The influence of hexactinellid sponge (Pheronema carpenteri) spicules on the patchy distribution of macrobenthos in the Porcupine Seabight (Bathyal NE Atlantic)

Article *in* Ophelia · November 1992

Impact Factor: 0.96 · DOI: 10.1080/00785326.1992.10430372

OPHELIA 36 (3): 217-226 (November 1992)

THE INFLUENCE OF HEXACTINELLID SPONGE *(PHERONEMA CARPENTERI)* SPICULES ON THE PATCHY DISTRIBUTION OF MACROBENTHOS IN THE PORCUPINE SEABIGHT (BATHYAL NE ATLANTIC)

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ABSTRACT

The hexactinellid sponge *Pheronema carpenteri* occurs in high densities (1.5 m^{-2}) over a narrow bathymetric range (1000-1300 m) in the Porcupine Seabight, to the southwest of Ireland. The possible influence of sponge spicule mats, which may cover ⅓ of the seafloor, on macrobenthic communities is assessed. Three box core samples were collected from the high density sponge zone (1250 m) and ~~three cores were~~ taken at each of two comparative non-sponge stations (900 and 1500 m). Analysis of data on the abundance and taxonomic composition of major groups of the larger (> 1 mm) macrobenthos suggests that the presence of sediment surface sponge spicule mats substantially modifies the fauna at the 1250 m station. The numerical abundance of macrobenthos within this station increases in an almost linear fashion with the volume of spicules present in a sample; in a single sample with the highest spicule volume, abundance was nearly an order of magnitude higher than that expected in the absence of spicule mats. The possible nature of sponge-macrobenthos interaction and the wider significance of the results are considered further.

INTRODUCTION

Barthel (1992) has recently suggested that the presence of hexactinellid sponges significantly influences the nature of Antarctic sponge populations, and potentially the benthos as a whole, by modifying the substrate. She further suggests that hexactinellids may play a similar role in benthic communities outside Antarctica, noting in particular the mass occurrences of species of the genus *Pheronema* as possible examples. This paper reports data from such a *Pheronema* population that appear to support Barthel's suggestion.

The present study was sited in an abundant population of *Pheronema carpenteri* (Thomson, 1869) in the Porcupine Seabight to the southwest of Ireland as reported by Rice et al. (1990). The sponges occur within a narrow bathymetric range, 1000 to 1300 m depth, reaching abundances in excess of 1.5 m^{-2} and a peak ash-

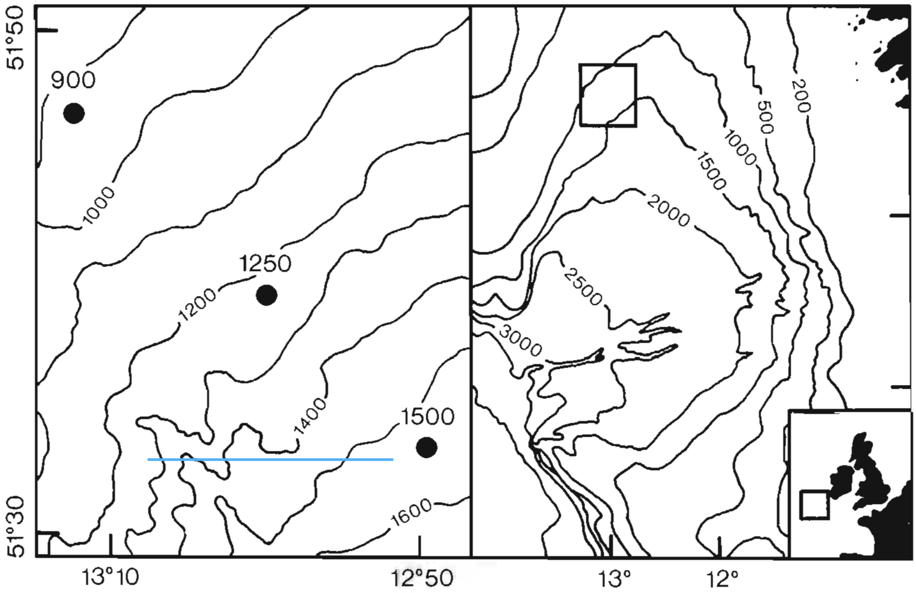

Fig. 1. Location and bathymetry of the Porcupine Seabight are shown to the right, box core sampling stations are shown to the left (all depths in metres).

free dry weight biomass of over 10 g m^{-2}, more than an order of magnitude higher than the total megabenthic biomass immediately above or below the sponge zone (Lampitt et al. 1986). There is no evidence for an increase in the total supply of organic matter to the sponge zone. Instead, Rice et al. (1990) suggested that local hydrographic conditions, particularly topographic enhancement of near-bottom currents, may favour suspension feeders in this area. Here we report an investigation of the possible influence of sponge spicule accumulations on the macrobenthos of the region.

We are grateful to our IOSDL colleagues, particularly Mike Thurston, for their assistance in obtaining the samples. Our thanks are also due to Drs Dagmar Barthel and Lisa Levin for their valuable comments which improved the paper. The work was funded partly under contract 0037 of the EEC MAST programme.

METHODS

Sampling was carried out from RRS Challenger (cruise 79) between 29 May and 1 June 1991. A study site within the presumed sponge zone was located, at a nominal depth of 1250 m, to correspond approximately with the area of high sponge densities recorded on photosledge transect 52018 as reported by Rice et al. (1990). Comparative sites were located upslope and downslope of this position at nominal depths of 900 m and 1500 m respectively (see Fig. 1).

Table 1. Summary of spade box core samples collected between 29 May and 1 June 1991 in the Porcupine Seabight from RRS Challenger.

Sample	Nominal depth (m)	Measured depth (m)	Position latitude North	Position longitude West	IOSDL station number
A	900	905	51°46.8′	13°13.4′	52707 #1
B	900	905	51°47.3′	13°13.8′	52707 #4
C	900	900	51°46.6′	13°13.6′	52707 #6
D	1250	1241	51°39.0′	13°00.6′	52708 #2
E	1250	1239	51°39.1′	13°00.3′	52702 #5
F	1250	1238	51°39.6′	12°59.5′	52702 #2
G	1500	1536	51°33.7′	12°49.7′	52703 #3
H	1500	1539	51°33.4′	12°50.1′	52709 #1
I	1500	1534	51°33.7′	12°49.9′	52709 #2

Three spade box core (USNEL type, 0.25 m^2) samples were recovered at each of the three study sites (see Table 1). The top 10 cm layer of sediment was removed from each box core, washed through a 1 mm mesh sieve and the residues fixed in buffered formalin. These samples were sorted in the laboratory and all metazoans identified to major taxa and counted. The presence and quantity of spicules was also determined for each sample. For the comparative sites at 900 and 1500 m this was simply a count of all recognisable siliceous spicules; this approach was not practical for the 1250 m samples where, instead, the volume occupied by the loose packed spicule mass in the original sample container was recorded.

RESULTS

In addition to the sampling programme detailed above, an IOSDL WASP (Wide-Angle Survey Photography) camera system was also deployed in the vicinity of the 1250 m station. The photographs obtained (see e.g. Fig. 2) confirmed the presence of dense *Pheronema* populations and indicated that sponge spicule mats consistently covered about one third of the seafloor in the sponge zone.

Obvious sponge spicule accumulations were present on the surfaces of two of the box core samples (cores E and F); in core E they were relatively diffuse, in core F the accumulations were dense and could be lifted almost intact from the surface of the core. Examination of the sieved residues revealed siliceous spicules in all but one of the samples (core B). In relative terms, very few spicules were present in the samples from the 900 and 1500 m stations. Exact counts of the numbers of spicules present in the 1250 m station samples were not attempted but it was clear that they contained at least two orders of magnitude more spicules than any of the other samples.

Fig. 2. Photograph taken with the IOSDL WASP (Wide Angle Survey Photography) system in the vicinity of the 1250 m station during box core sampling. Numerous sponges and spicule mats (darker areas) of varying densities are visible in this vertical view of c. 15 $m^2$of seafloor.

The abundance and composition of the fauna in the nine cores studied is given in Table 2 together with the quantity of sponge spicules recorded in each sample.

Statistical comparisons of the variation in abundance between stations, using the Kruskal-Wallis test (Sokal & Rohlf 1969), yield, few significant results. Significant ($p < 0.05$) differences were detected in the abundance of gastropods, nematodes, and sipunculids, but not in the abundance of the fauna as a whole. Gastropods were consistently more abundant at the 1250 m station, and sipunculids were consistently more abundant at the 900 m station. The 'large' nematodes included in the analysis constitute an artificial group that was formed in an attempt to avoid the likely bias in the recovery of nematodes, ie due to small forms being retained preferentially in the presence of large quantities of sponge spicules. Given the artificial nature of the 'large' nematode group the biological significance of apparent changes in their abundance must be viewed with caution.

Changes in faunal composition were examined using a number of classification and ordination techniques, all of which provided broadly similar results. Relatively discrete and distinct groupings were formed by the replicates from the 900 m and 1500 m stations respectively. The two highest spicule influence samples from the 1250 m station constituted a third distinct group, with the remaining replicate from this station being located closer to the samples from the other stations. Figure 3 illustrates the results of a principal components analysis (Heip

Table 2. Numerical abundance of the larger (> 1 mm) macrobenthos from the top 10 cm sediment layer of spade box core samples (0.25 m^2) taken in the Porcupine Seabight. The numbers or loose packed volume of sponge spicules present in each sample is also given. ([1]headed specimens only, [2]colonial forms considered unitary, [3]large specimens only).

Depth	900 m			1250 m			1500 m		
Sample	A	B	C	D	E	F	G	H	I
Taxon									
Polychaeta[1]	19	17	5	4	43	101	9	15	9
Ophiuroidea	1	7	1		17	186	1		2
Bivalvia	13	15	5	7	18	39	11	15	8
Echinoidea	28	8	4		18	14	1	4	
Gastropoda	2		2	22	13	12	1	1	
Bryozoa[2]					38	12		1	
Nematoda[3]				3	12	19	2		3
Cumacea	8	3	2	2	6	8		2	4
Porifera					4	14	6	4	3
Amphipoda		7	1	1	2	8	3	6	2
Tanaidacea	1	2		1	5	9		4	6
Ascidiacea	1	1				9	4	3	7
Scaphopoda	3	2		6		5	2	3	1
Sipuncula	5	5	8			3			
Isopoda					1	4	7	5	1
Hydrozoa[2]					3	7			
Anthozoa	1	2	3	1		1		1	1
Aplacophora	1			4		3			
Echiura		7						1	
Ostracoda	1	1				1			
Holothuroidea					1				
Indeterminate	2				6	5			1
Total	86	77	31	51	187	460	47	65	48
Spicules									
number	13	0	6	–	–	–	60	150	15
volume (ml)	-	-	-	250	500	1250	-	-	-

et al. 1988) based on a covariance matrix of the log (x + 1) transformed abundances of the 15 most abundant taxa. The eigenvalues of the first two axes are 1.523 and 0.564, which together account for 70% of the variance in the dataset.

The two trends revealed by the principal components analysis seem to be explicable in simple terms. The first, represented by axis 1, appears to be related to the degree of spicule influence; samples from the 1250 m station are ordered according to the measured volume of spicules present in each. More realistically, perhaps, it differentiates samples where coherent sediment surface spicule mats were present from those where they were not present. The second trend, represented by axis 2, is clearly related to water depth, since all the samples are ordered according to nominal station depth. The Spearman rank correlation

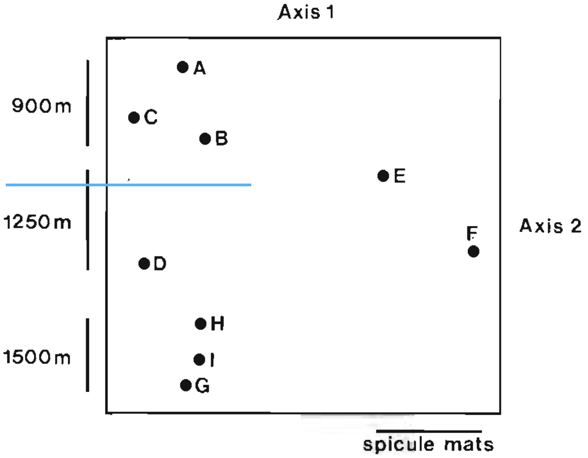

Fig. 3. Ordination (principal components analysis, see text for details) of the nine box core samples taken in the Porcupine Seabight. The first axis appears to relate to the presence or absence of sediment surface spicule mats, and the second axis to a depth gradient.

(Sokal & Rohlf 1969) between nominal depth and axis 2 score is significant ($p < 0.002$), as is that between measured depth and axis 2 score ($p < 0.01$).

An illustration of the faunal changes that underlie these two trends is given in Fig. 4. In terms of average abundance there is one group of taxa that exhibit a gradation in their distributions with depth. These range from the sipunculids that are most abundant at the 900 m station and absent from the 1500 m station, through the polychaetes and bivalves that are most abundant at the 1250 m station and somewhat less abundant at the other two stations, to the isopods that are most abundant at the 1500 m station and rare or absent from the 900 m station. A second group of taxa, including the gastropods, ophiuroids and bryozoans, are virtually restricted to the 1250 m station.

There is considerable variation in the abundance and composition of the fauna in the 1250 m station replicates. Most of this variation appears to be related to the quantity of spicules present; of the ten most abundant taxa, seven increase in abundance with the degree of spicule influence. Overall, total abundance increases in an almost linear relationship with the degree of spicule influence (Table 2).

DISCUSSION

Bathymetric changes in the numerical abundance, biomass, and diversity of the bathyal benthos have been studied extensively (see Gage & Tyler 1991 for review). Variation in the supply of organic matter is usually implicated as a major factor in the generally observed decrease in abundance and biomass with increasing depth (Lampitt et al. 1986). Over the comparatively narrow bathymetric range studied here, the average numerical abundance of macrofauna dropped from 260 m^{-2} at the 900 m station to 220 m^{-2} at the 1500 m station, though the difference is not statistically significant. Abundance in the low spicule influence sample

	900m	1250m	1500m
Sipuncula	**********	**	
Echinoidea	**********	********	*
Cumacea	********	**********	****
Bivalvia	*****	**********	*****
Polychaeta	***	**********	**
Porifera		**********	*******
Ascidiacea	*	******	**********
Isopoda		****	**********
Gastropoda	*	**********	
Ophiuroidea		**********	
Bryozoa		**********	

Fig. 4. An illustration of the change in average numerical abundance of selected taxa between stations. Two groups are shown, those (upper) that exhibit a graded distribution with depth, and those (lower) more restricted to the 1250 m station.

from the 1250 m station was broadly similar at around 200 m^{-2}, perhaps supporting the suggestion by Rice et al. (1990) that the sponge zone does not receive a significantly greater organic supply than the zones on either side.

In contrast, the abundance in the high spicule influence core from the 1250 m station was almost an order of magnitude higher (1800 m^{-2}) and may well be related, in part at least, to locally enhanced supplies of organic matter associated with sponges and their ~~spicule mats~~.

The richness of life associated with *Pheronema* populations in the north-eastern Atlantic has been appreciated for more than a century (e.g. Thomson 1873). Early investigators relied on dredges and trawls and consequently failed to recognise ~~small-scale patchiness~~ in the distribution of organisms. Subsequent improvements in sampling techniques have provided more detailed evidence for the interactions between hexactinellid sponges, accumulations of their spicules, and other members of the ~~benthos. The most~~ dramatic observations are from Antarctica, where hexactinellids are a conspicuous element of the sublittoral fauna; in places their spicules may contribute 50-70% of the sediment bulk, with spicule mats over half a metre thick (Dell 1972). Dayton et al. (1970) report a significant influence of sponges on the zonation of the benthos in McMurdo Sound where their spicule mats provide a suitable substrate for infaunal organisms but reduce the exposed rock surface available to sessile organisms.

Barthel (1992) envisages a different process operating in open sediment areas that is relevant to the present study. Barthel & Gutt (1992) noted the key role of substrate type in determining the characteristics of sponge associations in the eastern Weddell Sea. Barthel (1992) subsequently suggested a form of successional change in sponge associations controlled by hexactinellids: areas of open sediment are colonised by hexactinellids which modify the sediment by the deposition of their spicules, providing a suitable substrate for a variety of demosponge species otherwise unable to colonise the open sediment. She also suggests that the effect may not be limited to sponges, but that other members of the benthos may also benefit from this modification of the sediment.

Direct evidence for interaction between hexactinellids and macrobenthos is limited, but the work reported by Jumars (1976) and Jumars & Eckman (1983) is particularly relevant. Hexactinellid sponge fragments were found in five box core samples from the Santa Catalina Basin (1130 m) and were quantified by estimating the area of all fragments retained on a 1 mm mesh sieve. Polychaete abundance was significantly correlated with the area of sponge fragments encrusted with foraminiferans, but not with total sponge fragment area. A perfect co-ranking, and hence significant correlation, is evident between the abundance of macrobenthos as a whole and the area of sponge fragments encrusted with foraminiferans (see Jumars 1976, table 5). Our data also show a similar correspondence in the rank order of spicule volume and total macrofaunal abundance from the 1250 m station samples.

Jumars and Eckman (1983) imply that it is the presence of hexactinellid fragments at the sediment surface, and therefore accessible to encrusting foraminiferans, that is important in determining the nature of the spicule influence. Levin (1991) has reviewed the interactions between benthic metazoans and large agglutinating protozoans (Foraminiferida and Xenophyophorea), providing a good model for assessing the possible relationships between hexactinellids, their spicule mats, and the macrobenthos. She divides the possible interactions into two major groups (a) direct effects local to the biogenic structure, and (b) indirect effects operating in the near-field. Three categories of direct effect are particularly relevant here:

(i) *Provision of hard substrate in an open sediment situation.* All of the ascidians recovered in the high spicule influence sample from the 1250 m station were comparatively large, solitary, gelatinous forms that were firmly attached to sponge spicules. In contrast, all of the ascidians from the other two stations were small infaunal forms. Other sessile taxa, hydroids and bryozoans, were very largely restricted to the two high spicule influence samples from the 1250 m station.

(ii) *Provision of refugia from predation or physical hazard.* As Levin (1991) discusses, sediment stabilisation and the inhibition of predators by marsh or seagrass rhizomes may be a good shallow-water analogue in this context. It is easy to imagine similar functions for hexactinellid spicules. Organisms inhabiting the prostalia of living sponges, those within spicule mats, and potentially those in sediment rich in spicules may well be afforded some protection; the feeding activities of large predators may be inhibited by the spicules.

(iii) *Provision of an enhanced food supply.* Of the various mechanisms suggested by Levin (1991), access to trapped particulate matter within the biogenic structure, and access to an elevated feeding position are potentially the most important in the present case. Ophiuroids and ascidians certainly appear to use sponges and spicule mats as perches to gain access to the presumably higher water flow rates above the sediment-water interface (see fig. 4 in Rice et al. 1990). The Porcupine ~~Seabight is known~~ to be an area subject to a highly seasonal input of phytodetrital material (Billett et al. 1983, Rice et al. 1986). Once on the seabed, this material is redistributed by the near-bottom currents and accumulates around mounds and in depressions. We suggest that the sponges and their spicule mats act in this way to trap phytodetrital material and thus attract the ~~associated macro~~fauna.

The natural history of the sponge zone within the Porcupine Seabight is intriguing in its own right, but it may have a much wider relevance to deep-sea ecology as a whole. The increased awareness of 'patchiness' in the deep-sea (Rice & Lambshead 1992) suggests that patch-dynamics, or contemporaneous disequilibrium, may be important in structuring deep-sea benthic communities. Gage & Tyler (1991) note that the study of these mechanisms will be difficult since patches are generally rare and may be unpredictable, transient and fragile. Moreover, experimental studies risk complicating subsequent interpretations. Nevertheless, it is to be expected that "opportunities in the shape of natural disturbances of different sorts will present themselves" (Gage & Tyler 1991). The sponge zone in the Porcupine Seabight may offer just such an opportunity.

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