

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

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4 Rui P. Vieira^{a,b,c,1,*}, Brian J. Bett^b, Daniel O.B. Jones^b, Jennifer M. Durden^{a,b}, Kirsty J.
5 Morris^b, Marina R. Cunha^c, Clive N. Trueman^a, Henry A. Ruhl^{b,2}

6

7 ^a Ocean and Earth Science, University of Southampton, Southampton SO14 3ZH, UK.

8 ^b Ocean Biogeochemistry and Ecosystems, National Oceanography Centre, Southampton
9 SO14 3ZH, UK.

10 ^c Departamento de Biologia & CESAM, Universidade de Aveiro, Campus de Santiago,
11 3810-193 Aveiro, Portugal

12

13 Present address:

14 ¹ Centre for Environment, Fisheries & Aquaculture Science, Lowestoft Laboratory, Pakefield
15 Road, Lowestoft, Suffolk NR33 0HT, UK

16 ² Monterey Bay Aquarium Research Institute, 7700 Sandholdt Rd, Moss Landing, CA 95003,
17 USA

18

19 * Corresponding author at: Centre for Environment, Fisheries & Aquaculture Science,
20 Lowestoft Laboratory, Pakefield Road, Lowestoft, Suffolk NR33 0HT, UK.

21 Tel.: +441502524572. E-mail address: rui.vieira@cefas.co.uk (R.P. Vieira).

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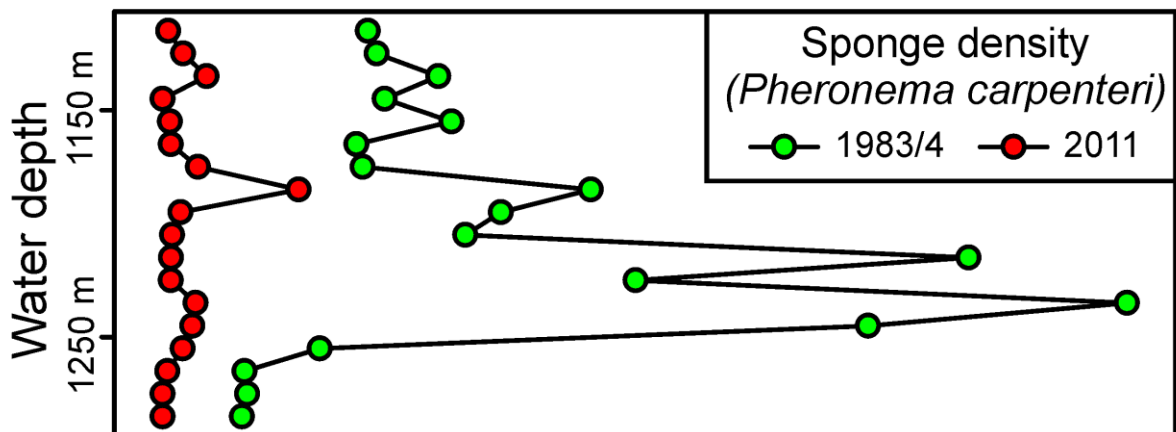
23 **Abstract**

24

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

54

55 **Graphical abstract**



56

57

58 **Highlights**

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

64

65

66 **Keywords**

67 Porifera; Sponges; Deep water; Bottom trawling; Zoobenthos; Nature conservation;

68 Vulnerable marine ecosystem; NE Atlantic; Porcupine Seabight; bathyal zone

69

70 **1. Introduction**

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

92
93 The presence of substantial sponge populations can increase local habitat complexity and
94 may enhance ecosystem functioning by providing refugia to a wide range of organisms
95 (Kenchington et al., 2013), substratum for sessile fauna, and habitat for an abundant and
96 diverse associated fauna (Bett and Rice, 1992; Klitgaard, 1995; Beaulieu, 2001; Kazanidis et
97 al., 2016). As a result of their nutrient remineralisation role in carbon and silicon cycles (Chu
98 et al., 2011; Maldonado et al., 2011; Rix et al., 2016), sponges may also contribute to pelagic-
99 benthic coupling (Yahel et al., 2007; Bell, 2008; Kahn et al., 2015). Sponge habitats are often
100 referred to as ecological “hotspots”, areas of enhanced biological diversity (Beazley et al.,
101 2015), and ecosystem function (Cathalot et al., 2015), and of potential importance to fisheries

102 (Bailey et al., 2009; Hogg et al., 2010; Priede et al., 2011; Pham et al., 2015). Sponge
103 aggregations are considered to be vulnerable marine ecosystems (VMEs; UNGA, 2006; FAO,
104 2009), and are listed as “Threatened and/or Declining” habitats (OSPAR, 2008). Bottom
105 trawl fishing has likely impacted European deep-sea habitats for over 100 years (Thurstan et
106 al., 2010). The effects of bottom trawling on benthic communities are often direct and
107 immediate, and may persist for decades. Direct and indirect effects of bottom-contact fishing
108 gears include direct biomass removal and other damage to benthic communities, increased
109 sediment resuspension / redeposition, with consequent changes in the geochemical and
110 physical properties of the sediments and modified seafloor topography (Puig et al., 2012;
111 Clark et al., 2016; Amaro et al., 2016; Huvenne et al., 2016). It is, therefore, likely that the
112 benthic communities of many continental slope areas have already been significantly
113 modified by bottom trawling (Roberts et al., 2000; Gage et al., 2005; Puig et al., 2012). Our
114 understanding of these impacts is hampered by limited direct observations, knowledge gaps
115 concerning the structure and function of deep-sea ecosystems, and natural variations in time
116 and space (Glover et al., 2010; Ruhl et al., 2011; Levin and Sibuet, 2012; Vieira et al., 2019).

117

118 In the present study, we specifically reoccupy the key photo-transects reported by Rice et al.
119 (1990) as the core of the *P. carpenteri* distribution in the Porcupine Seabight. Our aim was to
120 assess the current status of the sponge aggregations using comparable photographic survey
121 methods, the intervening decades having seen the development of a substantive deep-water
122 trawl fishery in the region (Bailey et al. 2009). Specifically, we aimed to address the
123 following questions: 1) Are *P. carpenteri* aggregations still a dominant habitat-forming
124 feature at those sites? 2) If so, have they changed in character, e.g. standings stocks, body
125 size distribution, etc.? 3) Is there any evidence of bottom trawling in the study area? 4) And
126 specifically, is there evidence of potential trawl impact within our new survey data?

127

128 **2. Material and Methods**

129 **2.1. Photographic surveys 1983/4**

130 The surveys described by Rice et al. (1991) were undertaken using an IOS epibenthic sledge
131 (see e.g. Gage and Bett, 2005), the design and operation of which is detailed by Rice et al.
132 (1982). The sledge carried an IOS Mark IVa conventional film stills camera recording in
133 half-frame 35 mm format (image c. 24 × 18 mm) and an IOS 10 J flashgun. The camera lens

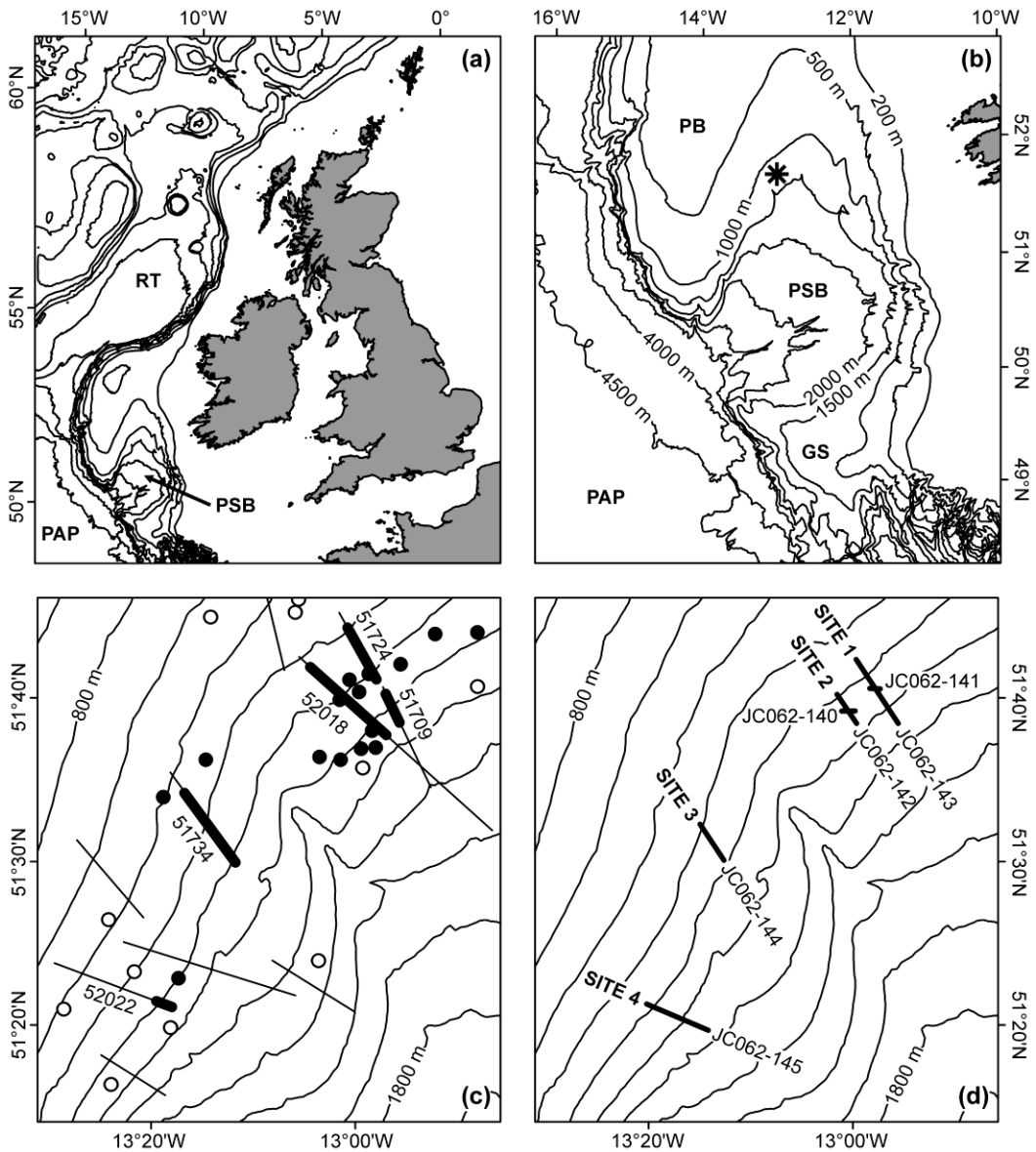
134 was located c. 80 cm above the seafloor level and angled 30° below the horizontal. The
135 proximal 3/4 of the resultant oblique image was analysed, representing c. 1.0 m² (Rice et al.,
136 1982). The sledge was operated by reference to an acoustic telemetry system, enabling the
137 user to record seabed contact, camera activation, and in situ (calibrated) pressure. The
138 sledge's geographic position was estimated by 'lay-back' calculation, i.e. a distance behind the
139 towing vessel based on the length of wire deployed and the water depth (from pressure) of
140 the sledge. Consequently, geolocation is somewhat approximate, however, the depth of
141 operation is well constrained and is used in the following comparative assessment.

142

143 **2.2. Photographic survey 2011**

144 Photographic transects were conducted in August 2011 from RRS *James Cook* cruise 062
145 (Ruhl, 2012), at four sites in the northern Porcupine Seabight (Fig. 1; Table 1), as previously
146 surveyed during the Institute of Oceanographic Sciences Porcupine Seabight Benthic
147 Biological Survey (Rice et al., 1990). The 2011 transects were carried out using the National
148 Oceanography Centre Wide-Angle Seabed Photography (WASP) off-bottom, towed camera
149 system (Jones et al., 2009). WASP was towed at c. 0.5 knots, at about 1-3 m above bottom,
150 by reference to an acoustic telemetry system. A vertically mounted, 35 mm film stills camera
151 (Ocean Scientific International Limited Mk 7) was fitted during all deployments and
152 augmented with an obliquely mounted digital stills camera (Kongsberg OE14-208). Note that
153 images from the latter were only used for qualitative assessment. The processed 35 mm film
154 negatives were digitised to 4096 × 3112 pixels; all faunal analyses reported here are based on
155 data derived from those digitised images. For quality control, images taken outside a 1-3 m
156 altitude range were discounted from the analyses, as were those where the full seafloor area
157 was not visible (e.g. as a result of flash shadowing or sediment resuspension). In the
158 remaining 1713 images, covering c. 5500 m² seafloor area (Table 1), all invertebrate
159 megafauna (body size > 1 cm; Bett, 2019) were identified to morphotype and counted. The
160 identification process was informed by reference to extensive specimen collections of
161 Porcupine Seabight megafauna available in the *Discovery Collections* at the National
162 Oceanography Centre (Chidgey, 1983; Jackson et al., 1991) and by direct consultation with
163 taxonomic experts (see Acknowledgements). Specimen body size and seafloor area imaged
164 were estimated from camera altitude and the known optical geometry of the camera system
165 (Jones et al., 2007). Geolocation and water depth data for the camera platform were derived

166 from an ultra-short baseline navigation transponder attached directly to the WASP vehicle
 167 (Ruhl, 2012).



168
 169 **Figure 1.** a) General location of the Porcupine Seabight (PSB; Porcupine Abyssal Plain,
 170 PAP; Rockall Trough, RT). b) General location of the study area (*) within the PSB
 171 (Porcupine Bank, PB; Goban Spur, GS). c) Locations of photosledge transects (lines) and
 172 other benthic samples (symbols) reported by Rice et al. (1990); solid symbols represent the
 173 presence and open symbols the absence of *Pheronema carpenteri*; thickened lines similarly
 174 mark the regions where *P. carpenteri* was present on transects (numbering, 5xxxx, refers to
 175 original station numbers). d) Location of the 2011 WASP camera system transects of the

- 176 present study, with corresponding station numbers (JC062-xxx) and site names (SITE x).
- 177 Mercator projection. <1.5 column>

178 **Table 1.** Details of the photographic transects undertaken in the present study (2011), with
 179 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 Latitude (°N) Longitude (°E)		Vertical images assessed	Seabed area imaged (m ²)	Oblique images reviewed
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

180

181 **2.3. *Pheronema carpenteri***

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

189

190 **2.4. Megabenthos assemblage analysis**

191 Composite samples were formed by pooling data from individual images, in water depth
 192 order within site, to contain c. 100 individuals. This was done to achieve a similar level of
 193 accuracy and precision in morphotype diversity and composition measures across the
 194 sampling units (Durden et al., 2016; Benoist et al., 2019). Variations in faunal diversity, as
 195 Hill's diversity numbers N0 (species richness), N1 (exponential form of the Shannon index),
 196 and N2 (inverse form of Simpson's index), together with corresponding 95% confidence
 197 intervals, were estimated for a rarefied sample size of 100 individuals using the iNEXT R
 198 package (Hsieh et al., 2016). Although rarefied, interpretation of variations in diversity was
 199 complicated by covariation in the seabed area assessed resulting from variation in megafauna
 200 density with depth and Site (see Sections 3 and 4). Among individual composite samples, the
 201 seafloor area assessed varied from 22 to 290 m² (median 41 m², interquartile range 60 – 88
 202 m²). Consequently, we carried out some exploratory assessments by simple and partial non-

203 parametric Spearman's rank correlation. Partial correlations were calculated using the R
204 package 'ppcor' (Kim, 2015), and the p-values associated with the simple correlation values
205 were adjusted for multiplicity using the false discovery rate method (Benjamini and
206 Hochberg, 1995) in the R function 'p.adjust'. The relationships between diversity measures
207 and the physical area of the sampling units indicated the need for caution in the interpretation
208 of the diversity data (see Section 3). This was addressed by reference to the general case of
209 the species-area-relationship, where a power function is thought to most appropriately
210 describe that relationship (Dengler, 2009). Variations in diversity between sites were then
211 assessed by an analysis of covariance incorporating that power function (i.e. $\log[\text{number of}$
212 $\text{taxa}] \sim \log[\text{sampled area}]$) in a linear model, as implemented in Minitab 18.1 (Minitab Inc.).

213

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

228

229 **2.5. Bottom trawling indicators**

230 Seafloor images, including the oblique digital stills (Table 1), were reviewed for any
231 evidence of bottom contact fishing activity. We recorded the number of trawl marks,
232 discerned as various forms of parallel lineations in the seafloor, which could be ascribed to
233 the effects of bottom-towed fishing gear (e.g. Bett, 2000). In addition, we examined the
234 recorded annual bottom fishing intensity data available for the area in the OSPAR Data and

235 Information System (ODIMS; period 2009-2017; data accessed February 2019). These data
236 estimate swept area ratio, seafloor area trawled per year / seafloor area, at a grid resolution of
237 0.05×0.05 degrees.

238

239 **3. Results**

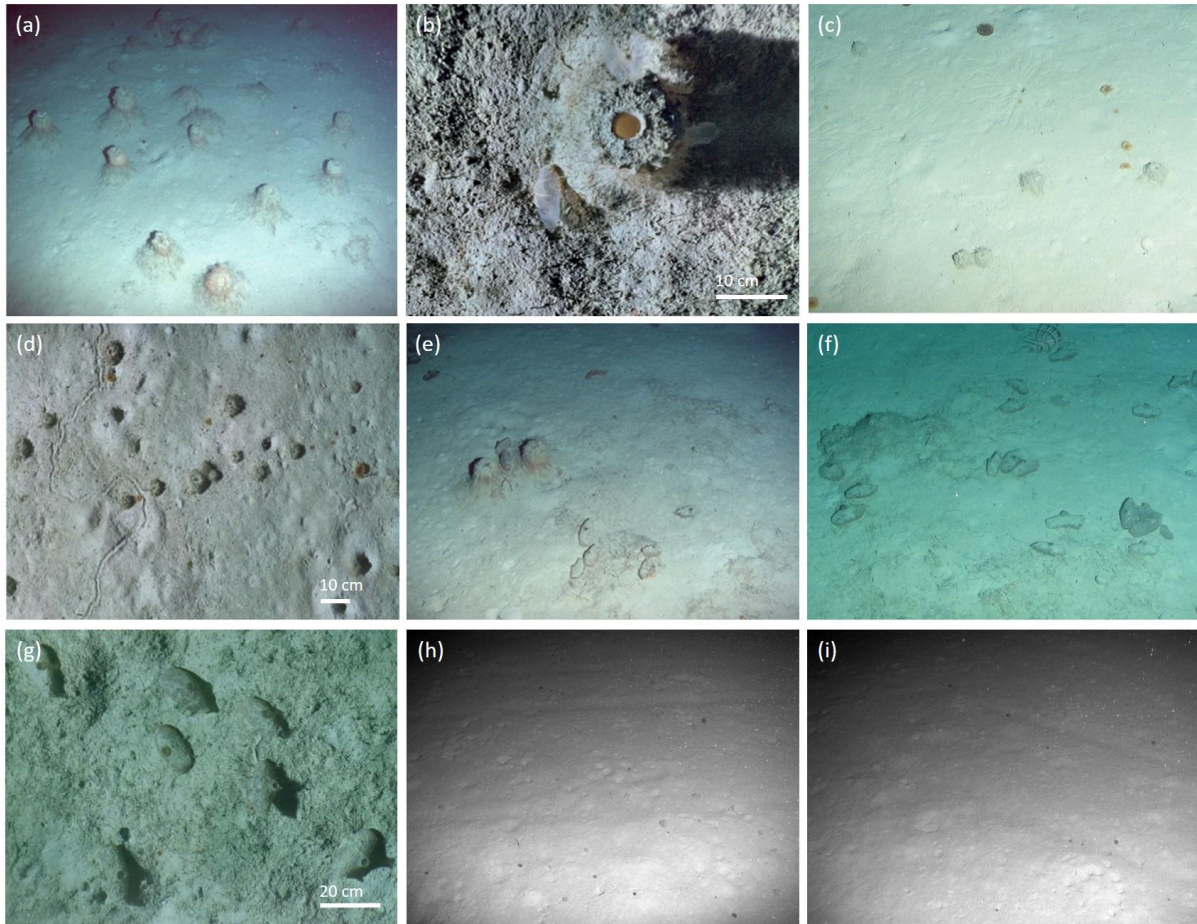
240 Our initial observations of the seafloor photographs from the 2011 survey indicated that
241 individuals and aggregations of a hexactinellid sponge consistent with *Pheronema carpenteri*
242 were still present at the locations originally documented by Rice et al. (1990), and indeed
243 were abundant at Site 4 where they were previously rare (Fig. 2). Accepting differences in the
244 angle of view and the camera altitude, there were no obvious gross differences in the
245 appearance of the sponges or the seafloor environment between the surveys conducted in
246 2011 and 1983/4 (or 1991; Rice, 1992; Bett and Rice, 1992).

247

248 **3.1. *Pheronema carpenteri* 1983/4 versus 2011**

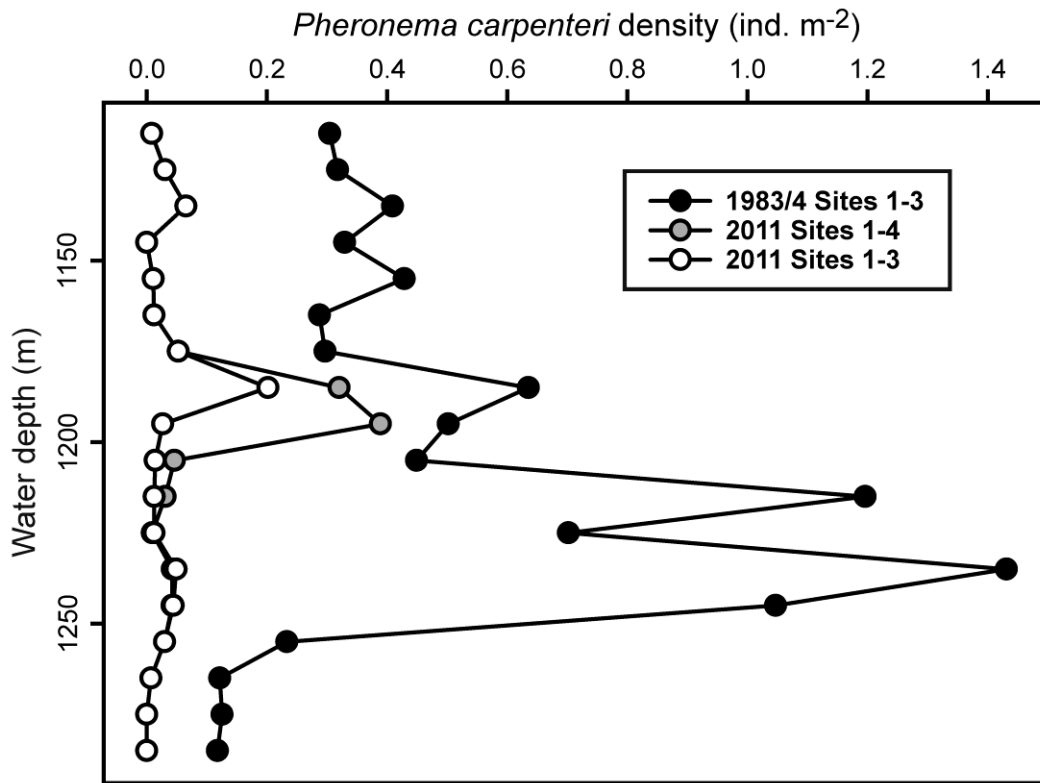
249 Across commonly assessed 10 m depth intervals, 1110-1290 m, the geometric mean density
250 of *P. carpenteri* appeared to have dropped c. 20-fold between the 1983/4 surveys and the
251 2011 survey. The geometric mean density in 1983/4 was 0.39 (95% CI 0.27-0.56) ind m⁻²; in
252 2011 the geometric mean density for Sites 1-4 was 0.02 (0.01-0.05) ind m⁻², and for Sites 1-3
253 (most directly comparable with Rice et al., 1990) it was 0.02 (0.01-0.03) ind m⁻². When
254 compared as samples paired by depth, across the commonly assessed 10 m depth intervals,
255 Wilcoxon paired-sample signed rank tests of 1983/4 and 2011 suggested a highly significant
256 difference ($V = 171$, $p < 0.001$) for both the Sites 1-4 and Sites 1-3 combined data (Fig. 3). A
257 similar change in biomass density seems likely, although this cannot be formally assessed
258 (see further in section 4.2.). Maximum recorded biomass declined by an order of magnitude
259 between the 1983/4 and 2011 surveys (Table 2).

260



261

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



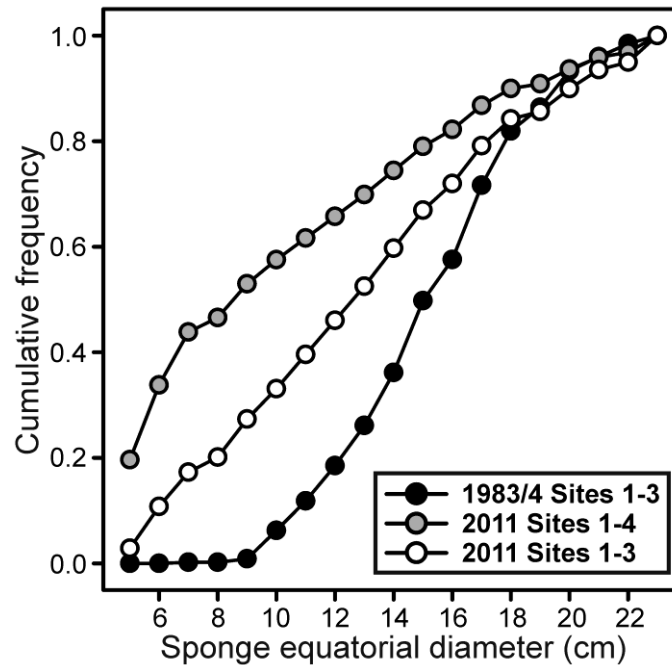
265
 266 **Figure 3.** Variation in the numerical density of *Pheronema carpenteri* with water depth, in
 267 10 m horizons, as recorded during 1983/4 and 2011 surveys. <1.5 column>
 268

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

Survey	Site 1		Site 2		Site 3		Site 4
	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

271
 272 There was a substantial shift in the distribution of sponge equatorial diameters between the
 273 1983/4 and the 2011 surveys (Fig. 4). Two-sample Kolmogorov-Smirnov tests of all 1983/4
 274 data with 2011 data from Sites 1-4 (D = 0.660) and Sites 1-3 (D = 0.296) yielded statistically
 275 significant differences in both cases (p < 0.001). Similar results were returned when those
 276 comparisons were limited to the commonly reported range of equatorial diameters between

277 1983/4 and 2011 (5-23 cm); all 1983/4 data with all 2011 data from Sites 1-4 ($D = 0.521$) and
 278 Sites 1-3 ($D = 0.277$), with statistically significant differences in both cases ($p < 0.001$; Fig.
 279 4).
 280



281
 282 **Figure 4.** Size frequency distribution of *Pheronema carpenteri* as observed in 1983/4 and
 283 2011 surveys. For presentation, sponge size range was truncated to the commonly observed
 284 range (5-23 cm diameter). <1 column>
 285

286 A formal statistical comparison of temporal change in the standing stock biomass of *P.*
 287 *carpenteri* between surveys is not possible. However, we are able to make a first order
 288 estimation using Rice et al.'s (1990) equation relating individual wet weight mass to
 289 equatorial diameter (Section 2.2). When assessed over the common water depth range
 290 surveyed at the same sites (1110 – 1290 m, Sites 1-3): the 1983/4 survey had a mean sponge
 291 diameter of 15.8 cm and a standing stock of 83 gwwt m⁻² while the 2011 survey had a mean
 292 sponge diameter of 13.0 cm and a standing stock of only 2 gwwt m⁻². When that assessment
 293 was limited to Rice et al.'s (1990) peak density depth range (1210 – 1250 m) the decline was
 294 even more marked, from 246 gwwt m⁻² in 1983/4 to 4 gwwt m⁻² in 2011. The modest
 295 reduction in equatorial diameter from 16 to 13 cm at Sites 1-3 between 1983/4 and 2011,
 296 nevertheless corresponds with a c. 50% drop in average individual body mass from 229 to

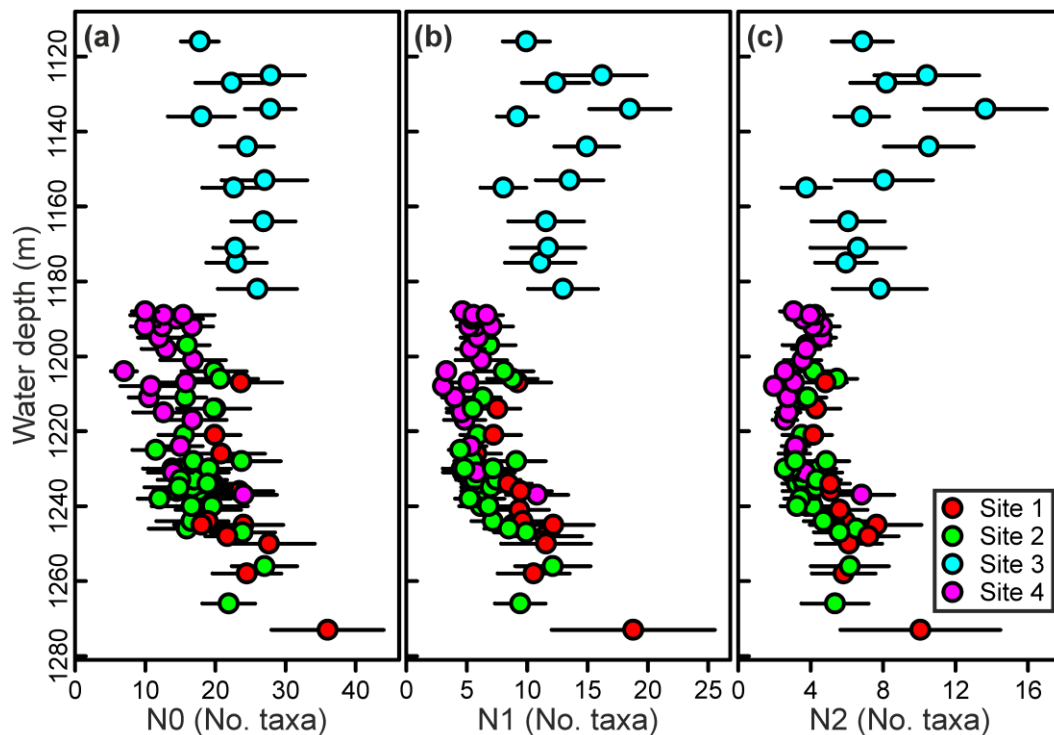
297 140 gwwt. That decline was even greater at Site 4, where average equatorial diameter in our
298 2011 survey was only 4.7 cm, and the corresponding individual body mass 33 gwwt.

299

300 **3.2. Megafaunal diversity 2011**

301 The patterns in rarefied diversity measures were somewhat complex (Fig. 5), with enhanced
302 diversity at the shallower Site 3, and some indication of a common increase in diversity with
303 water depth among the data from Sites 1, 2, and 4. In terms of simple correlations, assessed
304 across all samples, sampled seabed area was substantially and statistically significantly
305 positively correlated ($r_s = 0.58-0.78$, $p < 0.001$) with all three diversity measures (N0, N1,
306 N2; Table 3). Note, however, that these relationships were not apparent when the data from
307 individual Sites were assessed separately, i.e. the range in megafaunal density and therefore
308 seabed area sampled was much reduced. Within individual Sites, there were appreciable and
309 statistically significant positive correlations ($r_s = 0.45-0.71$, $p < 0.05$) between water depth
310 and rarefied taxon richness (N0). The apparent relationship between *P. carpenteri* density
311 and faunal diversity was complicated; across all Sites there was a statistically significant
312 moderate negative correlation ($r_s = -0.37$, $p < 0.05$) with taxon richness (N0). In contrast,
313 within Site 1, there were statistically significant strong positive correlations ($r_s = 0.82-0.89$, p
314 < 0.001) between *P. carpenteri* density and the N1 and N2 diversity measures. When water
315 depth, *P. carpenteri* density, and seabed area sampled were jointly assessed in partial
316 correlations with the diversity measures, all diversity measures exhibited statistically
317 significant strong positive partial correlations ($p_r_s = 0.68-0.78$, $p < 0.001$) with seabed area
318 sampled. All diversity measures also exhibited statistically significant moderate positive
319 partial correlations ($p_r_s = 0.29-0.45$, $p < 0.05$) with *P. carpenteri* density. In addition, water
320 depth exhibited a statistically significant modest positive partial correlation ($r_s = 0.28$, $p <$
321 0.05) with rarefied taxon richness (N0).

322



323

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

328

329 **Table 3.** Simple and partial Spearman's rank correlations between rarefied diversity
 330 measures (N₀, N₁, N₂) and potentially related variables (water depth, *Pheronema carpen-teri*
 331 density, and sampled seabed area); adjusted p-values: * p < 0.05, *** p < 0.001.

332

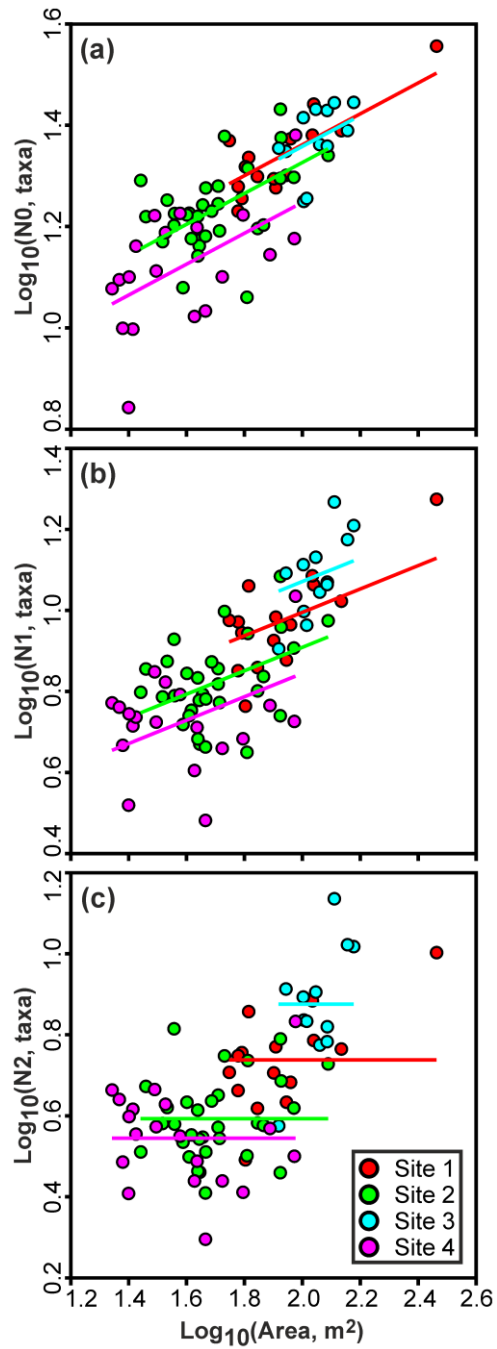
		N ₀	N ₁	N ₂
		Species	Exponential	Inverse
		richness	Shannon	Simpson's
Simple correlation				
All sites (n = 77)	Water depth	0.091	0.052	-0.019
	<i>P. carpen-teri</i>	-0.364*	-0.215	-0.086
	Sampled area	0.778***	0.709***	0.583***
Site 1 (n = 15)	Water depth	0.711*	0.579	0.475
	<i>P. carpen-teri</i>	0.457	0.825***	0.893***
	Sampled area	-0.231	0.055	0.086
Site 2 (n = 31)	Water depth	0.448*	0.294	0.180
	<i>P. carpen-teri</i>	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
	<i>P. carpenteri</i>	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
	<i>P. carpenteri</i>	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
	<i>P. carpenteri</i>	0.292*	0.444***	0.448***
	Sampled area	0.777***	0.768***	0.685***

333

334 Given the strong relationships between seabed area sampled and all three diversity measures,
335 whether assessed by simple or partial correlation (Table 3), our subsequent analyses of
336 between Site variations in diversity were undertaken with reference to covariation with
337 seabed area sampled. In the case of rarefied species richness (N0), there was no statistically
338 significant interaction between Site and sampled area (LM $F_{[3,69]} = 0.41$, $p = 0.748$), but a
339 statistically significant relationship between richness and area (ANCOVA $F_{[1,72]} = 34.48$, $p <$
340 0.001), and a statistically significant effect of Site (ANCOVA $F_{[3,72]} = 5.49$, $p = 0.002$).
341 Subsequent pairwise comparisons (5% Tukey) between Sites indicated statistically significant
342 differences in richness in all comparisons with Site 4, but not in any other comparisons (Fig.
343 6). In the case of the exponential Shannon index (N1), there was no statistically significant
344 interaction between Site and sampled area (LM $F_{[3,69]} = 2.42$, $p = 0.073$), but a statistically
345 significant relationship between diversity and area (ANCOVA $F_{[1,72]} = 16.89$, $p < 0.001$), and
346 a statistically significant effect of Site (ANCOVA $F_{[3,72]} = 7.42$, $p < 0.001$). Subsequent
347 pairwise comparisons (5% Tukey) between Sites indicated statistically significant differences
348 in diversity between Site 4 and Sites 1 and 3, but not Site 2 (Fig. 6). In the case of the inverse
349 Simpson's index (N2), there was a statistically significant interaction between Site and
350 sampled area (LM $F_{[3,69]} = 3.75$, $p = 0.015$). Consequently, between Site comparisons were
351 limited to a one-way ANOVA, which indicated a statistically significant effect of Site
352 (Welch's test $F_{[3,30.3]} = 19.23$, $p < 0.001$). Subsequent pairwise comparisons (Games-Howell
353 5%) indicated statistically significant differences in diversity between Site 4 and Sites 1 and
354 3, but not Site 2 (Fig. 6).

355



356

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

362

363 **3.3. Megafaunal assemblage composition 2011**

364 Ordination of the full set of composite samples demonstrated an obvious separation of all
365 four Sites in terms of assemblage composition (Fig. 7a). Additional exploratory analyses also
366 indicated statistically significant trends in the ordination scores with key variables:

367 Spearman's rank correlations between MDS y-ordinate and *P. carpenteri* density ($r_s = 0.613$,
368 $p < 0.001$; Fig. 7b) and between MDS x-ordinate and water depth ($r_s = 0.680$, $p < 0.001$; Fig.

369 7c). A global ANOSIM test confirmed the initial visual assessment of the ordination,

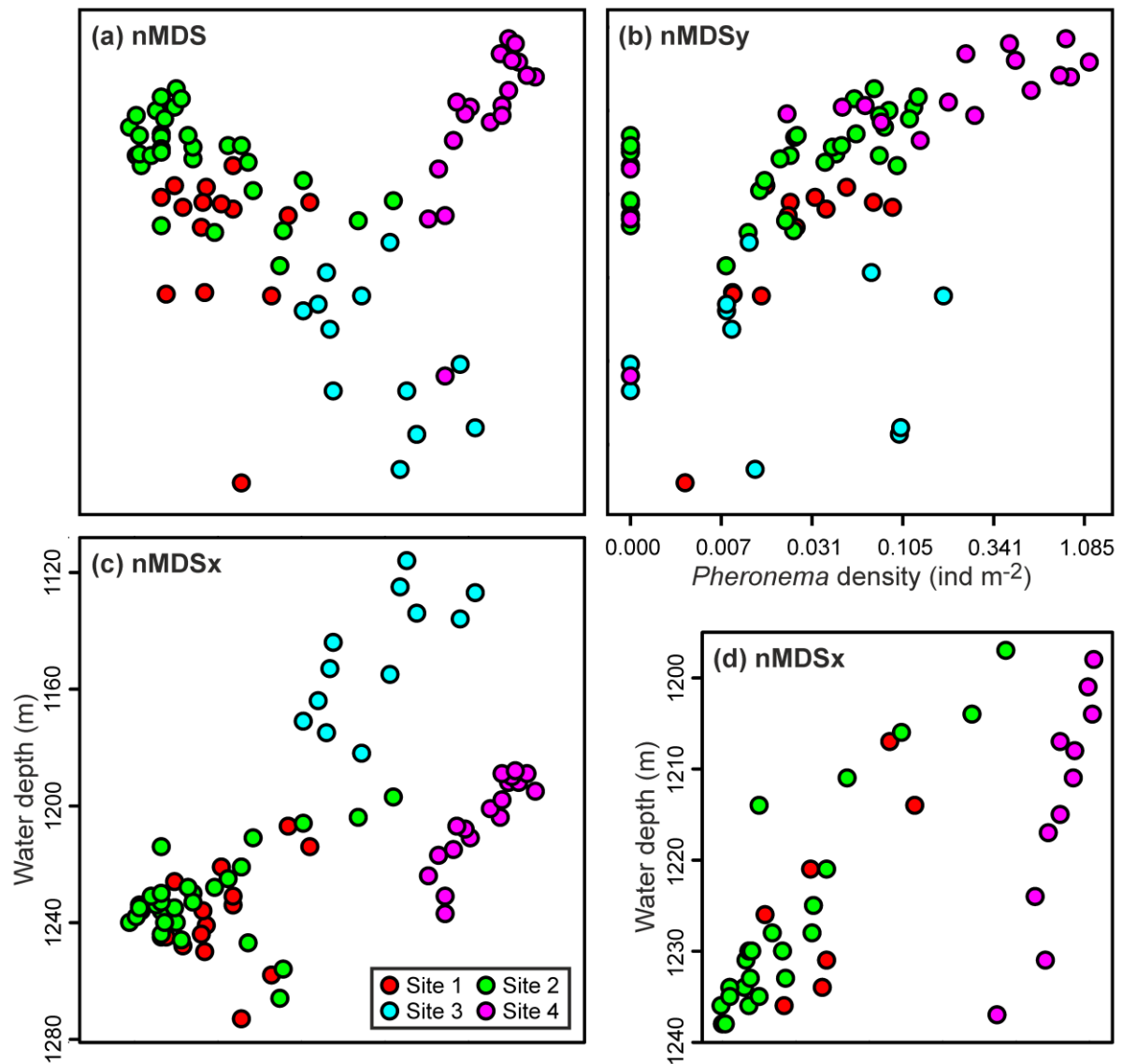
370 indicating substantial, statistically significant variation in assemblage composition between

371 Sites ($R = 0.738$, $p < 0.001$), with follow-up pairwise tests suggesting modest, statistically

372 significant differentiation of Sites 1 and 2 ($R = 0.272$, $p < 0.001$), and substantial, statistically

373 significant differentiation in all other cases ($R > 0.697$, $p < 0.001$).

374



375

376 **Figure 7.** Variations in megafaunal assemblage composition by: (a) Site (2D stress = 0.091),
 377 (b) numerical density of *Pheronema carpenteri*, and (c, d) water depth. Faunal composition
 378 was assessed by 2D non-metric multidimensional scaling ordination (nMDS; see main text
 379 for detail). <2 column>

380

381 When the composite sample set was reduced to only those in a common depth range (Sites 1,
 382 2, and 4), statistically significant Spearman's rank correlations between the MDS x-ordinate
 383 and water depth were detected among all samples ($r_s = 0.755$, $p < 0.001$) and for Sites 1 and 2
 384 assessed separately ($r_s = 0.793$, $p < 0.001$), and Site 4 assessed separately ($r_s = 0.943$, $p <$
 385 0.001 ; Fig. 7d). The corresponding global ANOSIM test yielded a substantial, statistically
 386 significant difference in assemblage composition between Sites ($R = 0.657$, $p < 0.001$), with

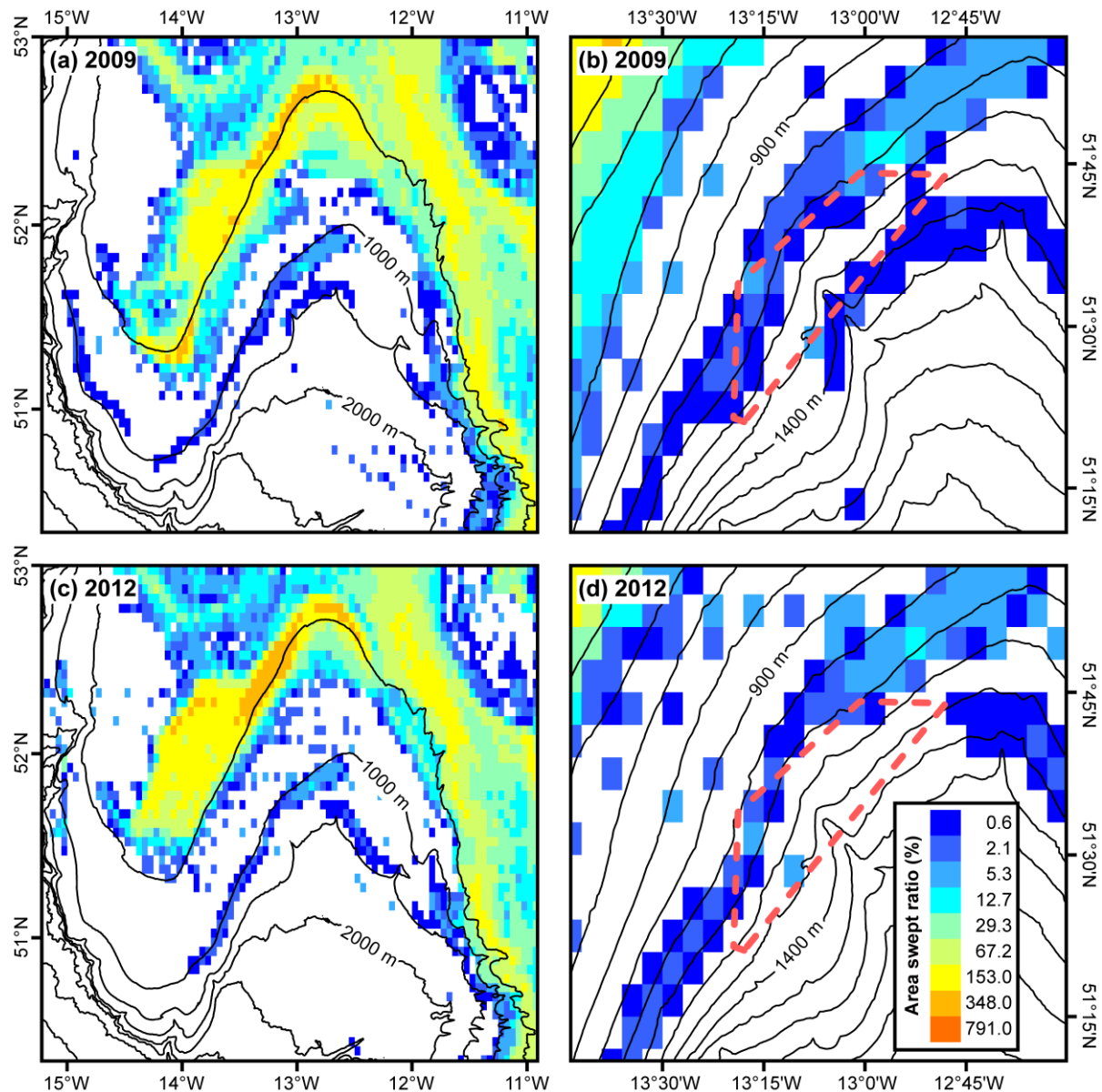
387 follow-up pairwise tests indicating modest, statistically significant differentiation of Sites 1
388 and 2 ($R = 0.228$, $p = 0.036$), and substantial, statistically significant differentiation between
389 Site 4 and both Sites 1 and 2 ($R \geq 0.823$, $p < 0.001$). When the composite samples from Sites
390 1 and 2 were combined as a single ‘low / no trawling’ case and Site 4 considered as a
391 ‘trawled’ case (see Section 3.4), the corresponding ANOSIM test yielded a very substantial,
392 statistically significant difference in assemblage composition between those cases ($R = 0.893$,
393 $p < 0.001$).

394

395 **3.4. Bottom trawling activity**

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

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Figure 8. Annual fishing intensity, as swept area ratio, for selected years in the northern Porcupine Seabight: (a, b) 2009, (c, d) 2012. Red dashed polygon bounds the area of the present study (see Fig. 1). Depth contours are illustrated at 500 m intervals in (a, c) and at 100 m intervals in (b, d). 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

415 hexactinellid sponge *Pheronema carpenneri* were still present (Fig. 2). However, there
416 appeared to have been a very substantial reduction in the standing stock of sponges. Our
417 observations also revealed what appeared to be seafloor trawl marks, and our assessment of
418 the available OSPAR fishing pressure data indicated the occurrence of commercial deep-sea
419 demersal trawling in the area. Although we cannot provide direct evidence of bottom trawl
420 fishing impact on these deep-sea sponge aggregations, there is certainly reason for suspicion
421 and consequently cause for concern.

422

423 **4.1. Demersal fishing pressure**

424 The available OSPAR fishing pressure data (2009-2017) indicates that commercial bottom
425 trawling may have occurred in the general area of our survey. Indeed, those data potentially
426 indicate targeted fishing in the 1000-1200 m water depth range (Fig. 8) coincident with the
427 previously established core of the local *P. carpenneri* bathymetric distribution (Rice et al.,
428 1990), and that predicted more generally in recent modelling studies (Ross and Howell, 2013;
429 Ross et al., 2015). In addition, it has been suggested that the indirect effects of demersal
430 trawling extend to greater water depths than the fishing activity itself (Bailey et al., 2009;
431 Puig et al., 2012; Trueman et al., 2014). These effects may cause a reduction in the biomass
432 of both target and bycatch species, and may be reflected in the secondary production,
433 population body size, and trophic structure of benthic assemblages (Jennings et al., 2001;
434 Jennings and Blanchard, 2004; Hiddink et al., 2016). We did directly observe apparent
435 seafloor trawl marks at Sites 3 and 4 (Fig. 2), though cannot unequivocally attribute these to
436 commercial fishing operations. Broader-scale seafloor mapping, done visually or
437 acoustically, would likely provide a better assessment of these features (see e.g. Huvenne et
438 al., 2016; Meyer et al., 2019). Given the very marked decline in *P. carpenneri* numerical
439 density between the 1983/4 and 2011 surveys, considered in Section 4.2, it is conceivable that
440 all four sites may have been impacted by demersal trawling. Consequently, the between Site
441 differences in faunal diversity and composition recorded in the 2011 survey may represent
442 local ecological variations, for example bathymetric and / or near-bottom tidal current
443 velocities, rather than variations in fishing pressure per se.

444

445 **4.2. Temporal change in *Pheronema carpenneri* standing stocks**

446 Rice et al. (1990) reported high densities of *P. carpenteri* (mean 0.3 ind m⁻²) at water depths
447 between 1000 and 1300 m, with a maximum density of 1.6 ind m⁻² at 1210 m water depth.
448 Our best comparable estimate of numerical density for 2011 was 0.03 ind m⁻², i.e. an order of
449 magnitude lower. Similarly, peak recorded sponge density (in any 10 m depth band) reduced
450 by a factor of seven between 1983/4 and 2011, and most notably, average sponge density in
451 Rice et al.'s (1990) peak density depth range (1210 – 1250 m) declined by a factor of 36
452 between the surveys (Section 3.1; Fig. 3). We characterise this decline as dramatic. Estimated
453 *P. carpenteri* standing stock numerical density is certainly variable geographically, for
454 example: Rosemary Bank 0.1 ind m⁻² (McIntyre et al., 2016); Morocco Margin 0.2 ind. m⁻²
455 (Barthel et al., 1996); Goban Spur 1.5 ind m⁻² (Hughes and Gage, 2004); and Le Danois Bank
456 7.4 ind m⁻² (Sánchez et al., 2008). Nevertheless, our results suggest a very substantial decline
457 in the Porcupine Seabight sponge population between the 1983/4 and 2011 surveys. Change
458 in standing stock biomass, potentially, offers a more valuable assessment as it incorporates
459 change in both numerical density and individual body mass. Our first order approximation of
460 that change was a factor of 40 decline generally, and a factor of 60 decline in Rice et al.'s
461 peak density depth range (Section 3.1). Again, we would tend to characterise that decline as
462 dramatic.

463

464 We cannot provide any direct evidence that demersal fishing was the direct or indirect cause
465 of the apparent decline in sponge standing stocks observed. However, we would suggest that
466 it is one plausible cause (Section 4.1). Our observations of somewhat variant response /
467 change at Site 4 are intriguing, but it is difficult to assess their potential ecological
468 significance. Rice et al. (1990) provide very little information for this Site (their Station
469 52022), simply noting that only three sponge specimens were photographed. Indeed, the latter
470 authors considered the Site 4 location to represent the western limit of the distribution of *P.*
471 *carpenteri* in the Porcupine Seabight. In contrast, our 2011 survey data from Site 4 suggest an
472 abundant population of small sponges in a narrow bathymetric band centred on 1190 m water
473 depth (Fig. 3). Given that we observed apparent seafloor trawl marks at Site 4, but not at
474 Sites 1 and 2, it is conceivable that the marked shift in sponge body size distributions might
475 be attributable to more, or more recent, demersal trawling at Site 4. However, given the
476 absence of earlier data on sponge body size distributions for Site 4, and the appreciable shift

477 in the centres of bathymetric distribution between these sites, it is at least equally likely that
478 other environmental factors may have been involved.

479

480 **4.3. Spatial variation in the megafaunal assemblage**

481 Despite the apparently substantial decline in the standing stock of *P. carpenteri* between the
482 1983/4 and 2011 surveys, our results suggest that the presence of sponge aggregations
483 continued to exert a positive influence on the diversity of the megafaunal assemblage
484 (Fig. 6). These results are consistent with the identification of deep-sea sponge aggregations
485 as 'hotspots' of biological diversity (Thomson, 1873; Bett & Rice, 1992; Hawkes et al., 2018;
486 Meyer et al., 2019), even in an apparently degraded state. If we accept that Site 4 was subject
487 to more, or more recent, trawling impact than Sites 1 and 2, then that impact may have
488 resulted in a statistically significant reduction in species richness (Section 3.2; Fig. 6). There
489 are likely to be multiple mechanisms by which the presence of sponges, and their spicule
490 mats, enhance the biological diversity of the associated assemblage. Perhaps most obviously
491 in the present case is a habitat-mosaic effect (see e.g. Benoist et al., 2019). The environment
492 studied here, in effect, comprises three habitats: (i) open sediment surface, (ii) sponge spicule
493 mats, and (iii) living sponges. Each of the constituent habitats may have associated unique
494 species and preferentially occurring species. Consequently, when these habitats are assessed
495 in toto as a composite environment, biological diversity is increased both by an increase in
496 species richness (addition of unique species restricted to individual habitats) and by a
497 reduction in dominance (amalgamation of different dominant species from individual
498 habitats). The influence of the presence of spicule mats on the diversity of the benthic fauna,
499 and on the occurrence of particular taxa, has previously been examined by Bett & Rice
500 (1992) for the macrobenthos. The potential significance of spicule mats in the present study is
501 further considered in Section 4.4.

502

503 In common with our assessment of assemblage diversity, faunal composition also exhibited
504 statistically significant trends with both *P. carpenteri* numerical density and water depth (Fig.
505 7b-d). These results suggest that the presence of sponges, even at markedly reduced standing
506 stock levels, continues to exert an appreciable influence on the composition of the
507 megafaunal assemblage, and equally cautions the comparison of assemblages drawn from
508 different bathymetric horizons. If we accept that Site 4 was subject to more, or more recent,

509 trawling impact than Sites 1 and 2, then that impact may have resulted in a statistically
510 significant change in faunal composition (Fig. 7d). Assessed only over the common water
511 depth range surveyed, the faunal composition of Sites 1 and 2 was jointly highly distinct from
512 that of Site 4. However, as considered in Section 4.2, note that Rice et al. (1990) only
513 encountered three *P. carpenneri* specimens at Site 4, with a fourth specimen taken in a nearby
514 trawl, and considered the location to be at the Westerly limit of the sponges' core distribution
515 in the Porcupine Seabight. Consequently, we must similarly caution that it is certainly
516 conceivable that other environmental factors might also have been involved in the
517 differentiation of Site 4 from Sites 1 and 2.

518

519 **4.4. Potential impact of demersal fishing**

520 Differences in benthic faunal assemblage composition and diversity have been observed
521 between locations subject to different trawling intensities (Hiddink et al., 2006; Ramalho et
522 al., 2017). The degree of assemblage change has been linked to the frequency and / or
523 intensity of disturbance (Rooper et al., 2011; van Denderen et al., 2015; Sorte et al., 2017). In
524 the present case, it is conceivable that the status of Site 4 represents a more recent and / or
525 more intense impact than had been experienced at Sites 1-3, though our limited prior
526 knowledge of Site 4 suggests the need for cautious interpretation (Section 4.3). Nevertheless,
527 the evidence of demersal fishing activity in the general area of our study (Section 4.1), and
528 the dramatic reduction in *P. carpenneri* standings stocks between 1983/4 and 2011 (Section
529 4.2) is suggestive of a substantive impact by demersal fishing. The continental slope of the
530 Porcupine Seabight has been subject to increased demersal trawling since at least 1989
531 (Priede et al., 2011; Vieira et al., 2019). Previous surveys in the Hatton Bank area of the NE
532 Atlantic have suggested that bottom trawling was a plausible cause for reduced standing
533 stocks of corals and sponges (Muñoz et al., 2012). Similarly, long-term changes in the
534 numerical and biomass density of deep-water fish populations in the Porcupine Seabight have
535 been attributed to commercial fishing pressure (Bailey et al., 2009; Godbold et al., 2013;
536 OSPAR, 2017).

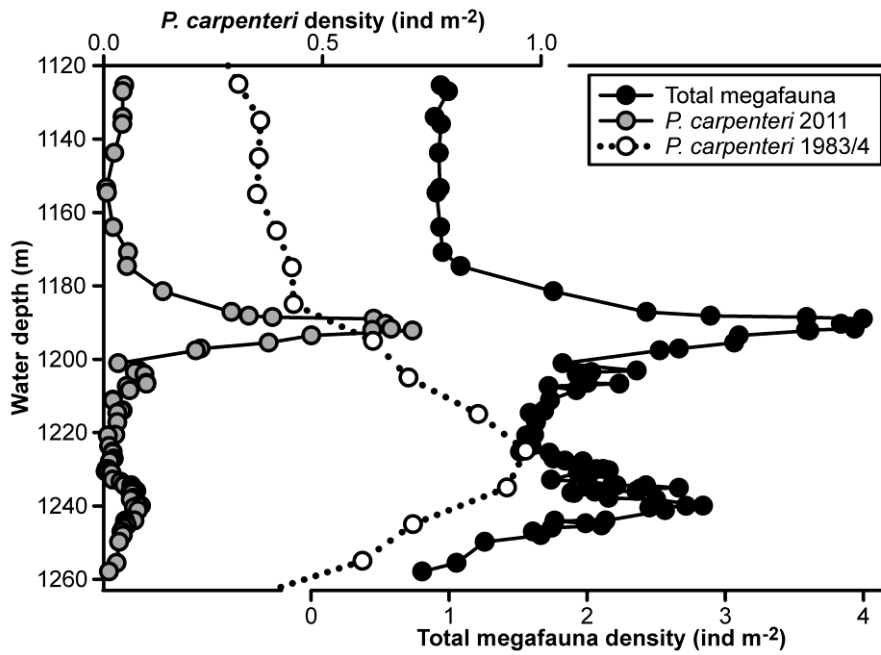
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538 It is both the mass occurrence, and habitat forming characteristics, of deep-sea sponges that
539 primarily attract their classification as features of conservation interest and as vulnerable
540 marine ecosystems (e.g. FAO, 2009; ICES, 2009). Taken in total, our 2011 survey data

541 indicate an order of magnitude decline in the numerical density of *P. carpenteri* in the core of
542 the previously determined distribution (1210-1240 m water depth; Rice et al., 1990) and a
543 narrow dramatic 'spike' in sponge density at c. 1180-1200 m, that reaches values broadly
544 comparable with Rice et al.'s (1990) observations (Fig. 9). Our data also appear to indicate an
545 enhanced numerical density ($>1.5 \text{ ind m}^{-2}$) of all megafauna in a comparable total depth range
546 (1180-1250 m). It is perhaps notable that there are two 'spikes' in megafauna density, one
547 corresponding to peak sponge density at c. 1190 m water depth, and one approximately
548 corresponding with the 1983/84 peak in sponge density at c. 1225-1245 m. The first
549 megafauna density spike potentially representing the expected enhancement of the fauna
550 associated with a living sponge aggregation, the second potentially reflecting the residual
551 effect of sponge spicule mats (skeletal remains) from the former sponge aggregation (see e.g.
552 Bett and Rice, 1992; Laguionie-Marchais et al., 2015). Some evidence for the latter effect
553 may be present in the markedly enhanced densities of large ascidians (Fig. 2) in a
554 bathymetric range (1210-1250 m; Fig. 10) that is well matched to the zone of abundant
555 sponges identified by Rice et al. (1990). It is at least conceivable that these filter feeders have
556 'opportunistically' replaced the former dense aggregation of sponges, using the remaining
557 spicule mats as a substratum.

558

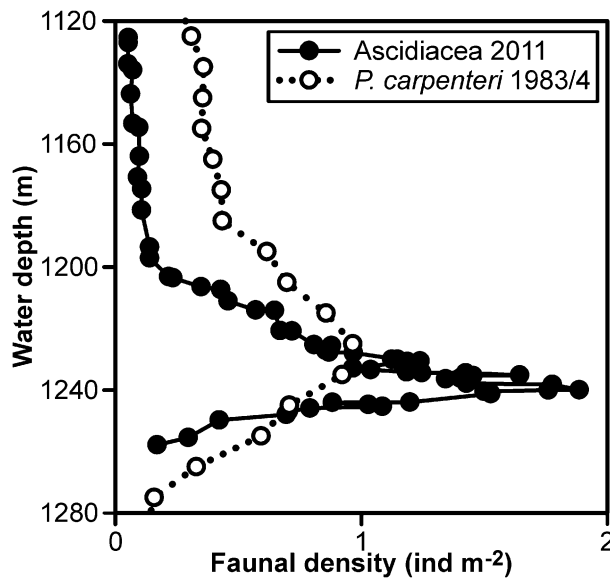
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560
 561 **Figure 9.** Variation in the numerical density of the megafaunal assemblage, and that of
 562 *Pheronema carpenteri* alone, with water depth. Data presented as 5-sample running mean
 563 with water depth across Sites 1-4 for 2011 and Sites 1-3 for *P. carpenteri* 1983/4. <1.5

564 column>

565



566
 567 **Figure 10.** Variation in the numerical density of ascidians in 2011, and that of *Pheronema*
 568 *carpenteri* in 1983/4. Data presented as 5-sample running mean with water depth across Sites
 569 1-3. <1 column>

570

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

586

587 We similarly note the exceptional long-term observations of Dayton et al. (2016) that indicate
588 the potential for very dramatic shifts in sponge recruitment and growth in an Antarctic shelf
589 sea environment. Works by Kahn et al. (2012) and Strand et al. (2017) have indicated the
590 scope for responses to temporal change in particulate organic flux and bottom water
591 temperatures in deep-water sponge populations. Other shelf sea hexactinellid aggregations,
592 such as those of the Salish Sea (Conway et al., 2005; Dunham et al., 2018), have been subject
593 to small-scale experimental disturbance (deliberate crushing by ROV) that revealed no
594 recovery after three years (Kahn, et al., 2016). Other experimental studies have examined the
595 potential impact of increased suspended sediment loads, such as may occur as a result of
596 bottom trawling, and indicate the scope for physiological effects (Tjensvoll et al., 2013; Kutti
597 et al., 2015). In general, the natural history of deep-water sponges, not least the
598 hexactinellids, remains very poorly known despite their classification as features of
599 conservation interest and vulnerable marine ecosystems. As key deep-sea 'ecosystem
600 engineers' (e.g. Coleman and Williams, 2002; Hogg et al., 2010; Grant et al., 2019), a better
601 understanding of their fundamental biological characteristics would improve the basis for
602 resource management decisions.

603

604 **4.5. Conservation and policy**

605 We have provided evidence for the degradation of deep-sea sponge aggregations in the
606 Porcupine Seabight potentially resulting from bottom trawl fishing, as indicated by fishing
607 pressure data (Fig. 8), the presence of seabed trawl marks at two of our four study sites (Fig.
608 2), and an apparent order of magnitude reduction in the local sponge population (Section 4.2).
609 Examples of human impacts on deep-sea habitats continue to accumulate (e.g. Ramirez-
610 Llodra et al., 2011; Clark et al., 2016; Huvenne et al., 2016), suggesting an on-going need for
611 the development of, or extension of, conservation and environmental protection measures in
612 deep-water environments (European Union, 2008). The European Parliament has now
613 approved the adoption of a regulation aimed at the sustainability of deep-sea fisheries,
614 indicating the prohibition of deep-sea fishing with bottom trawls below 800 m water depth,
615 and an obligation for vessels to report encounters with vulnerable marine ecosystems at water
616 depths greater than 400 m (European Union, 2016). That regulation would certainly apply in
617 the case of the Porcupine Seabight *P. carpentieri* population studied here, with Annex III
618 VME indicator species including, 3. (c) Deep-sea sponge aggregations, Glass sponge
619 communities, Rossellidae and Phoronematidae. The regulation represents a European Union
620 commitment to implement the resolutions of the General Assembly of the United Nations
621 (61/105 and 64/72) that call for the protection of vulnerable deep-sea marine ecosystems
622 from the impact of bottom fishing gears (UNGA, 2006, 2009).

623

624 The use of water depth-related management measures has a clear logic and evidence base in
625 the case of deep-sea demersal fishing in EU waters (Clarke et al., 2015) and could perhaps be
626 implemented elsewhere. How such a measure might be applied and enforced in areas beyond
627 national jurisdiction (High Seas) will require further consideration. It potentially falls to the
628 regulatory authority of the United Nations Convention on the Law of the Sea (Harrison et al.,
629 2017) and the role that Regional Fisheries Management Organisations, under the auspices of
630 the Food and Agricultural Organisation, and the International Seabed Authority, have in
631 managing activities in Areas Beyond National Jurisdiction. Such organisations, and the
632 scientific community, typically advocate an ecosystems-based approach and the use of the
633 precautionary principle in deep-sea environmental management (Thompson et al., 2016;
634 Huvenne et al., 2016; Kenny et al., 2018). Our observations of the status of the deep-sea

635 sponge aggregations in the Porcupine Seabight suggest that such efforts would greatly benefit
636 from an increase in the sustained observation of selected deep-sea habitats / species /
637 ecosystems of conservation interest (see also Kazanidis et al., 2019) and a much better
638 understanding of the natural history of the key species in those environments. A 'Deep
639 Essential Ocean Variable' of seafloor sponge cover, is currently under consideration by the
640 Deep Ocean Observing Strategy team (Levin et al., 2019), that could readily be achieved via
641 the use of autonomous underwater vehicles (e.g. Benoist et al., 2019; Simon-Lledó et al.,
642 2019) as have recently been employed in the investigation of deep-water sponge grounds
643 (Meyer et al., 2019).

644

645 **Acknowledgements**

646 The authors are grateful to the captain, crew and scientists of RRS *James Cook* cruise 062.
647 Thanks also to D.S.M. Billett, A.J. Gooday, P.A. Tyler, R. Milligan, C. Mah and A.
648 Rogacheva for their help in the megafauna identification, V. Huvenne for her assistance
649 producing maps, and to A. Kenny, A.R. Santos, and S. Ramalho for useful comments. RPV
650 was supported by a doctoral grant from the Portuguese Science Foundation
651 (SFRH/BD/84030/2012). Thanks are due to FCT/MCTES for the financial support to
652 CESAM (UID/AMB/50017/2019), through national funds. DOBJ was supported by funding
653 from the European Union's Horizon 2020 research and innovation programme under the
654 MERCES (Marine Ecosystem Restoration in Changing European Seas) project, grant
655 agreement No 689518. For BJB, DOBJ, and HAR, this article represents a contribution to the
656 Climate Linked Atlantic Sector Science (CLASS) project and was supported by UK Natural
657 Environment Research Council National Capability funding, grant number NE/R015953/1.
658 The data produced to support this article are available on request from the lead author.

659

660 **Author contributors**

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

665

666 **Declaration of interest: None**

667

668 **Submission declaration**

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

672

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