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Deep-sea sponge grounds enhance diversity and abundance of epibenthic megafauna in the Northwest Atlantic

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The influence of structure-forming deep-water sponge grounds on the composition, diversity, and abundance of the local epibenthic megafaunal community of the Flemish Pass area, Northwest Atlantic was statistically assessed. These habitats are considered vulnerable marine ecosystems and, therefore, warrant conservation measures to protect them from bottom fishing activities. The epibenthic megafauna were quantified from four photographic transects, three of which were located on the western slope of the Flemish Cap with an overall depth range of 444–940 m, and the fourth in the southern Flemish Pass between 1328 and 1411 m. We observed a diverse megafaunal community dominated by large numbers of ophiuroids and sponges. On the slope of the Flemish Cap, sponge grounds were dominated by axinellid and polymastid sponges, while the deeper sponge ground in the southern Flemish Pass was formed mainly by geodiids and *Asconema* sp. The presence of structure-forming sponges was associated with a higher biodiversity and abundance of associated megafauna compared with non-sponge habitat. The composition of megafauna significantly differed between sponge grounds and non-sponge grounds and also between different sponge morphologies. Surface chlorophyll *a* and near-bottom salinity were important environmental determinants in generalized linear models of megafaunal species richness and abundance.

Keywords: deep-water sponge grounds, Flemish Pass, megafauna, Northwest Atlantic, vulnerable marine ecosystem (VME).

Introduction

Epibenthic megafauna (herein referred to only as megafauna), i.e. the group of organisms inhabiting the sediment-water interface and ≥1 cm (Grassle *et al.*, 1975; Rex, 1981), are not well documented on the Canadian margin of the Atlantic Ocean and in adjacent deep waters. Despite the importance of megafauna in the function of deep-water ecosystems, descriptions of entire megafaunal communities in the Northwest Atlantic remain scarce, particularly for the continental slopes. Megafauna are important contributers to total benthic biomass (Billett, 1991; Lampitt *et al.*, 1995; Renaud *et al.*, 2007) and carbon cycling (Piepenburg *et al.*, 1995; Renaud *et al.*, 2007) and can be indicators of long-term environmental change (Bluhm, 2001). They have a strong impact on the microscale environment through bioturbation and remineralization processes (Smith *et al.*, 1993), and through the creation of mounds, burrows, and traces, they increase habitat heterogeneity and consequently increase diversity of sediment-dwelling fauna (Soltwedel and Vopel, 2001; Quéric and Soltwedel, 2007; Hasemann and Soltwedel, 2011).

Recently, the United Nations General Assembly (UNGA) Resolution 61/105 (http://www.un.org/Depts/los/general_assembly/general_assembly_resolutions.htm) drew attention to a component of the benthic megafauna, specifically, vulnerable marine ecosystems (FAO, 2009). Criteria for identifying vulnerable marine ecosystems (VMEs) include uniqueness or rarity of species or habitats, the functional significance, structural complexity and fragility of habitats or ecosystems, and life-history characteristics of component taxa that make recovery difficult (FAO, 2009). Some taxa and communities considered to epitomize the definition of a VME include deep-water corals and hydroids, sponge grounds, and seep and vent environments (FAO, 2009). As a result of UNGA 61/105, the general distribution of deep-water corals (e.g. Breeze *et al.*, 1997; Wareham and Edinger, 2007; Kenchington *et al.*, 2010; Murillo *et al.*, 2011a; Baker *et al.*, 2012), sponges (ICES, 2009;

Kenchington *et al.*, 2010; Fuller, 2011; Murillo *et al.*, 2012), and other taxa indicative of VMEs (e.g. Murillo *et al.*, 2011b) have been documented in the Northwest Atlantic. This resolution explicitly links the need for protecting VMEs with the biodiversity that they contain.

Large, structurally complex megafauna, such as deep-water corals, increase the number and complexity of available microhabitats (Tissot *et al.*, 2006), which become more important as depth increases and habitat heterogeneity decreases (Buhl-Mortensen *et al.*, 2010). Dense aggregations of megafauna may also create habitat, especially in areas of low topographical relief (Tissot *et al.*, 2006). These biogenic habitats can be utilized by other biota as refuge from predators, as spawning and nursery grounds, and as attachment substrate for sessile invertebrates (Bett and Rice, 1992; Krautter *et al.*, 2001; Fosså *et al.*, 2002; Reed, 2002; Henkel and Pawlik, 2005). As a result, biogenic habitats may exhibit different and/or more diverse and abundant assemblages of fauna than surrounding non-biogenic habitats (Mortensen *et al.*, 1995; Krautter *et al.*, 2001; Costello *et al.*, 2005). This is exemplified in studies on deep-water reef-building corals such as *Lophelia pertusa*, whose reefs exhibit a higher diversity of fish and macrofauna species than surrounding soft bottom communities (Mortensen *et al.*, 1995; Husebo *et al.*, 2002; Costello *et al.*, 2005; Buhl-Mortensen *et al.*, 2010).

Like corals, sponges in the deep sea also provide additional microhabitats, thus increasing biodiversity of local fauna (Bett and Rice, 1992; Klitgaard, 1995; Kunzmann, 1996; Bo *et al.*, 2012). Sponge associates may live inside the intricate canals formed by the sponge host and feed on food particles not utilized by the sponge or feed on the sponge itself (McClintock *et al.*, 2005; Buhl-Mortensen *et al.*, 2010). The accumulation of sediment and organic detritus on the surface of sponges has also been linked to large numbers of associated epifaunal species, especially deposit feeding taxa of the phyla Nematoda, Polychaeta, and Sipuncula (Klitgaard, 1995). Spicule mats formed by dead sponges may provide hard substratum for settlement by other organisms and refuge from predators (Bett and Rice, 1992).

In the North Atlantic, many deep-water sponge species are relatively common and occur as isolated individuals over much of their distribution (ICES, 2009). However, under favourable environmental conditions, deep-water sponges may form dense, multispecies communities known as sponge grounds (ICES, 2009; Hogg *et al.*, 2010; OSPAR, 2010). Until recently, the function of sponge grounds in the deep ocean has been poorly understood (Hogg *et al.*, 2010). Much like deep-water corals, sponge grounds provide spawning and nursery areas, feeding areas, and refuge from predators for a number of invertebrates and fish species (Klitgaard, 1995; Freese and Wing, 2003; Amsler *et al.*, 2009; Kenchington *et al.*, 2013). Sponges play a role in benthic-pelagic coupling and biogeochemical processing, which may be intensified in sponge grounds. The large amount of water processed by such benthic filter-feeders [Vogel (1977) reported that a 1-kg sponge filters 24 000 l daily] and empirical evidence for the magnitude of the carbon flux in some species indicates that they form a strong link between the pelagic microbial foodweb and the benthos (Pile and Young, 2006).

As with many other biological features in the deep sea, sponge grounds are poorly mapped, with much of our knowledge limited to areas of commercial and scientific exploration (Hogg *et al.*, 2010). However, some sponge grounds have been identified from specific studies in the Northeast Atlantic (Rice *et al.*, 1990; Klitgaard, 1995; Barthel *et al.*, 1996; Klitgaard and Tendal, 2004), and through the initiatives of the Northwest Atlantic Fisheries Organization (NAFO, the Regional Fisheries Management Organization for the Northwest Atlantic), several areas that constitute sponge grounds in the NAFO Regulatory Area (NRA) have also been identified (ICES, 2009; Murillo *et al.*, 2012) and protected through fisheries closures. However, in contrast to the Northeast Atlantic, the assessments of deep-water sponge ground biodiversity and associated species are generally lacking from the Northwest Atlantic (but see Fuller, 2011; Kenchington *et al.*, 2013).

NEREIDA, a Spanish-led multidisciplinary and international project with contribution from Canada, the UK, and Russia, was initiated in response to the UNGA Resolution 61/105. The main objective of the NEREIDA project is to gather information for the identification and delineation of VMEs in the NRA with special focus on those dominated by deep-water corals and sponges. Several research cruises for the NEREIDA project were carried out on board the Spanish Research Vessel "Miguel Oliver" and the Canadian Coast Guard Ship "Hudson" in 2009 and 2010. During these surveys, high-resolution multibeam and seismic data were collected, and rock dredges, boxcores, drop cameras, and ROVs were used to sample and survey the benthos.

As part of the NEREIDA project, we analysed benthic photographic transects collected from the western slope of the Flemish Cap and the Flemish Pass, a deep basin situated between the Grand Bank off Newfoundland and the Flemish Cap in international waters (Figure 1). Previous assessments of the benthic megafaunal community in the Flemish Cap area have been based solely on identifications from research groundfish stock assessment surveys (NAFO, 2009a; Murillo *et al.*, 2011a, 2012). This study represents the first *in situ* assessment of the benthic megafauna in this area.

In light of the recent discovery of diverse sponge grounds at several locations within the vicinity of the Flemish Cap, including the Flemish Pass (Murillo *et al.*, 2012), we assess the influence these VMEs have on the composition, diversity, and abundance of the epibenthic megafaunal ($\geq$1 cm) community. We test the hypothesis underpinning the policy objective that structure-forming sponge grounds increase the biodiversity and abundance of the local epibenthic megafauna. The relative importance of structure-forming sponges in influencing species richness and abundance is assessed against other environmental variables.

Methods

In situ photographic surveys

In 2009, the Department of Fisheries and Oceans, Canada (DFO), collected *in situ* photographic and video data in the NRA as part of the NEREIDA surveys of the NRA. Four photographic/video drift transects of the seabed were conducted aboard the CCGS "Hudson" in the western areas of the Flemish Cap, and in the Flemish Pass, a deep basin separating the Flemish Cap from Grand Bank off Newfoundland (Figure 1). Three of those transects (28–30) were conducted on the western Flemish Cap slope in an area with little fishing effort (NAFO, 2009b) and thought to contain gorgonian and antipatharian corals and sponges (Antonio Vazquez, Institute of Marine Research, Vigo, Spain; personal communication). The fourth (transect 38) directly targeted an area where a large concentration (4000 kg) of sponge was caught as bycatch at 1446-m depth by a DFO trawl survey (2004 DFO unpublished data) and where large catches (>1000 kg haul) of sponge have been reported previously (NAFO, 2009a). Since January 2010, this area has been closed to bottom fishing (NAFO, 2012) to

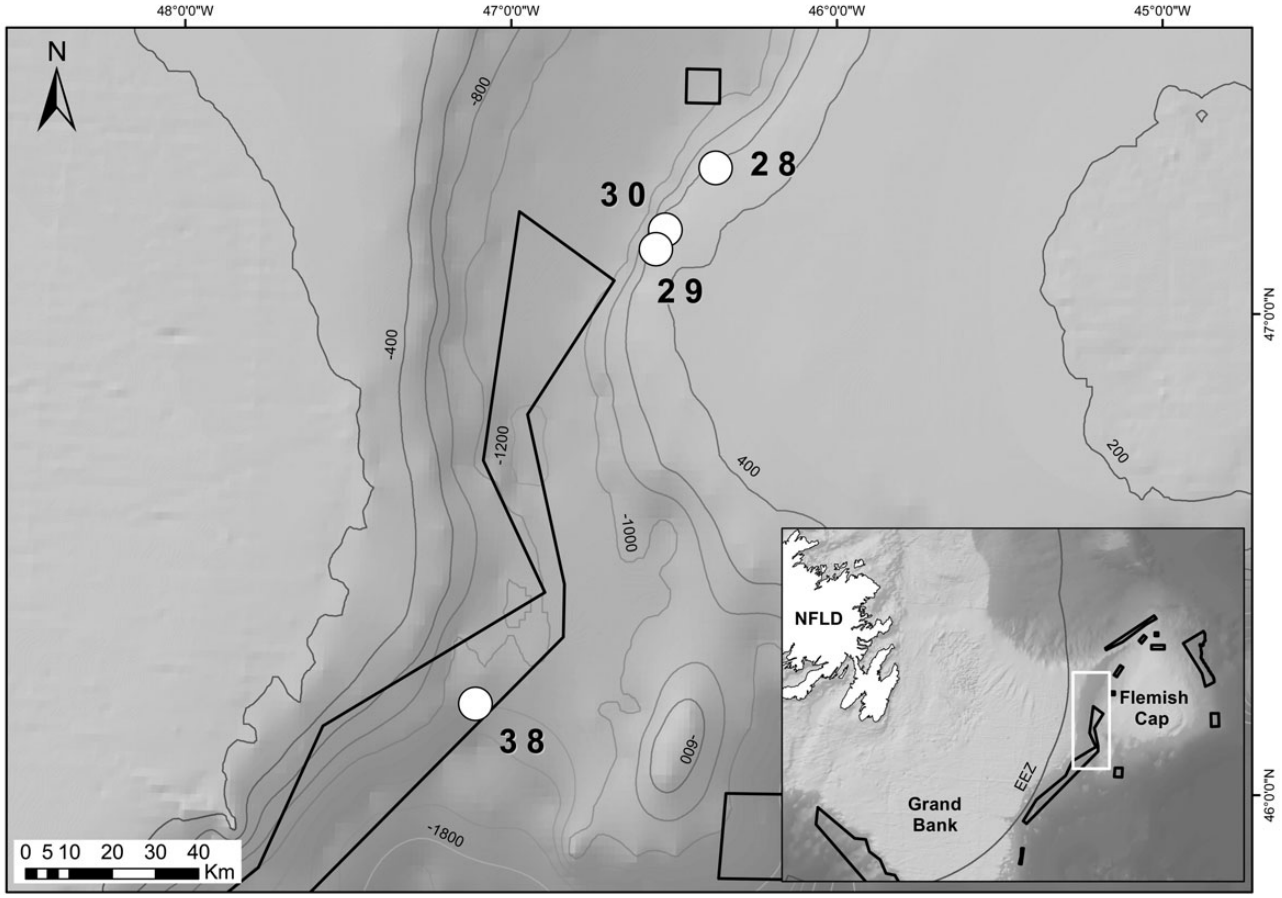


Figure 1. Map of the Flemish Pass area east of St John's, Newfoundland, Canada. White circles indicate the location of photographic transects taken during the CCGS "Hudson" 2009 mission. Black boxes indicate the VME closure areas in the NRA.

protect large gorgonians and sponges, although heavy trawling has not occurred here within the past 20 years (NAFO, 2009b).

Two digital camera systems were used to collect photographic/video imagery of the seabed. Campod is a light-weight tripod camera system that is deployed on station and controlled via a winch on deck. Campod is equipped with a Sony XC-999 colour video camera mounted obliquely to provide a forward-looking, wide view of the seabed; a downwards-facing Sony DXC-950 colour video camera; and a high-resolution Nikon D300 digital still camera mounted to face downwards along with two high-speed flashes. The height of the downwards-facing digital camera above the seabed is roughly 1 m when Campod is landed. Two laser beams calibrated at 10 cm apart are mounted on Campod and are used in the photographs as a size reference. On transects 28 and 29, Campod was used to collect downwards-facing photos that were taken at ∼1 min intervals when the tripod was landed on the seabed.

Imagery from the two deeper photographic transects, 30 and 38, was collected using a digital still camera system called the 4 K Camera (coined the "4KCam"), built by the Geological Survey of Canada in 2008. This system is capable to 4000-m depth, and houses a Canon Rebel Eos Ti 12 megapixel camera and two Canon flashes enclosed inside an aluminium roll cage. The non-conductor hydrostatic wire of the 4KCam was used to lower it via a winch to the seabed where it hovered near bottom; approximately every 1 min the winch operators lowered the camera causing an attached lead weight to touch the bottom triggering the camera and flashes. Due to an issue with the camera trigger wire on transect 30, the 4KCam was raised and redeployed further along the line, causing a large gap (∼970 m) between photographs taken before and after redeployment.

Imagery analysis and identification of fauna

To reduce autocorrelation in the data, photos that were taken less than 10 m apart from adjacent photos were not analysed. Photos that were taken too far or too close to the bottom, blurry photos, and photos containing sediment clouds that significantly impeded the identification of the fauna were also removed. In all, 473 photos drawn from the four transects were processed.

A 4 × 3 grid was placed over each image using batch processing in Adobe Photoshop version CS2 to assist the consistency of data recording. All epibenthic megafauna, defined as any organism ≥1 cm living on or near the seabed, were identified and counted. This included mobile organisms, such as fish and crustaceans that were present on or very near the seabed.

All organisms were identified down to the lowest taxonomic classification possible. Taxonomic identification of organisms from the photos was aided by voucher specimens collected during the NEREIDA surveys using a rock dredge and mega-boxcorer onboard the RV "Miguel Oliver". The Integrated Taxonomic

Information System (ITIS) was adopted as the taxonomic authority. Organisms that could not be identified down to species were given mutually exclusive morphotype designations either at a level higher than species (e.g. Actiniaria 1) or according to shape and other superficial features (unidentified taxa). Animal tubes, mounds, tracks, burrows, casts, and filaments were also quantified from each photo.

The average area covered in the Campod photos (mean ± s.d., $0.71 \pm 0.13\ m^{-2}$) was determined by randomly sampling 50 Campod photos across both Campod transects (28 and 29) and using the two calibrated laser beams as a size reference. For 4KCam transect 30, a subset of 50 suitable photos was selected based on the orientation of the lead weight used to scale the photos, and the average area covered ($0.47 \pm 0.05\ m^{-2}$) was determined using the length or width of the weight as a reference. For transect 38, height above bottom and orientation of the photos was more variable; therefore, area covered was calculated for each photo using the lead weight. For photos with no visible lead weight, biological features with a known size (e.g. central disc of large ophiuroids) were used to calculate the area covered in each photo (mean ± s.d., $0.70 \pm 0.33\ m^{-2}$). These areas were used to standardize the data to number m^2.

Environmental variables

Water depth and temperature were continuously recorded *in situ* using an SBE 39 temperature and pressure recorder attached to both the Campod and 4KCam systems and were extracted for the positions corresponding to the photos. Salinity profiles were extracted from CTD casts taken during NEREIDA cruises in the western Flemish Cap slope/Flemish Pass area during July–August 2009 and June–July 2010. Salinity values closest to the bottom were interpolated using ordinary and simple kriging methods in ArcMap version 10.0 (ESRI, 2011) to create continuous prediction surfaces of salinity for the Flemish Pass area. To assess the quality of the resulting surface prediction maps, the prediction errors (root mean square, mean standardized error, root-mean-square standardized error, and average standard error) from cross-validation were examined and compared between models, with the optimal model having the smallest root-mean-square error, a mean standardized error closest to zero, a root-mean-square standardized error closest to 1, and similar root-mean-square and average standard error values. A prediction value and the associated standard error were generated for the location of each photo from the interpolated surface using the "GA Layer to Points" tool in the Geostatistical Analyst toolbox of ArcMap.

SeaWiFS surface chlorophyll *a* estimates were obtained from NASA's Ocean Colour Web (http://oceancolor.gsfc.nasa.gov/). Level-3 monthly composites at 9 km resolution were retrieved from the period January 2001 to December 2010. The original 9 km dataset was resampled to a 1-km resolution and the annual average chlorophyll *a* ($mg\ m^3$) was calculated across all years. The 1-km resolution raster was converted to points and kriged using the methods above to create a continuous prediction surface of chlorophyll.

Near bottom minimum and maximum temperature (°C) and salinity (psu), mean temperature gradient (°C km), and mean current speed (ms) data modelled for the Northwest Atlantic were extracted for our study area. In addition, mean temperature and salinity were also extracted to compare against the *in situ* values for these variables. The model used was a North Atlantic 1/12 degree model with data spanning from 1990 to 2010 and developed at the Bedford Institute of Oceanography, Nova Scotia, Canada. It is based on NEMO version 2.3 (Nucleus for European Modelling of the Ocean), which includes both an ocean component (OPA, Ocean PArallelise) and a sea ice module (LIM2, the Louvain-la-Neuve sea ice model). The model horizontal resolution is 1/12 degree, corresponding to ~6.4 km in the Flemish Pass area. The surface forcing data used in the model include CORE2 (from 1990 to 2007) and NCEP (2008 to 2010). Each of these variables was kriged over the spatial extent of the Flemish Pass area and the resulting predictions extracted for each image using the methods above.

Data analysis

Data preparation

The large number of rare taxa called for a data reduction scheme to focus the analyses on more abundant and reliably sampled taxa. Only taxa/morphotypes that contributed 1% or greater to the total abundance of any one transect were quantitatively assessed. The resulting taxon abundance by the sample matrix was $\log(X + 1)$ transformed, and Bray–Curtis similarity calculated in Primer v.6 (Clark and Gorley, 2006). Species-accumulation curves using the number of taxa and their abundances per photo were also generated in Primer.

Spatial autocorrelation

Spatial autocorrelation is particularly important to evaluate when analysing transect data, since the serial nature of this type of data can lead to small-scale autocorrelative effects, violating assumptions of data independence. Also, species richness and abundance data often exhibit spatial autocorrelation in the residuals of regression models, thus violating the assumption of independently distributed errors required for classical tests of significance of correlation or regression coefficients (Legendre and Legendre, 1998; Legendre *et al.*, 2002). Failure to account for spatial autocorrelation can lead to inflated rates of type I error due to wrongly estimated confidence intervals (Legendre *et al.*, 2002; Kissling and Carl, 2007), biased regression coefficients (Kissling and Carl, 2007), and can invert the effects of environmental variables on species distribution (Kühn, 2007).

Before data analysis, autocorrelation in the unmodified species richness (i.e. the number of taxa/morphotypes) and abundance data of the most abundant taxa (≥1% of total transect abundance) was assessed on each transect using Moran's *I* correlograms computed using the "correlog" function in package "ncf" in R statistical software (version 2.15.3; R Core Team, 2013). Following Fortin and Dale (2005), the resulting correlograms were used to describe any spatial patterns in the data. Second, correlograms were computed on the residuals of the species richness and abundance generalized linear models (GLMs) to determine whether the errors were independently distributed after GLM implementation (GLM methods described below). Significance of the Moran's *I* correlation coefficients at each distance class was assessed by computing 1000 permutations using the "resamp" argument in the correlog function. The correlograms were considered globally significant if at least one correlation coefficient was significant at the Bonferroni corrected level, $\alpha' = \alpha/k$, where k equals the number of distance classes, and α equals the 0.05 significance level (Legendre and Legendre, 1998; Fortin and Dale, 2005).

Influence of structure-forming sponge

The sponge taxa observed in our study were designated as "structure formers" based on a list provided by the ICES-NAFO Working Group on Deep-water Ecology (WGDEC) of 25 structure-forming deep-water sponge species known to occur in the North Atlantic between 200- and 1500-m depth (ICES, 2009). However, as the majority of sponge taxa observed in this study have not been identified below the family level, our designations may include non-structure-forming members of the families represented in the ICES list. For example, all morphotypes of the family Polymastiidae observed in this study were designated as "structure formers", as they may represent any one of the three structure-forming *Polymastia* species listed in ICES (2009). None of the designated structure-forming sponges were present in the megafaunal taxa dataset comprising 1% abundance and greater. Structure-forming sponge abundance was used as a covariate in some analyses.

Sponge grounds were used as a factor in assessing their association with megafauna composition, diversity (species richness and Shannon diversity H'), evenness, and abundance. The definition of a sponge ground varies in the literature and often depends on gear type. For *in situ* photographic surveys, estimates of one sponge every 1–30 m^2 on sponge grounds have been reported (ICES, 2009). This definition was not adopted in our study, as sponges often exist in patches that may have been surveyed only in part in the photographic transects, thereby biasing the results when photos outside of the patches are considered within sponge grounds. In this study, entire transects or sections of transects with structure-forming sponges present in a continuous or semi-continuous fashion were classified as within a sponge ground. The spatial distribution of sponge grounds along the transects was examined using ArcMap.

Using R software, the species richness and abundance data were tested for normality and equal variances between sponge grounds and non-sponge grounds using the Shapiro–Wilk and Levene tests (Levene test in package "car"), respectively. Shannon diversity H' and Pielou's evenness J' were calculated for each photo in Primer and were subsequently tested for normality and equal variances in R as above. After all datasets failed to meet one or both assumptions, the non-parametric Wilcoxon rank sum test with continuity correction was applied to test for significant differences in these four variables between sponge grounds and non-sponge grounds. Differences in megafauna composition between these two groups was then tested using a one-way analysis of similarities (ANOSIM) based on Bray–Curtis similarity in Primer, and the taxa driving those differences were identified using the SIMPER (similarity percentages) routine. These two groups were further divided into four different classifications: (i) within sponge ground, sponge present; (ii) within sponge ground, sponge absent; (iii) outside sponge ground, sponge present; and (iv) outside sponge ground, sponge absent. ANOSIM was then used to determine differences in composition between these four groups.

Lastly, to assess whether sponge morphology had an effect on megafaunal composition, each structure-forming sponge taxon was classified into different morphological types, and a one-way ANOSIM was performed on the community data. Morphology categories were: (i) thin-walled/foliose, (ii) fan-shaped, (iii) massive/globular, and (iv) papillate/globular. Only two photos contained small/spherical sponges (*Craniella* sp.), and so this morphology type was not included. Photos without sponge or with a mix of sponge morphologies were also not included. This analysis will provide insight into the influence of the different structure-forming sponges which constitute the sponge grounds in shallower water (papillate/globular and fan-shaped) and in deeper water (massive/globular and thin-walled/foliose). SIMPER was then used to identify those taxa contributing most to the differences between the four different sponge morphology types.

Relative influence of structure-forming sponges on megafauna vs. other environmental variables

A GLM approach was used to determine the relative importance of structure-forming sponges against other environmental variables in determining patterns in megafaunal species richness and abundance. First, a Spearman's rank correlation coefficient matrix was created in R to determine the relationship between explanatory variables. As most of the variables were moderately to highly correlated, only very strongly correlated variables (Spearman's $\rho \geq 0.9$; Iman and Conover, 1983) were removed before analysis. When comparing strongly correlated variables, annual chlorophyll *a* was chosen to remain over others, as gradients in food supply have often been identified as the main factor in controlling changes in benthic biomass, diversity, distribution, and zonation (Levin *et al.* 2001; Carney, 2005; Soltwedel *et al.*, 2009; MacDonald *et al.*, 2010; Papiol *et al.*, 2012). The remaining explanatory variables included in the models were structure-forming sponge abundance, *in situ* water depth (m), *in situ* bottom salinity (psu), mean annual chlorophyll *a* (mg m^3), and mean temperature gradient (°C km).

GLMs were fitted and evaluated in R. Model fit was evaluated by examining diagnostic plots of the residuals generated by the plot function. For the species richness dataset, a full model was initially fitted containing all explanatory variables and their interactions. Overdispersion (φ) in the residuals of the final model was tested by dividing the generalized Pearson statistic χ^2 (squared sum of the Pearson residuals) by the residual degrees of freedom (Zuur *et al.*, 2009). If φ is greater than 1, overdispersion exists in the data. The megafauna abundance data, once rounded to the nearest integer, was initially fitted with a Poisson distribution and log link. However, a large overdispersion parameter and erroneous diagnostic plots led to the fitting of a negative binomial distribution with a log link function (package "MASS"). Following Zuur *et al.* (2009), optimal models always were found using the backward "step" function in R, with further fine-tuning using the hypothesis-testing function "drop1". The most parsimonious model was the one with the lowest Akaike Information Criterion (AIC).

The $\log(X + 1)$-transformed taxon abundance matrix was ordinated with principal components analysis (PCA) in Primer. As a visual aid, photos were labelled both according to whether they fell inside sponge grounds and also by depth class after photos were divided into arbitrary 200-m depth bins (400–600, 600–800, 800–1000, and 1300–1500 m). The scores of the two axes explaining the highest variation (PC1 and PC2) were extracted and used in bivariate regression against Structure-Forming Sponge Abundance and the other environmental variables. The strength and significance of the relationships were testing using Spearman's rank correlation.

Results

In total, 473 photos were analysed across all four transects, covering a total area of 293.2 m^2. Details of the number of photos analysed and the total area covered per transect are summarized in Table 1.

Table 1. Summary of photographic transects collected using Campod and the 4KCam in the Flemish Pass area.

	Position (dec. degrees)		Depth (m)							
Transect	Start (°N/°W)	End (°N/°W)	Min	Max	Mean ± s.d.	Gear	Transect length (m)	Number photos analysed	Total area covered (m^2)	Number of photos inside/ outside sponge grounds
28	47.2956/−47.0353	47.3038/−46.3452	461	479	474 ± 3.1	Campod	2 431	92	65.5	0/92
29	47.1241/−46.5415	47.1486/−46.5272	444	471	462 ± 4.7	Campod	3 197	132	94.0	132/0
30	47.1653/−46.5153	47.1817/−46.5895	455	940	699 ± 140.7	4KCam	6 101	174	81.3	109/65
38	46.1712/−47.0550	46.1849/−47.0353	1328	1 411	1 397 ± 11.7	4KCam	2 978	75	52.4	31/44

Position, depth (minimum, maximum, and mean ± s.d.), gear used, and transect length. Number of photos analysed, total area covered (m^2), and number of photos inside and outside of sponge grounds also shown.

Table 2. Abundance (standardized to m^2) and number of taxa/ morphotypes for each phylum observed in the Flemish Pass area.

Phylum/group	Total abundance	Number of taxa/ morphotypes
Annelida	1 145 (3.8)	9 (1.7)
Arthropoda	2 152 (7.2)	35 (6.6)
Brachiopoda	362 (1.2)	2 (0.4)
Chordata	1 973 (6.6)	12 (2.3)
Cnidaria	3 019 (10.1)	93 (17.6)
Echinodermata	6 983 (23.4)	34 (6.5)
Ectoprocta	512 (1.7)	8 (1.5)
Mollusca	483 (1.6)	24 (4.6)
Nemertea	28 (0.1)	6 (1.1)
Platyhelminthes	6 (0.02)	2 (0.4)
Porifera	11 091 (37.2)	182 (34.5)
Unidentified	2 072 (6.9)	120 (22.8)
Total	29 826	527
Tubes, filaments, tracks, casts, burrows, mounds	36 517	–

Numbers in brackets indicate the percentage of total.

In total, 29 826 individuals were recorded, representing 527 taxa and morphotypes (Table 2). A further 36 517 counts consisted of biogenic structures such as tubes, tracks, and casts. Of the 527 taxa and morphotypes designated, 120 could not be placed into a particular phylum and were classified as unidentified morphotypes. These represented 7% of the total biota observed. Eleven phyla were represented by the remaining 407 taxa/morphotypes that could be identified to some level. Sixty-six taxa/morphotypes were identified to the family level, whereas 43 were identified to the genus or species level. The Porifera, Echinodermata, and Cnidaria were the most abundant and diverse phyla across all transects, comprising 37, 23, and 10% of the total abundance and 182, 34, and 93 taxa/morphotypes, respectively (Table 2). The least abundant and speciose phylum was the Platyhelminthes, represented by two morphotypes and six individuals. The three most abundant taxa overall were the Ophiuroidea spp. ($n = 5198$), Porifera spp. ($n = 2603$), and soft corals of the family Alcyoniidae ($n = 1429$).

The taxa/morphotypes (herein referred to only as taxa) included in all further quantitative analyses are listed in Table 3 (constitute 1% abundance or more on any one transect). Of these 51 taxa, Ophiuroidea spp. were the most abundant on each of the four transects. Porifera spp. were also abundant and had the second highest abundance on transect 38 following Ophiuroidea spp. The number of taxa was highest on transect 29, followed by transect 30, whereas the mean abundance was highest on transect 38.

Species-accumulation curves of each transect (Figure 2) closely approached or reached the asymptote, suggesting that the amount of sampling was sufficient to describe the megafaunal communities within and among transects. Transects 29 and 30 had the steepest curves and closely approached the asymptote at ∼20 samples (photos). Transects 28 and 38, with fewer samples overall, approached the asymptote more slowly.

Spatial autocorrelation

On transects 28 and 29, Moran's *I* correlation coefficients were small and oscillated along the zero value for both species richness and abundance of megafauna (Figures 3 and 4, respectively), suggesting a random spatial pattern in both these parameters (Fortin and Dale, 2005). For these two transects, only the correlogram for abundance on transect 29 was globally significant at the α' level, where deviations occurred over one of the largest distance classes (2.6 km, mean distance in class) and hence is not of concern for the analyses undertaken. The correlogram for species richness on transect 38 had larger oscillations of Moran's *I* between positive and negative values, which is indicative of a patchy distribution. The abundance correlogram for this transect showed small positive values of Moran's *I* at small distances and small negative ones at larger distances. Both correlograms for transect 38 were globally significant but the deviations appear minor and reflective of a weak gradient in the data (at least for abundance). In contrast, the species richness and abundance correlograms for transect 30 showed significant positive values at short distances, and significant negative values at larger distances ranging from ∼0.5 to −1.0, indicative of a sharp gradient in the data. No spatial dependence was detected in the residuals of the GLM on species richness or negative binomial on abundance (correlograms not shown).

Structure-forming sponges and their influence on megafauna diversity, abundance, and composition

Structure-forming sponges were present in 99 of the 473 photos analysed (Table 4). The only member of the class Hexactinellida designated as a structure-forming sponge was a species of *Asconema* (family Rossellidae). Structure-forming members of the class Demospongiae included seven Polymastiidae morphotypes, Polymastiidae spp., *Geodia barretti*, *Geodia* sp., *Geodia* spp., *Craniella* sp., and Axinellidae spp. The most abundant taxon was Axinellidae spp., followed by *Asconema* sp. and Polymastiidae sp. 4. In terms of overall structure-forming sponge abundance, members of the family Polymastiidae dominated the three shallower transects (28–30; Figure 5). Axinellidae was the second most abundant taxon on these transects. The deepest transect (38) was

Table 3. Per cent abundance of the taxa/morphotypes that constitute 1% or more of the total abundance (standardized to 1 m^2) of any one transect.

			Transect			
Phylum	**Taxa/morphotypes**	**Description**	**28**	**29**	**30**	**38**
Annelida	Sabellidae (F.) sp. 3	Long tube (∼20 cm or more) with white to light-brown brachial plume. Often occurred in dense clusters anchored in soft substrate	2.8 (52.0)			
	Sabellidae (F.) sp. 12	Short tube (∼0.5 cm) with brown brachial plume. Often occurred in dense clusters anchored in soft substrate			3.0 (316.6)	
	Sabellidae (F.) spp.		2.4 (45.0)	2.1 (174.2)	2.6 (273.8)	
Arthropoda	*Meganyctiphanes norvegica*			4.5 (379.3)		
	Mysidae (F.) sp. 1	Small (∼0.5 cm), light-pink carapace with translucent lower body. Found close to bottom	1.0 (18.3)			
	Mysidae (F.) sp. 4	Slightly larger carapace than Mysidae sp. 1. Light-pink to orange carapace with translucent lower body. Found close to bottom	1.0 (18.3)			
	Pandalidae (F.) spp.		2.0 (36.5)			
	Malacostraca (C.) spp.				8.0 (840.8)	1.7 (154.3)
Brachiopoda	Brachiopoda (P.) spp.			1.0 (80.1)	2.6 (269.6)	
Chordata	Didemnidae (F.) sp.	Body form ranged from distinct individuals to fused colonies. Porous, with several large oral siphons when fused				4.6 (416.7)
	Ascidiacea (C.) sp. 2	Ovate-shaped, with single oral siphon. Smaller pores more conspicuous when large. Not colonial		1.8 (147.5)	3.5 (368.0)	6.7 (605.5)
	Ascidiacea (C.) spp.		3.2 (59.0)		1.0 (100.6)	
Cnidaria	Actiniaria (O.) sp. 1	Small (<0.5 cm), with orange oral disc and tentacles. Occurs in clusters on soft substrate	2.2 (40.7)			
	Actiniaria (O.) sp. 9	Large, whitish to light pink, with two rows of tentacles. Oral disc darker; purple when small, light pinkish when larger. Appears to be anchored directly in soft substrate		1.5 (122.2)		
	Actiniaria (O.) spp.		2.6 (47.8)	1.0 (81.5)		
	Tubularia sp.	Stem thin, with small light pink polyp at end. Found attached to underside of boulder	2.1 (39.3)			
	Hormathiidae (F.) spp.		1.8 (33.7)			
	Alcyoniidae (F.) spp.		3.4 (63.2)	8.2 (686.9)	6.4 (673.9)	
	Anthozoa (C.) spp.				1.0 (102.7)	
Echinodermata	*Psolus* spp.			4.7 (394.7)	5.0 (532.7)	
	Bourgueticrinida (O.) spp.				1.2 (124.1)	3.3 (299.7)
	Ophiuroidea (C.) spp.		33.8 (630.7)	13.9 (1 164.5)	12.7 (1 345.7)	22.9 (2 057.5)
Ectoprocta	Ectoprocta (P.) spp. [a]				1.7 (175.4)	1.1 (97.2)
Mollusca	Bivalvia (C.) spp.				1.0 (107.0)	
	Scaphopoda (C.) spp.				1.2 (126.2)	
Porifera	*Stylochordyla borealis*/ *Rhizaxinella* sp.[b]				2.3 (248.2)	
	Demospongiae (C.) sp. 6	Cushion, bright white in colour. Found encrusted on rocks	1.0 (18.3)			
	Demospongiae (C.) sp. 7	Ball-shaped to globular, whitish in colour. Osculum clearly visible when small; several pores visible when large. Possibly *Craniella* sp.		1.5 (125.0)	1.1 (119.8)	

Continued

Table 3. *Continued*

Phylum	Taxa/morphotypes	Description	Transect			
			28	29	30	38
	Demospongiae (C.) sp. 9	Encrusting. White to yellowish in colour, often translucent. Occurred on soft substrate		8.1 (677.1)	4.0 (425.7)	
	Demospongiae (C.) sp. 14	Cylindrical, sometimes pinched at osculum. White to pinkish in colour. Attached to rocks		1.1 (88.5)		
	Demospongiae (C.) sp. 16	Thin, encrusting sheets. Grey translucent. Occurred on soft substrate			1.8 (192.5)	
	Demospongiae (C.) sp. 36	Massive-globose, with many osculae visible. Found on soft substrate, and often partially covered with sediment				2.9 (261.5)
	Demospongiae (C.) sp. 38	Encrusting, bright Bellow. Occurred on soft substrate.				4.8 (427.7)
	Porifera (P.) sp. 4	Cushion/encrusting, in colour. Attached to rocks	7.4 (139.1)	2.9 (240.2)	1.0 (102.7)	
	Porifera (P.) sp. 26	Thin, encrusting on rocks. Sometimes observed partially covered in sediment	3.3 (61.8)	1.4 (118.0)		
	Porifera (P.) sp. 28	Small, globular. White in colour, and found on soft substrate	1.0 (18.3)	1.5 (123.6)	1.5 (156.2)	
	Porifera (P.) sp. 39	Small globose, translucent. Occurred on soft substrate	2.4 (45.0)	2.4 (205.1)	1.1 (117.7)	
	Porifera (P.) sp. 43	Small, globose. Whitish to grey in colour. Attached to rocks		1.8 (151.7)		
	Porifera (P.) sp. 57	Cushion, encrusting on rocks. Grey-translucent in colour	1.1 (19.7)			
	Porifera (P.) sp. 72	Very small, grey-translucent. Osculum sometimes visible. Occurred on soft substrate		1.8 (150.3)		
	Porifera (P.) sp. 78	Cylindrical, yellow in colour. Single osculum often visible at tip. Attached to small hard substrate, sometimes tipped over		2.1 (177.0)		
	Porifera (P.) sp. 96	Cushion, translucent white. Several large osculate visible. Found on both hard and soft substrate		1.0 (80.1)	1.0 (107.0)	
	Porifera (P.) sp. 99	Globular to sheet-like, white in colour. Occurred on soft substrate		1.3 (108.2)		
	Porifera (P.) sp. 257	Cylindrical-shaped, whitish in colour. Osculum at end often visible. Occurred on soft substrate				10.1 (908.8)
	Porifera (P.) sp. 266	Globular, yellow in colour. One osculum, with several pores visible. Occurred on soft substrate				1.4 (129.3)
	Porifera (P.) spp.		2.5 (46.4)	3.6 (300.6)	5.6 (596.9)	18.4 (1 658.8)
Unidentified	Unidentified 29	Orange in colour, oblong-shaped. Often partially covered in sediment. Possibly Bivalvia sp.	1.8 (33.7)	1.1 (88.5)	2.1 (222.5)	
	Unidentified 441	Translucent, scale-like. Attached to rocks and boulders	1.1 (19.7)			
	Unidentified 511	Flattened shape, white. Found in sediments. Could be member of Ectoprocta			1.1 (117.7)	
	Unidentified 889	Translucent base with possible tentacles attached. Occurs in clusters. Possibly Octocorallia sp.		2.7 (230.4)		

Continued

Table 3. *Continued*

Phylum	Taxa/morphotypes	Description	Transect 28	Transect 29	Transect 30	Transect 38
	Unidentified 1132	Grey, translucent. Web-like, stringy. Sometimes with large "pore" visible. Found attached to sediment or other organisms				6.2 (556.4)
		Total abundance of all taxa	1 867	8 397	10 571	8 995
		Mean abundance of 1% taxa (ind. m^{-2})	17	51	48	88
		Number of 1% taxa	33	44	41	33
		Number of rare taxa	95	238	235	146

Letters in brackets in Taxa column indicate the taxonomic level, where P, phylum; C, class; O, order; and F, family. Values in parenthesis are the total abundance. Empty cells indicate the absence of taxa on transect. Description provided for morphotype designations. Note than the mean abundance of 1% taxa (taxa/morphotypes that constitute 1% abundance) was calculated using the total number of individuals (unstandardized) divided by the total area covered per transect in Table 1. Rare taxa are those which constitute $<1\%$ total abundance on any one transect.
[a]Consistent with Bryozoa (Halanych, 2004).
[b]May include either or both species (Best *et al.*, 2010).

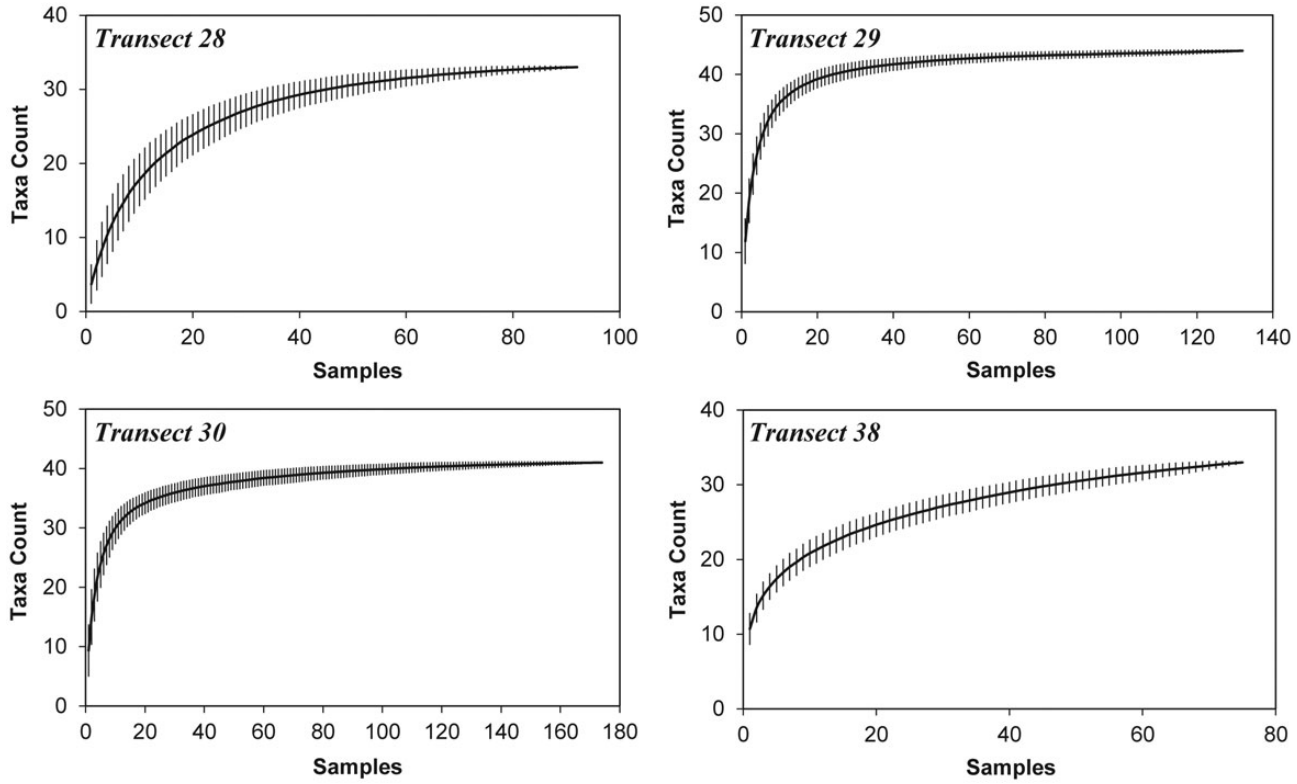


Figure 2. Species-accumulation curves for megafauna taxa/morphotypes identified from four photographic transects taken from the Flemish Pass area. Bars indicate the standard deviation.

dominated by *Asconema* sp. and Geodiidae members, with the latter occurring only on this transect.

The mean species richness and abundance of the megafauna significantly differed between sponge grounds and non-sponge grounds (richness: $W = 7944$, $p \leq 0.001$; abundance: $W = 11\,523$, $p \leq 0.001$), with sponge grounds having both a higher richness and abundance of megafauna (Figure 6). The mean Shannon diversity H' and Pielou's evenness J' were also significantly different between sponge grounds and non-sponge grounds (Shannon H': $W = 8001$, $p \leq 0.001$; Pielou's J': $W = 21\,060$, $p \leq 0.009$), with both indices being higher in sponge grounds compared with non-sponge habitat (Figure 6).

The composition of megafauna was significantly different between sponge grounds and non-sponge grounds (ANOSIM global $R = 0.36$, $p = 0.001$). Distinction between these two groups was indicated by a high SIMPER average dissimilarity (76.35%; Table 5). This dissimilarity was driven mainly by higher abundances of Porifera spp., Demospongiae 9, alcyoniid soft corals, and Ophiuroidea spp. in sponge grounds. Of the 22 taxa contributing to ~70% of the dissimilarity (Table 5), only a few

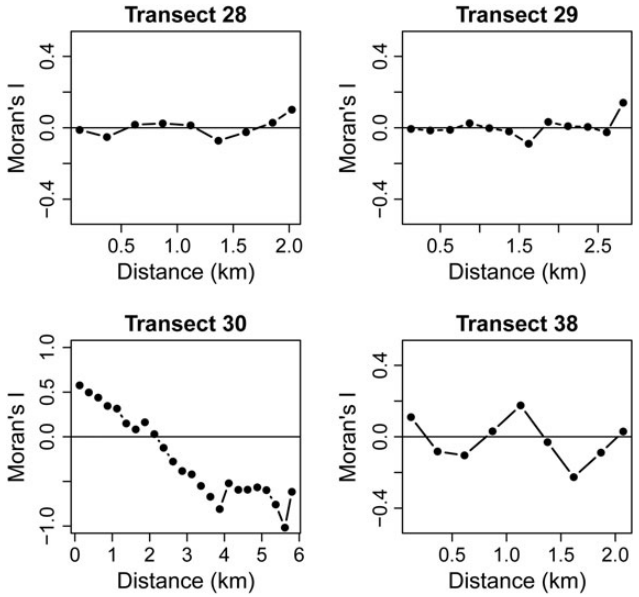


Figure 3. Spatial correlograms of megafauna species richness for each transect. Moran's *I* calculated for every 0.25 km.

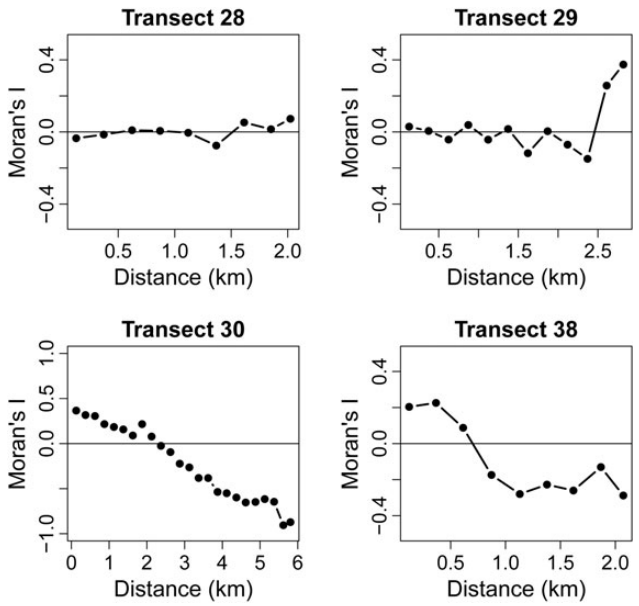


Figure 4. Spatial correlograms of megafauna abundance for each transect. Moran's *I* calculated for every 0.25 km.

were more abundant in non-sponge grounds: Malacostraca spp., Porifera 257, Didemnidae sp., and stalked crinoids of order Bourgueticrinida. All other taxa had higher abundances in sponge grounds. Of the taxa contributing to 100% of the dissimilarity (only 70% shown in Table 5), two taxa were exclusive to sponge grounds (Demospongiae 14 and Unidentified 889), whereas three were exclusive to non-sponge habitat (Actiniaria 1, Tubularia 1, and Unidentified 441).

Megafaunal composition significantly differed between the four different classifications of sponge ground presence/absence (ANOSIM global $R = 0.27$, $p = 0.001$). Pairwise comparisons indicated that the largest difference in megafaunal composition occurred between photos in sponge grounds with sponges present and photos outside of sponge grounds with sponges present ($R = 0.52$, $p = 0.001$). Within sponge grounds, there was no significant difference among photos with sponges present and those without ($R = 0$, $p = 0.479$), suggesting that the habitat effects of sponges on megafaunal composition within sponge grounds exceeds the photo ($\sim 1\ m^2$) scale.

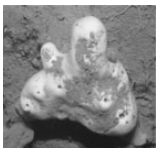
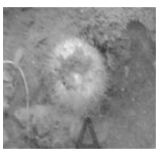
Significant differences in megafaunal composition between the four different structure-forming sponge morphologies were indicated by ANOSIM (global $R = 0.21$, $p = 0.001$; Table 6). The greatest separation in species composition occurred between massive/globular and fan-shaped sponges ($R = 0.83$, $p = 0.001$), which are constituents of the deep and shallow-water structure-forming sponge grounds, respectively. No significant differences were found between the dominant morphologies of the structure-forming sponges within the shallower (i.e. papillate/globular and fan-shaped sponges) and deeper sponge grounds (i.e., thin-walled/foliose and massive/globular; Table 6). This is consistent with the previous analysis that showed a strong habitat effect of the sponge ground itself. Several taxa that are associated with massive/globular sponges but are completely absent from fan-shaped sponges (Porifera 257, Demospongiae 38, and Demospongiae 36) drive the high dissimilarity (79.11%) between these two morphology types (Supplementary Table S1). The high dissimilarities between thin-walled/foliose sponges and both fan-shaped and papillate/globular sponges (70.56 and 68.25%, respectively, Supplementary Table S1) were mainly driven by higher abundances of Porifera spp. associated with thin-walled/foliose sponges.

Relative importance of structure-forming sponges on megafauna vs. other environmental variables

Although the entire Flemish Pass area was chosen as the final spatial extent over which environmental variables were kriged, we noted that the resulting surface prediction values and consequently, the GLM results, were sensitive to changes in the spatial extent of certain variables, especially Salinity. This did not affect the prediction errors of the surfaces, and so this issue was not transparent. For example, in our analysis, changes in the extent of the salinity data before kriging produced large changes in the deviance explained by this variable and other main effects and interactions in the GLMs. This is because the data were not spatially uniform within the spatial extent of the Flemish Pass, and therefore, salinity values located at the periphery greatly affected the kriged surface prediction values. Other variables that were more spatially uniform, such as those from the 1/12th degree model data, were not affected to the same degree. Various iterations of the GLMs were run to produce robust conclusions. However, the absolute values of the deviance explained by the models should be cautiously interpreted. We compared the *in situ* salinity data with the modelled data kriged over similar spatial extents in the GLMs and found similar deviance results. Because of this, and the knowledge that salinity is recognized as an important factor in determining patterns in benthic diversity and biomass (Cartes *et al.*, 2008; Papiol *et al.*, 2012), we chose to keep the *in situ* Salinity variable in the model.

The optimal GLM carried out on megafaunal species richness explained 63% of the total deviance in this variable (Table 7). Depth alone was not significant, but significant interactions between Depth and the other covariates, such as Salinity, were identified. The single term explaining the highest amount of deviance

Table 4. Classification, morphology type, representative, total abundance (standardized to 1 m^2), and transect observed of structure-forming sponges in the Flemish Pass area.

Class	Family	Morphology	Representative	Taxa	Total abundance	Transect observed
Hexactinellida	Rossellidae	Thin-walled/foliose		*Asconema* sp.	46.92	29, 30, 38
Demospongiae	Axinellidae	Fan-shaped		Axinellidae spp.	57.90	28, 29, 30
	Geodiidae	Massive/globular		*Geodia barretti*	11.40	38
				Geodia sp.	4.10	38
				Geodia spp.	9.60	38
	Tetillidae	Small/spherical		*Craniella* sp.	2.91	38
	Polymastiidae	Papillate/globular		Polymastiidae 1	2.81	28
				Polymastiidae 2	5.62	28, 29
				Polymastiidae 4	42.40	29, 30
				Polymastiidae 5	1.40	29
				Polymastiidae 6	6.35	29, 30
				Polymastiidae 7	6.54	29, 30
				Polymastiidae 10	3.47	38
				Polymastiidae spp.	26.36	28, 29, 30, 38

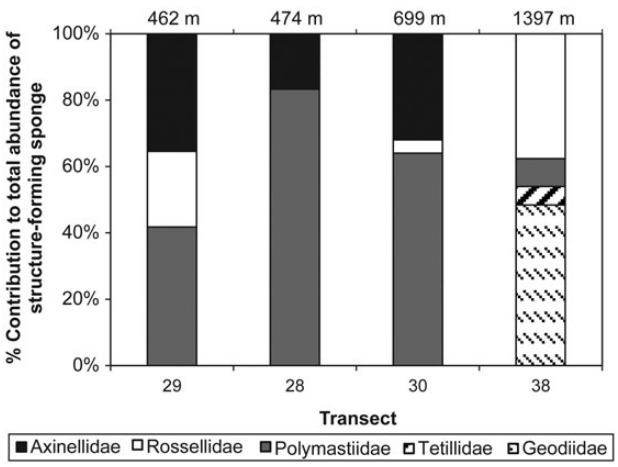


Figure 5. Contribution (per cent of total) to total abundance of structure-forming sponges on each transect. Order of transects is by increasing mean depth. Structure-forming sponges are grouped by family.

was Annual Chlorophyll *a* (35%), followed by Salinity (14%). Structure-Forming Sponge Abundance explained only 3% of the deviance in species richness, but was still a significant term. The interaction between Structure-Forming Sponge Abundance and Salinity was significant, but its interaction with Depth was non-significant.

The optimal model performed on the abundance of the megafauna explained 63% of the total deviance (Table 8). In contrast to the Species Richness model, Depth was significant and explained the second highest amount of deviance (14%). Annual Chlorophyll *a* explained the highest amount of deviance (22%), whereas Structure-Forming Sponge Abundance was significant and explained 5% of the deviance. Several interactions with Structure-Forming Sponge Abundance were significant.

Ordination of the megafauna abundance data with PCAs reduced the dimensionality of the data into five axes accounting for 50.6% of the variability (Table 9, Figure 7). The first two axes accounted for 36.7% of the variability in the abundance data. A plot of the photos against the first two axes showed a clear separation of photos on PC1 in the 1300–1500-m depth class (corresponding to transect 38) from the shallower depth classes/transects located in the upper Flemish Pass/slope of the Flemish Cap (Figure 7a). On PC2, there was great overlap between photos in the 400–600- and

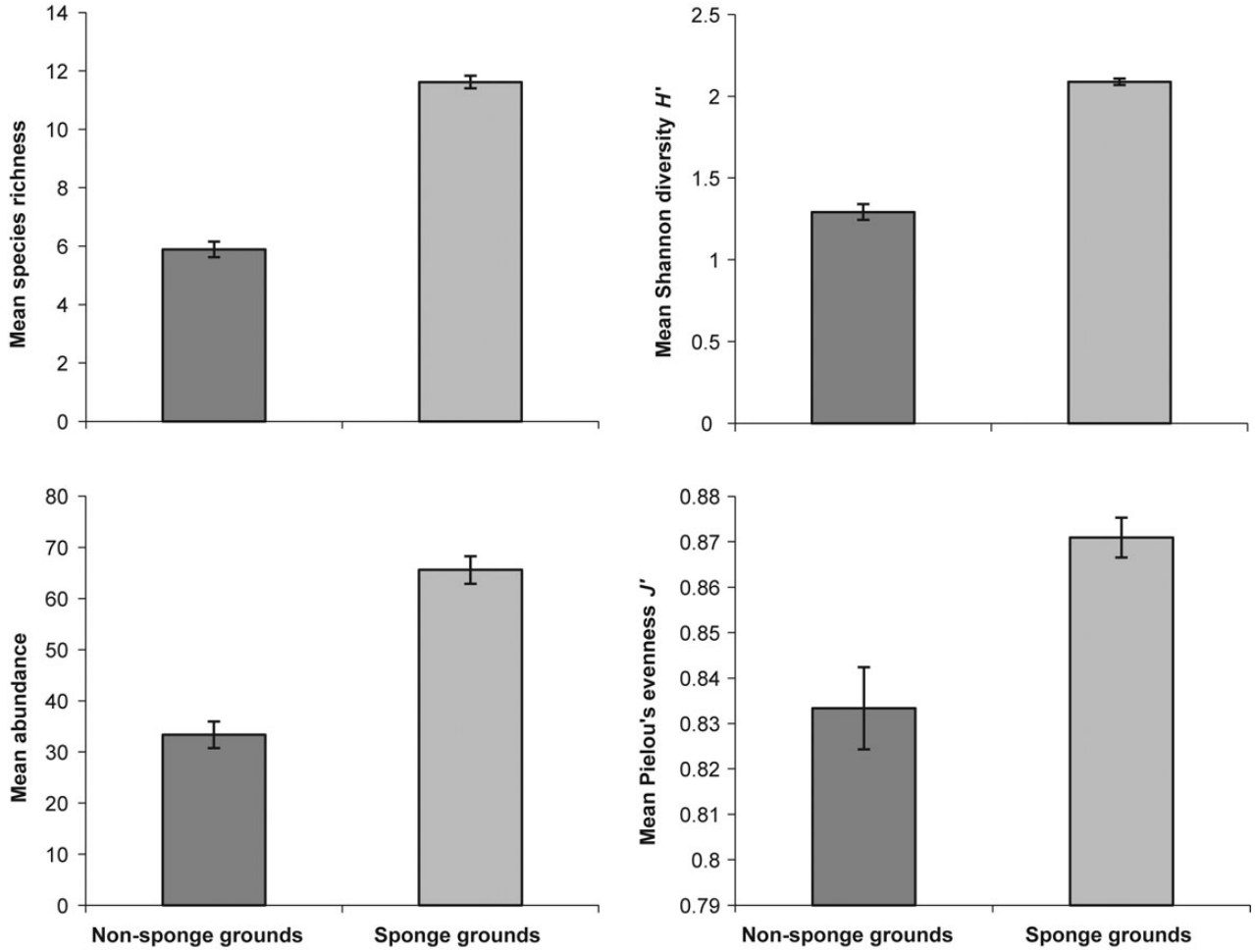


Figure 6. Mean species richness, mean abundance, mean Shannon diversity H', and mean Pielou's evenness per photo of megafauna (see Supplementary Table S1) within sponge grounds and non-sponge grounds. Error bars represent the standard error.

Table 5. Taxa contributing to 70% of the dissimilarity between sponge grounds and non-sponge grounds.

	Average abundance					
Taxa	Sponge grounds	Non-sponge grounds	Average dissimilarity	Dissimilarity/s.d.	Contribution (%)	Cumulative (%)
Porifera spp.	1.30	0.91	4.89	1.27	6.41	6.41
Demospongiae 9	1.20	0.14	4.60	1.11	6.03	12.43
Alcyoniidae spp.	1.23	0.20	4.45	1.16	5.83	18.26
Ophiuroidea spp.	2.21	1.94	4.09	1.08	5.36	23.63
Malacostraca spp.	0.68	0.75	3.71	0.91	4.86	28.49
Ascidiacea 2	0.83	0.44	3.30	0.92	4.32	32.80
Psolus spp.	0.76	0.03	2.80	0.72	3.67	36.47
Porifera 39	0.49	0.14	2.12	0.75	2.78	39.25
Unidentified 29	0.41	0.27	2.12	0.77	2.77	42.02
Sabellidae spp.	0.54	0.12	2.11	0.71	2.76	44.78
Porifera 257	0.31	0.42	1.92	0.56	2.51	47.30
Stylochordyla borealis/*Rhizaxinella* sp.	0.43	0.11	1.91	0.61	2.51	49.80
Didemnidae sp.	0.35	0.36	1.83	0.70	2.40	52.20
Brachiopoda spp.	0.44	0.13	1.79	0.69	2.34	54.54
Bourgueticrinida spp.	0.32	0.33	1.74	0.68	2.29	56.83
Unidentified 1132	0.28	0.37	1.71	0.59	2.24	59.07
Ectoprocta spp.	0.41	0.13	1.65	0.65	2.16	61.23
Porifera 4	0.35	0.16	1.61	0.55	2.10	63.34
Porifera 28	0.33	0.15	1.60	0.60	2.10	65.43
Demospongiae 7	0.41	0.05	1.60	0.68	2.09	67.52
Ascidiacea spp.	0.24	0.23	1.47	0.60	1.92	69.44
Porifera 78	0.41	0.01	1.46	0.64	1.92	71.36

Based on the $\log(X + 1)$ transformed species abundance matrix. Average dissimilarity = 76.35%.

Table 6. One-way ANOSIM testing the hypothesis of no significant difference in community composition among four different sponge morphology types and between pairs of morphology types.

Sponge morphology		
Global test: $R = 0.21$, $p = 0.001$		
Comparison group	***R* statistic**	***p*-value**
Thin-walled/foliose, massive/globular	0.09	0.120
Thin-walled/foliose, papillate/globular	0.13	0.021
Thin-walled/foliose, fan-shaped	0.27	0.001
Massive/globular, papillate/globular	0.42	0.001
Massive/globular, fan-shaped	0.83	0.001
Papillate/globular, fan-shaped	−0.01	0.571

600–800-m depth classes, although the separation of the photos from the 800–1000-m class was apparent. Although there was overlap between the two habitats, a clear transition between photos located inside sponge grounds and outside sponge grounds was apparent on PC2 (Figure 7b). Taxa with high positive loadings on the PC1 axis include three sponges (Porifera spp., Porifera 257, and Demospongiae 38), one unidentified taxon (Unidentified 1132), and two ascidians (Ascidiacea 2 and Didemnidae sp.), all of which are indicative of the deeper transect (Table 9). Alcyoniidae spp. and Demospongiae 9 had the highest negative loadings on both PC1 and PC2. The highest positive loading on PC2 was achieved by Malacostraca spp.

The PC1 community scores were most highly correlated with Annual Chlorophyll *a* and Depth (Table 10). The scores were positively correlated only with Depth and Structure-Forming Sponge Abundance and were negatively correlated with all other variables. The relationship between the PC1 scores and all explanatory variables was significant except for Structure-Forming Sponge Abundance, whose relationship with PC1 was negligible (Spearman's $\rho = 0.04$). The relationships between all explanatory variables and the PC2 scores were significant except for Structure-Forming Sponge Abundance. PC2 scores were most highly correlated with Salinity and Temperature Gradient (negative correlations; Table 10). Structure-Forming Sponge Abundance explained a higher amount of variability in PC2 compared with PC1 (Spearman's $\rho = -0.33$).

Discussion

Sponge grounds have only been recently recognized as important drivers of biodiversity and ecological function in deep-sea ecosystems (Hogg *et al.*, 2010). Generally, as depth increases along the continental margin, the availability of hard substrate and thus habitat complexity decreases (Buhl-Mortensen *et al.*, 2010, and references therein). The presence of sponges increases the number and complexity of microhabitats in an otherwise homogeneous environment. Increased habitat complexity has been shown to result in higher diversity and abundance of local fauna by increasing surface area for settlement, increasing niche availability, and decreasing competition among organisms (Tissot *et al.*, 2006; Wulff, 2006; Buhl-Mortensen *et al.*, 2010). Despite increasing awareness of the presence of sponge grounds in the Northwest Atlantic (ICES, 2009; Murillo *et al.*, 2012) and their importance in maintaining biodiversity (Hogg *et al.*, 2010), little quantitative data exist on how the habitat formed by these organisms, especially at small spatial scales, influence the surrounding megafaunal community.

Table 7. Analysis of deviance results of the GLM performed on megafauna species richness (Poisson distribution, log link).

Variables	**Explained deviance**	**Residual deviance**	**% Explained**	**Pr(>Chi)**
NULL		1 236.22		
Depth	1.72	1 234.50	0.14	0.189
Salinity	174.59	1 059.90	14.12	<0.001
Annual Chlorophyll *a*	427.28	632.62	34.56	<0.001
Temperature Gradient	0.88	631.74	0.07	0.349
Structure-Forming Sponge Abundance	34.99	596.75	2.83	<0.001
Depth × Salinity	67.59	529.16	5.47	<0.001
Depth × Annual Chlorophyll *a*	0.09	529.06	0.01	0.759
Salinity × Annual Chlorophyll *a*	1.55	527.51	0.13	0.214
Salinity × Temperature Gradient	10.39	517.13	0.84	0.001
Annual Chlorophyll *a* × Temperature Gradient	20.61	496.52	1.67	<0.001
Depth × Structure-Forming Sponge Abundance	3.37	493.15	0.27	0.066
Salinity × Structure-Forming Sponge Abundance	12.54	480.61	1.01	<0.001
Annual Chlorophyll *a* × Structure-Forming Sponge Abundance	0.49	480.12	0.04	0.485
Temperature Gradient × Structure-Forming Sponge Abundance	0.47	479.65	0.04	0.493
Depth × Salinity × Annual Chlorophyll *a*	1.04	478.61	0.08	0.309
Salinity × Annual Chlorophyll *a* × Temperature Gradient	5.19	473.43	0.42	0.023
Depth × Salinity × Structure-Forming Sponge Abundance	0.15	473.28	0.01	0.699
Depth × Annual Chlorophyll *a* × Structure-Forming Sponge Abundance	3.23	470.05	0.26	0.072
Salinity × Annual Chlorophyll *a* × Structure-Forming Sponge Abundance	1.90	468.15	0.15	0.168
Salinity × Temperature Gradient × Structure-Forming Sponge Abundance	5.17	462.98	0.42	0.023
Annual Chlorophyll *a* × Temperature Gradient × Structure-Forming Sponge Abundance	0.09	462.89	0.01	0.764
Depth × Salinity × Annual Chlorophyll *a* × Structure-Forming Sponge Abundance	0.21	462.68	0.02	0.651
Salinity × Annual Chlorophyll *a* × Temperature Gradient × Structure-Forming Sponge Abundance	4.27	458.41	0.35	0.039
Total			62.92	

Table 8. Analysis of deviance results of the GLM performed on the abundance of megafauna (negative binomial distribution, log link).

Variables	Explained deviance	Residual deviance	% Explained	Pr(>Chi)
NULL		1 378.55		
Depth	191.12	1 187.43	13.86	<0.001
Salinity	96.22	1 091.21	6.98	<0.001
Annual Chlorophyll *a*	302.68	788.53	21.96	<0.001
Temperature Gradient	1.37	787.16	0.10	0.242
Structure-Forming Sponge Abundance	69.49	717.67	5.04	<0.001
Salinity × Annual Chlorophyll *a*	4.10	713.57	0.30	0.043
Salinity × Temperature Gradient	64.77	648.80	4.70	<0.001
Annual Chlorophyll *a* × Temperature Gradient	69.11	579.69	5.01	<0.001
Depth × Structure-Forming Sponge Abundance	4.14	575.55	0.30	0.042
Salinity × Structure-Forming Sponge Abundance	49.28	526.27	3.57	<0.001
Annual Chlorophyll *a* × Structure-Forming Sponge Abundance	0.36	525.92	0.03	0.550
Temperature Gradient × Structure-Forming Sponge Abundance	0.02	525.89	0.00	0.876
Salinity × Annual Chlorophyll *a* × Temperature Gradient	9.50	516.40	0.69	0.002
Salinity × Annual Chlorophyll *a* × Structure-Forming Sponge Abundance	0.01	516.39	0.00	0.937
Salinity × Temperature Gradient × Structure-Forming Sponge Abundance	1.17	515.22	0.08	0.279
Annual Chlorophyll *a* × Temperature Gradient × Structure-Forming Sponge Abundance	7.16	508.06	0.52	0.007
Salinity × Annual Chlorophyll *a* × Temperature Gradient × Structure-Forming Sponge Abundance	2.96	505.10	0.21	0.085
Total			63.36	

To our knowledge, our study may be the first quantitative assessment of the diversity and abundance of the megafauna associated with structure-forming sponges compared with non-sponge habitat in the Northwest Atlantic.

The sponge grounds observed in our study appeared to exist in patches over potentially large (~140 km) spatial scales, with the largest, densest, and most diverse patch occurring at mid-slope depths on the western Flemish Cap slope. Our results show that biodiversity and abundance of the local epibenthic megafauna is significantly enhanced on these sponge grounds compared with non-sponge ground habitat in the Flemish Pass/western Flemish Cap slope. Enhanced biodiversity associated with sponge habitat has also been observed in the Northeast Atlantic (Bett and Rice, 1992; Klitgaard, 1995), the Mediterranean (Bo *et al.*, 2012), the Pacific Ocean off British Columbia, Canada (Cook *et al.*, 2008), and the Weddell Sea, Antarctica (Kunzmann, 1996). The extent to which sponges create habitat may depend on several characteristics: surface features (Klitgaard, 1995), canal volume (Wulff, 2006), and the size of the sponge itself and ability to form dense aggregations (Tissot *et al.*, 2006). Our study focused only on the larger size class of fauna; therefore, we are unable to discuss the importance of sponge habitat for fauna living inside the canals of sponges, infauna found in surrounding sediments, and mobile organisms not clearly visible or adequately surveyed by photographic surveys. Many shallow-water or tropical studies have focused on the vast diversity of endofauna that live inside the intricate canals of their host, utilizing the continuous flow of suspended matter filtered from the water column, or feeding on the sponge itself (Wulff, 2006). Other studies have noted the influence of sponge habitat on the macro/infauna community (Bett and Rice, 1992; Barrio Froján *et al.*, 2012). Barrio Froján *et al.* (2012) examined the macro/infauna in and around an area closed to fishing by NAFO in the Sackville Spur, a sediment drift feature which marks the northern limit of the Flemish Pass, and found that community composition and relative abundances were greatly altered by the presence of dense sponge spicule mats. A similar result was also found by Bett and Rice (1992) in spicule mats of *P. carpenteri* in the Porcupine Seabight, Northeast Atlantic. The importance of structure-forming sponge grounds to the epibenthic megafauna community has only been highlighted in a few studies (e.g. Klitgaard, 1995; Bo *et al.*, 2012). Klitgaard (1995) recorded at least 242 epi- and infauna species associated with 11 demosponge species in deep waters off the Faroe Islands, Northeast Atlantic. The majority of these species were using the sponges as substrate (93% of the total number of taxa were epifauna). In large open areas dominated by soft sediments, epifauna are thought to utilize sponges for attachment sites, for protection from predators, and for increased food resources (Buhl-Mortensen *et al.*, 2010).

The composition of taxa significantly differed between sponge grounds and non-sponge grounds in our study. Furthermore, this influence was greater than that imposed by individual sponges over smaller (~1 m^2) spatial scales, since community composition was most similar within sponge grounds whether sponges were present in the photos or not. This suggests that the large structure-forming sponges, which shape the sponge grounds, modify the habitat in some way. This is presumably via current baffling and the concentration of food resources (Krautter *et al.*, 2006; Schlacher *et al.*, 2007). The majority of taxa were present in higher abundances in sponge grounds, suggesting that the sponge grounds have a concentration effect, at least for the more abundant taxa. The small number of taxa exclusive to sponge grounds suggests more facultative than obligate relationships between sponge associates and their hosts. Perhaps through our exclusion of the rarest taxa, we have missed important associations between sponge hosts and rare species, which may be more sensitive to the presence of biogenic habitat than common ones. Further studies comparing the composition of fauna within sponge grounds with that of the ambient background are required to understand the degree of association between associates and their sponge hosts (Klitgaard, 1995).

Echinoderms, in particular crinoids and ophiuroids, and non-structuring sponges are often found in high abundances in sponge grounds (Klitgaard, 1995; Barthel *et al.*, 1996; Henkel and Pawlik,

Table 9. Eigenvalues, per cent variation explained, cumulative variance all five principal component axes, and taxa loadings for the first two axes based on log-transformed megafauna abundances.

	Principal components				
	PC1	**PC2**	**PC3**	**PC4**	**PC5**
Eigenvalue	4.01	2.46	1.08	0.70	0.67
Variance explained (%)	22.7	13.9	6.1	4.0	3.8
Cumulative variance (%)	22.7	36.7	42.8	46.8	50.6
Taxa loadings					
Porifera spp.	0.465	−0.241			
Porifera 257	0.411	0.015			
Unidentified 1132	0.344	0.008			
Ascidiacea 2	0.312	−0.216			
Demospongiae 38	0.281	0.016			
Didemnidae sp.	0.279	−0.049			
Ophiuroidea spp.	0.253	−0.125			
Bourgueticrinida spp.	0.215	−0.036			
Demospongiae 36	0.185	0.02			
Porifera 266	0.125	0.005			
Malacostraca spp.	0.086	0.041			
Ectoprocta spp.	0.08	−0.097			
Ascidiacea spp.	0.024	−0.012			
Tubularia 1	−0.001	−0.001			
Demospongiae 16	−0.002	−0.096			
Sabellidae 12	−0.005	−0.117			
Unidentified 441	−0.005	0.005			
Demospongiae 6	−0.006	0.001			
Sabellidae 3	−0.006	−0.015			
Porifera 57	−0.008	−0.03			
Scaphopoda spp.	−0.008	−0.017			
Actiniaria 1	−0.009	0.024			
Hormathiidae spp.	−0.009	0.006			
Unidentified 511	−0.01	−0.038			
Demospongiae 14	−0.012	−0.042			
Anthozoa spp.	−0.015	−0.027			
Porifera 99	−0.015	−0.114			
Porifera 26	−0.017	−0.062			
Mysidae 4	−0.018	−0.003			
Sabellidae spp.	−0.021	−0.215			
Bivalvia spp.	−0.023	−0.094			
Mysidae 1	−0.024	−0.01			
Stylochordyla borealis/ *Rhizaxinella* sp.	−0.025	−0.076			
Porifera 96	−0.026	−0.049			
Pandalidae spp.	−0.029	−0.041			
Meganyctiphanes norvegica	−0.03	−0.016			
Unidentified 29	−0.03	−0.037			
Demospongiae 7	−0.031	−0.176			
Porifera 43	−0.039	−0.062			
Porifera 72	−0.04	−0.084			
Brachiopoda spp.	−0.041	−0.159			
Unidentified 889	−0.043	−0.159			
Porifera 28	−0.044	−0.08			
Actiniaria spp.	−0.047	−0.086			
Actiniaria 9	−0.049	−0.07			
Porifera 78	−0.05	−0.191			
Porifera 4	−0.061	−0.162			
Psolus spp.	−0.068	−0.359			
Porifera 39	−0.069	−0.109			
Demospongiae 9	−0.079	−0.399			
Alcyoniidae spp.	−0.156	−0.527			

Data are sorted by descending values on PC1.

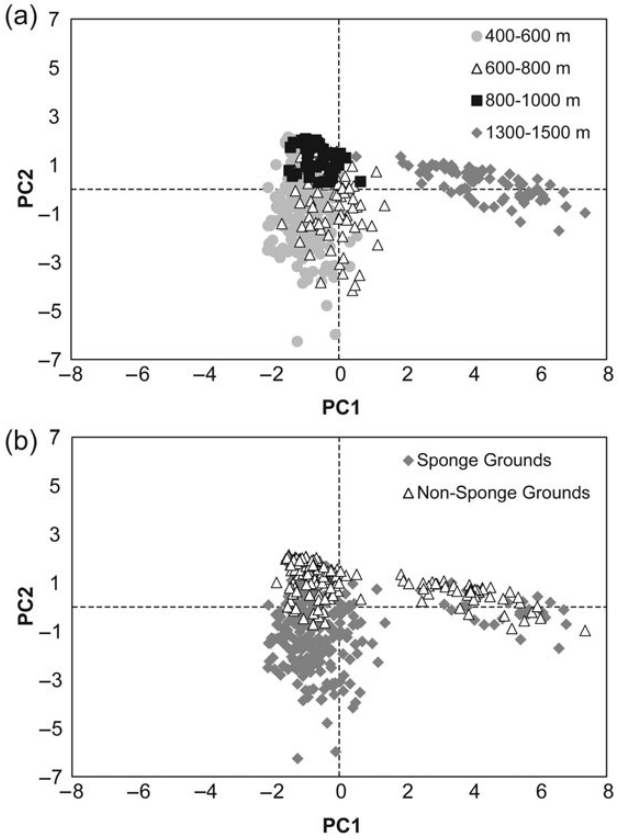


Figure 7. PCA of log-transformed megafaunal abundance data. Images are labelled by (a) depth class and (b) according to whether they fall inside or outside of sponge grounds. PC1 accounts for 23% of the variation, and PC2 accounts for 14%. Loadings of the megafauna on both PC1 and PC2 can be found in Table 9.

Table 10. Spearman's ρ and significance of correlation between environmental explanatory variables and PC1 and PC2 scores generated from the PCA analysis on log-transformed megafaunal abundances.

	PC1		**PC2**	
Variable	**Spearman's ρ**	***p*-value***	**Spearman's ρ**	***p*-value***
Depth	0.62	<0.001	−0.31	<0.001
Structure-Forming Sponge Abundance	0.04	0.433	−0.33	<0.001
Salinity	−0.41	<0.001	−0.51	<0.001
Annual Chlorophyll *a*	−0.64	<0.001	0.09	0.055
Temperature Gradient	−0.43	<0.001	−0.57	<0.001

*p-value reported is approximate due to the presence of ties. $\alpha = 0.05$.

2005). In our study, Ophiuroidea taxa were present in both habitats, although they were more abundant in sponge grounds. Perhaps, the feeding type of sponge-associated ophiuroids differs from those in

non-sponge habitat, where suspension feeders are more commonly found in association with sponges, and deposit feeders on open sediments. The higher abundances of Porifera spp. on sponge grounds contributed most to the differences between the two habitats. Other studies have reported close associations between structure-forming sponges and other sponge taxa, such as encrusting (Klitgaard, 1995) and stalked species (Barthel *et al.*, 1996). The most diverse sponge grounds documented to date consisting of multispecies assemblages occur in Faroese waters (ICES, 2009). In these grounds, *Geodia* and *Stryphnus* species dominate, while other structure-forming and non-erect sponges are present in high abundances.

Multispecies assemblages of sponges may form in areas where particular environmental conditions occur. Murillo *et al.* (2012) observed sponge grounds to occur in areas with a narrow range of temperature (between 3.38 and 3.84°C) and salinity (34.85 and 34.90‰) along the slope of Grand Bank, Flemish Pass, and Flemish Cap. These results are similar to those reported for the distribution of "ostur" in the Northeast Atlantic (Klitgaard and Tendal, 2004). Klitgaard and Tendal (2004) discuss large aggregations of sponges in areas of presumed enhanced food supply resulting from resuspension by internal waves, whereas Rice *et al.* (1990) discussed an association between the distribution of *P. carpenteri* and enhanced near-bottom tidal currents. These conditions may enhance food supply and favour the accumulation of suspension feeding taxa. The highly zero-inflated nature of the structure-forming sponge abundance data prevented us from conducting any formal tests on the influence of environmental conditions on these organisms. Nonetheless, the presence of other suspension feeders in high abundances in sponge grounds (sponge morphotypes and alcyoniid soft corals) supports the assumption that conditions favourable to this feeding guild are present.

Several studies have noted the importance of sponge morphology on the composition, diversity, and abundance of associated species (Koukouras *et al.*, 1992; Klitgaard, 1995). For instance, Klitgaard (1995) noted a difference in the occurrence of epi- and infauna between demosponges of different morphologies, where infauna were found exclusively in axinellid sponges. Also, the largest number of epifauna taxa was present on sponge species with spicule "fur". In our study, we found significant differences in the composition of the megafauna between the four different sponge morphologies assigned. The strongest differences were between the massive/globular sponges and both the fan-shaped and papillate/globular sponges, but this likely reflects depth-related community differences as massive sponges were found only on the deepest transect where fan-shaped sponges were absent and papillate sponges occurred in low abundances. However, the significant differences between thin-walled/foliose and both the papillate/globular and fan-shaped sponges likely reflect actual influences of the different morphologies as these taxa co-occur on the same transects in our study. Thin-walled/foliose sponges typically had higher abundances of associated Porifera spp. than fan-shaped or papillate/globular sponges. We did not observe any unusual associations between *Asconema* sp. (i.e. thin-walled/foliose) and other unidentified sponges. Although they did not contribute greatly to the dissimilarity, we observed more Ophiuroidea spp. associated with thin-walled/foliose sponges than fan-shaped or papillate/globular sponges. In the photographs, we commonly observed ophiuroids on or inside the canals of *Asconema* sp. and around the rim or base of fan-shaped sponges. Several crinoids were observed attached to the upper portion of *Asconema* sp. This may be a tactic to increase their position in the water column where presumed higher flow rates occur (Buhl-Mortensen *et al.*, 2010), to utilize the continuous flow of suspended matter filtered from the water column by the sponge itself (Ilan *et al.*, 1994), or to collect particles accumulated on the poral sieves (Klitgaard, 1995). No ophiuroids were observed on top of, or inside the oscular cavities of massive geodiid sponges as observed by Klitgaard (1995), but some were observed partially hidden by the base of these sponges, which may represent a tactic to avoid predation.

Structuring of megafauna community by structure-forming sponges and other environmental variables

The dynamic physical environment of the Flemish Pass and slopes of Flemish Cap shapes the habitat for both the sponges and other megafauna observed in our study. GLMs showed a link between sponge grounds (abundance of structure forming sponge taxa) and increased biodiversity (as measured by species richness) and abundance of the local megafauna. Compared with other environmental correlates, however, the influence of the sponges was relatively small. Species richness on transect 30 on the western slope of Flemish Cap uniquely showed significant autocorrelation over scales of 0.25–6 km, consistent with the presence of a strong gradient correlated with depth. However, depth could not account for variation in species richness over larger scales in the GLMs where chlorophyll *a* and salinity were the most important determinants. Depth became more important in predicting patterns in megafaunal abundance and likely explains the strong gradient in this variable on transect 30.

Surface chlorophyll *a* concentration has been used to calculate particulate organic carbon (POC) and to estimate POC flux to the seabed (Loisel *et al.*, 2002; Johnson *et al.*, 2007). Variations in POC flux have often been linked to changes in the standing stock of deep-sea benthos (Johnson *et al.*, 2007; Wei *et al.*, 2010). In areas where POC to the seabed has been measured directly, there is a linear relationship between POC flux and the abundance of all major size classes of biota (Smith *et al.*, 2008), both of which decrease with increasing depth (Gage and Tyler, 1991; Rowe *et al.*, 1991; Rex and Etter, 2010). The relationship between diversity and surface productivity is not as clear. Several studies on macrofauna diversity patterns found positive correlations between POC flux and diversity (Tietjen, 1984; Cosson-Sarradin *et al.*, 1998), whereas others found relationships between POC flux and abundance, but not diversity (Paterson *et al.*, 1998). Bivariate regression indicated that both megafaunal abundance and species richness declined with increasing levels of surface chlorophyll *a* in our study. Levin *et al.* (2001) proposed several explanations as to why species diversity would decrease in areas with high productivity: (i) differential responses among species to increased nutrients, where a small number of opportunistic species increase in abundance, lowering evenness and diversity measures that incorporate it, (ii) faster rates of competitive exclusion, (iii) increased variability in productivity, which often occurs with higher levels of productivity, and (iv) physical stress from hypoxia related to an increase in oxygen demand. However, we cannot preclude the effects of lateral transport of productivity away from the location of the transects in this study.

Unlike in nearshore environments where steep gradients in temperature and salinity may occur, both these variables tend to vary little in the deep ocean environment (Thistle, 2003). Although the effect of salinity on megafauna species richness and abundance was significant, it varied less than 0.01 psu across our study region (34.896–34.903 psu). Papiol *et al.* (2012) found that, although

correlated with depth, temperature and salinity were important factors in controlling changes in composition, biomass, and diversity of megafauna assemblages in the middle slope of the Balearic Basin, Mediterranean. Narrow ranges in salinity have been correlated with suprabenthos-zooplankton biomass at bathyal depths in the Mediterranean (Cartes *et al.*, 2008), which may in turn affect the availability of food resources to the benthos. Variations in salinity may also reflect changes in water masses, which may also influence megafaunal boundaries (Flach *et al.*, 1998; Howell *et al.*, 2002; Arantes *et al.*, 2009). Water masses typically have unique hydrographic characteristics, such as speed of flow, temperature, salinity, and pH, and can thus influence food availability in the deep-sea benthic environment (Arantes *et al.*, 2009). The transects located on the slope of the Flemish Cap may be affected by different water masses than the transect lower in the Flemish Pass basin. The Labrador Current from the north bifurcates as it reaches the Flemish Pass, with the major branch flowing southward through the Pass as Slope Water Current to meet North Atlantic Current water at the southern slopes of the Grand Bank (Stein, 2007). This transports cold, relatively low salinity Labrador Slope water into the Pass (Colbourne and Foote, 2000). In the south the North Atlantic Current transports warmer, higher salinity water to the northeast along the slope of the Grand Bank and Flemish Cap, with waters pervading into the southern Flemish Pass (Colbourne and Foote, 2000). Examination of the modelled near-bottom salinity data averaged over the 20-year period indicated that waters in the southern Flemish Pass are more saline than those of the upper Pass where the slope transects lie, suggesting that the higher-saline waters of the North Atlantic Current pervade into deep waters in the southern Flemish Pass. Thus, differences in the composition, diversity, and abundance of the fauna on the southern transect may be related not only to depth, but to differences in the innate hydrographic characteristics between the two water masses within the Flemish Pass and their influence on food availability.

Annual chlorophyll *a* (negative correlation) and depth (positive correlation) had the greatest explanatory power in community structure among the environmental correlates with the first principal component. The second principal component served to separate the photos from the shallower depths (400–800) along a gradient negatively correlated with temperature gradient, salinity, and the abundance of structure-forming sponges. It is well recognized that community composition and abundance of epibenthic fauna exhibit clear changes as depth increases from the shelf to abyssal plains (Carney *et al.*, 1983; Gage and Tyler, 1991; Carney, 2005). This zonation is often attributed not to depth itself, but to various environmental parameters that are correlated with depth and may have more of a direct influence on species distributions, such as temperature, food availability, and bottom type (Carney, 2005). Carney (2005) suggested three global depth boundaries that mark gradual shifts in species composition: shelf-slope zone of transition (300–500 m), an upper slope depth (1000 m), and a lower slope zone of transition (2000–3000 m). However, these boundaries become less distinct as the depth range of individual species widen with increasing latitude and width of the continental margin (Carney, 2005). Boundaries in megafaunal assemblages between 400 and 700 m and around 1200 m were discussed by Hecker (1990), who stated that the near-universality of these boundaries suggests that parameters important for controlling zonation are likely associated with these depths. Our results indicate that the change in megafaunal composition with depth was gradual between ~400 and ~1000 m, although the assemblage was much more distinct between 800 and 1000 m from 400 to 800 m. The most distinct faunal transition occurred somewhere between ~1000 and ~1300 m with the community below 1300 m being markedly different from that shallower than 1000 m. The boundary in which abyssal fauna begin to replace bathyal has been described at ~1500 m (Carney, 2005). The low taxonomic resolution of the fauna observed between 1300 and 1500 m prevents us from determining whether they are indicative of abyssal taxa and therefore also negates this explanation for our observations. This depth class/transect was dominated by large numbers of an undetermined Porifera taxa and Ophiuroidea spp. Several taxa of stalked crinoids of the order Bourgueticrinida were also abundant and some families of this order, such as Bathycrinidae, are common on soft sediments in the deep ocean (Gage and Tyler, 1991).

Conclusion

In conclusion, our results indicate a diverse community of epibenthic megafauna in the Flemish Pass/western slope of the Flemish Cap. This community was dominated by large numbers of ophiuroids and sponges and is host to multispecies sponge grounds. Our results support an increased biodiversity (as measured by species richness and Shannon diversity) and abundance of megafauna associated with these sponge grounds compared with non-sponge grounds, consistent with the UNGA resolution 61/105. This controlling factor intercedes with mesoscale patterns (several km to ~140 km) of species richness influenced by chlorophyll *a* and salinity and of abundance largely determined by depth and chlorophyll *a*. The functional significance of sponge habitat to the biodiversity of the local megafaunal community indicates that efforts by NAFO to close areas dominated by sponge grounds to bottom-tending gears will serve to meet the conservation objectives of the UNGA Resolution 61/105.

Supplementary material

The following supplementary material is available at *ICESJMS* online: similarity of percentages (SIMPER) results of the taxa contributing to 70% of the dissimilarity in megafaunal composition among photos classified by four different sponge morphology types.

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