



The distribution of deep-sea sponge aggregations (Porifera) in relation to oceanographic processes in the Faroe-Shetland Channel

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ABSTRACT

Deep-sea sponge aggregations have been identified as potential Vulnerable Marine Ecosystems under United Nations General Assembly Resolution 61/105. Understanding the distribution of these habitats is critical to future spatial management efforts, and central to this understanding are quantitative data on the environmental drivers of that distribution. Accumulations of large suspension feeders are hypothesised to aggregate in regions of internal wave formation. The causal link is thought to be an increase in the supply of food related to the incidence of internal waves, which results in resuspension of particulate organic matter on which the sponges feed. There is, however, almost no empirical evidence to support this hypothesis for deep-sea sponge aggregations, although there is strong circumstantial evidence. We tested the relationship between sponge density and 1) temperature range (as a measure of internal wave presence in this region), and 2) optical backscatter (a measure of particulate flux) for a known sponge aggregation in the Faroe-Shetland Channel where internal wave interaction with the slope is further well-documented. 25 benthic video transects, ranging from 422 to 979 m water depth were conducted in the study region. 225 images were analysed and all taxa identified to morphotypes and quantified. Temperature and optical backscatter data were drawn from archived CTD data, and data from long term (4 months) and 2 seasonal short term (11 days) mooring deployments from the region. A generalised linear model was used to test the relationship between sponge density and temperature range (ΔT), and sponge density and optical backscatter. The results showed a statistically significant positive relationship between sponge density and temperature range, with the highest sponge densities occurring at depths of greatest temperature range. They showed a statistically significant positive relationship between sponge density and optical backscatter for long term and one short term seasonal deployment (Sep–Oct), but a weak negative relationship for the other short term mooring deployment (April–May). We conclude that sponge aggregations in the Faroe-Shetland Channel are associated with slope regions that are subjected to abrupt and pronounced changes in temperature due to intensified internal wave activity over the slope between depths of 400–600 and that lead to intensified near-bed currents and elevated resuspension of particulate. Our data provide empirical evidence of the relationship between internal wave processes and deep-sea sponge aggregations. These data modify current theory on drivers of deep sea sponge aggregation distribution, suggesting aggregations also occur directly within regions of internal wave breaking, rather than simply proximal to these regions.

1. Introduction

Deep-sea sponge aggregations are communities of large sponges that form under specific biological, hydrological and geological conditions (Hogg et al., 2010). They are a global phenomenon (Van Soest et al., 2012), examples of which include: *Pheronema* (formerly known as *Holtenia*) grounds characterised by *Pheronema carpenteri* (Thomson, 1869) in the NE Atlantic (Rice et al., 1990), dense Hexactinellid reefs found off the coast of British Columbia, Canada (Krautter et al., 2001)

and ostur grounds characterised by large demosponges on the Faroese slope and shelf (Klitgaard and Tendal, 2004; Murillo et al., 2018). Deep-sea sponge aggregations have been identified as potential Vulnerable Marine Ecosystems (VME) (UNGA, 2006) under the FAO's guidelines for the management of deep-sea fisheries (FAO, 2009), and are listed under the OSPAR Convention as a threatened and declining habitat (OSPAR, 2010). Furthermore, a recent Convention on Biological Diversity (CBD) Decision XX/4 emphasised the ecological importance and sensitivity of these aggregations and the need to study and conserve them; and the

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United Nations Environment Programme have called for international engagement in mapping and modelling sponge distribution (Hogg et al., 2010).

Effective management and conservation of these habitats relies on a firm understanding of their spatial distribution. While there are a number of growing datasets on the presence of individual sponge taxa, data on the presence of sponge aggregations is limited, and so recent studies have attempted to predict their distribution using habitat suitability modelling approaches (Knudby et al., 2013; Ross and Howell, 2013; Howell et al., 2016). The construction of models requires data on the presence/absence/abundance of a species and spatial layers of data on relevant environmental parameters. Models can then be developed that formalise the relationship between species presence/absence/abundance and the environmental drivers (or surrogates for those drivers) of their distribution within a statistical framework. However, questions remain around the accuracy and reliability of modelled maps, particularly where there is only a very basic understanding of the underlying ecology and environmental drivers of species distributions (Howell et al., 2016).

The distribution of deep-sea sponge aggregations is thought to be related to the interaction of internal waves (IWs) with sloping boundaries, typically the continental slope (Rice et al., 1990; Klitgaard et al., 1997; White, 2003) and raised features like the Mid-Atlantic Ridge (van Haren et al., 2017). Rice et al. (1990) postulated that accumulations of hexactinellid sponges in the Porcupine Seabight (NE Atlantic) aggregated near regions with a critical slope where the bottom slope matches the slope of propagation of internal tidal waves and near-bed currents are intensified. The causal link was suggested to be an increase in the supply of food related to the occurrence of the internal waves. Sponges are filter-feeders and represent an important link between carbon in the water column in the form of ultraplankton (2–20 µm) and picoplankton (< 2 µm) (Reiswig, 1975), dissolved organic carbon (Yahel et al., 2003; de Goeij et al., 2008) and potentially viral particles (Hadas et al., 2006), and the benthos. Rice et al.'s hypothesis was extended by Klitgaard et al. (1997) for aggregations characterised by the demosponge *Geodia* spp, who put forward two mechanisms by which food availability in the form of suspended material might be increased: 1) increased primary production where internal wave mixing promotes nutrient flux to the surface, and 2) leakage of food-particle rich water from the bottom-mixed layer to the stratified ocean interior. To date there has been no formal testing of this hypothesis.

Within the Faroe-Shetland Channel (FSC) sponge aggregations are known to occur on shelf areas around the Faroe Islands (Klitgaard and Tendal, 2004) as well as on the continental slope west of the Shetland Islands (Bett, 2001). These sponge aggregations have been classified as 'Boreal Ostur' (Klitgaard and Tendal, 2004). They are characterised by sponges of the genus *Geodia*, specifically *Geodia barretti* Bowerbank 1858, *G. macandrewi* Bowerbank 1858, *G. atlantica* (Stephens, 1915) and *G. phlegraei* (Sollas, 1880).

The FSC is also a site with particularly intense IW processes (Van Raaphorst et al., 2001; Hosegood et al., 2004a, 2004b) that result in dramatic short-term changes in temperature (Hosegood, 2004a, 2004b). In addition to the generation of internal tides at a semidiurnal frequency throughout the channel (Hosegood and van Haren, 2006; Hall et al., 2011), resuspension may be promoted by the propagation of 'solibores' up the continental slope. Defined as features that resemble both internal bores and nonlinear internal wave trains, solibores have been observed to generate a temperature decrease of > 4 °C in less than one minute at a depth of 470 m. In the FSC, particulate fluxes are two orders of magnitude larger than background levels for 2 days following the passage of solibores (Hosegood et al., 2004a). Key to their generation, and the continuous critical reflection of the internal tide over the slope that occurs further to the south in the FSC and generates similar near-bed intensified currents (Hall et al., 2011), is the intersection of the strongly stratified permanent pycnocline over the Shetland slope at depths of 400–600 m. Separating the poleward flowing surface

waters of Atlantic origin and the equatorward flowing waters of polar origin, the pycnocline persistently renders the slope critical to internal wave reflection at the depth where it intersects the bottom, but whose location varies over time due to tidal, and lower frequency, modulations of the current regime (Hosegood and van Haren, 2006).

Within the depth range of 400–600 m in the FSC, resuspension of particulate material is thus persistently driven by the internal tide whereby near-bed currents and temporal changes in temperature are bottom intensified with a semidiurnal frequency. Due to changes in background stratification, the signature of such resuspension in moored OBS signals is effectively switched on and off at a given location due to the location of internal tide generation (Bonnin et al., 2005); as the background stratification evolves in response to regional scale, sub-inertial forcing such as coastal trapped waves (Hosegood et al., 2006), the precise depth at which the slope is critical to the semidiurnal internal tide changes within the 400–600 m range (Hosegood and van Haren, 2006). The FSC has thus long been a site of multidisciplinary study due to these unique biological and hydrographic characteristics and is an excellent site for investigating relationships between IW processes and sponge aggregations.

Whilst the association between ostur aggregations in this region and IW processes has been suggested by previous authors (Bett, 2001; Klitgaard and Tendal, 2004), there has been no robust analysis of these relationships. This study aims to consolidate our understanding of the role of IW in driving the distribution of ostur in the FSC, contributing to the development of more complex habitat suitability models and a deeper understanding of how this valuable and threatened ecosystem is generated and sustained. Our hypotheses are: H1 – The abundance of sponges is associated with the generation of internal waves at the slope, H2 – The abundance of sponges is related to the amount of particulate matter in suspension.

2. Methods

2.1. Study area

The FSC is a roughly symmetrical, widening trench bounded by the Faroe Islands in the west and the Shetland Islands in the east (Fig. 1). It has a roughly southwest to northeast orientation. In the southwest the channel terminates in sills at a depth of 850 m and 500 m at the Faroe Bank Channel and Wyville-Thomson Ridge, respectively. To the Northeast the FSC meets the Norwegian Sea at between 1500 and 2000 m (Van Raaphorst et al., 2001). The hydrography of the FSC is primarily underpinned by the constituents of the water column, which comprises 5 distinct water masses described in Turrell et al. (1999).

2.2. Biological data

Biological data were derived from 25 benthic video/image transects conducted by the M/V Franklin during the combined Strategic Environment Assessment 7/Special Area for Conservation survey in 2006 (Jacobs and Howell, 2007). Transects were conducted on two separate sites; FSC_NE ($n = 9$) (62°00′–00″N, 1°00′–00″W) and FSC_SW ($n = 16$) (61°00′–00″N, 3°30′–00″W) (Fig. 1) and ranged from 473 m to 2591 m in length. Sea-floor image data were collected with the SEATRONICS drop frame camera system (Howell et al., 2010). The system comprised an integrated DTS 6000 digital video telemetry system, which provided a real time video link to the surface, a digital stills camera (5 mega pixel, Kongsberg OE14–208) and a colour video camera (Kongsberg OE14–366). The stills camera was mounted at an oblique angle (22°) to the seabed. Sensors monitored depth, altitude and temperature, and an Ultra Short Base Line (USBL) beacon provided position data accurate to 1 m (Howell et al., 2007). The drop frame was towed in the water column between one and three metres above the seabed. At approximately 1 min intervals the camera was landed on the seabed and a still image taken. This ensured a consistent size field of

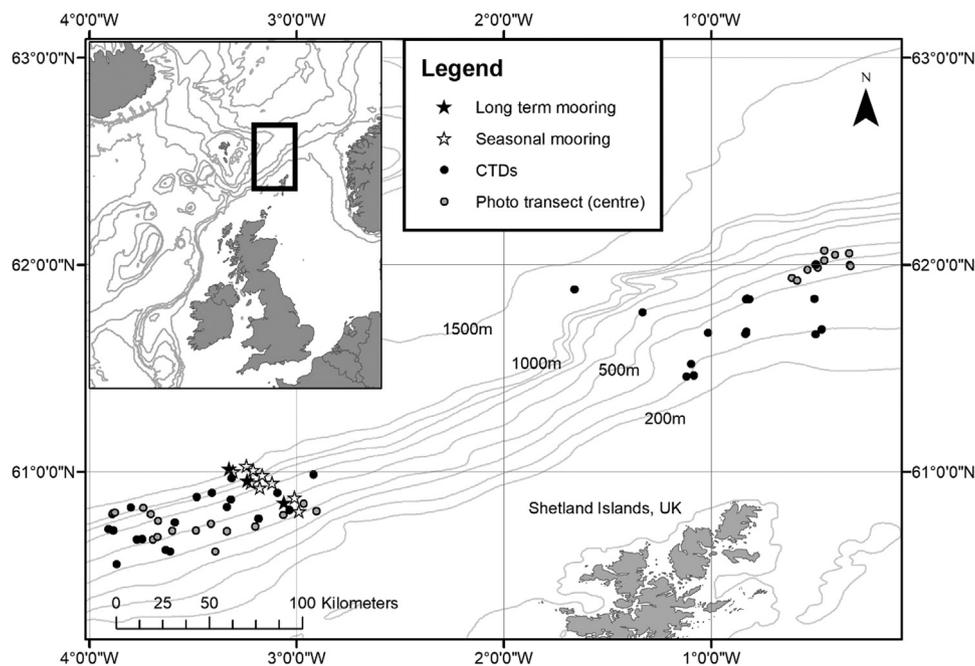


Fig. 1. Map of the Faroe-Shetland Channel detailing the locations of areas of study, CTD casts, image transects (mid point shown), and PROCS-1–3 mooring sites, North of Scotland, Shetland and Orkney shown in grey.

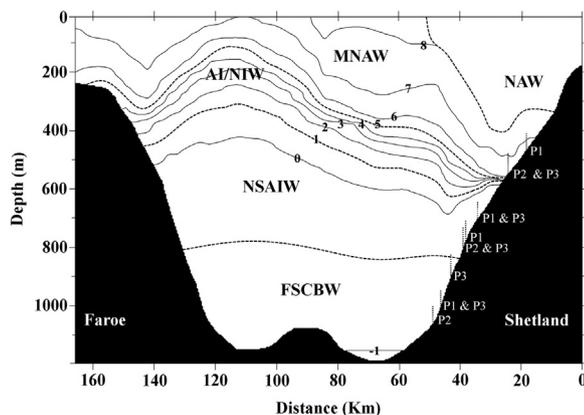


Fig. 2. Cross section of the Faroe-Shetland Channel showing detailed temperature and water masses as described by Turrell et al. (1999). PROCS-1-3 (P1-3) mooring depths are indicated by vertical dashed lines. Numbers 0–8 are isotherms in °C; water masses are North Atlantic Water, Modified North Atlantic Water, Arctic Intermediate/North Icelandic Water, Norwegian Sea Arctic Intermediate Water, Faroe-Shetland Channel Bottom Water (Redrawn from Hosegood, 2005).

view for images.

For each transect 9 images were quasi-randomly selected for analysis, giving 225 images for analysis. Compromised images (e.g. high sediment, large obstructions, resolution or contrast issues) were omitted and an alternative image selected. Selected images were quantitatively analysed in the following manner: all sponges > 1 cm were identified and counted, percentage cover of sponges was also calculated using a calibrated grid superimposed over the image (data were rounded to the nearest 0.25 of a grid square). Sponge taxa were identified as distinct Operational Taxonomic Units (OTUs) following Howell and Davies (2010). OTUs may not conform to established taxonomy. Sponge OTUs were defined by colour, shape, and specific terminology found within Ackers et al. (2007) and grouped into distinct morphologically similar groups as a result of the difficulty in identifying sponges using images. Image data were then pooled by transect.

2.3. Oceanographic data

Variation in the temperature range with depth was chosen as an indicator for the presence of internal waves at the seabed as recorded by Nansen (1902). Archived CTD casts for the immediate region of study (FSC_NE = 18 n, FSC_SW = 18 n) were obtained from the British Oceanographic Data Centre (BODC) (Fig. 1). The CTD profiles all reach to within approximately 10 m of the sea bed. These data spanned a period of 28 years (1984–2012). Mean, range and standard deviation were calculated for temperature (°C) at 20 m depth intervals from all CTD casts ($n = 36$) from 0 to 1300 m (Supplementary material, Fig. S1). These data are considered low temporal resolution data and will be referred to as such henceforth.

Higher resolution data on temperature, and data on turbidity (optical back scatter, (OBS)) were obtained from moorings deployed over the Shetland continental slope by the Royal Netherlands Institute of Sea Research (NIOZ) during the ‘Processes on the Continental Slope’ (PROCS) programme (Fig. 1). Medium temporal resolution data (hereinafter referred to as PROCS-2 data) were derived from three ‘long term’ moorings deployed for a period of 132 days (May–Sept 1999) at 552, 803, 1043 m depth. Temperature and optical backscatter were recorded hourly. In addition seasonal high temporal resolution data were obtained from two further sets of moorings deployed for an 11 day period in April–May (PROCS-1 research cruise, 4 moorings at 471, 700, 777, 1000 m) and Sept–Oct (PROCS-3 research cruise, 5 moorings at 550, 700, 800, 900, 1000 m) (Fig. 2). Temperature and optical backscatter was logged every 4 mins.

Optical backscatter was measured using a Seapoint STM optical backscatter sensor (OBS). Optical backscatter indicates the presence of suspended particulate matter with the limitation that the raw signal (measured in Volts, with a higher voltage indicating a greater proportion of suspended particles) depends heavily on the particle size in accordance with Bunt et al. (1999), who found that optical devices are most sensitive to particles < 20 µm in diameter. The OBS in this study is capable of detecting particles in the ultra and picoplankton size range (size fraction on plankton known to be utilised by sponges as a food resource), but it must be noted that OBS is a bulk measure of suspended material and its use here as a proxy for availability of potential food

resource for sponges is limited and this is acknowledged in the discussion.

For medium and high resolution moorings data mean, range and standard deviation were calculated for temperature (°C) and OBS over the full deployment period for each mooring. To investigate the relationship between sponge abundance and temperature variation/OBS, each photo transect was paired with the nearest mooring from each of the PROCS1, PROCS2 and PROCS3 datasets.

2.4. Statistical analysis

Preliminary analysis demonstrated that temperature range data (ΔT) from CTDs, long term and short term moorings were highly correlated therefore only CTD data were used in further analyses. In addition, sponge abundance and sponge percent cover were highly correlated (Kendall's Rank (Tau) $T = 0.646$, $P < 0.001$) and so only sponge abundance was used in further analyses. Scatter plots of sponge abundance vs temperature range suggested a log-linear or polynomial relationship was present. Simple linear, log linear and polynomial models were fitted to the data, however a log-linear model provided the best fit and explained substantially more variance than other models trialled. To test H1 a linear model was used to test for a significant relationship between log sponge abundance and ΔT from archived CTD data.

Scatter plots of sponge abundance vs OBS again suggested a log-linear or polynomial relationship was present between sponge abundance and OBS. However, the limited data available for OBS from only 3 or 4 moorings (depending on whether long term or seasonal datasets) meant it was inappropriate to fit a model to these datasets. Instead for long term (PROCS-2) data, sponge abundance data were grouped by mooring (OBS) and a Kruskal–Wallis test was used to test for a significant differences in sponge abundance between moorings and thus long term (PROCS-2) OBS data. The relationship between sponge abundance and short term seasonal (PROCS-1 and PROCS-3) OBS data were not formally tested but are described. Data analysis was conducted using R-Studio (RStudio Team, 2015) a wrapper for the program R (version 3.3.2 (R Core Team, 2016)).

3. Results

3.1. Sponge abundance and variation in temperature (indicative of the influence of internal waves)

ΔT for all datasets peaked between 400 and 600 m, with a maximum range of around 9 °C (Fig. 3, Fig. S1). Sponge abundance peaked at approximately 500 m (498 m = 361 individuals), and transects with the highest recorded abundances were all located between ~400–600 m (Fig. 3). Sponge abundance declines rapidly deeper than 600 m. There is a highly significant linear relationship between log sponge abundance and ΔT ($p < 0.001$, Multiple R-squared: 0.73 on 23 df, Supplementary material, Fig. S2).

3.2. Sponge abundance and the resuspension of particulate material

Box plots of mean long term OBS data (PROCS-2) appeared to show a log-linear relationship with sponge abundance although this was not formally tested as a result of limited data. A Kruskal–Wallis test confirmed there was a significant difference in sponge abundance between moorings and therefore low, medium, and high OBS values (p -value = 0.01238). These data suggest that sponge abundance is related to mean long term particulate resuspension at the seabed (Fig. 3) However, the data are confounded by depth, and have limited resolution as photo transect data have been assigned to the nearest mooring, and data are only available from 3 moorings (Supplementary material Fig. S3). High resolution seasonal data for Sept-Oct (PROCS-3) appeared to have a positive log-linear relationship with sponge

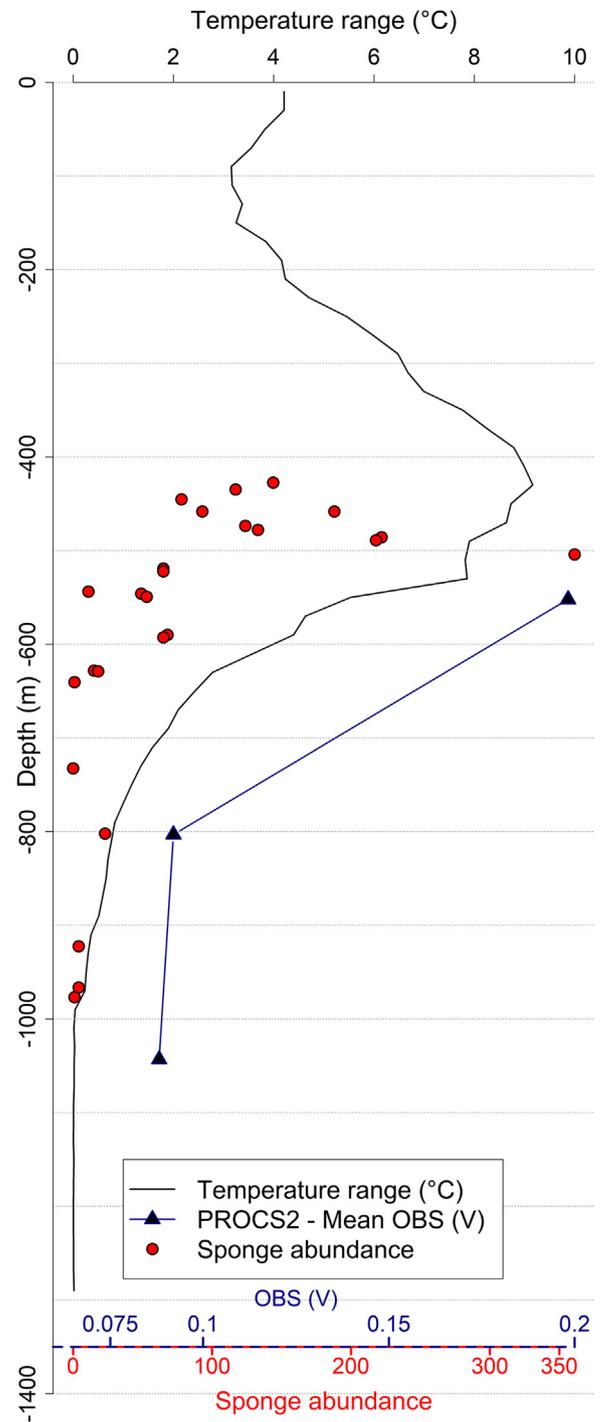


Fig. 3. Sponge abundance determined from pooled image data by transect, temperature variation (ΔT) from CTD casts, and long term optical backscatter (PROCS-2) as a function of depth.

abundance, however seasonal data for April-May (PROCS-1) showed a more complex relationship with sponge abundance, where sponges abundance was low at very high OBS values (Supplementary material Fig. S4). This suggests that sponge abundance has a more complex relationship with short term seasonal observations of OBS. However, again it must be considered that data are only available from 4 moorings.

4. Discussion

4.1. Sponge abundance and temperature variations

Large temperature changes are observed between 400 and 600 m depth in this region of the FSC which, on the basis of previous studies, are attributed to internal wave activity (Fig. 3). This depth-range is consistent with the established critical slope angle for internal semi-diurnal tidal waves (M_2 waves), calculated to be 350–550 m on the SE slope of the FSC (Van Raaphorst et al., 2001) but also the depth range over which solibores propagate up, and along, the slope (Hosegood et al., 2004b). The highest densities of sponges are also located at between 400 and 600 m, and our results suggest there is a significant linear relationship between temperature range and sponge abundance, suggesting that sponge abundance is highest in the region of internal wave activity at the seabed. The mechanism responsible for the generation of the solibores in this particular location have been suggested to be the nonlinear evolution of the permanent pycnocline that subsequently evolves into various forms of an internal wave train (Hosegood et al., 2006). Internal tides are not necessarily responsible but we note that Hall et al. (2011) observed dynamically similar features in the southern prion of the FSC to occur with semidiurnal frequency leading to the conclusion that the critical slopes at this depth range lead to nonlinear internal tide reflection. The common factor in either scenario is a rapid drop in temperature accompanied by intense near-bed currents.

Although in general agreement, this is contrary to the current theory, which suggests sponge aggregations are found near to, but not in, regions of internal wave breaking (Rice et al., 1990; Klitgaard et al., 1997; White, 2003). Increased velocities associated with regions of critical slope angle and therefore internal wave propagation were postulated to be too severe for sponge species to persist (White, 2003). Sponge aggregations were postulated to form ‘downstream’ of regions of breaking internal waves, such that they benefitted from material transported by turbulent mixing but were not subject to breaking waves. In this study the highest densities of sponges were found at ~500 m (Fig. 3) which corresponds well with the highest cross-slope enhancement of velocity at 502 m on the SE shelf of the FSC (Van Raaphorst et al., 2001). This study suggests that ostur aggregations are capable of withstanding strong bottom currents. The initial theory was postulated for aggregations of *P. carpenteri*, which grow mainly on fine sediments and weakly anchor themselves via a spicule matt (Rice et al., 1990). Ostur species are characteristically found physically attached to gravel, small cobblestones or hard sediments (Klitgaard and Tendal, 2001). Furthermore, ostur sponges are regularly found to have gravel incorporated into the cortex (Klitgaard and Tendal, 2001), which could enable them to more strongly anchor to the seafloor, allowing them to resist faster current speeds.

The flow rate through a sponge is also dictated by the ambient flow (Vogel, 1977). *Geodia barretti* (Bowerbank, 1858), a defining species of ostur grounds, has been shown, in a combination of laboratory and in situ conditions, to have pumping rates 6 times slower than shallow water sponges (Kutti et al., 2013), therefore it is possible that if ostur are able to resist higher current regimes this may lead to greater food acquisition. This could be achieved by increased flow through the sponge as a result of the significantly enhanced bottom currents due to internal wave breaking, where peak current velocities in this region can reach $> 75 \text{ cm s}^{-1}$ (Masson, 2001).

4.2. Sponge abundance and the resuspension of particulate material

We found significant differences in sponge abundance between areas of low, medium and high OBS, and our data suggest there may be a positive log-linear relationship between sponge abundance and OBS from long term mooring data as well as seasonal short term mooring data (PROCS-3), although available data were insufficient to formally

test this. High OBS values are indicative of high levels of suspended particulate material.

Current theory suggests that sponge aggregations are promoted by the presence of internal waves as a result of either: 1) increased primary production that may occur where internal wave mixing promotes nutrient flux to the surface, or 2) leakage of food-particle rich water from the bottom-mixed layer to the stratified ocean interior. Our data would suggest the latter mechanism may operate in the FSC. Due to the presence of tidally driven internal waves (Van Raaphorst et al., 2001; Hosegood et al., 2006) and solibores generated by subinertial processes (Hosegood et al., 2004b), there is likely to be a permanent intermediate nepheloid layer between the intermediate and deep water masses (Turrell et al., 1999) around 500–550 m (Van Raaphorst et al., 2001). This nepheloid layer could provide the sponges with a sustained and reliable food source and thus support the formation of aggregations. A recent study focused on sponge aggregations on the summit of an Arctic seamount also suggested sponge densities were associated with elevated near-bed suspended particulate material concentrations, likely as a result of local/near-field resuspension by tidal currents, the driver being improving food supply to the sponges (Roberts et al., 2018). However, we do not know if the resuspended material observed here is utilised by the sponges as a food source. Nor do we know the nutritional value of the material to the sponge. Thus we cannot demonstrate that it is the resuspension of material that drives sponge abundance through provision of food resource.

Although our data suggest a positive log-linear relationship between sponge abundance and OBS data from long term moorings and short term seasonal moorings deployed in Sep-Oct, there is a more complex relationship between sponge abundance and OBS data from seasonal short term moorings deployed in April-May when the most intense solibores were observed (Hosegood et al., 2004a).

Within the April-May short term mooring deployment (PROCS-1) a solibore event occurred on day 112 during a barotropic neap tide, the period where internal tidal forcing would be expected to be the weakest (Hosegood et al., 2004b). Solibore events were observed to occur approximately every 4–7 days and are not directly associated with tidal forcing (Hosegood et al., 2004b; Hosegood et al., 2006), therefore they are not likely to be reliable for frequent particulate resuspension. However, during a solibore event the amount of particulate that can be resuspended is up to 100 times the amount than that can be resuspended by typical steady currents (Fig. S4). During the solibore event observed during PROCS-1 the total max flux at $> 700 \text{ m}$ was shown to be 2 orders of magnitude higher than that at 470 m during the day following the solibore occurrence (Hosegood et al., 2004a). Sponge abundance is low at 700 m where PROCS-1 seasonal OBS is highest (Supplementary material Fig. S4). It is possible that this concentration of particulate matter in the water column might exceed the tolerance levels for the sponges resulting in the clogging of the osculum and ostia, leading to a depressed metabolism and possible mortality (Klitgaard and Tendal, 2004). It is possible that sponge aggregations do not extend deeper in the FSC as a result of these episodic mass flux events. However, geodid sponges are able to tolerate high exposure to suspended particulate by reducing respiration rates by up to 86%, for a short time (Tjensvoll et al., 2013). In addition more recent studies have shown that chronic (29 day) cyclic exposure to natural bottom sediment did not affect geodid respiration (Kutti et al., 2015). It is therefore more likely that the consistently lower temperatures below 600 m ($\sim 0^\circ \text{C}$) may lie outside the thermal tolerance of the sponge species observed. Species characteristic of boreal ostur, including *G. barretti*, *G. macandrewi*, *G. atlantica* and *G. phlegraei*, have been observed over a temperature range of -0.62 – 10.75°C (Cardenas et al., 2013; Howell et al., 2016), with the lower figures coming from the FSC where the lower temperatures are only experienced periodically not consistently.

4.3. Further observations and remarks

This study has shown a significant log-linear relationship between temperature range and sponge abundance, suggesting that sponge abundance is highest in the region of internal wave activity at the seabed. If the relationship between sponge abundance and internal wave processes can be shown to be consistent across multiple sites globally, it would provide a powerful predictor in the further development and application of habitat suitability modelling approaches to predictively map the distribution of sponge aggregations in the deep sea. Our study is of one site in one basin and does not enable such a generalisation to be made. It does however provide quantitative data on the nature of that relationship at this site, such that a more comprehensive test of this relationship can be made in future.

This study has also shown that sponge aggregations of the FSC are subjected to rapid and large changes in temperature as result of the extreme thermal gradient in the FSC and the propagation and breaking of internal waves. Sites with sponge aggregations consistently experience 6 °C shifts in temperature, with the highest variation being over 9 °C (Supplementary material, Fig. S1)). Aggregations are frequently subjected to water < 0 °C due to the movement of the pycnocline, but temperature varies between approximately –1 and 9 °C and is on average around 3.5 °C. Changes in temperature of this magnitude might be expected to induce heat shock and possibly mortality. *G. barretti*, a key constituent of these aggregations, has been observed to be intolerant to sustained rises in temperature. Guihen et al. (2012) observed that 95% of specimens were killed during two heat shock events in 2006 and 2008, by a 4 °C rise in temperature in < 24 h, which was then sustained for several days. Temperatures peaked at 12.6 °C. These authors suggested that 12.6 °C exceeded the thermal tolerance for *G. barretti* and that observed mortality was caused by microbially induced anaerobic degradation. Our data suggest that *G. barretti* is able to tolerate rapid but sustained fluctuations in temperature of between –1 and 9 °C.

Interestingly a recent study from the Scotian Shelf in the Western Atlantic found that sponge grounds in the Emerald Basin formed by the hexactinellid *Vazella pourtalesi* occurred in areas of historically high inter-annual variability in bottom temperature and salinity (Beazley et al., 2018). Temperature ranged from 4 °C in the mid 1960's to upwards of 12 °C in more recent years, giving a similar level of shift in temperature (8 °C) to that observed in this study over short time-scales. These data suggest that sponge grounds may be tolerant to some level of temperature fluctuation on both short and long-term time-scales. Beazley et al. (2018) suggest that these types of observations can give insight into how deep-sea sponge species will respond to future climate change.

5. Conclusions

This paper offers a formal test of the relationship between sponge aggregations and temperature variation (ΔT). Large temperature changes observed between 400 and 600 m depth in this region of the FSC have been attributed to internal wave activity, and this depth-range is consistent with the established critical slope angle for internal semi-diurnal tidal waves (M2 waves). While we cannot rule out the involvement of other oceanographic processes in driving these variations in temperature, available data suggest the abundance of sponges in the FSC is associated with the generation of internal waves at the slope (H1). We have also demonstrated a relationship between sponge abundance and long term (132 days) mean suspended particulate matter in support of H2. The highest values of long term OBS and highest abundance of sponges also occur between 400 and 600 m, where breaking internal waves are known to resuspend particulate material. Formal testing of this relationship is confounded by depth and limited data from only 3 moorings

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Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.dsr.2019.03.005.

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