The Diversity and Ecological Role of Non-scleractinian Corals (Antipatharia and Alcyonacea) on Scleractinian Cold-Water Coral Mounds

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Cold-water coral carbonate mounds, created by framework-building scleractinian corals, are also important habitats for non-scleractinian corals, whose ecology and role are understudied in deep-sea environments. This paper describes the diversity, ecology and role of non-scleractinian corals on scleractinian cold-water coral carbonate mounds in the Logachev Mound Province, Rockall Bank, NE Atlantic. In total ten non-scleractinian species were identified, which were mapped out along eight ROV video transects. Eight species were identified as black corals (three belonging to the family Schizopathidae, one each to the Leiopathidae, Cladopathidae, and Antipathidae and two to an unknown family) and two as gorgonians (Isididae and Plexauridae). The most abundant species were *Leiopathes* sp. and *Parantipathes* sp. 2. Areas with a high diversity of non-scleractinian corals are interpreted to offer sufficient food, weak inter-species competition and the presence of heterogeneous and hard settlement substrates. A difference in the density and occurrence of small vs. large colonies of *Leiopathes* sp. was also observed, which is likely related to a difference in the stability of the substrate they choose for settlement. Non-scleractinian corals, especially black corals, are an important habitat for crabs, crinoids, and shrimps in the Logachev Mound Province. The carrier crab *Paromola* sp. was observed carrying the plexaurid *Paramuricea* sp. and a black coral species belonging to the genus *Parantipathes*, a behavior believed to provide the crab with camouflage or potentially a defense mechanism against predators. More information on the ecophysiology of non-scleractinian corals and fine-scale local organic matter supply are needed to understand what drives differences in their spatial distribution and community structure.

Keywords: cold-water coral mounds, fine-scale spatial patterns, biodiversity, associated megafauna, Antipatharia, Alcyonacea, Logachev Mound Province

INTRODUCTION

Lophelia pertusa and *Madrepora oculata*, the dominant reef-forming scleractinian corals in the deep sea, have been widely studied over the last 20 years. However, due to the high biodiversity and the numerous symbiotic associates they have, non-scleractinian corals should not be overlooked (e.g., Buhl-Mortensen and Mortensen, 2005; Etnoyer and Morgan, 2005; Tazioli et al., 2007; Cerrano et al., 2010; Wagner et al., 2012; Corbera Pascual, 2015; Cúrdia et al., 2015; De Clippele et al., 2015). This is because non-scleractinian corals are known to be an important habitat for a diverse range of organisms providing, e.g., a feeding platform, a place to shelter or a substrate for fish to lay their eggs on (Buhl-Mortensen and Mortensen, 2004; Le Guilloux et al., 2010; Wagner et al., 2012; De Clippele et al., 2015). In this study, we will discuss the non-scleractinian corals belonging to the Antipatharia and Alcyonacea.

Antipatharia also referred to as black corals (Cnidaria: Anthozoa: Hexacorallia) encompass seven families (Wagner et al., 2012) with 75% (c. 180 species) found below 50 m depth (Cairns, 2007). The black corals' lifespan is greater than most other deep-sea coral species (Andrews et al., 2001, 2009; Roark et al., 2009). A *Leiopathes annosa* (Wagner and Opresko, 2015), colony from Hawaiian (United States) waters was estimated to be 4,265 years old with radial growth rates between 0.005 and 0.022 mm yr^{-1} (Roark et al., 2009; Sherwood and Edinger, 2009).

Gorgonians (Cnidaria: Anthozoa: Octocorallia) belong to the Order Alcyonacea can be found at virtually any depth, with records found as deep as 5850 m (Madsen, 1956). They can be found in most ocean basins and can live over 100 years (Hill et al., 2011; Watling et al., 2011; Lacharite and Metaxas, 2013). Octocorals grow faster and have lower lifespans than black coral species, with radial growth rates between 0.05 and 0.44 mm yr^{-1} (Watling et al., 2011).

Given their slow growth rates and great longevity, cold-water black corals and octocorals are particularly vulnerable to anthropogenic damage. Disturbance and removal through bottom fishing (Althaus et al., 2009) and exploitation for commercial therapeutic and jewelry/art use (Grigg, 2001) are significant threats. Deep-water black and octocorals are part of "Vulnerable Marine Ecosystems" (VME) as defined by United Nations General Assembly Resolutions 61/105 and 64/72 (Fuller et al., 2008).

This study focussed on the non-scleractinian corals that grow on the cold-water coral carbonate mounds in the Logachev Mound Province, Rockall Bank. While black corals and deep-sea gorgonians corals have been reported in this area in previous studies (Duineveld et al., 2007; Roberts et al., 2008; Henry et al., 2014) their community characteristics, ecology and functional roles have not been studied.

Cold-water coral carbonate mounds are topographic structures that owe their existence, partially or entirely, to the growth of scleractinian framework building corals, such as *Lophelia pertusa* and *Madrepora oculata* (Freiwald, 2002; Roberts et al., 2006). These mound structures have developed over glacial-interglacial time periods and vary widely in size and shape (Kenyon et al., 2003; Van Weering et al., 2003;

Mienis et al., 2007; Wheeler et al., 2007). Both box core samples and video footage have revealed that cold-water coral carbonate mounds are associated with a high diversity of organisms (Raes et al., 2003; Raes and Vanreusel, 2005, 2006; Wheeler et al., 2005; Henry and Roberts, 2007). Corals are suspension feeders and have been shown to be more abundant on- vs. off-mound (Henry and Roberts, 2007). Soetaert et al. (2016) showed that at Rockall Bank, there is a significant interaction between tidal currents and cold-water coral formed mounds which induce downwelling events of surface water that brings the organic matter to 600 m deep. Therefore, the greater resuspension of particulate organic matter and the high currents keeping sedimentation rates low could explain why both filter and suspension feeders are more abundant on the mounds (Henry and Roberts, 2007). These characteristics make cold-water coral mounds important features to study regarding non-scleractinian coral presence and diversity. The dominant non-scleractinian fauna varies across European cold-water coral reef ecosystems with, for example, black corals dominating the Belgica Mound Province (Henry and Roberts, 2007), while gorgonians corals dominate reefs in Norwegian fjords (Mortensen et al., 1995). This difference could be a consequence of variability in hydrography, topography, and the biological traits of the species themselves, which is interrelated to the mound or reefs' size and complexity of the habitat (Ricklefs and Lovette, 1999).

Therefore, this study aims to: (1) document the diversity of these non-scleractinian corals on cold-water coral carbonate mounds, (2) determine what environmental conditions influence differences in their density, and (3) investigate their potential ecological role. The goal of this study is to provide more information on these non-scleractinian corals to ensure that better-informed decisions can be made to protect these long-lived organisms.

MATERIALS AND METHODS

Study Area

The Logachev Mound Province is located on the south-eastern slope of Rockall Bank in the northeast Atlantic (Kenyon et al., 2003; **Figure 1**). Within Rockall Trough, the upper layers down to 1,200–1,500 m are occupied by Eastern North Atlantic Water (ENAW) (Holliday et al., 2000). The cold-water coral carbonate mounds are between 5 and 360 m tall, up to a few kilometers long and located between 600 and 1000 m depth, which is within the boundaries of the ENAW (Kenyon et al., 2003; Mienis et al., 2007, 2009; de Haas et al., 2009). The ENAW circulates through an anticyclonic gyre in Rockall Trough with a net northward flow direction, while around the mounds there is a local residual current flow toward the south-west that ranges between 5 and 15 cm s^{-1} (Huthnance, 1986; Holliday et al., 2000; Mienis et al., 2007; White et al., 2007; Soetaert et al., 2016). There is also a stronger bottom-magnified diurnal tidal flow of 15–28 cm s^{-1}. It is these strong northwest-southeast directed currents that affect the growth direction of the mounds, which is perpendicular to the regional contours (Mienis et al., 2007; White et al., 2007).
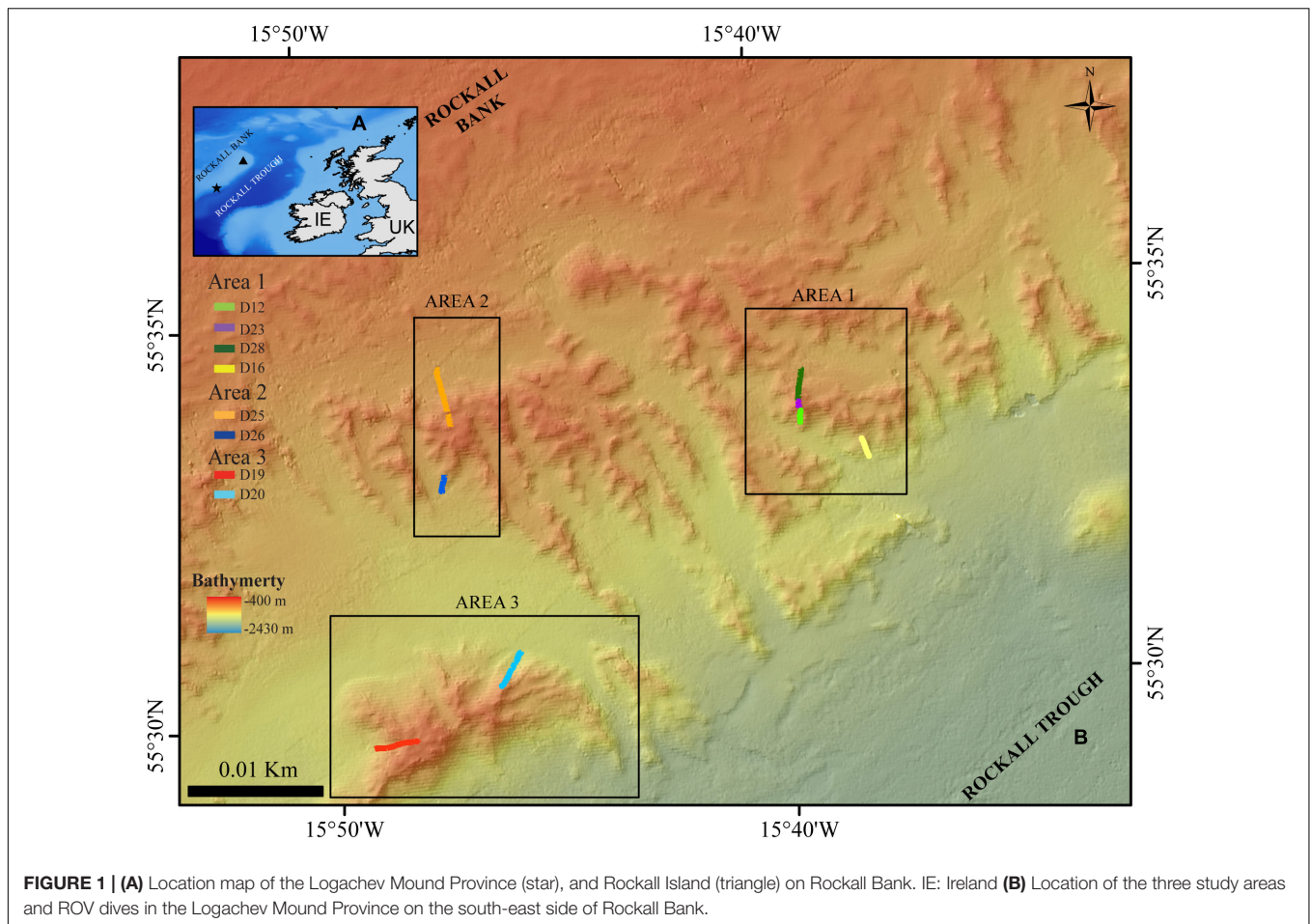
FIGURE 1 | (A) Location map of the Logachev Mound Province (star), and Rockall Island (triangle) on Rockall Bank. IE: Ireland **(B)** Location of the three study areas and ROV dives in the Logachev Mound Province on the south-east side of Rockall Bank.

The Logachev Mound Province consist of a cluster of mounds that are built of accumulated fine sediments baffled by coral reef framework, dead coral fragments and live coral on the summit. The mound bases are covered by bio- and siliciclastic sands with various amounts of pebbles, cobbles and boulders (de Haas et al., 2009). The flanks of the mounds are covered with patches of coral rubble, dead coral branches and living corals, while the summits of the mounds are characterized by dense *L. pertusa* patches at 500–600 m depth (Kenyon et al., 2003; Van Weering et al., 2003; de Haas et al., 2009).

Food is supplied to the suspension-feeding corals through different mechanisms. First, the presence of the coral framework will slow down the currents allowing the corals to gather food, but also trap sediments, which can then accumulate between the coral branches ensuring further growth of the mounds as a whole (Roberts et al., 2006; Dorschel et al., 2007; de Haas et al., 2009; Mienis et al., 2009; Roberts et al., 2009). Secondly, the interaction of the diurnal tidal currents with the slope of Rockall Bank and the topographies of the cold-water coral mounds themselves, induces downwelling of the productive Rockall Bank surface waters due to the formation of internal waves (Kenyon et al., 2003; Davies et al., 2009; Wagner et al., 2011; Findlay et al., 2013; Cyr et al., 2016; Soetaert et al., 2016). Thirdly, the interaction of internal waves and tidal currents with seabed sediments also

causes nepheloid layers, which contain increased amounts of suspended seabed sediment that can supply the corals with food at deeper depths (Kenyon et al., 2003; Mienis et al., 2007). Intermediate Nepheloid Layers (INL) have been identified as turbidity clouds between 450 and 900 m depth and varied in depth and shape coincidingly with the diurnal cycle. The largest turbidity cloud can be found between 200 and 500 m depth, just above the carbonate mounds. A second smaller turbidity cloud can be found 25 km from Rockall Bank between 500 and 700 m depth (White et al., 2003; Mienis et al., 2006, 2007).

High-Definition Video Data
Video Data Acquisition
In the Logachev Mound Province, genera belonging to the Order Antipatharia Milne-Edwards and Haime (1857) (black corals), as well as the Order Alcyonacea Lamouroux 1816, were present and studied here using high definition (HD) video recordings from remotely operated vehicles (ROVs). High-definition video data were collected in the Logachev Mound Province in 2012 (RRS *James Cook* Cruise 073, May 18–June 15, 2012) as part of the Changing Oceans 2012 expedition, using the ROV *Holland-1*. The data were recorded with a combination of cameras mounted on the ROV: an HD Insite

mini-Zeus video camera with a direct HDSDI fiber output, a Kongsberg 14–208 digital stills camera, a Kongsberg 14–366 pan and tilt camera and an Insite Pegasus-plus fixed zoom camera. Four lights were used: two 400-W deep-sea power and light SeaArc2 HMI lights and two 25,000 lumen Cathx ocean APHOS LED lights. Two lasers spaced 10 cm were also mounted on the HD camera. The position and depth of the ROV were determined by USBL (Sonardyne) underwater positioning system and recorded using the OFOP (Ocean Floor Observation Protocol) software.

During the Changing Oceans Expedition, a total of eight video transects were recorded in the Logachev Mound Province with a total length of ∼3.4 km and an average width of 2.74 m ±0.5 m. These eight video transects only covered small parts, on alternating sides of three large clustered cold-water coral carbonate mounds within the Logachev Mound Province (**Figure 1** and **Table 1**). Since the transects only cover a section and not the whole of the clustered mound, they are referred to as area 1, 2, and 3. Based on Soetaert et al. (2016), it is known that the supply of organic matter varies with depth along the flank of Rockall Bank. It is therefore relevant to note that these three areas are located at different distances on the slope of Rockall Bank from the shallowest point, i.e., Rockall Island (**Figure 1**). Area 1, at 560–700 m depth, is located ∼26.1 km from Rockall Island, area 2 at 530–700 m depth is located ∼25.7 km and area 3 at 530–850 m depth is located ∼26.8 km from Rockall Island.

Substrate Classification

Substrate types were identified from the HD videos according to the classes listed in **Table 2** (see **Table 2** and **Figure 2**) and noted in Excel. The dominant substrate class was noted every meter from the HD videos for which the percentage cover for each substrate class were calculated per flank and area.

Coral Identification and Associated Fauna

The presences of non-scleractinian coral species were noted for every meter in Excel, alongside the notes on the dominant substrate class. Preliminary evaluation of the HD videos indicated a large number of occurrences of different size classes of the black coral species *Leiopathes* sp., which was therefore classified as small (<30 cm), medium (30–100 cm), or large (>100 cm).

The associated mobile megafauna was identified from the HD video and their location on the coral colonies specified as central branch versus the outer branch, and on the base, middle or top part of the colonies.

Analyses

The HD video dive transects that were used for analyses varied from 40 to 1040 m in length (**Table 1**). The video transects were systematically subsampled into a total of 84 groups located at a distance of 40 m to reduce the influence of spatial autocorrelation for statistical analyses (**Table 1**). The length of 40 m was chosen as this length gave the best representation of the substrate and species variability in relation to a changing bathymetry and rugosity. The ArcGIS "Join" function was used to calculate the total number of counts for each non-scleractinian coral species per sub-sample.

Diversity, Evenness, and Density

The species diversity, density, and evenness of all non-scleractinian corals were calculated in the PRIMER software (Clarke and Warwick, 2001). The data matrix composed of the sub-sample number (*y*-axis) and the counts of the non-scleractinian species found per 40 m sub-sample (x-axis). Two types of factors were added. A first identifying the location of the sub-sample (area 1, 2 or 3), and a second factor identifying the flank the sub-sample was located on (NE, S, NW, SW). Shannon diversity index (H′) and Pielou value were used to calculate the diversity and evenness of the non-scleractinian corals in the study area. The Pielou's evenness value can range from 0 to 1, and gives an indication of dominant species being present in a sample (∼0) or if there is an equal abundance of all species (∼1). Density was calculated for all the non-scleractinian corals together and for the species separately, by dividing their total counts by the total square meter which covered per 40 m sub-sample. When the video transects were recorded the ROV varied in height, affecting the average width, and thus the total area of the transect. The average width of the video transects can be found in **Table 1**. When a density calculation was made including two or more different video transects, their average width was used to calculate the total area covered. The number of different species counted per area and flank were also calculated in Excel.

TABLE 1 | Remotely operated vehicle dive information.

Dive (area)	Start Lon (decimal degrees)	Start Lat (decimal degrees)	End Lon (decimal degrees)	End Lat (decimal degrees)	Aspect/ flank	Depth range (min-max) (m)	Length/ Width (m)	No. Sub-samples
12 (1)	−15.65523	55.55799	−15.65557	55.55567	NE	(640–722)]	200/2.36	5
16 (1)	−15.63350	55.55119	−15.63142	55.547439	S	(758–874)	240/2.82	6
23 (1)	−15.65630	55.55847	−15.65571	55.55965	NE	(563–584)	40/2.55	1
28 (1)	−15.65585	55.56014	−15.65389	55.56674	S	(575–701)	240/2.91	6
25 (2)	−15.78718	55.57206	−15.78421	55.56013	NW	(547–705)	1040/3.37	26
26 (2)	−15.78795	55.55020	−15.78918	55.54672	SW	(702–768)	360/2.79	9
19 (3)	−15.82089	55.49419	−15.80442	55.49478	NE	(559–801)]	880/2.62	22
20 (3)	−15.76447	55.51220	−15.77232	55.50529	NW	(610–873)]	360/2.97	9

Average aspect represents the side of the area/clustered mound at which the video transects were collected.

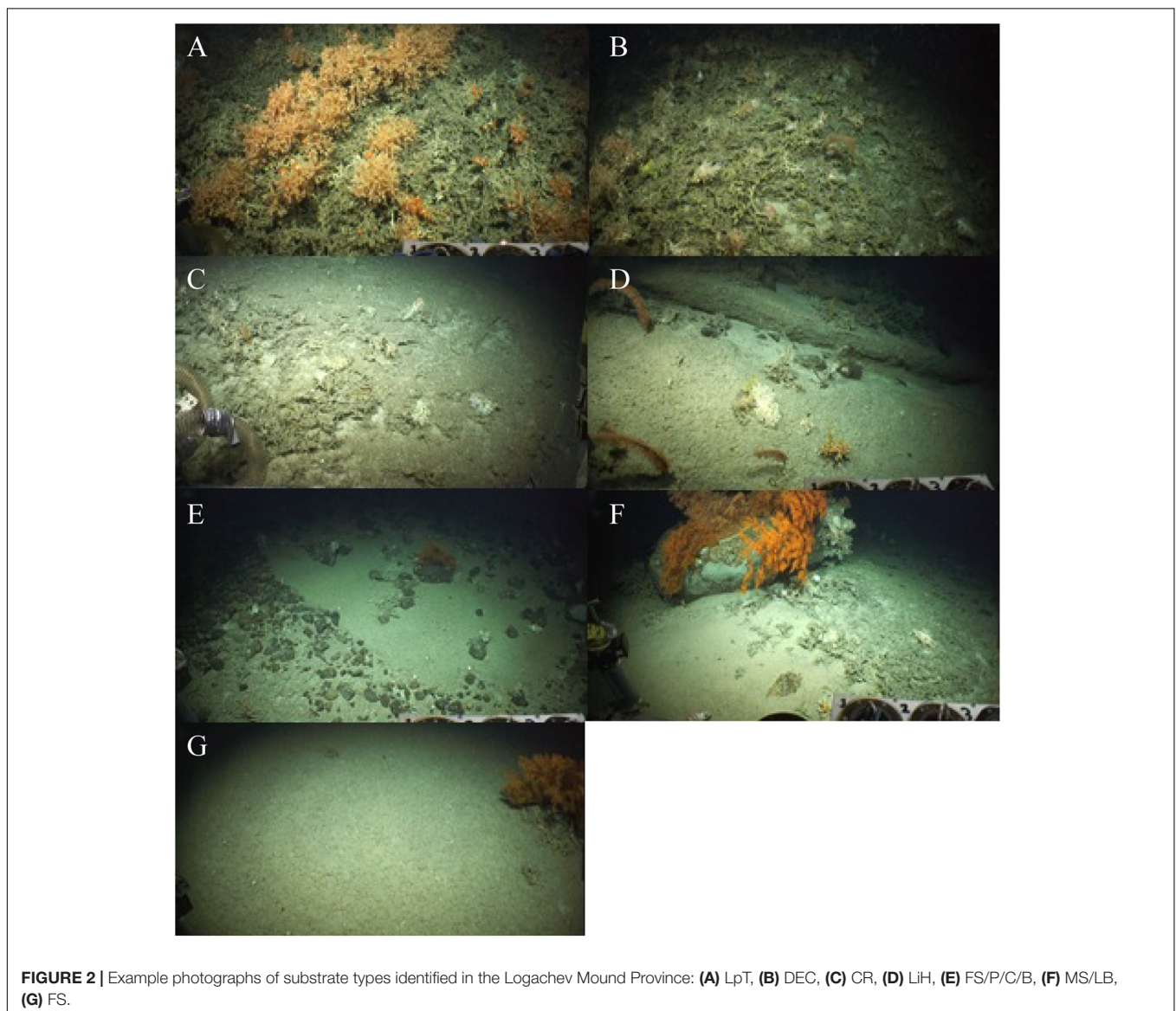**TABLE 2 |** Substrate classes identified in HD video data.

Substrate type	Abbreviation
L. pertusa thicket	LpT
Dead exposed *L. pertusa* framework with scarce live *L. pertusa* colonies	DEC
Coral rubble	CR
Lithified hardground	LiH
Fine sediment with pebbles, cobbles, and boulders (<100 cm diameter)	FS/P/C/B
Mixed sediment with large boulders (>100 cm)	MS/LB
Fine sediment	FS

Environmental Drivers of Spatial Variation in Density

The change in the density of the non-scleractinian species was studied in relation to the substrates and to environmental variables that were extracted from bathymetry data. Substratum information was obtained from video data (see section "Substrate Classification"). Terrain characteristics were extracted from a bathymetry dataset that was provided by the Irish National Seabed Survey programme (INSS) at a 20 m× 20 m resolution[1]. Several topographic variables were derived from the bathymetric grid using the ArcGIS 10.1, ESRI Software and the Benthic Terrain Modeler (Wright et al., 2012): slope, aspect (eastness and northness), rugosity (calculated at two spatial scales, using a square kernel window of respectively 3 × 3 and 9 × 9 pixels) and bathymetric positioning index (BPI; calculated at two spatial scales using an annulus kernel window with inner and outer radius of respectively 3 × 6 and 6 × 9 cells). More information on these variables can be found in De Clippele et al. (2017) and,

[1]www.gsiseabed.ie

FIGURE 2 | Example photographs of substrate types identified in the Logachev Mound Province: **(A)** LpT, **(B)** DEC, **(C)** CR, **(D)** LiH, **(E)** FS/P/C/B, **(F)** MS/LB, **(G)** FS.

for example, in Wilson et al. (2007), Guinan et al. (2009), and Henry et al. (2010).

Because the response variables did not follow a normal Gaussian distribution, the more flexible Generalized Linear Modeling (GLM) approach was used. The probability distributions of the coral density data analyzed here belong to the exponential quasi-Poisson family (McCullagh and Nelder, 1989; Dobson and Barnett, 2008). The statistical software package R was used to perform the GLM (R Development Core Team, 2010).

Linear regression cannot include missing values. Hence sub-samples that had no abundances of the analyzed species present were excluded (McCullagh and Nelder, 1989; Dobson and Barnett, 2008). Backward stepwise regression decided what environmental variables (% occurrence of the seven substrate types and the variables derived from the bathymetry) contributed the most to the performance of the model. The best model was chosen based on the Akaike Information Criterion (AIC), which estimates if there is any uncertainty over the model (Cnaan et al., 1997; Symonds and Moussalli, 2011). Once the variables were selected, a GLM was performed. By taking the exponent of the coefficient values, the percentage change in the abundance of the coral per unit change of each explanatory variable was calculated. Species that had less than 50 individuals present were excluded from the statistical analyses due to the small sample size.

RESULTS

Substrate Types

Coral rubble (33.4%), dead exposed *L. pertusa* framework (25.7%), and fine sediment with pebbles, cobbles, and boulders (23.2%), were the most abundant substrate types recorded in the entire studied area (area 1, 2, and 3). *L. pertusa* thickets covered 10.8%, lithified hardground covered 4.2%, fine sediment covered 2.3% while mixed substrate with large boulders covered just 0.4%.

Dead exposed *L. pertusa* framework and coral rubble were present in high percentages in all the areas (**Table 3**). *L. pertusa* thickets were found predominantly in area 1 on the NE flank of the mound. A total of ~39% of the terrain surveyed in area 2
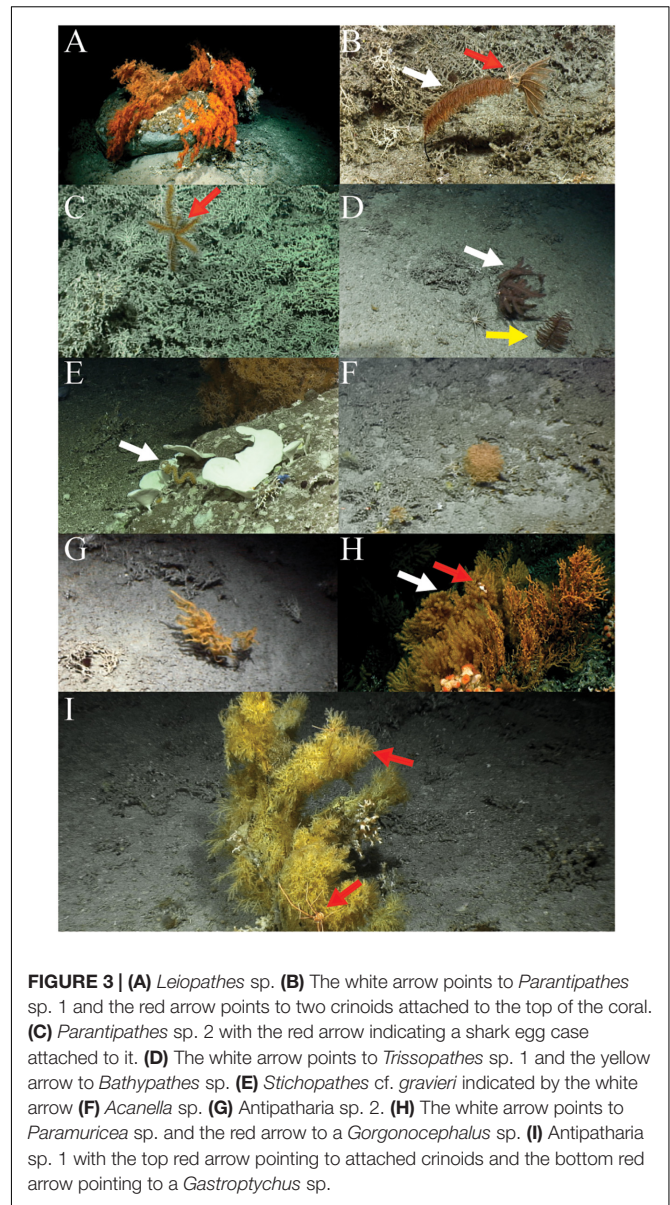

FIGURE 3 | (A) *Leiopathes* sp. **(B)** The white arrow points to *Parantipathes* sp. 1 and the red arrow points to two crinoids attached to the top of the coral. **(C)** *Parantipathes* sp. 2 with the red arrow indicating a shark egg case attached to it. **(D)** The white arrow points to *Trissopathes* sp. 1 and the yellow arrow to *Bathypathes* sp. **(E)** *Stichopathes* cf. *gravieri* indicated by the white arrow **(F)** *Acanella* sp. **(G)** Antipatharia sp. 2. **(H)** The white arrow points to *Paramuricea* sp. and the red arrow to a *Gorgonocephalus* sp. **(I)** Antipatharia sp. 1 with the top red arrow pointing to attached crinoids and the bottom red arrow pointing to a *Gastroptychus* sp.

and 3 were covered with the hard substrates (pebbles, cobbles, boulders, large boulders, and lithified hardgrounds), mostly on the NW flank of their mounds. Area 1 had only 4% of these hard substrates present.

Non-scleractinian Species

Ten non-scleractinian coral species with a total 1,707 specimens were counted across the three Logachev mound areas. Black corals were the most abundant non-scleractinian corals, overall, with 1,695 individual black corals recorded. In total eight different black coral species were identified: three species belonging to the family Schizopathidae (*Bathypathes* sp., *Parantipathes* sp. 1, *Parantipathes* sp. 2), one species belonging to the families Leiopathidae (*Leiopathes* sp.), Cladopathidae (*Trissopathes* sp.), and Antipathidae (*Stichopathes* cf. *gravieri*) and

TABLE 3 | Percentage contribution of the different substrates calculated from the HD video dive transects per area and per flank.

Area	LpT	DEC	CR	LiH	FS/P/C/B	MS/LB	FS
1 (total)	**31.92**	**38.72**	**20.16**	**1.59**	**1.66**	**0.24**	**5.71**
1 NE	24.93	19.84	1.40	0	0	0	0
1 S	6.99	18.88	18.76	1.59	1.66	0.24	5.71
2 (total)	**0.16**	**13.49**	**41.79**	**7.64**	**27.91**	**3.14**	**5.88**
2 NW	0.16	7.58	11.41	4.15	20.52	2.43	1.31
2 SW	0	5.92	30.37	3.49	7.39	0.71	4.56
3 (total)	**1.72**	**20.84**	**38.82**	**5.11**	**33.22**	**0.12**	**0.17**
3 NE	0.01	3.13	3.30	0	0	0.01	0.06
3 NW	1.71	17.70	35.52	5.11	33.22	0.11	0.12

The dives included per flank and area can be found in Table 1.

two unidentified species which we refer to as Antipatharia sp. 1, Antipatharia sp. 2. Only two species belonging to the Order Alcyonacea were identified: one gorgonian coral belonging to the Isididae family (*Acanella* sp.) and one gorgonian belonging to the Plexauridae family (*Paramuricea* sp.). The different species are shown in **Figure 3**.

The black coral *Leiopathes* sp. was the most abundant antipatharian with a total of 1,583 individuals. The second most abundant coral was also a black coral species, *Parantipathes* sp. 1, with 60 individuals. The other non-scleractinian species were more rare, ranging between 1 and 11 counts and their densities varied with depth (**Table 4** and **Figure 4**).

Leiopathes sp. occurred in all three study areas and on all substrates except *L. pertusa* thickets (**Table 5**). The larger sized *Leiopathes* sp. colonies occurred mostly in areas with large boulders while the smaller sized colonies preferred dead exposed *L. pertusa* framework. Medium sized colonies occurred both on dead exposed *L. pertusa* framework and big boulders. *Leiopathes* sp. species has the largest depth range in the Logachev Province and was the deepest (874 m) recorded species (**Table 4**).

Like *Leiopathes* sp., *Parantipathes* sp. 1 was found in all three study areas, on all substrates, except for fine sediment. This species occurred mostly on dead exposed *L. pertusa* framework. Lower occurrences were found on large boulders and fine sediment with pebbles, cobbles, boulders (**Table 5**). This species had a much narrower depth range of 565–691 m depth (**Table 4**).

Parantipathes sp. 2 had a similar depth range (**Table 4**) and substrate preference to *Parantipathes* sp. 1 and also occurred in all the study areas. The only difference was that this species was also found in fine sediments (**Table 5**).

Stichopathes cf. *gravieri* was found in all the studied areas, on three substrates; mostly on large boulders, but also on dead exposed *L. pertusa* framework and *L. pertusa* thicket (**Table 5**). This species had the narrowest depth range and was only found between 663 and 696 m (**Table 4**).

Bathypathes sp. occurred mostly in areas with dead exposed *L. pertusa* framework, but also on large boulders and fine sediment with pebbles, cobbles and boulders (**Table 5**). This species occurs at greater depths between 678 and 859 m. This species was only found in area 1 and 2 (**Table 4**).

All four individuals of Antipatharia sp 1 together with one Antipatharia sp. 2 individual were found in one particular location in area 1 with coral rubble (**Table 5**) as a substrate at 860 m depth (**Table 4**).

All three *Trissopathes* sp. individuals were found within dead exposed *L. pertusa* framework (**Table 5**), at a wide depth range of 629–860 m, in area 1 and 2 (**Table 4**).

Only two records of *Acanella* sp. were made, one was located in an area with dead exposed coral framework, the other in coral rubble (**Table 5**). This species was only found at deeper depths of 772 m (area 2) and 860 m (area 1) (**Table 4**).

Seven of the *Paramuricea* sp. colonies were observed on dead exposed *L. pertusa* framework, while two were observed in *L. pertusa* thickets and one in coral rubble (**Table 5**). This species was found at depths of 546–796 m in all the study areas (**Table 4**).

Diversity, Evenness, and Density

The highest total diversity of non-scleractinian corals was recorded in area 2, with an H′ of 0.40 with a total of eight different species. The SW flank had a higher diversity of non-scleractinian corals compared to the transect on the NW flank. In area 1, a total of nine non-scleractinian coral species were recorded, but the overall H′ was slightly lower (0.33), with the S side of this area being higher in diversity. The lowest number of species and diversity was found in area 3, with, respectively, six species and an H′ of 0.11. Here, the highest diversity was found on the NW flank (**Table 6**). After calculating these parameters per area and the mounds' flank, these indices were also calculated per 40 m transect to reveal more fine-scale spatial variations. An H′ of 1.389 and 1.386 were recorded in area 1 at, respectively, 616 and 860 m depth. In area 2, the highest H′ of 1.175 and 1.039 were found at, respectively, 679 and 753 m depth.

The distribution of the most abundant and therefore dominant species, *Leiopathes* sp., also differed and affected the evenness on the different mounds. Area 3 had the lowest evenness with a value of 0.06, followed by area 1 with 0.15 and area 2 with 0.19. In area 1 an evenness of 1 was found at 616 and 655 m depth. Area 2 had an evenness of 1 at 663 and 728 m depth. The evenness in the different areas was always higher on the flanks, where a higher diversity of non-scleractinian species was found (**Table 6**).

Area 2 had a high average density of non-scleractinian corals with 0.136 ind. m^{-2}. Even though the diversity is low in area 3, it had the highest average densities of non-scleractinian corals (0.143 ind. m^{-2}) present, which was predominantly caused by the presence of a high density of *Leiopathes* sp. Area 1 had the lowest average density of corals present of only 0.034 ind. m^{-2} (**Table 6**). The density of non-scleractinian corals was highest on the flanks of the areas, which had a lower diversity and evenness.

As mentioned earlier, the black coral *Leiopathes* sp. is the most abundant non-scleractinian coral found in the Logachev Province (**Table 4**). Small sized colonies (<30 cm) were the most abundant size class, with the highest total density of 9.436 ind. m^{-2} recorded at depths between 546 and 874 m. Medium sized colonies (30–100 cm) were the least represented, had a density of 0.125 ind. m^{-2} and were found between 571 and 780 m depth. Large sized colonies (>100 m) were recorded at depths between 565 and 874 m. The large colonies had their highest densities of 0.364 ind. m^{-2}.

Environmental Drivers of Spatial Variation in Density

Statistical analyses to identify the environmental variables that cause differences in the density of non-scleractinian species were limited to the two most abundant species; *Leiopathes* sp. and *Parantipathes* sp 1. The analyses for *Leiopathes* sp. was performed for its most abundant size classes (small and large). Due to the small sample size of the remaining species, no significant results were found.

Leiopathes sp.: Percentage cover of dead exposed *L. pertusa* framework, depth and eastness ($p < 0.0001$) significantly affected the density of small-sized *Leiopathes* sp. When these variables increase with one unit (respectively percentage per 40 m, 40 m,

TABLE 4 | Observed recorded depth range and density (m^{-2}) of non-scleractinian species.

Species	Min depth (m)	Max depth (m)	Depth range (m)	Total	Area 1		Area 2		Area 3		
					NE	S	NW	SW		NE	NW
Acanella sp.	772	860	88	0.013	0.022	0.000	0.030	0.018	0.000	0.000	0.001	0.034	0.000
Antipatharia sp. 1	860	860	0	0.025	0.087	0.000	0.120	0.000	0.000	0.000	0.002	0.000	0.000
Antipatharia sp. 2	628	628	0	0.006	0.000	0.000	0.000	0.000	0.022	0.000	0.000	0.000	0.000
Bathypathes sp.	678	859	181	0.082	0.152	0.000	0.211	0.018	0.112	0.090	0.004	0.000	0.000
Leiopathes sp. (all)	547	874	327	9.925	2.130	4.230	1.324	14.539	14.342	2.599	0.208	26.581	1.333
Leiopathes sp. (large)	565	874	309	0.364	0.152	0.078	0.181	0.090	0.989	0.448	0.009	0.000	0.070
Leiopathes sp. (medium)	571	780	209	0.125	0.022	0.078	0.000	0.090	0.292	0.090	0.003	0.136	0.035
Leiopathes sp. (small)	547	874	327	9.436	1.957	4.073	1.143	14.359	13.061	2.061	0.197	26.445	1.228
Paramuricea sp.	546	796	250	0.063	0.065	0.157	0.030	0.072	0.067	0.000	0.002	0.136	0.000
Parantipathes sp. 1	565	691	126	0.376	0.630	0.235	0.782	0.144	0.495	0.358	0.017	0.136	0.035
Parantipathes sp. 2	565	699	134	0.069	0.065	0.078	0.060	0.036	0.135	0.000	0.002	0.068	0.000
Stichopathes cf. *gravieri*	663	696	33	0.125	0.109	0.000	0.150	0.054	0.270	0.179	0.004	0.034	0.000
Trissopathes sp.	629	860	231	0.019	0.022	0.000	0.030	0.000	0.045	0.000	0.001	0.000	0.000

*The total density and the densities for the three different areas and for the mound flanks are listed. The dives included per flank and area can be found in **Table 1**. When more than one dive transect was recorded, as is the case for area 1 NE and Se and the areas overall, the average width of their transects were used to calculate the total area covered.*

degree per 40 m), the density of the colonies increased with, respectively, 2 and 0.8% and decreased by 48%. For large *Leiopathes* sp. individuals, only the mixed sediment with large boulders contributed significantly to changes in their density ($p < 0.001$). The density of large *Leiopathes* sp. individuals increases by 27% when mixed sediment with large boulders increases 1% per 40 m. This observation was also clear from the video observations.

Parantipathes sp. 1: Only lithified hardground contributed significantly to changes in the density of *Parantipathes* sp. 1 ($p < 0.01$). Its density increases 6% when the percentage cover of lithified hardground increases 1% per 40 m.

Associated Fauna

Depending on the speed and height of the ROV, species associated with non-scleractinian corals were not always visible. Therefore, no quantitative data are presented here. Instead, a qualitative overview is given describing which non-scleractinian coral species had associated organisms present, with notes of their location on the coral colonies.

On both small and large sized *Leiopathes* sp. colonies the anomuran crab *Gastroptychus* sp. were found on the middle and uppermost outer branches (**Figures 5A,B**). Small sized colonies would always host one specimen, while larger sized colonies hosted up to three specimens at the same time. On one occasion, a *Munida* sp. was found sheltering under a small *Leiopathes* sp. colony (**Figure 5H**). Ophiuroids and crinoids were only observed on larger sized colonies.

A close-up of a *Parantipathes* sp. 2 showed a small shrimp in between the branches (**Figure 5C**). But also *Gastroptychus* sp. (**Figure 5C**) and crinoids were found using this species (**Figure 5D**). On one occasion, a shark egg case was found attached to the top middle branch of a *Parantipathes* sp. 2 individual (**Figure 3C**).

One *Parantipathes* sp. 1 coral had two crinoids attached to the top central branch (**Figure 3B**). *Parantipathes* sp. 1 was found carried by three *Paromola* sp. crabs (**Figure 5F**). Two crabs were found carrying the plexaurid coral *Paramuricea* sp. (**Figure 5E**), ten crabs carried a sponge (**Figure 5F**), nine carried nothing, and on six occasions, it was unclear whether they were carrying something.

Antipatharia sp. 1 was only found in one location, where large numbers (∼10) of crinoids had attached themselves to it, together with one *Gastroptychus* sp. specimen (**Figure 3I**).

Finally, *Gastroptychus* sp. was also found on the top central branch of three *Bathypathes* sp. individuals (**Figure 5G**).

One large *Paramuricea* sp. was observed with a *Gorgonocephalus* ophiuroid attached to it in the central top branches (**Figure 3H**).

No large megafauna was visible on the corals *Acanella* sp., Antipatharia sp. 2, *Stichopathes* cf. *gravieri* and *Trissopathes* sp.

DISCUSSION

A total of ten different non-scleractinian coral species were identified in the ROV video data collected from the Logachev Province, Rockall Bank, NE Atlantic. Of these, eight belonged to the Order Antipatharia (Black corals) and two to the Order Alcyonacea. Even though it is accepted that, like scleractinian corals, non-scleractinian corals prefer areas where high current speeds enhance food availability and where hard substrate is available for settlement (Genin et al., 1986; Thiem et al., 2006; Davies et al., 2009; Roberts et al., 2009), their fine-scale spatial distribution is more complex and both the density and diversity
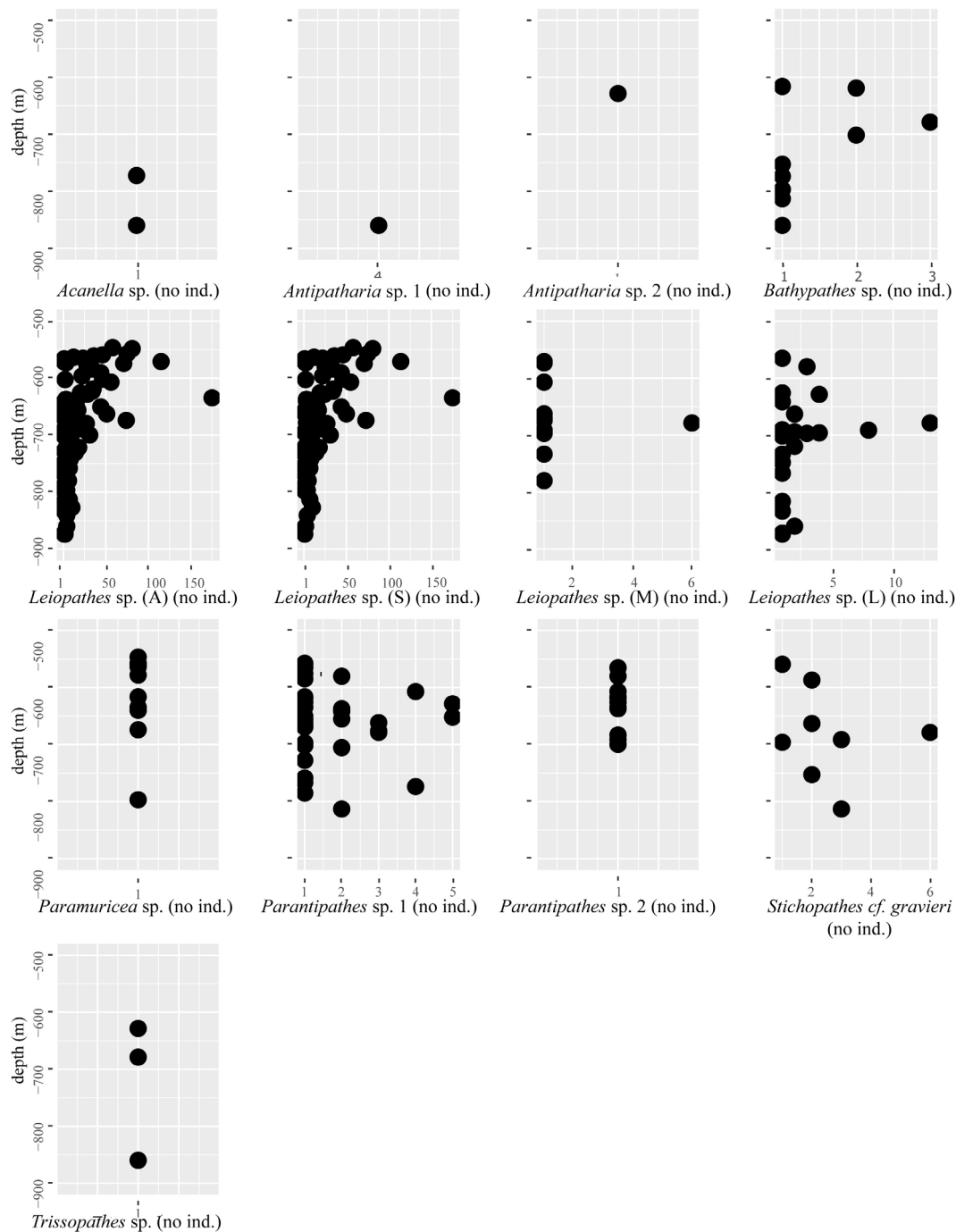
FIGURE 4 | The number of individuals (no ind.) of a certain species counted in the Logachev Mound Province (*X*-axis) plotted against depth (*Y*-axis). This gives an indication of the densities of certain species at certain depths. For *Leiopathes* sp., the abbreviations A, S, M, and L stand for, respectively, all, small, medium, and large.

of non-scleractinian corals varied within and between the areas examined in this study. It is important to note that it is likely that the depth range of the non-scleractinian corals studied in this area is wider than suggested here, as some could have been overlooked due small colony sizes or poor video quality.

High concentrations of organic matter (mixture of, e.g., dissolved organic matter, bacteria, marine snow, and small zooplankton) which are produced in the photic zone above Rockall bank, can be observed above the Logachev Mound Province, while off-reef seafloor areas at comparable depths are

TABLE 5 | Number of specimens found by substrate.

Species	LpT	DEC	CR	LiH	FS/P/C/B	MS/LB	FS
Acanella sp. (2 ind.)	0	1	1	0	0	0	0
Antipatharia sp. 1 (4 ind.)	0	0	4	0	0	0	0
Antipatharia sp. 2 (1 ind.)	0	0	1	0	0	0	0
Bathypathes sp. (13 ind.)	0	11	1	0	2	3	1
Leiopathes sp. (all) (1583 ind.)	0	2201	50	3	23	69	12
Leiopathes sp. (large) (58 ind.)	0	8	2	0	1	49	3
Leiopathes sp. (medium) (20 ind.)	0	12	0	1	1	11	0
Leiopathes sp. (small) (1505 ind.)	0	2181	48	2	21	9	9
Paramuricea sp. (10 ind.)	2	7	1	0	0	0	0
Parantipathes sp. 1 (60 ind.)	3	50	2	1	5	4	0
Parantipathes sp. 2 (11 ind.)	0	13	0	0	1	1	2
Stichopathes cf. *gravieri* (20 ind.)	2	9	0	0	0	12	0
Trissopathes sp. (3 ind.)	0	3	0	0	0	0	0

TABLE 6 | The diversity, evenness, average density, and number of different species counted per area and mound flank.

Area	Diversity (H′)	Evenness	Density (ind. m^{-2})	No. species
1	**0.33**	**0.15**	**0.034**	**9**
1 NE	0.29	0.26	0.046	3
1 S	1.48	0.67	0.028	9
2	**0.40**	**0.19**	**0.136**	**8**
2 NW	0.38	0.18	0.155	8
2 SW	0.67	0.48	0.032	4
3	**0.11**	**0.06**	**0.143**	**6**
3 NE	0.14	0.07	0.270	6
3 NW	0.49	0.35	0.014	4

depleted in suspended organic matter (Duineveld et al., 2007; Soetaert et al., 2016). When scleractinian cold-water corals, like *L. pertusa* and *M. oculata*, form mounds of a certain size, they can engineer the environment by altering the local hydrodynamics to their benefit. The clustered Logachev cold-water coral carbonate mounds have reached this size, and therefore induce tidal up- and downwelling, internal waves, and as a consequence also large INL, which supply the corals together with other filter feeders in their community with food (Mienis et al., 2007; Soetaert et al., 2016). This increased concentration of organic matter was reflected through healthy dense live *L. pertusa* thickets on the summits of the clustered mounds in our study area at a relatively shallow depth (between 560 and 610 m depth). These areas coincided with low densities and diversity of non-scleractinian corals even though this is precisely where organic matter concentrations are the highest (Soetaert et al., 2016). There are two explanations for this observation. Firstly, the permanent mucus layer (coenosarc) on the skeleton of live scleractinian corals prevents attachment of most epibiotic species (Freiwald, 2002; Buhl-Mortensen et al., 2010). Secondly, in our study area, the scleractinian corals might outcompete other filter and suspension feeders for food on mound summits. The food capture rates for different species can strongly depend on

current velocity, seawater temperature and polyp size. High flow velocities can deform coral polyps reducing the exposed feeding surface area (Dai and Lin, 1993; Purser et al., 2010; Wijgerde et al., 2012; Gori et al., 2015). Higher flow speeds may also make the polyps less efficient at holding prey (Sebens et al., 1998; Orejas et al., 2011). Colder temperatures may cause the polyps to contract or affect nematocyst function (Gori et al., 2015). Warmer temperatures may increase the metabolism of corals, but can cause starvation if food supply is not met (Dodds et al., 2007; Davies et al., 2009). Some coral species with larger polyps can remove particles from their environment more efficiently compared to those with smaller polyps (Porter, 1976; Palardy et al., 2005; Wang et al., 2012). The effect of flow velocity, temperature and polyp size are unknown for the non-scleractinian corals described in this study. Since food supply is essential to maintain the basic physiological processes (Naumann et al., 2011), understanding what affects coral food capturing rates may help to explain the distribution pattern of the non-scleractinian corals in the Logachev Mound Province.

Dead exposed *L. pertusa* framework, and coral rubble become more abundant with increasing depth as the concentration of fresh organic matter decreases, and food becomes scarce toward deeper waters (Kenyon et al., 2003). Consequently, the first peak in non-scleractinian diversity was observed, right below the *L. pertusa* thickets in area 1. Food supply will still be relatively high at these depths, and an increased range of substrates such as coral rubble, dead *L. pertusa* framework and hard substrates (lithified hardgrounds, pebbles, cobbles, boulders) become available and can be used as settlement substrates (Mortensen and Fosså, 2006; Buhl-Mortensen et al., 2010). A significant correlation was found between lithified hardgrounds and the density of *Parantipathes* sp. Only a small percentage (22%) of the substrates in the study area consisted of these hardgrounds, but they are an important aspect of overall mound growth and development as they provide stability to the steep slopes of the mounds and can be used as substratum for mound-building invertebrates (Noé et al., 2006). Hardgrounds on the coral carbonate mounds
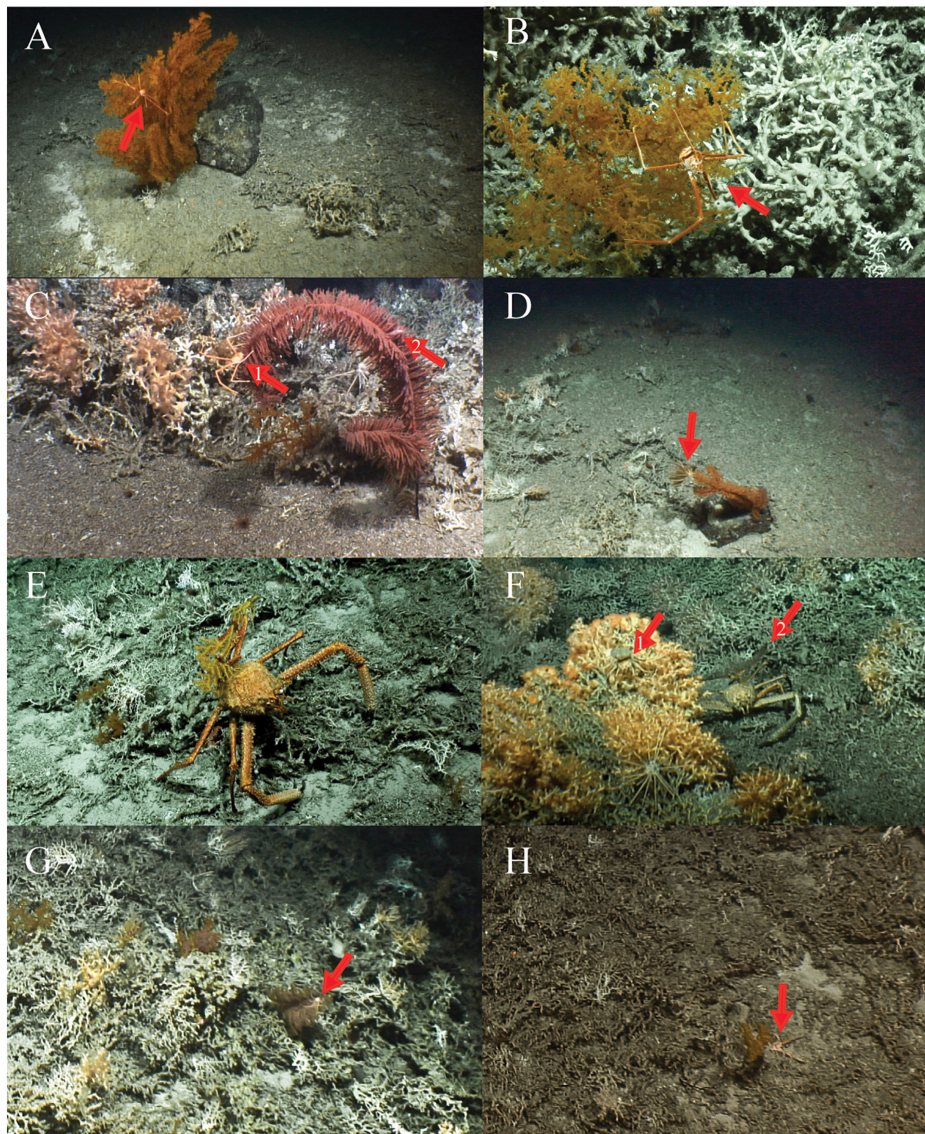
FIGURE 5 | (A,B) large and small-sized *Leiopathes* sp. colonies with the arrow pointing to a *Gastroptychus* sp. **(C)** *Parantipathes* sp. 2 with the first arrow pointing to a *Gastroptychus* sp. and the second arrow to a small shrimp. **(D)** *Parantipathes* sp. 2 with the arrow pointing to an attached crinoid. **(E)** *Paramuricea* sp. carried by *Paromola cuvieri*. **(F)** The first arrow points to *Paromola cuvieri* carrying a sponge and the second arrow points to *Paromola cuvieri* carrying a *Parantipathes* sp. 1. **(G)** The arrow points to a *Gastroptychus* sp. on the top central branch of *Bathypathes* sp. **(H)** The arrow points to *Munida* sp. sheltering under a small *Leiopathes* sp. colony.

in the Rockall area have been identified in the past (Van Weering et al., 2003). These hardgrounds can be completely exposed, showing signs of erosion by currents and sponge borings or can have different degrees of sediment cover with live and dead coral colonies (Wheeler et al., 2005, 2007). The exposure of these hardgrounds is associated with strong bottom currents (Noé et al., 2006), which could mean an increase in the food-encounter rate for cold-water corals that were able to settle there.

Differences observed in densities of non-scleractinian corals could be related to local variations in food supply. Soetaert et al. (2016) model's output of vertical current velocities and organic matter concentration in the water column of the Logachev Mound Province, appears to suggest that mounds that are located closer to Rockall Bank access more optimal food and hydrodynamic conditions. Therefore, the distance of the studied areas from the shallow bank to the deeper located mounds could affect the concentration of the organic matter reaching the corals. The lowest diversity and highest density of non-scleractinian corals was calculated for area 3. Even though the nutritional quality may not be so good, NLs could be an additional source of food, which could explain why we see high densities in area 3, which is located approximately ~25 km from the bank (Mienis et al., 2007). From both shallow water

and land based ecosystems it is known that higher nutrient input can lead to a lower diversity and higher density for a rather low number of species (Hector et al., 1999; Chapin et al., 2000; Wiedenmann et al., 2013). This would suggest that area 3 is receiving higher concentrations of organic matter. The flanks of the areas with higher densities of corals were located perpendicular to the SW orientated residual current. It is likely that this current also facilitates the supply of additional food sources.

The most abundant non-scleractinian coral in our study areas is *Leiopathes* sp. Our data showed that *Leiopathes* sp. occupied all available substrates. From this observation, it seems this species is a generalist for settlement substrates, this could explain why it thrives in all our studied areas, even when the range of available substrates is low. *Leiopathes* sp. has a slow radial growth rate of 0.005–0.022 mm yr^{-1} and is one of the longest living species on earth (Roark et al., 2009; Carreiro-Silva et al., 2013). The slower radial growth rates and their longevity might be of an advantage in areas where food supply is scarcer.

An interesting difference in the density of the various size classes of *Leiopathes* sp. was observed. The vast majority (95%) of the colonies in our area were small sized (>30 cm), while 1% was medium (30–100 cm) and 4% were large (>100 cm). A high density of small-sized colonies could indicate a successful dispersal event with a high survival rate after settlement or that they are growing from regenerating fragments (Molodtsova, 2011). However, substrate stability might be another factor influencing the distribution of the different size classes. Small sized colonies were found in areas with dead exposed *L. pertusa* framework (95% of total individuals), while the large sized colonies were mainly found in areas with large boulders (78% of total individuals). Medium sized colonies were found in similar densities on both substrates. We suggest that this difference in survival could be related to the stability large boulders provide to a large colony. Colonies growing on dead exposed *L. pertusa* framework are inclined to fall over when exposed to high current speeds. Toward the summit of the cold-water coral mounds, large boulders become rare as they are covered with live and dead *L. pertusa* and therefore are unavailable as a stable substrate for large-sized *Leiopathes* sp. colonies. Therefore, the higher percentage cover of dead exposed *L. pertusa* framework versus large boulders could also explain why a difference in the densities of the different size classes is observed.

In past studies as well as here, shrimps, crabs, crinoids and ophiuroids were found to be using non-scleractinian coral species as a feeding platform and a place to shelter (e.g., Vytopil and Willis, 2001; Burkepile and Hay, 2007; De Clippele et al., 2015). No associates were observed visually on the corals *Acanella* sp., Antipatharia sp. 2, *Stichopathes* cf. *gravieri*, *Trissopathes* sp. and only one observation was made for the plexaurid *Paramuricea* sp. For *Paramuricea* sp. this was surprising as it has been found occupied abundantly by megafauna elsewhere (Rosenberg et al., 2005; De Clippele et al., 2015). Higher numbers of organisms occupied non-scleractinian coral colonies that were larger. This is expected as smaller sized colonies are unable to have more

than one organism attached due to competition for perch sites. These associated organisms were mainly located on the top outer parts of the colonies, which increases their food encounter rate as their elevated position is further away from the slower current in the near-bottom boundary and therefore closer to the main flow (Fujita and Ohta, 1988). Generally, it is the corals' size, the number of branches and the availability of sufficient food that will impact the presence of associates on colonies. On one occasion, the squat lobster *Munida* sp. was found sheltering under a small *Leiopathes* sp. colony. This behavior was also observed under the sea pen *Kophobelemnon stelliferum* (De Clippele et al., 2015).

Even though non-scleractinian corals function as a habitat, only a minority of them had associated fauna present. This low occurrence of associated fauna could be caused by the lack of detailed surveying in our study, the high flexibility of the coral branches, and the relatively low availability of large-sized colonies. The non-scleractinian corals in our study have a more flexible skeleton compared to, e.g., the gorgonian *Paragorgia arborea* which commonly has abundant associated fauna present (Buhl-Mortensen and Mortensen, 2004, 2005; De Clippele et al., 2015). The skeleton of black corals is more flexible and chitinous, which is an adaptation for living in areas with very strong currents. To withstand strong currents, *P. arborea* grows much thicker branches compared to other corals (Mortensen and Buhl-Mortensen, 2004) which provide the associated organisms with a more robust and larger surface area to inhabit. A negative relationship between the presence of associated fauna and the flexibility and size of the colonies and branches has been shown before and therefore explains our lower presence of these associates (Buhl-Mortensen and Mortensen, 2004; Santavy et al., 2013).

Aside from functioning as a feeding platform and as a shelter, non-scleractinian corals were also used by the carrier crab *Paromola cuvieri* as camouflage or more likely, as anti-predator defense. In total, 30 carrier crabs were observed in this study, of which most were carrying a sponge, but also the black coral species, *Parantipathes* sp. 1 and the plexaurid *Paramuricea* sp. Antipatharians and alcyonaceans have previously been reported being carried by *P. cuvieri* between the dactyls and propodi of the fifth pereiopods (Wicksten, 1985; Guinot et al., 1995; Weaver et al., 2009; Braga-Henriques et al., 2012). Braga-Henriques et al. (2012) studied the behavior of 16 carrier crabs (*P. cuvieri*) in the Azores. The Braga-Henriques et al. (2012) study observed that damage of the fifth pereiopods could be a reason for when there was no object being carried. In the study presented here, no damage was observed, but this could be related to the distance between the ROV and seabed limiting the resolution of the video. The species that are carried by *P. cuvieri* varies depending on what species are available in the surrounding habitat. However, it will not necessarily be the most common invertebrates in that habitat (Braga-Henriques et al., 2012). The selection process of which species is carried is still unclear but is possibly related to weight, size and palatability (Braga-Henriques et al., 2012). In the Azores study, and in this study, camouflage-type behavior

was observed, as in some occasions the crab would lift the object above their carapace when disturbed by the ROV and its lights. However, Capezzuto et al. (2012) only observed such behavior as an adaptation to an anti-predator defense. At present, there are no indications of *P. cuvieri* using the carried species to attract other crabs or species. The sponges and cnidarians can distract predators, but also can protect the crabs with spicules and secondary metabolites against predators (Coll et al., 1982; Hill and Hill, 2002; Barsby and Kubanek, 2005; Hill et al., 2005).

CONCLUSION

Amongst the clusters of cold-water coral carbonate mounds, differences in the diversity and density of non-scleractinian corals were observed. In this study, the balance between food supplied by intermediate nepheloid layers and tidal downwelling, together with the presence of *L. pertusa* thickets and a variety of substrates seem to affect the diversity and density patterns observed. Substrate availability and stability is an important contributor to the differences observed in diversity and density, but also for the size class distribution of *Leiopathes* sp. The explanations that are given here for the differences in the fine-scale spatial distribution of non-scleractinian corals remain speculative. To fill in the gaps in our knowledge, more information on their ecophysiology and specific local organic matter concentrations for each area are needed.

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