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Distribution of sponges on the Mauritanian continental shelf

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Key words: Biogeography, faunal barrier, Porifera

Abstract

Transect sampling on the continental shelf off the Banc d'Arguin, Mauritania, revealed a patchy distribution of sponge species and populations. Major sponge habitats are inshore coastal sandstone flats harbouring a diverse infaunal sponge fauna, and the moving substrate of shells of live gastropods or empty shells occupied by hermit crabs which harbour a numerically important but species-poor incrusting sponge fauna. The latter forms occur over most of the depth profile. Horizontal distribution of the sponges shows a distinct gap in species and numbers associated with a muddy bottom area where the sediment-rich Banc d'Arguin run-off is found. North and south of this gap the specific composition of the infaunal sponges is considerably different and this is explained as evidence for limitation of range extensions, notably of the southern sponge fauna, by the muddy area.

Introduction

Somewhere along the sandy continental platform off Mauritania or Senegal, the Mediterranean-Atlantic marine shallow-water biota reach their southern border to be replaced by the tropical marine biota of West Africa. Often quoted faunal borders are Cabo Verde (Senegal) and Cap Blanc (Mauritania) (e.g. Briggs, 1974; for sponges: Boury-Esnault & Lopes, 1985). Abiotic and ecological factors responsible for the faunal changes in these localities are, however, barely documented. One of the purposes of the Tyro Mauritania II Expedition (1988) (Van der Land, 1988) was to examine in detail the bottom conditions and quantitative distributions of the benthic organisms in a North-South series of transects set off at right angles to the coast of Mauritania. The results of this study, of which the part concerning the distribution of the sponges is presented

here, may contribute in understanding the nature of the faunal barriers in this area.

To date, no published reports are available on sponges from Mauritanian waters. A major reason for this lack of distributional data from that area may be the sandy nature of the sea bottom of the continental shelf off Mauritania, which does not invite the study of hard substrate dwellers such as sponges. The Tyro Mauritania II Expedition nevertheless secured approximately one hundred different species of sponges between 0 and 1900 m, and the majority of these were not collected from the often hard-bottomed continental slope as might be expected, but came from shallow waters on the continental platform between 0 and 100 m. There, two major substrates are available to sponges: the mobile substrate presented by extremely common gastropod shells and their empty shells inhabited by hermit crabs, and the hard sandstone platforms and ridges cov-

ered by a sufficiently thin layer of sand or mud, which harbour stalked or infaunal species. Less importantly, sponges may be epizoic on stems of hydroids, algae and gorgonids.

Study area and methods

The Tyro Mauritania II Expedition was part of a large programme of multidisciplinary marine biological investigations in the period of April to October, 1988, aimed at studying the area of the Banc d'Arguin ($20^{\circ}55' - 18^{\circ}49' \text{ N}$). The expedition used the Dutch research vessel Tyro as a platform for making eight bottom sampling transects at right angles to the coast of Mauritania from Cap Blanc in the north to just south of Cap Timiris (I–VIII in Fig. 1). The surface currents in the area are well known from previous oceanographic expeditions. In summary, there is a strong relatively cool current coming from the north (Canary Current), present all the year round, which gives off a branch into the Banc d'Arguin area south of Cape Blanco through the Passe de Lévrier. This branch leaves the Banc d'Arguin north of Cape Timiris. In the south a weak northwardly directed coastal current is present in the summer months. Eight transects were chosen at approximately equal distances of 15 geographic minutes (cf. Fig. 1: I–VIII), each from inshore coastal waters (depth limitation of the research vessel was 16 m) westward to continental slope depths (400–1900 m).

Sampling along the transects was done at regular depth intervals, using a variety of bottom gear, with a fixed routine for each gear-type: Van Veen grab (4 grabs at each station), Hamon grab (idem), Agassiz 1.2, 2.4 and 3.5 m trawls (single hauls with standard bottom time), rectangular dredge (idem). Samples were sorted immediately when on deck; sponges were isolated from the samples, characterized briefly, pre-identified, and preserved in ethanol. Of grab samples, bottom sediment was noted (categories: sandstone, sand, gravel, muddy sand, mud); distribution of these bottom sediments in the depth range of 10–100 m is presented in Fig. 2. In the area where the run-

off of Banc d'Arguin water is concentrated (transects IV–VI), bottom sediment samples were almost exclusively mud. Hard bottoms with thin layers of sediment are found mostly inshore, although here and there hard bottoms occur at depths of 50–60 m. The continental slope between 100 and 1000 m may be quite steep and canyon-like; in such areas the bottom is often rocky and may carry deep-water reefs (*Lophelia*). These deep-water reefs were found to contain an extensive sponge fauna. Species composition was found to resemble that of similar Northern Atlantic deep-water reefs, with such typical representatives as *Pachastrella monilifera* (Schmidt, 1868), *Desmacidon fruticosa* (Montagu, 1818), *Myxilla incrustans* (Johnston, 1842) and *M. rosacea* (Lieberkühn, 1859). Few if any species were found both there and in the shallow-waters. In other areas the slope is gradual and the bottom muddy, and sponges are absent. Deep-water samples (> 100 m) were identified to species level, but are ignored in the present study, because they clearly appear to belong to a separate fauna with a different ecological range and geographic distribution.

Sampling efforts varied somewhat over the various transects; the distribution over the eight transects of a total of 96 grab and trawl/dredge stations, and another 4 stations (3, 4, 7 and 8) involving wading/snorkling or other means of collecting, is presented in Fig. 3. Depths covered by the sampling efforts also varied, dictated by the nature of the continental platform in the various transects. The distribution of 100 stations over the depth profile in 10 m depth intervals is given in Fig. 4. In both Figs 3 and 4 sampling by grabs and trawls/dredges are presented also separately because they are widely different in area covered and have different capture efficiency with regard to mobile vs. infaunal sponges. Graphs of depth- and horizontal distributions of sponges presented below need to be compared with Figs 3 and 4.

Drs C. Franssen identified the hermit crab associates of 'mobile sponges'; Mr R. Moolenbeek identified the gastropod associates. Mr J. J. Vermeulen assisted in collecting and preserving the sponges. Dr J. van der Land allowed me to join

Fig. 1. Map of the continental shelf off northern Mauritania with the positions of the eight sampling transects (I–VIII) of the Tyro Mauritania-II Expedition; numbers along the transects refer to individual stations details of which are found in Van der Land (1988).

Fig. 2. Bottom conditions on the continental shelf off Mauritania as found in the eight sampling transects of the Tyro Mauritania-II Expedition. Symbols indicate subjective categories: black circles: mud, triangles: muddy sand, squares: sand, open circles: sandstone flats and ridges, diamonds: gravel.

Fig. 3. Sampling efforts of the Tyro Mauritania-II Expedition over the eight transects; black bars: total number of samples, white bars: Agassiz-trawl and rectangular dredge samples, hatched bars: Van Veen grab samples (4 grab attempts each).

the expedition and provided the maps of Figs 1 and 2.

Results

Vertical distribution

The dominant substrate of the continental shelf off Mauritania (and indeed of large areas off the

Moroccan, Saharan and North Senegal coasts) is sand. This habitat presents such difficulties for sponges (almost no settlement surface for larvae, clogging of inhalant and exhalant orifices), that only specially adapted growth forms can successfully thrive there. Depending of the thickness of the sediment layer, there are two ecological sponge groups, viz. stalked or long-papillated sponges, and those incrusting on shells of gastropods and hermit crabs ('mobile sponges'). The

Fig. 4. Sampling efforts of the Tyro Mauritania-II Expedition over the depth profile; the attempts of the eight transects are here combined to number of attempts at 10 m depth intervals.

Fig. 5. Depth distribution of sponge diversity on the shelf off the Banc d'Arguin. The results of the eight transects are combined to species numbers found at 10 m depth intervals.

former group is only viable when the sand overlies a hard surface (bigger shells of molluscs and sandstone platforms and ridges).

Diversity of sponges over the 0–100 m depth profile (expressed as the total no. of species found in 10 m depth intervals over the entire area, see Fig. 5) shows a peak (for both grab and trawl/dredge samples) at 10–20 m. This is contrary to the sampling efforts which were highest in the 20–30 m depth interval (see Fig. 4). This inshore high diversity is caused by the high frequency and diversity of the stalked-papillated sponges at these depths, correlated with the occurrence of sandstone platforms and ridges close inshore. Fig. 5, in fact, presents a rather misleading picture of gradual decline of diversity towards greater depths. Six of the 100 stations contribute disproportionately towards the diversity counts (station 11: 13 species, 27: 9, 49: 28, 53: 11, 63: 15, 72: 22), and together account for almost half the number of collected samples (*i.e.* one or more specimens

of a given species collected at a given station) and 81% of the recorded species (0–100 m). Of these six stations five were inshore and made on hard bottom covered with a thin layer of sand (the sixth station was made on a gravel bottom at 40–50 m). Growth forms of the various species were either stalked (examples: *Suberites* aff. *syringella* (Schmidt, 1862) (Plate 1c), *Adreus micraster* (Burton, 1956), and *Dictyonella plicata* (Schmidt, 1862) (Plate 1d) or massively sprawling with long papillae sticking out beyond the sediment (*Topsentia porrecta* (Topsent, 1928) (Plate 1a, b).

Most stations yielded a low number of species: average diversity was 3.5 sponge species per station; if the above mentioned six stations are omitted, average diversity of the remaining stations was only 2.1. Most of the stations other than the six mentioned above had bottoms consisting of a thick layer of sand or muddy sand, and the only viable sponge group in such habitats are the 'mo-

Plate 1

Figs. a-d. Stalked/papillated sponges found on inshore sand stone platforms off the coast near the Banc d'Arguin.

a. *In-situ* photo of *Topsentia porrecta* papillae sticking out from under the sediment at approximately 20 m depth off the coast near Cap Timiris.

b. *Topsentia porrecta* (Topsent, 1928), specimen photographed upon collection.

c. *Suberites* aff. *syringella* (Schmidt, 1868), photographed upon collection.

d. *Dictyonella plicata* (Schmidt, 1868), photographed upon collection.

Figs. e-f. 'Mobile' sponges found occurring widely on the continental shelf off the Banc d'Arguin.

e. *Clathria* (*Microciona*) *atrasanguinea* (Bowerbank, 1866) incrusting on gastropod *Clavatula*, photographed upon collection.

f. *Suberites domuncula* (Olivi, 1791) photographed upon collection.

Table 1. Depth distribution and frequency of occurrence (% of samples containing specimens) of six species of 'mobile' sponges on the continental platform of the Banc d'Arguin, Mauritanian, between 0 and 100 m.

Depth (m)	10–20	20–30	30–40	40–50	50–60	60–70	70–80	80–90	90–100
Species									
<i>Suberites domuncula</i>	27	44	88	100	66	20	33	0	33
<i>Suberites ficus</i>	0	0	0	0	34	40	0	50	100
<i>Clathria atrasanguinea</i>	45	22	30	33	80	20	0	0	0
<i>Clathria</i> spec. (beige)	0	0	8	0	0	20	0	0	0
<i>Hymedesmia coriacea</i>	10	0	15	66	17	60	0	0	100
<i>Tricheurypon</i> spec.	10	0	0	0	0	0	0	0	0
Number of trawl attempts	11	19	15	3	6	5	3	2	2

bile sponges'. These comprised the following six species (see also Table 1 for a summary of distributional data): *Suberites domuncula* (Olivi, 1871), (Plate 1f) almost exclusively the 'marmorated' form (see Topsent, 1900 for an extensive description of this species). These are by far the most numerous of the mobile sponges. They form big (up to 11 cm in greatest dimension) ellipsoid potato-shaped, mottled orange-brown-slate coloured, associations of sponges and hermit crabs. The gastropod shell (mostly either of *Turritella* or of *Natica*) originally colonized by the hermit crabs

and subsequently incrustated by the sponge, is often completely 'dissolved' in the later growth stages, presumably by acidic agents secreted by the sponges. However, the gastropod cavity is still preserved by the residing hermit crab, which also keeps a wide passage open to the outside of the sponge. The sponges host at least three different hermit crab associates: *Dardanus* spec., *Pagurus* spec. 1 and spec. 2, and there seems to be a clear size partitioning (Fig. 6) with small sponges hosting small hermit crab species (*Pagurus* spec. 1 in sponges up to 3.3 cm in greatest dimension, *Pagu-*

Fig. 6. Relationship between sponge length and carapax length of the *Suberites domuncula* (Olivi, 1791) – hermit crab association found abundantly off the Banc d'Arguin. Note that the hermit crabs belong to three different species.

Fig. 7. Number of specimens of *Suberites domuncula* (Olivi, 1791) – hermit crab associations collected over the depth profile on the shelf off the Banc d'Arguin. The results of the eight transects are combined to numbers found at 10 m depth intervals. The numbers for the 30–60 m depth intervals were very much higher (up to 300 specimens or more in individual trawl samples) than the 100 limit.

rus spec. 2 in sponges up to 4.0 cm) and large sponges hosting large hermit crabs (*Dardanus* spec. in sponges of 4–11 cm). Depth distribution is from 18 to 95 m, with a clear optimal depth range between 30 and 70 m (Fig. 7). *S. domuncula* is a Mediterranean-Atlantic species occurring at least as far south as the Gulf of Guinea (Lévi, 1959).

At the most shallow stations (and upwards into the littoral region), this symbiotic association is replaced by a similar association of hermit crabs and large nodular calcareous bryozoa; the two associations were not collected together, so presumably there is a form of resource partitioning. *Suberites ficus* (Esper, 1794): dull light grey-brown coloured incrustations on gastropod shells (a.o. *Xenophora* and *Calliostoma*) with hermit crabs. The incrustations of this species seldom exceed 0.5 cm in thickness. Depth distribution 50–>100 m (down to at least 200 m). This distribution may point to habitat partitioning between *S. domuncula* and *S. ficus*. The latter is known from the North Sea, Mediterranean, and the west coast of Africa as far south as Namibia (Uriz, 1989).

Clathria (Microciona) atrasanguinea (Bowerbank, 1866): (Plate 1e) thin reddish or orangy velvety crusts on both live gastropods (often *Clavatulula*) and empty shells with hermit crabs.

Common between 10 and 40 m, found down to 60 m. It is a North Eastern Atlantic species.

Clathria (Microciona) spec.: thin velvety beige-coloured crusts on mostly live gastropods (*Clavatulula*). Found at 30–40 m and 60–70 m.

Tricheurypon spec.: thin red, very hispid crust on *Favaria emersoni* resembling the cosmopolitan species *T. viridis* (Topsent, 1889), but red in colour instead of blue-green. Found only once at 10–20 m.

Hymedesmia coriacea (Fristedt, 1887) is a smooth, slippery, dull greyish brown crust with a delicate faint blue venal pattern on gastropod shells (a.o. *Marginella*) with hermit crabs. The taxonomy of this sponge has recently been revised (Van Soest, 1987); it occurs on various substrates (shells, gravel, rocks) from Norway southwards, to reach its southern border in the studied area.

Occasionally sponges were found attached to legs and thorax of spider crabs, mostly at depths exceeding 70 m.

Horizontal distribution

Although sampling efforts in the mid-transects (IV–VI, cf. Fig. 1) were considerably lower than those in other transects, both the number of

Fig. 8. Number of sponge samples (i.e. one or more specimens of a given species in a given sampling attempt) collected in the eight transects off the Banc d'Arguin. Black bars: total sample number, white bars: Agassiz- trawl and rectangular dredge samples, hatched bars: Van Veen grab samples.

sponge samples (7), and the number of species (4) caught in these transects were disproportionately low compared to those from the other transects (Figs 8 and 9). The only species found in low numbers (2–4 specimens) were *Cliona* spec. (a sponge boring in empty shells), the mobile *Clathria* spec., and the ubiquitous mobile sponges *Suberites domuncula* and *Clathria atrasanguinea*.

The overall horizontal distribution (Fig. 8) of collected sponge samples shows distinct northern (transects I–III) and southern (transects VII–VIII) maxima, with a gap in the area of transects IV–VI. If we compare Figs 1 and 2 with Fig. 8, it is obvious that the observed gap coincides with muddy bottoms, caused by the Banc d'Arguin run-off of sediment-rich waters.

Fig. 9. Number of sponge species collected in the eight transects off the Banc d'Arguin subdivided in Mediterranean-Atlantic (black bars) and West African (hatched bars) species.

Although habitats and growth forms of stalked and papillated sponges in the northern and southern transects are similar (cf. above), species composition differs dramatically: only about 23% of the species (18 species) is shared between the two areas. These are for the most part (17%) species with a wide distribution to the north (Mediterranean-Atlantic), and relatively few (6%) with a southern distribution (West African endemics) (for a listing of West African sponges and their affinities cf. Van Soest, in press). If we tabulate the main distribution of the species found in the various transects (Fig. 9), we observe going southwards an expected increase of West African endemics and an expected decrease of Mediterranean-Atlantic species. However, this is not a proportional increase-decrease phenomenon: of the 53 species occurring in the southern transects 23 (43%) are known from the Mediterranean-Atlantic, whereas of the 49 species occurring in the northern transects only 10 (20%) are known only from the coasts of West Africa (most of these are undescribed). Combined these figures point to a low proportion of West African forms in the northern transects and a relatively high proportion of Mediterranean-Atlantic forms in the southern transects. Some care with the interpretation of the data is in order as about half the species were collected only once.

Discussion

The observed horizontal and vertical distribution patterns as well as the high proportion of single records point to a patchy distribution of sponge species and populations in the area off the Banc d'Arguin, especially for the sedentary species. The only habitat available for these are the hard bottoms found mostly at shallow depths and these are patchily distributed and only available to species especially adapted to living in the sediment. The high diversity and regionality found in these forms is surprising: dozens of different species with similar morphology living closely sympatrically (e.g. 13 different species in 4 Van Veen grab samples at station 11 in the south, and 15 differ-

ent species in 4 Van Veen grab samples at station 63 in the north, but only 2 shared species!). A likely explanation for the differences in species composition between these similar habitats in the north and the south seems to be the restricted exchange of species and larvae between these areas caused by the unfavourable muddy area of transects IV–VI. It is quite conceivable that this unfavourable habitat is a barrier for southern species attempting to extend their range northwards, because of lack of settlement substrate and adverse currents from the north. Only 10 species known exclusively from West Africa occur in the northern area of these only two species are known from previous records, viz. *Burtonanchora myxilloides* Lévi (1959) and *Adreus micraster* Burton (1956); the others are undescribed species and have consequently few distributional data). Of these 10 species 5 are shared between the northern and the southern transects, and thus presumably have (had) the ability to cross the mud area in northern direction. In contrast there are 23 species in the southern area which have a predominantly Mediterranean-Atlantic distribution, pointing to the mud area being a less efficient barrier for species extending their range southwards. In view of the prevailing Canary Current, which may transport larvae southwards, this conforms to the expectation. One might conclude that the mud area off the Banc d'Arguin functions as a semi-permeable barrier allowing a good percentage of Mediterranean-Atlantic species to extend their distribution, but largely preventing the reverse range extension of West African endemics.

Compared to the sponge-rich areas of the rocky coasts in the north (Mediterranean, Canary Islands and Madeira Archipelago) and to the south (Cape Verde Islands and Dakar area) the entire north West African continental platform is probably impoverished and constitutes a large scale barrier to all sponges other than those specialized for mobile or infaunal substrates. For the latter, the Banc d'Arguin run-off area is an important barrier

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