



# Distribution of Deep-Sea Sponge Aggregations in an Area of Multisectoral Activities and Changing Oceanic Conditions

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Discovery and understanding of fragile deep-sea habitats like sponge aggregations, are being outpaced by anthropogenic resource exploitation. Sustainable ocean development in the Faroe-Shetland Channel Nature Conservation Marine Protected Area (FSC NCMPA; northeast Atlantic), which harbors sponge aggregations, now requires adaptive management in the face of encroachment of multisectoral activities in this area (e.g., fishing, oil and gas, shipping) and climate change. We examined sponge morphotype composition, richness, diversity, density and body-size distribution inside and outside the FSC NCMPA, and the role of environmental variability and human impact in these sponge aggregations. Analyses were based on the examination of 465 high resolution images from 13 towed-camera transects. A catalog for regional sponge morphotypes was also developed and applied for these analyses. Analysis revealed that morphotype composition did not differ between inside and outside the FSC NCMPA but richness, diversity and densities of massive/spherical/papillate and flabellate/caliculate sponges were higher inside than outside the boundary. The sponge aggregations occurred within a narrow zone between 450 and 530 m depth, within relatively warm and saline water masses. Furthermore, multiple size cohorts of sponges were recorded inside the FSC NCMPA, in contrast to the single cohort outside. Distance-based linear modeling showed that demersal fisheries, substratum, salinity and temperature explained a statistically-significant amount of variation (48%,  $p < 0.001$ ) of sponge density across the study area. Findings on density and size cohorts suggest that the FSC NCMPA boundary currently encloses the most vulnerable area, which also demonstrates normal ecosystem functions (e.g., recruitment). However, sponges were constrained to a narrow environmental niche shaped by fisheries and interactions of FSC NCMPA water masses with the slope that in turn likely determine, food supply to the sponge aggregations. Our study illustrated the vulnerability of the FSC NCMPA sponge aggregations to fisheries and changes to water mass properties over time. The morphotype catalog and suite of indicators (i.e., density and body-size

distribution) allow for baseline and future assessments of anthropogenic and climate change impacts on sponge aggregations' environmental status in the FSC NCMPA, thus guiding management as sectoral encroachment continues in this area.

**Keywords:** deep-sea sponges, marine protected area, fisheries, oil and gas, environmental health, climate change

## INTRODUCTION

Sponges (Phylum Porifera) are widespread benthic organisms being found from the intertidal zone down to the abyss (Maldonado et al., 2017). Studies on shallow-water ecosystems have revealed the important role of sponges in habitat supply and nutrient cycling (e.g., Bell, 2008 and references therein). On the contrary, available information about sponges in the deep sea (i.e., generally areas below 200 m water depth), even for basic aspects like sponges' biogeographic distribution, biology and ecological roles, is very limited (Klitgaard and Tendal, 2004; Cathalot et al., 2015; Kazanidis et al., 2016, 2018).

Technological developments like the use of towed cameras, remotely operated vehicles (ROVs) and autonomous underwater vehicles (AUVs) can help us map the distribution of deep-sea sponges and the ecosystems they form i.e., deep-sea sponge grounds (Hogg et al., 2010). However, in order to maximize the impact of these video/image-based methods, there is an urgent need to develop and establish common protocols and procedures (Henry and Roberts, 2014a,b). Method standardization (e.g., units used in reporting faunal density) will enable the comparability of findings among studies and will enable the identification of gaps, challenges, strengths, and opportunities for the exploration of sponge grounds and deep-sea ecosystems, in overall. Another important step for advancing our understanding on deep-sea sponge grounds is to unravel the environmental parameters that shape their distribution, which in turn will facilitate the development of efficient conservation strategies (Howell et al., 2016; Johnson et al., 2018). This is of uttermost importance as deep-sea sponges are slow-growing organisms which makes them particularly vulnerable to human activities such as bottom trawling (Kenchington et al., 2014; Pusceddu et al., 2014; Victorero et al., 2018) and oil and gas activities (Vad et al., 2018). Indeed, deep-sea sponge grounds fulfill the Food and Agriculture Organization of the United Nations (FAO) definition of Vulnerable Marine Ecosystems (VMEs) and have also been included in the Oslo/Paris Convention for the Protection of the Marine Environment of the North-East Atlantic (OSPAR) List of threatened and/or declining species and habitats in the northeast Atlantic (OSPAR, 2008). Existing studies (both modeling and observations) about the role of water mass properties on the environmental parameters shaping the distribution of deep-sea sponge grounds suggest important roles of hydrography and temperature (Rice et al., 1990; Bett, 2001; Murillo et al., 2012), ocean chemistry (e.g., salinity and silicate) (Beazley et al., 2015; Howell et al., 2016), and biological parameters such as the concentration of particulate organic carbon (Barthel et al., 1996; Howell et al., 2016).

The Faroe-Shetland Chanel (FSC, hereafter) in the northeast Atlantic hosts complex hydrographic and sedimentary features (Bett, 2003). Multisectoral collaborations between industry, government and academia have allowed detailed investigations of how the ecology of deep-sea benthic communities is shaped by the hydrography and sedimentary regimes in FSC (Bett, 2001; Henry and Roberts, 2004; Jones et al., 2006; Narayanaswamy et al., 2010), including the discovery of sponge aggregations within a narrow bathymetric zone (Bett, 2001; Axelsson, 2003). The area hosting these deep-sea sponge aggregations was designated in 2014 as the "Faroe-Shetland Channel Nature Conservation Marine Protected Area" (FSC NCMPA hereafter)<sup>1</sup>. Mixed sponge assemblages are recorded there including boreal "ostur" communities (Klitgaard and Tendal, 2004) a mixture of geodiid sponges such as *Geodia barretti*, *G. macandrewi*, *G. atlantica*, *G. phlegraei* (reported as *Isops phlegraei*) and several other flabellate, lobose, stipitate and encrusting species (Bett, 2001; Howell et al., 2010; Henry and Roberts, 2014a<sup>2</sup>). Sponge density ranged from 0.001 to 0.818 sponges/m<sup>2</sup> (Axelsson, 2003; Henry and Roberts, 2014a). More detailed information on density, bathymetric distribution and body size of different species is currently missing. Furthermore, how anthropogenic activities and environmental parameters shape the distribution of FSC NCMPA sponge aggregations is also unknown. This is an important knowledge gap because sponges in FSC NCMPA provide habitat for *Munida* crabs, the ophiuroid *Ophiactis balli* and sessile polychaetes (Howell et al., 2010) and also because of oil and gas, shipping and telecommunications<sup>3</sup> encroachment in the region. Oil exploration and production activities take place in the FSC since early 1990s (Vad et al., 2018). Investigations on the physical disturbance caused from drilling on the megafaunal communities in FSC have shown smothering of the seafloor in a radius of 50–120 m around the drilling site (Jones et al., 2006). This disturbance caused significant reduction in abundance, diversity and species richness of megafauna (e.g., sponges, cnidarians, molluscs) (Jones et al., 2006, 2007, 2012). Furthermore, studies on FSC have shown that a part of the fishing activity (8% of total time) is carried out sub-zero temperatures; however, best catches of Greenland halibut (*Reinhardtius hippoglossoides*) and Roughhead grenadier (*Macrourus berglax*) and most of the fishing activity were recorded in boundary waters (0–4°C) (Bullough et al., 1998). In addition, surveys in the area have revealed disturbance in sediments and sponges, assumed to result from trawling (Bett, 2000). Currently, there are no FSC NCMPA specific

<sup>1</sup><http://jncc.defra.gov.uk/page-6483>

<sup>2</sup>[http://jncc.defra.gov.uk/pdf/NEFSC\\_SACO\\_v1.0.pdf](http://jncc.defra.gov.uk/pdf/NEFSC_SACO_v1.0.pdf)

<sup>3</sup><https://marinescotland.atkinsgeospatial.com/nmpi/>

management measures in place (e.g., for fisheries) and the statutory agency Marine Scotland is in the process of developing a joint recommendation to implement measures under the Common Fisheries Policy (Marine Scotland, 2017)<sup>4</sup>.

Hátún et al. (2017) have shown a decline over the last 25 years in silicate concentrations in North Atlantic including the FSC NCMPA. Changes in the temperature and salinity profiles of FSC NCMPA water masses over the last two decades, have also been shown (Turrell et al., 1999; Sherwin et al., 2006; Berx et al., 2013; Broadbridge and Toumi, 2015; McKenna et al., 2016). Reduction in concentration of silicate can have detrimental effects on deep-sea sponges as silicate concentrations shape primary production (and thus food-supply) and also silicate is an integral compound of sponges' skeleton (Maldonado et al., 2011).

Deep-sea sponge aggregations of the FSC NCMPA are impacted by both human activities and climate change. Advancing, thus, our knowledge is essential for evaluating the existing FSC NCMPA boundary and for the development of conservation strategies for these VMEs (Johnson et al., 2018).

In the present study we have analyzed video/image material from inside and outside the FSC NCMPA to address three fundamental questions:

- (1) Which sponge morphotypes are encountered inside and outside the NCMPA?
- (2) How does sponge morphotype (a) richness and diversity, (b) density and (c) body-size distribution differ between inside and outside the FSC NCMPA?
- (3) Which is the role of environmental variability and human activities in controlling the distribution and density of sponge morphotypes?

## MATERIALS AND METHODS

### Faroe-Shetland Channel Hydrography and Habitat Features

The Faroe-Shetland Channel (FSC) is characterized by complex hydrography as five water masses flow through it: North Atlantic Water (NAW), Modified North Atlantic Water (MNAW), Modified East Icelandic Water (MEIW), Norwegian Sea Arctic Intermediate Water (NSAIW), and Norwegian Sea Deep Water (NSDW) (Hansen and Østerhus, 2000). The distribution of these five water masses in the FSC is indicated by their characteristic temperature and salinity values which are accompanied by a specific spectrum of chemical and biological characteristics (see Table 1 in McKenna et al., 2016 for details). In the FSC, water masses above 400 m water depth are composed from NAW (9.5–10.5°C; 35.35–35.45 psu) or MNAW (7–8.5°C; 35.10–35.30 psu). NAW flows along the Shetland Shelf Edge while MNAW enters the FSC from the north of the Faroe Islands and recirculates within it. At greater depths (~400–800 m) water masses are composed from MEIW (2–4.5°C; 34.76–34.99 psu) and NSAIW (–0.5–0.5°C; 34.89–34.91 psu). Bottom water mass NSDW (<–0.5°C; 34.91–34.92 psu) which has the greatest

contribution in the southwards overflow through the Faroe Bank Channel and across the Wyville Thomson Ridge (Berx, 2012; Broadbridge and Toumi, 2015; McKenna et al., 2016). The boundary area occurring between the warm and cold-waters (found between ~350–650 m) is particularly interesting as within it (~550 m) rapid changes in seawater temperature (decrease up to 7°C within 1 h) have been recorded (Bett, 2001). These changes in seawater temperature are thought to be created by internal waves created by water flow across the Wyville Thomson Ridge. These internal waves propagate in the FSC at the boundary between warm and cold-water masses (Sherwin, 1991). Apart from the unusual temperature profile, the FSC is also interesting in terms of sedimentary habitat types that include areas of iceberg ploughmarks and North Sea Fan among others (Masson, 2001 for details; see also Bett, 2003; Narayanaswamy et al., 2010).

### Visual Survey of Sponge Aggregations

In September 2014, a visual survey was conducted by Marine Scotland on board the MRV *Scotia* ("MoreDeep" cruise) to investigate the deep-sea sponge aggregations inside and outside the FSC NCMPA. The visual survey was conducted using a Seatronics<sup>5</sup> towed body hosting a Kongsberg Maritime OE14-366 PAL color zoom camera<sup>6</sup>. The system was also equipped with six high-intensity lights and sensors that measured at 1 s intervals, the altitude (the distance between the camera system and the seabed), depth ( $\pm 0.1$  m), and pitch and roll of the system (see McIntyre et al., 2013, 2016 for details). Seawater temperature was recorded ( $\pm 0.01$ °C) through the sensor attached to the camera system. In total, 13 camera transects were conducted, which were grouped into one area inside (i.e., Area 2) and three areas (i.e., Area 1, Area 3, and Area 4) outside the FSC NCMPA (Figure 1). The average duration of each transect was ~1 h 21 min at a speed of 1.5 m/sec. The altitude was 2–6 m. Because a camera positioning system was not available, positions recorded are those of the ship. Starting-ending points and depth range of the camera transects as well as values of temperature are given in Table 1. Sponge samples during the transects were not collected.

### Image Analysis

The camera recorded continuous high definition (HD) video from which individual image frames were extracted every 20 s. Extraction was carried out with freely available software VLC. The frames were subjected to quality check with low-visibility frames been discarded. The resolution in images was 6544 × 3680 pixels in dimension with a 350 pixel/inch DPI. In total, 465 high quality image frames were subjected to further analysis (see below).

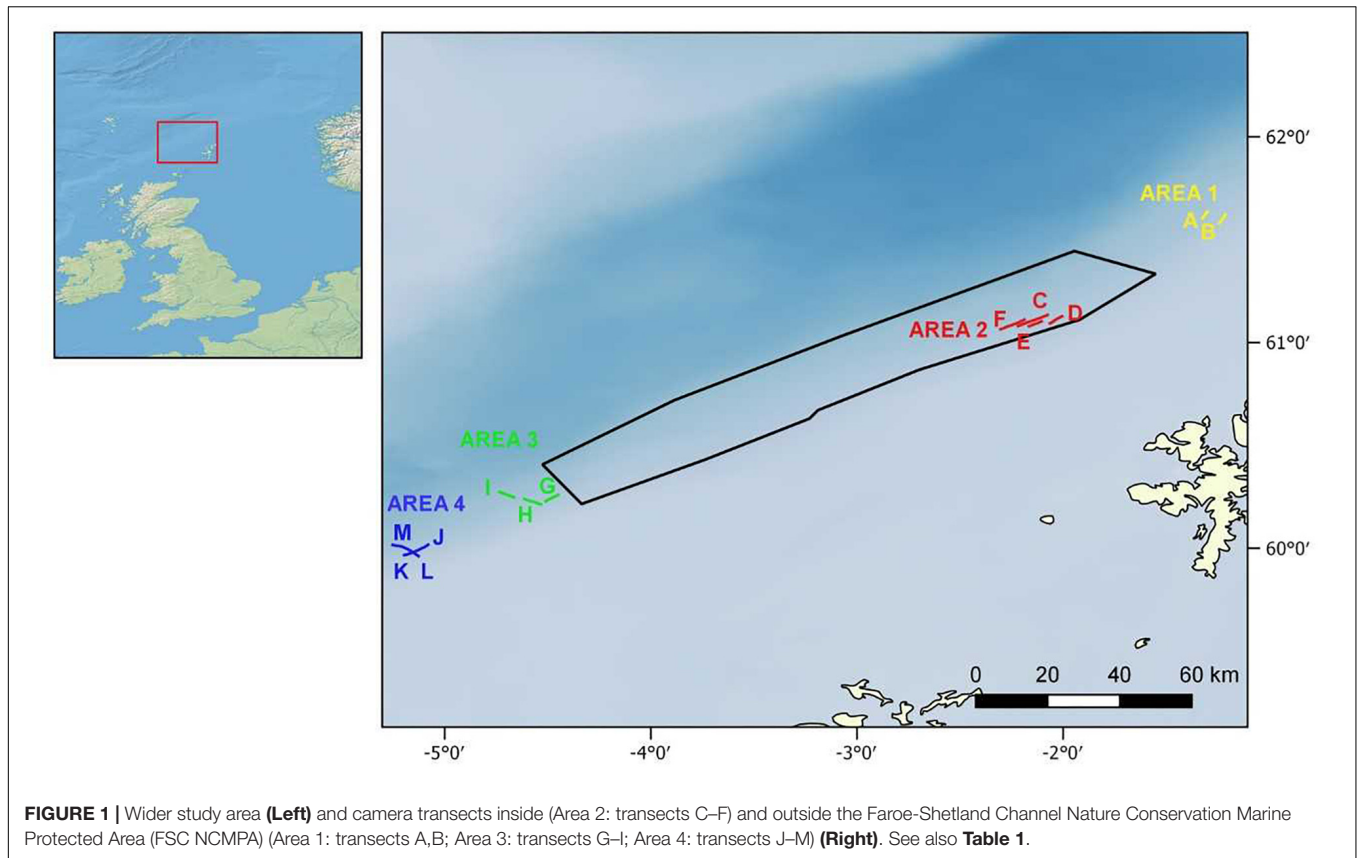
### Sponge Morphotype Categories

Sponge morphotype categories were mainly based on the "Thesaurus of Sponge Morphology" (Boury-Esnault and Rützler, 1997) accompanied by studies on the distribution and structure of deep-sea sponge aggregations in the North Atlantic (Bett,

<sup>4</sup><https://www.gov.scot/Topics/marine>

<sup>5</sup><http://www.seatronics-group.com>

<sup>6</sup>[www.km.kongsberg.com](http://www.km.kongsberg.com)



**TABLE 1 |** Coordinates and depth values for each of the transects inside (Area 2) and outside (Area 1, Area 3, Area 4) the Faroe-Shetland Channel Nature Conservation Marine Protected Area (FSC NCMPA).

Area	Transect	Min latitude	Max latitude	Min longitude	Max longitude	Min depth	Max depth	T (°C)	Salinity (psu)	Images per transect
1	A	61.60633	61.62217	-1.32350	-1.31133	529.5	532.9	3.12	34.89	19
1	B	61.58617	61.61350	-1.23833	-1.21850	431.4	440.5	5.61	34.90	50
2	C	61.08700	61.13350	-2.20250	-2.07733	492.0	500.6	8.51	35.13	93
2	D	61.09467	61.12117	-2.06200	-2.01800	449.8	454.0	8.98	34.91	32
2	E	61.07967	61.09950	-2.16433	-2.11283	467.7	473.0	8.55	34.95	44
2	F	61.06500	61.10667	-2.30267	-2.19767	516.0	523.3	6.52	35.00	65
3	G	60.23017	60.25433	-4.50783	-4.46117	497.4	501.1	8.01	35.16	40
3	H	60.21600	60.23167	-4.59000	-4.53883	502.0	574.6	7.92	35.22	19
3	I	60.24983	60.26617	-4.71200	-4.66933	661.5	715.1	2.41	34.89	11
4	J	59.98650	60.00900	-5.13933	-5.09250	498.7	511.8	8.49	35.19	93
4	K	59.96767	59.97567	-5.19300	-5.16500	482.5	496.3	9.29	35.24	32
4	L	59.99133	60.01183	-5.22533	-5.17100	547.1	631.3	5.67	35.21	44
4	M	59.96400	59.98950	-5.16850	-5.13017	452.4	534.9	8.73	35.24	65

Depth and temperature data were available for each of the images collected, while salinity data were available at lower spatial resolution. Average values (per transect) of temperature (T, °C), salinity (psu), number of images analyzed are given.

2001; Axelsson, 2003; Klitgaard and Tendal, 2004; Ackers et al., 2007; Cárdenas et al., 2013; Henry and Roberts, 2014a; McIntyre et al., 2016). The construction of the sponge morphotype catalog was also based on the examination of images collected by ROVs over several years in the wider FSC area. Five sponge morphotype categories were used (Table 2). Each sponge specimen recorded in the high-quality image frames of the

present study was grouped in one of the five morphotype categories, and counted. Sponge morphotype categories were based on the “Thesaurus of Sponge Morphology” (Boury-Esnault and Rützler, 1997). Sponges were grouped in the five following categories: **Category 1:** encrusting (Figure 2A); **Category 2:** arborescent (“tree-like”) (Figure 2A); **Category 3:** massive, spherical and papillate (Figures 2B,C,G); **Category 4:** flabellate

**TABLE 2** | Categories of sponge morphotypes in the Faroe Shetland Channel Nature Conservation Marine Protected Area (FSC NCMPA).

Categories	Morphotypes	Genus/Species names
Category 1	encrusting	Possibly <i>Aplysilla sulfurea</i> , <i>Hymedesmia</i> spp.
Category 2	arborescent	“–”
Category 3	massive	<i>Geodia</i> spp. (e.g., <i>G. barretti</i> , <i>G. macandrewi</i> , <i>G. atlantica</i> , <i>G. phlegraei</i> )
	spherical	“–”
	papillate	Possibly <i>Oceanapia robusta</i>
Category 4	flabellate	Possibly <i>Phakellia ventilabrum</i>
	caliculate	Possibly <i>Axinella infundibuliformis</i>
Category 5	stipitate	Possibly <i>Stylocordila borealis</i>
	clavate	Possibly <i>Chondrocladia gigantea</i>

Genus/species names have tentatively been suggested for each category. “–” means lack of confidence.

(“fan-shaped”) and caliculate (“cup-shaped”) (**Figures 2F,G**); **Category 5**: stipitate (“stalked”) and clavate (“club-shaped”) (**Figures 2D,E**).

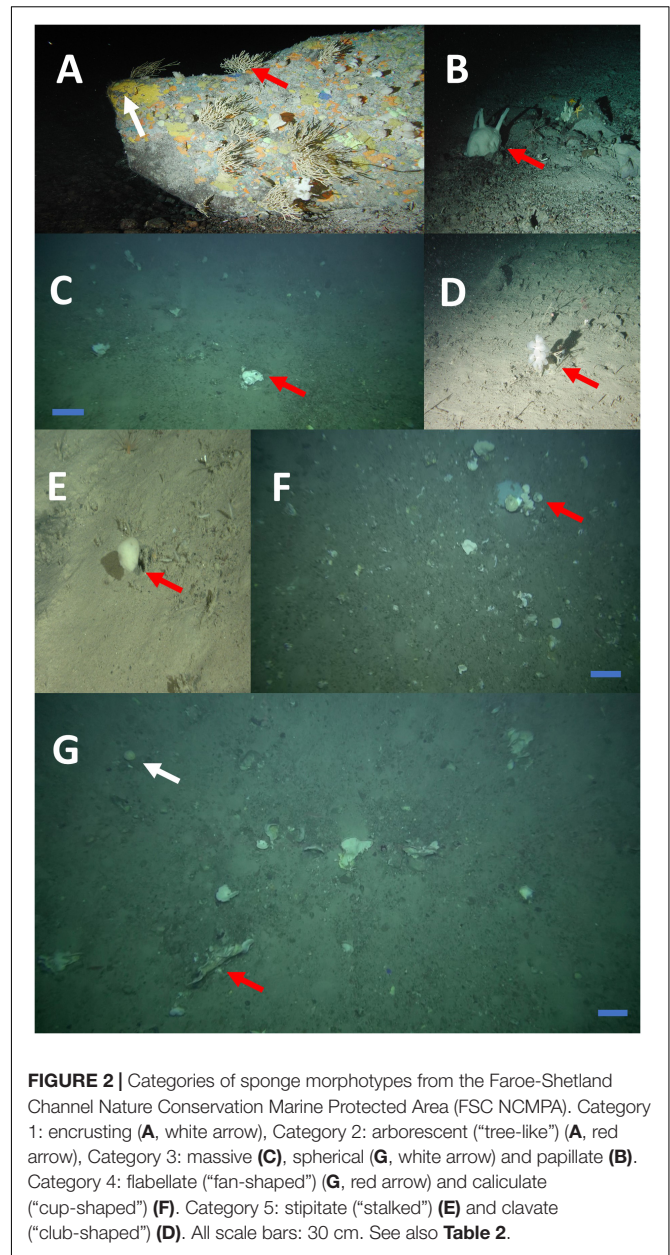
### Density and Body Size of Sponge Morphotypes

The surface of the seabed seen in each of the HD image frames (field of view) was quantified (in m<sup>2</sup>) by matching the time point that a frame was captured with the relevant data (altitude and pitch angle of the towed camera system) provided by the sensor attached to the system. A detailed description of the methodology followed for measuring the field of view is given in McIntyre et al. (2013). In brief, altitude and pitch of the towed body were used in the survey area calculations using trigonometric equations. To correct for the effect of the distance on the visibility of the seabed, image analysis techniques in MATLAB<sup>7</sup> Image Processing Toolbox were used to construct a correction factor. The latter was a proportion of visible seabed in each image (see McIntyre et al., 2013 for details).

Using the number of sponge specimens from each morphotype Category recorded in each image and the surface of the seabed, values of sponge density were measured (sponge individuals per Category/m<sup>2</sup>). These measurements of sponge morphotype density were carried out for categories 2, 3, 4, and 5 while specimens from sponge morphotype Category 1 (“encrusting”) were logged in terms of presence/absence. Furthermore, using the camera’s laser points as a reference (7.5 cm), we measured the width of flabellate sponges and the average value between “length” and “width” for the massive/spherical/papillate and the caliculate sponges (**Figure 3**). Body size measurements were grouped into 5 cm size classes following Bo et al. (2012). Measurements on body size were mainly carried out for transects A, B, C, D, E, F; unfortunately the position of the camera did not allow appropriate measurements to be taken in transects G, H, I, J, K, L, and M (**Figure 1**).

### Fisheries and Environmental Data

The distribution of sponge aggregations inside and outside the FSC NCMPA was investigated in relation to water depth (m), type

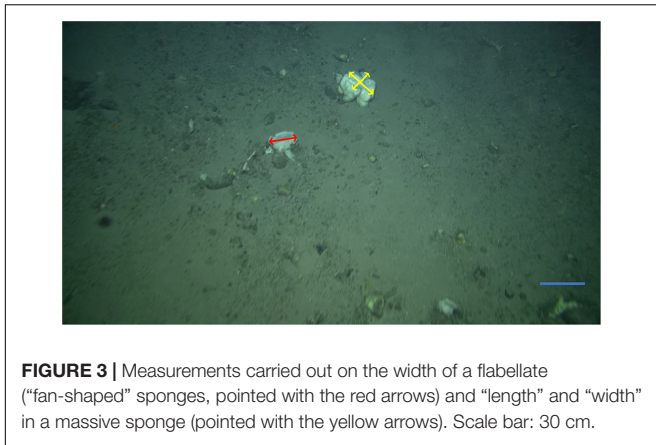


**FIGURE 2** | Categories of sponge morphotypes from the Faroe-Shetland Channel Nature Conservation Marine Protected Area (FSC NCMPA). Category 1: encrusting (**A**, white arrow), Category 2: arborescent (“tree-like”) (**A**, red arrow), Category 3: massive (**C**), spherical (**G**, white arrow) and papillate (**B**). Category 4: flabellate (“fan-shaped”) (**G**, red arrow) and caliculate (“cup-shaped”) (**F**). Category 5: stipitate (“stalked”) (**E**) and clavate (“club-shaped”) (**D**). All scale bars: 30 cm. See also **Table 2**.

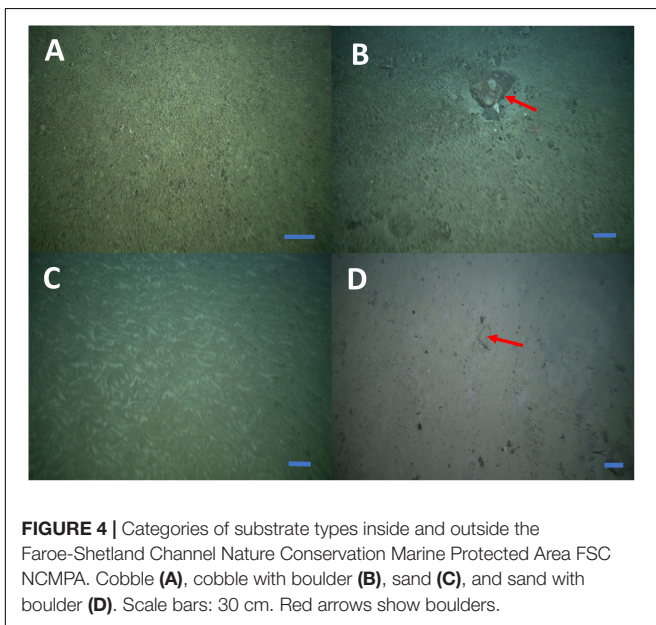
of substratum, temperature (°C), salinity (psu), water density (g/ml), oxygen saturation and demersal fisheries. Data on depth, type of substratum and temperature were available for each of the images collected during the visual survey of the present study. The type of the substratum in each of the 465 high quality image frames was grouped in one of the four categories (following Bett, 2003): (1) cobble (**Figure 4A**), (2) cobble with boulder (**Figure 4B**), (3) sand (**Figure 4C**), and (4) sand with boulder (**Figure 4D**). Data on salinity, water density and oxygen saturation (derived from equivalent temperature and salinity using a MATLAB routine<sup>8</sup>) from the FSC were supplied from Marine Scotland, at a coarser spatial scale. These data came

<sup>7</sup>Release, 2017b; www.matlab.com

<sup>8</sup><http://mooring.ucsd.edu/software/matlab/doc/ocean/oxsat.html>



**FIGURE 3** | Measurements carried out on the width of a flabellate (“fan-shaped” sponges, pointed with the red arrows) and “length” and “width” in a massive sponge (pointed with the yellow arrows). Scale bar: 30 cm.



**FIGURE 4** | Categories of substrate types inside and outside the Faroe-Shetland Channel Nature Conservation Marine Protected Area FSC NCMPA. Cobble (A), cobble with boulder (B), sand (C), and sand with boulder (D). Scale bars: 30 cm. Red arrows show boulders.

from locations inside the transects of the visual survey (Table 1) at similar depths.

Data on demersal fishing activity for Area 1, Area 2, Area 3, and Area 4, were extracted with qGIS<sup>9</sup> from the Marine Scotland MAPS NMPI (National Marine Plan Interactive) website using the layer entitled “Fishing statistics – Demersal landings (tons) from Scottish waters [per International Council for the Exploration of the Sea (ICES) statistical rectangle]”<sup>10</sup>. Data for this layer were available only for 5 years (2012–2016) enabling thus an assessment of recent demersal fishing impact on the sponge communities. For each of the ICES rectangles taken into account (i.e., rectangle 52E8 for Area 1; 51E7 for Area 2; 49E5 for Area 3; 48E4 for Area 4) an average value was calculated over the time period 2012–2016. The average value for the annual demersal landings were: 113

tons in Area 1, 64 tons in Area 2, 2836 tons in Area 3, and 3011 tons in Area 4.

### Statistical Analysis

The number of sponge morphotypes (S) and Shannon’s diversity index (H) were calculated using Primer-7 (Clarke et al., 2014) and these indices were compared between inside and outside the FSC NCMPA. Furthermore, the density of sponges was compared (1) inside versus outside the FSC NCMPA, (2) across the four areas (i.e., Area 1, Area 2, Area 3, and Area 4), and (3) across all transects. Sponge size was compared inside versus outside the FSC NCMPA. These comparisons were carried out in the software R (R Core Team, 2018). The Shapiro-Wilk test was applied to test for normality, followed by the Bartlett-test or the F-test to verify the equality of variances (for two or three groups, respectively). If the distributions were normal and the variances were equal, then the hypothesis that the groups have the same mean was tested using the two-sample *t*-test or the one-way ANOVA (for two or three groups, respectively). If distributions were normal but variances were not equal, the hypothesis that the means of the groups were the same was examined through the Welch’s two sample *t*-test or one-way analysis of means (not assuming equal variances) (for two groups or three groups, respectively). If distributions were not normal, the hypothesis that the groups have the same median was tested through a Wilcoxon rank sum test or a Kruskal-Wallis rank sum test (for two or three groups, respectively). All values in the text are presented as mean  $\pm$  standard error (SE).

The size-frequency distributions were analyzed applying the Bhattacharya analysis using the FISAT software package (Gayanilo and Pauly, 1997<sup>11</sup>). Size-frequency distributions were compared between inside and outside the FSC NCMPA; comparisons were carried out for morphotype Categories 3, 4 and for all morphotypes.

The grouping of the transects was analyzed in Primer-7. Specifically, non-transformed data on the density (individuals/m<sup>2</sup>) of each sponge morphotype were used in the calculation of Bray–Curtis similarities and similarity matrices. Based on these matrices, clustering analysis was carried out. Finally, the role of environmental parameters and demersal fisheries in shaping the density of sponge morphotypes was analyzed through distance-based linear modeling (“Dist-LM” routine) in Primer 7.

## RESULTS

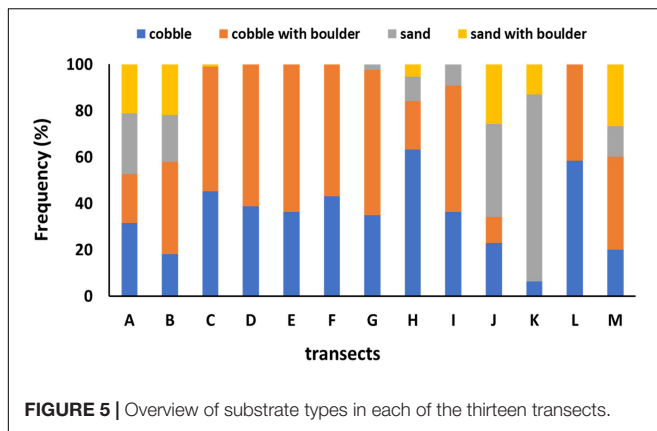
### Environmental Data

Preliminary investigation of environmental parameters (i.e., Draftsman Plots in Primer-7 software; see below for details) showed high correlations between salinity-density and between salinity-oxygen saturation and thus density and oxygen saturation data were not used further (see below for details). Average values of temperature ranged from 2.41°C (transect I) to 9.29°C (transect K) and average salinity ranged

<sup>9</sup>www.qgis.org/en/site/

<sup>10</sup>https://marinescotland.atkinsgeospatial.com/nmpi/

<sup>11</sup>http://www.fao.org/fishery/topic/16072/en



from 34.89 psu (A, I transects) to 35.24 psu (transects K, M) (Table 1). Hard substrata (i.e., cobble, cobble with boulder) dominated most transects while soft sediments were the major type of substrate only in J and K transects (Figure 5).

## Biological Data

### Sponge Morphotypes Encountered Inside and Outside the FSC NCMPA

In the present study we recorded only three categories (Category 1, Category 3, and Category 4 in Table 2) out five previously recorded in FSC; there were no records of Category 2 or Category 5 (Figures 2, 6 and Table 2). Category 1 sponges were recorded in all transects except from transect I. Sponge morphotypes from Categories 1, 3, and 4 were found both inside and outside the FSC NCMPA (Figure 6). In Category 3, >90% of sponge specimens recorded were massive; similarly, in Category 4, >90%

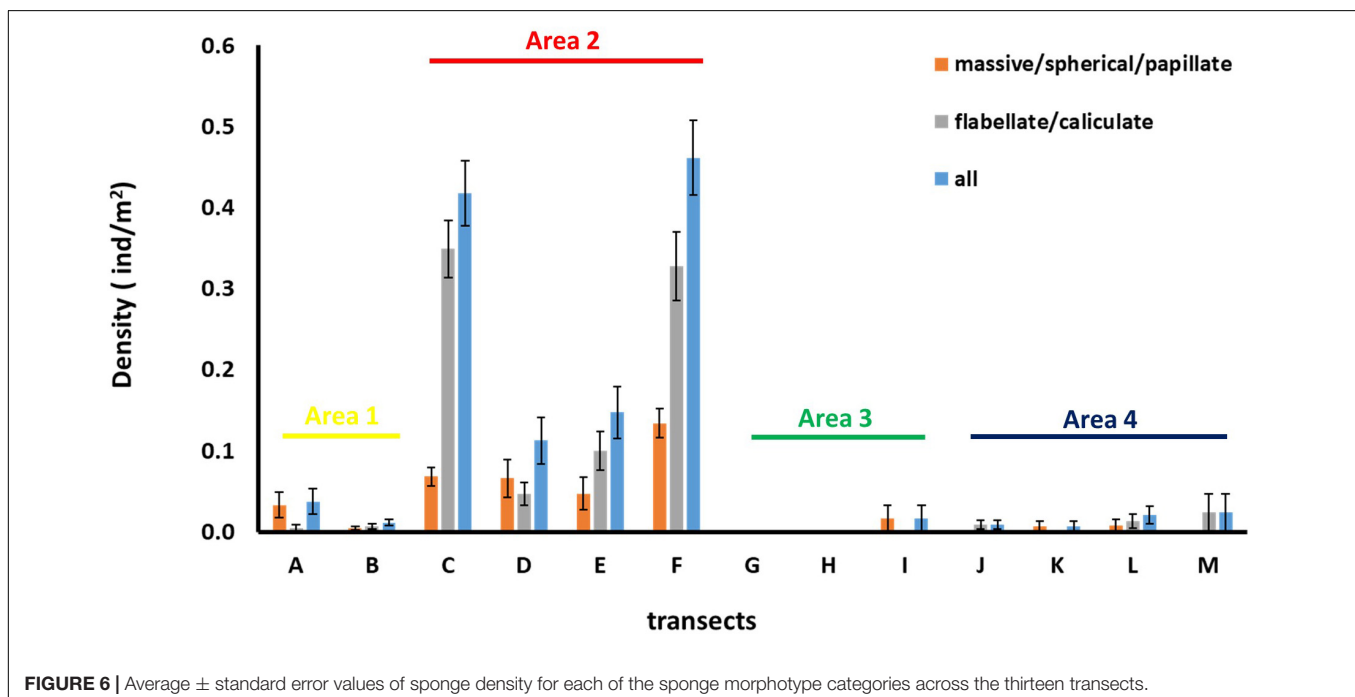
of sponges were flabellate. The number of sponge morphotypes (S) was significantly higher inside than outside the FSC NCMPA. Specifically, the number of sponge morphotypes (S) inside the FSC NCMPA was  $1.2 \pm 0.0$  sponge morphotypes vs.  $0.1 \pm 0.0$  sponge morphotypes outside the FSC NCMPA (Wilcoxon rank sum test = 46716,  $p < 0.0001$ ;  $n = 465$ ). Similarly, (H) was significantly higher inside than outside the FSC NCMPA. (H) inside the FSC NCMPA was  $0.22 \pm 0.01$  while (H) outside the FSC NCMPA was  $0.01 \pm 0.00$  (Wilcoxon rank sum test = 36628,  $p < 0.0001$ ,  $n = 465$ ).

### Density of Sponge Morphotypes Inside and Outside the FSC NCMPA

Density of all sponge morphotypes was significantly higher inside than outside the FSC NCMPA (Table 3). Significant differences were also detected across the four areas (i.e., Area 1, Area 2, Area 3, and Area 4); higher values were recorded in Area 2 (Table 3 and Figure 6). Clustering analysis using density values for each sponge morphotype revealed a higher level of similarity (~50%) for transects in Area 2 (i.e., inside the FSC NCMPA) than transects in Area 1, Area 3, and Area 4 (i.e., outside the FSC NCMPA) (Figure 7). Finally, significant differences in density were recorded across all transects (Table 3 and Figure 6). The highest density for Category 3 was found in transect F, for Category 4 in transect C and for all sponge morphotypes in transect F (Table 3 and Figure 6).

### Density of Sponge Morphotypes Across Depth

Density values for both Categories 3 and 4 showed a peak within a narrow zone (450–530 m) (Figures 8A–C). This peak was recorded inside the FSC NCMPA. The maximum values of density recorded for Category 3 was



**TABLE 3 |** Density of Category 3 (massive/spherical/papillate) and Category 4 (flabellate/caliculate) sponges inside and outside the Faroe-Shetland Channel Nature Conservation Marine Protected Area (FSC NCMPA), across areas (Area 1, Area 2, Area 3, and Area 4) and across transects.

	<b>Category 3 (massive/ spherical/ papillate) (average ± SE) (individuals/m<sup>2</sup>)</b>	<b>Category 4 (flabellate/ caliculate) (average ± SE) (individuals/m<sup>2</sup>)</b>	<b>All morphotypes (average ± SE) (individuals/m<sup>2</sup>)</b>
Inside FSC NCMPA	0.082 ± 0.009	0.256 ± 0.021	0.338 ± 0.024
Outside FSC NCMPA	0.006 ± 0.002	0.005 ± 0.002	0.011 ± 0.003
<b>Analysis of variance inside vs. outside FSC NCMPA</b>	Wilcoxon rank sum test = 37767, ***, <i>n</i> = 465	Wilcoxon rank sum test = 45800, ***, <i>n</i> = 465	Wilcoxon rank sum test = 47454, ***, <i>n</i> = 465
Area 1	0.01 ± 0.00	0.01 ± 0.00	0.02 ± 0.01
Area 2	0.08 ± 0.01	0.26 ± 0.02	0.34 ± 0.02
Area 3	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Area 4	0.01 ± 0.00	0.01 ± 0.01	0.01 ± 0.01
<b>Analysis of variance across areas</b>	Kruskal-Wallis chi-squared = 98.016, ***, <i>n</i> = 465	Kruskal-Wallis chi-squared = 218.71, ***, <i>n</i> = 465	Kruskal-Wallis chi-squared = 240.56, ***, <i>n</i> = 465
transect A	0.033 ± 0.015	0.005 ± 0.005	0.037 ± 0.016
transect B	0.005 ± 0.002	0.007 ± 0.003	0.011 ± 0.004
transect C	0.068 ± 0.011	0.349 ± 0.035	0.417 ± 0.040
transect D	0.066 ± 0.024	0.046 ± 0.014	0.112 ± 0.029
transect E	0.047 ± 0.020	0.100 ± 0.024	0.147 ± 0.032
transect F	0.134 ± 0.018	0.327 ± 0.042	0.461 ± 0.046
transect G	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000
transect H	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000
transect I	0.017 ± 0.017	0.000 ± 0.000	0.017 ± 0.017
transect J	0.000 ± 0.000	0.009 ± 0.005	0.009 ± 0.005
transect K	0.007 ± 0.007	0.000 ± 0.000	0.007 ± 0.007
transect L	0.008 ± 0.008	0.013 ± 0.009	0.021 ± 0.011
transect M	0.000 ± 0.000	0.023 ± 0.023	0.023 ± 0.023
<b>Analysis of variance across transects</b>	Kruskal-Wallis chi-squared = 133.07, ***, <i>n</i> = 465	Kruskal-Wallis chi-squared = 279.38, ***, <i>n</i> = 465	Kruskal-Wallis chi-squared = 289.18, ***, <i>n</i> = 465

Mean values, standard error (S.E), results of statistical test, *P* values (\*\*\**P* ≤ 0.001, \*\*0.001 < *P* ≤ 0.01, \*0.01 < *P* ≤ 0.05, ns: no significant) and number of measurements (*n*), are given.

0.79 individuals/m<sup>2</sup> (Figure 8A) and for Category 4 was 1.93 individuals/m<sup>2</sup> (Figure 8B).

### Size of Sponge Morphotypes Inside and Outside the FSC NCMPA

The average size for Category 3 inside the FSC NCMPA was significantly higher than outside the FSC NCMPA i.e., 13.3 ± 0.8 vs. 9.2 ± 3.1 cm, respectively (Wilcoxon rank sum test = 944.5, *p* < 0.05, *n* = 145). In Category 4, there were no statistically-significant differences in the average size between transects inside and outside the FSC NCMPA i.e., 12.3 ± 0.4 vs. 11.7 ± 2.4 cm, respectively (Wilcoxon rank sum test = 2713.5, *p* > 0.05, *n* = 469).

For all the sponge morphotypes, the average size inside the FSC NCMPA was not different from the average size outside the FSC NCMPA i.e., 12.6 ± 0.4 vs. 10.5 ± 1.9 cm, respectively (Wilcoxon rank sum test = 7621.5, *p* > 0.05, *n* = 614).

The analysis of the body-size distribution through the Bhattacharya method revealed clear differences between inside and outside the NCMPA. Specifically, in Category 3 there were two size cohorts in transects inside the FSC NCMPA and one size cohort outside the FSC NCMPA. In Category 4 there were three size cohorts inside the FSC NCMPA and one outside the NCMPA. The analysis of Categories 3 and 4 pooled together showed the existence of four size cohorts inside the FSC NCMPA and one size cohort outside the FSC NCMPA (Table 4 and Figure 9).

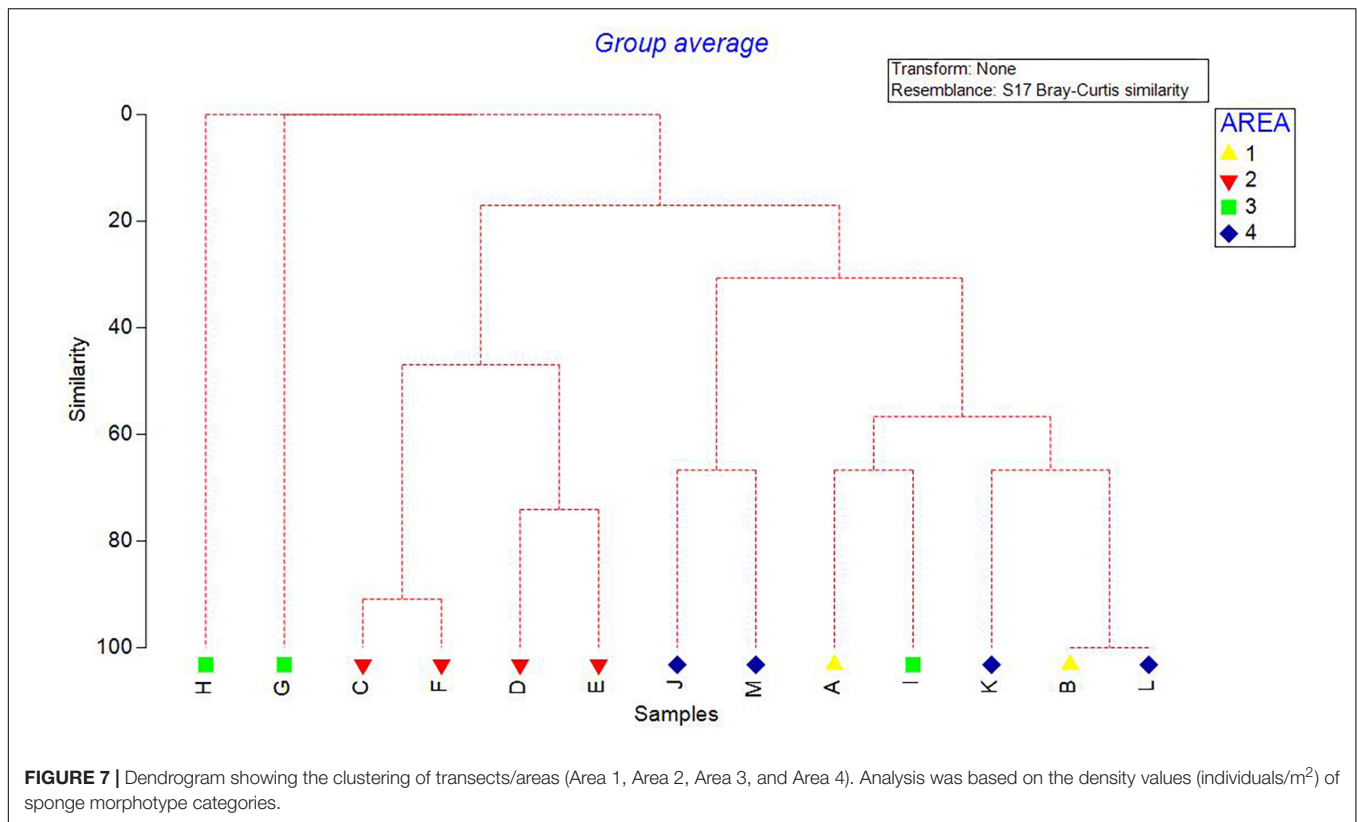
### Role of Fisheries and Environmental Parameters in Density of Sponge Morphotypes

Fisheries and environmental variability explained a total of 47.98% of the variation in the density of sponge morphotypes. Variables that explained significant amounts of variation included demersal fisheries pressure (29.75%), cobble with boulder (12.02%), salinity (4.89%) and temperature (1.07%) (Table 5). Inside the FSC NCMPA the density of Category 3 and Category 4 sponges was higher than outside the FSC NCMPA. Furthermore, the highest densities of Category 3 and Category 4 sponges were found in transects dominated by cobble with boulder substrata. The temperature and salinity values in transects with highest measured densities ranged from 6.52 to 8.98°C and 34.91 to 35.13 psu, respectively, indicating that the sponge aggregations were mainly sitting within the relatively warm and saline NAW, MNAW, and MEIW.

### DISCUSSION

The present study showed that sponge morphotype composition did not differ between inside and outside the FSC NCMPA boundary, but richness, diversity and densities of Category 3 and Category 4 sponges (Tables 2, 3 and Figures 2, 6) were higher inside than outside this boundary. Multiple size cohorts of sponges were recorded inside the FSC NCMPA, in contrast to the single cohort outside (Table 4 and Figure 9). Variation in density of sponges was mostly explained by fisheries pressure: higher densities of sponges were found in the area- with lowest values of demersal landings (i.e., Area 2) while densities were significantly lower in the areas with higher demersal landings (i.e., Area 1, Area 3, and Area 4). Type of substratum explained also a significant amount of variation in sponge density: highest densities were found in cobble with boulder. Finally, water temperature and salinity explained also a significant (but lower compared to fisheries and substratum) amount of variation in sponge density: highest values were found in Area 2 where temperature and salinity ranged from 6.52 to 8.98°C and 34.91 to 35.13 psu, respectively, indicating that the sponge aggregations were mainly sitting within the relatively warm and saline NAW, MNAW, and MEIW.





## Richness/Diversity, Body-Size Distribution and Density of Sponge Morphotypes Inside and Outside the FSC NCMPA – The Role of Human Activities and Environmental Variability

### Richness and Diversity of Sponge Morphotypes

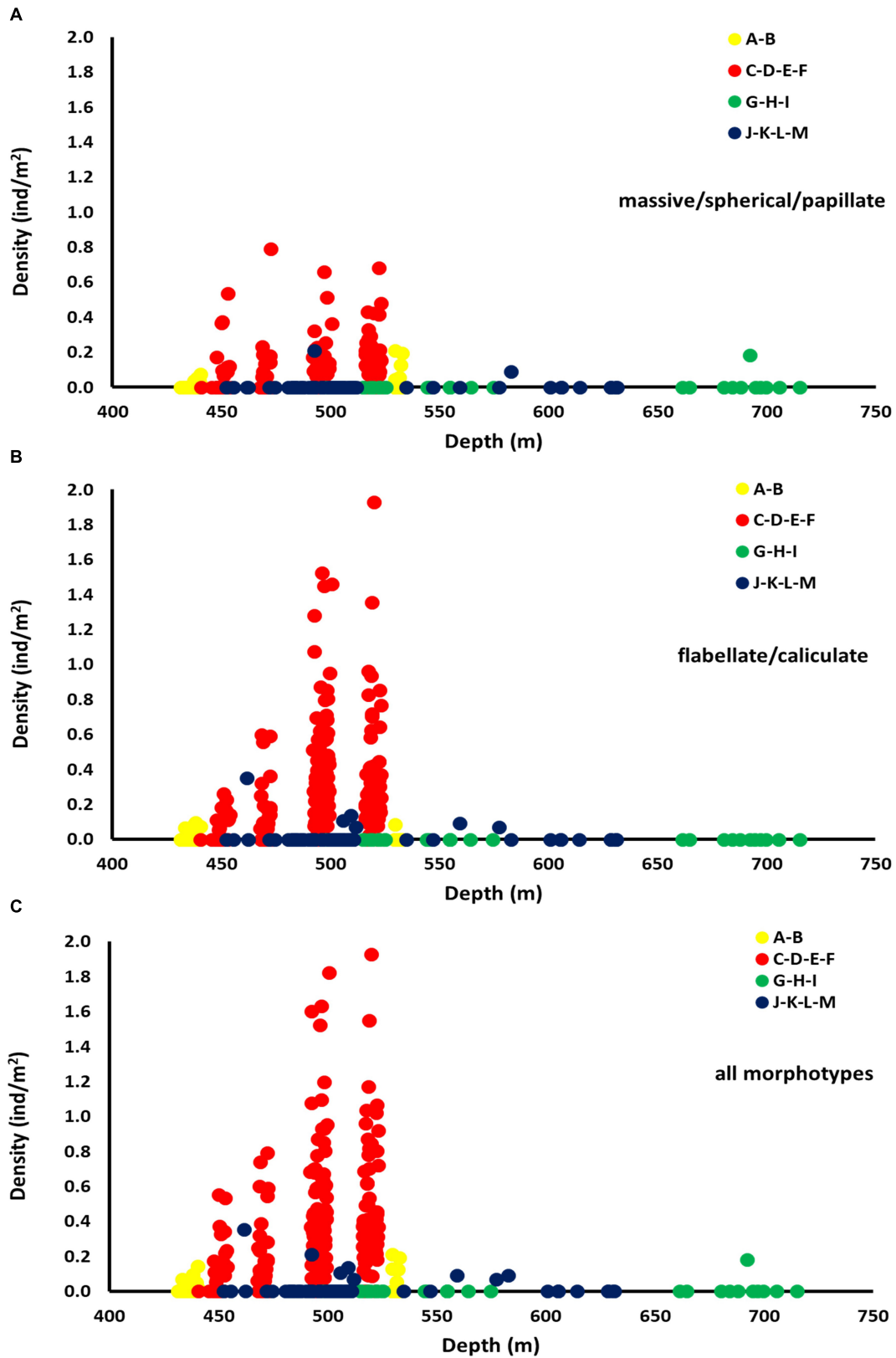
Sponge aggregations inside and outside the FSC NCMPA were mainly composed of massive (most likely *Geodia* spp.) and flabellate (most likely *Phakellia ventilabrum*) sponges (**Table 2**). Unfortunately, biological samples were not collected during the transects and thus the taxonomic identification of specimens seen in images was not possible. Findings of the present study are in agreement with previous studies in the wider FSC that recorded *Geodia* and *Phakellia* in this area (Bett, 2001; Axelsson, 2003; Klitgaard and Tendal, 2004; Howell et al., 2010; Henry and Roberts, 2014a).

Although the same morphotypes were encountered inside and outside the FSC NCMPA, their richness and diversity were significantly higher inside than outside this boundary. Studies have shown that bottom fishing has an impact on the morphotypes of benthic organisms and the same may hold true for our findings on FSC NCMPA. Specifically, a photographic survey in the Georges Bank (northwest Atlantic Ocean) provided evidence that erect forms like hydrozoans, bushy bryozoans, sponges and sedentary polychaetes had higher cover in undisturbed sites while encrusting bryozoans were the only colonial group not affected by fishing (Asch and Collie, 2008).

As regards the role of hydrography, Bell and Barnes (2000) have shown that massive and encrusting sponge morphotypes were more abundant at high-flow areas in the sublittoral zone, due to a high basal area to volume ratio which decreases removal from the substrates; on the contrary, pedunculate, papillate and arborescent morphotypes were more abundant at the low flow areas as these morphotypes may prevent sedimentation on sponges (see also Ginn et al., 2000; Bell et al., 2002; George et al., 2018). Bell and Barnes (2000) also showed that diversity of sponge morphotypes decreased with increasing flow due to the removal of delicate morphotypes. Studies on the hydrography of the FSC have shown the existence of active mesoscale variability (Sherwin et al., 2006). The role, however, of this hydrographic variability in shaping richness and diversity of FSC NCMPA sponge aggregations, is currently unknown.

### Body-Size Distribution of Sponge Morphotypes

Our study showed that the number of body-size cohorts sponges was higher inside than outside the FSC NCMPA (**Table 4** and **Figure 9**). Although the available time series on demersal fisheries inside and outside the FSC NCMPA are limited the findings indicate the impact that fisheries can have on the FSC NCMPA sponge aggregations. However, due to this limited data availability, the impact of fisheries should be treated with caution. Actually, we did not observe trawl marks in any of the 465 images analyzed (see Figure 4 in Roberts et al., 2000). Hydrography, however, in FSC NCMPA is dynamic

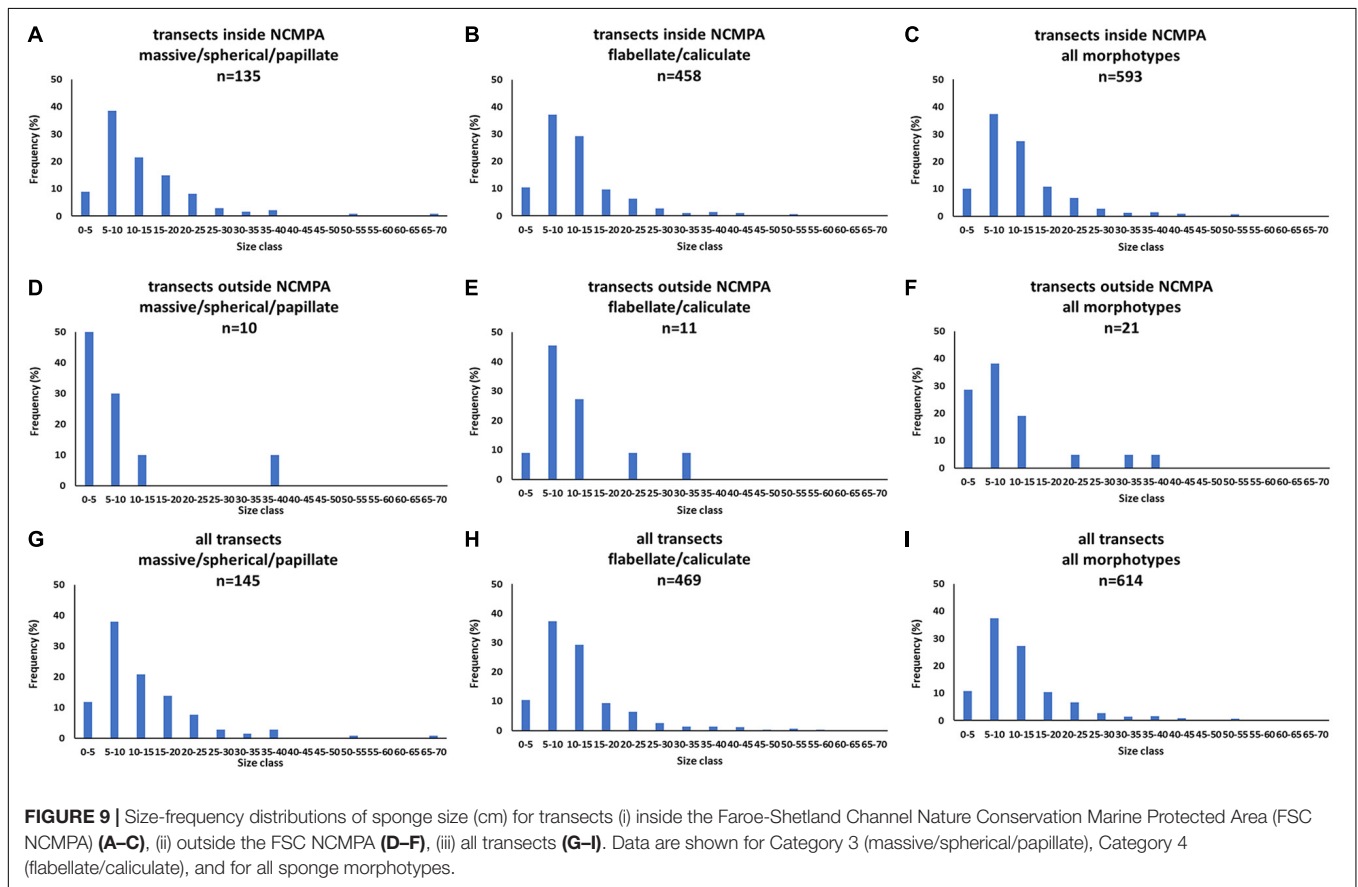


**FIGURE 8 |** Density (individuals/m<sup>2</sup>) of sponge morphotypes across depth in each of the four areas: Area 1 (transects A-B), Area 2 (transects C-D-E-F), Area 3 (transects G-H-I), Area 4 (transects J-K-L-M). Data shown for Category 3 (massive/spherical/papillate) (A), Category 4 (flabellate/caliculate) (B), and for all sponge morphotypes (C).

**TABLE 4 |** Size cohorts (mean ± standard deviation for each cohort) in transects (a) inside the Faroe-Shetland Channel Nature Conservation Marine Protected Area (FSC NCMPA), (b) outside the FSC NCMPA, and (c) across all transects.

Transects	Morphotype Category 3			Morphotype Category 4			Morphotype All categories		
	Size cohort	Mean	SD	Size cohort	Mean	SD	Size cohort	Mean	SD
Inside FSC NCMPA	1	12.8	7.1	1	9.9	4.6	1	9.0	3.9
	2	40.0	5.1	2	37.0	5.3	2	20.6	5.0
	3			3	50.0	4.9	3	37.9	4.3
	4			4			4	53.7	2.2
Outside FSC NCMPA	1	NA	NA	1	8.80	3.4	1	6.5	5.1
All transects	1	8.3	3.8	1	9.9	4.6	1	9.0	4.0
	2	40.0	6.0	2	36.3	5.6	2	20.9	4.8
	3			3	50.0	5.9	3	37.5	4.7
	4			4			4	50.0	4.3

“NA” refers to cases of limited data where Bhattacharya analysis could not be carried out. Category 3: massive/spherical/papillate sponges; Category 4: flabellate/caliculate sponges; All categories: Categories 3 and 4 pooled together. See also **Figure 9**.



(Sherwin et al., 2006) and trawl marks could have been erased. In addition, fishermen may intentionally now avoid the FSC NCMPA sponge aggregations in order to limit damage to fishing gear or due to relatively little fish biomass present in sponge aggregations (e.g., see Munoz et al., 2012; Kenchington et al., 2013; Kutti et al., 2014).

Present findings on sponge richness/diversity and body-size distribution are a strong indication about the presence

inside the FSC NCMPA of more favorable conditions for reproduction, recruitment and growth of sponges. Data on these very important parameters, however, and their role in shaping deep-sea sponge aggregations are extremely limited (Witte, 1996; Fallon et al., 2010). Long-term studies in the abyssal northeast Pacific have shown a correlation between the increase in food supply and density of two glass sponges, suggesting that increased flux of particulate organic carbon

**TABLE 5** | Outcome of distance-based linear modeling on the role of environmental parameters in the variation of density of sponge morphotypes.

Sequential tests					
Variable	R <sup>2</sup>	Pseudo-F	p	Individual proportion	Cumulative
+Depth	0.0002	0.10	0.798	0.0002	0.0002
+Temperature	0.0109	4.98	0.018	0.0107	0.0109
+Cobble	0.0114	0.25	0.718	0.0005	0.0114
+Cobble with boulder	0.1315	63.65	0.001	0.1202	0.1316
+Sand	0.1329	0.71	0.448	0.0013	0.1329
+Sand with boulder	0.1334	0.26	0.793	0.0005	0.1334
+Demersal fisheries	0.4309	238.86	0.001	0.2975	0.4309
+Salinity	0.4798	42.86	0.001	0.0489	0.4798

may cause recruitment or regeneration in deep-sea sponges (Kahn et al., 2012). Furthermore, studies on reef-forming glass sponges in British Columbia showed that recruitment took place where hard substrate (sponge skeletons) was available (Kahn et al., 2016). Apart from the parameters shaping body-size distribution information on the number and structure of body-size cohorts themselves is also limited and when available, a detailed analysis like the one carried out here has not been completed. Available studies have shown unimodal distribution with long tails (e.g., in *Pachastrella monilifera* and *Poecillastra compressa* – Bo et al., 2012; various taxa – Rooper et al., 2016) and multimodal distributions (e.g., in *Pheronema carpenteri* – Rice et al., 1990; in *Geodia mesotriaena* – Klitgaard and Tendal, 2004).

## Density

Density had significantly higher values inside than outside the FSC NCMPA (Table 3 and Figure 6). The average value when all sponge morphotypes within the FSC NCMPA were summed, was 0.28 individuals/m<sup>2</sup> which is well within the range reported for deep-sea areas in the North Atlantic e.g., the Traena Coral Field (0.14 individuals/m<sup>2</sup> for geodiids and unidentified sponges – Cathalot et al., 2015), the Rosemary Bank Seamount Nature Conservation Marine Protected Area (1.2 individuals/m<sup>2</sup> for various demosponges – McIntyre et al., 2016), the Norwegian shelf (~0.2 individuals/m<sup>2</sup> for various demosponges – Buhl-Mortensen et al., 1995), and Norwegian cold-water coral reefs (from 0.007 to 2.254 individuals/m<sup>2</sup> for *Mycale lingua*; from 0.011 to 0.139 individuals/m<sup>2</sup> for *Geodia barretti* – Purser et al., 2013) (see also Rice et al., 1990; Barthel et al., 1996; Kutti et al., 2013).

Densities of sponges peaked within a highly constrained depth zone of about 80 m (Figure 8) with substratum having a statistically-significant contribution. Highest values were recorded where cobble/cobble with boulder were the dominant or even the only type of substrate recorded (Tables 2, 3 and Figures 5, 6). This finding is in agreement with available information about the presence of *Geodia* and *Phakellia* sponges on hard substrates (Hoffmann et al., 2003;

Klitgaard and Tendal, 2004; Ackers et al., 2007; Gates and Jones, 2012; Tjensvoll et al., 2013).

Apart from fisheries pressure and substratum, a whole suite of other variables related to chemical oceanography exerted strong control over sponge aggregations in the FSC NCMPA in similar ways found in other North Atlantic regions. This suggests that these same factors shape distribution and structure of sponge grounds at the basin scale. These variables include water temperature, salinity and silicate concentrations (Murillo et al., 2012; Knudby et al., 2013; Beazley et al., 2015; Howell et al., 2016), topography, internal waves, current speeds, food supply (Rice et al., 1990; Klitgaard and Tendal, 2004; Knudby et al., 2013; Howell et al., 2016). Establishing a precise relationship between the contribution of each of the environmental parameters mentioned above and the distribution of deep-sea sponges/deep-sea sponge aggregations is still an open question given the limited availability of data on (a) species' physiological tolerances, (b) geographical/bathymetric distribution of these organisms and (c) measurements of environmental data at appropriate spatial scales (Tjensvoll et al., 2013; Beazley et al., 2015; Strand et al., 2017). In the present study, the values of temperature per transect inside the FSC NCMPA ranged from 6.5°C (transect F) to ~8.9°C (transect D) and salinity values ranged from 34.9 psu (transect D) to 35.1 psu (transect C; Table 1); these values fall within the temperature and salinity range reported up to now for *Geodia* sponges in the North East Atlantic (Klitgaard and Tendal, 2004; Bett, 2012). Despite this agreement, it is not clear to what extent the high density of sponge aggregations recorded inside the FSC NCMPA is due to the physical/chemical parameters of the water masses *per se* and/or due to the outcome of the interaction of these water masses (i.e., NAW, MNAW, MEIW, NSAIW, NSDW) with the slope creating internal waves supplying food particles to deep-sea benthos (Mienis et al., 2009; Mohn et al., 2014). Taking into account, however, that (a) rapid changes in temperature have been recorded at the Faroe-Shetland Channel (up to 7°C within 1 h) at a depth of 550 m (Bett, 2001) and that deep-sea sponges feed mainly on particulate organic matter (e.g., Kazanidis et al., 2018 and references therein), it is likely that the hydrographic conditions (i.e., internal waves) play a more important role than temperature and salinity themselves in promoting the proliferation of sponges within the FSC NCMPA. Previous works have also highlighted the role of enhanced kinetic energy increasing the supply of food particles to sponges (Rice et al., 1990; Klitgaard and Tendal, 2004; Beazley et al., 2015).

Suggestions made above about the role of water mass characteristics and hydrography in promoting the proliferation of sponge aggregations within the FSC NCMPA gain further interest considering long-term changes in major chemical features in North Atlantic including the FSC NCMPA (Hátún et al., 2017). On top of changes in silicate concentration, long-term measurements (1994–2011) in the FSC NCMPA have also shown that surface layers (NAW and MNAW) have become warmer and more saline over the past two decades: temperatures have been increasing by 0.5°C per decade and salinities by approximately 0.07 (Berx et al., 2013). These temperature- and

salinity-related changes in FSC water masses may pose additional pressures on the vulnerable sponge aggregations through changes like a decrease in oxygen concentration (e.g., Sweetman et al., 2017).

## Conclusion and Suggestions Facilitating Adaptive Management in the FSC NCMPA

The present study provided evidence that the FSC NCMPA boundary currently encloses the most vulnerable area encompassing sponge communities with high richness, diversity, density and several size classes. Sponge communities were constrained to a narrow environmental niche shaped by relatively low fishing impact and the interactions of the five FSC water masses with the slope, supplying in this way food to sponges. This suggests that the deep-sea sponge aggregations are vulnerable not only to demersal fishing but could also be susceptible to changes in oceanic conditions over time.

The findings of the present study can contribute to the establishment of monitoring programs and efficient conservation strategies in the FSC NCMPA. Our study presents simple indicators that can be monitored during annual demersal camera surveys of the FSC NCMPA, including sponge richness/diversity, density, and body-size distribution. The present study serves both baseline and future assessments of anthropogenic and climate change impacts on deep-sea sponge ecosystem environmental status in the FSC NCMPA guiding thus adaptive management in FSC NCMPA.

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## AUTHOR CONTRIBUTIONS

FN designed and led the ship survey and collated the video footage. GK and JV processed the video/image material. GK, JV, and L-AH designed the statistical comparisons, while GK and JV analyzed the data with assistance from KG. BB provided oceanographic data from the FSC. All authors helped to write the manuscript.

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**Conflict of Interest Statement:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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