Macrobenthic assemblages across deep-sea pockmarks and carbonate mounds at Santos Basin, SW Atlantic

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ABSTRACT

The SE Brazilian continental margin is rich in geomorphological features that create different seascapes, where diverse benthic communities thrive. The seafloor is composed of a mixture of pockmarks of different sizes and shapes and tall carbonate mounds that may form extensive chains. Mounds are colonized by deep-water corals which are the main responsible organisms promoting growth over geological time. Depressions and mounds affect the benthic ecosystem in multiple ways owing to water flow, sedimentation rates and food availability. This paper presents new data on macrofaunal composition and community structure associated with deep-sea coral habitats and pockmark areas along the upper continental slope of Santos Basin. Ten sites were sampled using a 0.25 m2 box corer on board R/V Alpha-Crucis, totaling 27 sediment samples. A total of 182 taxa were found, including new records for the Southwestern Atlantic, as well as several potential new species to science. In general, we observed an association of the macrobenthic fauna with the geomorphology of the area and the most important variables, mainly substrate composition and water flux. The abundance, taxonomic composition and also the feeding modes varied across the deep-water coral sites and pockmarks, reflecting in a mosaic of benthic habitats. As deep-sea corals and pockmarks are extremely sensitive to anthropogenic influence and natural shifts, in addition to the economic value associated to fisheries, this study provides baseline information on these special habitats in Santos Basin that can be used for future research, monitoring activities, and conservation strategies.

Descriptors: Continental slope, Macroinfauna, Gas Seep, Salt tectonic, Cold-water corals

INTRODUCTION

The deep sea is the largest environment on Earth representing almost 90% of all oceans, but it is also the least explored and understood habitat (Ramirez-Llodra et al., 2010; McClain and Hardy, 2010; Danovaro et al., 2014). Historically, habitats beyond the continental shelf (>200m depth) have been considered homogeneous and with low biomass and bio-diversity, mainly due to extreme environmental conditions and lack of suitable technology

(Ramirez-Llodra et al. 2010). However, recent studies have shown that deep oceans exhibit a broad spectrum of geomorphological and ecological features that define a mosaic of habitats where different benthic communities thrive. One of these features, called pockmarks, are abundant in the Brazilian continental margin, especially at the Santos Basin (Sumida et al., 2004, 2022; de Mahiques et al., 2017).

Pockmarks are circular or elliptical-shaped depressions with an average diameter of 1 km and 100 m depth (Schattner et al., 2016). They are formed when gases escape from faults caused by the tectonic uplift of salt diapirs (de Mahiques et al., 2017; Schattner et al., 2018). Pockmarks also act as traps of particulate organic matter (Ramos et al., 2020) and alter near-bed circulation (Pau et al., 2014). A constant and slow flow of light hydrocarbon fluid passes through the sediments building up authigenic carbonates that can further be colonized by cold-water corals, normally at the edge of pockmarks (Sumida et al., 2004). The build up of corals over geological time resulted in large carbonate mounds (Hovland and Thomsen, 1997; Wheeler et al., 2005).

Seafloor depressions and mounds affect the benthic ecosystem in multiple ways, e.g., water flow, sedimentation rates and food availability. The depositional environment formed in pockmarks is colonized by an invertebrate infauna mainly composed of annelids, mollusks and crustaceans (Sumida et al., 2004; Sánchez et al., 2021). On the other hand, the elevated areas of carbonate mounds are exposed to stronger currents and are dominated by large filter-feeding animals, such as cnidarians, sponges and corals (Henry and Roberts, 2007). In places where deep-sea corals thrive, a remarkable proportion of the macrofauna species is associated with coral skeletons. These associated organisms seek shelter in the complex three-dimensional structure of the dead coral fragments, frequently living among coral rubble, in crevices and perforating coral debris (Roberts et al., 2008). Coral rubble can occur both at the top and on the sides of carbonate mounds and within the pockmarks (Sumida et al., 2004).

Deep-sea habitats have been mostly described and studied for the northern hemisphere, while in other ocean basins they still remain practically unknown. Recent advances have been made to survey the deep Southwest Atlantic, mainly in areas of interest for oil and gas exploration, such as the Santos Basin, where several new features have been discovered. An extensive pockmark field was described at the SB, containing deep (up to 100 m) and large (~ 1000 m of diameter) depressions associated with salt tectonics in subsurface (de Mahiques et al., 2017). Cold-water coral reefs are also a common habitat found in the Southwest Atlantic, sometimes located at the edge of pockmarks (Sumida et al., 2004) and also over large carbonate mounds (Maly et al., 2019).

Considering the scarce knowledge about deep-sea environments in the SW Atlantic and the importance of SB from both a geological and an ecological perspective, this paper presents new data on macrofaunal composition and community structure associated with deep-sea coral habitats and pockmark areas along the upper continental slope of SB. This study, under the scope of the BiOil Project ('Biology and Geochemistry of Oil and Gas Seepages, SW Atlantic'), aimed to identify and map seep areas along the Santos Basin (Sumida et al., 2022).

METHODS

STUDY AREA

The study area comprises the continental slope of Santos Basin (SB), between the isobaths of 350 and 1000 m (Figure 1). Detailed information on the study area, as well as the methods used in this study, are available in Sumida et al. (2022). The circulation pattern of SB is influenced by the western portion of the South Atlantic Subtropical Gyre (SASG) (Peterson and Stramma 1991; Stramma and England 1999; Marcello et al. 2018). On the slope, two main flows of the SASG reach and shape the SB slope, with the Brazil Current (BC) flowing southwestwards and the Intermediate Western Boundary Current (IWBC) flowing northeastwards (Figure 1B) (Biló
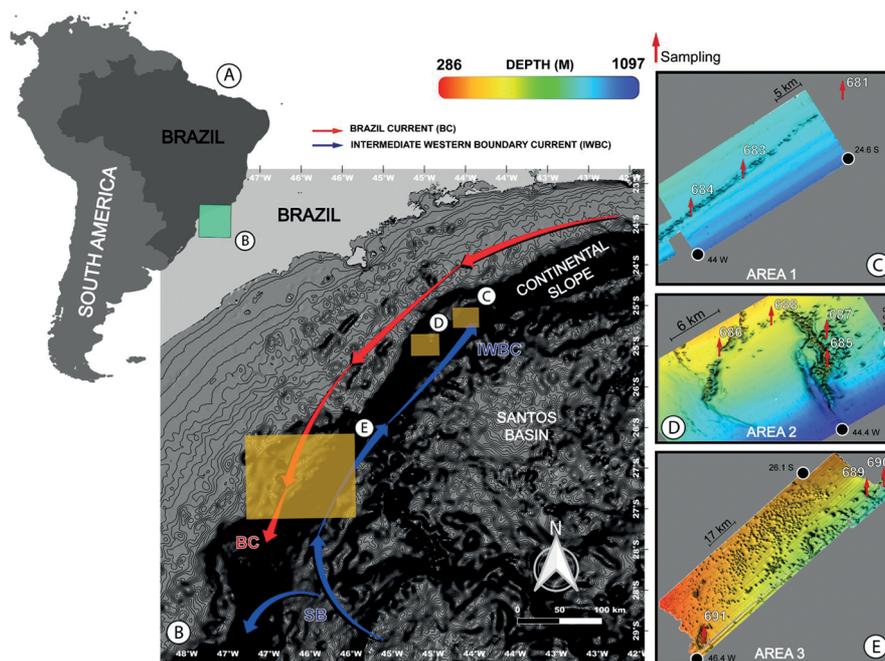
Figure 1. A. General view of SE Brazilian continental margin investigated during Project BIOIL oceanographic cruise in November 2019 using the R/V Alpha Crucis. B. Santos Basin region with main currents (arrows) and the three sampling areas. Insets C. (Area 1 - 681, 683 and 684), D. (Area 2 - 685, 686 and 687) and E. (Area 3 - 689, 690 and 691) show in detail the ten sampled stations in each of the sampling areas. BC = Brazilian currents; SB = Santos Bifurcation; IWBC = Intermediate Western Boundary Current.

et al., 2014). The Brazil Current carries Tropical Water (TW) at the surface and the South Atlantic Central Water (SACW) at the pycnocline. It has a maximum speed of 75 cm/s in the water column (Silveira et al., 2000). The IWBC transports the AAIW and represents the northern branch of the Santos Bifurcation (Figure 1B) (Biló et al., 2014). On the shelf edge, the BC exhibits a meandering pattern in conjunction with intense flows which favors the development of extensive bedform fields or seafloor sediment reworking with subsequent generation of relict surfaces (de Mahiques, 2002; Dias de Araujo et al., 2021).

Three areas of interest (A1, A2, and A3) were previously delimited for sampling (Figure 1). Area 1 (stations 681, 683 and 684, Figure 1C) consists of a carbonate seabed and an environment with a high concentration of nutrients (Trevizani et al., 2022). Area 2 (stations 685, 687 and 688, Figure 1D) contains a ring-shaped carbonate mound province known as *Alpha Crucis Carbonate Ridge*

(ACCR) formed by carbonate walls and ridges that elevates over 300 m over the seafloor (Maly et al., 2019). The composition of carbonate mounds is a mixture of fine sediments and coral skeletons, the latter used by benthic organisms as shelter or settling areas (Maly et al., 2019). The structure of ACCR is determined and shaped by the dominant bottom current, the IWBC. On the mound flanks, elongated and comet-like depressions are observed as the result of the interaction of the water flux with the obstacle offered by the mounds. Area 3 (stations 689, 690 and 691, Figure 1E) is a pockmark field with 984 mapped depressions on the continental slope (Sumida et al., 2004; de Mahiques et al., 2017). In this field are observed exhumed diapirs surrounded by pockmarks, indicating the genetic relationship between halokinesis and the formation of these depressions (de Mahiques et al., 2017; Schattner et al., 2018). The region is strongly influenced by the BC-IWBC current system, with the presence of asymmetric

depressions generated by the flow contact with the pockmarks (Schattner et al., 2016). Currents also interact with diapirs, forming moats originated from erosion and not from deposition of sediments by the flow (Schattner et al., 2018). From a depositional point of view, the high depth of the pockmarks presents in this region into contact with the flow give these features the status of natural sediment traps, with sediments inside distinct from the adjacent seafloor (Ramos et al., 2020).

Sampling

The oceanographic cruise of Project BIOIL occurred on November 11-24th, 2019, on board of R/V Alpha-Crucis, from Instituto Oceanográfico of the University of São Paulo (IOUSP) (Sumida et al., 2022). All sites along the three areas were sampled with multibeam echosounder to map the ocean floor, CTD-rosette sampler to determine water parameters, and box corer (Ocean Instruments, model BX-650) for sediment and macrofauna analysis. Detailed information on the sampling procedures and locations is provided by Sumida et al. (this volume). Box-corer samples were collected in triplicate at ten sites, totaling 27 sediment samples (Figure 1). At some sites (684 and 690), triplicate sampling was not possible due to the nature of the seabed. After the recovery of the box corer, the 50x50 cm sediment samples were divided into two equal parts (~0.125 m² of area each). One half of the box corer sample was destined for macrofaunal studies. The samples were carefully elutriated and then sieved using a 500 μm and a 300 μm mesh. Specimens destined for molecular analysis were preserved in 96% ethanol and organisms destined for morphological identification and taxonomic studies were fixed in 4% formaldehyde diluted in sea water.

Laboratory analyses

The macrofauna was sorted under a stereomicroscope and some specimens were photographed alive immediately after collection. Organisms destined for morphological and taxonomic studies were fixed in seawater formaldehyde 4% and stored at room temperature. The remaining specimens were bulk preserved in 96% ethanol and stored at 4ºC for molecular analyses. The specimens selected for scanning electron microscopy (SEM) were fixed in trialdehyde (glutaraldehyde + paraformaldehyde + sodium cacodylate) at 4ºC for 2 h and stored in sodium cacodylate at room temperature. To ensure the best results for DNA extraction, selected specimens were fixed in molecular-grade absolute ethanol and stored at -20 ºC. At the Laboratório de Ecologia e Evolução de Mar Profundo (LAMP) the preserved sediment samples were sorted under stereomicroscope and the organisms identified to the lowest possible taxonomic level, according to standard taxonomic literature. Species names were verified using relevant literature and the World Register of Marine Species (WoRMS Editorial Board, 2022). Count of individuals of all species in a sample were performed and the density was expressed as ind.m⁻².

Community descriptors such as species richness (S), Shannon-Wiener diversity index (H'), Pielou's evenness index (J') were calculated for each station replicate. These indexes as well the organism density for each station were graphically represented with the calculated mean and standard error (SE).

The most representative macrobenthic species were categorized under their respective feeding guilds according to the available literature (Macdonald et al. 2012, Jumars et al. 2015). The feeding guilds were the following: (C) carnivores - feeding on meiofauna or macrofauna; (OM) omnivores - feeding on large particulate matter; (SRD) surface deposit feeders - collecting and ingesting particles from the sediment surface; (SSD) sub-surface deposit feeders - feeding on particles below the sediment surface; and (SU) suspensivores - feeding exclusively on particles from the water column; (FD) facultative detritivores - may feed as suspensivores, surface deposit feeders or subsurface deposit feeder; (FC) facultative carnivores - feed as predators or scavengers on macro or meiofauna, but also deposit feed. The relative abundance of each feeding guild category was calculated for each site.

Samples used for the determination of the grain size and nutrient concentration of the sediments were prepared, analyzed and the detailed results information are available in Santos et al. (this volume).

STATISTICAL ANALYSES

Differences in the macrofauna density and ecological indexes (S, H', and J') among stations were tested with a one-way Analysis of Variance (ANOVA). Pairwise differences between stations were evaluated with a post-hoc Tukey-HSD test. Prior to every parametric test, data was respectively checked for normality and homoscedasticity with Shapiro-Wilk test and Levene's test.

Multivariate analyses of the species abundance matrix were conducted using PRIMER (Plymouth Routines in Multivariate Ecological Research) (version 6.1.3) (Clarke and Warwick, 2001). The taxonomic groups selected for the multivariate statistical analysis were Annelida, Crustacea, Echinodermata and Mollusca, considering only the taxa identified at species level or morphotypes, whose accumulated abundance reached 90% of the total abundance. Multivariate analyses were performed using the average ranked values of Bray-Curtis similarity in log-transformed [log(x+1)] species abundance data to give more weight in the analysis to the less abundant species. Ordination of the stations according to this similarity matrix was visualized by non-metric multidimensional scaling (nMDS) plot. In order to conduct multivariate community analyses, one factor was considered in this study, the habitat type. According to previous study in the same area, we classified the sampled sites in four habitats: (1) Carbonate mound (CM) – influenced by biogenic reefs (685 and 687); (2) Carbonate mounds surroundings (CMS) – bottom sediments influenced by dead coral skeletons (683 and 684); (3) Pockmark (P) – circular depressions in the seafloor, with tens or hundreds of meters in diameter, usually associated with the infiltration of gas and/or saline diapir (689, 690, and 691); and (4) Pockmark surroundings (PS) – adjacent sediments at the border of the pockmarks (681, 686, 688). Global and pairwise differences in composition of the macrofaunal communities in each of these habitats were tested with one-way Analysis of Similarity (ANOSIM).

Similarity of Percentages (SIMPER) routine (log-transformed) was used to identify species that typify in terms of abundance in the studied sites. Principal Component Analysis (PCA) was used to identify the environmental variables most related to the spatial variability of macrofauna. The environmental variables used were sediment grain size contribution, nutrient concentration (ammonium, phosphate, nitrate and silicate) at the sea bottom, and station depth (in meters).

RESULTS

ENVIRONMENTAL VARIABLES

The four habitats were typically sandy, especially in the pockmark area with greater predominance of the sand fraction in the pockmark surroundings (stations 686 and 688) (Table 1, Figure 2). Carbonate mound areas showed a greater presence of finer sediment fractions with coarser silt in stations on the top of CM (stations 685 and 687), and finer silt fractions in the CM surroundings (stations 683 and 684). Pockmarks and carbonate mound surroundings had higher concentration of nutrients such as nitrates, phosphates and silicates whereas carbonate mounds had a higher concentration of ammonia. The higher concentration of nitrates, phosphates and silicates was also linked to deeper stations (650 - 811 m depth), which are probably under influence of the AAIW (Table 1, Figure 2).

MACROBENTHIC COMPOSITION AND STRUCTURE

A total of 182 taxa were found but only 90 have been named at genus or species level (about 50%), the remaining have been identified into morphotypes at either family level, or higher taxa (Table 2). In general, annelids represented the most frequent group, present in all 27 stations, followed by echinoderms (f = 55.6%), mollusks (f = 51.9%), crustaceans (f = 48.1%), sponges (f = 22.2%), cnidarians (f = 18.5%), and bryozoans (f = 7.4%) (Table 2). About 30% of the total taxa occurred only once, with only a single individual, and were classified as rare (see Table 2). Of the total number of organisms (1912 ind.) the most abundant group was Annelida (60.6%), followed by Echinodermata (23%), Arthropoda: Crustacea (7.1%), Mollusca (1.8%), Cnidaria (6.5%), Porifera

Table 1. Depth, temperature, concentration of dissolved nutrients in the bottom water and sediment grain composition in the stations of the Project BIOIL Cruise 1 (November 2019).

Station	Depth	Temperature	Salinity	Phosphate	Silicate	Nitrate	Ammonium	Fine Sand	Very Fine Sand	Very Coarse Silt	Coarse Silt	Medium Silt	Fine Silt	Very Fine Silt	Clay
	(m)	(°C)	(PSU)			(μmol L^{-1})					(%)				
683	811	4.7	34.3	1.363	13.767	24.676	0.111	0.00	10.60	27.96	23.40	15.19	11.10	6.43	5.32
684	800	4.6	34.3	1.915	20.245	27.513	0.136	0.28	16.10	32.07	21.33	11.43	8.60	5.30	4.89
685	550	7.6	34.5	1.372	8.734	19.277	0.111	0.74	14.47	31.98	25.52	13.27	7.19	3.62	3.22
686	530	8.4	34.6	1.582	50.324	21.366	0.161	3.56	22.40	30.18	20.11	11.07	6.20	3.25	3.23
687	560	6.7	34.4	1.410	10.875	19.510	0.136	0.25	14.62	31.33	23.14	12.58	8.55	4.95	4.58
688	530	8	34.5	1.086	6.883	13.149	0.087	6.52	29.31	29.85	15.54	8.75	5.07	2.53	2.42
689	650	-	-	1.944	16.543	27.721	0.099	2.95	20.88	30.52	20.75	11.26	6.30	3.59	3.76
690	740	5.8	34.4	1.782	16.370	24.276	0.111	0.46	10.95	30.03	28.72	14.15	7.13	4.36	4.20
691	519	10.5	34.8	1.258	6.768	17.468	0.161	0.25	17.72	35.70	24.93	10.27	4.91	2.88	3.33

(0.8%), and Bryozoa (0.2%). Some species corresponding to the most important taxonomic groups are illustrated in Figures 3–6.

Macrofauna density was lowest (< 250 ind. m^{-2}) at stations 681, 683, 684 and 688 (Figure 7). The highest densities were found in the areas of pockmarks and carbonate mounds (Figure 7). The station at the top of Alpha Crucis Carbonate Ridge (ACCR) (685) exhibited the highest density of organisms reaching 1584 ind. m^{-2} (ANOVA F=52.55; d.f.=5; p=0.008), followed by the pockmark stations, 689 (613 ind.m^{-2}), 690 (948 ind.m^{-2}) and 691 (812 ind.m^{-2}) (Figure 7). Among the samples from the surrounding sites, station 686 had the highest density of organisms (Figure 7).

Annelids represented the most dominant group of macrofauna in all stations (Figure 8). Crustaceans and mollusks were less abundant in all sites (Figure 8). At the pockmark areas, (within and at its surroundings), annelids represented 70-90% of all macrofauna (681, 686, 688, 689, 690, and 691). At the sites under influence of hard substrate or carbonate mounds (683, 684, 685 and 687), we observed greater contribution of other macrofauna groups, such as echinoderms and cnidarians, especially at the 685 (Figure 8).

Among annelids, nine families corresponded to 80% of the group (Table 3). In Echinodermata, four ophiuroid families were dominant, Ophiacanthidae (67.5%), Ophiactidae (9%), Amphiuridae (4.7%), Astrophiuridae (3.8%). The most representative arthropods were peracarid crustaceans (Table 3). Most mollusks were morphotyped at higher taxonomic levels (H.T.L.), which corresponded to almost 80% of the abundance. The families comprised the gastropods Eulimidae, Olividae and Anatomidae, and the bivalves Limopsidae and Verticordiidae (Table 3).

Station 685 was the only one where a live deep-water reef-building species were found (i.e., *Solenosmilia variabilis*), and other large fauna such as sponges *Sarostegia oculata* and *Aphrocalistes* cf. *beatrix*, as well as hydrozoan colonies. Associated with these reefs, we found
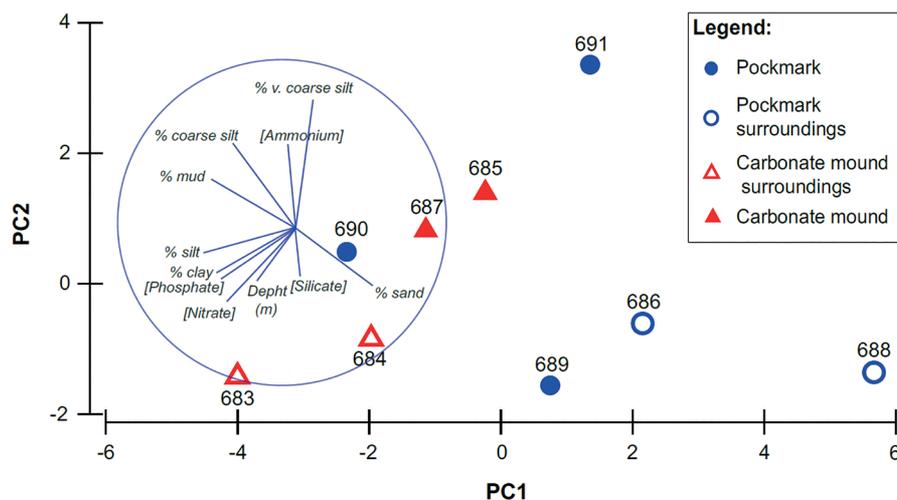
Figure 2. Principal component analysis (PCA) on the environmental variables (standardized and normalized) of the Project BIOIL Cruise 1 (November 2019). The two main axes (PC1 and PC2) represent, respectively, 55.7% and 17.8% of the total variation in the analysis. Environmental variables vectors (in blue) indicate the direction of the influence of each variable in the station features. Station 681 was not included in the analysis due missing nutrient data.

Table 2. Number of taxa, frequency of occurrence (%), number of rare taxa, and relative abundance (%) of macrobenthic groups found at the stations sampled in the Santos Basin. Single-occurring taxa with only one individual were classified as 'rare taxa'.

	Number of taxa	Frequency of occurrence (f) (n = 27)	Number of rare taxa	Relative abundance (n = 1912)
Annelida	95	100%	15	60.6%
Arthropoda	26	48.1%	10	7.1%
Echinodermata	37	55.6%	18	23.0%
Mollusca	17	51.9%	10	1.8%
Cnidaria	5	18.5%	-	6.5%
Porifera	4	22.2%	-	0.8%
Bryozoa	1	7.4%	-	0.2%

several invertebrates living both inside (endo-) and on the surface (epifauna) of substrates, comprehending omnivores, carnivores, suspensivores, facultative detritivores, and also sub- and surface-deposit feeders. Echinoderms were the most abundant (62%), followed by cnidarians (20%), annelids (15%), and crustaceans (< 5%) (Figure 8). The glass sponges *Sarostegia oculata* and *Aphrocalistes* cf. *beatrix*, presented numerous symbiotic zoanthids (*Thoracactis topsenti*), and several annelids living in their association, including syllids, nereidids, and polynoids (Figure 6). Many eunicid and nereidid annelids were found inside the corals, and a range of small marine

invertebrates was found living at the surface of corals and hydrozoans colonies, including annelids, ophiuroids, tanaidaceans, isopods, aplacophorans, among others (Figure 6). The sediments at the carbonate mounds surroundings were composed of dead coral fragments, with several endofaunal deposit-feeder annelids. Station 687 was composed of sediment associated with dead coral fragments, with fauna living among and inside coral rubble. Annelids represented more than 90% of all macrofauna, followed by a lower contribution (<5%) of echinoderms, mollusks and crustaceans. A single live colony of *S. variabilis* was found at the station 683, but all fauna found was associated
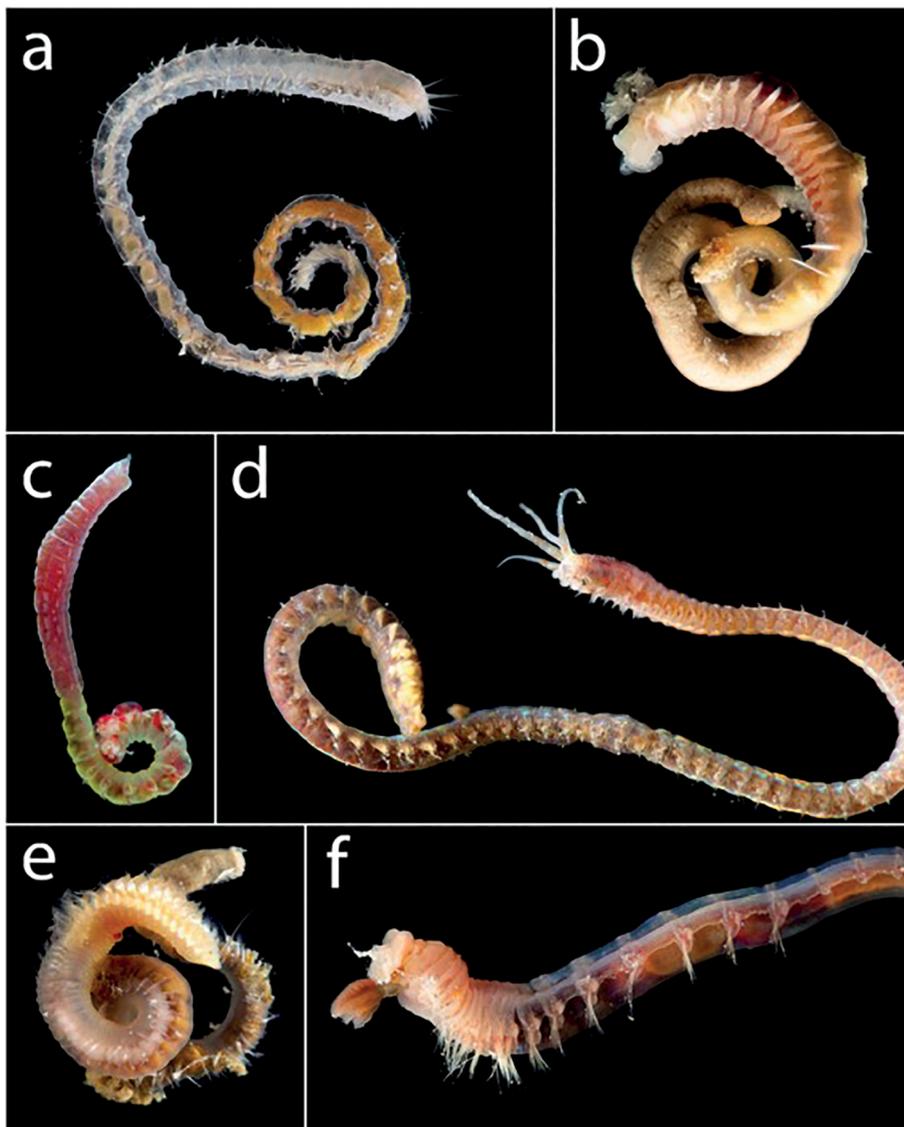
Figure 3. Annelids collected during Project BIOIL Cruise I in November 2019 at Santos basin. **a** eyeless specimen of *Ceratocephale* sp. 1; **b** *Aurospio* sp. 1; **c** *Notomastus* sp. 1; **d** *Kimbergonuphis* sp. 1; **e** *Paradoneis* sp. 1; **f** *Terebellides* sp.

with the dead corals (*Desmophyllum pertusum, S. variabilis* and *Enallopsammia rostrata*) and in surrounding sediments. The same was found at the station 684. Echinoderms were also more abundant in both stations, with 53% and 33%, respectively (Figure 8). Crustaceans were more abundant at stations 681 (26%) and 688 and 690 (15%), and Mollusca was the least abundant taxon along the studied sites (Figure 8).

Although there were no differences in species richness between tested stations (ANOVA F=21.17; d.f.=5; p=0.13), mean richness found in the area suggests higher values in the pockmark areas and in the areas surrounding the pockmarks (686, 688). Carbonate mounds presented an average richness higher than 20 species per station (685 and 687). The surroundings of carbonate mounds (683 and 684) presented the lowest richness, with an average of 8 species or less (Figure 9A). The same pattern can be observed for the diversity index (H´) that did not show differences between stations (ANOVA F=0.79; d.f.=5; p=0.57)
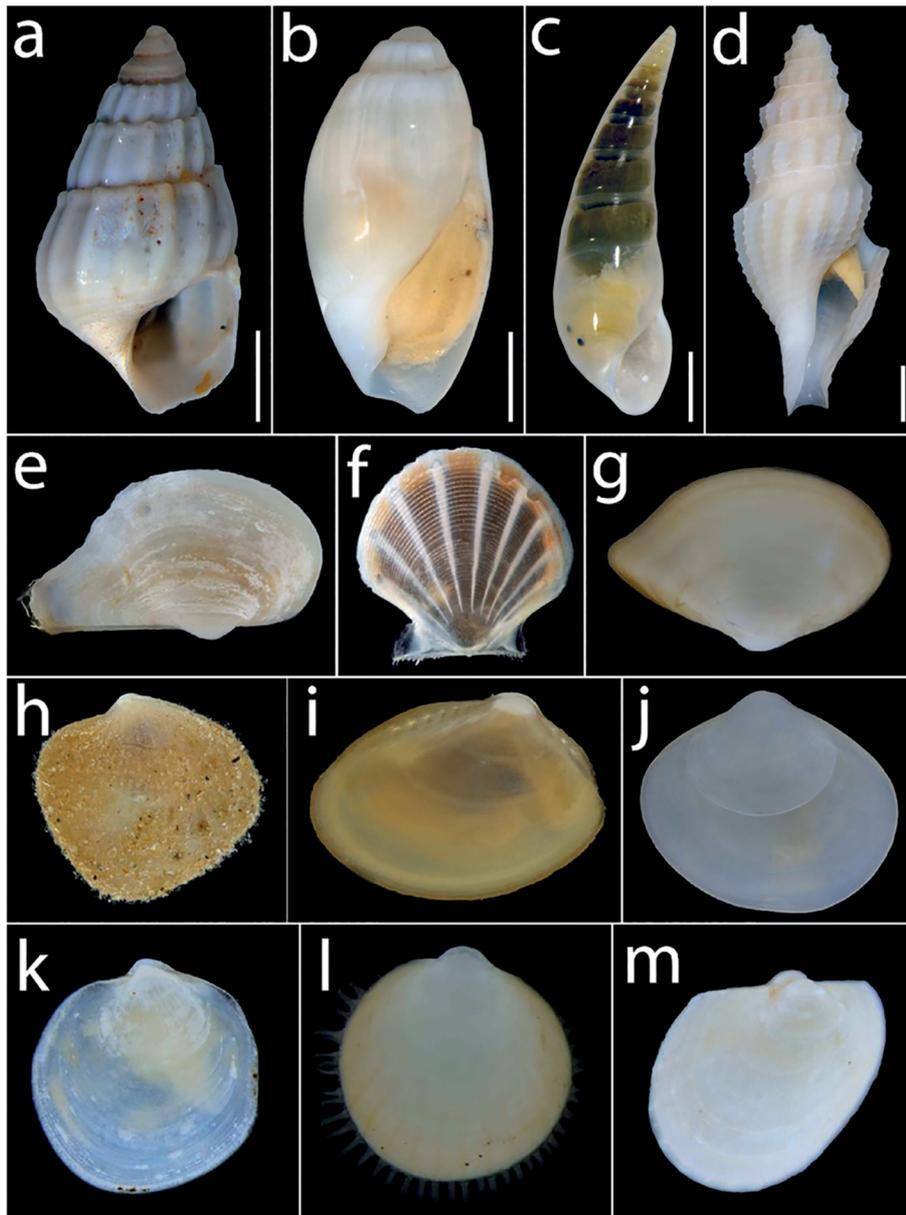
Figure 4. Mollusks collected during Project BIOIL Cruise I in November 2019 at Santos Basin. **a** *Benthonella xanthias*; **b** *Olivella careorugula*; *Melanella* sp. 1; **d** specimen of Conoidea; **e** Cuspidariidae sp. 1; **f** Pectinidae; **h** Verticordiidae; **i** Nuculidae; **k** *Axinulus croulinensis*; **l** Limopsidae; **m** Arcidae.

(Figure 9B). Pielou's evenness (J') was lower at some sites, such as 685 (0.94), and the station 689 (0,93), there were no significant differences in species dominance between stations (ANOVA F=19.99; d.f.=5; p=0.15) (Figure 9C).

In terms of community structure, multivariate analysis revealed distinct patterns, mainly associated with different habitat types (ANOSIM global test: R_{global}=0.501, p<0.001). We tested the influence of some previously classified environments on the distribution of organisms, including the influence of carbonate mounds and pockmark areas (Figure 10). Stations were grouped into two main groups: one group formed by samples collected at the top of the carbonate mound (685 and 687), a larger group with samples collected in the extensive area of pockmarks, either inside or at surrounding (pairwise ANOSIM: R_{CM-P}=0.777, p<0.01
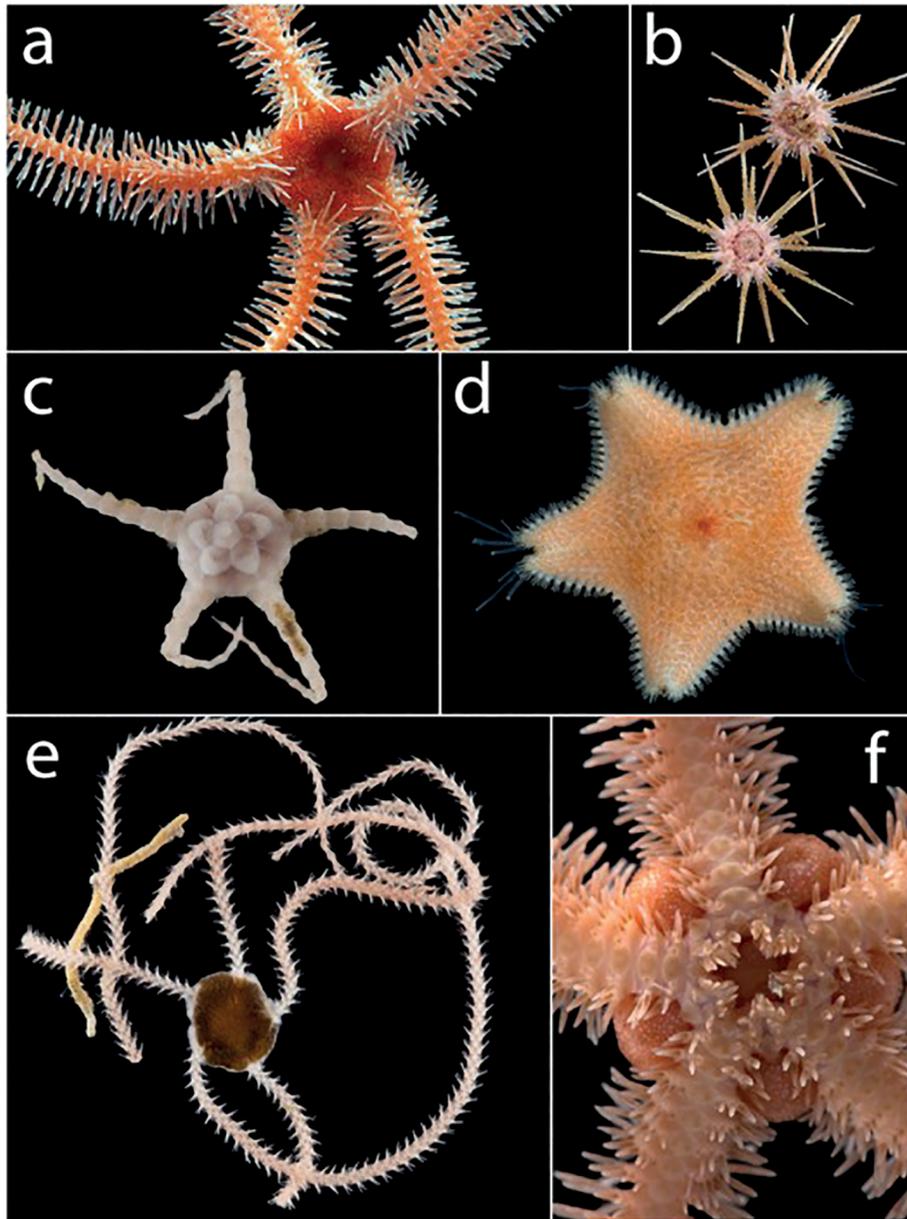
Figure 5. Echinoderms collected during Project BIOIL Cruise I in November 2019 at Santos Basin. **a** *Ophiacantha* sp., aboral view; **b** two specimens of the order Cidaroida, oral view; **c** *Ophiomisidium tommasii*, aboral view; **d** Asterinidae, aboral view; **e** specimen of the class Ophiuroidea, aboral view; **f** *Ophiacantha* sp., oral view.

and R_{CM-PS}=0.707, p<0.01) (Figure 10). Samples collected from the surroundings of carbonate mounds appear as intermediary sites (pairwise ANOSIM: R_{CMS-CM}=0.571, p<0.01; R_{CMS-P}=0.603, p<0.01 and; R_{CMS-PS}=0.575, p<0.01). There were no significant differences between pockmarks and their surroundings (pairwise ANOSIM: R_{P-PS}=-0.036, p=0.61). Similarity between groups varied from 18 to 27% (Figure 10).

SIMPER analysis indicated the percent contribution of species for the formation of the groups shown in Figures 10 and 11 (Table 4). The group 'Pockmark surroundings' had an average similarity (AS) of 18.06% and was formed mainly by annelids with the highest contribution of *Ceratocephale* sp. 1. 'Carbonate mound surrounding' (AS 10.46%) had the contribution of *Chloeia pocicola* and *Amphiura* sp. 1. 'Carbonate Mound' (AS
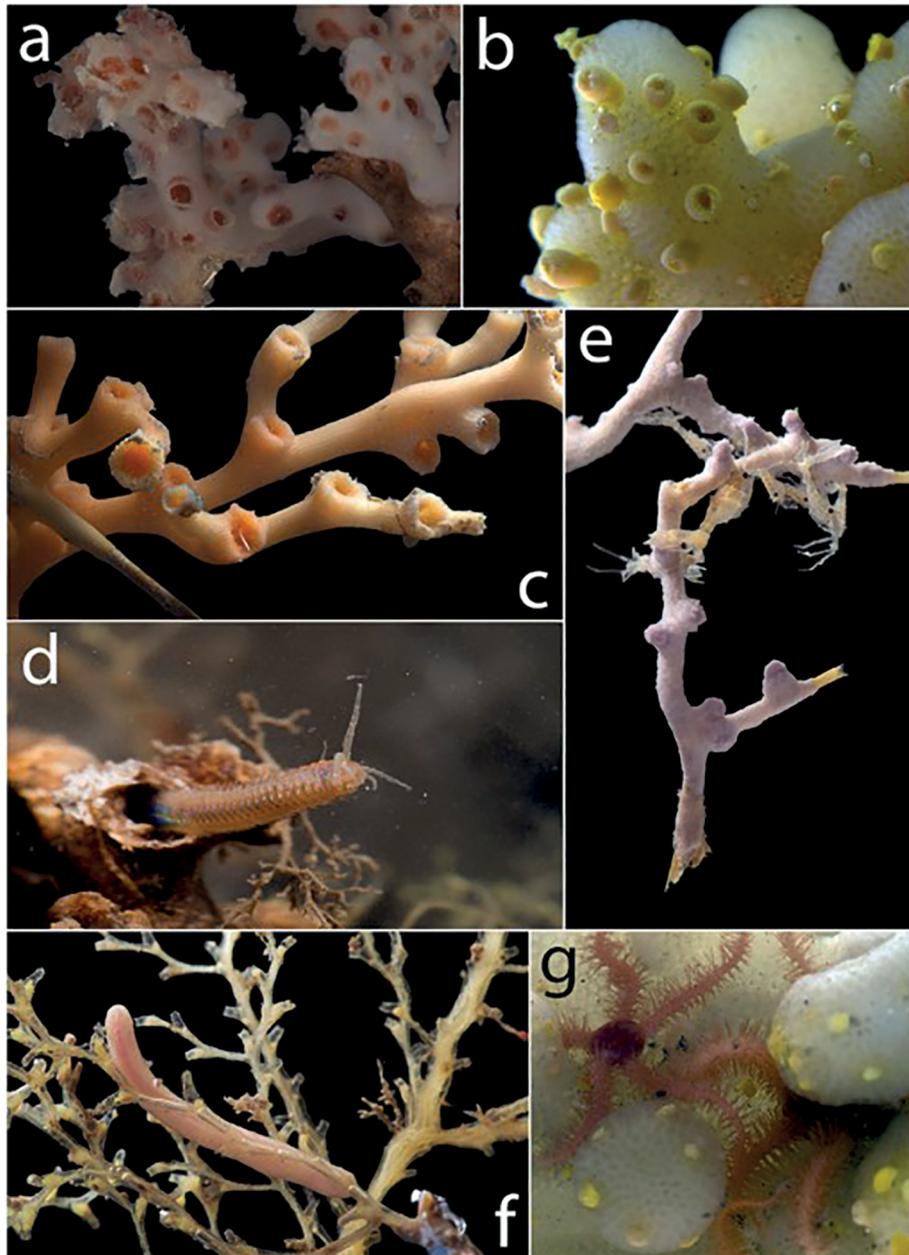
Figure 6. Corals, sponges and associated macrofauna collected during Project BIOIL Cruise I in November 2019 at Santos Basin. **a** branch of the glass sponge *Sarostegia oculata* with the symbiotic zoanthid *Thoracactis topsenti*; **b** branch of the glass sponge *Aphrocallistes* cf. *beatrix* with a symbiotic zoanthid; **c** branch of the stony coral *Solenosmilia variabilis*; **d** specimen of Eunice sp. living inside of a dead coral branch; **e** specimens of the isopod Arcturidae sp. on top of an octocoral; **f** aplacophoran solenogaster mollusk on top of a hydrozoan colony; **g** *Ophiacantha* sp. living on top of the glass sponge *Aphrocallistes* cf. *beatrix* sponge.

23.03%) had the main contribution of Polynoidae sp. 2, *Ophiacantha* sp. 1 and Anthozoa sp. 1. 'Pockmark' (AS 27.91%) had the highest contribution mainly of *Ceratocephale* sp. 1, *Laonice* sp. 1, *Tharyx* sp. 2, and *Tharyx* sp. 1 (Table 4).

Based on SIMPER results, the main taxa of each habitat were classified according to their feeding mode and are presented in Table 3. The contribution of each feeding mode varies along different habitat types, as shown in Figure 11.
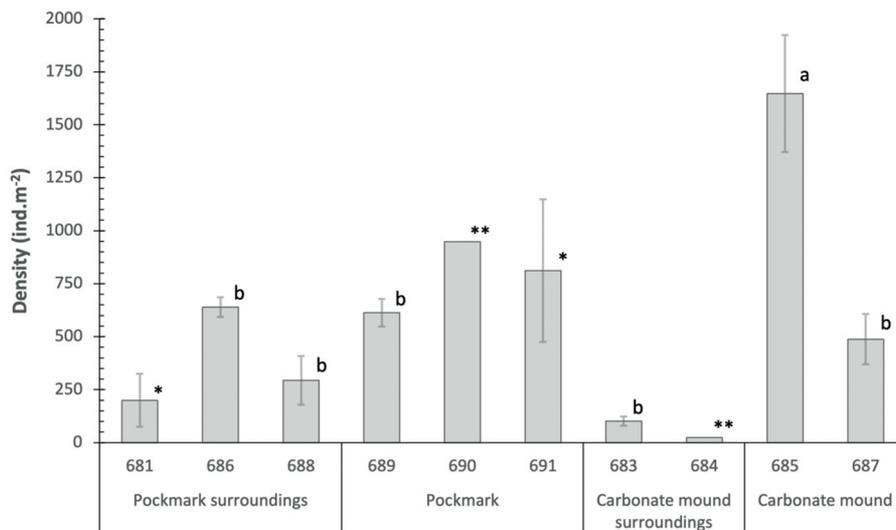
Figure 7. Mean macrofauna density (ind.m^{-2}) found at ten stations sampled in Santos Basin during Project BIOIL Cruise I in November 2019. Error bars are standard error. Same letters above columns indicate no significant differences in Tukey-HSD test. Stations indicated with * and ** were not included in statistical testing as they present two replicates and one replicate respectively. The total number is presented for stations 684 and 690 due to the absence of replicates.
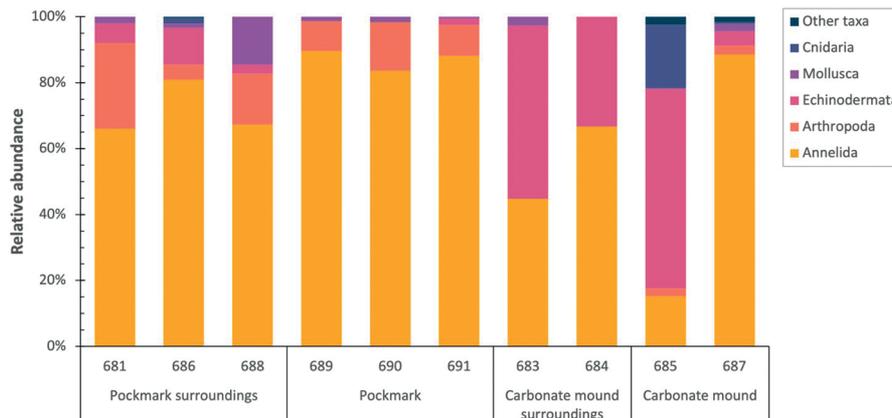

Figure 8. Relative abundance (%) of the main macrofauna groups found in slope environments in the 10 stations sampled in the Santos Basin during the Project BIOIL Cruise 1 in November 2019. The data represent the mean abundance values of the stations.

In general, the 'Pockmark surroundings' and 'Pockmark' groups showed certain similarities regarding feeding habits (Figures 11A, C). At these stations, higher densities of OM, SRD, SSD, and FD organisms were found; in this case animals classified as OM and FD are generalists and could also feed on deposits (Figures 11A, C). In stations under the influence of carbonate mounds and surroundings, there was a greater abundance of detritivorous or suspension-feeding (FD) and facultative carnivores (FC) organisms. In the top of

Carbonate Mound, we observed the contribution of more feeding modes, absent in other sites, direct suspensivores (SU) and direct carnivores (C).

DISCUSSION

The present study demonstrated that geological heterogeneity found at the Santos Basin directly influences macrobenthic structure patterns. The sampled sites comprise an area characterized by an extensive pockmark field formed by intense subsurface salt tectonic activity, indicated

Table 3. Relative abundance (%) and frequency of occurrence (%) of the main macrofauna families, in the 10 stations of the Santos Basin collected during the Project BIOIL Cruise 1 in November 2019. N = Total number of individuals. H.T.L. = Higher Taxonomic Level.

Families	Relative abundance (%)	Frequency of occurrence (%)	Families	Relative abundance (%)	Frequency of occurrence (%)
Annelida	**(n = 1159)**	**Freq.**	**Arthropoda**	**(n = 136)**	**Freq.**
Nereididae	16.0	56	Apseudidae	29.8	22
Paraonidae	12.3	59	Tanaidae	26.1	30
Capitellidae	12.1	48	Phoxocephalidae	11.1	19
Cirratulidae	10.9	41	Anthuridae	8.2	19
Spionidae	8.8	37	Gnathiidae	8.9	19
Syllidae	8.5	41	Ampeliscidae	2.9	7
Orbiniidae	6.8	44	Janiridae	2.9	4
Polynoidae	2.3	22	Arcturidae	3.7	11
Onuphidae	2.2	22	Corophiidae	1.4	7
Ampharetidae	1.8	15	Cirolanidae	0.7	4
Eunicidae	1.8	19	Maeridae	0.7	4
Cossuridae	1.5	33	Lyssianassidae	0.7	4
Glyceridae	1.2	22	Caprellidae	0.7	4
Goniadidae	1.0	26	Gammaridae	0.7	4
Opheliidae	1.0	26	**Echinodermata**	**(n = 440)**	**Freq.**
Amphinomidae	0.9	15	Ophiacanthidae	67.5	11
Hesionidae	0.9	30	Ophiactidae	9.0	19
Lumbrineridae	0.9	22	Amphiuridae	4.7	33
Magelonidae	0.8	19	Astrophiuridae	3.8	19
Flabelligeridae	0.7	4	Ophiothamnidae	1.8	15
Mollusca	**(n = 34)**	**Freq.**	Ophionereididae	1.3	15
Eulimidae	5.8	7	Ophioscolecidae	0.9	7
Olividae	5.8	7	Ophiuridae	0.6	7
Anatomidae	2.9	4	Cassidulidae	0.2	4
Limopsidae	2.9	4	Ophiopezidae	0.2	4
Verticordiidae	2.9	4	Amphiuridae	0.2	4
H.T.L.	79.4	37	H.T.L.	9.3	15

by several exhumed salt diapirs (Mahiques et al., 2017). In Santos Basin, these geological features are frequently associated to cold-water coral reefs (Sumida et al., 2004; Mahiques et al., 2017; Schattner et al., 2018) and also giant carbonate mounds that can coalesce into long ridges (Maly et al., 2019) (Figure 1). In general, the specific conditions of these environments influence the food availability, sediment and organic matter flux, and flow regime which reflect on the benthic community structure (Levin et al., 2001; Carvalho et al.,

2013). Indeed, our PCA showed the heterogeneity of area evidencing that physical-chemical characteristics such as the composition of substrates and nutrients were important factors in grouping the sites into habitat (Table 1, Figure 2), except for the pockmarks sites which were heterogeneous (Table 1, Figure 2).

The formation of two macrobenthic faunal groups related to the top of Alpha Crucis Carbonate Ridge and to pockmarks and surrounding areas emphasizes the importance of these
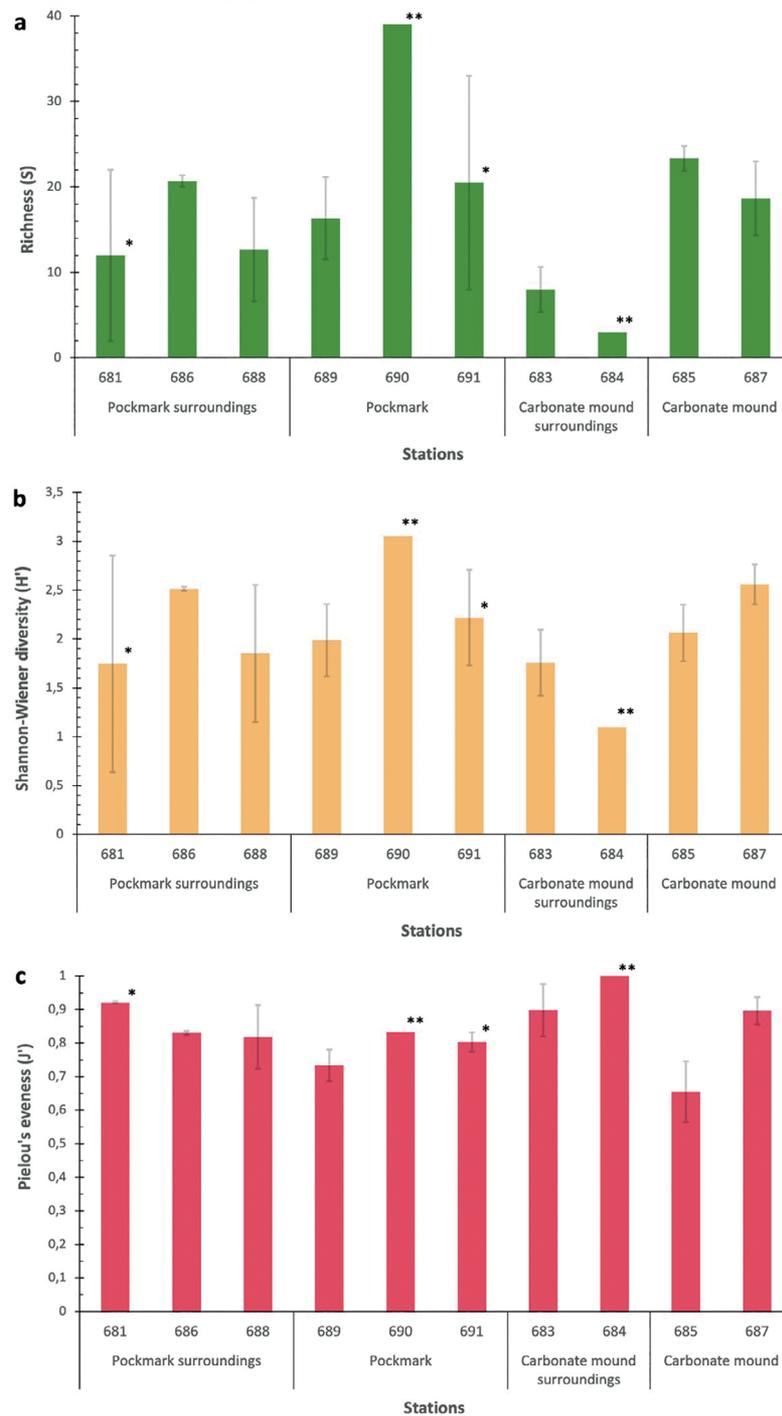
Figure 9. Ecological indicators of macrofauna found in the 10 stations sampled in the Santos Basin during the Project BIOIL Cruise 1 in November 2019. Mean values ± standard error. **a**. Richness (average number of morphotypes); **b**. Shannon-Wiener diversity index (H′− log2); **c**. Pielou's evenness (J'). ANOVA tests did not show significant differences between stations. Stations indicated with * and ** were not included in statistical testing as they present two replicates and one replicate respectively. The total number is presented for stations 684 and 690 due to the absence of replicates.
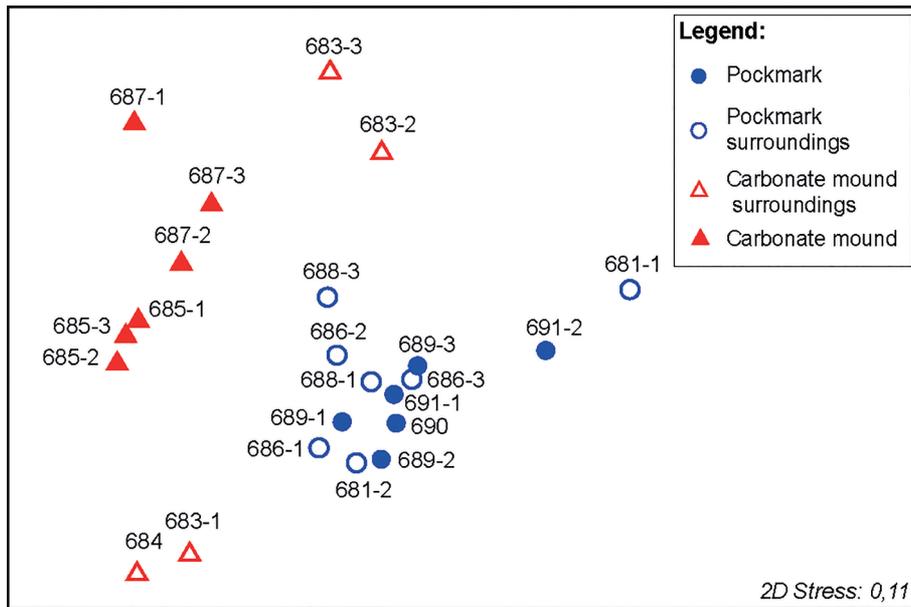
Figure 10. Non-metric multidimensional scaling (nMDS) plot of station replicates of the Project BIOIL Cruise 1 (November 2019) based on Bray-Curtis distance matrix from transformed [log(x+1)] species abundance data (with a minimum number of 5 individuals in a sample).
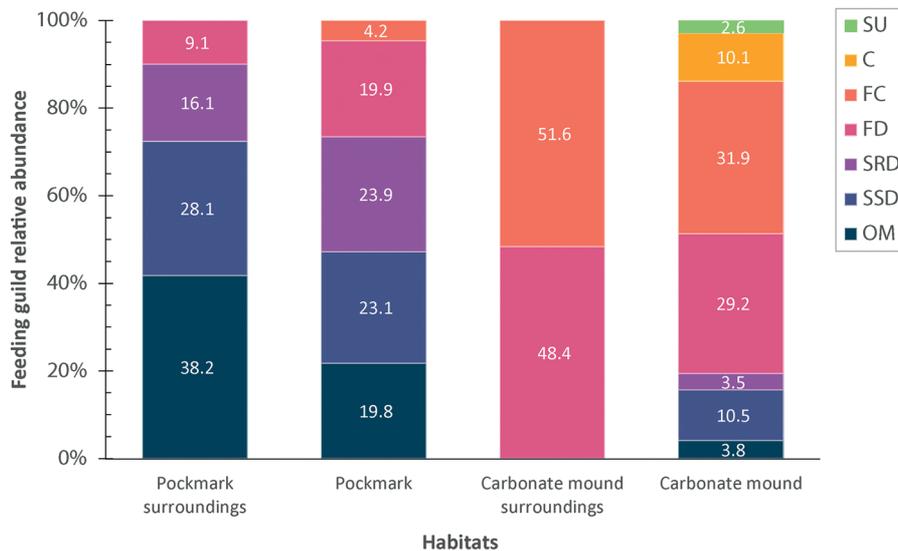

Figure 11. Contribution of feeding guilds (SU - suspensivores, C - carnivores, FC - facultative carnivores, FD - facultative detritivores, SRD - surface deposit feeders, SSD - subsurface deposit feeders, and OM - omnivores) of the most important taxa for the formation of the different habitat groups (SIMPER analysis).

physiographic features in the biodiversity and eco-system function in bathyal areas of SE Brazil. The remaining stations 683 and 684 were a mixture of dead coral fragments and soft sediments exhibiting intermediate characteristics. The distribution of macrofaunal organisms appears to be related to

the substrate type (hard- and soft nature of substrates and by their mixture).

Fauna density was also highly related to substrate type, which also influenced feeding habits. At the top of the ACCR (685), density was higher probably due to the presence of Deep-water coral

Table 4. Species that contribute up to 90% of the similarity values found between samples of each isobath (SIMPER). A.S.: Average similarity. Taxonomic groups (TG): An – Annelida, Tan – Tanaidacea, Cni – Cnidaria, Oph – Ophiuroidea. Feeding modes (FM): Omnivores (OM), Subsurface deposit feeders (SSD), Surface deposit feeders (SRD), Carnivore (C), Facultative detritivores (FD), Facultative carnivores (FC), Suspensivores (SU).

Group	Species/ morphotypes	Average Abundance	Contribution (%)	Cumulative Contribution%	TG	FM
Pockmark surroundings (Stations 681, 686, 688) A.S.: 18.06	*Ceratocephale* sp. 1	1.53	31.06	31.06	An	OM
	Paraonidae sp. 2	0.35	6.67	37.73	An	SSD
	Magelonidae sp. 1	0.53	5.71	43.44	An	SRD
	Opheliidae sp. 1	0.55	5.5	48.94	An	SSD
	Sipuncula sp. 1	0.68	5.5	54.45	An	SRD
	Apseudidae sp. 1	0.62	4.91	59.36	Tan	FD
	Paraexogone sp. 1	0.58	4.54	63.9	An	OM
	Cossuridae sp. 1	0.58	4.04	67.94	An	SSD
	Notomastus sp. 1	0.81	3.93	71.87	An	SSD
	Maldanidae sp. 1	0.45	3.68	75.55	An	SSD
	Tharyx sp. 1	0.58	2.77	78.32	An	SRD
	Kinbergonuphis sp. 1	0.45	2.56	80.88	An	OM
	Paradoneis sp. 1	0.68	2.17	83.05	An	SSD
	Tanaidae sp. 1	0.46	2.11	85.16	Tan	FD
	Laonice sp. 1	0.6	2.09	87.25	An	FD
	Tharyx sp. 2	0.63	2.09	89.34	An	SRD
	Mediomastus sp. 1	0..3	2.08	91.42	An	SSD
Carbonate mound surrounding (Stations 683, 684) A.S.: 10.46	Chloeia sp. 1	0.35	51.63	51.63	An	FC
	Amphiura sp. 2	0.45	48.37	100	Oph	FD
Carbonate mound (Stations 685, 687) A.S.: 23.03	Polynoidae sp. 2	1.3	12.96	12.96	An	FC
	Ophiacantha sp. 1	2.14	12.37	25.33	Oph	FD
	Anthozoa sp. 1	1.5	10.06	35.39	Cni	FC
	Neanthes sp. 1	0.9	6.93	42.33	An	FC
	Ophiactis sp. 1	1.19	6.36	48.69	Oph	FD
	Paraonidae sp. 3	0.61	5.84	54.53	An	SSD
	Lysidice sp. 1	1.05	5.57	60.09	An	FC
	Marenzelleria sp. 2	0.57	4.95	65.05	An	FD
	Capitellidae sp. 2	0.77	4.66	69.71	An	SSD
	Syllis sp. 2	0.66	3.8	73.51	An	OM
	Sipuncula sp. 2	0.61	3.51	77.02	An	SRD
	Glyceridae sp. 2	0.58	3.33	80.35	An	FC
	Chloeia sp. 1	0.48	3.08	83.43	An	FC
	Histampica sp. 1	0.48	2.89	86.33	Oph	FD
	Ophiuroidea sp. 1	0.77	2.62	88.95	Oph	FD
	Sabellariidae sp. 1	0.53	2.62	91.57	An	SU

Continued **Table 4.**

Pockmark (Stations 689, 690, 691) A.S.: 27.91	*Ceratocephale* sp. 1	2,09	13,42	13,42	An	OM
	Laonice sp. 1	1,77	13,35	26,77	An	FD
	Tharyx sp. 2	1,41	12,25	39,02	An	SRD
	Tharyx sp. 1	1,57	11,63	50,65	An	SRD
	Paradoneis sp. 1	1,24	5,82	56,47	An	SSD
	Paraonidae sp. 1	1,07	5,62	62,09	Na	SSD
	Mediomastus sp. 1	1,34	5,01	67,09	An	SSD
	Kinbergonuphis sp. 1	0,97	4,64	71,74	An	OM
	Cossuridae sp. 1	0,53	4,35	76,09	An	SSD
	Tanaidae sp. 1	0,89	4,26	80,35	Tan	FD

reefs that increase habitat heterogeneity and modify the abiotic environment providing a new habitat for macrobenthic fauna (Jensen and Frederiksen, 1992, Henry et al., 2008, van Oevelen et al., 2009; Webb et al., 2009, Levin et al., 2015, Ross et al., 2017).

Macrobenthic fauna at the 685 was characterized by the presence of voluminous live biogenic substrates, formed by glass sponge colonies of *Sarostegia oculata* and *Aphrocalistes* cf. *beatrix*, hydrozoans and live *Solenosmilia variabilis* colonies, in addition to dead-coral fragments mixed in the sediments at the base of reefs. In these samples, the density of organisms was the highest among the collected samples (1584 ind. m^{-2}), mainly due the presence of suspensivore epifauna and detritivore ophiuroids, carnivore annelids living inside sponges and corals, as well as other deposit-feeding annelids in the associated mixed sediments. Many studies on deep-water reefs found macrofauna distribution closely associated with three-dimensional structures producing "macrohabitats" or "vertical zonations". Therefore, they comprise zones of significant invertebrate species turnover ranging from the reef summit to its flank, including living coral framework, sediment-clogged mostly dead coral framework, rubble coral, and underlying sediments (Mortensen et al., 1995; Raes and Vanreusel, 2005; Roberts et al., 2006).

Despite the high density in these locations (basically formed by the increase of detritivores/suspensivores ophiuroids) and high taxon richness, diversity was lower than what is reported in the literature. In particular, invertebrate diversity was estimated to be up to three times higher than the surrounding seabed (Henry and Roberts, 2007), and even higher in areas dominated by coral rubble and sediments. In our samples, both richness of morphotypes and Shanon-Weaver diversity index were similar to other type habitats studied herein. Low diversity and high density have already been registered for *Desmophyllum pertusum* rubble at the base of coral mounds (macrofauna, Mortensen et al., 1995; Mortensen and Fosså, 2006).

The 687 station is also located on top of the ACCR, but both density values and taxonomic composition were different compared to station 685 (density: ~500 ind.m^{-2} x 1584 ind.m^{-2}; taxonomic composition: 90% of annelids x 60% of Echinodermata and only 10% of annelids). Despite the divergences observed, however, SIMPER analysis suggest that the two stations are grouped by the similarity of organisms with varied feeding habits including carnivores, detritivores, both sub- and surface deposit feeders, omnivores and suspensivores, as expected for the habitat type.

Differences in communities may be related to the complexity of the carbonate mound sampled, or particularly for what part of the mound the samples are representing. In fact, the difference in complexity between the samples collected at stations 685 and 687 is evident, both in terms of structure and composition of the substrate (although PCA analyses did not indicate strong differentiation between these sites). The heterogeneity and hard substrate availability in coral mounds allowed suspension-feeder animals such as sponge colonies (*Sarostegia oculata* and *Aphrocalistes* cf. *beatrix*), live corals (*Solenosmilia variabilis*), hydrozoans, anemones and a great abundance of ophiuroids

to be present at station 685. Variation in community composition due to changes in aspect strongly relates to how species respond to differences in water flow (Best, 1988; Glasby, 2000; Glasby and Connell, 2001). Biological functioning of suspensivores, such as feeding efficiency, often vary between upstream and downstream flow (Holland et al., 1987). On the ACCR, the structure is determined and shaped by the dominant bottom current, the IWBC, and are tidally driven and flow in an approximately south to north direction (Figure 1), which would make the southward-facing station 685 exposed to the local hydrodynamics, allowing the presence of filter-feeding animals (Maly et al., 2019).

Furthermore, the structure and diversity of mounds seem vary with the gradual differentiation of communities as one moves from top to the mound to the flank and bottom and as increasingly different or distant environments are compared (Jonsson et al., 2004, Mortensen and Fossa, 2006, Henry and Roberts, 2007, van Soest et al., 2007, Cordes et al., 2008, Roberts et al., 2008, Roberts et al., 2009, Henry et al., 2009). That's the case to explain the lower densities and diversity at the station 683, located close to carbonate substrates (Ramos, pers. obs.). Samples were composed of sediments intermingled with several dead coral fragments forming a massive matrix. Only one living colony of *Solenosmilia variabilis* and a few solitary corals (*Caryophyllia* sp. 1) were found. No sponge or hydrozoan colonies were found at these stations.

This low structural complexity reflected in observed differences and low densities. Most of the animals were found in the associated sediments and very few within the coral skeletons. It is worth mentioning that station 684 may have been affected because only one sample was collected and therefore it was not possible to fully assess such a pattern. However, in terms of composition, stations 683–684 had basically annelids and ophiuroids, mostly composed of facultative carnivores and detritivores or suspensions which are common to reef habitats. As already discussed, structures formed by deep-water corals usually alter the local flow, facilitating the deposition of organically enriched sediments and thus modifying the

characteristics of the adjacent sediments and the benthos (Jumars and Nowell, 1984), even though these effects are often considered localized and highly variable at distances less than 10 m from the reef (Posey et al., 1994; Danovaro et al., 2008; Demopoulos et al., 2014). Both stations 683 and 684 showed the highest amounts of silt sediments and nutrient concentration (Table 1). Therefore, the sites seem to show an intermediate habitat between the carbonate sediments and sites dominated by background sediments.

Most of the studies on pockmark communities have been related with the fluid or gas seepage and the establishment of a chemosynthesis-based ecosystem. Indeed, when active the chemosynthetic production can increase the beta diversity of deep sea (Hovland and Judd, 1988; Dando et al., 1991; Ondreas et al., 2005). However, even when inactive or when fluid/gas emission is diffuse, the diversity in pockmarks can be higher compared with outside regions due to increase of seafloor profile heterogeneity (Cordes et al., 2010).

Macrobenthic assemblage composition can be different between areas inside and outside pockmarks and sometimes considered as a refuge for the benthic community (Dando et al., 1991; Dubois et al., 2015). Thus, as with positive geologic formations, negative features also affect benthic species distribution and community structure. In fact, the macrofauna found within the pockmark was abundant and species-rich. Some taxa, for example, were found only in these environments. The three pockmark stations (689-691) are in different depths (Table 1), and possibly at different water masses (Table 1). Consequently, factors such as circulation, sedimentation and accumulation of nutrients are different between stations grouped in pockmarks, and therefore the sites were slightly dissimilar to each other, as shown by the PCA (Figure 2). In general, however, pockmark fauna has a strong relationship with the surrounding fauna, which we call here the 'pockmark surrounding' (Figure 10). Most of these sites exhibited high taxon dominance, with annelids representing the community dominant in all sampled habitats and typical of deep-sea sediments (Levin and Gooday, 2003). At these stations, we had a greater predominance of deposit-feeding organisms (Table 4).

According to Ramos et al. (2020), pockmarks function as sediment traps for fine particles, and could favor the presence of marine deposit-eating organisms. Furthermore, such negative structures could still act to interfere with the flow of larvae between populations of other features, depending on the depths and dimensions of the pockmarks. However, apparently the pockmarks found here did not show considerable depth or other peculiar characteristics enough to shape or sustain a different fauna.

Although we did not find the presence of seepages or directly specialized fauna in cold-seeps habitat, we did find some animals that usually are associated with these environments living inside pockmarks, such as the annelids *Melinna* sp. 1, *Melinnopsis* sp. 1, *Anobothrus* sp. 1 (Ampharetidae), *Sirsoe* sp. 1. (Hesionidae), *Siboglinum besnardi* (Siboglinidae), and bivalves of the family Thyasiridae. The presence of these animals in pockmark areas may indicate the presence of diffused gas, or proximity to areas with methane exudation. Biological evidence based on the presence of a correlated fauna corroborates the geophysical work in progress in the BS area showing the presence of gas in subsurface (Mahiques et al., 2017).

CONCLUSION

The present study contributes to a better understanding of deep-sea benthic habitats and their communities in an important area from a geological, ecological and also economic perspective, such as the Santos Basin. Our results show the presence of a great species richness of marine invertebrate taxa, most of them corresponding to rare species (35% of all taxa), in addition to the presence of new records for the SW Atlantic, and potentially new species for science that will be formally published soon. We also showed a strong correlation of the macrobenthic fauna from the upper slope of the BS with the geomorphology of the area and the most important variables that act on the sites, mainly substrate composition, inclination and orientation to water flux. We describe the fauna of important BS environments, from an

ecological, geological and also economic point of view, such as the carbonate mounds that harbor a large special fauna associated with cold-water coral reefs. It is a sensitive and important environment in regard to biodiversity conservation on the Brazilian margin. As deep-sea corals and pockmarks are extremely sensitive to anthropogenic and natural events, this study provides baseline information on macrobenthic communities from these special deep-sea habitats in the BS that can be used to help inform future research, monitoring activities, and conservation strategies. Although we did not find evidence of cold seeps and the communities characteristic of such environments, we found some animals that could indicate the presence of gas, either diffuse or residual, in nearby areas. This data together with both geophysical and microbiological data could help in the resolution and mapping of potential cold seep environments in the BS.

ACKNOWLEDGMENTS

AUTHOR CONTRIBUTIONS

O.C.: Conceptualization; Data curation; Formal analysis; Investigation; Visualization; Writing – original draft; Writing – review & editing.

A.Z.G.: Investigation; Data curation; Formal analysis; Visualization; Writing – review & editing.

G.B.: Investigation; Visualization; Writing – review & editing.

B.H.M.S., T.N.S.B.: Investigation; Writing – review & editing.

P.D.N.P.: Investigation; Project administration; Writing – review & editing.

J.M., A.C.: Investigation.

R.B.R.: Investigation – review & editing.

P.Y.G.S.: Conceptualization; Funding acquisition; Investigation; Project administration; Resources; Supervision; Writing – review & editing.

REFERENCES

ARAÚJO, L. D., LOBO, F. J. & DE MAHIQUES, M. M. 2021. The imprint of sedimentary processes in the acoustic structure of deposits on a current-dominated continental shelf. *Journal of South American Earth Sciences*, 105, 103005.

BEST, B. A. 1988. Passive suspension feeding in a sea pen: effects of ambient flow on volume flow rate and filtering efficiency. *Biology Bulletin*, 175(3), 332–342.

BILÓ, T. C., SILVEIRA, I., ROCHA, C. B. & CECCOPIERI, W. 2014. On the Brazil current thickening in Santos Basin (23-28 S). *OSM,* ID14707.

CARVALHO, R., WEI, C., L., ROWE, G. & SCHULZE, A. 2013. Complex depth-related patterns in taxonomic and functional diversity of polychaetes in the Gulf of Mexico. *Deep-Sea Research Part I*, 80, 66-77.

CORDES, E. E., CUNHA, M. R., GALÉRON, J., MORA, C., ROY, K., SIBUET, M., GAEVER, S. V., VANREUSEL, A. & LEVIN, L. A. 2010. The influence of geological, geochemical, and biogenic habitat heterogeneity on seep biodiversity. *Marine Ecology*, 31(1), 51-65, DOI: https://doi.org/10.1111/j.1439-0485.2009.00334.x

CORDES, E. E., MCGINLEY, M. P., PODOWSKI, E. L., BECKER, E. L., LESSARD-PILON, S., VIADA, S. T. & FISHER, C. R. 2008. Coral communities of the deep Gulf of Mexico. *Deep-Sea Research Part I*, 55(6), 777-787.

DANDO, P. R., AUSTEN, M., BURKE, R., KENDALL, M., KENNICUTT, M., JUDD, A. G., MOORER, D., O'HARA, S., SCHMALJOHANN, R. & SOUTHWARD, A. 1991. Ecology of a North Sea pockmark with an active methane seep. *Marine Ecology Progress Series*, 70(1), 49-63.

DANOVARO, R., GAMBI, C., DELLANNO, A., CORINAIDESI, C., FRASCHETTI, S., VANREUSEL, A., VINCX, M. & GOODAY, A.J. 2008. Exponential decline of deep-sea ecosystem functioning linked to benthic biodiversity loss. *Current Biology,* 18(1), 1-8.

DEMOPOULOS, A. W. J., BOURQUE, J. R. & FROMETA, J. 2014. Biodiversity and community composition of sediment macrofauna associated with deep-sea *Lophelia pertusa* habitats in the Gulf of Mexico. *Deep-Sea Research I*, 93, 91-103.

DE MAHIQUES, M. M., SCHATTNER, U., LAZAR, M., SUMIDA, P. Y. G. & SOUZA, L. A. P. 2017. An extensive pockmark field on the upper Atlantic margin of Southeast Brazil: spatial analysis and its relationship with salt diapirism. *Heliyon*, 3, e00257.

DE MAHIQUES, M. M., SILVEIRA, I. C. A., SOUSA, S. H. D. M. & RODRIGUES, M. 2002. Post-LGM sedimentation on the outer shelf-upper slope of the northernmost part of the São Paulo Bight, southeastern Brazil. *Marine Geology*, 181(4), 387-400.

DORSCHEL, B., HEBBELN, D., FOUBERT, A., WHITE, M. & WHEELER, A. J. 2007. Hydrodynamics and cold-water coral facies distribution related to recent sedimentary processes at Galway Mound west of Ireland. *Marine Geology*, 244(1-4), 184-195.

DUBOIS, S. F., D'ERIAN, F., CAISEY, X., RIGOLET, C., CAPRAIS, J. & THIEBAUT, E. 2015. Role of pockmarks in diversity and species assemblages of coastal macrobenthic communities. *Marine Ecology Progress Series*, 529, 91-105.

GLASBY, T. M. 2000. Surface composition and orientation interact to affect subtidal epibiota. *Journal of Experimental Marine Biology and Ecology*, 248(2), 177-190.

GLASBY, T. M. & CONNELL, S. D. 2001. Orientation and position of substrata have large effects on epibiotic assemblages. *Marine Ecology Progress Series,* 214, 127-135.

HENRY, L. A., DAVIES, A. J. & MURRAY, R. 2009. Beta diversity of cold-water coral reef communities off western Scotland. *Coral Reefs*, 29(2), 427-436.

HENRY, L. A., NIZINSKI, M. S. & ROSS, S. W. 2008. Occurrence and biogeography of hydroids (Cnidaria: Hydrozoa) from deep-water coral habitats off the southeastern United States. *Deep Sea Research Part I*, 55, 788-800.

HENRY, L. A. & ROBERTS, J. M. 2007. Biodiversity and ecological composition of macrobenthos on cold-water coral mounds and adjacent off-mound habitat in the bathyal Porcupine Seabight, NE Atlantic. *Deep Sea Research Part I,* 54(4), 654-672.

HOLLAND, N. D., LEONARD, A. B. & STRICKLER, J. R. 1987. Upstream and downstream capture during suspension feeding by *Oligometra serripinna* (Echinodermata: Crinoidea) under surge conditions. *Biology Bulletin,* 173(3), 552-556.

HOVLAND, M. & JUDD, A. G. 1988. *Seabed pockmarks and seepages. Impact on geology, biology and the marine environment.* Oxford: Graham and Trotman.

HOVLAND, M. & THOMSEN, E. 1997. Cold-water corals—are they hydrocarbon seep related? *Marine Geology,* 137(1-2), 159-164.

JENSEN, A. & FREDERIKSEN, R. 1992. The fauna associated with the bank forming deep-water coral *Lophelia pertusa* (Scleractinia) on the Faroe Shelf. *Sarsia,* 77(1), 53-69.

JONSSON, L. G., NILSSON, P. G., FLORUTA, F. & LUNDA, T. 2004. Distributional patterns of macro- and megafauna associated with a reef of the cold-water coral *Lophelia pertusa* on the Swedish west coast. *Marine Ecology Progress Series*, 284, 163-171.

JUMARS, P. A., DORGAN, K. M. & LINDSAY, S. M. 2015. Diet of worms emended: an update of polychaete feeding guilds. *Annual Review of Marine Science*, 7, 497-520, DOI: https://doi.org/10.1146/annurev-marine-010814-020007

JUMARS, P. A. & NOWELL, A. R. M. 1984. Fluid and sediment dynamic effects on marine benthic community structure. *American Zoologist,* 24(1), 45-55.

LEVIN, L. A., ETTER, R. J., REX, M. A., GOODAY, A. J., SMITH, C. R., PINEDA, J., STUART, C. T., HESSLER, R. R. & PAWSON, D. 2001. Environmental influences on regional deep-sea species diversity. *Annual Review of Ecology and Systematics*, 132, 51-93.

LEVIN, L. & GOODAY, A. J. 2003. The deep Atlantic Ocean. *In*: TYLER, P. A. (ed.). *Ecosystems of the world volume 28: ecosystems of the deep ocean.* Amsterdam: Elsevier, pp. 111-178.

LEVIN, L. A., MENDOZA, G. F., GRUPE, B. M., GONZALEZ, J. P., JELLISON, B., ROUSE, G., THURBER, A. R. & WAREN, A. 2015. Biodiversity on the rocks: macrofauna inhabiting authigenic carbonate at Costa Rica methane seeps. *PloS One*, 10(8), e0131080.

MACDONALD, T. A., BURD, B. J. & ROODSELAAR, A. V. 2012. Facultative feeding and consistency of trophic structure in marine soft-bottom macrobenthic communities. *Marine Ecology Progress Series*, 445, 129-140.

MALY, M., SCHATTNER, U., LOBO, F. J., DIAS, R. J. S., RAMOS, R. B., COUTO, D. D. M. & DE MAHIQUES, M. M. 2019. The Alpha Crucis Carbonate Ridge (ACCR): discovery of a giant ring-shaped carbonate complex on the SW Atlantic margin. *Scientific reports*, 9(1), 1-10.

MCCLAIN, C. R. & HARDY, S. M. 2010. The dynamics of biogeographic ranges in the deep sea. *Proceedings of the Royal Society B: Biological Sciences*, 277, 3533-3546.

MORTENSEN, P. B. & FOSSA, J. H. 2006. Species diversity and spatial distribution of invertebrates on deep-water Lophelia reefs in Norway. *In: Proceedings of 10th International Coral Reef Symposium*. Okinawa, Japan, 28 Jun-02 July, 2003. Okinawa: ICRS, pp. 1849-1868.

MORTENSEN, P. B., HOVLAND, M., BRATTEGARD, T. & FARESTVEIT, R. 1995. Deep water bioherms of the scleractinian coral *Lophelia pertusa* (L.) at 64N on the Norwegian shelf: structure and associated megafauna. *Sarsia*, 80, 145-158.

ONDRÉAS, H., OLU, K., FOUQUET, Y. & CHARLOU, J. L. 2005. ROV study of a giant pockmark on the Gabon continental margin. *Geo-Marine Letters*, 25(5), 281-292.

PAU, M., HAMMER, Ø. & CHAND, S. 2014. Constraints on the dynamics of pockmarks in the SW Barents Sea: evidence from gravity coring and high-resolution, shallow seismic profiles. *Marine Geology*, 355, 330-355.

PETERSON, R. G. & STRAMMA, L. 1991. Upper-level circulation in the South Atlantic Ocean. *Progress in Oceanography*, 26(1), 1-73.

POSEY, M. H. & AMBROSE, W. G. 1994. Effects of proximity to an offshore hard-bottom reef on infaunal abundances. *Marine Geology*, 118(4), 745-753.

RAES, M. & VANREUSEL, A. 2005. *The metazoan meiofauna associated with a cold-water coral degradation zone in the Porcupine SEABIGHT (NE Atlantic)*. *In*: FREIWALD, A. & ROBERTS, J. M. (eds.). *Coldwater corals and ecosystems*. Heidelberg: Springer-Verlag, pp. 821-847.

RAMIREZ-LLODRA, E., BRANDT, A., DANOVARO, R., DE MOL, B., ESCOBAR, E., GERMAN, C. R., LEVIN, L. A., MARTINEZ ARBIZU, P., MENOT, L., BUHL-MORTENSEN, P., NARAYANASWAMY, B. E., SMITH, C. R., TITTENSOR, D. P., TYLER, P. A., VANREUSEL, A. & VECCHIONE, M. 2010. Deep, diverse and definitely different: unique attributes of the world's largest ecosystem. *Biogeosciences*, 7(9), 2851-2899.

RAMOS, R. B., SANTOS, R. F., SCHATTNER, U., FIGUEIRA, R. C. L., BÍCEGO, M. C., LOBO, F. J. & DE MAHIQUES, M. M. 2020. Deep pockmarks as natural sediment traps: a case study from southern Santos Basin (SW Atlantic upper slope). *Geo-Marine Letters*, 40(6), 989-999.

ROBERTS, J. M., HENRY, L. A., LONG, D. & HARTLEY, J. P. 2008. Cold-water coral reef frameworks, megafaunal communities and evidence for coral carbonate mounds on the Hatton Bank, northeast Atlantic. *Facies*, 54, 297-316.

ROBERTS, J. M., WHEELER, A. J. & FREIWALD, A. 2006. Reefs of the deep: the biology and geology of cold-water coral ecosystems. *Science*, 312, 543-547.

ROBERTS, J. M., WHEELER, A. J., FREIWALD, A. & CAIRNS, S. D. 2009. *Cold water corals: the biology and geology of deep-sea coral habitats*. Cambridge: Cambridge University Press.

ROSS, S. W., RHODE, M. & BROOKE, S. 2017. Reprint of – Deep-sea coral and hardbottom habitats on the west Florida slope, eastern Gulf of Mexico. *Deep-Sea Research Part I*, 127, 114-128.

SÁNCHEZ, N., ZEPPILLI, D., BALDRIGHI, E., VANREUSEL, A., GASIMANDOVA, M., BRANDILY, C., PASTOR, L., MACHERIOTOU, L., GARCÍA-GÓMEZ, G., STÉPHANNIE, D. & OLU, K. 2021. A threefold perspective on the role of a pockmark in benthic faunal communities and biodiversity patterns, *Deep Sea Research Part I: Oceanographic Research Papers*, 167, 0967-0637, DOI: https://doi.org/10.1016/j.dsr.2020.103425

SCHATTNER, U., LAZAR, M., SOUZA, L. A. P., TEN BRINK, U. & DE MAHIQUES, M. M. D. 2016. Pockmark asymmetry and seafloor currents in the Santos Basin offshore Brazil. *Geo-Marine Letters*, 36(6), 457-464.

SCHATTNER, U., LOBO, F. J., GARCÍA, M., KANARI, M., RAMOS, R. B. & DE MAHIQUES, M. M. (2018). A detailed look at diapir piercement onto the ocean floor: New evidence from Santos Basin, offshore Brazil. *Marine Geology*, 406, 98-108.

SILVEIRA, I. C. A. D., SCHMIDT, A. C. K., CAMPOS, E. J. D., GODOI, S. S. D. & IKEDA, Y. 2000. A corrente do Brasil ao largo da costa leste brasileira. *Revista Brasileira de Oceanografia*, 48(2), 171-183.

STRAMMA, L. & ENGLAND, M. 1999. On the water masses and mean circulation of the South Atlantic Ocean. *Journal of Geophysical Research: Oceans*, 104(C9), 20863-20883.

SUMIDA, P. Y. G., PELLIZARI, V. H., LOURENÇO, R. A., SIGNORI, C. N., BENDIA, A. G., CARRERETTE, O., NAKAMURA, F. M., RAMOS, R. B., BERGAMO, G., SOUZA, B. H. M., BUTARELLI, A. C. A., PASSOS, J. G., DIAS, R. J. S., MALY, M., BANHA, T. N. S., GÜTH, A. Z., SOARES, L. F., PERUGINO, P. D. N., SANTOS, F. R., SANTANA, F. R. & DE MAHIQUES, M. M. D. 2022. Seep hunting in the Santos Basin, Southwest Atlantic: sampling strategy and employed methods of the multidisciplinary cruise BIOIL 1. Ocean and Coastal Research, 70(Suppl 2), e22031, DOI: https://doi.org/10.1590/2675-2824070.22077pygs

SUMIDA, P. Y. G., YOSHINAGA, M. Y., MADUREIRA, L. A. S. P. & HOVLAND, M. 2004. Seabed pockmarks associated with deepwater corals off SE Brazilian continental slope, Santos Basin. Marine Geology, 207(1-4), 159-167.

TREVIZANI, T. H., NAGAI, R. H., FIGUEIRA, R. C. L., SUMIDA, P. Y. G. & DE MAHIQUES, M. M. 2022. Chemical characterization of deep-sea corals from the continental slope of Santos Basin (southeastern Brazilian upper margin). Ocean and Coastal Research, 70(Suppl 2), e22018, DOI: http://doi.org/10.1590/2675-2824070.21108tht

VAN OEVELEN, D., DUINEVELD, G., LAVALEYE, M., MIENIS, F., SOETAERT, K. & HEIP, C. H. R. 2009. The cold-water coral community as a hot spot for carbon cycling on continental margins: a food-web analysis from Rockall Bank (northeast Atlantic). Limnology and Oceanography, 54(6), 1829-1844.

VAN SOEST, R. W. M., CLEARY, D. F. R., DE KLUIJVER, M. J., LAVALEYE, M. S. S., MAIER, C. & VAN DUYL, F. C. 2007. Sponge diversity and community composition in Irish bathyal coral reefs. Contributions to Zoology, 76(2), 121-142.

WEBB, K. E., BARNES, D. K. A. & GRAY, J. S. 2009. Benthic ecology of pockmarks in the inner Oslofjord, Norway. Marine Ecology Progress Series, 387, 15-25.

WHEELER, A. J., BETT, B. J., BILLETT, D. S. M., MASSONT, D. G. & MAYOR, D. 2005. The impact of demersal trawling on northeast Atlantic deepwater coral habitats: the case of the Darwin Mounds, United Kingdom. American Fisheries Society Symposium, 41, 807-817.