



Sandy beach macroinfauna response to the worst oil spill in Brazilian coast: No evidence of an acute impact

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ABSTRACT

This study provides the first assessment of the impact of the worst oil spill ever faced by Brazilian sandy beaches by analyzing changes in the community structure of intertidal macroinfauna. Four sandy beaches were sampled three times after the oil spill, and the results were compared with previous data. The first sampling, conducted 15 days after the oil spill (October 2019), showed higher abundance of macroinfauna, which decreased in subsequent sampling conducted 60 and 120 days later, but never reached a lower level than in previous sampling. Of the macroinfauna species, *Scolecopsis* sp. was most abundant in October 2019, while *Donax gemmula* was predominant during the other time periods. Changes observed in macroinfauna were due to natural fluctuations rather than a response to this disturbance. Characteristics of both the oil spill and macroinfauna contributed to the lack of acute impacts.

1. Introduction

Since late August 2019, crude oil began to wash up onto the beaches of the northeastern Brazilian coastline; four months after the first report, oil had already been found along >3000 km of the coast, making this oil spill the most extensive and severe environmental disaster ever recorded in Brazilian history (Soares et al., 2020a, 2020b, 2022). This disaster reached more than 55 marine protected areas, and a range of coastal ecosystems have also been affected, including mangroves, estuarine systems, seagrass beds, intertidal rocky shores, rhodolith beds, coral reefs, and sandy beaches (Magris and Giarrizzo, 2020; Soares et al., 2020b). Moreover, this oil spill also resulted in various socioeconomic impacts that negatively affected tourism, fishery, and food sectors in the region (Câmara et al., 2021; Estevo et al., 2021).

The source of this crude oil remains unknown; most likely, the spillage occurred approximately 700 km off the Brazilian coast, where the oil was then transported closer to the continental shelf by the southern branch of the South Equatorial Current and, subsequently, was moved northward by the North Brazil Current and then southward by the Brazil Current (Lessa et al., 2021; Zacharias et al., 2021). The stranded oil along the entirety of the northeastern Brazilian coast had the same origin and was characterized as solid tar, denser than seawater, with the formation of stable or meso-stable emulsion from some weathering processes (Lourenço et al., 2020; Oliveira et al., 2020; Araújo et al., 2021). Due to these characteristics, the oil drift occurred in

the subsurface (Lessa et al., 2021), making its prior detection difficult.

The ecological effects of the oil spill can be divided into two phases, an initial or acute impact characterized by high mortality of fauna, followed by chronic effects resulting from the long-term persistence of toxic compounds, mostly hydrocarbons, within sediments (Schlacher et al., 2011; Bejarano and Michel, 2016). Previous assessments of the oil spill's impacts on sandy beach macroinfauna have confirmed this acute impact, which resulted in a reduction in the total abundance and diversity of macroinfauna just a few weeks after the spill (de la Huz et al., 2005; Junoy et al., 2005; Schlacher et al., 2011).

Sandy beaches are considered one of the most resilient ecosystems to oil spills (Schlacher et al., 2011; Junoy et al., 2014), with a recovery of affected macroinfauna occurring in periods ranging from weeks to a couple of years (Bejarano and Michel, 2016). However, the macroinfaunal recovery depends on several factors, including site-specific physical properties and processes (e.g., beach morphodynamics), the degree of shoreline oiling and depth of oil burial, as well as biological characteristics of the community (Bejarano and Michel, 2016).

The main problem for assessing the ecological effects of either the oil spill or any other disturbances is the lack of baseline studies in many of the ecosystems affected. In fact, the sandy beaches of the northeastern region are among the least studied along the Brazilian coast (Amaral et al., 2016). The Sergipe coast was the third most heavily affected by the stranded oil, with approximately 570 tons of residues (i.e., crude oil and underlying sediments) having been collected mainly from its sandy

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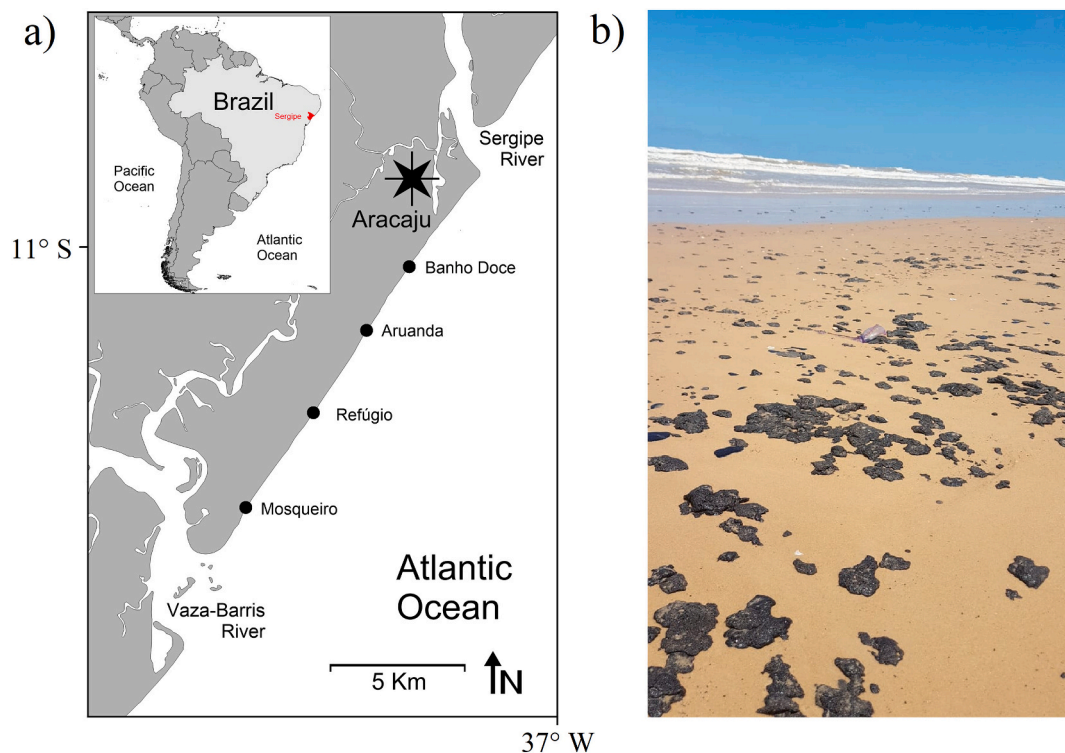


Fig. 1. Location of the studied sandy beaches along the central portion of the Sergipe coast, northeastern Brazil (a) and a photograph of the stranded crude oil at Mosqueiro Beach (b).

beaches (Soares et al., 2020a, 2020b; Zacharias et al., 2021; Soares et al., 2022). In this Brazilian state, studies on sandy beach ecology are incipient (e.g., Rosa et al., 2018; Rosa, 2021), and the results of most of the existing studies are not yet published. Therefore, the present study assessed the immediate impacts of this oil spill on the macroinfauna of Sergipe coast. For this purpose, four sandy beaches were sampled three times each (at approximately days 15, 75, and 135) after the oil arrived at the end of September 2019. The results were compared with previously unpublished data, mainly from 2013 and 2014, which were obtained using the same procedures; this allowed a more robust assessment of this disaster.

2. Material and methods

The coast of the state of Sergipe corresponds to approximately 160 km of intermediate/dissipative sandy beaches distributed between the mouths of the São Francisco and Piauí rivers (Dominguez et al., 2016). East-southeast waves with periods of 6 and 8 s and heights ranging from 1 to 2 m are prevalent along the coast (Pianca et al., 2010). Tides are semidiurnal, with a maximum tidal range of 2.6 m (Dominguez et al., 2016). The local climate is tropical, with a wet season occurring from April to August (Alvares et al., 2013).

Samplings were carried out at four different beaches: Banho Doce (11°00'33" S; 37°03'42" W), Aruanda (11°02'11" S; 37°04'54" W), Refúgio (11°04'14" S; 37°06'17" W), and Mosqueiro (11°06'41" S; 37°07'58" W), all situated along the central portion of Sergipe coast (Fig. 1). These beaches were chosen for having been identified as those most affected by stranded oil, as well because previous macroinfaunal data was available for them.

The beaches had been sampled previously in August 2013 and June 2014 and were then sampled at intervals of approximately 15 (October 2019), 75 (December 2019), and 135 days (February 2020) after the discovery of stranded crude oil and after the posterior clean-up activities had taken place. At each beach, macroinfauna was sampled at five transects spaced 2 m apart along the beach. Transects comprised 10

samples that were equally spaced from the water line to the high tide mark (Rosa-Filho et al., 2015) and were taken using a corer (inner diameter 200 mm, 200 mm deep). Each sample was washed through 0.5 mm mesh bags, and all of the resulting retained material was preserved in 70% ethanol *in situ*. Additional samples were taken from a single transect to carry out granulometric analyses. Beach slope was measured using a dumpy level, and wave regime (wave height and period) was characterized through visual estimation.

Macroinfaunal organisms were sorted from sediment, identified, and counted in a laboratory setting. The mean grain size was obtained by sieving dried sediment samples following Suguio (1973), for methodology, and Wentworth (1922), for grain size scale. Beach morphodynamic states were obtained by applying both Dean's parameter (Ω) and Beach Index (BI), according to Short (1996) and McLachlan and Dorvlo (2005), respectively.

For analytical purposes, all of the samples obtained from each transect were grouped, and the density of each species was determined for the transect sampled area (Schlacher et al., 2008). Then, the biological data were arranged in an $n \times p$ matrix, with the species in rows and the transects (five replicates per sampling period) in columns. Species occurring in only one sampled transect were not included in the analysis. Square root data transformation was performed and all tests were based on the Bray-Curtis's resemblance function.

Firstly, differences in the structure of macroinfauna between beaches and sampling periods were assessed by a two-way permutational analysis of variance (Permanova) (Anderson et al., 2008). Non-metric multidimensional scaling (nMDS) and hierarchical agglomerative clustering (CLUSTER analysis), with the unweighted pair-group average cluster model, were also used to compare macroinfauna structure between sampling periods for each beach individually (Clarke and Warwick, 2001). The similarity profile routine (SIMPROF) test was applied to determine significant differences between the clusters considering a 5% significance level (Clarke et al., 2008). The contributions of individual taxa to the overall disparities between clusters were identified through similarity percentages breakdown (SIMPER) analysis (Clarke

Table 1
Mean values (\pm SD) of abiotic variables obtained to each analyzed beach.

Variables	Banho Doce	Aruanda	Náufragos	Mosqueiro
Intertidal width (m)	125.67 \pm 8.50	135.13 \pm 14.20	121.33 \pm 16.50	134.33 \pm 10.02
1/Slope (m)	46.46 \pm 3.94	50.54 \pm 2.30	42.07 \pm 4.16	47.34 \pm 5.75
Grain size (mm)	0.141 \pm 0.02	0.128 \pm 0.02	0.139 \pm 0.01	0.132 \pm 0.01
Wave height (m)	0.70 \pm 0.15	0.70 \pm 0.10	0.73 \pm 0.21	0.73 \pm 0.21
Wave period (s)	9.40 \pm 2.85	8.87 \pm 2.10	9.37 \pm 2.44	10.03 \pm 2.54
Ω	4.91 \pm 1.20	6.36 \pm 0.96	5.32 \pm 0.75	5.44 \pm 1.07
BI	2.66 \pm 0.05	2.72 \pm 0.03	2.62 \pm 0.04	2.68 \pm 0.07

and Warwick, 2001). All analyses were performed using Primer 6 + PERMANOVA add-on software.

3. Results

All beaches showed similar morphodynamic characteristics throughout the sampling periods. Intertidal width ranged from 121.33 \pm 16.50 (Refúgio) to 134.33 \pm 10.02 m (Mosqueiro), with slopes ranging from \sim 1/42 (Mosqueiro) to \sim 1/50 m (Aruanda). Sediment was composed of fine sands, while the wave regime comprised waves with \sim 0.7 m in height and periods of 8 to 10 s. According to Dean's parameter (Ω), beaches were classified as dissipative, except for Banho Doce, which was classified as an intermediate beach. Contrastingly, the BI classified all beaches as mesotidal intermediate beaches. Table 1 shows a summary of all characteristics of the beaches.

A total of 9719 individuals belonging to 32 species were collected. The most abundant species were the polychaete *Scolecipis* sp. and the bivalve *Donax gemmula*, corresponding to \sim 79% of the total number of individuals (i.e., 55.86% and 23.08%, respectively). Other abundant organisms were the mysid *Chlamydopleon dissimile* (3.58%), the polychaete *Hemipodia californiensis* (2.98%), as well as the isopod *Excirrolana armata* (2.60%).

Overall, the number of species recorded throughout the sampling periods at each beach ranged from 11 (February 2020, Banho Doce) to 20 (December 2019, Mosqueiro) (Fig. 2). For all beaches, higher

densities of macroinfauna were recorded for the first sampling carried out after the oil spill (October 2019) compared to previous samplings (August 2013 and June 2014) (Fig. 2). The macroinfauna densities recorded in October 2019 were the highest mainly because of the high densities of the polychaete *Scolecipis* sp. (Fig. 3).

The multivariate analyses indicated significant differences in the macroinfauna between both beaches (Permanova: Pseudo-F = 8.842; P (perm) = 0.001) and sampling periods (Pseudo-F = 39.476; P (perm) = 0.001). However, the changes in the macroinfauna structure observed between the sampling periods were distinct for each beach, as indicated by significant interaction (Pseudo-F = 6.073; P (perm) = 0.001). This spatiotemporal variability was also highlighted by both clustering and ordination analyses, where a distinct grouping pattern in the sampling periods was detected for each beach (Fig. 4).

The lowest temporal variability of macroinfauna was recorded at Refúgio Beach, where only three of the August 2013 samples were grouped apart from all the others (Fig. 4). This difference resulted mainly from the absence of polychaetes *Scolecipis* sp. and *H. californiensis* in these three samples (Table 2). At Banho Doce Beach, two distinct sampling groups were also recorded (Fig. 4). October 2019 samples contained the highest macroinfaunal densities, especially for *Scolecipis* sp. (Table 3), and were grouped apart from other sampling periods. Three groups were recorded at Aruanda Beach (Fig. 4). Again, the highest macroinfauna densities, especially of *Scolecipis* sp., were recorded in October and December 2019 and resulted in one group apart (Table 4). The February 2020 sample group resulted from the highest densities of *D. gemmula*, while the third group (August 2013/June 2014) corresponded to periods of lowest macroinfaunal densities (Table 4). Contrastingly, the highest variability was recorded at Mosqueiro Beach, where five groups were formed, each corresponding to a distinct sampling period (Fig. 4). The highest densities of *Scolecipis* sp. in October 2019 resulted in the formation of one distinct group, whereas other groups resulted from both lower macroinfaunal densities and shifts in prevalence between *D. gemmula* and *C. dissimile* (Table 5).

4. Discussion

All beaches were very similar regarding morphodynamics and did not show any significant differences between sampling periods. Despite

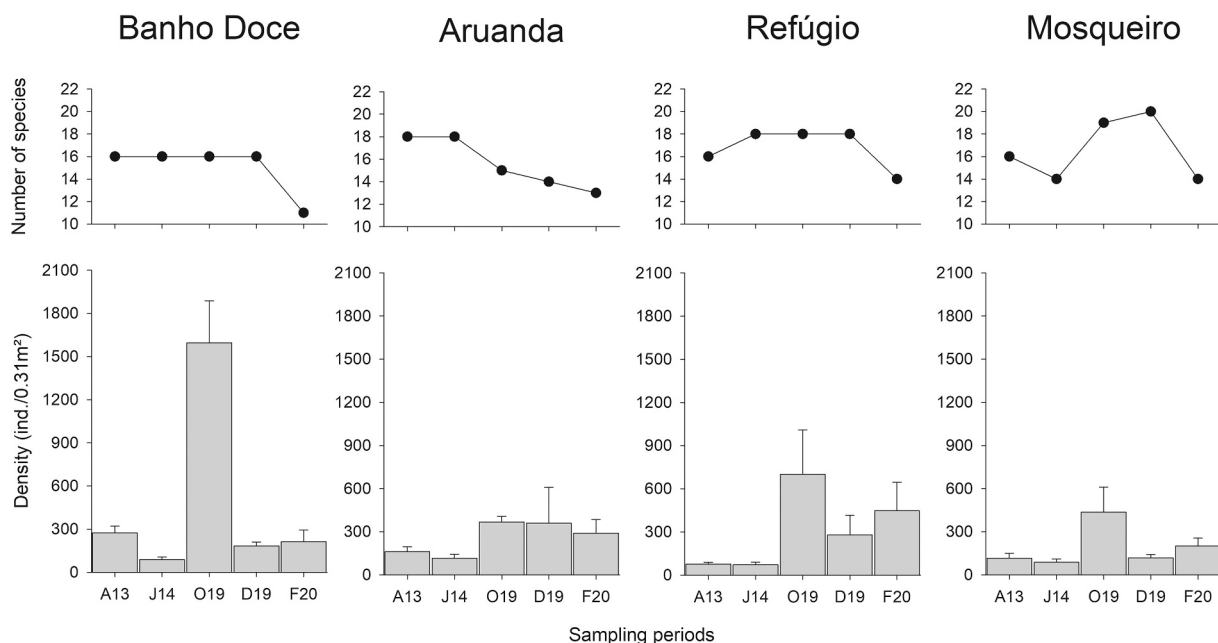


Fig. 2. Number of species and mean values (\pm 1 standard deviation) of total macroinfauna density at each analyzed sandy beach along the sampling periods (A13: August 2013, J14: June 2014, O19: October 2019, D19: December 2019, F20: February 2020).

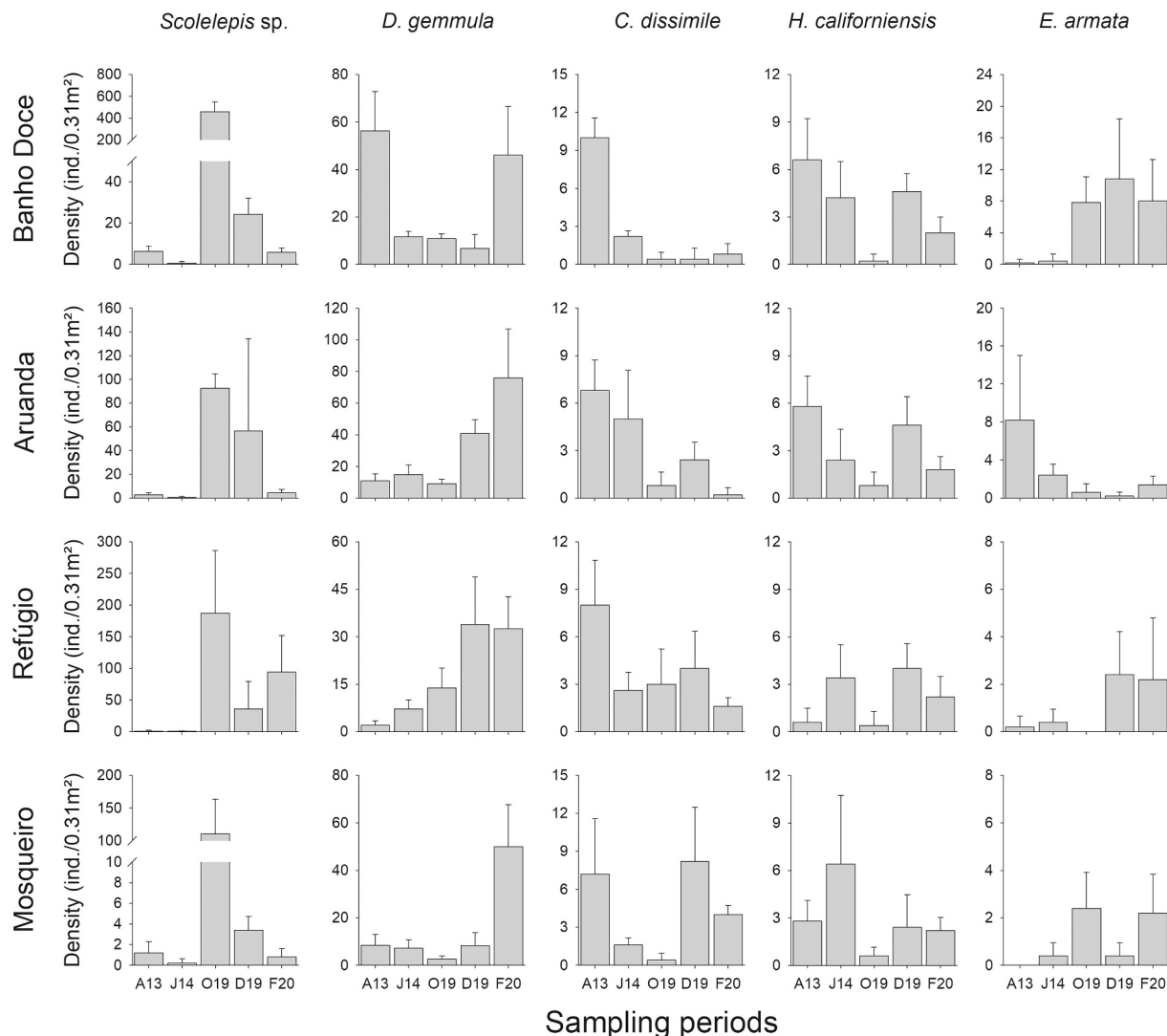


Fig. 3. Mean density (± 1 standard deviation) of the dominant macroinfaunal species at each analyzed sandy beach along the sampling periods (A13: August 2013, J14: June 2014, O19: October 2019, D19: December 2019, F20: February 2020).

the similarities in abiotic environments, the macrofauna highly varied between the beaches analyzed and the sampling periods. Differences in the structure of macrofauna had been previously recorded at these same beaches and were attributed to natural along-shore variability due to different patterns of recruitment and posterior along-shore migration (Rosa, 2021). Observed temporal differences mainly occurred due to macrofaunal densities, which were higher during the first sampling carried out after the oil spill (October 2019), and which were driven mainly by the polychaete *Scolelepis* sp.

In general, an increase in macrofauna abundance soon after oil spill events are associated with increased densities of opportunistic species (Junoy et al., 2014; Bejarano and Michel, 2016; Craveiro et al., 2021). In addition, the polychaete *Scolelepis* sp. has been pointed out as an opportunistic species which adapts easily to oil spill scenarios (Rizzo and Amaral, 2001). However, some previous studies have shown that these polychaetes were negatively affected by oil spills at two distinct events, the “Prestige” off the Galician coast (de la Huz et al., 2005; Junoy et al., 2005) and the “Pacific Adventurer” in Eastern Australia (Schlacher et al., 2011); in both cases, its abundance decreased.

Scolelepis is represented by conspicuous and very abundant species on intertidal sandy beaches worldwide. These polychaetes are considered interface feeders, which catch particles that are either in suspension or deposited in sediments (Pardo and Amaral, 2004). *Scolelepis* spp. is

the dominant species in southern Brazil, accounting for over 70% of total macrofauna in most of the sandy beaches analyzed (Souza and Gianuca, 1995; Borzone et al., 1996; Souza and Borzone, 2000; Amaral et al., 2003). In that region, these polychaetes had higher densities during the austral winter than in the summertime (Souza and Gianuca, 1995; Borzone et al., 1996; Souza and Borzone, 2000). Furthermore, inter-annual variations in *S. squamata* abundance were also observed (Souza and Borzone, 2000). Based on samplings carried out monthly from February 1992 to February 1993 at one of these beaches, Souza and Borzone (2000) recorded two peaks in *S. squamata* abundance: one, which was more intense, in July 1992 (austral winter) and another in February of 1993 (austral summer). According to these authors, this inter-annual variability in polychaete abundance was related to a successful recruitment of more than one cohort.

Previous studies of these same beaches' macrofauna had revealed low levels of abundance for *Scolelepis* sp., as well as for the community as a whole (Rosa, 2021). Indeed, the macrofauna on Sergipe coast was very poor compared to beaches in southern Brazil, where total abundance was about two orders of higher magnitude. This pattern of low macrofaunal density is attributed to the latitudinal gradient, which establishes that macrofauna abundance decreases toward lower latitudes as a result of lower food availability (see McLachlan and Defeo, 2018).

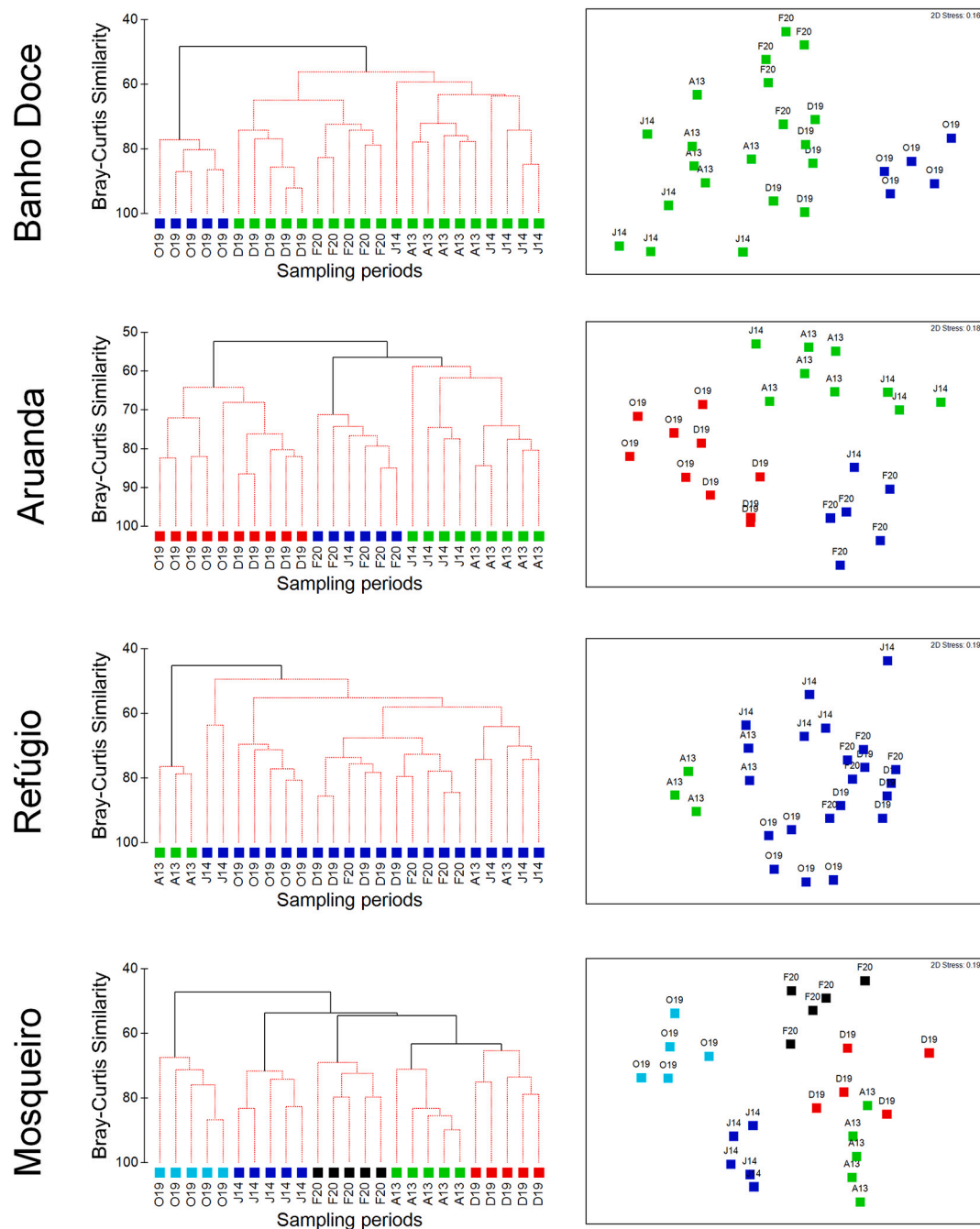


Fig. 4. Cluster dendrograms and plots of MDS on similarity in the structure of macroinfauna assemblages along the sampling periods (A13: August 2013, J14: June 2014, O19: October 2019, D19: December 2019, F20: February 2020) at each analyzed sandy beach. Colored symbols indicate different groups pointed by SIMPROF test. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Unfortunately, there are no temporal studies on the macroinfauna of Sergipe beaches, except for the callinassid shrimp *Callichirus major* (Rosa et al., 2018). This burrowing shrimp is a conspicuous filter-feeding species that inhabits intertidal areas of sandy beaches along the western Atlantic; they are customarily caught to be used as live baits by recreational fishers (Souza and Borzone, 2003; Botter-Carvalho et al., 2007; Costa et al., 2020). Populational aspects of this species were analyzed at Aruanda Beach in a previous study, in which higher densities of burrow openings and juveniles were observed from June to September, evidencing a clear seasonal pattern of recruitment (Rosa et al., 2018). According to the authors, the recruitment of *C. major* during the wet season was related to the greater availability of food since an increase in the fluvial discharge results in the enrichment of the coastal water.

A similar pattern was observed by Araújo and Rocha-Barreira (2012), who studied the population dynamics of *Olivella minuta*, a common sandy beach gastropod, along the beaches of the state of Ceará, also located on the northeastern coast of Brazil. The authors observed that the recruitment of this gastropod was from March to September (wet season), resulting in the highest densities being observed in November. In this same state, higher densities of *Scolecopsis* sp. have been observed during rainy rather than dry seasons (Rocha-Barreira et al., 2001; Viana et al., 2005). With the limited data available, it is difficult to assess whether *Scolecopsis* sp. is an opportunistic species favored by oil spills. However, it is plausible that the highest densities of *Scolecopsis* sp. soon after the spill might also be a natural occurrence resulting from the seasonality promoted by the wet season.

Table 2

Summary of SIMPER analysis identifying the contribution of individual species to total similarity in each temporal grouping recorded to macroinfauna in the Naufragos Beach. Only species with a Sim/SD ratio > 1 are included (Av. Den: Average density; Av. Sim: Average Similarity; Sim/SD: average contribution/standard deviation; Contr. (%): % species contribution; Cum. (%): cumulation of % species contribution).

Species	Av. Den	Av. Sim	Sim/SD	Contr. (%)	Cum. (%)
Group ■ (three samples from Aug 2013) Average similarity: 77.23					
<i>Chlamydopleon dissimile</i>	10.04	17.67	15.67	22.88	22.88
<i>Donax gemmula</i>	1.69	10.11	17.4	13.09	35.97
Group ■ (all others samples) Average similarity: 59.25					
<i>Donax gemmula</i>	15.37	14.27	4.24	24.08	24.08
<i>Scolecipis</i> sp.	23.85	11.47	1.30	19.37	43.45
<i>Chlamydopleon dissimile</i>	2.29	8.91	2.69	15.05	58.49
<i>Hemipodia californiensis</i>	1.17	6.57	1.32	11.09	69.58

Table 3

Summary of SIMPER analysis identifying the contribution of individual species to total similarity in each temporal grouping recorded to macroinfauna in the Banho Doce Beach. Only species with a Sim/SD ratio > 1 are included (Av. Den: Average density; Av. Sim: Average Similarity; Sim/SD: average contribution/standard deviation; Contr. (%): % species contribution; Cum. (%): cumulation of % species contribution).

Species	Av. Den	Av. Sim	Sim/SD	Contr. (%)	Cum. (%)
Group ■ (Oct 2019) Average similarity: 80.36					
<i>Scolecipis</i> sp.	451.65	31.92	23.34	39.72	39.72
<i>Donax gemmula</i>	10.73	12.52	25.49	15.58	55.3
Group ■ (Aug 2013/Jun 2014/Dec 2019/Feb 2020) Average similarity: 61.77					
<i>Donax gemmula</i>	21.37	16.57	3.32	26.83	26.83
<i>Hemipodia californiensis</i>	3.84	11.56	5.62	18.71	45.54
<i>Scolecipis</i> sp.	4.18	8.98	1.50	14.53	60.07

Overall, recorded changes in the macroinfauna were in a period of both higher macroinfauna abundance and prevalence of the polychaete *Scolecipis* sp., during the first instances following the oil spill (October 2019), followed by periods of both lower macroinfaunal densities and the prevalence of the bivalve *D. gemmula* in the previous samplings (August 2013 and June 2014). This pattern of lower macroinfaunal densities and the prevalence of *D. gemmula* were previously recorded in April 2012 (dry season) at the same beaches (Rosa, 2021), supporting that the macroinfaunal changes were observed due to natural seasonal variability instead of a response to the oil spill. However, this seasonality in the macroinfauna with shifts in the prevalence of species and higher densities associated with higher food availability during the wet season need to be investigated further.

As pointed out by Bejarano and Michel (2016), each oil spill is a unique event, and the response of sandy beach macroinfauna depends on several factors, like the type and quantity of oil spilled, as well as beaches' characteristics and the communities associated with them. Regarding the volume of the spilled oil, more than 5000 tons of oil residues were removed from the ~3000 km of coastline from August 2019 to January 2020, of which 570 tons (<12% of total) were removed from Sergipe coast. Based on the quantity of oil present in these residues, quantitative estimations suggested that the total volume of oil spilled

Table 4

Summary of SIMPER analysis identifying the contribution of individual species to total similarity in each temporal grouping recorded to macroinfauna in the Aruanda Beach. Only species with a Sim/SD ratio > 1 are included (Av. Den: Average density; Av. Sim: Average Similarity; Sim/SD: average contribution/standard deviation; Contr. (%): % species contribution; Cum. (%): cumulation of % species contribution).

Species	Av. Den	Av. Sim	Sim/SD	Contr. (%)	Cum. (%)
Group ■ (Aug 2013/Jun 2014) Average similarity: 66.34					
<i>Donax gemmula</i>	11.22	12.20	7.58	18.39	18.39
<i>Chlamydopleon dissimile</i>	5.06	9.65	5.83	14.54	32.93
<i>Excirrolana armata</i>	3.95	8.35	5.88	12.59	45.52
<i>Hemipodia californiensis</i>	2.94	7.50	1.82	11.31	56.82
Group ■ (Feb 2020) Average similarity: 75.13					
<i>Donax gemmula</i>	60.59	23.22	5.46	30.90	30.90
<i>Scolecipis</i> sp.	3.52	11.27	8.94	15.00	45.91
<i>Hemipodia californiensis</i>	1.57	9.47	10.04	12.61	58.52
<i>Excirrolana armata</i>	0.98	6.85	1.34	9.12	67.64
Group ■ (Oct 2019/Dec 2019) Average similarity: 69.33					
<i>Scolecipis</i> sp.	57.19	19.27	4.29	27.80	27.80
<i>Donax gemmula</i>	20.20	15.16	5.33	21.87	49.67
<i>Hemipodia californiensis</i>	1.17	5.73	1.22	8.26	57.93
<i>Chlamydopleon dissimile</i>	0.75	5.27	1.24	7.61	65.54

ranged between 5000 and 12,500 m³ (Zacharias et al., 2021). Considering these estimates and the proportion of oil stranded on Sergipe beaches, this disaster could be regarded as a low-volume spill. Additionally, the oil stranded along the northeastern coast of Brazil had the appearance of tar balls; it had a solid aspect and was denser than water, suggesting a high degree of weathering (Lourenço et al., 2020; Oliveira et al., 2020). These characteristics make the stranded oil have a lower rate of percolation into sediments and result in it being more easily removed from the beaches. Furthermore, these characteristics resulted in oil patches that were stranded randomly along the beaches.

In conclusion, the characteristics of the spillage (i.e., the quantity, type, and how this oil was stranded on the beaches) along with a poor density of fauna contributed to a lack of evidence regarding the immediate impact on macroinfauna of the sandy beaches of Sergipe coast. Furthermore, it is more plausible that the observed differences result from the natural temporal variability rather than as a response of the macroinfauna to the oil spill.

CRediT authorship contribution statement

Leonardo Cruz da Rosa: Conceptualization, Resources, Methodology, Formal analysis, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data associated with this article can be found in the online version, at <https://doi.org/10.1016/j.marpolbul.2022.113753>. These data include the Google map of the most important areas

Table 5

Summary of SIMPER analysis identifying the contribution of individual species to total similarity in each temporal grouping recorded to macrofauna in the Mosqueiro Beach. Only species with a Sim/SD ratio > 1 are included (Av. Den: Average density; Av. Sim: Average Similarity; Sim/SD: average contribution/standard deviation; Contr. (%): % species contribution; Cum. (%): cumulation of % species contribution).

Species	Av. Den	Av. Sim	Sim/SD	Contr. (%)	Cum. (%)
Group					
■ (Aug 2013) Average similarity: 79.54					
<i>Donax gemmula</i>	7.59	11.08	10.94	13.93	13.93
<i>Chlamydopleon dissimile</i>	6.39	10.57	7.67	13.28	27.21
<i>Hemipodia californiensis</i>	2.60	8.59	9.10	10.80	38.01
<i>Scolecopsis sp.</i>	0.55	4.29	1.16	5.39	43.40
Group					
■ (Jun 2014) Average similarity: 74.49					
<i>Donax gemmula</i>	6.08	12.13	3.47	16.28	16.28
<i>Hemipodia californiensis</i>	5.20	11.11	3.79	14.92	31.20
<i>Chlamydopleon dissimile</i>	1.52	9.05	6.25	12.15	43.35
Group					
■ (Oct 2019) Average similarity: 72.23					
<i>Scolecopsis sp.</i>	100.98	23.76	8.47	32.90	32.90
<i>Donax gemmula</i>	2.36	9.33	6.69	12.92	45.82
<i>Excirolana armata</i>	1.22	6.05	1.15	8.37	54.19
Group					
■ (Dec 2019) Average similarity: 69.27					
<i>Chlamydopleon dissimile</i>	7.23	10.94	11.31	15.79	15.79
<i>Donax gemmula</i>	6.72	10.61	3.62	15.31	31.11
<i>Scolecopsis sp.</i>	3.22	9.41	5.97	13.59	44.69
<i>Hemipodia californiensis</i>	1.08	4.66	1.14	6.73	51.42
Group					
■ (Feb 2020) Average similarity: 72.54					
<i>Donax gemmula</i>	47.84	27.04	9.83	37.28	37.28
<i>Chlamydopleon dissimile</i>	3.95	14.99	12.90	20.66	57.94
<i>Hemipodia californiensis</i>	2.07	12.31	6.87	16.96	74.90
<i>Excirolana armata</i>	1.04	7.61	1.15	10.50	85.40

described in this article.

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