fig. 5).

Individual substratum types are dominated by different taxa. 'Sediment' substratum contained the highest percentage of Isididae (Table 3). This was mainly attributed to large *Acanella* aggregations. Both '*Lophelia* and rock' and '*Lophelia* reef' had fewer coral higher taxa represented. 'Mixed Sediment and Rock' had a high occurrence of the alcyonarian *Anthomastus* and 94% of the schizopathid *Bathypathes* were observed on the substratum. Pennatulacea were found within the 'Mixed Sediment and Rock' and 'Sediment' substrata. 100% of the Primnoidae occurred on the 'Mixed Sediment and Rock' substratum (Table 3).

Multi-dimensional scaling (MDS) (Fig. 6) illustrates a separation of the '*Lophelia* reef' and '*Lophelia* and rock' to the top left of the plot. 'Mixed Sediment and Rock' occurred in the centre with 'Sediment' and 'Sediment Slope' occurring close together. However, ANOSIM Global R ($N=17$, $R=0.501$, $P=0.001$) indicates no difference of the overall assemblage composition among substratum types (Table 4). Despite this, when pairs of substrata are considered, there are significant differences at the 5% level between both '*Lophelia* reef' and '*Lophelia* and rock' substrata and both the 'Mixed Sediment and Rock' and 'Sediment' substrata (Table 4). This indicates that the *Lophelia* substratum types are mainly responsible for the differences observed among

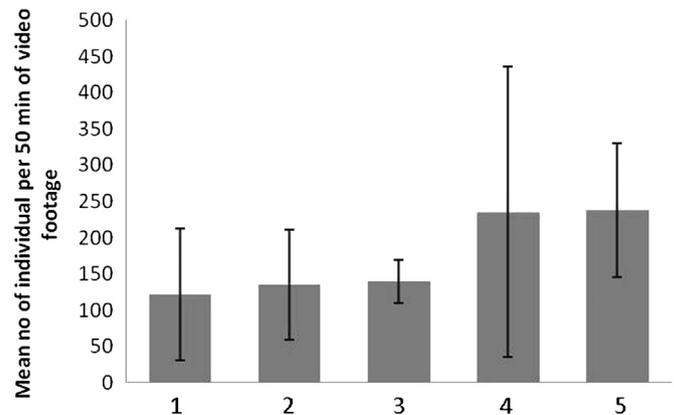


Fig. 5. Average number of individuals observed within a 50 min period on different substrata types with the Whittard Canyon. Each 50-min period is made up of ten 5-min segments accumulated together. Error bars indicate standard error from the mean. $N=17$. 1='sediment', 2='sloped sediment', 3='mixed rock and sediment', 4='Lophelia and rock', 5='Lophelia reef'.

Table 3

Coral taxon occurrence expressed as a % of the total number of coral colonies observed per substratum type. Each row totals 100%.

	Sediment	Sediment slope	Mixed rock and sediment	'Rock with <i>Lophelia</i> '	' <i>Lophelia</i> reef'
Schizopathidae	0	5.6	94.4	0	0
Carophylliidae	0	0	1.7	39.7	58.6
Gorgonacea sp.	0	0	0	0	100
Whip coral	8.6	5.8	80.8	2.9	1.9
Alcyoniidae	3.1	32.6	63.9	0.3	0
Paragorgiidae	0	0	50	50	0
Chrysogorgiidae	8.2	90.2	1.6	0	0
Isididae	55.9	13.1	27.2	0.3	3.4
Primnoidae	0	0	100	0	0
Stylasteridae	0	0	100	0	0
Pennatulacea	39.7	2.6	57.6	0	0
Unknown	2.5	2.5	75	20	0

assemblages. By plotting the MDS X ordinate against substratum type it is possible to visualise a change in the assemblage structure with an increase in habitat complexity and hard substratum (Fig. 7). SIMPER tests indicate *Lophelia*, *Acanella* and *Anthomastus* are important in the determination of the assemblage composition, accounting for the majority of dissimilarity between communities (Table 5).

4. Discussion

The present study shows differences in community structure depending on the substratum type.

Large patches of *Acanella* observed throughout this study resulted in Isididae dominating coral communities in the 'Sediment' substratum, e.g. Dive 114 (Supplementary Fig. 3). This is consistent with Mortensen et al. (2008) who found that *Acanella* dominated some sediment areas along the Mid-Atlantic Ridge (MAR). Species from the family Isididae have a root-like system which allows them to colonise and survive in sedimented areas (Gass and Willison, 2005; Woodby et al., 2009). This system is analogous to the peduncle in pennatulids which typically allows pennatulids to dominate coral communities in sedimented areas as shown at 450N on the MAR (Morris et al., 2012). Chrysogorgiidae also colonise areas of sediment (Mortensen and

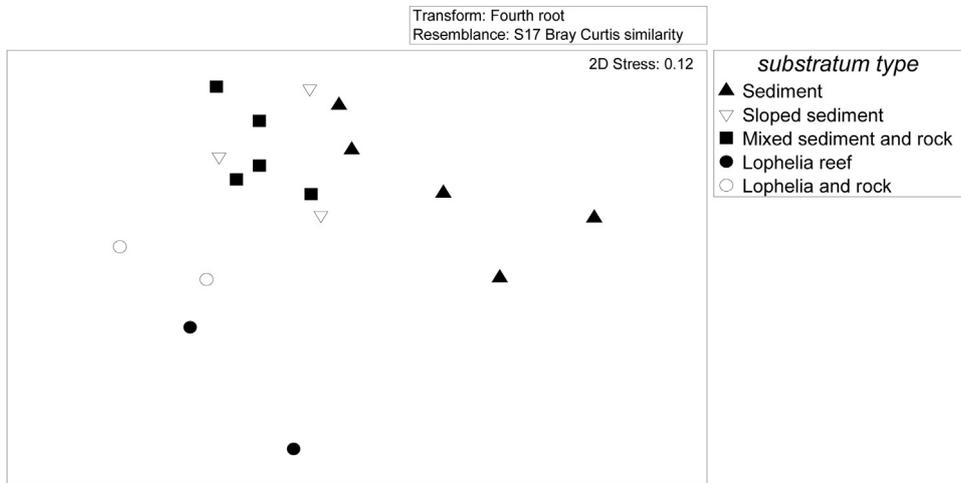


Fig. 6. Multi-dimension scaling ordination of coral assemblages structure from different substrata types across the Whittard Canyon dives.

Table 4
Results of ANOSIM tests comparing coral assemblages composition upon different substrata across Whittard Canyon Dives. N=17.

Global R=0.102, P=0.13	'Sediment Slope'	'Mixed Sediment and Rock'	'Lophelia reef'	'Lophelia and Rock'
	R=0.138 P=0.26	R=0.468 P=0.02	R=0.836 P=0.04	R=0.709 P=0.04
		R=0.231 P=0.16	R=1 P=0.1	R=0.833 P=0.1
			R=0.945 P=0.04	R=0.836 P=0.04
				R=0.5 P=0.33

R levels below 0.4 considered to have no difference.
R levels > 0.4 and < 0.7 considered to be the same as they are different.
R levels > 0.7 considered different.
P values < 0.05 considered significant at 5% level.
P Values < 0.1 considered significant at 10% level (indicated in bold).

Table 5
Results of SIMPER tests comparing significantly different coral assemblage compositions relative to different substrata in the Whittard Canyon. Number represents the percentage of dissimilarity between the two substrata types. The three most important taxa contributing to the dissimilarity are listed in each case.

	'Lophelia reef'	'Lophelia and Rock'
'Sediment'	92.0% <i>Lophelia</i> <i>Acanella</i> <i>Pennatula aculeata</i>	88.98% <i>Lophelia</i> <i>Primnoa</i> <i>Anthomastus</i>
'Sediment Slope'	88.98% <i>Lophelia</i> <i>Acanella</i> <i>Acanthogorgia</i>	75.88% <i>Acanella</i> <i>Lophelia</i> <i>Primnoa</i>
'Mixed Sediment and Rock'	86.12% <i>Lophelia</i> <i>Anthomastus</i> <i>Acanella</i>	67.19% <i>Acanella</i> <i>Lophelia</i> <i>Primnoa</i>

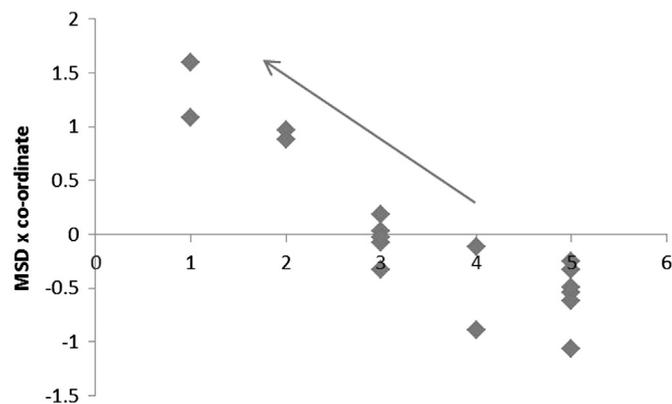


Fig. 7. Multi-dimension scaling x ordinate of coral assemblages against substrata type in the Whittard Canyon. 1="Lophelia reef", 2="Lophelia and rock", 3='mixed rock and sediment', 4='sloped sediment', 5='sediment'.

Buhl-Mortensen, 2004; Woodby et al., 2009; Morris et al., 2012). In the Whittard Canyon Chrysogorgiidae were prevalent in the 'Sediment Slope' substratum (Table 3), with fewer individuals in flat 'Sediment' areas. *Anthomastus* was also a key coral taxon in areas of sedimented slope (Supplementary Figs. 1–4). However, a difference in mean number of individuals observed per time period was

not discernible between 'Sediment Slope' and 'Sediment' (Fig. 5). It is likely that most of the 'Sediment Slope' areas are rock draped in sediment. Such structures are prone to periodic slump events which could wipe out the coral assemblages present and lead to a reduced density than would otherwise be observed (Okey, 1997). A sediment drape may indicate that despite the Whittard Canyon being an active canyon system, current flows are reduced in at least some areas, preventing erosion of the sediment and promoting the development of 'Sediment' coral taxa, such as *Acanella*. This would indicate that there are complex interactions of factors other than the steepness of the slope, which has been believed to lead to an enhanced abundance of fauna as a result of changed oceanographic conditions (Genin et al., 1986, 1989).

Lophelia was generally observed on overhangs and on boulders surrounded by sediment. 'Lophelia reef' and 'Lophelia and rock' substrata had the greatest densities of coral, although the coral distribution was extremely patchy (Fig. 5). In areas where *Lophelia* occurred in high abundance octocorals were less abundant and showed a reduced taxa richness (Table 3). This could indicate that although *Lophelia* increases regional diversity by providing a structural habitat for other organisms (Buhl-Mortensen and Mortensen, 2005; Clark et al., 2006), it could possibly be outcompeting other coral taxa within the North East Atlantic. Within this study *Lophelia* was found in dives with a depth range of 520–2448 m

(Tables 1 and 2). The Aragonite Saturation Horizon (ASH) may limit the distribution of *Lophelia* (Turley et al., 2007). It occurs at a depth of about 2000 m within the Bay of Biscay (de Mol et al., 2011; Davies et al., 2008). Therefore the lower distribution limit of *Lophelia* in the Whittard Canyon (2448 m) may be associated with the Aragonite Saturation Horizon. Clark et al. (2006) also found that the ASH was a major factor determining the distribution of scleractinian corals on seamounts. Below the ASH there have been reports of reduced abundance of Scleractinia (Roberts et al., 2009) with the possibility that other corals taxa fill the available niche. This would result in the increased taxon richness away from *Lophelia* areas observed in this study (Table 3). However, it has been found that there are areas where the substratum type present appears optimal for colonisation, yet no corals are present. This agrees with Mortensen and Buhl-Mortensen (2004) who found areas of cobble and boulder devoid of gorgonians, despite being within the optimal depth range. From this it can be suggested that factors other than substratum type and ASH, such as oceanographic regime and associated food availability, play an important role in small-scale coral distribution patterns within the canyon, producing a very heterogeneous and patchy environment for different coral taxa.

The deep sea is a food limited environment (Smith et al., 2009). Corals are passive suspension feeders and thus require a particle flux high enough to meet their metabolic needs, suggesting that not all areas are suitable for colonisation (Thistle, 2003). During cruise JC36 Stand Alone Pump Systems (SAPs) were used to measure the concentration of particles sinking to the sea floor within the canyon (Masson, 2009). Although particulate organic carbon (POC) is directly related to surface production, the preliminary results from the SAPs demonstrate that some areas within the canyon are subject to higher organic input than others. When the POC composition was analysed it was found that the eastern and western branch had different molecular signatures (Huvenne et al., 2011). Changes in the composition of POC input may influence the community structure of the Whittard Canyon, as seen, for instance, on the adjacent abyssal plain (Billett et al., 2001, 2010). Although very little work has been undertaken on cold-water coral lipid content, Hamoutene et al. (2008) found that there were differences in lipid content between species. Gorgonians were found to have lower lipid content than soft corals, sea-pens and Antipatharia (Hamoutene et al., 2008). *Ancathogorgia armata* has also been found to feed at a higher trophic level than *Primnoa* species (Sherwood et al., 2008). This indicates that different coral species thrive under different organic matter input conditions and that the composition, as well as freshness of the POC, has an impact on the coral assemblages.

The Whittard Canyon is a very active and open system, acting as a conduit of sediment into the deep sea (de Stigter et al., 2007; Arzola et al., 2008). It funnels organic matter to depth via a variety of mechanisms including tidal currents, internal waves and turbidity flows (Duineveld et al., 2001; Quaresma et al., 2007). The greater hydrodynamic activity in the canyon leads to an increase in organic matter input and increased food quality within the canyon in comparison to less active areas on the open continental slope. Kiriakoulakis et al. (2011) found that sediments in canyons on the Portuguese Margin are enriched in organic matter in comparison to slope sediments. Similarly, Rowe (1971) found increased sediment transport within canyons led to enhanced food availability at depth. This may account for the apparent lack of a significant effect of depth on the coral communities in the Whittard Canyon (Fig. 5), because greater food is available at all depths. On the open continental slope the sharp decrease in food with increasing depth leads to major changes in community structure. It is also possible that this is a result of the patchiness of the coral community and the relative small sample size attainable from the studies.

5. Conclusion

This study has shown that substratum type has an effect on the cold-water coral assemblages in the Whittard Canyon. Coral densities were greatest on '*Lophelia reef*' and '*Lophelia* and rock' substrata. However, the taxon richness of coral was reduced in areas with *Lophelia*, possibly because *Lophelia* out-competes other suspension feeding coral taxa. In this respect, although depth is not shown to have an effect on the assemblage structure *per se* in the Whittard Canyon, the loss of *Lophelia* with increasing depth, due in part to the Aragonite Saturation Horizon, may prevent *Lophelia* from dominating coral communities in deeper parts of the canyon. Substratum type, changed oceanographic regimes, topography, and the interaction of topography and physics produce a very heterogeneous and patchy environment for different coral taxa. These factors lead to enhanced POC inputs in the Whittard Canyon in leading to greater taxon richness and greater abundances than in other more nutrient poor areas.

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Appendix A. Supplementary Information

Supplementary data associated with this article can be found in the online version at <http://dx.doi.org/10.1016/j.dsr2.2013.03.036>.

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