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Visual evidence of reduced seafloor conditions and indications of a cold seep ecosystem from the Hatton–Rockall basin (NE Atlantic).

Francis C. Neat*[1], Alan J. Jamieson[2], Heather A. Stewart[3], Bhavani E. Narayanaswamy[4], Neil Collie[1], Michael Stewart[1], Thomas D. Linley[2]

***Corresponding author: francis.neat@msc.org**

[1]Marine Scotland Science, Marine Laboratory, Aberdeen, U.K. AB11 9DB

[2]School of Marine Science and Technology, Newcastle University, Newcastle Upon Tyne, U.K. NE1 7RU

[3]British Geological Survey, Lyell Centre, Research Avenue South, Edinburgh, U.K. EH14 4AP

[4]Scottish Association for Marine Science, Scottish Marine Institute, Oban, Argyll, U.K. PA37 1QA

Abstract

High definition video from a towed camera system was used to describe the deep sea benthic habitats within an elongate depression located at the western margin of Rockall Bank in the Hatton–Rockall Basin. At depths greater than 1190 m, an extensive area (10 km long by 1.5 km wide) of what appeared to be reduced sediments, bacterial mats and flocculent matter indicated possible cold seep habitat. Plumes of sediment rich fluid were observed alongside raised elongate features that gave topographic relief to the otherwise flat seafloor. In the deepest section of the depression (1215 m) dense flocculent matter was observed suspended in the water column, in places obscuring the seabed. Away from the bacterial mats, the habitat changed rapidly to sediments dominated by tube-dwelling polychaete worms and then to deep-sea sedimentary habitats more typical for the water depth (sponges and burrowing megafauna in areas of gentle slopes, and coral gardens on steeper slopes).

Keywords: reduced sediment environment, chemosynthetic, bacterial mats

Running Head: Camera survey of putative cold seep

Introduction

Reduced environments are found throughout the world’s ocean seafloor and sediments and typically arise from a lack of dissolved oxygen or excessive organic inputs to the seabed, such as particulate organic matter (marine snow) or large animal carcasses (Tunnicliffe *et al.* 2002). They also arise from geological conditions, for example, cold seeps that are typically located along continental margins and associated with sub-seabed reservoirs of hydrocarbons (often methane) and sulphide rich fluid expelled to the seafloor by gravitational and tectonic forces (Levin, 2005). Methane seeps, mud volcanoes, pock marks, carbonate slabs and brine pools are all examples of cold-seep chemosynthetic habitats (Cordes *et al.,* 2010). At cold seeps, microbial consortia anaerobically oxidise methane, reduce sulphate to sulphide and chemically acquire the necessary energy for metabolism, growth and replication (Boetius *et al*., 2000; Orphan *et al.,* 2002; Joye *et al.,* 2004; Dubilier *et al.,* 2008; Boetius & Wenzhöfer, 2013). The biochemical reactions result in the precipitation of authigenic carbonate which can lead to the formation of solid crusts surrounding seeps and vents that in turn provide substrate for other fauna (Bayon *et al.,* 2013).

The bacteria occur either as chemosynthetic symbionts of other organisms (Dubilier *et al.,* 2008) or as free-living bacteria. The free-living bacteria often form extensive filamentous mats across the seafloor (Boetius & Wenzhöfer, 2013). Only a few higher marine taxa have evolved the specialised adaptations to tolerate high concentrations of sulphide and live symbiotically with the bacteria (Dubilier *et al.,* 2008). These include, among others; mussels of the subfamily Bathymodiolinae; bivalve clams of the family Vesicomyidae, Thyasiridae, Lucinidae and Solemyidae;

annelid worms of the family Siboglinidae; and sponges of the family Cladorhizidae. The species and communities of cold-seep sediments are often dominated by endemic fauna (Olu *et al.,* 1997; Levin, 2005; Vanreusel *et al.,* 2009). Cold seep habitats are highly heterogeneous (Cordes *et al.,* 2010) and contrast starkly with adjacent deep-sea habitats (Bowles *et al*., 2016). The biomass of cold-seep communities can be orders of magnitude greater than the surrounding deep-sea habitat (Tunnicliffe*,* 1992).

Although world-wide less than 100 active seeps have been described (German *et al.* 2011), they are thought to be much more widespread along continental margins than currently documented. This is likely to be the case in the deep north-east Atlantic, where as far as we know, they are few and far between. Only three confirmed sites have so far been described; at approximately 72 °N lies the Haakon Mosby mud volcano in the Barents Sea (Niemann *et al.,* 2006; Jerosch *et al.* 2007), at around 64 °N, offshore from Norway, is found the Nyegga pock-mark region (Krylova *et al.,* 2011), and south of Spain, at 36 °N, are found the mud volcanoes of the Gulf of Cadiz (Cunha *et al.* 2013; Rodrigues *et al.,* 2010). This apparent rarity of cold seeps in the northeast Atlantic is unlikely to be real and highlights a major gap in our knowledge of deep-water benthic ecosystems. Most of the sedimentary basins of the North Atlantic margin contain potential hydrocarbon source rocks and this includes the Hatton–Rockall basin, a large expanse of submerged continental crust that lies approximately 500 km west of the British Isles (Hitchen, 2004). The underlying sediments of the Hatton–Rockall Basin are characterised by an extensive polygonal fault system which has been suggested to be a currently active process resulting in fluid expulsion (Berndt *et al.,* 2012). As seabed fluid expulsion is often associated with chemosynthetic ecosystems (Sibuet & Olu-Le Roy, 1998), the Hatton–Rockall Basin is a candidate area for harbouring cold-seep ecosystems.

In 2012 a benthic sampling net deployed at the deepest point (1200 m) of the western margin of Rockall Bank recovered two new species of chemosymbiotic bivalve of the families Vesicomyidae and Thyasiridae (Oliver & Drewery 2014). These specimens suggested a cold seep ecosystem (hereafter referred to as the *Scotia Seep*) within the UK continental shelf claim. However, the occurrence of these 'indicator' species is not itself proof of a cold-seep, as they may be associated with reduced sediments arising from biotic inputs. In order to assess the seabed habitats in the vicinity of where these species were found, a visual survey of the area was made using a towed camera to produce the first account of the site and map the seabed habitats present.

Materials and Methods

Study Site

The Hatton–Rockall Basin is a large, sedimentary deep-water habitat (1000-1500 m water depth). Bounded by the Rockall Bank to the east and the Hatton Bank to the west and north, it is located around 500 km west of the United Kingdom in international waters, but within the extended continental shelf claim of the United Kingdom (Figure 1, inset map). The study site (provisionally named the *Scotia Seep* after MRV Scotia) was located at approximately 57° 57' N and 15° 33' W at the bottom of the western slope of the Rockall Bank at depths of between 1100 and 1216 m.

Visual survey

Eight towed camera transects were made aboard *MRV Scotia* totalling approximately 12.5 hours and 40 km of video footage (Figure 1, main map). Transects spanned a depth range of 1040-1216 m. Seabed imagery was obtained using a towed body, consisting of an aluminium frame fitted with a Kongsberg Maritime colour HD video camera and six high-intensity undersea lamps and 30 cm spaced lasers for scale (McIntyre *et al.*, 2016). The camera also had the option to take strobe-lit stills which was done to obtain images for close inspection. In addition, the frame housed sensors for pressure (depth), bearing, altitude from seabed, pitch and heave, all recording at 1 s intervals throughout. The towed body was attached to the research vessel with a 4000 m 'Netsonde' co-axial cable and towed at a speed of between 1.5 – 2.5 knots at an elevation of between 2 to 5 m above the seafloor. An ultra-short baseline beacon (USBL) provided positional information on the towed camera, calculating the position of the body relative to the vessel. Transmission from the USBL was, however, intermittent and for many video sequences the position of the camera had to be estimated from the length of wire out and the seabed depth using standard spherical geometry (assuming the body to lie directly behind the vessel). Comparison of estimated positions with known positions from the USBL indicated estimated positions were on average within 164 m (+/- 22 m) of the known position. In addition to the towed video five point observations were made from a free fall baited lander system with time-lapse cameras that took horizontal digital stills of the seabed (Linley 2016). These were used to supplement the towed camera data.

Habitat classification

The identification of species from digital stills images and HD video is frequently problematic in the absence of physical samples; however visible species were identified to the lowest possible taxonomic level. Following detailed analysis of the HD video that involved species identification when possible and an assessment of the seabed type, six broad habitat types were evident that appeared to be generally exclusive of one another. These were; bacterial mats covering flat seabed and raised areas; sponges in bioturbated sediment; coral gardens; sand-rich sediment; sediment with tube-dwelling worms; zero visibility (when the seabed was obscured by dense flocculent matter). Segments of video were classified to one of these habitat types and using time referenced positions were then mapped in ArcGIS.

Bathymetry mapping

The ship-board Olex seabed mapping system (www.olex.no) generated a bathymetric map of the area based on echo-sounder readings. This was used to generate 10 m depth contours from 1100 to 1210 m water depth in ArcGIS on which to results are presented.

Results

Location and topography

The putative cold seep habitat was revealed within a distinct narrow depression (Figure 1) beneath a steep escarpment to the east (Rockall Bank) and a more gradual ascent to the west (the Hatton–Rockall Basin). At its deepest point the depression reached 1216 m. There were two distinct basins along the north-south axis of the basin where water depth exceeded 1200 m, separated by a ridge that rose to around 1180 m water depth. To the south and north of the trench, the seabed gradually shallowed before levelling out at around 1100 m water depth.

Habitats and distribution

1. Bacterial mats. Large expanses of the seafloor appeared to be covered in dense bacterial mats. The bacterial mats appeared as patches on the seabed (Figure 2a and Supplementary video) between areas of fine sediment (Figure 2b) and areas where flocculent matter had settled to form a fluffy lighter brown layer (Figure 2a, b). The bacterial mats were mainly devoid of any emergent epifauna with the exception of sporadic, small unidentified anemones (supplementary video). The bacterial mats were encountered mainly at depths of 1190 m and deeper (Table 1). At times the bacterial mats covered distinct three-dimensional features referred to as ‘green mounds’ in Figure 2c and Table 1. These mounds rose an estimated 1 m above the surrounding seafloor, forming elongate ridges and mounds. At least four separate sediment rich fluid plumes emanating from the seafloor were observed (Figure 2d, e and supplementary video). Small concentric features of the seabed were sometimes evident (Figure 2f) that resembled holes or burrows. Visibility was variable along transects a result of often dense flocculent matter in the water column. Fish (e.g.

Corephaeneoides rupestris, Chimaera opalesence, Synaphobranchus kaupi) were seen swimming above the bacterial mats.

2. Sponges in bioturbated sediment. This habitat was characterised by soft, bioturbated sediment (Figure 3a). Megafauna included sponges, of which the hexactinellid *Pheronema carpenteri,* the encrusting yellow sponge *Hexadella* sp*.* and a stalked sponge of the genus *Hyalonema* were identified. What appeared to be Xenophyophores were evident, although at times it was difficult to distinguish these from species of sponge. The squat lobster *Munida sp.* was seen frequently, sometimes partially burrowed in the sediment. The biotope was further characterised by cerianthid anemones, of which *Pachycerianthus sp.* was identified. Other commonly observed taxa included holothurians of the genus *Benthogone* and various large echinoids including *Calveriosoma sp.* This habitat was characteristic of the shallower western slopes (1130-1180 m) of the study area (Table 1). Fish were observed including *Lepidon eques.* This habitat rapidly disappeared at depths of around 1180 m and greater, transitioning into either the bacterial mat or tubeworm dominated habitats.

3. Coral gardens. This habitat (Figure 3b) was typified by the presence of gorgonian corals (sea fans) of the genus *Placogorgia,* stony coral (*Madrepora oculata*), alcyonaceans (soft corals) and the anemone *Bolocera sp.* The slope was steep and the seabed composed of outcrops of rock and areas of gravel with intermittent patches of fine-grained sediments. Fish were observed including *Lepidon eques.* This habitat was only observed in the eastern reaches of the study area, coincident with the steep flank of Rockall Bank along a narrow depth range of between 1140 and 1167 m (Table 1).

4. Sand-rich sediment. In this habitat the sediment comprised muddy sand with occasional gravel sized clasts. It was predominantly not bioturbated and lacked sponges. Occasional boulders were colonised by an unidentified species of barnacle. Other benthic fauna included small cerianthid anemones and holothurians including *Benthogone* sp. This habitat was observed on the ridge between the two basins, but also extended into the basins in places and was characteristic of the southern limit of the basin as the depth decreased.

5. Tube-dwelling polychaete worm sediment. This habitat was characterised by the presence of high densities of small unidentified tube-dwelling polychaete worms (Figure 3 c, d). At times there appeared also to be a light covering of bacterial mat. There was no evidence of bioturbation and no sponges or other benthic megafauna. This habitat was typically seen adjacent to and at marginally shallower water depths than the bacterial mats habitat (Table 1).

6. Zero-visibility. This category was reserved for sections of transects where the seabed was completely obscured by dense flocculent matter in the water column (see supplementary video). The location of this cloud of flocculent matter was predominantly encountered in the deepest sections of the study area (Table 1), although in two transects areas of zero-visibility was encountered at shallower water depths and in one instance it was encountered where the seabed had been visible on another transect.

Discussion

Extensive areas of what appeared to be bacterial mats smothering the seafloor were observed in this study. The localised nature of the mats and their absence from adjacent shallower areas suggest a focal source of reduced sediments, hydrogen sulphide production and/or methane. The bacterial mats could be indicative of a chemosynthetically active cold seep ecosystem as has been reported from numerous sites across the world's oceans (Boetius & Wenzhöfer, 2013). Alternatively they could be sustained through excessive accumulation of photosynthetically derived particulate organic matter (Gooday & Lambshead, 1989). This would fit with the bacterial mats being found predominantly in the deepest part of the study area (below 1190 m) and, also with the survey being undertaken in mid-summer following the spring phytoplankton bloom in the NE Atlantic. The presence of bacterial mats together with the initial discoveries of chemosynthetic clams (Oliver & Drewery, 2014) provides strong evidence for the presence of a reduced sediment conditions and possibly the first cold-seep ecosystem to have been found within the continental shelf limits of the UK. In places the seafloor was obscured due to dense flocculent matter in the water column, but again it is not clear at this stage if this is bacterially derived flocculants from the seabed or is pelagic derived phytodetritus. Bacterial mats and dense particulate matter in the water column have been previously reported from cold-seeps from the Barents Sea (Grunke *et al.* 2012), the Gulf of Mexico (Sassen *et al.,* 1993), the Californian slope (Levin, 2003) and the New

Zealand margin (Baco *et al.,* 2009). The near-bottom water throughout the area was clearly not toxic to fish as numerous species were observed swimming directly above the seabed.

Assuming that most of the seabed below 1190 m water depth is covered in bacterial mats this would equate to an area of at least 10 km^2 similar in scale to cold seeps found on the slope of the Gulf of Mexico (Sibuet & Olu 1998). While there was no evidence for gas bubbling or 'shimmering water' from the seabed, as is often reported from cold-seeps and mud volcanoes (Neimann *et al.,* 2006; Skarke *et al.,* 2014), sediment rich fluid plumes were observed that might suggest an active geological process. Water currents, fish motion and pressure waves from the towed camera could have caused sediment disturbance, but the plumes were sporadic and very localised, occurring both in absence and presence of fish (see supplementary video). The fluid plumes were seen in association with unusual elongate three-dimensional features on the seabed. Directed sampling of the sediments, mounds and plumes is needed to confirm their origin and nature.

The video footage did not reveal any obvious aggregations of bivalves in the bacterial mats as has been reported from other cold seep sites (Barry *et al.* 1996; Sibuet & Olu, 1998; Baco *et al.,* 2009), but this may simply reflect the small size and burrowing habits of the Vesicomyidae and Thyasiridae clams described by Oliver & Drewery (2014). Overall there was a scarcity of benthic epifauna associated with the bacterial mats, with the exception of small, dark red anemones that appeared sporadically. These remain to be identified and it is not known if they belong to the several genera of cerianthid anemones that are known to associate with reduced deep-sea habitats (Rodriguez & Daly 2012). Dense fields of what appeared to be small (2-3 cm in height) tube-dwelling polychaete worms were observed in areas adjacent to the bacterial mats. They clearly were not large enough and did not have the characteristic bright red tentacles to suggest they were species of the family Siboglinidae (that are well known from cold seeps) and is not clear whether they are chemosynthetic or not. It is interesting however that they appeared in a transition zone between the bacterial mats and the sponges and bioturbated sediment habitat observed at shallower depths.

In the area beyond the reduced sediments, on the shallower flanks of the depression, numerous sessile and more typical deep-sea species were observed. These included hexactinellid sponges *Hyalonema* sp. (stalked sponge) and *Pheronema carpenteri,* the ophiuroid *Ophiocten gracilis* and possibly Xenophyophores. This habitat occurred primarily on the shallower western slope of the study area and was characterised by bioturbation of the sediment and the presence of the squat lobster *Munida sp.* and the holothurian, *Benthogone* sp. These species and similar biotopes have been reported from numerous sites nearby in the Rockall Trough and Hatton–Rockall Basin (Hughes & Gage, 2004; Narayanaswamy *et al.,* 2013; McIntyre *et al.,* 2016). The coral garden habitat occurred on the steep eastern slope of the study area and again contrasted sharply with the seabed in the depression. Various gorgonians, the anemone *Phelliactis* sp. and soft corals (alcyonaceans) were seen in this area. Coral gardens are frequently associated with escarpment features with steep gradients, boulders and exposed bedrock (Davies *et al.,* 2015).

The habitats observed at the *Scotia Seep* contrasted starkly from the surrounding deep seafloor and slopes. A concentric pattern of habitats was apparent with a central area located in the deepest part of the depression covered with dense bacterial mats, elongate raised features and sediment rich fluid plumes. Away from the bacterial mats there appears to be transition into sediments with tube-dwelling worms, and in turn to more typical deep-sea bioturbated sediments and communities. Concentric patterns of chemosynthetic habitat radiating out from active seep areas have been previously described (Olu *et al.,* 1997; Levin *et al.,* 2003, 2005, 2016).

Chemosynthetic ecosystems are currently understood to be rare in the NE Atlantic with only the three sites previously mentioned confirmed to date. Given that these are thousands of kilometres away from the current study site, it is perhaps not surprising that species from the *Scotia Seep* have turned out to be new to science (Oliver & Drewery 2014). Interestingly, west of the Scotia *Seep* there is a network of kilometre-scale polygonal faults that extend across the Hatton–Rockall Basin (Berndt *et al.,* 2012). It is possible the *Scotia Seep* is connected in some way to this geological fault system. The observation of flocculent matter above the seabed suggests it could have a significant effect on the overlying water column. Methane plumes from cold seeps in the Gulf of Mexico, at depths similar to this study are thought to support planktonic microbial communities from the seabed into the surface water (Rakowski *et al.,* 2015).

In conclusion while the habitats described are clearly atypical of the seabed sediments in the north Atlantic for these depths, it is not clear whether it is a geological driven cold seep ecosystem or a biologically driven reduced environment. It might even arise from both if geological conditions (emissions of hydrogen sulphide rich fluids) give rise to toxic seafloor conditions for detritivores, the absence of which allows phytodetritus to build-up. Geochemical analyses of sediment samples and genetic bar-coding of the microbial and invertebrate communities are currently underway and should better define the biogeochemical nature of the *Scotia Seep*.

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References

Baco, A., Rowden, A., Levin, L.A., Smith, C.R. and Bowden, D.A. (2009) Initial characterization of cold seep faunal communities on the New Zealand Hikurangi margin. *Marine Geology* 272, 251-259

Barry, J.P., Greene, H.G., Orange, D.L., Baxter, C.H., Robison, B.H., Kochevar, R.E., Nybakken, J.W. and McHugh, C.M. (1996) Biologic and geologic characteristics of cold seeps in Monterey Bay, California. *Deep Sea Research Part I*, *43*, 1739-1762.

Bayon, G., Dupre, S., Ponzevera, E., Etoubleau, J., Cheron, S., Mascle, J., Boetius, A. and de Lange, G.T. (2013). Formation of carbonate chimneys in the Mediterranean Sea linked to deep-water oxygen depletion. *Nature Geosciences* 6, 755-760.

Berndt, C., Jacobs, C., Evans, A., Gay, A., Elliott, G., Long, D. and Hitchen, K. (2012). Kilometre-scale polygonal seabed depressions in the Hatton Basin, NE Atlantic Ocean: Constraints on the origin of polygonal faulting. *Marine Geology, 332*, 126-133.

Boetius, A., Ravenschlag, K., Schubert, C.J., Rickert, D., Widdel, F., Gieseke, A., Amann, R., Barker Jùrgensen, B., Witte, U. and Pfannkuche, O. (2000) A marine microbial consortium apparently mediating anaerobic oxidation of methane. *Nature* 427, 623-626.

Boetius, A. and Wenzhöfer, F. (2013). Seafloor oxygen consumption fuelled by methane from cold seeps. *Nature Geosciences* 6, 725–734.

Bowles, M., Hunter, K.S., Samarkin, V. and Joye, S. (2016). Patterns and variability in geochemical signatures and microbial activity within and between diverse cold seep habitats along the lower continental slope, Northern Gulf of Mexico. *Deep Sea Research Part II*, 129, 31-40.

Cordes, E.E., Cunha, M.R., Galeron, J., Mora, C., Olu-Le Roy, K., Sibuet, M., Van Gaever, S., Vanreusal, A. and Levin, L. (2010) The influence of geological, geochemical and biogenic habitat heterogeneity on seep biodiversity. *Marine Ecology*, 31, 51-65.

Cunha, M. R., Rodrigues, C. F., Genio, L., Hilario, A., Ravara, A., and Pfannkuche, O. (2013). Macrofaunal assemblages from mud volcanoes in the Gulf of Cadiz: abundance, biodiversity and diversity partitioning across spatial scales, *Biogeosciences*, 10, 2553–2568.

Davies, J.S., Stewart, H.A., Narayanaswamy, B.E., Jacobs, C., Spicer, J., Golding, N., and Howell, K.L. (2015). Benthic Assemblages of the Anton Dohrn Seamount (NE Atlantic): Defining deep-sea biotopes to support habitat mapping and management efforts with a focus on vulnerable marine ecosystems. *PLoS ONE*, 10: e0124815.

Dubilier, N., Bergin, C. and Lott, C. (2008). Symbiotic diversity in marine animals: the art of harnessing chemosynthesis. *Nature Reviews in Microbiology*, 6, 725-740.

German, C.R., Ramırez-Llodra, E., Baker, M.C. and Tyler, P.A. (2011) Deep-water chemosynthetic ecosystem research during the Census of Marine Life decade and beyond: A proposed deep-ocean road map. *PLOS One* 6, 1-16.

Gooday, A.J. and Lambshead, P.J.D. (1989).Influence of seasonally deposited phytodetritus on benthic foraminiferal populations in the bathyal northeast Atlantic: the species response. *Marine Ecology Progress Series.* 58, 53-67.

Grunke, S., Lichtschlag, A., de Beer, D., Felden, J., Salman, V., Ramette, A., Schulz-Vogt, H.N. and Boetius, A. (2012). Mats of psychrophilic thiotrophic bacteria associated with cold seeps of the Barents Sea. *Biogeosciences*, 9, 2947–2960.

Hitchen, K. (2004). The geology of the UK Hatton–Rockall margin. *Marine Petroleum Geology*, 21, 993-1012.

Hughes, D.J. and Gage, J.D. (2004). Benthic metazoan biomass, community structure and bioturbation at three contrasting deep-water sites on the northwest European continental margin. *Progress in Oceanography*, 63, 29-55.

Jerosch K., Schluter M., Foucher J.P., Allais A.G., Klages M., Edy C. (2007). Spatial distribution of mud flows, chemoautotrophic communities, and biogeochemical habitats at Hakon Mosby Mud Volcano. *Marine Geology*, 243, 1–17.

Joye, S.B., Boetius, A., Orcutt, B.N., Montoya, J.P., Schulz, H.N., Erickson, M.J. and Lugo, S.K. (2004). The anaerobic oxidation of methane and sulfate reduction in sediments from Gulf of Mexico cold seeps. *Chemical Geology*, 205, 219-238.

Juniper, S.K. and Brinkhurst, R.O. (1986). Water-column dark CO2 fixation and bacterial-mat growth in intermittently anoxic Saanich Inlet, British Columbia. *Marine Ecology Progress Series*, 33, 41−50.

Krylova, E.M., Gebruk, A.V., Portnova, D.A., Todt, C., Haflidason, H. (2011) New species of the genus Isorropodon (Bivalvia: Vesicomyidae: Pliocardiinae) from cold methane seeps at Nyegga (Norwegian Sea, Vøring Plateau, Storrega Slide). *Journal of the Marine Biological Association of the United Kingdom*, 91, 1135-1144.

Levin, L.A. (2003). Spatial heterogeneity of macrofauna at northern California methane seeps: influence of sulphide concentration and fluid flow. *Marine Ecology Progress Series*, 265, 123-139.

Levin, L.A. (2005). Ecology of cold-seep sediments: Interactions of fauna with flow, chemistry and microbes. *Oceanography and Marine Biology*, 43, 1-46.

Levin L.A., Baco, A.R., Bowden, D.A., Colaco, A, Cordes, EE, Cunha, M.R., Demopoulos, A.W.J., Gobin, J., Grupe, B.M., Le, J., Metaxas, A., Netburn, A.N., Rouse,G.W., Thurber, A.R., Tunnicliffe, V., Van Dover, C.L., Vanreusel, A., Watling L. (2016). Hydrothermal Vents and Methane Seeps: Rethinking the Sphere of Influence. *Frontiers in Marine Science*, 3.DOI:10.3389/fmars.2016.00072

Linley,T.D. (2016). *Fishes of the pacific abyssal and hadal zones: new technology and advances in geographic and bathymetric resolution*. PHD thesis. University of Aberdeen.

McIntyre, F.D., Drewery, J., Eerks-Medrano, D. and Neat, F. (2016) Diversity and distribution of deep-sea sponge grounds on the Rosemary Bank Seamount, NE Atlantic. *Marine Biology*, 163, 143-153.

Narayanaswamy, B.E., Hughes, D.J., Howell, K.L., Davies, J. and Jacobs, C. (2013). First observations of megafaunal communities inhabiting George Bligh Bank, northeast Atlantic. *Deep Sea Research Part II* 92, 79-86.

Niemann,H., Lösekann, T., de Beer, D., Elvert, M., Nadalig, T., Knittel, K., Sauter, E.J., Schluter, M., Klages, M., Foucher, J.P. and Boetius, A. (2006) Novel microbial communities of the Haakon Mosby mud volcano and their role as a methane sink. *Nature* 443, 854-8.

Oliver, P.G. and Drewery, J. (2014). New species of chemosymbiotic clams (Bivalvia: Vesicomyidae and Thyasiridae) from a putative 'seep' in the Hatton–Rockall Basin, north-east Atlantic. *Journal of the Marine Biological Association of the United Kingdom 94,* 389-403.

Olu, K., Lance, S., Sibuet, M., Henry, P., Fiala-Médioni, A. and Dinet, A. (1997). Cold seep communities as indicators of fluid expulsion patterns through mud volcanoes seaward of the Barbados accretionary prism. *Deep Sea Research Part I*, 44, 811-841.

Orphan, V.J., House, C.H., Hinrichs, K., McKeegan, K.D. and DeLong, E.F. (2002). Multiple archaeal groups mediate methane oxidation in anoxic cold seep sediments. *Proceeding of the National Academy of Sciences USA*, 99, 7663–7668.

Rakowski, C., Magen, C., Bosman, S., Gillies, L., Rogers, K. and Chanton, J. (2015). Methane and microbial dynamics in the Gulf of Mexico water column. *Frontiers in Marine Science*, 2, 69.doi:10.3389/fmars.2015.00069

Rodríguez, E. and Daly, M. (2010) Phylogenetic relationships among deep-sea and chemosynthetic sea anemones: Actinoscyphiidae and Actinostolidae (Actiniaria: Mesomyaria). *PLoS ONE* 5(6), e10958.

Rodrigues, C.F., Webster, G., Cunha, M.R., Duperron, S. and Weightman, A.J. (2010). Chemosynthetic bacteria found in bivalve species from mud volcanoes of the Gulf of Cadiz. *FEMS Microbiology and Ecology*, 73, 486-499.

Sassen, R., Roberts, H.H., Aharon, P., Larkin, J., Chinn, E. and Carney, R. (1993) Chemosynthetic bacterial mats at cold hydrocarbon seeps, Gulf of Mexico continental slope. *Organic Geochemistry*, 20, 77-89.

Sibuet, M. and Olu, K. (1998) Biogeography, biodiversity and fluid dependence of deep-sea cold-seep communities at active and passive margins. *Deep Sea Research Part II*, 45, 517-567.

Skarke, A., Ruppel, C., Kodis, M., Brothers, D., Lobecker, E. (2014) Widespread methane leakage from the sea floor on the northern US Atlantic margin. *Nature Geoscience*, 7, 657–661.

Tunnicliffe, V. (1992). Hydrothermal-vent communities of the deep sea. *American Scientist*, 80, 336-349.

Tunnicliffe, V., Juniper, S. K. and Sibuet, M. (2003). Reducing environments of the deepsea floor. In (Tyler, P. A. ed.) *Ecosystems of the World: The Deep Sea.* Chapter 4, pp. 81 - 110. London, Elsevier Press.

Van Dover, C.L .(2000). *The ecology of deep-sea hydrothermal vents*. Princeton University Press, 448 pp.

Vanreusel, A., Andersen, A.C., Boetius, A., Connelly, D., Cunha, M.R., Decker, C., Hilario, A., Kormas, K.A., Maignien, L., Olu, K., Pachiadaki, M. (2009) Biodiversity of cold seep ecosystems along the European margins. *Oceanography* 22, 110-127.

Figure Captions

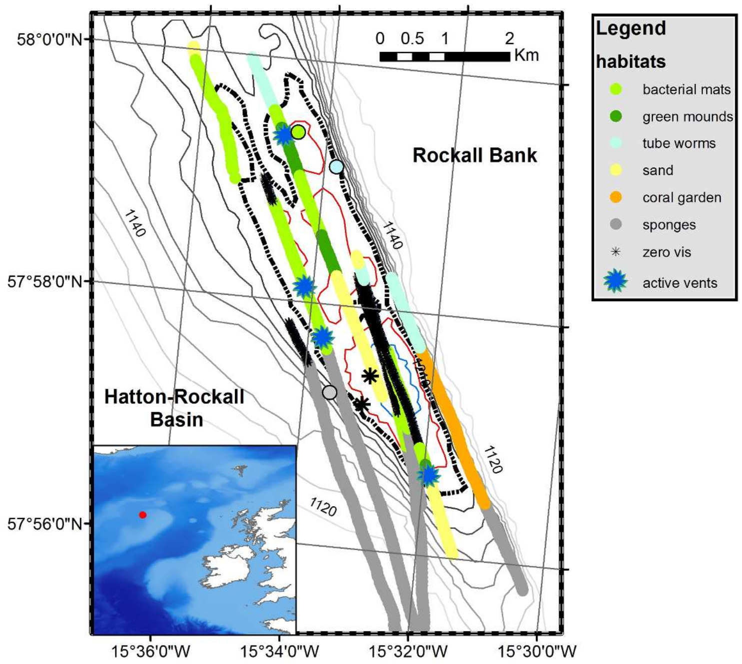
Figure 1. Map of the study site and the habitats found along the towed camera transects. Baited camera deployments are also indicated (circles) as are the sites of active vents. Bathymetric contours are plotted every 10 m from 1100 m to 1210m. The 1190 m isobaths is shown in black to indicate the area in which the majority of cold seep habitats were observed. Inset map gives location of the putative cold seep (red dot).

Figure 2. Seabed imagery of cold seep habitats. (a) and (b) The bacterial mats shrouding the seabed. The paler areas are flocculent matter that has settled from the water column onto the mats. (c) An example of the raised elongate mounds on the seabed covered with bacterial mats. (d) and (e) Active fluid seepage in association with the raised mounds. (f) An example of what appears to be a hole in the seabed between the bacterial mats. Red laser points are 30 cm apart

Figure 3. Seabed imagery of habitats on slopes adjacent to the cold seep. (a) Bioturbated sediments with sponges/and or xenophyophores. (b) Coral gardens with gorgonian corals, stony corals and anenomes. (c) Tube-dwelling worm dominated sediments. (d) Close up of the tube-dwelling worm dominated sediments (image acquired from a baited lander deployment).

Table 1. Depth ranges (derived from pressure sensor on towed camera) for each of the habitat types observed in the study.

habitat	average depth (m)	max depth (m)	min depth (m)
bacterial mats	1193.3	1211.2	1070.8
green mounds	1201.4	1208.1	1188.2
tube worms	1174.1	1200.0	1149.7
sand	1191.2	1210.8	1117.5
sponges	1132.5	1197.4	1068.9
coral garden	1157.0	1167.7	1140.4
zero visibility	1201.8	1216.6	1140.1



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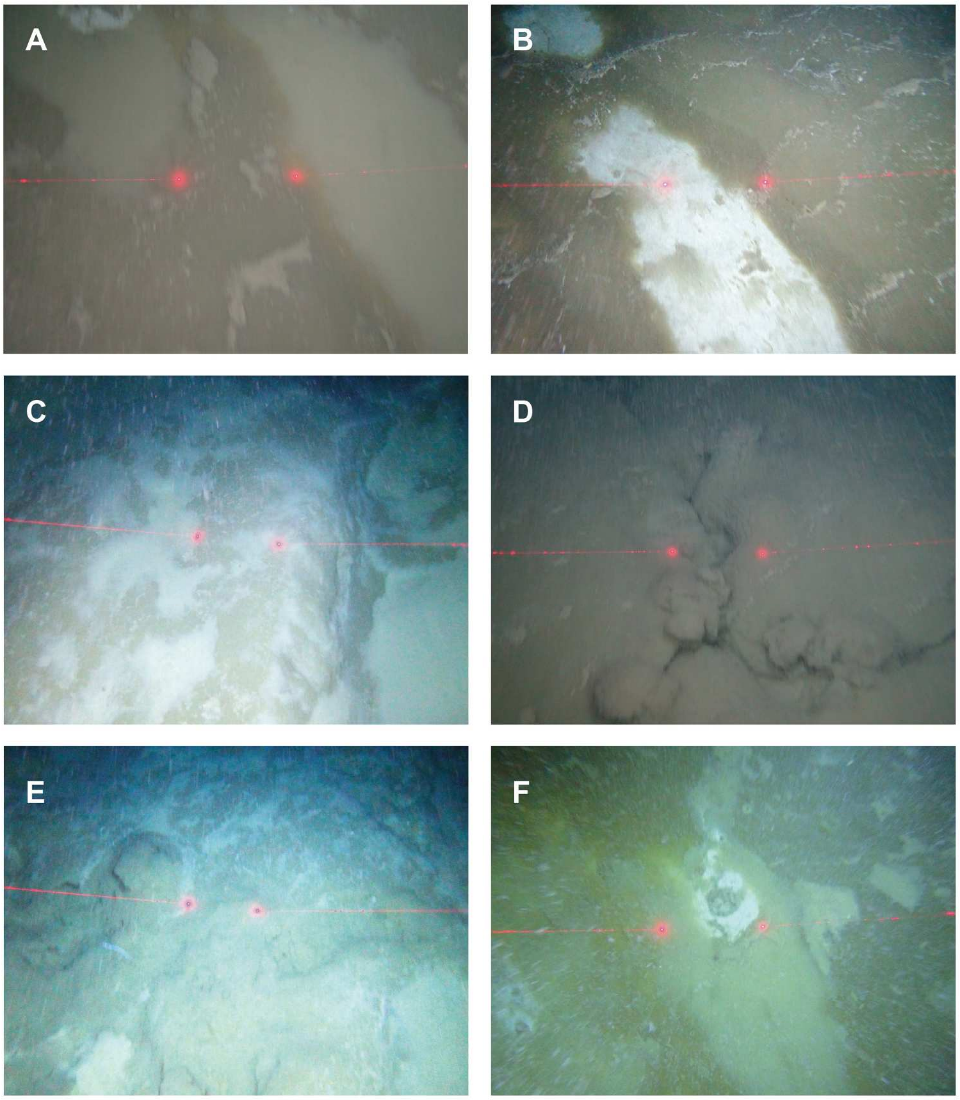

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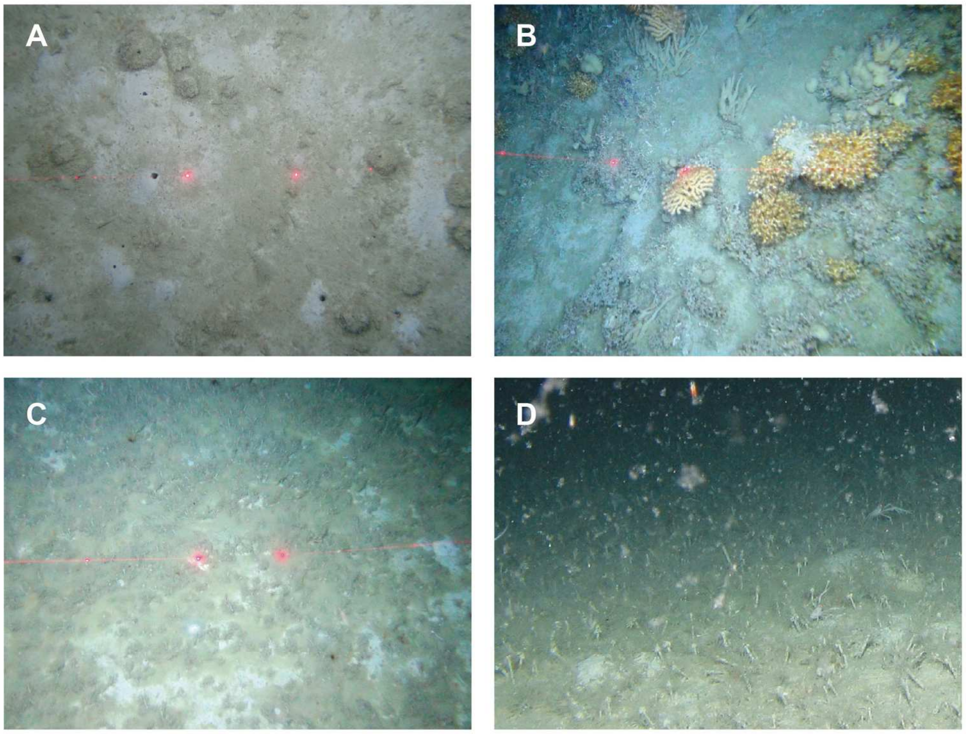

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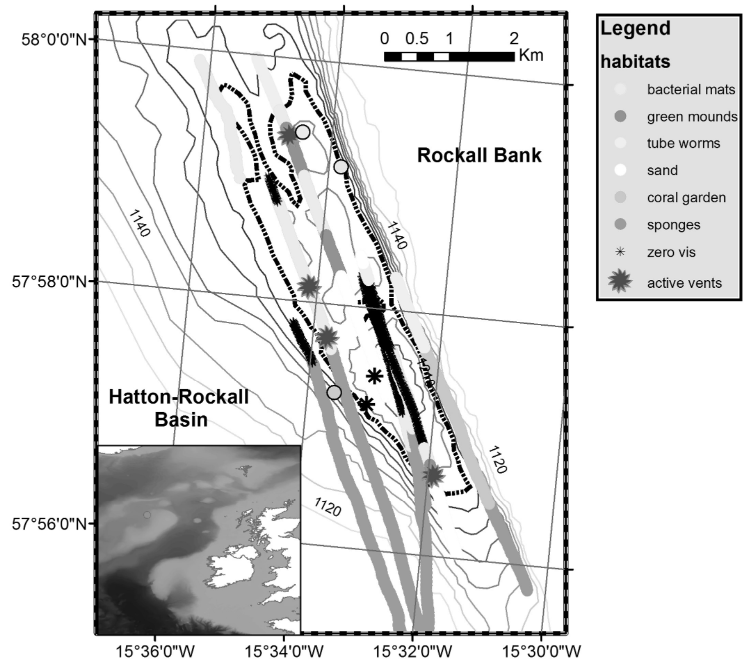

Black and white version of Figure 1

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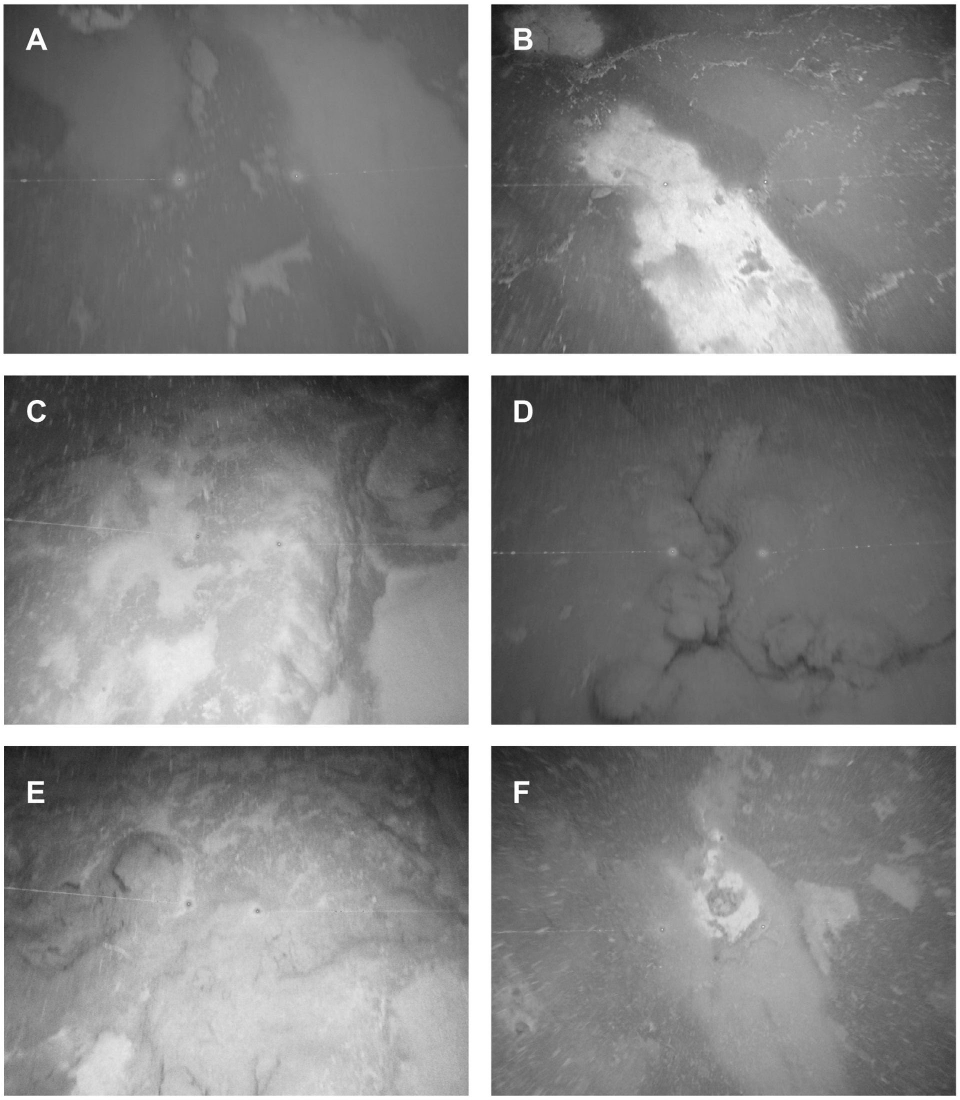

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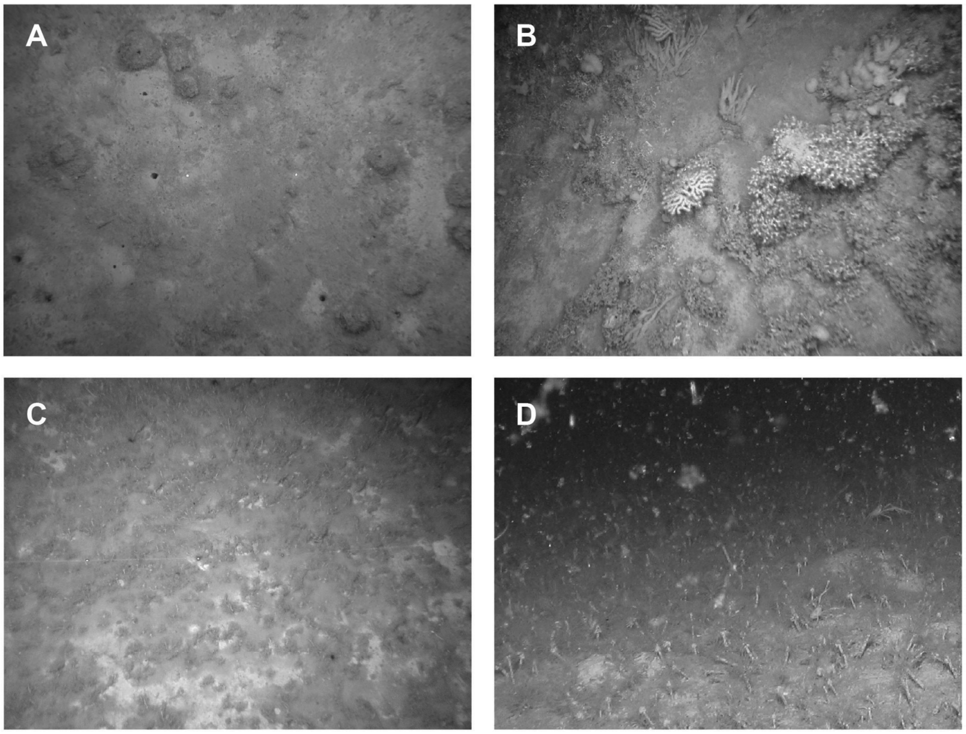

Black and white version of Figure 3

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