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An uncommon or just an ecologically demanding species? Finding of aggregations of the brittle-star *Ophiothrix maculata* on the Northwest African slope

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ABSTRACT

Ophiuroidea constitutes the largest class of the phylum Echinodermata. It includes families with suspension-feeder behaviour that can be found in dense aggregations in all oceans worldwide. *Ophiothrix maculata* was known as a rare suspension-feeder brittle star, with only four records in the Eastern Central Atlantic dating from almost 100 years ago.

During the ten multidisciplinary Spanish and Norwegian surveys carried out from 2004 to 2012 off Northwest Africa, between the Gibraltar Strait and the Sierra Leone border from 19 to 1888 m depth, we sampled 1298 stations. We gathered about one million individuals and 124 kg of brittle stars at 501 of the stations. Eight hundred and thirty-two specimens of *Ophiothrix maculata* were collected at six localities on the continental slope off Mauritania, Western Sahara and Guinea Bissau, at depths between 155 and 594 m. The Guinea Bissau samples represent the southernmost current record for the species. Even though *Ophiothrix maculata* has been previously recorded only in isolation, we discovered dense concentrations on the Mauritanian slope on the Wolof's Seamount (580 individuals) and off the Western Sahara, in a *Lophelia pertusa* reef (202 individuals).

In this paper, we describe these findings and discuss the association of this species to hard-bottom habitats and high primary production areas, outside of the oxygen minimum zone (OMZ). We also analyse what other factors may explain the patchy distribution of *O. maculata* on the Northwest African slope.

1. Introduction

Ophiuroidea is the largest class within the phylum Echinodermata. About 2200 species are distributed in all oceans, from the intertidal to hadal depths (Stöhr et al., 2012), constituting a common component of megabenthic communities (Metaxas and Giffin, 2004). Brittle stars can be numerically dominant in bathyal and abyssal bottoms, with almost half of its species found at depths between 100 and 1000 m (Metaxas and Giffin, 2004).

Some suspension-feeder ophiuroids—mostly belonging to the families Ophiotrichidae, Ophiactidae, Amphiuridae, Ophiocomidae and Ophiacanthidae (Warner and Woodley, 1975; Metaxas and Giffin, 2004)—can be extremely abundant at some localities. Thus, dense aggregations of suspension-feeder ophiuroids have been found in all oceans (Metaxas and Giffin, 2004). Those large patches, sometimes called "*ophiuroid seabed*", are composed of hundreds to thousands of individuals—sometimes exceeding 2000 individuals per m^2—and have been recorded in both shallow and deep waters (Allen, 1998). Nevertheless, the ophiuroid beds generally appear in shallow waters up to 15 m, being rarely observed at bathyal and abyssal depths. Although most of these aggregations are located on hard bottom exposed to tidal currents, they generally seem not to be specific to physical substrate characteristics (Warner and Woodley, 1975).

Several studies reporting aggregations of some *Ophiothrix* species in different Northeast Atlantic localities, particularly *Ophiothrix fragilis* (Abildgaard, 1789), were published in the 1970s (Broom, 1975; Warner and Woodley, 1975). Madsen (1967) also reported dense aggregations of *Ophiothrix (Ophiothrix) aristulata* Lyman, 1879 off Tasmania. Nevertheless, *Ophiothrix maculata* Ljungman (1872), is a yet poorly known species, only recorded in isolation, over a century ago, at four localities in the Eastern Central Atlantic.

The first one, from the original species description of two exemplars found on the Josephine Bank (36°40'N) at 210 m depth during the corvette *Josefina* expedition, dates back to the end of the 19th century (Ljungman, 1872, p. 623). Subsequently, Koehler, p. 29, pl. I, Figs. 17, 19) (1906) described a new species that he called *Ophiothrix inducta*, from five specimens caught at two stations off Western Sahara during the 1883 *Talisman* survey. One of them was caught at 400 m depth, at

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Table 1
Sample data for all, previous and new records, of *Ophiothrix maculata*. (Acronyms: RD: Rock dredge; BT: Beam-trawl; OT: Otter-trawl).

Zone	Survey	Date	Gear	Station	Longit W	Latit N	Depth (m)	Habitat	Indiv. No	Size (mm)	Reference
Mauritania	*Maurit-1011*	Nov. 2010	RD	MUDR23	16°46′38"	17°08′46"	240	Seamount	580	10.8–19.2	Present paper
Mauritania	*Maurit-0911*	Nov. 2009	BT	MUBV14	16°47′34"	16°45′56"	291	Sand	11	12.2–15.1	"
Western Sahara	*Maroc-0611*	Nov. 2006	OT	MO221	17°16′33"	22°36′46"	590	Mud	1	13.5	"
Western Sahara	*Maroc-0611*	Nov. 2006	OT	MO263	16°26′06"	24°36′54"	410	Coral	202	3.4–11.0	"
Guinea Bissau	*Bissau-0810*	Oct. 2008	OT	BS183	16°25′27"	10°10′14"	170	Muddy sand	11	17.0	"
Guinea Bissau	*Bissau-0810*	Oct. 2008	OT	BS211	17°02′20"	10°29′08"	160	Sandy mud	20	9.0–13.5	"
Josephine Bank	*Josephine Exp.*	July 1869	n.a.	n.a.	14°12.13′	36°42.12′	209	n.a.	2	12.0	Ljungman (1872)
Morocco	*Dana*	1930	n.a.	4020	09°00′	33°12′	114	n.a.	4	2.0–14.0	Madsen (1970)
Western Sahara	*Talisman*	1883	n.a.	69	18°16′[a]	25°41′	400	Sand, coral	1	11.0	Koehler (1906)
Western Sahara	*Talisman*	1883	n.a.	103	19°47′[a]	21°47′	225	Sand, rock	4	6.0–9.0	Koehler (1906)

[a] París Meridian (2°20′14.025″ E) (*Talisman* stations).

25°41'N, 660 nautical miles south of the Josephine Bank; four other juveniles were gathered during the same expedition at 21°47'N, also at the coast of Western Sahara but at 225 m depth. Mortensen (1927) subsequently synonymised Koehler's species with *O. maculata*. Afterwards, Madsen (1970) reviewed the ophiuroid collections of the *Atlantide* and other northern and tropical West African expeditions. He identified as *O. maculata* four other specimens collected off Northern Morocco at 114 m depth during the *Dana* expedition in 1930 (Madsen, 1970, p. 216, fig. 36e) (Table 1). This synonymy is currently accepted by the WoRMS taxonomic database (http://www.marinespecies.org/).

In this study, we describe for the first time dense aggregations of this species from a deep-water coral reef in Western Saharan waters and associated with the recently discovered Wolof's Seamount on the continental slope off Mauritania (Sanz et al., 2017a). Other isolated records from Western Sahara, Mauritania and Guinea Bissau are also included. The Guinea Bissau finding constitutes the southernmost confirmed record for this species in the Northeast Atlantic.

2. Material and methods

2.1. Sampling on board

The specimens of *Ophiothrix maculata* come from an intense megabenthos-sampling programme developed, between 2004 and 2012, over 10 multidisciplinary Spanish and Norwegian surveys along the Northwest African continental margin, from the Strait of Gibraltar to the northern border of Sierra Leone. During these surveys, 1298 stations were sampled from 19 to 1888 m depth (Fig. 1). Most samples were taken with a commercial demersal trawl over soft bottoms; were also used a beam trawl and a rock dredge over the soft and hard bottoms on Mauritanian slope.

At all stations, brittle stars were sorted on board to morphospecies, counted, weighed and fixed in 70% ethanol for later study. Pictures of living specimens and details of the external morphology were also taken during the cruises.

2.2. Laboratory work

We studied the complete ophiuroid collections from Northwest Africa (EcoAfrik collections), at the Marine Zoology Laboratory of the Vigo University (Spain). These collections contain by almost 4000 specimens, taken at 501 trawl stations from Gibraltar Strait to Sierra Leone, during the above mentioned surveys.

From the total 1298 stations sampled, *Ophiothrix maculata* was collected at only six stations (see Table 1). In these six stations we took 832 specimens which were preliminary identified on board as *Ophiothrix maculata*. Among them, seventy-six specimens were preserved to confirm the identification in the laboratory. The disc diameter (dd) on the dorsal side of each specimen, from the base of one arm to the opposing disc side in the inter-radius, was measured to the millimetre.

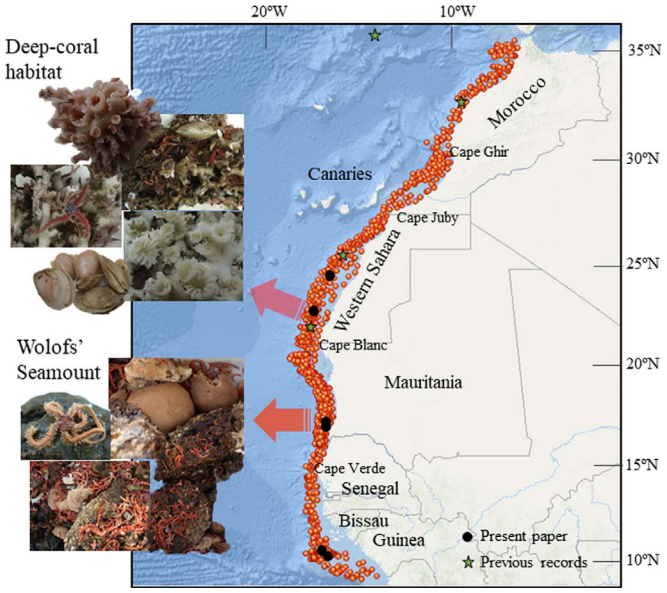

Fig. 1. Map with the 1298 stations carried out during the ten Northwest Africa surveys (orange points) and locations where *Ophiothrix maculata* was found (black points: present study; green stars: previous records), and location of the two main aggregations on the slope hard-bottom habitats: over the Wolof's Seamount on the Mauritanian slope, associated to a Geodidae sponges assemblage; and off Western Sahara, in a cold-water coral thicket composed of *Lophelia pertusa* and *Acesta excavata*. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Data related to the location, habitat type and sizes of all the EcoAfrik collection specimens, as well as the historical records for the species, are included in Table 1.

3. Results

3.1. Taxonomic considerations

Ophiothrix maculata was first described by Ljungman in 1872, almost 150 years ago, and based entirely on preserved material. Here we provide a new diagnosis and description of the species, based on recently collected fresh material.

Diagnosis: Species belonging to the family Ophiotrichidae, characterized by its large naked (without spines) radial shields, which can reach or even surpass four fifths of the radius of the disc; dorsal arm plates rhomboid with a convex distal margin that is not keeled; a dark spot on some dorsal arm plates and sometimes also on the radial shield (Fig. 2).

New description: Circular disc with a diameter of 3.4–19.2 mm. Very large radial shields, reaching or even surpassing four fifths of the disc radius. The large radial shields are naked, triangular in shape, with

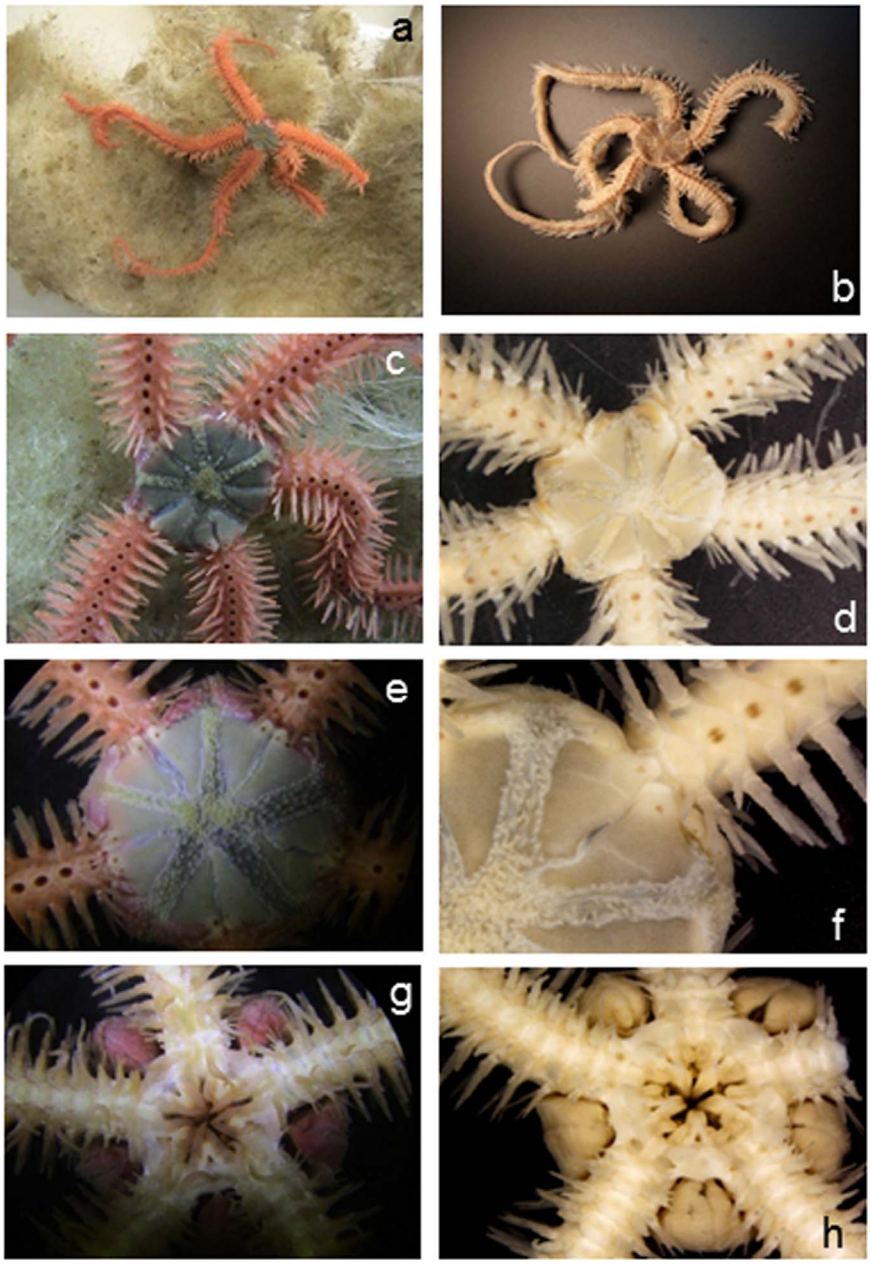

Fig. 2. Complete individual (a, b) and detailed images of dorsal view (c, d), dorsal disc and arms (e, f) and ventral view (g, h), of *Ophiothrix maculata* specimens collected off Northwest Africa: fresh (left panels: a, c, e, g) and preserved (right panels: b, d, f, h).

a little process on the internal distal end (Fig. 2); and sometimes with a dark spot on the process.

The dorsal face of the disc carries some small plates, provided with short spines either bearing a crown of thorns or developed into serrated spinules. Radial shields are separated by one (sometimes two) rows of plates, and inter-radially by four or five rows of plates. These plates are more elongated than those from the central area.

The oral face is naked. Oral shields are rhomboid, wider than long, with acute proximal and distal angles, and slightly rounded lateral edges. Dorsal plates are short and stout. Genital slits are well developed.

Tooth papillae placed on four rows of teeth at the jaw apex, the outermost larger than the two inner rows of teeth.

The dorsal arm plates are large, wider than long, diamond-shaped but with a prominent distal angle that is slightly raised and which abut on the succeeding plate. Dorsal arm plates are without a keel but usually (but not always) have a dark central spot similar but bigger than that on the radial shields.

The first ventral arm plate is small and rectangular, longer than broad, with a sunken middle area. The second is similar in shape, but slightly broader. Distally the ventral plates become broader than long and hexagonal in shape; both the proximal and distal edges are slightly concave, separated by a thick skin.

Each lateral plate has eight serrate spines on each side, increasing in size from a very small first ventral spine to the sixth that reaches a length of three arm segments; the seventh and eighth spines are smaller than the sixth. Each tentacle pore bears a small, oval tentacle scale.

The living specimens have a characteristic orange or pink colour, which is lost after preservation in ethanol (Fig. 2).

3.2. Distribution and habitat

During the surveys off Northwest Africa, we collected 832 specimens of *O. maculata*, with a wet weight of 2942 g. The species was gathered at only six stations (four with commercial otter trawl, one with beam trawl, and another one in a rock dredging) of the 501 stations where ophiuroids were caught (1.2%) and of the total 1298 stations (0.46%).

Most of the *O. maculata* specimens (580 individuals, 70%; Fig. 3a,

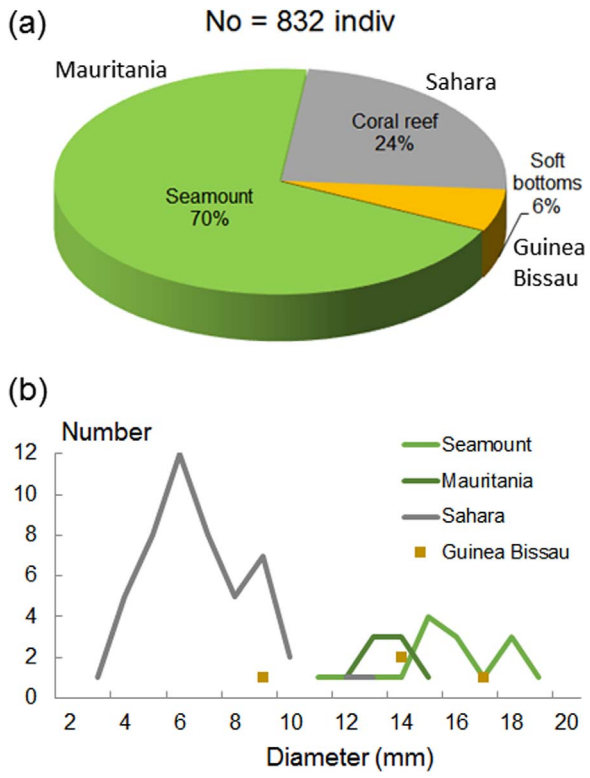

Fig. 3. Composition (numerical abundances in percentage, %) by type of substrate and geographical zone (a), and size composition of measured specimens of *Ophiothrix maculata* from Northwest Africa (b).

Table 1) were collected with a rock-dredge from rocky substrata on Wolof's Seamount, on the Southern Mauritanian slope, at 17°08´46"N and 240 m depth (Sanz et al., 2017a) (Fig. 1). Eleven more specimens were obtained with a beam-trawl at similar depths in the surrounding area (16°45´56"N), on soft bottoms.

Another location with remarkable concentration of *O. maculata* (202 specimens, 24%; Fig. 3a, Table 1) was located further north, at 24°37´N, in Western Saharan waters at 410 m depth.

The remaining records include one specimen obtained on the Western Sahara slope, off northern Cape Blanc, at 22°36´46"N between 586 and 594 m depth, and 38 specimens collected from two nearby localities off southern Guinea Bissau (10°10´37"N and 10°28´44"N), at 155–178 m depth on soft bottoms.

As in Mauritanian slope, as in Western Sahara, the brittle star aggregations appears clearly linked to highly diverse suspension-feeder communities: in the case of the Mauritanian seamount (Sanz et al., 2017a), from an assemblage of Geodidae sponges, and on the Western Sahara slope from a cold-water coral reef constituted mainly by *Lophelia pertusa* (Linnaeus, 1758), supporting a rich assemblage dominated by *Acesta excavata* (Fabricius, 1779), crinoids, pectinids and hydrozoans (Fig. 1). Although less abundant, the small aggregation found in Guinea Bissau also occurs where there is a significant diversity of suspension-feeders, as for example hydrozoans (Gil González, 2017).

3.3. Size

The size distribution of *O. maculata* individuals in the EcoAfrik collections is shown in Fig. 3b. Individuals off Mauritania are larger than those found further north, in Western Saharan waters. Thus, while the disc diameter of Western Saharan brittle stars ranged between 3.4 and 13.5 mm, the individuals inhabiting the southern Mauritanian slope, mostly from the Wolof's Seamount, had a minimum size of 10.8 mm, and reached almost 20.0 mm.

The seven exemplars collected by Ljungman and Koehler from Josephine's Bank and Western Saharan waters measure between 6.0 and 12.0 mm disc diameter.

4. Discussion

Prior to this study, the brittle star *Ophiothrix maculata* had only been recorded as isolated individuals by Ljungman (1872) on the Josephine Bank, by Koehler (1906) at two different sites in Western Saharan waters, and by Madsen (1970) in northern Moroccan waters.

Considering the difficulty of identifying species belonging to the genus *Ophiothrix*, it is possible that the apparent scarcity of *O. maculata*, or lack of geographical continuity recorded along the Northwest African slope, has been caused by misidentification. Although *Ophiothrix maculata* is relatively easy to identify—due to their large radial shields, absence of a keel and presence of black spots on dorsal arm plates—it may be confused with other *Ophiothrix* species that are harder to characterise, particularly in the case of juveniles.

We identified a collection of almost 4000 specimens of ophiuroids taken from 1298 stations off Northwest Africa between 19 and 1888 m depth. Besides *O. maculata*, we have found four more species of the genus *Ophiothrix*: *Ophiothrix fragilis, Ophiothrix luetkeni* Thomson, 1873, *Ophiothrix cotteaui* (de Loriol, 1900) and *Ophiothrix congensis* Koehler, 1911. The two former ones—*O. fragilis* and *O. luetkeni*—have a wide distribution in the Northeastern Atlantic and/or Mediterranean Sea, while *O. congensis* and *O. cotteaui* are restricted to western African waters (Madsen, 1970). However, despite the large number of stations sampled in our cruises and the considerable number of specimens examined, we collected *O. maculata* at only six stations. Two of them were located in Western Saharan waters, very close to Koehler's reported sites (Fig. 1). Two other stations were from the adjacent southern Mauritanian slope. The two last records were collected from the southern part of Guinea Bissau. Our findings constitute the first record of the species off Mauritania and Guinea Bissau, as well as from the southern Cape Blanc. Nevertheless, we did not find any specimens of *O. maculata* further north, in Moroccan waters, or further south, off Senegambia and Guinea—with the exception of some questionable records from this last zone. No previous records for this species exist in the literature or databases on biodiversity for Morocco (Menioui, 1998), the Canary Islands (Hernández et al., 2013; Gobierno de Canarias, 2016, www.biodiversidadcanarias.es/atlantis/) or the Cape Verde archipelago (Entrambasaguas, 2008). Nor does the Ocean Biogeographic Information System (OBIS, 2017) registers any reports of the species. Only the old findings of Ljungman and Koehler are mentioned in the World Register of Marine Species (WoRMS Editorial Board, 2016), and Global Biodiversity Information Facility (GBIF, 2017).

Our results appear to confirm that *Ophiothrix maculata* is an uncommon species mainly restricted to the Northwest African slope where it exhibits a patchy distribution. Nevertheless, despite its scarcity and restricted location, we found dense aggregations of the species, not previously recorded. The two main concentrations of *O. maculata* were associated with hard-bottoms and sessile suspension-feeder communities, which are uncommon in this continental margin. The densest aggregation was recorded on rocky bottom on the Wolof's Seamount (southern Mauritania) at 240 m depth, while the second one was located in a cold-water coral reef, off the Western Sahara at 410 m depth.

Although our findings constitute the first records of these ophiuroid aggregations in Northwest Africa, some associations of dense populations of brittle stars with cold-water corals and other suspension-feeder assemblages have been described worldwide. Thus, Brooks et al. (2007) mentioned associations of *Ophiacantha bidentata* (Bruzelius, 1805) with deep-water coral reefs, in particular with *Lophelia pertusa,* in the southeastern coast of the United States. O'Hara (2007) and O'Hara et al. (2008) reported associations of ophiuroids with coral reefs of *Solenosmilia variabilis* Duncan, 1873 in Australia and New Zealand. Bowden et al. (2011) described dense populations of ophiuroid species and large stalked crinoids at Admiralty Seamount in the Ross Sea (Southern

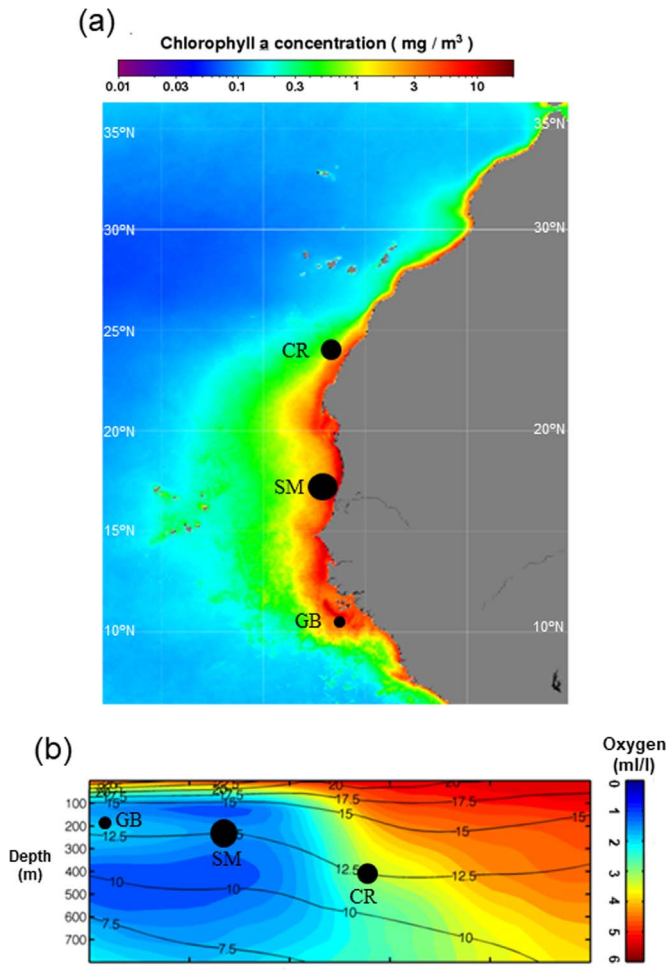

Fig. 4. Location of the three main *Ophiothrix maculata* aggregations (black circles), superimposed on maps of (a) chlorophyll a concentrations and (b) vertical oxygen content along the Northwest Africa continental slope between 35°N and 10°N (circles size are proportional to density). Adapted from Pelegrí and Peña Izquierdo (2015). (Acronyms: CR: Deep-water coral reef; SM: Wolof's Seamount; GB: Guinea Bissau).

Ocean).

The Northwest African region constitutes one of the most highly productive areas worldwide, linked to upwelling phenomena and to the seasonal displacement of a thermal front, between Cape Blanc (Mauritania) and Cape Verde (Senegal) (Fig. 4a) (Pelegrí and Benazzouz, 2015a). Particularly the Western Sahara-Mauritania coast is characterized by permanent upwelling conditions throughout the year (Pelegrí and Peña-Izquierdo, 2015b) and by the presence of important eddies and filaments that export highly productive waters to the slope up to 600 km offshore (Sangrá, 2015).

These oceanographic features likely provide environmental conditions favourable for suspension-feeding fauna. Rich assemblages of long-lived suspension-feeders have been reported from soft bottoms off the Moroccan and mainly Western Sahara slopes, where the diversity seems to reach the highest values for the entire Northwest African region (Ramos et al., 2015a; b). Nevertheless, despite the high productivity, such suspension-feeder assemblages are exclusively linked to hard-bottom habitats—northern canyons, Wolof's Seamount and southern area of the coral carbonate mounds barrier (Ramos et al., 2017). More than 90% of the Mauritanian slope between 100 and 2000 m depth is characterized by the dominance of muddy bottoms, large landslides of sediments (Sanz et al., 2017b), and weak bottom currents (Colman et al., 2005). All of these factors constitute unfavourable environmental conditions for suspension-feeders (Castillo et al., 2017; Ramil and Ramos, 2017). Moreover, the Mauritanian slope, almost up to the latitude of Cape Blanc, is, to a large extent, occupied by low oxygen waters (Pelegrí et al., 2017). This oxygen depleted zone ranges between 300 and 600 m depth over the entire tropical northeast Atlantic (Pelegrí and Peña-Izquierdo, 2015b; Stramma et al., 2015) (Fig. 4b) and seems to effectively limit the presence of some epibenthic taxa, particularly echinoderms (Calero et al., 2017).

The finding of a high density and abundant *Ophiothrix maculata* aggregation exclusively concentrated on the Wolof's Seamount indicates the existence of particular environmental conditions in this slope area, highly favourable for this species to flourish. Although the large aggregation of *Ophiothrix maculata* in a cold-water coral habitat in Saharan waters is also remarkable, it does not seem to achieve the density and above all the size of those on the southern Mauritanian slope. We need to take into account that the Saharan aggregation is found at more than 400 m depth, while that on the Mauritanian seamount inhabits between 200 and 240 m. The limited range of the bathymetric distribution very likely constitutes an important factor affecting the density and size reached by *O. maculata*. Sanz et al. (2017a) point out that this brittle star species constitutes one of the main components of the Mauritanian seamount assemblage and that besides the presence of hard substrata and the absence of sedimentation, the location of Wolof's Seamount on the upper slope would allow suspension-feeder species to benefit from the high productivity generated by the upwelling over the Mauritanian shelf and would promote the aggregation and growth of *O. maculata*. Ramos et al. (2017) reported that this area is characterized by a seasonal wind-induced upwelling and the presence of sandy ripples up to 5 m height. Upwelling mechanism and bottom currents enrich the continental shelf with emerging nutrient- and oxygen-rich waters and may induce the resuspension of sediments, favouring the suspension-feeder communities.

It is somewhat remarkable that both Geodidae sponges and the brittle star *Ophiothrix maculata* showed the same distribution pattern on the Western Saharan slope and over the Mauritanian seamount, 470 nautical miles south of the Sahara records. Similar to the Geodidae (Sanz et al., 2017a), the isolated *O. maculata* population on Wolof's Seamount could be a relict population that originated in the past when the oceanographic and environmental conditions on the Mauritanian slope were more favourable for the development of suspension-feeders.

Some authors have suggested that social behaviour or reduced predation intensity could help explain the persistence of suspension-feeder ophiuroid aggregations over time (Broom, 1975; Aronson and Harms, 1985; Aronson, 1989). However, at least in the case of *Ophiothrix maculata*, we consider that its occurrence is a response to other, more important, environmental factors. As other authors have suggested, we also highlight the nature of the substratum (Reese, 1966) and the potentially high food rates that are linked to high productivity and strong currents (Broom, 1975).

The discovery of only two dense aggregations in an area so intensively sampled, suggest that *Ophiothrix maculata* must be an obligate suspension-feeder species that requires particular environmental conditions to achieve such dense aggregations, including hard-bottom support and highly productive and oxygenated water masses.

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