Mar Biol (2016) 163:143
DOI 10.1007/s00227-016-2913-z

ORIGINAL PAPER

Distribution and diversity of deep-sea sponge grounds on the Rosemary Bank Seamount, NE Atlantic

F. D. McIntyre[1] · J. Drewery[1] · D. Eerkes-Medrano[1] · F. C. Neat[1]

Received: 18 December 2015 / Accepted: 17 May 2016 / Published online: 2 June 2016

Abstract A towed camera survey revealed extensive sponge grounds on the deep slopes of the Rosemary Bank Seamount in the NE Atlantic. An Agassiz trawl deployed in the same area yielded samples for taxonomic validation and comparison to the visual survey. The sponge grounds were observed between 1200 and 1440 m depth. Eight species were identified in the trawl samples from five genera: *Geodia*, *Thenea*, *Pheronema*, *Aphrocallistes* and *Craniella*. In addition, there were 2 unresolved species of *Craniella*, one of *Hexadella* and 2 other unidentifiable Porifera species. Seven taxa were consistently identified from the video footage. *Craniella longipilis* was numerically dominant across all depths, but other species showed significant change in abundance with depth. At shallower depths *Pheronema carpenteri* was more prevalent, whereas the encrusting species *Hexadella sp.* increased in frequency with depth. Although all species have been previously reported from the North Atlantic, community composition at Rosemary Bank appears to be more diverse than other regions. Estimates of the number of sponges within the surveyed area suggest around 88 million sponges may be present. The community appears to be largely in pristine condition and the recent designation of Rosemary Bank as a nature conservation MPA should help ensure it remains so.

Responsible Editor: D. Gochfeld.

Reviewed by D. Janussen, J. M. Roberts, O. Tendal.

✉ F. D. McIntyre
F.Neat@marlab.ac.uk

[1] Marine Scotland-Science, Marine Laboratory, Aberdeen, Scotland AB11 9DB, UK

Introduction

Sponges (Phylum: Porifera) contribute to the diversity and structural habitat of many seafloor ecosystems (Hogg et al. 2010). In deep-water ecosystems, sponge species can be widely distributed as isolated individuals or where local water currents enhance food supply, they occur in dense aggregations known as deep-sea sponge grounds (Hogg et al. 2010). Sponge grounds may form distinct bands that follow depth contours and are often found on or near to sloped environments such as seamounts and ridges (Klitgaard 1995; Cárdenas and Rapp 2015). Sponge grounds are, however, also reported from basins or flat areas, e.g. the Hatton Basin (Duran-Munoz et al. 2011) and the 'Tromsoflaket' area of the Barents Sea (Klitgaard and Tendal 2004). Generally, habitat complexity decreases as depth increases (Buhl-Mortensen et al. 2010), but the structural microhabitats that sponges form increase the heterogeneity of the seafloor environment (Bett and Rice 1992; Klitgaard 1995; Bo et al. 2012). This increased microhabitat complexity has been shown to result in higher species diversity (Kazanidis et al. 2016) and abundance of marine benthic fauna by increasing the surface area for settlement, providing shelter from predation and increasing niche availability (Wulff 2006; Buhl-Mortensen et al. 2010). Sponges play a significant role in ecosystem functioning by recycling dissolved organic matter and transforming it to particulate organic matter that becomes available to detritivores, and ultimately higher trophic levels (de Goeije et al. 2013; Rix et al. 2016). Sponge grounds are thus recognised as important drivers of biodiversity and ecological function in deep-sea ecosystems (Hogg et al. 2010). Deep-sea sponge grounds may take millennia to form (Murillo et al. 2016), and individual sponges may take decades to grow (Pusceddu et al. 2014). Consequently, they are vulnerable to chronic disturbance from human activities such as bottom trawling. As a result, deep-sea sponge grounds were listed by OSPAR as a habitat under immediate threat and/or decline (OSPAR 2008), and the Food and Agricultural Organisation of the United Nations (FAO 2009) classed them as a vulnerable marine ecosystem (VME).

Deep-sea sponge grounds vary throughout the North Atlantic from the Barents Sea, along the Norwegian coast, the European continental slope and out to the Faroe Islands, Iceland, southern Greenland and Newfoundland. In the fjordic waters of Iceland and Norway, sponge grounds are characterised by a number of species from the genera *Geodia*, *Stryphnus*, *Stelletta*, *Thenea* and *Phakellia* (Hogg et al. 2010). The genus *Stryphnus* dominates on the northern shelf edge of the Faroes (Hogg et al. 2010), whereas extensive sponge grounds dominated by *Geodia* sp. are found elsewhere around the Faroes (Klitgaard and Tendal 2004; Cárdenas et al. 2013) and in the north-west Atlantic (Knudby et al. 2013). Dense aggregations of the glass sponge *Pheronema carpenteri* occur on the Porcupine Sea Bight southwest of Ireland (Rice et al. 1990) and further south off the Iberian Peninsula and the Moroccan coast (Reiswig and Champagne, 1995; Barethel and Thiel 1996). The mid-Atlantic ridge has recently been shown to be a particularly diverse area with 22 species reported (Cárdenas and Rapp 2015).

Despite increasing awareness of sponge grounds in the North Atlantic (Murillo et al. 2012), sponge grounds remain poorly mapped, with much of our knowledge limited to areas of commercial fishing interest (Hogg et al. 2010) or one-off research investigations. Collecting data on benthic species from deep-water environments is difficult and expensive, especially in large areas far from land. Technological developments, including underwater video surveys, provide benign access to the deep sea (McIntyre et al. 2015) and quantifiable imagery of these habitats (Davies et al. 2015). Such data can eventually feed into habitat suitability models (Knudby et al. 2013; Ross et al. 2015) that allow prediction of sponge habitat beyond the surveyed areas and may ultimately provide the broad-scale understanding that is currently lacking.

The Rosemary Bank Seamount lies in the north-east Atlantic and is one of three seamounts in Scotland's seas (Howe et al. 2006). An extinct volcano, Rosemary Bank rises 1400 m above the surrounding seafloor. Although it has been geologically surveyed (Howe et al. 2006), the fauna is poorly studied with only occasional reports of deep-sea sponges and other benthos (Neat et al. 2008). The seamount was designated a nature conservation marine protected area (MPA) by the Scottish Government in 2014 on the basis of it being a seamount community and thus likely to harbour cold-water coral reefs and deep-sea sponges. The aim of this study was to use a towed video camera system in combination with physical sampling to describe, map and quantify a suspected sponge ground on the Rosemary Bank Seamount.

Materials and methods

Visual survey

In 2014, Marine Scotland conducted a visual survey of the eastern slopes of Rosemary Bank aboard *MRV* Scotia using a towed camera system described by McIntyre et al. (2015). The video transects targeted an area where a bottom trawl survey had reported deep-sea sponges as bycatch. Four towed video camera transects (Fig. 1) of the seabed were conducted. These were of varying lengths and durations (Table 1), with three following depth contours 1250, 1300 and 1350 m, and the fourth tow conducted perpendicular to the others, ascending the slope from 1420 to 1150 m depth. A sensor attached to the camera system recorded depth and temperature every 30 s. A summary of the mean depth and temperature recorded for each camera tow is included in Table 1.

The towed camera system recorded continuous high-definition (HD) video. The towed body consisted of an aluminium frame mounted with 6 high-intensity lights and sensors that measured and recorded, at 1 s intervals, the altitude, depth, pitch and roll of the system. The average tow duration was 2 h at a towing speed of 1.5 m s^{-1}. The video camera system was towed at an altitude of 3–7 m from the seabed, which gave a swath seabed view of 2–8 m width. At depths of 1200–1400 m, the camera is approximately 1400 m directly behind the vessel; however, as no camera positioning system was available, positions reported are those of the ship.

Agassiz trawl sampling

Two deployments of an Agassiz trawl were taken at depths of approximately 1300 and 1250 m close to the camera tow paths (small red lines in Fig. 1). The solid frame Agassiz trawl has a horizontal opening of 210 cm and a vertical opening of 55 cm with chain along the top and bottom leading into a fine mesh (20 mm) tapered collection net. The chain digs into the top-most layer of the seabed, and the opening is sufficiently large to take all but the very largest of *Geodia* specimens. It was towed for approximately 8 min at a speed of 1 knot. Touch down on and lift-off from the seabed was determined with a 'Scanmar' depth unit affixed to the trawl frame. The catch was sorted and each species was counted, weighed and photographed with voucher specimens preserved.

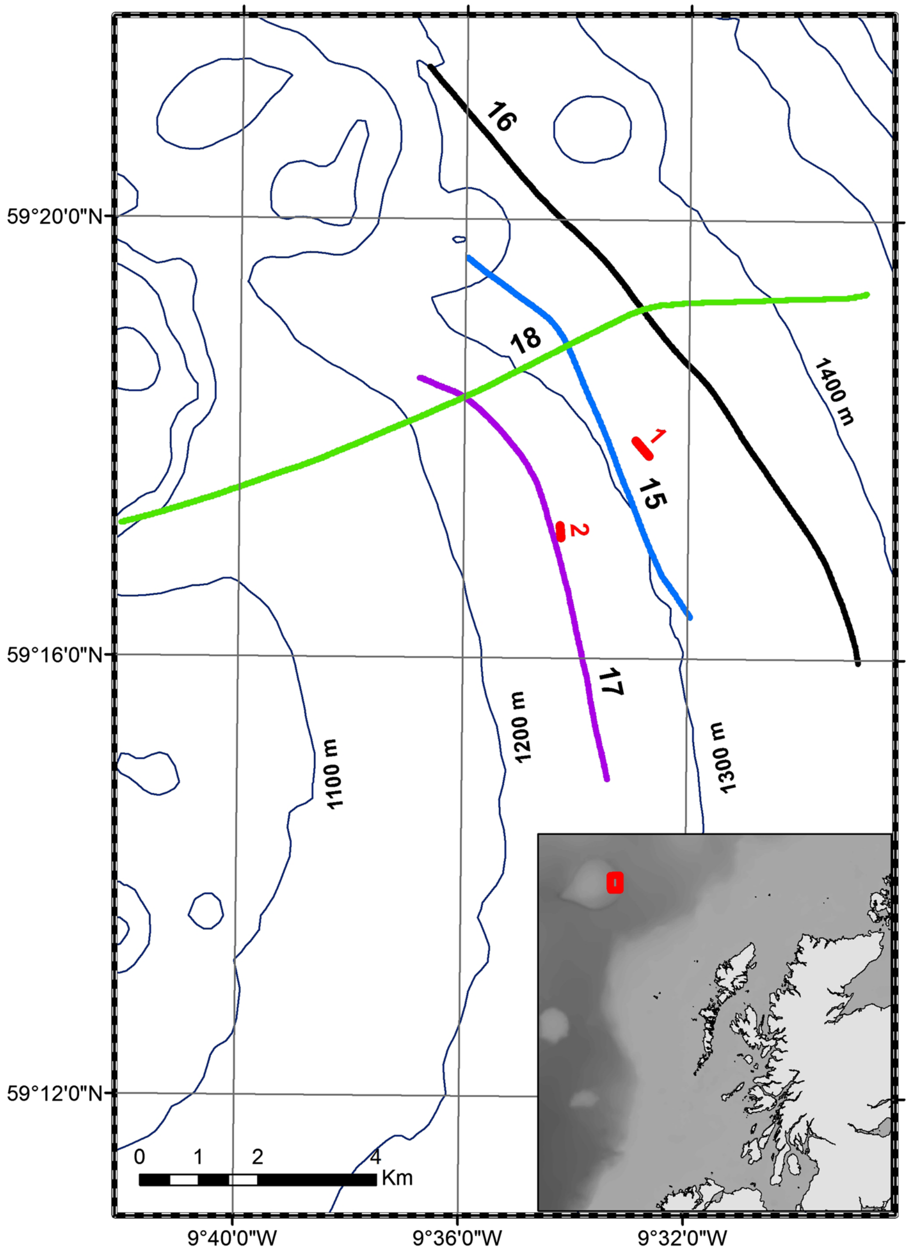

Fig. 1 Map showing survey area on east side of Rosemary Bank Seamount with video transects (*green*, *purple*, *blue* and *black* coloured lines numbered 15–18) and Agassiz trawl deployments (short *red lines* numbered 1, 2). *Inset* map shows study area (*red box*) in relation to the British Isles—shading of the seabed corresponds to depth

Table 1 Summary data for the video tows at Rosemary Bank, including temperature (°C), depth (m), area sampled (m^2)

Tow	Date	Start latitude	Start longitude	End latitude	End longitude	Mean temp (°C)	Max depth (m)	Transect length (km)	Area of sample (m^2)	Imaged area (m^2)	Number of images
15	15/09/2014	59.280	−9.542	59.328	−9.600	5.967	1290	6.26	9801	1015	135
16	15/09/2014	59.351	−9.602	59.266	−9.483	5.434	1360	11.61	7539	901	130
17	16/09/2014	59.305	−9.597	59.248	−9.557	6.217	1235	6.72	6925	877	112
18	16/09/2014	59.322	−9.501	59.287	−9.702	5.714	1440	12.05	7242	1450	189

Species identification

Specimens collected from the Agassiz trawl (Fig. 2) were identified on the basis of gross morphology (not spicule analysis) with reference to Steenstrup and Tendal (1982) and Cárdenas and Rapp (2012, 2015). These included: (1) *Geodia atlantica,* Stephens 1915. This species is smooth, irregular to vase-shaped with oscula and groups of small pores on distinctly different surfaces and is sometimes very large (>40 cm diameter). (2) *Geodia phlegraei*, Sollas 1880. This species is also irregular and vase-shaped but has larger and distinctly emarginated pores on upper surface, rarely larger than 20 cm. (3) *Geodia barretti*, Bowerbank 1858. This species is smooth, generally round with readily observable single osculum or multiple oscula. (4) *Geodia macandrewii*, Bowerbank 1858. This species is regular and round in shape with a flattened top and dense peripheral spicules, but no obvious oscula. (5) *Pheronema carpenteri,* Thomson 1869. This species is delicate and egg-shaped with a single large osculum surrounded by a fringe of elongate spicules. (6) *Aphrocallistes beatrix,* Gray 1858. This species is tubular, irregularly branched with a 'lace-like' surface composed largely of uniform hexagonal pores. Specimens were off-white to yellow, but it appeared lilac in the video. (7) *Craniella longipilis,* Topsent 1904. This species (until very recently in the genus *Tetilla*) is regular round/cone shaped with long, 'furry' spicules often displaying dimples on the upper side and with a root of long spicules attached to the seabed. (8) *Hexadella sp*. This is an encrusting yellow sponge growing on other sponges and on the spicule mat covering the seafloor. Examination under light microscopy revealed it to have no obvious fibrous internal structure indicating that it belongs to the genus *Hexadella*, rather than *Aplysilla sulphurae* (another yellow encrusting species generally found shallower). (9) *Thenea levis,* Lendenfeld 1907. This species is small, bean-shaped and elongate with longitudinal pore and oscula recesses. (10) Two further species of the genus *Craniella* were found in the Agassiz trawl sample (Fig. 2), but as the taxonomic status of this genus is currently undergoing revision (P. Cárdenas pers. comm.) these are referred to as *Craniella* sp. 1 and *Craniella* sp. 2.

Image analysis

The HD video was sub-sampled by extracting individual image frames at 20-s intervals. Image frames captured when the camera was at a high altitude from the seabed or that were blurry were not analysed. In total, 566 HD image frames from the four transects were processed. For each image frame examined, all sponges were identified to the lowest taxonomic classification possible and counted.

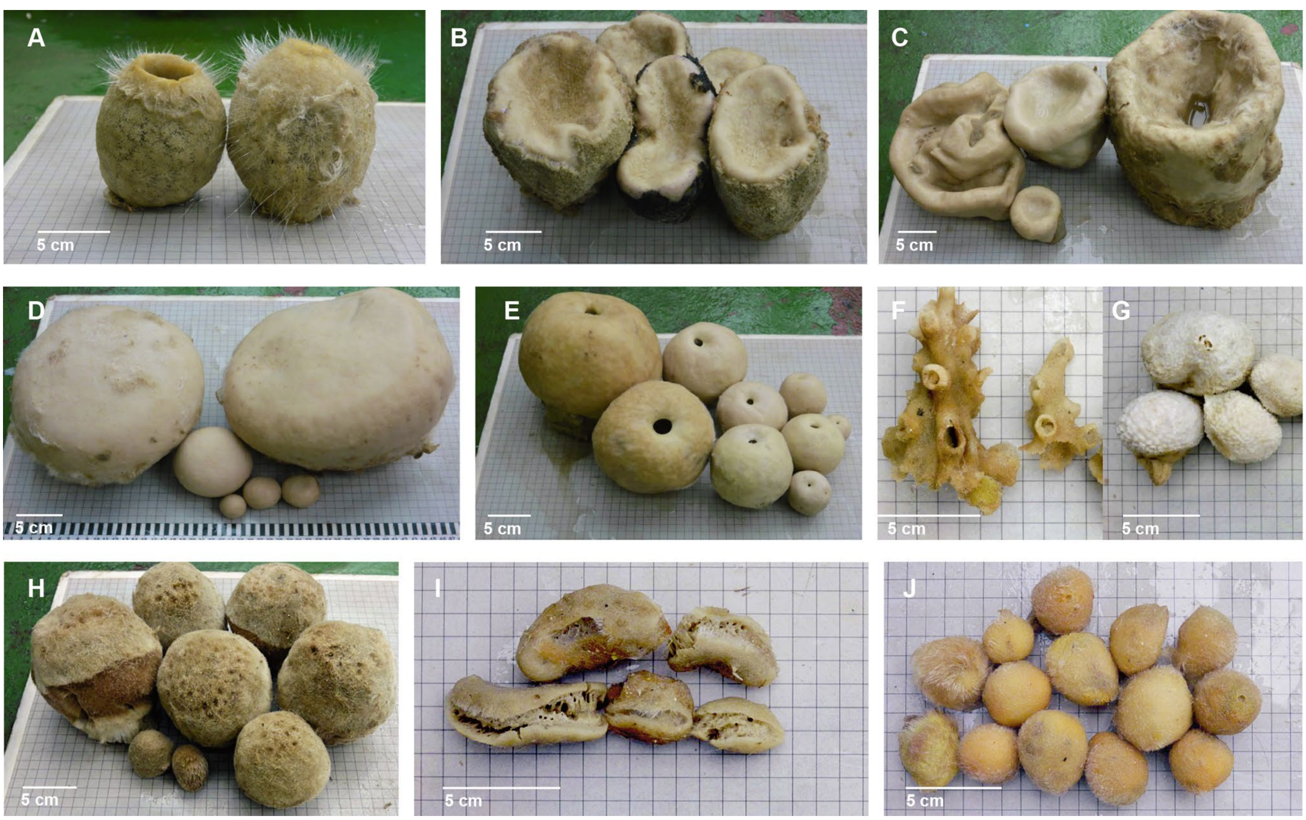

Fig. 2 Photographs of fresh samples of sponges derived from the Agassiz trawl. **a** *Pheronema carpenteri*. **b** *Geodia phlegraei.* Note central specimen has the encrusting species *Hexadella* sp. growing on its sides (it changes from *yellow* to *blue*/*purple* upon contact with air). **c** *Geodia atlantica* (smaller specimens on the *left*) and a more ambiguous larger specimen on the right that is possibly *G. phlegraei*. **d** *Geodia macandrewii* (large specimens). Smaller specimens are not of confirmed identity. **e** *Geodia barretti*. **f** *Aphrocallistes beatrix*. **g** *Craniella sp 1* (possibly *C. zetlandica*). **h** *Craniella longipilis.* **i** *Thenea levis*. **j** *Craniella sp 2*

Different species/genera of sponges grow in variable shapes and sizes that can be detected with variable taxonomic resolution with the HD video (Fig. 3). We were able to consistently recognise the following species or groups of species from the HD video footage: (1) *Geodia atlantica* and/or *Geodia phlegraei*; (2) *Geodia barretti;* (3) *Geodia macandrewii;* (4) *Pheronema carpenteri*; (5) *Aphrocallistes beatrix;* (6) *Craniella longipilis*; (7) *Hexadella sp.*

Data analysis

The area viewed for each image frame, the field of view (FOV), was calculated by matching the time stamp of the image frame to the sensor data and using the measurements of altitude of the camera from the seabed and the pitch angle of the camera system. McIntyre et al. (2015) provide a full description of the methods used to calculate the area surveyed. The density of each sponge taxon (per m^2) was calculated for each individual image frame based on the FOV of the image frame. To estimate abundance, the average density for each taxon was raised to the total areas of each transect and then to the minimal area bounding all transects. Relationships of sponge taxon abundance with depth and temperature were evaluated using the R package 'MASS' for generalised linear models (GLM) with a Poisson distribution and log link on density data of each sponge taxon.

Community analyses

From the perpendicular tow (1420–1150 m), the proportional representation of sponge taxon was summarised for each 50-m-depth band (1150–1200; 1200–1250; 1250–1300; 1300–1350; 1350–1400; and 1400–1420 m). For the other transects that followed the contours, three indices of community diversity were computed: the Shannon–Weaver diversity index (H'), Simpson's diversity index and the species evenness index (J). To assess interspecific associations, a probabilistic model of species taxon co-occurrence was calculated using the R package "co-occur". The algorithm calculates the observed and expected frequencies of co-occurrence between each pair of sponge taxa. The expected frequency is based on the distribution of each sponge taxa being random and independent of the other sponge taxa. The analysis returns the probabilities that a more extreme (either low or high) value of co-occurrence could have been obtained by chance. The output of the probabilistic model of the taxa co-occurrence is a data frame that classifies taxa pairs as having positive, negative and random associations.

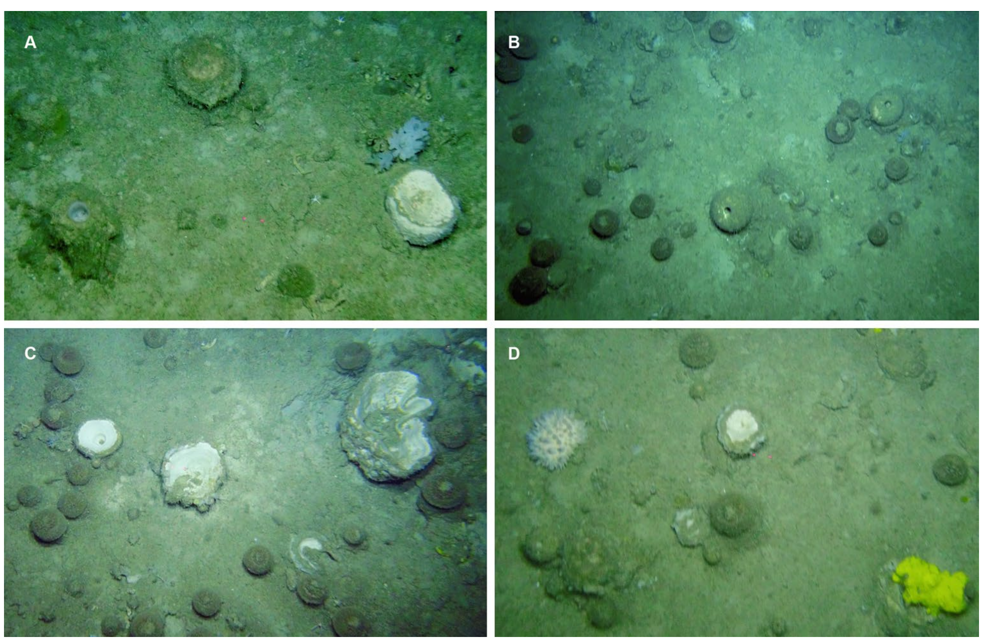

Fig. 3 High definition images from the towed video showing various species. **a** Four sponge species: *Pheronema carpenteri* (*lower left*), *Geodia macandrewii* (*top middle*), *Aphrocallistes beatrix* (*blue* branched, *upper right*) and *Geodia phlegraei* or *G. atlantica* (*white*, *lower right*). **b** *Geodia barretti* (round with hole on *top—middle* and *top right*) among *Craniella longipilis* (*round*, *brownish*—predominantly in *lower left*). **c** *Geodia atlantica* (large *white*, vase-like on *right hand side*), among *C. longipilis.* (*round*, *brownish*) and other *Geodia* (white—either *atlantica* or *phlegraei*). **d** *Craniella longipilis.* (*round*, *brownish*), *Geodia* (white—either *atlantica* or *phlegraei*), a species of *Polymastia* (*whitish* with spikes) and the *yellow* encrusting sponge, *Hexadella sp.* (*lower right corner*)

Table 2 Sponge densities (mean number of each sponge taxa per m^2) for each transect (±SE) and the overall mean for all transects

Tow	*Pheronema carpenteri*	*Geodia barretti*	*Craniella longipilis*	*Geodia atlantica/phlegraei*	*Aphrocallistes beatrix*	*Hexadella sp.*	*Geodia macandrewii*
15	0.067 (±0.01)	0.012 (±0.009)	0.755 (±0.05)	0.049 (±0.009)	0.005 (±0.001)	0.011 (±0.002)	0.005 (±0.002)
16	0.032 (±0.01)	0.071 (±0.01)	1.212 (±0.11)	0.059 (±0.01)	0.002 (±0.001)	0.046 (±0.01)	0.008 (±0.003)
17	0.168 (±0.024)	0.027 (±0.013)	0.098 (±0.08)	0.113 (±0.01)	0.067 (±0.01)	0.067 (±0.01)	0.011 (±0.001)
18	0.126 (±0.023)	0.040 (±0.01)	0.669 (±0.06)	0.068 (±0.009)	0.042 (±0.02)	0.253 (±0.02)	0.003 (±0.001)
Overall mean	0.098	0.038	0.862	0.068	0.041	0.094	0.007

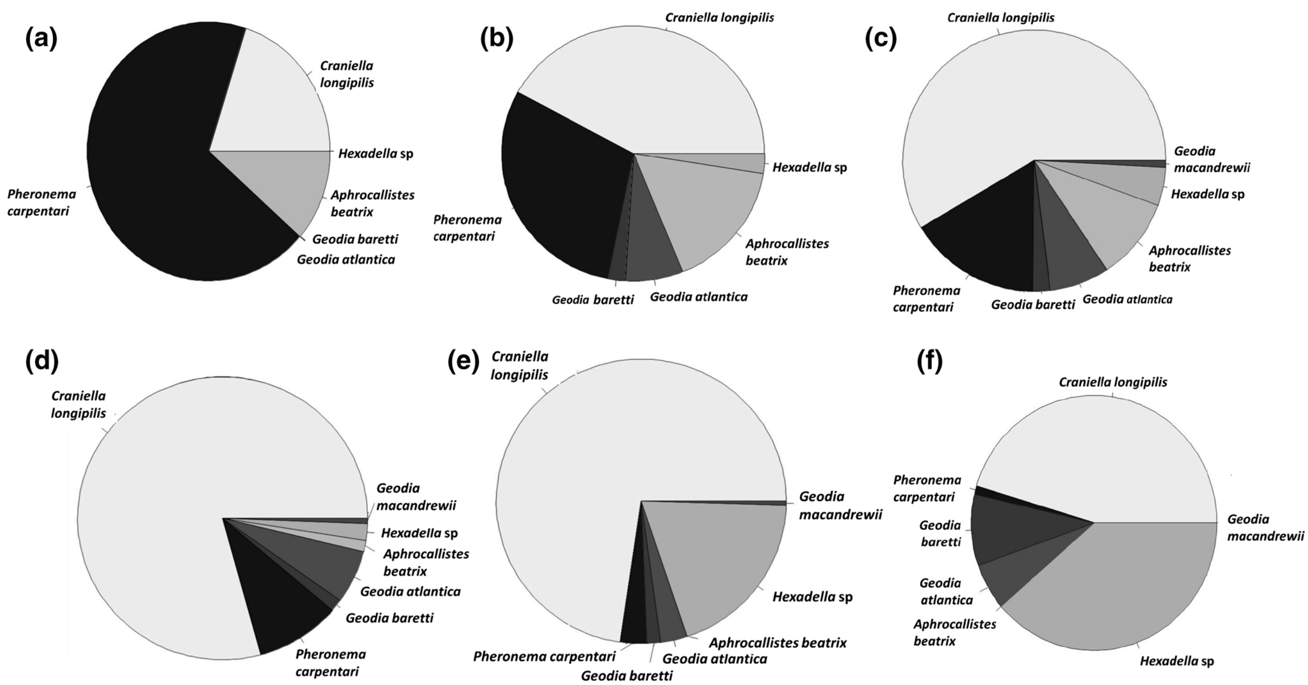

Fig. 4 Pie-charts showing contribution (percent of total) to total abundance of sponge taxa identified in Tow 18 for the depth bands. **a** 1150–1200 m; **b** 1200–1250 m; **c** 1250–1300 m; **d** 1300–1350 m; **e** 1350–1400 m; **f** 1400–1450 m

Results

Visual survey

In total, 566 image frames (covering a total area of 4243 m^2) were analysed across the four transects. The following taxa were consistently identified from the images: *Craniella longipilis*, *Geodia barretti*, *Geodia macandrewii, Hexadella sp., Pheronema carpenteri* and *Aphrocallistes beatrix*. Two other species of *Geodia* were present *(G. atlantica and G. phlegraei,)*, but these could not be distinguished when small and thus are considered as one taxonomic group. In between the live sponges there was what appeared to be an amorphous matted layer of dead sponge spicules. *Craniella longipilis* was found to be most dominant across all transects contributing a minimum of 64 % to the total abundance of sponge taxa identified in all transects (Table 2). *Craniella longipilis* was found in 514 (90 %) of the 566 image frames sampled where present density estimates ranged from 1 individual per m^2 to a maximum of 7 per m^2. *Pheronema carpenteri* and *Geodia atlantica/G. phlegraei* were the next most abundant, with a minimum contribution of 17 and 8 %, respectively. *Geodia macandrewii* and *Geodia barretti* were the least common species (Table 2). The species composition analyses from the perpendicular tow (Tow 18) show how species composition changes with depth (Fig. 4). *Pheronema carpenteri* was more abundant at shallower depths (1150–1250 m), whereas *Hexadella sp.* was more common at greater depths. The estimates of density for each sponge taxon for each tow are summarised in Table 2 and estimates of total abundance given in Table 3. These estimates indicate just how abundant the sponges were with the number of *Craniella longipilis* for a single tow calculated at 9137 sponges.

Table 3 Estimates of each sponge taxa raised to the total area of each tow and to the total area surveyed (73 km^2) based on the area of a minimum bounding polygon around all tows and using the average density of each sponge taxa (given at the bottom of Table 2)

Tow	Tow Area (m^2)	*Pheronema carpenteri*	*Geodia barretti*	*Craniella longipilis*	*Geodia atlantica/ phlegraei*	*Aphrocallistes beatrix*	*Hexadella* sp.	*Geodia macandrewii*	*Total number sponges*
15	9801	657 (7 %)	116 (1 %)	7397 (79 %)	483 (5 %)	48 (1 %)	106 (0.5 %)	48 (1 %)	8855
16	7539	243 (2 %)	536 (5 %)	9137 (84 %)	443 (4 %)	17 (0.5 %)	343 (3 %)	59 (1 %)	10,777
17	6925	1161 (13 %)	190 (2 %)	5630 (57 %)	679 (7 %)	782 (8 %)	466 (5 %)	79 (1 %)	8986
18	7242	914 (11 %)	290 (5 %)	4845 (86 %)	489 (9 %)	305 (5 %)	1833 (32 %)	25 (0.5 %)	8700
Total area	73,000,000	7,172,347 (8 %)	2,741531 (3 %)	62,937513 (71 %)	4,995616 (6 %)	2,958,319 (3 %)	6,875,152 (8 %)	502,715 (0.6 %)	88,183,194

The approximate percentage composition of each taxa is also given in parentheses

There were at least two other rare or small species evident in the video. One was likely to be from the genus *Polymastia* (Fig. 3d), while the other, a small and tubular species, remains unknown.

Regression relationships between densities of each sponge taxon and depth are illustrated in Fig. 5a–f. The hexactinellid sponges *Pheronema carpenteri* and *Aphrocallistes beatrix* were related to depth with densities of these sponges decreasing with increasing depth (Fig. 5b, e: GLM, $p = 0.001$ and $p = 0.0121$, respectively). The encrusting sponge *Hexadella sp.* was also found to be related with depth with higher densities at deeper depths (Fig. 5f: GLM, $p = 0.003$). This species grows both on other sponges and directly on the seabed which itself is largely dead sponge matter (spicules). Depth did not have a significant effect on the densities of *Craniella longipilis*, *Geodia barretti* and *Geodia atlantica/G. phlegraei*. Regression relationships between densities of each sponge taxon and temperature were not found to be significant.

Mean values for each towed camera transect of species diversity (Shannon H') and species richness are shown in Table 4. The perpendicular transect showed high diversity reflecting the wider range of depths covered. The transect at 1250 m had higher diversity indices than the deeper transects reflecting the frequent occurrence of *P. carpentari* and *A. beatrix* becoming increasingly rare at depths below this. Figure 6 illustrates a heat-map visualisation of the pairwise species associations revealed by the probabilistic model of species co-occurrence. *Craniella longipilis* shows a positive association with all other sponge taxa identified due to its occurrence in 90 % of the sampled image frames. A positive association was also found for *Geodia atlantica/G. phlegraei* with *Geodia barretti, Hexadella sp.* and *Aphrocallistes beatrix*. *Geodia barretti* had a positive association with *Hexadella sp.*, although it should be noted *Hexadella sp.* was observed alongside, but not actually growing on *G. barretti*. *Pheronema carpenteri* was found to have a high probability of co-occurrence with the other Hexactinellid species, *Aphrocallistes beatrix*.

Agassiz trawl survey

The number and total weight of each species identified in the trawl samples are given in Table 5. Specimens fresh from the trawl are shown in Fig. 2a–j. The species representation was similar to that recorded by the visual survey with *C. longipilis* being numerically dominant, followed by the *Geodia* species and *P. carpentari*. There were potentially a further three other species present in the sample: one which was large and globular, one which was small and round and one which was small and tubular. These unidentified species, however, represented a tiny proportion of the overall weights and numbers observed. There were also clumps of the amorphous mat (also seen on the video) which was a matrix of spicules and soft sediment.

Discussion

This study has characterised a previously unknown and extensive deep-sea sponge ground in the north-east Atlantic and suggests the Rosemary Bank Seamount may be a hotspot for sponge diversity. Our results almost certainly underestimate the actual diversity of this sponge ground, in part because we could not identify all specimens, but also because ongoing genetic research and systematic revision of the Porifera will likely reveal new species (Cárdenas et al. 2012; 2013; Morrow and Cárdenas 2015). The results from the video survey were in general agreement with those obtained from the Agassiz trawl from the same depth and area, at least for the dominant species. Minor discrepancies between the two survey methods included the smaller and rarer species such as *Craniella* sampled by the Agassiz trawl, but not apparent on the video, and a species of *Polymastia* observed on video, but not sampled by the Agassiz trawl.

Dense aggregations of mainly *Geodia* sponges have been reported throughout the north-east Atlantic, further to

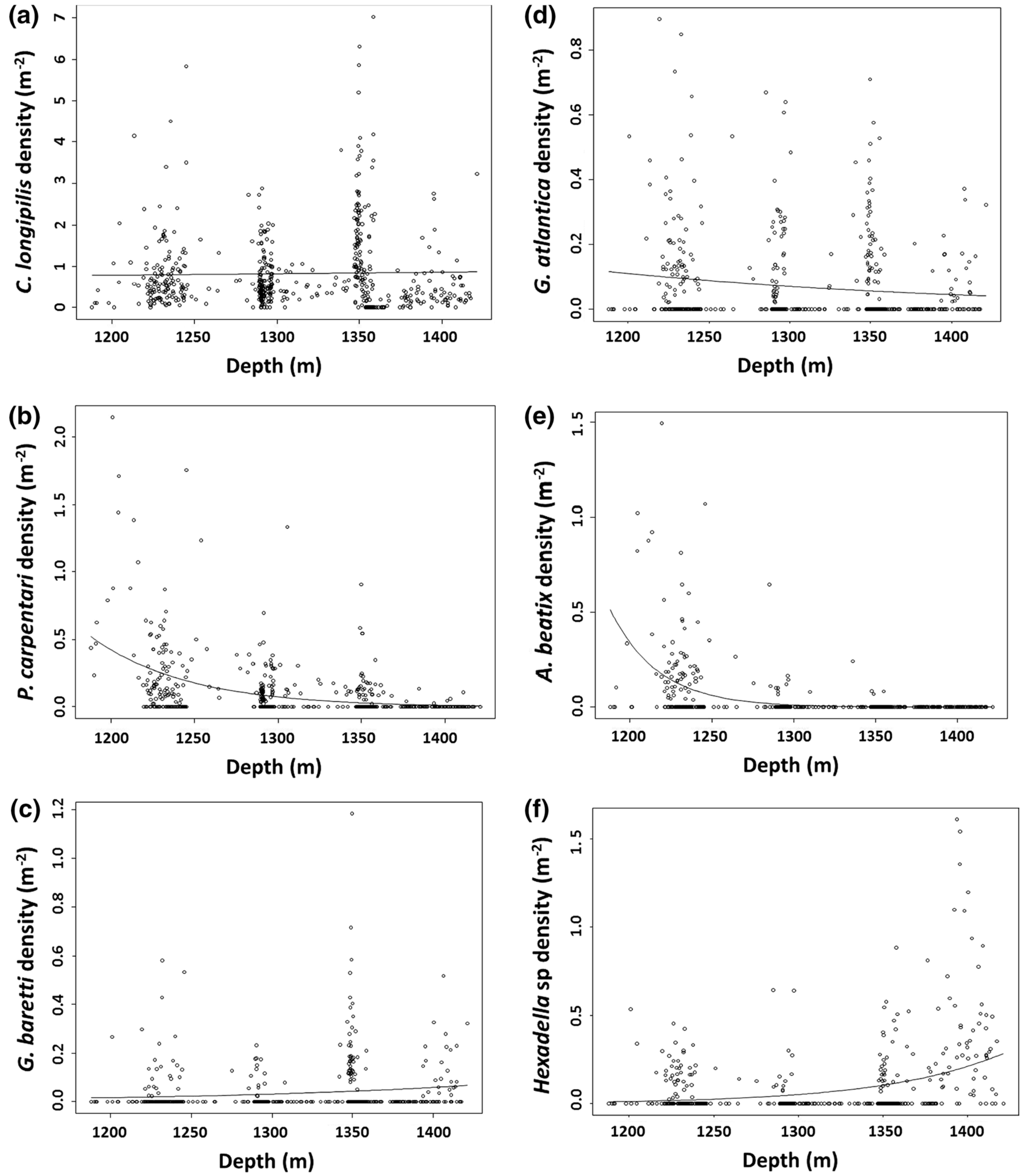

Fig. 5 Regression plots of the relationship with depth (m) of the main species observed: **a** *Craniella longipilis*, **b** *Pheronema carpenteri*, **c** *Geodia barretti*, **d** *Geodia atlantica/phlegraei*, **e** *Aphrocallistes beatrix*, **f** *Hexadella sp*

Table 4 Values of community diversity indices for each visual survey transect

Index	Tow number (depth)			
	15 (1300 m)	16 (1350 m)	17 (1250 m)	18 (1420–1150 m)
Shannon's Diversity Index (*H*)	0.697	0.678	1.359	1.337
Species evenness (*J*)	0.358	0.348	0.698	0.687
Simpson's Diversity Index	0.307	0.286	0.615	0.637

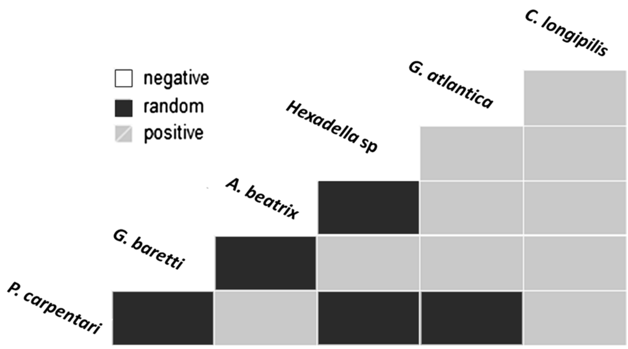

Fig. 6 Heat-map visualisation of the pairwise species associations revealed by the probabilistic model of species co-occurrence for the 6 more common sponge taxa identified. *Black* represents a positive association and *grey* a random association

Table 5 Summary data of weights and numbers for each species sampled by the Agassiz trawl

Haul	Depth (m)	Species	Weight (kg)	Number
1	1305	*Geodia barretti*	9.82	7
		Geodia phlegraei	0.31	2
		Geodia atlantica	3.10	6
		Craniella longipilis	42.32	279
		Thenea levis	0.11	8
		Pheronema carpenteri	1.31	5
		Craniella sp. 2	0.20	15
		Craniella sp. 1.	0.21	11
2	1250	*Geodia barretti*	17.30	23
		Geodia phlegraei	13.00	22
		Geodia atlantica	60.10	19
		Geodia macandrewii	9.80	4
		Craniella longipilis	98.97	293
		Thenea levis	0.02	3
		Pheronema carpenteri	5.10	18
		Craniella sp. 2	0.31	15
		Craniella sp. 1	0.41	12
		Aphrocallistes beatrix	0.57	N/A

N/A due to the encrusting and fragmented nature *of Hexadella* sp. it was not meaningful to count numbers. Three rare unidentifiable specimens not included

the north around the Faroe Islands, Norway, Iceland and off East Greenland (Klitgaard et al. 1997), whereas aggregations of *Pheronema carpenteri* have been reported further to the south of the study area from the Porcupine Bight west of Ireland (Rice et al. 1990; Barethel and Thiel 1996) to the continental slope off Morocco (Reiswig and Champagne 1995). The sponge community on Rosemary bank, however, is different from these communities described from other areas. First it appears to be more diverse, containing species from the two main classes of sponges, and second, the sponges were distributed fairly uniformly at high densities, which is contrary to previous observations of many small, but high density patches (Klitgaard and Tendal 2004). Perhaps the most notable difference was the dominance of *Craniella longipilis* at Rosemary Bank at all depths sampled. *Craniella longipinis* is normally reported as a minor constituent of deep-sea sponge communities (Cárdenas and Rapp 2015).

The apparent high diversity of the sponge grounds at Rosemary bank may relate to the fact that the site is deeper than other sites investigated and that this survey spanned a relatively wide depth range. This study is novel is being able to show how Porifera species composition changes with depth; *Pheronema carpenteri* was found in highest densities in the shallower depth bands, whereas the frequency of the yellow encrusting sponge *Hexadella sp.* increased with depth (although this itself may reflect the presence of host species or the spicule mat upon which it encrusts). At its base, the Rosemary Bank Seamount is at the junction of two different water masses; a deeper southerly flowing current known as Wyville Thomson Ridge overflow water and a northerly flowing current comprised mainly of Labrador Sea Water (Howe et al. 2006). These currents interact with the topography of the seamount to generate local hydrographic anomalies such as internal waves, turbulence and circular flow patterns (Howe et al. 2006). Deep-sea sponge grounds tend to occur in regions where the topography is irregular and where hydrographic conditions cause internal waves and the acceleration of local currents (Rice et al. 1990; Klitgaard et al. 1997). It is interesting that the sponge grounds discovered here were located on a gently sloped "terrace" environment between depths of 1175–1425 m. Rice et al. (1990) postulated that *Pheronema carpenteri* prefers areas close to high hydrodynamic flux, but not actually within such areas themselves. This hypothesis would fit with the current study—at depths shallower and deeper (<1000 and >1500 m) than where the sponges were found, the slope at Rosemary Bank is much steeper.

Sponge grounds are ecologically significant as they have high species richness and diversity compared to the surrounding seafloor (Buhl-Mortensen et al. 2010). The functional role of sponge grounds may be particularly important in creating structural habitat. Through habitat modification, deep-sea megafauna can have measurable influences on macrofauna (McClain and Barry 2010). Klitgaard (1995) found that large numbers of invertebrate taxa are associated with species (like *C. longipilis)* that have "furry" spicules which persist long after the sponge has died, creating a matted seafloor of increased heterogeneity. In functional terms, sponges are highly effective filter feeders processing a wide size spectrum of particles and a large volume of water (Leys et al. 2012; Kutti et al. 2013). In addition to sequestering dissolved silicon from the ocean (Maldonado et al. 2011), they remove dissolved organic matter from the water column and therefore significantly influence ecosystem functioning through carbon recycling (de Goeije et al. 2013; Rix et al. 2016) and bentho-pelagic coupling (Pile and Young 2006; Wulff 2006; Bell 2008). Nitrification rates have been measured in *Geodia barretti* (Hoffmann et al. 2009) indicating a substantial contribution to nitrogen turnover in the deep-sea environments. Raising the numbers of sponges found in this study to a boundary around the camera tows (~73 km^2) gives an abundance estimate of around 88 million visually detectable sponges. This gives some idea of the potential biomass in just one small area and suggests sponge habitats play fundamental roles in the functioning of deep-sea ecosystems (Buhl-Mortensen et al. 2010; Kutti et al. 2013; Rix et al. 2016).

The towed camera methodology employed in this study is clearly a useful survey tool for characterising and mapping deep-sea sponge grounds and other VMEs such as coral reefs. That it is non-extractive and non-damaging to benthic communities means it is ideal for monitoring MPAs and discovering new areas of VMEs. Video surveys, however, do have their limitations with respect to species identification (Howell et al. 2014), but the broad agreement between what we observed on the video and what was sampled by the Agassiz trawl samples gives confidence and a degree of quality assurance. The combination of methods is necessary to cover a representative area and acquire some degree of taxonomic certainty. The full extent of this sponge ground is not yet determined, and there is potentially a vast belt of sponges circling the Rosemary Bank Seamount. Rosemary Bank harbours a unique and extensive example of pristine deep-sea sponge habitat in the north-east Atlantic. The recent designation of the Rosemary Bank (Scottish Government 2014) as a marine protected area should ensure that these sponge grounds are safe guarded for the future.

Acknowledgments This research was funded by the Scottish Government (Project ST0150: MOREDEEP). We are most grateful for the technical support and expertise of Neil Collie and Mike Stewart as well as Matt Kinghorn and Rob Kynoch for making up the Agassiz trawl. We further thank the officers and crew of MRV Scotia and the scientific staff who participated on survey 1314S. We are grateful to Ole Tendal, Paco Cárdenas, Henry Reiswig, Ellen Kenchington, Javier Murrilo Perez and Gabrielle Tompkins-MacDonald for taxonomic advice. The editor and three anonymous reviewers provided very helpful criticism that improved the manuscript.

References

Barethel Tendal OS, Thiel H (1996) A wandering population of the hexactinellid sponge *Pheronema carpenteri* on the continental slope off Morocco, Northwest Africa. P.S.Z.N.I. Mar Ecol 17:603–616

Bell JJ (2008) The functional roles of marine sponges. Estuar Coast Shelf Sci 79:341–353. doi:10.1016/j.ecss.2008.05.002

Bett BJ, Rice AL (1992) The influence of hexactinellid sponge (*Pheronema carpenteri*) spicules on the patchy distribution of macrobenthos in the porcupine seabight (bathyal NE Atlantic). Ophelia 36:217–226

Bo M, Bertolino M, Bavestrello G, Canese S, Giusti M, Taviani M (2012) Role of deep sponge grounds in the Mediterranean Sea: a case study in southern Italy. Hydrobiology 219:163–177

Buhl-Mortensen L, Vanreusel A, Gooday AJ, Levin L, Priede IG, Buhl-Mortensen P, Gheerardyn H, King NJ, Raes M (2010) Biological structures as a source of habitat heterogeneity and biodiversity on the deep ocean margins. Mar Ecol 31:21–50. doi:10.1111/j.1439-0485.2010.00359.x

Cárdenas P, Rapp HT (2012) A review of Norwegian streptaster-bearing Astrophorida (Porifera: Demospongiae: Tetractinellida), new records and a new species. Zootaxa 3253:1–53

Cárdenas P, Rapp HT (2015) Demosponges from the Northern Mid-Atlantic Ridge shed more light on the diversity and biogeography of North Atlantic deep-sea sponges. J Mar Biol Assoc UK (online). doi:10.1017/S0025315415000983

Cárdenas P, Perez T, Boury-Esnault N (2012) Sponge systematics facing new challenges. Adv Mar Biol 61:79–209

Cárdenas P, Rapp HT, Klitgaard AB, Best M, Thollesson M, Tendal OS (2013) Taxonomy, biogeography and DNA barcodes of Geodia species (Porifera, Demospongiae, Tetractinellida) in the Atlantic boreo-arctic region. Zool J Linn Soc 169:251–311. doi:10.1111/zoj.12056

Davies JS, Stewart H, Narayanaswamy BE, Jacobs C, Spicer J, Golding N, Howell KL (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. doi:10.1371/journal.pone.0124815

de Goeij JM, van Oevelen D, Vermeij MJA, Osinga R, Middelburg JJ, de Goeij AFPM, Admiraal W (2013) Surviving in a marine desert: the sponge loop retains resources within coral reefs. Science 342:108–110. doi:10.1126/science.1241981

Duran-Munoz P, Murillo FJ, Sayago-Gil M, Serrano A, Laporta M, Otero I, Gomez C (2011) Effects of deep-sea bottom longlining on the Hatton Bank fish communities and benthic ecosystem, north-east Atlantic. J Mar Biol Assoc UK 91:939–952. doi:10.1017/s0025315410001773

FAO (2009) International guidelines for the management of deep-sea fisheries in the high seas. Food and Agriculture Organization of the United Nations, p 73

Hoffmann F, Radax R, Woebken D, Holtappels M, Lavik G, Rapp HT, Schläppy ML, Schleper C, Kuypers MMM (2009) Complex nitrogen cycling in the sponge *Geodia barretti*. Environ Microbiol 11:2228–2243. doi:10.1111/j.1462-2920.2009.01944.x

Hogg MM, Tendal OS, Conway KW, Pomponi SA, Van-Soest RWM, Krautter M, Roberts JM (2010) Deep-sea sponge grounds: reservoirs of biodiversity. UNEP-WCMC Biodiversity Series, Cambridge

Howe JA, Stoker MS, Masson DG, Pudsey CJ, Morris P, Larter RD, Bulat J (2006) Seabed morphology and the bottom-current pathways around Rosemary Bank Seamount, northern Rockall Trough, North Atlantic. Mar Petrol Geol 23:165–181

Howell KL, Bullimore RD, Foster NL (2014) Quality assurance in the identification of deep sea taxa from video and image analysis: response to Henry and Roberts. ICES J Mar Sci 71:899–906. doi:10.1093/icesjms/fsu052

Kazanidis G, Henry LA, Roberts JM, Witte UFM (2016) Biodiversity of *Spongosorites coralliophaga* (Stephens, 1915) on coral rubble

at two contrasting cold-water coral reef settings. Coral Reefs 35:193–208
Klitgaard AB (1995) The fauna associated with outer shelf and upper slope sponges (Porifera, Demospongiae) at the Faroe Islands, northeastern Atlantic. Sarsia 80:1–22
Klitgaard AB, Tendal OS (2004) Distribution and species composition of mass occurrences of large-sized sponges in the northeast Atlantic. Prog Oceanogr 61:57–98. doi:10.1016/j.pocean.2004.06.002
Klitgaard AB, Tendal OS, Westerberg H (1997) Mass occurrences of large sponges (Porifera) in Faroe Island (NE Atlantic) shelf and slope areas: characteristics, distribution and possible causes. The responses of marine organisms to their environments. University of Southampton, England: Southampton Ocenography Centre, pp. 129–142
Knudby A, Kenchington E, Murillo FJ (2013) Modelling the distribution of *Geodia* sponges and sponge grounds in the northwest Atlantic. PLoS One 8(12):e82306. doi:10.1371/journal.pone.0082306
Kutti T, Bannister RJ, Fosså JH (2013) Community structure and ecological function of deep-water sponge grounds in the Traenadypet MPA—Northern Norwegian continental shelf. Cont Shelf Res 69:21–30. doi:10.1016/j.csr.2013.09.011
Leys SP, Yahel G, Reidenbach MA, Tunnicliffe V, Shavit U (2012) The sponge pump: the role of current induced flow in the design of the sponge body plan. PLoS One 6(12):e27787. doi:10.1371/journal.pone.0027787
Maldonado M, Navarro L, Grasa A, Gonzalez A, Vaquerizo I (2011) Silicon uptake by sponges: a twist to understanding nutrient cycling on continental margins. Nat Sci Rep 1:30
McClain CR, Barry JP (2010) Habitat heterogeneity, disturbance, and productivity work in concert to regulate biodiversity in deep submarine canyons. Ecology 91:964–976
McIntyre F, Neat F, Collie N, Stewart M, Fernandes P (2015) Visual surveys can reveal rather different 'pictures' of fish densities: comparison of trawl and video camera surveys in the Rockall Bank, NE Atlantic Ocean. Deep Sea Res 95:67–75
Morrow C, Cárdenas P (2015) Proposal for a revised classification of the Demospongiae (Porifera). Front Zool 12:1–27. doi:10.1186/s12983-015-0099-8(2015)
Murillo FJ, Duran-Muñoz P, Cristobo J, Ríos P, González C, Kenchington E, Serrano A (2012) Deep-sea sponge grounds of the Flemish Cap, Flemish Pass and the Grand Banks of Newfoundland (Northwest Atlantic Ocean): distribution and species composition. Mar Biol Res 8:842–854. doi:10.1080/17451000.2012.682583
Murillo FJ, Kenchington E, Lawson JM, Li G, Piper DJW (2016) Ancient deep-sea sponge grounds on the Flemish Cap and Grand Bank, northwest Atlantic. Mar Biol. doi:10.1007/s00227-016-2839-5
Neat F, Burns F, Drewery J (2008) The deepwater ecosystem of the continental shelf slope and Seamounts of the Rockall trough: a report on the ecology and biodiversity based on FRS scientific surveys. Fisheries Research Services Internal Report No 02/08. http://www.gov.scot/Uploads/Documents/IR0208.pdf. Accessed 26 May 2016
OSPAR (2008) OSPAR List of Threatened and/or Declining Species and Habitats. Reference Number: 2008-6
Pile AJ, Young CM (2006) The natural diet of a hexactinellid sponge: benthic–pelagic coupling in a deep-sea microbial food web. Deep Sea Res I 53:1148–1156. doi:10.1016/j.dsr.2006.03.008
Pusceddu A, Bianchelli S, Martín J, Puig P, Palanques A, Masqué P, Danovaro R (2014) Chronic and intensive bottom trawling impairs deep-sea biodiversity and ecosystem functioning. PNAS 111:8861–8866. doi:10.1073/pnas.1405454111
Reiswig HM, Champagne P (1995) The NE Atlantic glass sponges *Pheronema carpenteri* (Thomson) and *P. grayi* Kent (Porifera: Hexactinellida) are synonyms. Zool J Linn Soc 115:373–384
Rice AL, Thurston MH, New AL (1990) Dense aggregations of a hexactinellid sponge. Prog Oceanogr 24:179–196
Ross LK, Ross RE, Stewart HA, Howell KL (2015) The influence of data resolution on predicted distribution and estimates of extent of current protection of three 'listed' deep-sea habitats. PLoS One 10(10):e0140061. doi:10.1371/journal.pone.0140061
Rix L, Goeij JM, Mueller CE, Struck U, Middelburg JJ, van Duyl FC, Al-Horani FA, Wild C, Naumann MS, van Oevelen D (2016) Coral mucus fuels the sponge loop in warm- and cold-water coral reef ecosystems. Nat Sci Rep 6:18715. doi:10.1038/srep18715
Scottish Government (2014) Rosemary Bank Seamount Marine Protected Area Order 2014. http://www.gov.scot/Resource/0045/00457018.pdf
Steenstrup E, Tendal OS (1982) The genus Thenea (Porifera, Demospongia, Choristida) in the Norwegian Sea and adjacent waters; an annotated key. Sarsia 67:259–268
Wulff JL (2006) Ecological interactions of marine sponges. Can J Zool 84:146–166. doi:10.1139/Z06-019