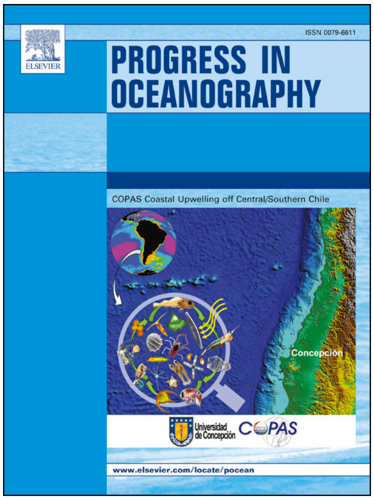

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Deep-sea sponge aggregations (*Pheronema carpenteri*) in the Porcupine Seabight (NE Atlantic) potentially degraded by demersal fishing

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Abstract

Deep-sea sponge aggregations are widely recognised as features of conservation interest and vulnerable marine ecosystems that may particularly require protection from the impact of commercial bottom trawl fishing. In 2011 we revisited deep-sea sponge aggregations in the Porcupine Seabight (NE Atlantic, c. 1200 m water depth) originally described by Rice, Thurston and New (1990, *Prog. Oceanogr.* **24**: 179-196) from surveys in 1983/4. Using an off-bottom towed camera system, broadly comparable to the bottom-towed system originally employed, we resurveyed four key transects detailed in that publication. In the intervening years, there has been a substantial increase in deep-water fishing activity; our primary objectives were therefore to establish the continued presence of *Pheronema carpenteri* (Hexactinellida, Pheronematidae), the current status of the sponge population, and whether there was any evidence of bottom trawl fishing impact on the sponges and their associated fauna. We noted a very substantial reduction in the standing stock of sponges: in Rice et al.'s (loc. cit.) peak abundance depth range (1210 – 1250 m) numerical density declined from 1.09 to 0.03 ind m^{-2}, and biomass density from 246 to 4 gwwt m^{-2}, between the surveys. Our assessment of available vessel monitoring data suggested that commercial bottom trawling had been occurring in the area, with some indication of focussed effort in the sponge's bathymetric range. We also recorded the presence of multiple apparent seafloor trawl marks on two of the transects. Despite the potential disturbance, the presence of sponge aggregations continued to exert a statistically significant positive influence on the diversity of the local megafaunal assemblage. Similarly, faunal composition also exhibited a statistically significant trend with *P. carpenteri* numerical density. Megafaunal numerical density, particularly that of ascideans, appeared to be enhanced in the core of Rice et al.'s (loc. cit.) peak abundance depth range potentially reflecting the residual effect of sponge spicule mats. Our observations were suggestive of a substantive impact by bottom trawl fishing; however, a definitive assessment of cause and effect was not possible, being hampered by a lack of temporal studies in the intervening period. Other causes and interpretations were plausible and suggested the need for: (i) a precautionary approach to management, (ii) an improved understanding of sponge natural history, and (iii) temporal monitoring (e.g. seafloor sponge habitat cover).

Graphical abstract

Will be added at a later stage of the submission.

Highlights

- Deep-sea sponge aggregations identified in the 1980s were resurveyed in 2011
- Sponge (*Pheronema carpenteri*) standing stocks had declined by an order of magnitude
- Seafloor trawl marks were observed in the sponge grounds
- Vessel monitoring data indicated commercial bottom trawling effort in the area
- Without protection this deep-sea habitat, and its species, may continue to decline

Keywords

Sponges; Deep water; Bottom trawling; Zoobenthos; Nature conservation; Vulnerable marine ecosystem; NE Atlantic; Porcupine Seabight; bathyal zone

1. Introduction

The first deep-sea sponge aggregations to be highlighted were those discovered in 1868 from HMS *Lightning* at about 1000 m water depth just to the south of the Wyville Thomson Ridge, NE Atlantic (Thomson, 1873). These aggregations, originally described as the "*Holtenia* Ground", were found to support a high associated biological diversity (Thomson, 1869). "*Holtenia"* is the glass sponge now known as *Pheronema* (Hexactinellida). The UK National Oceanography Centre (as the Institute of Oceanographic Sciences) undertook extensive surveys of the Porcupine Seabight, SW of Ireland, between 1977 and 1986 (Rice et al., 1991). These included the discovery and description of dense aggregations of *Pheronema carpenteri*, centred around 1200 m water depth (Rice et al., 1990). Subsequently, the sponge spicule mat habitat from the core of the sponge aggregation (c. 1240 m water depth) was found to be associated with substantially increased macrofaunal abundance and diversity (Bett and Rice, 1992). Rice et al. (1990) estimated a maximum *Pheronema* numerical density of 1.5 ind m^{-2} and a biomass density of c. 400 gwwt m^{-2} and suggested local enhancement of bottom water currents as the probable cause of the mass aggregations. *P. carpenteri* is now known to form aggregations on various NE Atlantic slopes and banks (Narayanaswamy et al., 2013; McIntyre et al., 2016). Other large populations have been recorded: off Morocco (Barthel et al., 1996), Bay of Biscay (OSPAR, 2010), Cantabrian Sea (Sánchez et al., 2008), Greenland (Burton, 1928), Norway (Klitgaard and Tendal, 2004) and the Mid-Atlantic Ridge south of Iceland (Copley et al. 1996). Modelling the available presence data, Howell et al. (2016) indicated that water depth and bottom water temperature were the best predictors of the distribution of these *Pheronema* aggregations.

The presence of substantial sponge populations can increase local habitat complexity and may enhance ecosystem functioning by providing refugia to a wide range of organisms (Kenchington et al., 2013), substratum for sessile fauna, and habitat for an abundant and diverse associated fauna (Bett and Rice, 1992; Klitgaard, 1995; Beaulieu, 2001). As a result of their nutrient remineralisation role in carbon and silicon cycles (Maldonado et al., 2011; Rix et al., 2016), sponges may also contribute to pelagic-benthic coupling (Bell, 2008). Sponge habitats are often referred to as ecological "hotspots", areas of enhanced biological diversity (Beazley et al., 2015), and ecosystem function, and of potential importance to fisheries (Bailey et al., 2009; Hogg et al., 2010; Priede et al., 2011; Pham et al., 2015).

Sponge aggregations are considered to be vulnerable marine ecosystems (VMEs; UNGA, 2006; FAO, 2009), and are listed as “Threatened and/or Declining” habitats (OSPAR, 2008). Bottom trawl fishing has likely impacted European deep-sea habitats for over 100 years (Thurstan et al., 2010). The effects of bottom trawling on benthic communities are often direct and immediate, and may persist for decades (Clark et al., 2016; Huvenne et al., 2016). It is, therefore, likely that the benthic communities of many continental slope areas have already been significantly modified by bottom trawling (Roberts et al., 2000; Gage et al., 2005; Puig et al., 2012). Our understanding of these impacts is hampered by limited direct observations, knowledge gaps concerning the structure and function of deep-sea ecosystems, and natural variations in time and space (Glover et al., 2010; Ruhl et al., 2011; Levin and Sibuet, 2012; Vieira et al., 2019).

In the present study, we specifically reoccupy the key photo-transects reported by Rice et al. (1990) as the core of the *P. carpenteri* distribution in the Porcupine Seabight. Our aim was to assess the current status of the sponge aggregations using comparable photographic survey methods, the intervening decades having seen the development of a substantive deep-water trawl fishery in the region (Bailey et al. 2009). Specifically, we aimed to address the following questions: 1) Are *Pheronema* aggregations still a dominant habitat-forming feature at those sites? 2) If so, have they changed in character, e.g. standings stocks, body size distribution, etc.? 3) Is there any evidence of bottom trawling in the study area? 4) And specifically, is there evidence of potential trawl impact within our new survey data?

2. Material and Methods

2.1. Photographic surveys 1983/4

The surveys described by Rice et al. (1991) were undertaken using an IOS epibenthic sledge (see e.g. Gage and Bett, 2005), the design and operation of which is detailed by Rice et al. (1982). The sledge carried an IOS Mark IVa conventional film stills camera recording in half-frame 35 mm format (image c. 24 × 18 mm) and an IOS 10 J flashgun. The camera lens was located c. 80 cm above the seafloor level and angled 30° below the horizontal. The proximal 3/4 of the resultant oblique image was analysed, representing c. 1.0 m^2 (Rice et al., 1982). The sledge was operated by reference to an acoustic telemetry system, enabling the user to record seabed contact, camera activation, and in situ (calibrated) pressure. The sledge's geographic position was estimated by 'lay-back' calculation, i.e. a distance behind the towing vessel based on the length of wire deployed and the depth (from pressure) of the sledge. Consequently, geolocation is somewhat approximate, however, the depth of operation is well constrained and is used in the following comparative assessment.

2.2. Photographic survey 2011

Photographic transects were conducted in August 2011 from RRS *James Cook* cruise 062 (Ruhl, 2012), at four sites in the northern Porcupine Seabight (Fig. 1; Table 1), as previously surveyed during the Institute of Oceanographic Sciences Porcupine Seabight Benthic Biological Survey (Rice et al., 1990). The 2011 transects were carried out using the Wide-Angle Seabed Photography (WASP) off-bottom, towed camera system (Jones et al., 2009). WASP was towed at c. 0.5 knots, at about 1-3 m above bottom, by reference to an acoustic telemetry system. A vertically mounted, 35 mm film stills camera (Ocean Scientific International Limited Mk 7) was fitted during all deployments and augmented with an obliquely mounted digital stills camera (Kongsberg OE14-208); images from the latter were only used for qualitative assessment. The processed 35 mm film negatives were digitised to 4096 × 3112 pixels; all faunal analyses reported here are based on data derived from those digitised images. For quality control, images taken outside a 1-3 m altitude range were discounted from the analyses, as were those where the full seafloor area was not visible (e.g. as a result of flash shadowing or sediment resuspension). In the remaining 1713 images, covering c. 5500 m^2 seafloor area (Table 1), all invertebrate megafauna (body size > 1 cm; Bett, 2019) were identified to morphotype and counted. Specimen body size and seafloor area imaged were estimated from camera altitude and the known optical geometry of the camera system (Jones et al., 2007). Geolocation and water depth data for the camera platform were derived from an ultra-short baseline navigation transponder attached directly to the WASP vehicle (Ruhl, 2012).

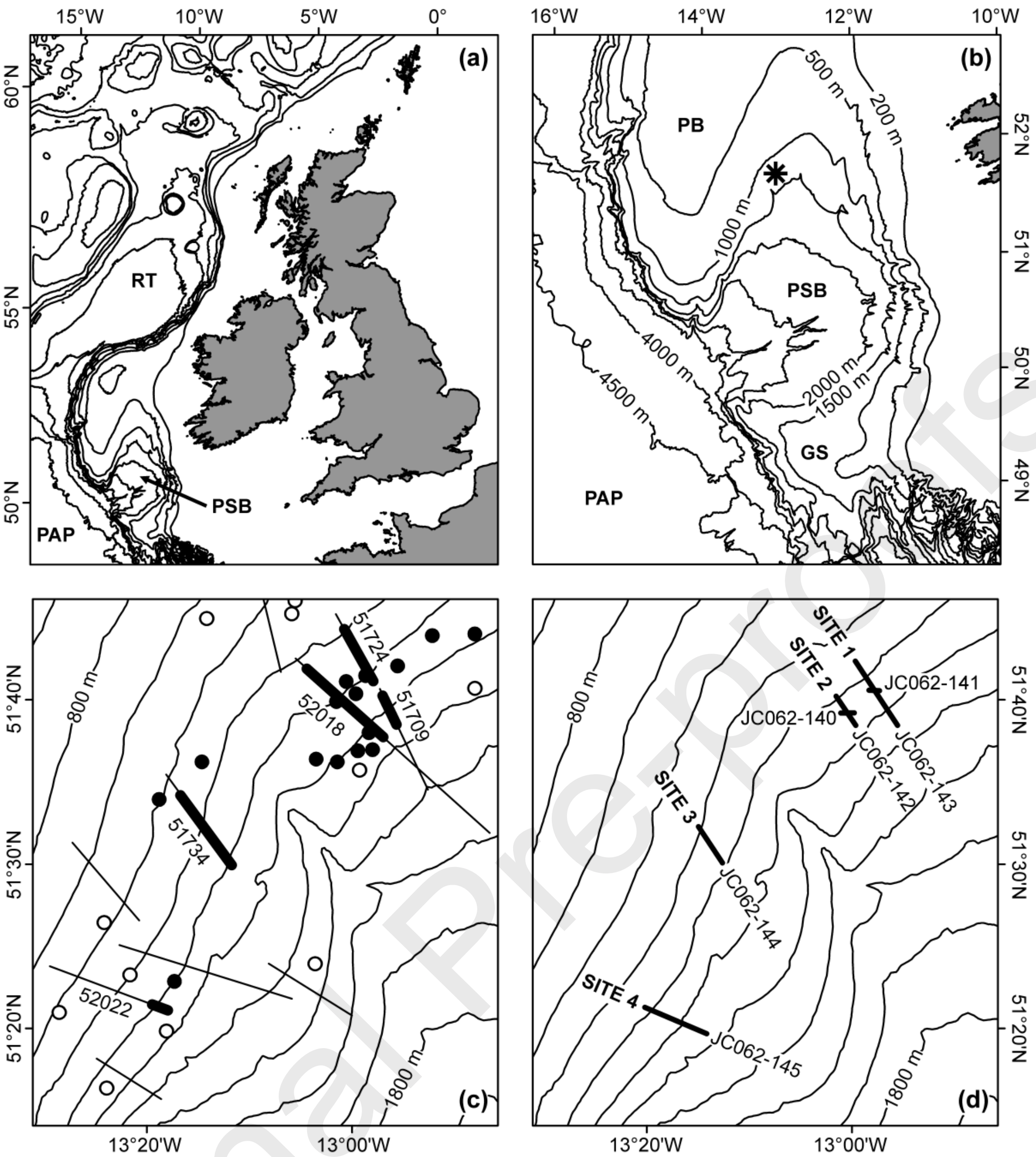

Figure 1. a) General location of the Porcupine Seabight (PSB; Porcupine Abyssal Plain, PAP; Rockall Trough, RT). b) General location of the study area (*) within the PSB (Porcupine Bank, PB; Goban Spur, GS). c) Locations of photosledge transects (lines) and other benthic samples (symbols) reported by Rice et al. (1990); solid symbols represent the presence and open symbols the absence of *Pheronema carpenteri*; thickened lines similarly mark the regions where *P. carpenteri* was present on transects (numbering, 5xxxx, refers to original station numbers). d) Location of the 2011 WASP camera system transects of the present study, with corresponding station numbers (JC062-xxx) and site names (SITE x). Mercator projection.<1.5 column>

Table 1. Details of the photographic transects undertaken in the present study (2011), with corresponding station numbers as occupied by Rice et al. (1990) in 1983/4.

Site	1983/4 station no.	2011 station no.	Water depth (m)	Central position		Vertical images assessed	Seabed area imaged (m^2)	Oblique images reviewed
				Latitude (°N)	Longitude (°E)			
1	51709/24	JC062-141	1236-1249	51.676	-12.962	90	243	-
1	51709/24	JC062-143	1203-1288	51.675	-12.963	353	1256	497
2	52018	JC062-140	1227-1249	51.653	-13.007	221	563	-
2	52018	JC062-142	1193-1266	51.656	-13.010	401	1183	37
3	51734	JC062-144	1114-1184	51.515	-13.224	389	1422	471
4	52022	JC062-145	1186-1246	51.350	-13.318	259	827	324

2.3. *Pheronema carpenteri*

The equatorial diameter of each observed specimen was measured and converted to estimated biomass using the equation provided by Rice et al. (1990): wet weight (g) = 0.0501 (diameter, cm)^3 + 27.9205. Sponge count and wet weight data from individual photographs were then compiled into 10 m bathymetric intervals and standardised to unit seabed area photographed. Differences in sponge numerical density and body size were assessed using the Wilcoxon paired sample signed-rank test and the two-sample Kolomogorov-Smirnov test respectively (e.g. Siegel and Castellan, 1988).

2.4. Megabenthos assemblage analysis

Composite samples were formed by pooling data from individual images, in depth order within site, to contain c. 100 individuals. This was done to achieve a similar level of accuracy and precision in morphotype diversity and composition measures across the sampling units (Durden et al., 2016; Benoist et al., 2019). Variations in faunal diversity, as Hill's diversity numbers N0 (species richness), N1 (exponential form of the Shannon index), and N2 (inverse form of Simpson's index), together with corresponding 95% confidence intervals, were estimated for a rarefied sample size of 100 individuals using the iNEXT R package (Hsieh et al., 2016). Although rarefied, interpretation of variations in diversity was complicated by covariation in the seabed area assessed resulting from variation in megafauna density with depth and Site (see Sections 3 and 4). Among individual composite samples, the seafloor area assessed varied from 22 to 290 m^2 (median 41 m^2, interquartile range 60 – 88 m^2). Consequently, we carried out some exploratory assessments by simple and partial non-parametric Spearman's rank correlation. Partial correlations were calculated using the R package 'ppcor' (Kim, 2015), and the p-values associated with the simple correlation values were adjusted for multiplicity using the false discovery rate method (Benjamini and Hochberg, 1995) in the R function 'p.adjust'. The relationships between diversity measures and the physical area of the sampling units indicated the need for caution in the interpretation of the diversity data (see Section 3). This was addressed by reference to the general case of the species-area-relationship, where a power function is thought to most appropriately describe that relationship (Dengler, 2009). Variations in diversity between sites were then assessed by an analysis of covariance incorporating that power function (i.e. log[number of taxa] ~ log[sampled area]) in a general linear model, as implemented in Minitab 18.1 (Minitab Inc.).

Variations in faunal composition were visualised by 2D non-metric multidimensional scaling (MDS) ordination following transformation of faunal density data to $\log(x + 1)$ and the calculation of Bray-Curtis similarities between samples. Follow-up investigations were carried out using Spearman's rank correlation to assess trends, and analysis of similarities (ANOSIM) to assess variation between sites and apparent levels of bottom trawling. The multivariate techniques were implemented using PRIMER (V6.1.11, Quest Research Ltd; Clarke and Gorley, 2006). We should here note that the process of forming composite samples involved depth ordering of images within site; consequently, the resultant composite samples do not represent independent replicates of a given site and so violate the underlying assumptions of ANOSIM. This process enabled the examination of bathymetric trends; however, the results of direct between-site comparisons should be viewed with some caution. Consequently, we examined variations for the full 2011 data set and for a restricted set that included data only from a common water depth range.

2.5. Bottom trawling indicators

Seafloor images, including the oblique digital stills (Table 1), were reviewed for any evidence of bottom contact fishing activity. We recorded the number of trawl marks, discerned as various forms of parallel lineations in the seafloor, which could be ascribed to the effects of bottom-towed fishing gear (e.g. Bett, 2000). In addition, we examined the recorded annual bottom fishing intensity data available for the area in the OSPAR Data and Information System (ODIMS; OSPAR, 2017). These data estimate swept area ratio, seafloor area trawled per year / seafloor area, at a grid of resolution of 0.05 × 0.05 degrees.

3. Results

Our initial observations of the seafloor photographs from the 2011 survey indicated that individuals and aggregations of a hexactinellid sponge consistent with *Pheronema carpenteri* were still present at the locations originally documented by Rice et al. (1990), and indeed were abundant at Site 4 where they were previously rare (Fig. 2). Accepting differences in the angle of view and the camera altitude, there were no obvious gross differences in the appearance of the sponges or the seafloor environment between the surveys conducted in 2011 and 1983/4 (or 1991; Rice, 1992; Bett and Rice, 1992).

3.1. *Pheronema carpenteri* 1983/4 versus 2011

Across commonly assessed 10 m depth intervals, 1110-1290 m, the geometric mean density of *Pheronema* appeared to have dropped c. 20-fold between the 1983/4 surveys and the 2011 survey. The geometric mean density in 1983/4 was 0.39 (95% CI 0.27-0.56) ind m^{-2}; in 2011 the geometric mean density for Sites 1-4 was 0.02 (0.01-0.05) ind m^{-2}, and for Sites 1-3 (most directly comparable with Rice et al., 1990) it was 0.02 (0.01-0.03) ind m^{-2}. When compared as samples paired by depth, across the commonly assessed 10 m depth intervals, Wilcoxon paired-sample signed rank tests of 1983/4 and 2011 suggested a highly significant difference ($V = 171$, $p < 0.001$) for both the Sites 1-4 and Sites 1-3 combined data (Fig. 3). A similar change in biomass density seems likely, although this cannot be formally assessed. Maximum recorded biomass declined by an order of magnitude between the 1983/4 and 2011 surveys (Table 2).

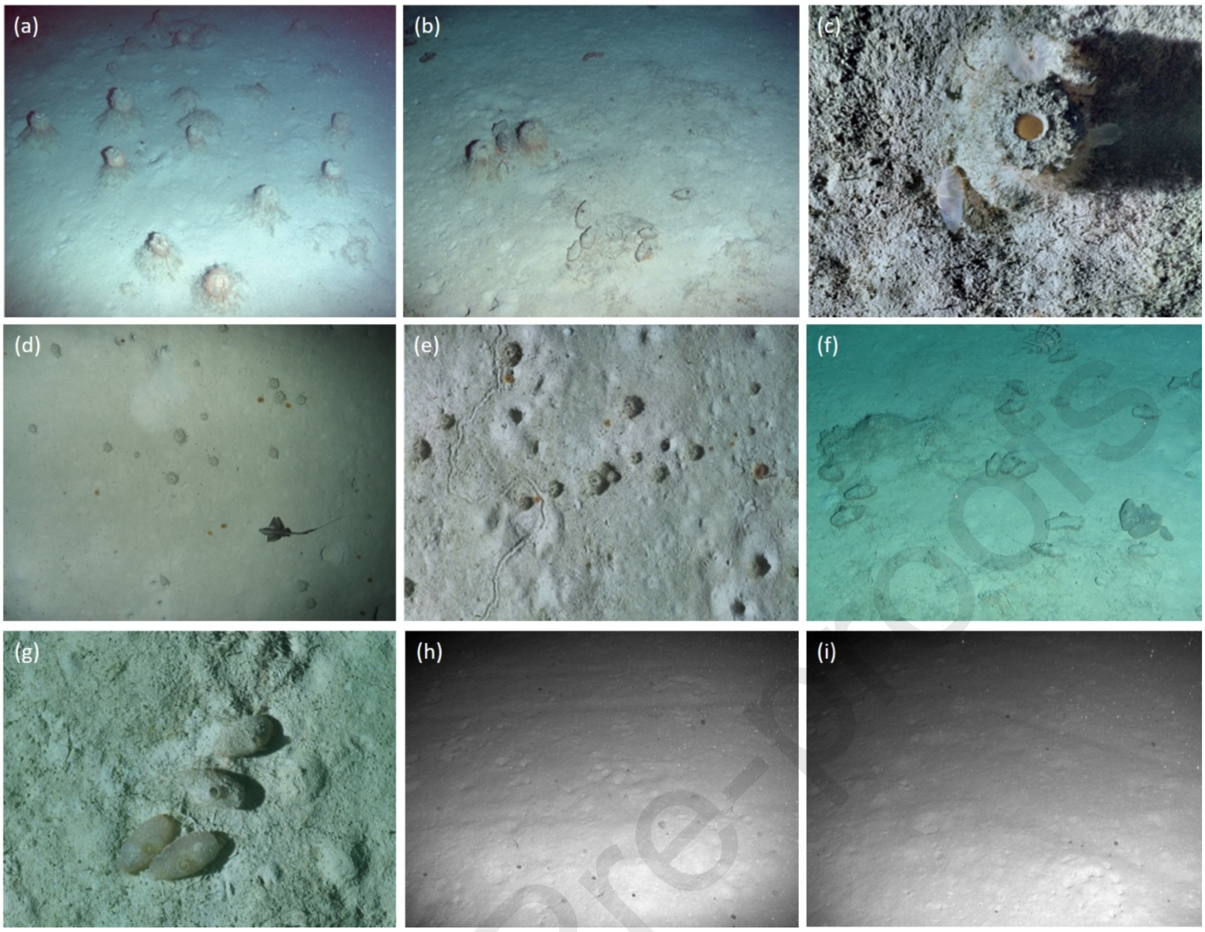

Figure 2. (a-e) Examples of *Pheronema carpenteri* observed in 2011 oblique and vertical images. (f, g) Examples of abundant large ascideans observed in 2011. (h, i) Examples of presumed seafloor trawl marks observed (at Site 4) in 2011.<2 column>

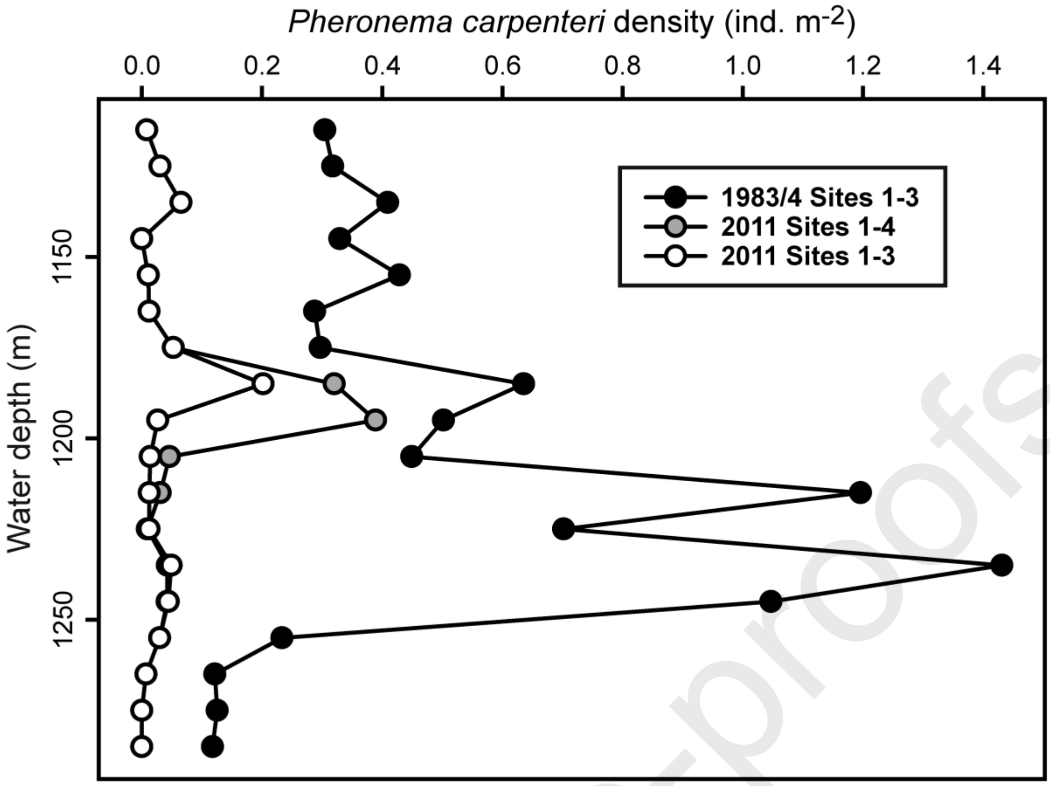

Figure 3. Variation in the numerical density of *Pheronema carpenteri* with water depth, in 10 m horizons, as recorded during 1983/4 and 2011 surveys.<1.5 column>

Table 2. Summary statistics of *Pheronema carpenteri* specimens assessed in the present survey, 2011, and during 1983/4 surveys by Rice et al. (1990).

	Site 1		Site 2		Site 3		Site 4
Survey	**1983/4**	**2011**	**1983/4**	**2011**	**1983/4**	**2011**	**2011**
Total specimens assessed	156	30	130	62	170	54	168
Overall mean diameter (cm)	17	12	13	14	16	14	5
Max. density in 10 m depth band (ind m^{-2})	1.60	0.04	1.40	0.07	0.80	0.20	0.64
Max. biomass in 10 m depth band (gwwt m^{-2})	453	4	204	16	199	14	21
Max. density in single image (ind m^{-2})	4.00	1.15	5.00	1.48	2.50	1.89	7.80
Max. biomass in single image (gwwt m^{-2})	1131	310	729	111	498	82	235

There was a substantial shift in the distribution of sponge equatorial diameters between the 1983/4 and the 2011 surveys (Fig. 4). Two-sample Kolmogorov-Smirnov tests of all 1983/4 data with 2011 data from Sites 1-4 ($D = 0.660$) and Sites 1-3 ($D = 0.296$) yielded statistically significant differences in both cases ($p < 0.001$). Similar results were returned when those comparisons were limited to the commonly reported range of equatorial diameters between

1983/4 and 2011 (5-23 cm); all 1983/4 data with all 2011 data from Sites 1-4 (D = 0.521) and Sites 1-3 (D = 0.277), with statistically significant differences in both cases ($p < 0.001$; Fig. 4).

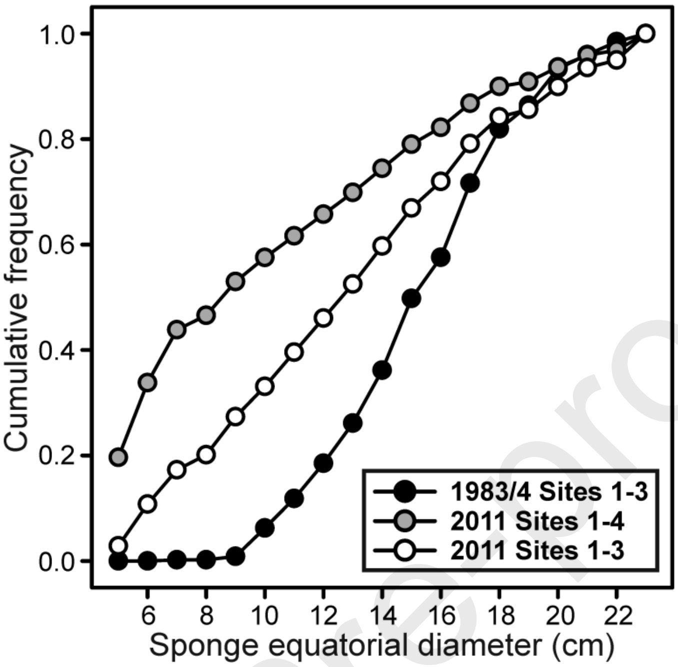

Figure 4. Size frequency distribution of *Pheronema carpenteri* as observed in 1983/4 and 2011 surveys. For presentation, sponge size range was truncated to the commonly observed range (5-23 cm diameter).<1 column>

3.2. Megafaunal diversity 2011

The patterns in rarefied diversity measures were somewhat complex (Fig. 5), with enhanced diversity at the shallower Site 3, and some indication of a common increase in diversity with water depth among the data from Sites 1, 2, and 4. In terms of simple correlations, assessed across all samples, sampled seabed area was substantially and statistically significantly positively correlated ($r_s = 0.58\text{-}0.78$, $p < 0.001$) with all three diversity measures (N0, N1, N2; Table 3). Note, however, that these relationships were not apparent when the data from individual Sites were assessed separately, i.e. the range in megafaunal density and therefore seabed area sampled was much reduced. Within individual Sites, there were appreciable and statistically significant positive correlations ($r_s = 0.45\text{-}0.71$, $p < 0.05$) between water depth and rarefied taxon richness (N0). The apparent relationship between *P. carpenteri* density and faunal diversity was complicated; across all Sites there was a statistically significant moderate negative correlation ($r_s = -0.37$, $p < 0.05$) with taxon richness (N0). In contrast, within Site 1, there were statistically significant strong positive correlations ($r_s = 0.82$-0.89, $p < 0.001$) between *P. carpenteri* density and the N1 and N2 diversity measures. When water depth, *P. carpenteri* density, and seabed area sampled were jointly assessed in partial correlations with the diversity measures, all diversity measures exhibited statistically significant strong positive partial correlations (${}_pr_s = 0.68$-0.78, $p < 0.001$) with seabed area sampled. All diversity measures also exhibited statistically significant moderate positive partial correlations (${}_pr_s = 0.29$-0.45, $p < 0.05$) with *P. carpenteri* density. In addition, water depth exhibited a statistically significant modest positive partial correlation ($r_s = 0.28$, $p < 0.05$) with rarefied taxon richness (N0).

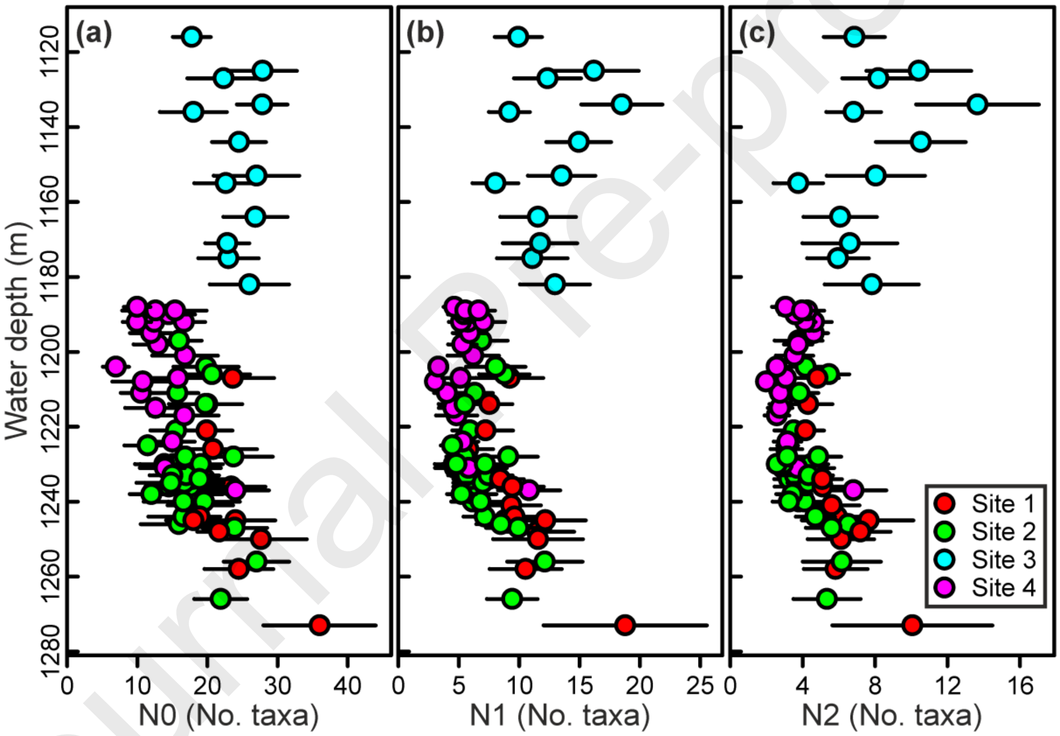

Figure 5. Variations in megafaunal assemblage diversity with water depth and Site observed in 2011 survey. Shown as Hill's diversity numbers: (a) N0 (species richness), (b) N1 (exponential Shannon index), and (c) N2 (inverse Simpson's index) rarefied to 100 individuals and illustrated with corresponding 95% confidence intervals.<1.5 column>

Table 3. Simple and partial Spearman's rank correlations between rarefied diversity measures (N_0, N_1, N_2) and potentially related variables (water depth, *Pheronema carpenteri* density, and sampled seabed area); adjusted p-values: * $p < 0.05$, *** $p < 0.001$.

		N_0 Species richness	N_1 Exponential Shannon	N_2 Inverse Simpson's
Simple correlation				
All sites (n = 77)	Water depth	0.091	0.052	-0.019
	P. carpenteri	**-0.364***	-0.215	-0.086
	Sampled area	**0.778*****	**0.709*****	**0.583*****
Site 1 (n = 15)	Water depth	**0.711***	0.579	0.475
	P. carpenteri	0.457	**0.825*****	**0.893*****
	Sampled area	-0.231	0.055	0.086
Site 2 (n = 31)	Water depth	**0.448***	0.294	0.180
	P. carpenteri	0.142	0.302	0.346
	Sampled area	-0.128	0.099	0.195
Site 3 (n = 12)	Water depth	**0.636***	0.643	0.455
	P. carpenteri	0.126	-0.189	-0.545
	Sampled area	0.387	0.352	0.169
Site 4 (n = 19)	Water depth	**0.574***	-0.007	-0.240
	P. carpenteri	0.318	-0.133	-0.291
	Sampled area	-0.418	0.163	0.431
Partial correlation				
All sites (n = 77)	Water depth	**0.278***	0.222	0.095
	P. carpenteri	**0.292***	**0.444*****	**0.448*****
	Sampled area	**0.777*****	**0.768*****	**0.685*****

Given the strong relationships between seabed area sampled and all three diversity measures, whether assessed by simple or partial correlation (Table 3), our subsequent analyses of between Site variations in diversity were undertaken with reference to covariation with seabed area sampled. In the case of rarefied species richness (N0), there was no statistically significant interaction between Site and sampled area (LM $F_{[3,69]} = 0.41$, $p = 0.748$), but a statistically significant relationship between richness and area (ANCOVA $F_{[1,72]} = 34.48$, $p < 0.001$), and a statistically significant effect of Site (ANCOVA $F_{[3,72]} = 5.49$, $p = 0.002$). Subsequent pairwise comparisons (5% Tukey) between Sites indicated statistically significant differences in richness in all comparisons with Site 4, but not in any other comparisons (Fig. 6). In the case of the exponential Shannon index (N1), there was no statistically significant interaction between Site and sampled area (LM $F_{[3,69]} = 2.42$, $p = 0.073$), but a statistically significant relationship between diversity and area (ANCOVA $F_{[1,72]} = 16.89$, $p < 0.001$), and a statistically significant effect of Site (ANCOVA $F_{[3,72]} = 7.42$, $p < 0.001$). Subsequent pairwise comparisons (5% Tukey) between Sites indicated statistically significant differences in diversity between Site 4 and Sites 1 and 3, but not Site 2 (Fig. 6). In the case of the inverse Simpson's index (N2), there was a statistically significant interaction between Site and sampled area (LM $F_{[3,69]} = 3.75$, $p = 0.015$). Consequently, between Site comparisons were limited to a one-way ANOVA, which indicated a statistically significant effect of Site (Welch's test $F_{[3,30.3]} = 19.23$, $p < 0.001$). Subsequent pairwise comparisons (Games-Howell 5%) indicated statistically significant differences in diversity between Site 4 and Sites 1 and 3, but not Site 2 (Fig. 6).

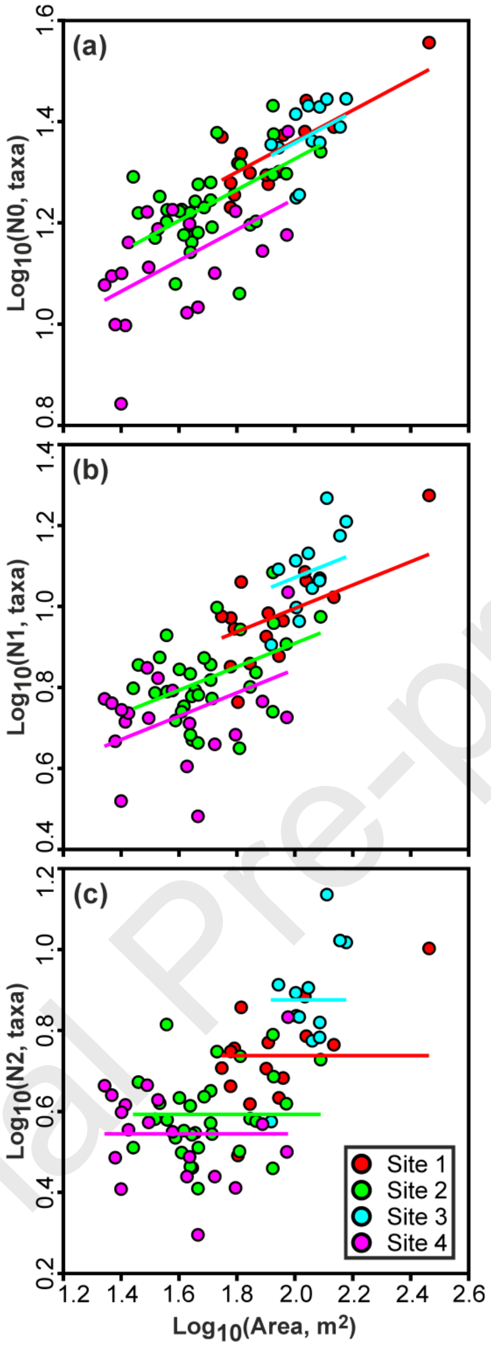

Figure 6. Summaries of ANCOVA (a, b) and ANOVA (c) assessments of variations in megafaunal assemblage diversity with seafloor area surveyed and Site in 2011. Illustrated as Hill’s diversity numbers: (a) N0 (species richness), (b) N1 (exponential Shannon index), and (c) N2 (inverse Simpson's index) for samples of c. 100 individuals, shown with trend lines by Site.<1 column>

3.3. Megafaunal assemblage composition 2011

Ordination of the full set of composite samples demonstrated an obvious separation of all four Sites in terms of assemblage composition (Fig. 7a). Additional exploratory analyses also indicated statistically significant trends in the ordination scores with key variables: Spearman's rank correlations between MDS y-ordinate and *Pheronema* density ($r_s = 0.613$, $p < 0.001$; Fig. 7b) and between MDS x-ordinate and water depth ($r_s = 0.680$, $p < 0.001$; Fig. 7c). A global ANOSIM test confirmed the initial visual assessment of the ordination, indicating substantial, statistically significant variation in assemblage composition between Sites ($R = 0.738$, $p < 0.001$), with follow-up pairwise tests suggesting modest, statistically significant differentiation of Sites 1 and 2 ($R = 0.272$, $p < 0.001$), and substantial, statistically significant differentiation in all other cases ($R > 0.697$, $p < 0.001$).

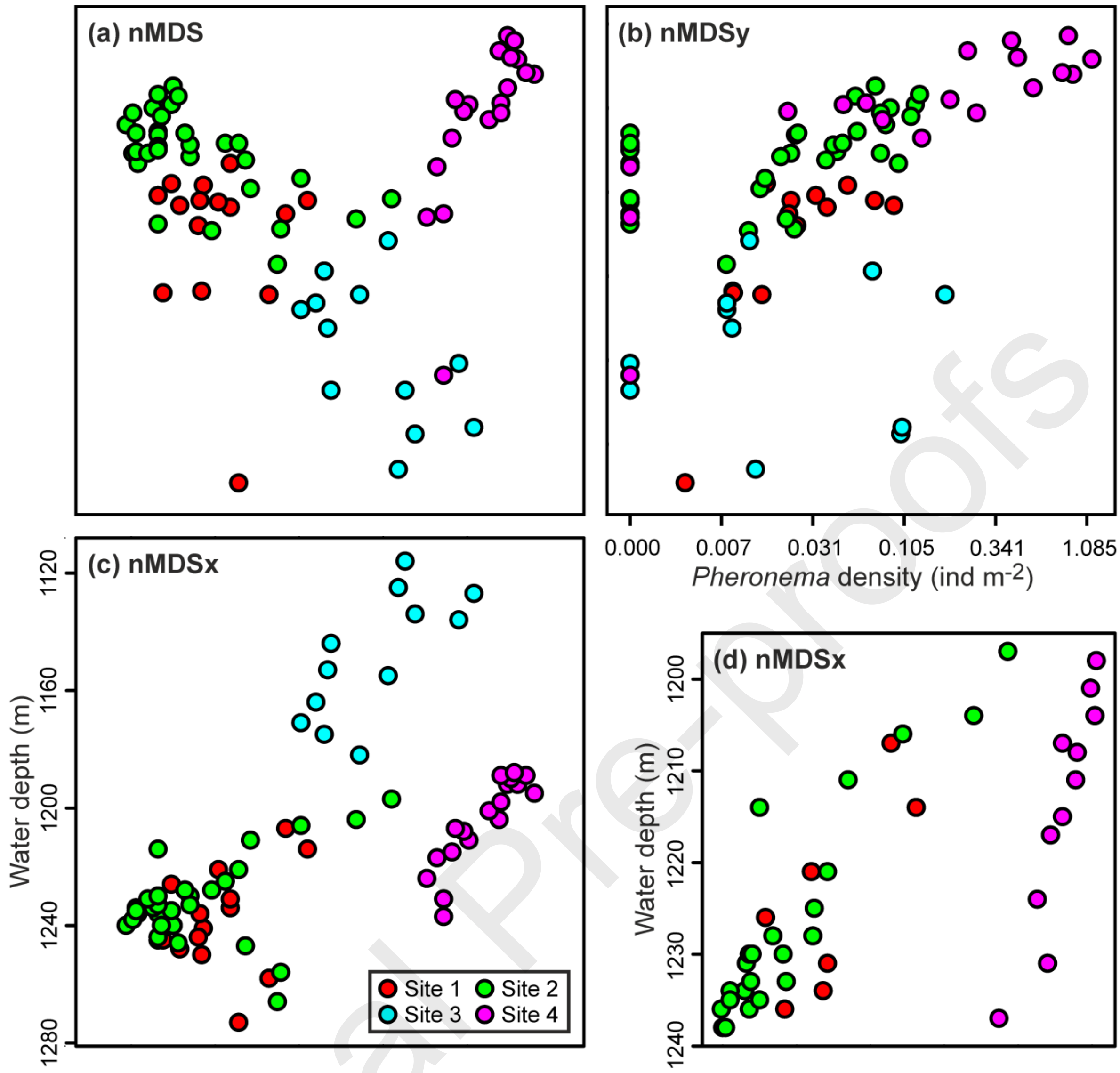

Figure 7. Variations in megafaunal assemblage composition by: (a) Site, (b) numerical density of *Pheronema carpenteri*, and (c, d) water depth. Faunal composition was assessed by 2D non-metric multidimensional scaling ordination (nMDS; see main text for detail).<2 column>

When the composite sample set was reduced to only those in a common depth range (Sites 1, 2, and 4), statistically significant Spearman's rank correlations between the MDS x-ordinate and water depth were detected among all samples ($r_s = 0.755$, $p < 0.001$) and for Sites 1 and 2 assessed separately ($r_s = 0.793$, $p < 0.001$), and Site 4 assessed separately ($r_s = 0.943$, $p < 0.001$; Fig. 7d). The corresponding global ANOSIM test yielded a substantial, statistically significant difference in assemblage composition between Sites ($R = 0.657$, $p < 0.001$), with follow-up pairwise tests indicating modest, statistically significant differentiation of Sites 1 and 2 ($R = 0.228$, $p = 0.036$), and substantial, statistically significant differentiation between Site 4 and both Sites 1 and 2 ($R \geq 0.823$, $p < 0.001$). When the composite samples from Sites 1 and 2 were combined as a single 'low / no trawling' case and Site 4 considered as a 'trawled' case (see Section 3.4), the corresponding ANOSIM test yielded a very substantial, statistically significant difference in assemblage composition between those cases ($R = 0.893$, $p < 0.001$).

3.4. Bottom trawling activity

The available fishing intensity data suggests that bottom trawling is likely to have occurred in the general study area in recent years (2009-15; Fig. 8). Visual inspection suggests that there may be a notable concentration of effort around the 1000 m bathymetric contour. Conversely, there was little or no indication of trawling pressure in the 600 to 800 m water depth range, or below the 1200 m bathymetric contour (Fig. 8). In our photographic assessment (2011 survey), we recorded 32 apparent seafloor trawl marks at Sites 3 and 4 (Fig. 2), but none at Sites 1 or 2.

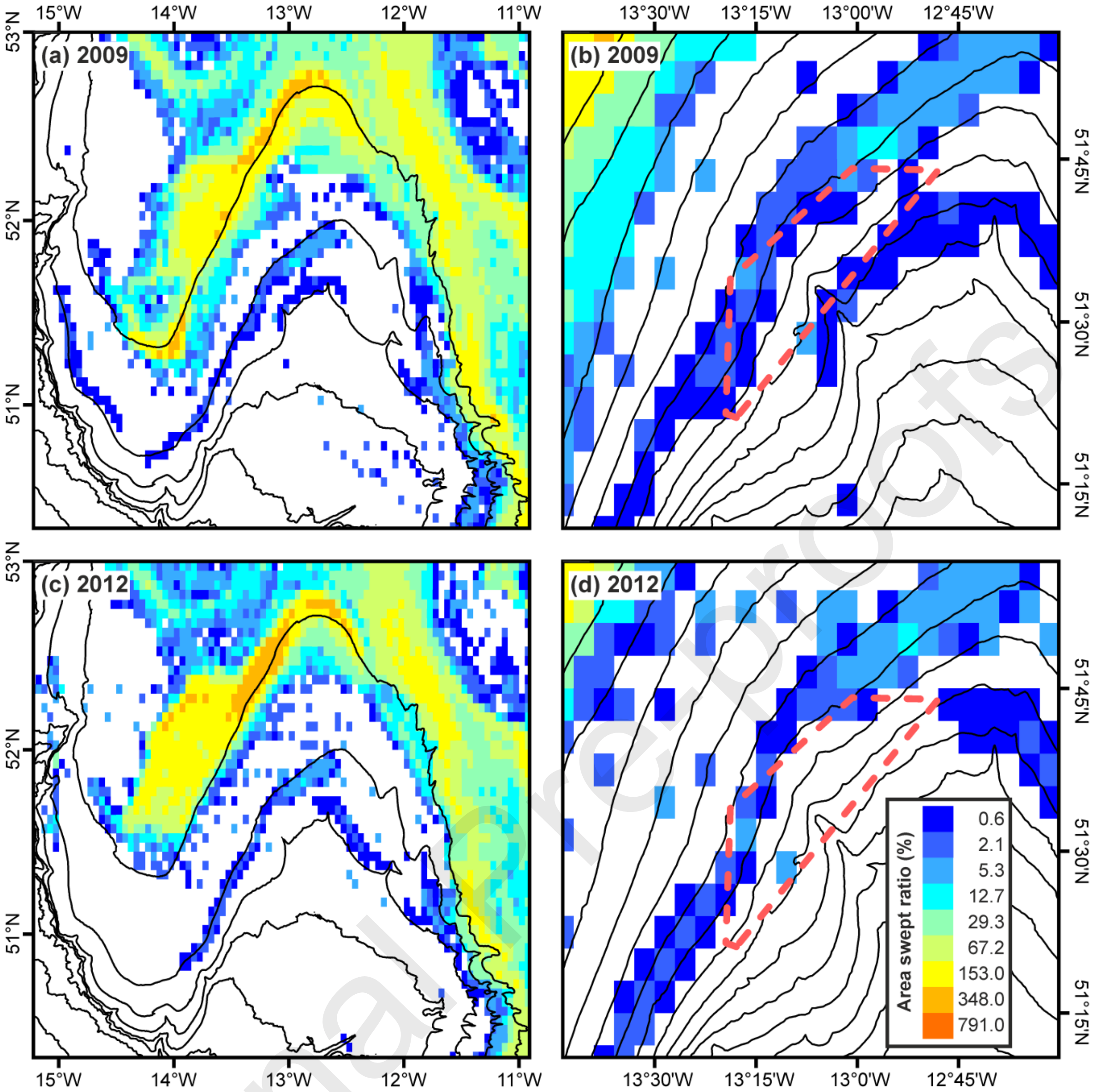

Figure 8. Annual fishing intensity, as swept area ratio, for selected years in the northern Porcupine Seabight: (a, b) 2009, (c, d) 2011. Red dashed polygon bounds the area of the present study (see Fig. 1). Mercator projection. Data source: https://odims.ospar.org/.<2 column>

4. Discussion

Our assessment of the current status of deep-sea sponge aggregations in the Porcupine Seabight suggests that they may have been impacted by bottom trawling. The 2011 photo-transects, repeating those of Rice et al. (1990) in 1983/4, confirmed that aggregations of the hexactinellid sponge *Pheronema carpenteri* were still present (Fig. 2). However, there appeared to have been a very substantial reduction in the standing stock of sponges. Our observations also revealed what appeared to be seafloor trawl marks, and our assessment of the available OSPAR fishing pressure data indicated the occurrence of commercial deep-sea demersal trawling in the area. Although we cannot provide direct evidence of bottom trawl fishing impact on these deep-sea sponge aggregations, there is certainly reason for suspicion and consequently cause for concern.

4.1. Demersal fishing pressure

The OSPAR fishing pressure data from 2009-2015 indicates that commercial bottom trawling may have occurred in the general area of our survey. Indeed, those data potentially indicate targeted fishing in the 1000-1200 m water depth range (Fig. 8) coincident with the previously established core of the local *Pheronema carpenteri* bathymetric distribution (Rice et al., 1990), and that predicted more generally in recent modelling studies (Ross and Howell, 2013; Ross et al., 2015). In addition, it has been suggested that the indirect effects of demersal trawling extend to greater water depths than the fishing activity itself (Bailey et al., 2009; Puig et al., 2012; Trueman et al., 2014). These effects may cause a reduction in the biomass of both target and bycatch species, and may be reflected in the secondary production, population body size, and trophic structure of benthic assemblages (Jennings et al., 2001; Jennings and Blanchard, 2004; Hiddink et al., 2016). We did directly observe apparent seafloor trawl marks at Sites 3 and 4 (Fig. 2), though cannot unequivocally attribute these to commercial fishing operations. Broader-scale seafloor mapping, done visually or acoustically, would likely provide a better assessment of these features (see e.g. Huvenne et al., 2016). Given the very marked decline in *P. carpenteri* numerical density between the 1983/4 and 2011 surveys, considered in Section 4.2, it is conceivable that all four sites may have been impacted by demersal trawling. Consequently, the between Site differences in faunal diversity and composition recorded in the 2011 survey may represent local ecological variations, for example bathymetric and / or near-bottom tidal current velocities, rather than variations in fishing pressure per se.

4.2. Temporal change in *Pheronema carpenteri* standing stocks

Rice et al. (1990) reported high densities of *P. carpenteri* (mean 0.3 ind m^{-2}) at water depths between 1000 and 1300 m, with a maximum density of 1.6 ind m^{-2} at 1210 m water depth.

Lampitt et al. (1986) had estimated a maximum density of 0.5 ind m^{-2} based on epibenthic sledge sampling in the region, with their value assumed to be underestimated given the likely inefficiency of net sampling relative to photographic assessment (see e.g. Rice et al., 1990). Assessed over the common water depth range surveyed at the same sites (1110 – 1290 m, Sites 1-3) our data indicate an average sponge density, 0.03 ind m^{-2} (2011 survey), an order of magnitude lower than the corresponding value from Rice et al.'s (1990) data of 0.50 ind m^{-2}. Similarly, peak sponge density in any 10 m depth band reduced from 1.43 to 0.20 ind m^{-2} between 1983/4 and 2011. Most notably, average sponge density in Rice et al.'s (1990) peak density depth range (1210 – 1250 m) declined from 1.09 to 0.03 ind m^{-2} between the surveys (Fig. 3). We characterise this decline as dramatic. *Pheronema carpenteri* standing stock numerical density is certainly variable geographically, for example: Rosemary Bank 0.1 ind m^{-2} (McIntyre et al., 2016); Morocco Margin 0.2 ind. m^{-2} (Barthel et al., 1996); Goban Spur 1.5 ind m^{-2} (Hughes and Gage, 2004); and Le Danois Bank 7.4 ind m^{-2} (Sánchez et al., 2008). Nevertheless, our results suggest a very substantial decline in the Porcupine Seabight sponge population between the 1983/4 and 2011 surveys.

Although we were unable to formally compare change in the standing stock biomass of *P. carpenteri* between surveys (Section 3.1), we would suggest that there has been a dramatic decline. Using Rice et al.'s (1990) equation relating individual wet weight mass to equatorial diameter (Section 2.2), when assessed over the common water depth range surveyed at the same sites (1110 – 1290 m, Sites 1-3): the 1983/4 survey had a mean sponge diameter of 15.8 cm and a standing stock of 83 gwwt m^{-2} while the 2011 survey had a mean sponge diameter of 13.0 cm and a standing stock of only 2 gwwt m^{-2}. When that assessment is limited to Rice et al.'s (1990) peak density depth range (1210 – 1250 m) the decline is even more marked, from 246 gwwt m^{-2} in 1983/4 to 4 gwwt m^{-2} in 2011.

The modest reduction in equatorial diameter from 16 to 13 cm at Sites 1-3 between 1983/4 and 2011, nevertheless corresponds with a c. 50% drop in average individual body mass from 229 to 140 gwwt. That decline was even greater at Site 4, where average equatorial diameter in our 2011 survey was only 4.7 cm, and the corresponding individual body mass 33 gwwt. It is difficult to assess the potential ecological significance of this observation, as Rice et al. (1990) provide very little information for this Site (their Station 52022), simply noting that only three sponge specimens were photographed. Indeed, the latter authors considered the Site 4 location to represent the western limit of the distribution of *P. carpenteri* in the Porcupine Seabight. In contrast, our 2011 survey data from Site 4 suggest an abundant population of small sponges in a narrow bathymetric band centred on 1190 m water depth (Fig. 3), having a local standing stock of c. 0.7 ind m^{-2} and 22 gwwt m^{-2}. Given that we observed apparent seafloor trawl marks at Site 4, but not at Sites 1 and 2, it is tempting to speculate that the marked shift in sponge body size distributions, median diameters 4.4 and 13.4 cm respectively, might be attributable to more or more recent demersal trawling at Site 4. However, given the absence of earlier data on sponge body size distributions for Site 4, and the appreciable shift in the centres of bathymetric distribution between these sites, 1190 m water depth at Site 4 and 1240 m water depth at Sites 1 and 2 combined, it is conceivable that other environmental factors may also have been involved.

4.3. Spatial variation in the megafaunal assemblage

Despite the apparently substantial decline in the standing stock of *P. carpenteri* between the 1983/4 and 2011 surveys, our results suggest that the presence of sponge aggregations continued to exert a positive influence on the diversity of the megafaunal assemblage. After applying statistical controls on the effect of water depth and sampling unit size, the numerical density of *Pheronema* exhibited a statistically significant positive correlation with all three diversity measures tested (Table 3). The effect was modest in the case of species richness (partial Spearman's rank correlation, ${}_{p}r_{s} = 0.292$ $p < 0.05$) and more notable in the case of exponential Shannon and inverse Simpson's diversity measures (${}_{p}r_{s} \geq 0.444$ $p < 0.001$). These results are consistent with the identification of deep-sea sponge aggregations as 'hotspots' of biological diversity (Thomson, 1873), even in an apparently degraded state. If we accept that Site 4 was subject to more or more recent trawling impact than Sites 1 and 2, then that impact may have resulted in a statistically significant reduction in species richness (Section 3.2; Fig. 6).

In common with our assessment of assemblage diversity, faunal composition also exhibited statistically significant trends with both *P. carpenteri* numerical density and water depth (Fig. 7b-d). These results suggest that the presence of sponges, even at markedly reduced standing stock levels, continues to exert an appreciable influence on the composition of the megafaunal assemblage, and equally cautions the comparison of assemblages drawn from different bathymetric horizons. If we accept that Site 4 was subject to more or more recent trawling impact than Sites 1 and 2, then that impact may have resulted in a statistically significant change in faunal composition (Fig. 7d). Assessed only over the common water depth range surveyed (1195 – 1240 m), the faunal composition of Sites 1 and 2 was jointly highly distinct from that of Site 4 (ANOSIM R = 0.893 $p < 0.001$). However, as considered in Section 4.2, note that Rice et al. (1990) only encountered three *P. carpenteri* specimens at Site 4, with a fourth specimen taken in a nearby trawl, and considered the location to be at the Westerly limit of the sponges' core distribution in the Porcupine Seabight. Consequently, we must similarly caution that it is certainly conceivable that other environmental factors might also have been involved in the differentiation of Site 4 from Sites 1 and 2.

4.4. Potential impact of demersal fishing

Differences in benthic faunal assemblage composition and diversity have been observed between locations subject to different trawling intensities (Hiddink et al., 2006; Ramalho et al., 2017). The degree of assemblage change has been linked to the frequency and / or intensity of disturbance (Rooper et al., 2011; van Denderen et al., 2015; Sorte et al., 2017). In the present case, it is conceivable that the status of Site 4 represents a more recent and / or more intense impact than had been experienced at Sites 1-3, though our limited prior knowledge of Site 4 suggests the need for cautious interpretation (Section 4.3). Nevertheless, the evidence of demersal fishing activity in the general area of our study (Section 4.1), and the dramatic reduction in *P. carpenteri* standings stocks between 1983/4 and 2011 (Section 4.2) is suggestive of a substantive impact by demersal fishing. The continental slope of the Porcupine Seabight has been subject to increased demersal trawling since at least 1989 (Priede et al., 2011; Vieira et al., 2019). Previous surveys in the Hatton Bank area of the NE Atlantic have suggested that bottom trawling was a plausible cause for reduced standing stocks of corals and sponges (Muñoz et al., 2012). Similarly, long-term changes in the numerical and biomass density of deep-water fish populations in the Porcupine Seabight have been attributed to commercial fishing pressure (Bailey et al., 2009; Godbold et al., 2013).

It is both the mass occurrence, and habitat forming characteristics, of deep-sea sponges that primarily attract their classification as features of conservation interest and as vulnerable marine ecosystems (e.g. FAO, 2009; ICES, 2009). Taken in total, our 2011 survey data indicate an order of magnitude decline in the numerical density of *Pheronema carpenteri* in the core of the previously determined distribution (1210-1240 m water depth; Rice et al., 1990) and a narrow dramatic 'spike' in sponge density at c. 1180-1200 m, that reaches values broadly comparable with Rice et al.'s (1990) observations (Fig. 9). Our data also appear to indicate an enhanced numerical density (>1.5 ind m^{-2}) of all megafauna in a comparable total depth range (1180-1250 m). It is perhaps notable that there are two 'spikes' in megafauna density, one corresponding to peak sponge density at c. 1190 m water depth, and one approximately corresponding with the 1983/84 peak in sponge density at c. 1225-1245 m. The first megafauna density spike potentially representing the expected enhancement of the fauna associated with a living sponge aggregation, the second potentially reflecting the residual effect of sponge spicule mats (skeletal remains) from the former sponge aggregation (see e.g. Bett and Rice, 1992; Laguionie-Marchais et al., 2015). Some evidence for the latter effect may be present in the markedly enhanced densities of large ascidians (Fig. 2) in a bathymetric range (1210-1250 m; Fig. 10) that is well matched to the zone of abundant sponges identified by Rice et al. (1990). It is at least conceivable that these filter feeders have 'opportunistically' replaced the former dense aggregation of sponges, using the remaining spicule mats as a substratum.

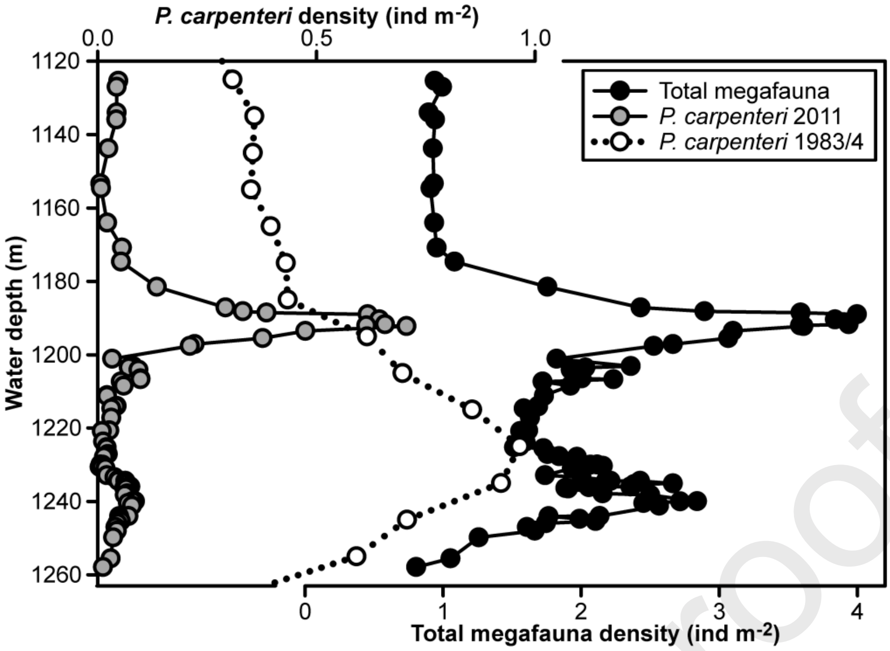

Figure 9. Variation in the numerical density of the megafaunal assemblage, and that of *Pheronema carpenteri* alone, with water depth. Data presented as 5-sample running mean with water depth across Sites 1-4 for 2011 and Sites 1-3 for *P. carpenteri* 1983/4.<1.5 column>

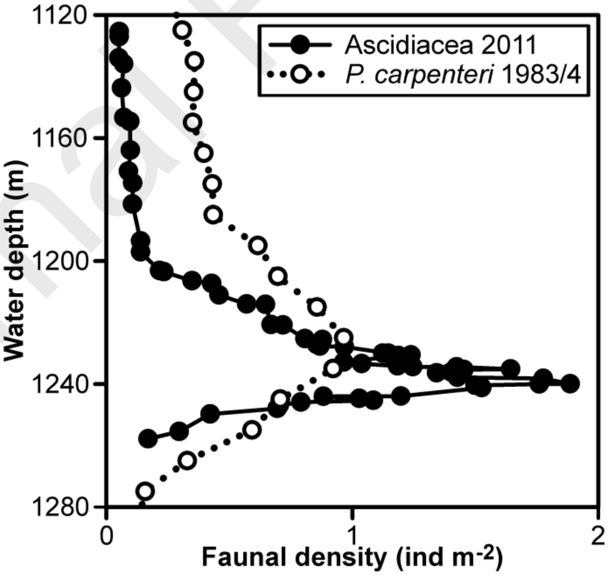

Figure 10. Variation in the numerical density of ascidians in 2011, and that of *Pheronema carpenteri* in 1983/4. Data presented as 5-sample running mean with water depth across Sites 1-3.<1 column>

While demersal fishing is an highly plausible cause for the very substantial reduction in the standing stocks of *P. carpenteri* that we have recorded in the present study, a definitive assessment of cause and effect is not possible. In particular, we are hampered by a lack of temporal studies (see e.g. Boolukos et al., 2019) that would assist in disentangling the effects of natural change from those that might arise from the direct and / or indirect effects commercial fishing. The need for more widespread, and more frequent, time-series monitoring of features of conservation interest and vulnerable marine ecosystems in the deep sea is clear (Vieira et al., 2019; Levin et al., 2019). We are also bound to note potential alternative explanations, perhaps the most interesting of which is the suggestion of a "wandering" population of *Pheronema carpenteri* on the Continental Slope off Morocco (NE Atlantic) proposed by Barthel et al. (1996). These authors reported the observation of an abundant living sponge population located immediately upslope of an equally abundant occurrence of dead and dying sponges. They further hypothesized that this reflected a natural, successional spatial drift in the centre of the population distribution, potentially driven by changes in local hydrography and / or the sponge population optimising to the best feeding horizon.

We similarly note the exceptional long-term observations of Dayton et al. (2016) that indicate the potential for very dramatic shifts in sponge recruitment and growth in an Antarctic shelf sea environment. Other shelf sea hexactinelid aggregations, such as those of the Salish Sea (Dunham et al., 2018), have been subject to small-scale experimental disturbance (deliberate crushing by ROV) that revealed no recovery after three years (Kahn, et al., 2016). In general, the natural history of deep-water sponges, not least the hexactinellids, remains very poorly known despite their classification as features of conservation interest and vulnerable marine ecosystems. As key deep-sea 'ecosystem engineers' (e.g. Coleman and Williams, 2002), a better understanding of their fundamental biological characteristics would improve the basis for resource management decisions.

4.5. Conservation and policy

We have provided evidence for the degradation of deep-sea sponge aggregations in the Porcupine Seabight potentially resulting from bottom trawl fishing, as indicated by fishing pressure data (Fig. 8), the presence of seabed trawl marks at two of our four study sites (Fig.

2), and an apparent order of magnitude reduction in the local sponge population (Section 4.2). Examples of human impacts on deep-sea habitats continue to accumulate (e.g. Ramirez-Llodra et al., 2011; Clark et al., 2016; Huvenne et al., 2016), suggesting an on-going need for the development of, or extension of, conservation and environmental protection measures in deep-water environments. The European Parliament has now approved the adoption of a regulation aimed at the sustainability of deep-sea fisheries, indicating the prohibition of deep-sea fishing with bottom trawls below 800 m water depth, and an obligation for vessels to report encounters with vulnerable marine ecosystems at water depths greater than 400 m (European Union, 2016). That regulation would certainly apply in the case of the Porcupine Seabight *Pheronema carpenteri* population studied here, with Annex III VME indicator species including, 3. (c) Deep-sea sponge aggregations, Glass sponge communities, Rossellidae and Pheronematidae. The regulation represents a European Union commitment to implement the resolutions of the General Assembly of the United Nations (61/105 and 64/72) that call for the protection of vulnerable deep-sea marine ecosystems from the impact of bottom fishing gears (UNGA, 2006, 2009).

The use of water depth-related management measures has a clear logic and evidence base in the case of deep-sea demersal fishing in EU waters (Clarke et al., 2015) and could perhaps be implemented elsewhere. How such a measure might be applied and enforced in areas beyond national jurisdiction (High Seas) will require further consideration. It potentially falls to the regulatory authority of the United Nations Convention on the Law of the Sea (Harrison et al., 2017) and the role that Regional Fisheries Management Organisations, under the auspices of the Food and Agricultural Organisation, and the International Seabed Authority, have in managing activities in Areas Beyond National Jurisdiction. Such organisations, and the scientific community, typically advocate an ecosystems-based approach and the use of the precautionary principle in deep-sea environmental management (Thompson et al., 2016; Huvenne et al., 2016; Kenny et al., 2018). Our observations of the status of the deep-sea sponge aggregations in the Porcupine Seabight suggest that such efforts would greatly benefit from an increase in the sustained observation of selected deep-sea habitats / species / ecosystems of conservation interest (see also Kazanidis et al., 2019) and a much better understanding of the natural history of the key species in those environments. A 'Deep

Essential Ocean Variable' of seafloor sponge cover, is currently under consideration by the Deep Ocean Observing Strategy (Levin et al., 2019).

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Author contributors

RPV, BJB, HAR conceived and contributed to the research and article preparation. BJB, DOBJ, HAR, carried out the field survey. RPV, JMD, KJM, carried out the data generation / image analysis. MRC and CNT contributed to article preparation. All authors approved the article for submission.

Declaration of interest: None

Submission declaration

All authors declare that the work described has not been published previously, that it is not under consideration for publication elsewhere, and if accepted it will not be published elsewhere in the same form (in any language etc.).

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