



OPEN Depth drive shifts in the fish and benthic assemblages of the South American Reef System

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The low-latitude habitats of the South American reef system have a high endemism and represent important stepping-stones due to the connectivity with Amazon and Caribbean reefs. We provide the first seabed mapping, and analyze the benthic cover and fish assemblages of these extreme reefs. Fleshy macroalgae (2–66% of cover), algal turfs (0–47%), and sponges (3–25%) are the dominant benthic groups. The main reef builders are crustose coralline algae (2–23%) and only four coral species (0 to 18%), mainly the weedy *Siderastrea stellata*. Cluster analysis distinguished two groups. The first group includes the shallowest reefs (~17 m deep) where fleshy macroalgae are abundant together with higher siltation on the reefs (~31% covered by sediments). The second group, by contrast, includes the deeper reefs (22.5–27 m), which have much higher algal turf cover, and the lowest sediment cover (4%). The deeper reefs also have the highest cover of corals (18%) and sponges (25%). We recorded a total of 63 fish species, with the deep reefs being the richest. Analysis indicated that the composition of the benthos was considerably more homogeneous across the study area than the composition of fish assemblages, which had a higher turnover of species among reefs. Moreover, we identified the depth of the reef as a variable structuring the benthic assemblages. The fish assemblage is influenced, in turn, by the benthos. Overall, the seabed mapping revealed the existence of a single reef system with high spatial heterogeneity. Our results provide new insights into the structure of these extreme reefs that have evolved under the influence of sediment resuspension, moderate turbidity, and are warmer than other West Atlantic reefs located at middle- and high-latitudes.

Keywords Tropical reefs, Spatial distribution, Benthic community, Corals, Sponges, Reef fish, South Atlantic

Over the past few decades, tropical shallow-water reefs have suffered from multiple human-related impacts such as increased sedimentation, pollution, overfishing, and climate change (e.g., marine heatwaves)^{1–3}. Assessing the spatial patterns in the benthic cover and fish assemblages represents an important step toward understanding how human impacts can modify the reef assemblages and their functioning^{4–8}. Moreover, studies of reef assemblages can contribute to effective science-based management practices by providing subsidies for conservation actions^{5,7,9,10}.

Research focusing on the spatial patterns of benthic and fish assemblages have been done mainly in shallow-water (<10 m depth) and nutrient-poor waters with low turbidity¹¹. These systems represent the “classical” coral reefs dominated by scleractinian corals that provide most of the reef framework and its structural complexity^{12–14}. However, there is an extreme lack of knowledge of reef assemblages in extreme and/or marginal habitats^{15–17}.

These extreme or marginal reefs are located in areas under suboptimal conditions for coral growth, such as moderate turbidity, wide temperature variations, and/or sediment resuspension^{17–19}. In this regard, these reef systems have unique reef assemblages, low coral diversity, and dominance of stress-tolerant reef-building species (e.g., genera *Montastraea*, *Porites*, and *Siderastrea*). These corals usually flourish and resist some short-term disturbances, such as marine heatwaves and siliciclastic sedimentation^{16,20,21}. Despite the importance of

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these habitats for understanding reef resilience to global environmental change^{16,22}, few data are available on the spatial heterogeneity in the composition of their benthic and fish assemblages^{18,23,24}.

The South American Reef system (SAR) is one of the largest semi-continuous tropical reef systems in the world together with the Great Barrier Reef and the Mesoamerican Barrier Reef (Central America)²⁵. This extensive reef system stretches from French Guiana and along the Brazilian tropical/subtropical coast where unusual nearshore environmental conditions for reef-building corals are generally found, such as high sedimentation inputs, periodic burials, and moderate water turbidity. Given this, these turbid reefs are considered to be potential climate-change refugia. This hypothesis has been widely discussed in recent years^{16,18,21,26,27}. Part of the difficulty of confirming this hypothesis is the lack of data on the composition and spatial heterogeneity of the reef assemblages²⁴, as in the case of the SAR system.

SAR is ~4,000 km long and has three main interconnected parts, being the Amazon reef system (~1,000 km), the Brazilian semi-arid coast reef system (~1,000 km), and the eastern Brazilian reef system (~2,000 km) (Fig. 1). This semi-continuous reef system spans from equatorial to subtropical region in the western Atlantic coast²⁵ (Fig. 1). The Pedra da Risca do Meio Marine State Park is a marine protected area located on the Brazilian semi-arid coast, and is a subunit of the SAR located approximately 10 nautical miles (~18 km) from the city of Fortaleza, the capital of Ceará state (Fig. 1).

Environmental factors (such as the depth and penetration of sunlight through turbid waters) represent important parameters that may control the heterogeneity of reef assemblages¹². Spatial heterogeneity occurs when the choice of descriptor (e.g., coral or sponge cover) fluctuates extremely at different locations within a restricted geographic area²⁸. However, data are scarce especially on reef habitats in the low-latitude portion of the SAR due to the complicated logistics of navigation and diving, and the limited visibility of the water^{29,30}.

In the present research, we describe the characteristics of the seabed, sediments, benthic cover, and the fish assemblages of the low-latitude reefs of the coast of Ceará, in northeastern Brazil (Fig. 1). We evaluate whether, and to what extent the depth and other key environmental factors (e.g., sediment cover) drive the distribution of the major components (the algae, reef fish, sediments, sponges, and corals) of these low-latitude reefs of the SAR system.

Results

Seabed mapping and unconsolidated sediments characterization

The seabed mapping revealed a reef bottom composed of a mosaic of high roughness (Fig. 2), with reef structures inserted among patches of bioclastic to lithobioclastic sands. The interconnected coralline reefs follow a typical formation pattern of deposits, with elongated circular and linear structures parallel to the coastline. Among the structures are observed some channels (Fig. 2). The model highlighted some low-latitude reefs that are used as

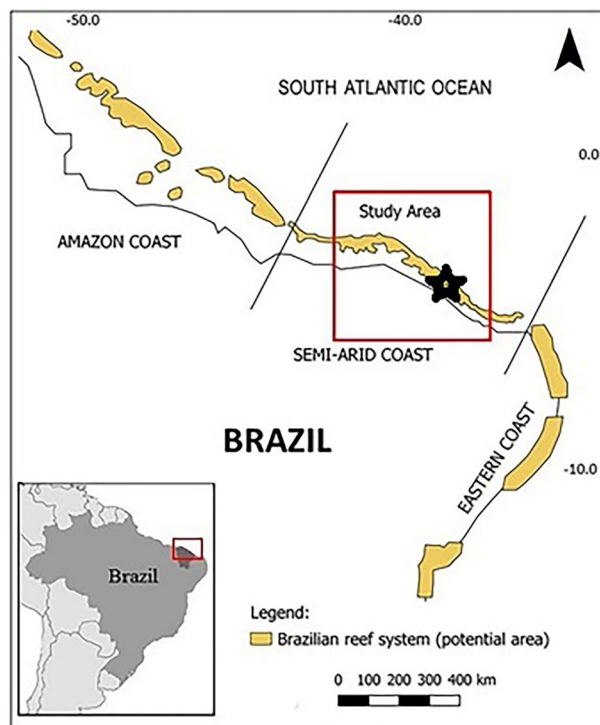


Fig. 1. Location of the study area in the Semi-arid coast on the South American Reef system in the Equatorial Atlantic. The black star shows the marine protected area (*Pedra da Risca do Meio* State Park) in which the data were collected. The area shaded dark gray on the map of Brazil is the state of Ceará (northeastern Brazil). Free software QGIS 3.32 was used to create the map (<https://www.qgis.org/>).

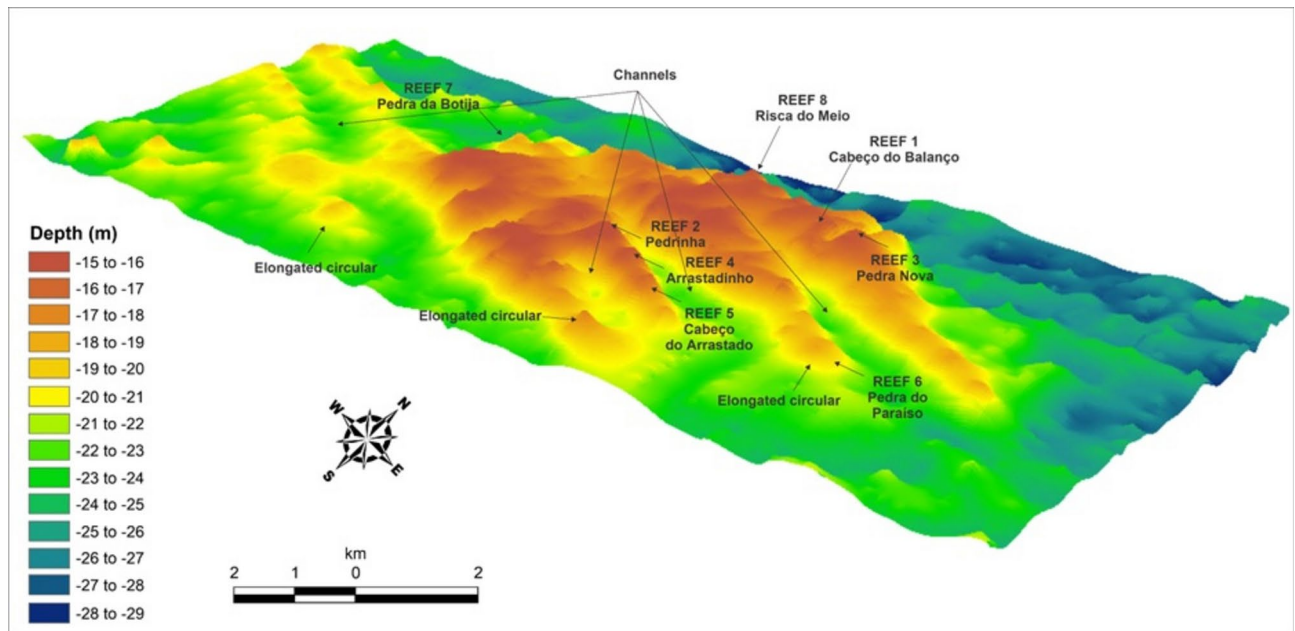


Fig. 2. 3D Digital Terrain Model (DTM) highlighting the eight low-latitude reefs in the Pedra da Risca do Meio Marine State Park in the southwestern Atlantic, off the coast of Ceará, in northeastern Brazil.

diving points, such as ‘Cabeço do Balanço’, ‘Pedra Nova’, ‘Pedrinha’, ‘Arrastadinho’ and ‘Cabeço do Arrastado’ (Table S1). The reefs are located between 15 and 20 m above sea level. The channels are at depths of 21 to 23 m (Fig. 2).

The unconsolidated material is formed by mainly sandy sediments of the coarse and very coarse fractions, rich in fragments of calcareous algae like *Halimeda*, *Lithothamnion*, and *Mesophyllum*, besides bivalve shells. This predominant granulometric and compositional characteristic is intrinsic to the CaCO_3 content that was between 57 and 82%. The medium sand grain size fraction was the third most representative of the unconsolidated material and contained a mixture of sediments composed of more fragmented biotrites and lithoclastic grains of quartz and other minerals such as mica (muscovite). The biotrital material in this grain size fraction represented the CaCO_3 content which was 10 to 40%. Less representative in the area are the unconsolidated sediments of the fine sand fraction, composed of lithoclastic sand rich in quartz and heavy minerals, and CaCO_3 content below 10% (Table S2).

Benthic cover and reef fish composition

The studied low-latitude reefs presented a high degree of spatial heterogeneity in the benthic cover of fleshy macroalgae (2 – 66%), algal turfs (0 – 47%), sponges (3 – 25%), crustose coralline algae or crusts (2 – 23%), live coral (0 – 18%), other organisms (0 – 2%), unconsolidated sediments (4 – 33%), and rocky bottom (0 – 6%). The indicators with the greatest range of variation were two most dominant benthic groups: macroalgae and algal turfs (Fig. 3; Table S3).

The algal benthic groups (macroalgae, turf, and crustose algae) dominated the benthos (mean cover of $58 \pm 3\%$ —Standard Error) over animals such as sponges ($12.3 \pm 3.1\%$) (Fig. 4) and corals ($4.9 \pm 2.4\%$) (Fig. 5). Overall, macroalgae ($31.9 \pm 9.1\%$) were the most abundant group, followed by turf ($16 \pm 6.7\%$) and crustose coralline algae ($9.9 \pm 2.5\%$). Moreover, the stress-tolerant and weedy coral species *Siderastrea stellata* ($4.00 \pm 1.95\%$), *Montastraea cavernosa* ($0.84 \pm 0.49\%$), *Mussismilia hispida* ($0.06 \pm 0.06\%$) and *Meandrina braziliensis* ($0.03 \pm 0.03\%$) indicate that the scleractinian community is composed of only four reef-building species, dominated by *S. stellata* (Figs. 3,5) and most of the corals have very low cover (<1%). A wide variation of unconsolidated sediment cover was observed over the reefs ($21.5 \pm 4.1\%$), although the coverage without organisms or unconsolidated sediment, that is, rocky ground, was low ($2.5 \pm 0.7\%$) (Fig. 3; Table S2).

Overall, 63 reef fish species were recorded in the present study, representing 45 genera distributed in 29 families (Supplementary Material I; Table S5). A total of 5,383 individuals were counted in the censuses, representing 55 species in 40 genera and 25 families, including three elasmobranchs. The families with the largest numbers of fish species were the Labridae (11 species) (Fig. 6), Haemulidae (7), and Carangidae and Lutjanidae (each with 4 species). The most abundant fish species were *Haemulon aurolineatum*, *H. squamipinna* (Fig. 6), *Acanthurus chirurgus*, *Myripristis jacobus* and *H. parra*. The most frequent species were *A. chirurgus*, *Sparisoma frondosum*, *H. aurolineatum*, *Stegastes pictus* and *Chaetodipterus faber*.

Influence of environmental variables on benthos and fish assemblages

The tBRDA identified depth as an important determinant of the composition of the benthos ($F_{1,6}=5.19$, $p=0.02$), explaining 46.4% of the variations (Fig. 7). Conversely, depth was not a significant determinant of fish

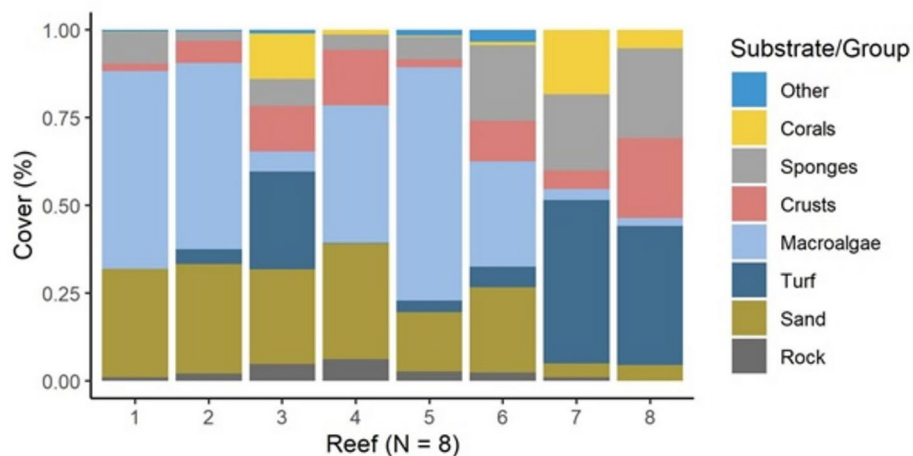


Fig. 3. Relative cover of the different substrate types and benthic groups on the eight studied reefs surveyed in the present study off the Brazilian semi-arid coast of Ceará, in the southwestern Atlantic. The mean depth of the reefs increased from reef 1 (~17 m deep) to reef 8 (~27 deep).

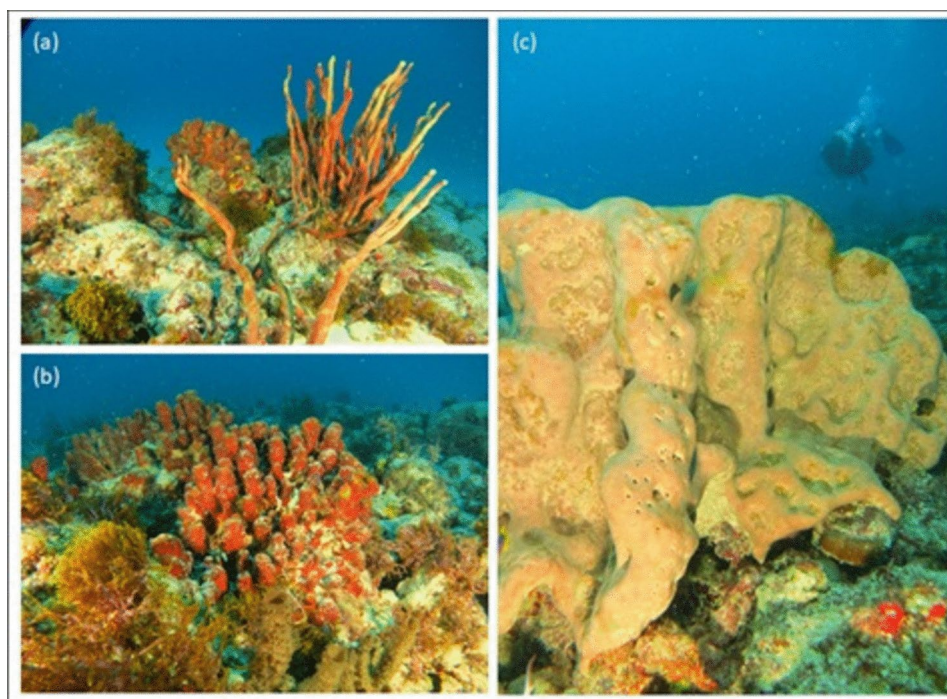


Fig. 4. Examples of massive sponges on the studied reefs surveyed off the Brazilian semi-arid coast of Ceará, northeastern Brazil, in the southwestern Atlantic: (a) *Aplysina fulva* (red color on the middle of the image), (b) *Aplysina* sp. (red color on the middle of the image) and *Callyspongia* (*Cladochalina*) *aculeata*, and (c) *Agelas dispar* (large brown sponge). Photos by the authors.

assemblages ($F_{1,6} = 1.24$, $p = 0.24$). The first axis (RDA1) of the tBRDA divided the studied reefs into two main groups. Reefs 3, 7, and 8, which are among the deepest formations and have a greater cover of reef-building corals, sponges, and turf algae, were separated from the other reefs which had a greater coverage of sand and macroalgae (Fig. 7). No such difference was apparent for the fish assemblages, reflecting the lack of significance in the analysis.

The main differences among reef benthic assemblages revealed by tBRDA were also evident in the IndVal analysis, which identified turf (0.896, $p = 0.002$) and corals (0.878, $p = 0.011$) as indicators of the group formed by reefs 3, 7 and 8, whereas macroalgae (0.967, $p = 0.013$) and sand (0.982, $p = 0.004$) were associated with the group formed by all the other reefs (Table 1). By contrast, the fish assemblages showed a much less clear pattern

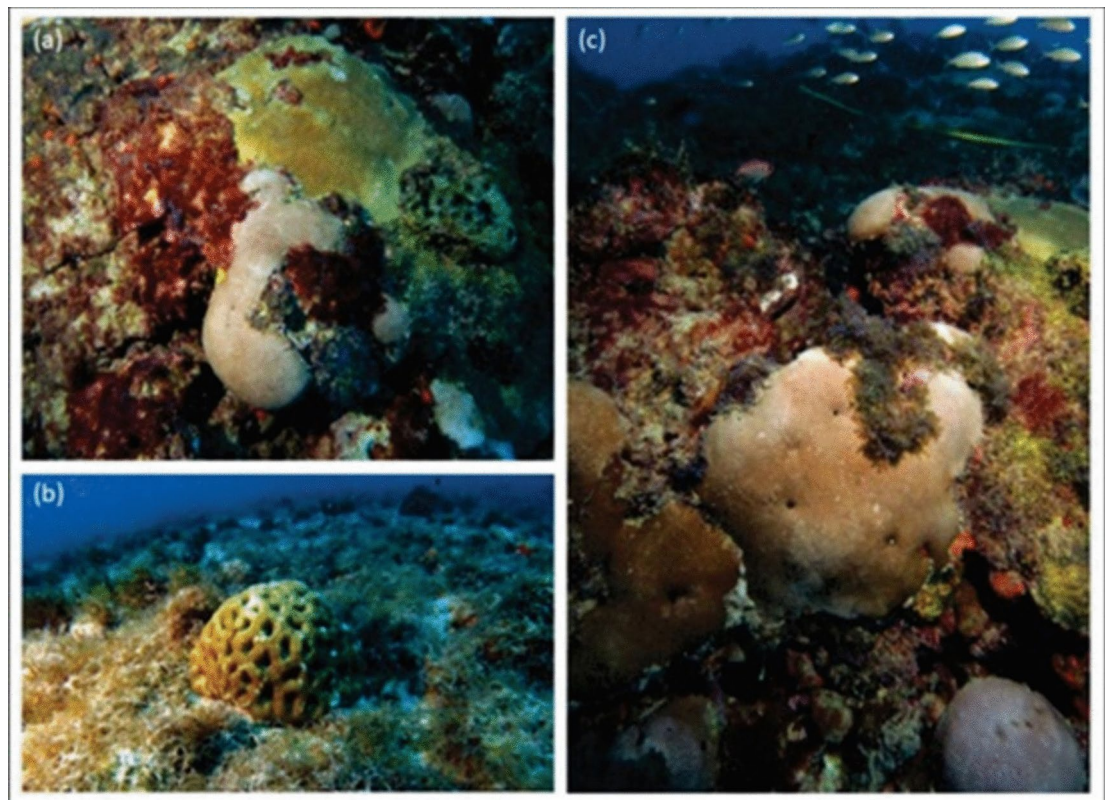


Fig.5. Reef-building massive corals on the studied reefs surveyed off the Brazilian semi-arid coast of Ceará, northeastern Brazil, in the southwestern Atlantic. (a) *Siderastrea stellata* (brown color) and *Montastraea cavernosa* (green color); (b) *Mussismilia hispida*; and (c) *Siderastrea stellata* (the dominant species in the coral community) (brown color). Photos by the authors. Table S4 (Supplementary Material) for coral species.



Fig.6. Mixed school of *Haemulon aurolineatum* (red arrow), *Haemulon plumieri* (white arrow) and *Haemulon squamipinna* (blue arrow) recorded at Cabeço do Arrastado (reef 5 – 19 m deep) in the southwestern Atlantic off Ceará, northeastern Brazil. Photograph: Marcus Davis/Mar do Ceará.

among the studied low-latitude reefs, with few species being associated with any specific set of reefs, reflecting the absence of any clear patterns.

The analysis considered both isolated reefs and random groups of reefs. Only significant indicator values are shown.

Regardless of the influence of depth, the co-correspondence analysis (CoCA) indicated a significant relationship between the composition of benthic and fish assemblages. While the first two CoCA axes explained 43.7% of the observed variation in the species composition of fish fauna, only the first axis (which explained 27.97% of the variation) was statistically significant ($p=0.02$). This suggests that only the most important

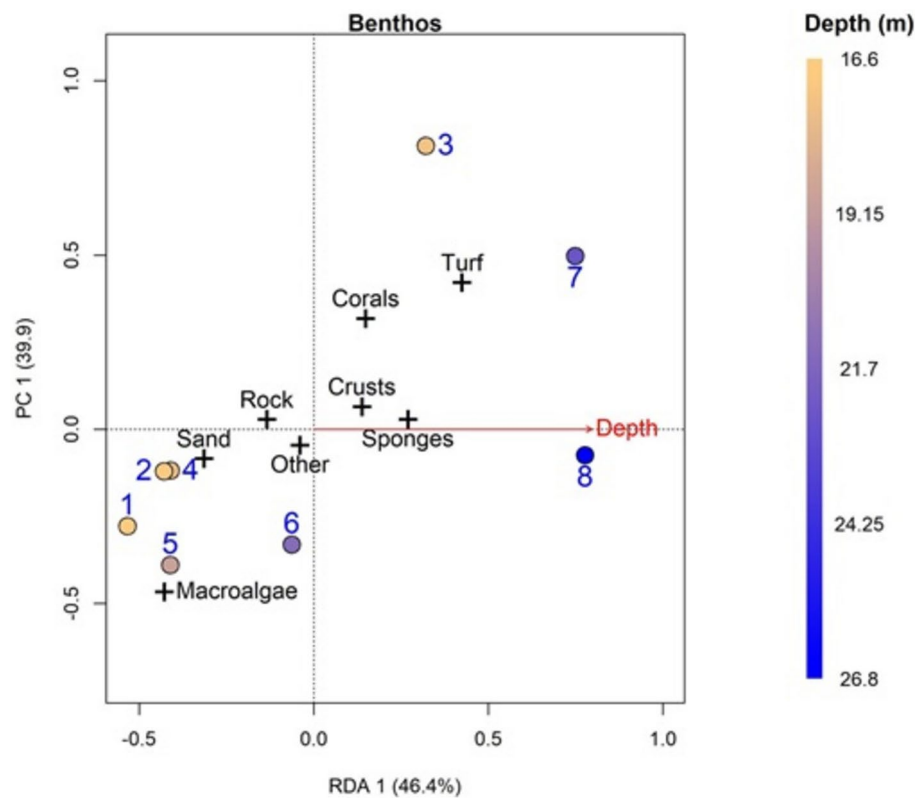


Fig. 7. Transformation-based Redundancy Analysis (tbrDA) of the benthic and fish assemblages recorded at eight studied reefs (circles 1 to 8) on the continental shelf of the Brazilian semiarid coast off Ceará, Brazil, in the southwestern Atlantic. The variable selection procedure identified the depth of reef as the most prominent explanatory factor, which supported a statistically significant model for the benthos ($F = 4.06$, $p = 0.04$, adjusted $R^2 = 0.47$), in particular along the first axis (RDA1). The significance of this pattern was reflected in the much clearer differences visible in the panel on the left. Fish abbreviations on Table S5 (Supplementary Material).

Stratum	Set of reefs	Category/ Species	Indicator value index	p-value
Benthos	3, 7, 8	Turf	0.90	0.004
		Corals	0.88	0.008
	1, 2, 4, 5, 6, 7	Macroalgae	0.97	0.01
	1, 2, 3, 4, 5, 6	Sand	0.98	0.004
Fish	5 5, 8 2, 5, 6	<i>Mycteroperca bonaci</i>	0.94	0.008
		<i>Scarus zelindae</i>	0.90	0.018
		<i>Lutjanus jocu</i>	0.85	0.03
	6	<i>Halichoeres dimidiatus</i>	0.88	0.019
	1, 4	<i>Pseudupeneus maculatus</i>	0.91	0.002
	5, 6	<i>Lutjanus alexandrei</i>	0.90	0.019
	1, 2, 4, 7, 8	<i>Myripristis jacobus</i>	0.93	0.004
	4, 5, 6, 7, 8	<i>Anisotremus virginicus</i>	0.84	0.035

Table 1. The indicator value indices of the benthic categories or fish species recorded in the eight low-latitude reefs surveyed on the continental shelf off the Brazilian semiarid coast in Ceará, Brazil, in the southwestern Atlantic.

differences in benthic composition (i.e. assemblages with a predominance of sand and algae versus assemblages with a predominance of corals, sponges and turf, similar to the differences detected by tbrDA) were influential on the composition of fish assemblages. Conversely, the analysis was not significant when the benthic structure was predicted from the composition of the fish fauna ($p = 0.33$). Therefore, there seems to be a mainly bottom-up relationship in the studied low-latitude reefs, with the benthos influencing the structure of the fish fauna (Figs. 7 and 8).

Discussion

In the present research, we provide the first joint analysis for seabed mapping, sedimentology, benthic cover and reef fish assemblages of low-latitude reefs on the South American Reef System²⁵. These reef systems are exposed to significant sediment resuspension, moderate turbidity³¹, and warmer waters (average 26–30 °C)^{29,32} than other West Atlantic reefs at high- and mid-latitude that usually experience wider seasonal seawater temperature variations^{7,18,27}. The low-latitude reef habitats surveyed in the present study have diversified fish assemblages and benthic cover (algae, sponges, and corals) which were influenced by the depth. These new insights are also important for the interpretation of structure of extreme and marginal reefs that are less studied globally^{16–18}.

Mapping and reef sediments characterization

The bottom mapping and 3D Digital Terrain Model (DTM) of the study area indicate that this region encompasses a complex reef system that is interconnected by hard-bottom habitats and channels. In particular, the reefs with the lowest sediment cover (4%) were the deepest (26.8 m and 22.5 m) while the sediment cover was much greater (31%) in the shallower reefs (16.6 to 16.7 m). This may reflect the more intense deposition and silting in the shallower reefs due to the greater influence of swell waves, tides, and coastal currents^{25,31}. The confirmation of these hypotheses will nevertheless require further research on sedimentation rates and dispersion modeling.

The three-dimensional arrangement of the reefs which are distributed longitudinally and parallel to the shoreline²⁵ with channel formations (Fig. 2) arranged in stripes. They are consistent with the transgression and regression events during the Pleistocene^{33–36}. But at least some of the structures observed (Fig. 1) were probably shaped by recent hydrodynamic processes, which were also responsible for the distribution of the unconsolidated material³⁷ that fills these channels. In the Continental Shelf of the Brazilian semiarid coast, a model of the formation of the features suggest that the transformation of channels or river valleys to submerged rocky reefs, in the region between the municipalities of Fortaleza and Icapuí, in Ceará, were the result of the marine regression that occurred 18,000 years Before Present (B.P.), in the Upper Pleistocene³⁸. During this period, the sea level was 130 m lower than in the present day, resulting in the formation of an extensive coastal plain, which persisted for approximately 8,000 years until the subsequent rise in sea level, which occurred during the Holocene (starting around 11,000 years B.P.)³⁸.

The genesis of these reef formations may have been associated with at least two depositional events, one related to the lithification of ancient coastal ridges or barrier islands deposited during the marine regression period, and the other to the deposition of the Pleistocene sediments of the Barreiras Formation³⁸. These reefs may be composed of the coralline calcareous algae and other reef building organisms^{39,40}, and further studies are urgently needed to investigate the extent, composition, age, and rates of accretion/erosion of these structures.

The unconsolidated sediment of the area was composed of sedimentary facies that correspond to bioclastic sand to lithobioclastic coarse to very coarse⁴¹, and constitute a sedimentary pattern that is characteristic of the Northeast Brazilian Shelf⁴². Despite the predominance of unconsolidated material of the coarse to very coarse

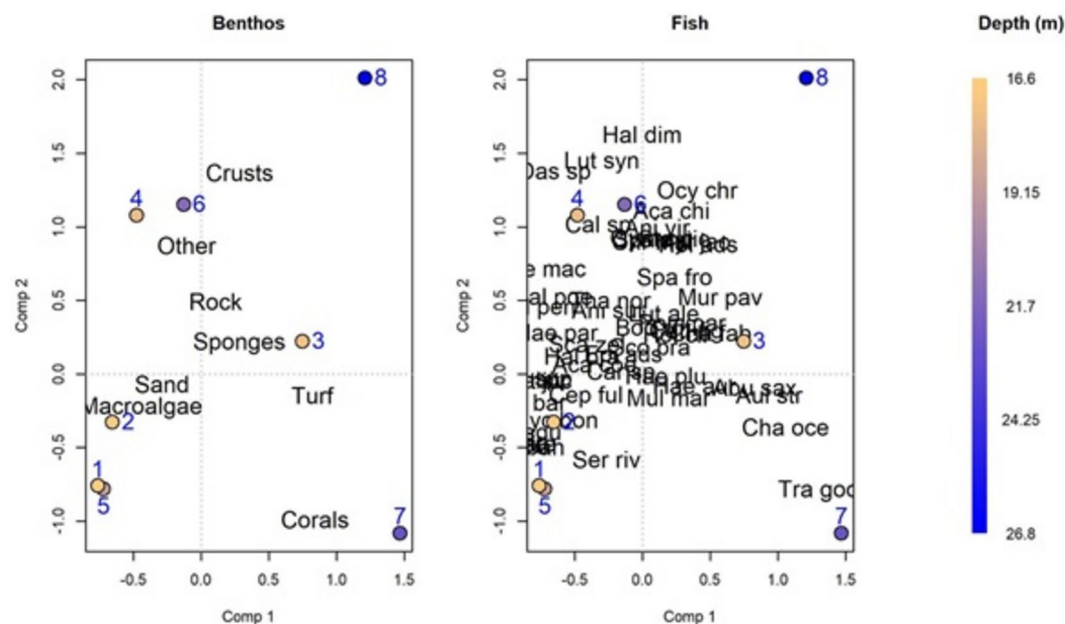


Fig. 8. Plots of the predictive co-correspondence analysis (CoCA) between the composition of benthic (as predictor) and fish (as response) assemblages of the eight reefs surveyed on the Brazilian semiarid continental shelf. Only the first CoCA axis was statistically significant (stat = 0.39, $p = 0.02$). Species situated in similar positions relative to the origin in each panel show positive associations. Note that the two groups have a similar ordination, i.e., concave downward along the composition gradients, reflecting a certain degree of relationship between the two biotic strata. Fish abbreviations on Table S5 (Supplementary Material).

fractions and rich in biotrites, the presence of finer material composed of quartz sand and other minerals, shows that there are two sedimentation environments in the reef area, a predominant marine and a less representative terrigenous one. The sedimentation on the continental shelf of northeastern Brazil has a reduced continental terrigenous contribution⁴², which reflects the semiarid climate of the adjacent coastal region and the reduced fluvial discharge. This pattern is consistent with the predominance of the carbonate sediments composed of biotrites and coralline algae identified here in the habitats of the studied reefs, together with the benthic cover.

Benthic cover

Fleshy macroalgae were widespread (benthic cover of 53–56%) on the four shallow reefs (depth of 16–17 m) that are subjected to high sediment cover (~31%). On the other hand, the lowest macroalgae cover (2–3%) was observed on the deeper reefs (22.5 to 26.8 m) which also have reduced sediment cover (4%). The algal turfs had the second highest benthic cover (Fig. 3) which also varied extensively in their distribution and had more extensive coverage on the two deepest reefs (22.5 m and 27 m deep). Overall, then, depth was maybe the driver of turf productivity rate, as observed in other tropical reefs⁴³. This may be explained by the opportunistic traits of some of these tiny and small algae in nutrient-poor waters, given that they have a high surface area to volume ratio which provides high net primary productivity due to their high nutrient uptake rates, resulting in rapid growth⁴⁴. The fast growth of these small algae also enables them to recover rapidly after disturbances³⁹ such as periodic sedimentation events on these extreme reefs³¹. In this context, algal turf-bound sediments are an abundant and highly productive benthic component on tropical reefs⁴⁵ including those of the present study area.

Sponges also constitute an important group in these reef habitats (3 to 25% cover). These sessile suspension feeders are able to tolerate or even thrive in areas that are affected by the wave force which are moderately turbid and have high sedimentation rates⁴⁶, which accounts for their occurrence in the habitats analyzed here. It is possible that on these extreme reefs the sponges are better adapted to the resuspension of sediments, which enhances their ability to survive and flourish⁴⁷ on these reefs^{16,18}. Adaptations such as morphological and structural modifications may represent a passive response, which prevent the accumulation of sediment on the surface of the sponge, while modifications or the interruption of pumping rates may be an active response that removes sediment from the sponge surface, as a means of avoid the clogging of the feeding and filtration systems⁴⁷.

Disturbances such as carbonaceous and siliciclastic sediment deposition described here²⁹ may contribute to an increase in sponge cover, which selects stress-tolerant species. High energy swell waves may also cause disturbances and sediment resuspension on these reefs³¹, which also selects disturbance-tolerant organisms that are able to cope with intense hydrodynamics and sediment deposition⁴⁸. Another important observation is that the highest mean percentage coverage of sponges (25%) was recorded on one of the deepest reefs (26.8 m), while the lowest sponge cover (3%) was found on one of the shallowest reefs (16.7 m). This may be accounted for by the presence of large sponges (*Agelas dispar*) (Fig. 5C) on the deep reefs and their competition with macroalgae in shallower waters, as well as the more intense hydrodynamic conditions of the shallowest reefs, which generate greater turbulence (swell waves) and higher siltation rates³¹.

Shifts of the benthic assemblages with increasing depth may represent a response to the biophysical gradients (e.g., light penetration and sediment deposition) observed within the study area. Similar to the depth-graded arrangement of the sponges, the most extensive coral cover (18%) was recorded in one of the deepest reefs (22.5 m). By contrast, the most reduced coral cover (less than 1%) was found on the shallower. The increased coral cover in deeper areas may thus reflect the more efficient heterotrophic capabilities of these mixotrophic organisms⁴⁹, less competition with algae, and the lower frequency of sediment-related disturbances (e.g., higher sediment deposition).

The corals recorded on the studied low-latitude reefs have biological characteristics that favor their presence in stressful and extreme reef environments. Despite the reduced diversity of massive corals (4 species) recorded here (Table S4), the most abundant species (Fig. 5), the weedy *Siderastrea stellata* and the stress-tolerant *Montastraea cavernosa*, are known for their tolerance to environmental disturbances, their mixotrophic trophic ecology^{22,50} and wider bathymetric distribution with *S. stellata* occurring at depths of up to 90 m and *M. cavernosa* up to 180 m²⁷.

Morphological and physiological adaptations of these reef-building corals are keys for their persistence on turbid reefs, including the capacity of the most abundant coral (*S. stellata*) to survive short-term burial events⁵¹. On the other hand, the massive-growth forms, have thicker tissue, which confers greater resistance to high-light stress. The endosymbiont community that includes species more tolerant of thermal anomalies may also be a factor, in addition to the feeding strategy adopted under turbid conditions²⁷. Corals with a greater heterotrophic feeding capacity (e.g., *S. stellata*)⁵⁰ are more resilient to stressful situations such as intense sedimentation²² and the mass bleaching observed in the study area in 2010 and 2020 had low mortality rates^{29,30}.

The dependence on a few reef-building coral species for carbonate construction and structural complexity represents a major risk in the face of predicted modeling that indicates significant future climate change impacts on *S. stellata*, *M. hispida*, and *M. cavernosa*⁵² and the increased erosion risk⁵³. The main reef builders in the study area are few scleractinians corals and the crustose coralline algae (2–23% of cover). In particular, coralline red algae appear to be key builders in these reefs, and they have an important functional role in many reef systems in the southwestern Atlantic⁵⁴. Further studies should analyze their calcification rates, carbonate budget, and also their reef growth potential as made previously on Caribbean reefs^{53,55}. These reefs are possibly biogenic, being primarily composed of sandstone³¹ and covered with non-framework (e.g., fleshy macroalgae) and framework building organisms (e.g., corals and coralline algae) as shown here by the 3D digital seabed mapping and reef samples.

Reef fishes

Reef fish assemblages are known to be associated with the benthic assemblages^{56,57}, with fish diversity being linked to the heterogeneity of rocky bottoms^{58,59}. The abundance of roving herbivores of the families Acanthuridae and Scaridae (actually recognized as Labridae) on Elkhorn Reef in Florida increased as coral cover decreased and the macroalgal cover increased⁶⁰.

One curious finding of our research may be related to the characteristics of the turbid reefs studied here²¹. The tbRDA indicated that only the benthos is influenced by depth, whereas the CoCA found a significant relationship between the benthos and fish assemblages. It is thus possible to conclude that depth affects the benthic assemblage which, in turn, has an influence on the reef fish assemblage. Similar results were obtained from two submerged reef systems located off the Pilbara coast on Australia's North West Shelf. The location, depth, and rugosity of the reefs were the factors that most influenced the benthic assemblage⁶¹.

Reef fish assemblage in the Ceará coast was previously assessed and 129 fish species, being six elasmobranchs and 123 teleosts⁶². While this estimate is much higher than that recorded in the present study (66 species), it does include qualitative data, published records, and additional reefs from the same area. The baseline results of the present study nevertheless represent a quantitative record of the fish fauna. They are especially important because they predate (2019) the invasion of the invasive lionfish (*Pterois volitans*), whose occurrence in the study area was confirmed in 2023^{63,64}.

Depth played an important role in spatial heterogeneity^{43,65} of reef composition studied here. It is possible that the cover of organisms, such as corals, sponges, and algae, is regulated by reduced wave energy and consequent lower turbulence and associated sedimentation, which contributes to higher covers of coral and sponges in deeper regions and lower abundance in shallower ones. Moreover, depth represents a keystone factor for reef fish assemblages in these reefs⁵⁷ and also for the benthic cover as detected by RDA analysis. These findings highlight the spatial heterogeneity of benthic cover and fish species richness within a small area, which further reinforces the conclusion that turbid-zone reefs are heterogeneous^{21,57,66}.

In the studied reefs, the benthos seemed much more spatially structured than the fish fauna. This may reflect the mobility of fish relative to the short distances among the reefs. The benthos, on the other hand, and especially the sessile groups considered here, are much more susceptible to small environmental changes. In this case, the depth of the reef is the major factor influencing the benthic composition. The studied reefs are located at relatively altophotic depths (~16–27 m), where the availability of light may already be decreasing. Even at these depths, sediment resuspension by the shelf currents may increase turbidity at least temporarily in the area⁶⁷. Therefore, the growth and production by ecosystem engineers, such as sponges, corals, and calcareous algae, may be limited by local adverse conditions, thus contributing to the observed spatial differences.

Despite the apparent absence of a direct relationship between environmental variables and the composition of fish fauna, this assemblage was influenced significantly by benthic composition. A similar association between fish and substrate characteristics has already been found in shallow tropical reefs on the coast of Brazil⁶⁸, as well as in various sublittoral ecosystems, located at altophotic, mesophotic and rariphotic depths^{69,70}. However, the present study is the first, to our knowledge, to record this pattern in a single habitat type within the deep altophotic zone of the Brazilian equatorial continental shelf. This result suggests that even fine-scale variations in benthic features may affect the fish fauna, which may have a series of implications for the ecology, conservation and management of the fish stocks of these low-latitude stepping stone habitats that connect the Caribbean and Amazon reefs.

In conclusion, the results of this research indicate the existence of significant spatial heterogeneity in the low-latitude reef habitats and assemblages in the southwestern Atlantic, which varies according to the depth and sunlight penetration of the reefs. The main reef builders are crustose coralline algae and only four coral species; although the benthic cover is usually dominated by fleshy macroalgae, algae turfs and sponges. Moreover, these novel results represent an essential first step toward the understanding of the composition of naturally-occurring algae- and sponge-dominated reefs in unique environmental conditions. Further studies of environmental drivers such as sedimentation rates and the impact of fish herbivory on benthic assemblages, and long-term monitoring will nevertheless be needed for a better understanding of the functioning of these unique tropical ecosystems.

Methods

Study area

The study area is characterized by intense trade winds, mesotides (2 to 4 m), oligotrophic waters, and seawater temperature ranging between 26 °C and 29 °C^{31,32}, but even higher during marine heatwaves^{29,30}. The cumulative action of the trade winds, especially during the second half of the year, and the nearshore coastal currents are responsible for moderate turbid waters through the maintenance of suspended particles on the water column⁴⁸.

In the present study we analyzed the biotic and abiotic components (e.g., sediment cover) on eight reef habitats (Table S1, Supplementary Material) within the area of *Pedra da Risca do Meio* Marine State Park. These turbid-zone reefs varied in depth from approximately 17 m to around 27 m (Table S1). These reef-like environments were old fishing spots described by local fishers. This low-latitude Marine Protected Area (MPA) encompasses a rectangular area of 33.20 km²⁷¹, and is the only totally submerged protected area within the SAR of the Equatorial SW Atlantic. The bottom of the marine protected area (MPA) has low relief and flat reef formations³¹, which have never been mapped. Their low-latitude position on the Brazilian semi-arid coast (Fig. 1) makes these reef habitats important stepping-stones due to their connectivity to the Amazon and the Caribbean reefs²⁵ enabled by fast-flowing northward currents⁴⁸.

The distance of the reefs from the shoreline ranged from 14.6 to 17.7 km (Table S1), and all are outside the area of influence of nutrient runoff and sedimentation processes of coastal and estuarine environments⁷².

Due to their distance from the coast (Table S1) and low river input due to the semi-arid climate⁷², sediment resuspension by swell waves is the main factor in increasing siltation of these low-latitude reefs.

Field sampling and data collection

Seabed mapping and unconsolidated sediments characterization

The seabed of the low-latitude reefs on SAR was mapped by the oceanographic vessel *Argo Equatorial*. We used the geophysical bathymetric method to determine the depths and seabed relief. For this, a Garmin echosounder coupled to a geographic positioning receiver (GPS) was used to record the raw data in real time during the navigation, following to the NMEA (National Marine Electronics Association) protocol³⁸. All variables collected (i.e., geographic coordinates of the points, depth of the water column and time of recording), were recorded in American Standard Code (ASCII) format, and then transformed into X, Y and Z files (X and Y coordinates, and Z depth). These XYZ data were subsequently corrected to the reduced level (hydrographic zero) based on the tide table of Mucuripe harbor (Fortaleza, Ceará), available on the website of the Directorate of Hydrography and Navigation (DHN) of the Brazilian Navy. From this data a digital terrain model (3D DTM) was generated in order to depict the surveyed hard-bottom habitats and reef relief.

The geological characterization was based on the analysis of the reefs and unconsolidated material (bottom sediments). These sediment samples were collected from 18 points within the area of each reef area using a Van Veen sampler in May and June 2019 which was deployed from the *Argo Equatorial*. The analysis of the unconsolidated sediments contemplated the textural aspects (granulometry)⁷³ and composition (calcium carbonate content—CaCO₃ and presence of biodegradable fragments)⁷⁴, and the Larsson classification, modified by Dias (1996), was used, which considers grain size and CaCO₃ content.

Benthic cover and reef fishes

The spatial distribution and heterogeneity of benthic components in the eight low-latitude reefs (Table S1), was assessed by the PIT (Point Intercept Transect) method following the methodology established by Leão et al.⁷⁵ for SAR reefs (modified from AGRRA – Atlantic and Gulf Rapid Reef Assessment). The approach of general benthic categories is a classical approach in coral reef studies. We classified the cover in eight benthic groups/categories: (i) Live hard coral; (ii) Fleshy Macroalgae; (iii) Turf; (iv) Crustose coralline algae (CCA) or crusts; (v) Sponge; (vi) Other organisms; (vii) Unconsolidated sediment, and (viii) Rocky ground (no biological cover or sediments). Cover data were obtained along four 10-m transects on each reef habitat during the first half year of 2019 (May–June) due to favorable sea conditions (e.g., lower wind incidence and better visibility for scientific diving) and the availability of oceanographic vessel.

Benthic cover elements were identified every 10 cm along the transect by scuba diving with a total of 100 points being surveyed per transect, and 400 points per reef. Percent (%) benthic cover was calculated by dividing the number of point records of each benthic group by the total number of points (400) surveyed on each studied reef.

At each reef the fish were identified and counted during three stationary visual census taken by 2 scuba divers between 09:00 and 16:00 h, in order to avoid crepuscular change. In order to delimit the area, a tape measure was laid across the bottom and small fish (< 10 cm in length), were recorded within 2 m radius, while larger specimens were recorded within a 5 m radius⁷⁶. To determine the species density, the area of a cylinder was used, taking into account the radius and depth of each reef.

Statistical analysis

We used a transformation-based Redundancy Analysis, tbrDA⁷⁷ to investigate the relationship between depth (measured by scuba divers in situ) species composition of the reefs, considering the benthic and fish assemblages independently. For this, transect data from each reef (including either substrate coverage or fish species abundance) were pooled and Hellinger-transformed prior to analysis, to reduce the weights of rare species and improve the resolution of linear relationships between dependent and independent variables⁷⁸.

Since geographic proximity among reefs may have affected both gradients in species composition and environmental features, we tested for spatial dependencies by relating the residuals of the tbrDAs to Moran's Eigenvector Maps (MEMs)⁷⁹. To build the MEMs, the connectivity (i.e., “neighbourness”) among formations was represented by a Gabriel graph. A forward- stepwise selection procedure was then used to select the best subset of MEMs in relation to the tbrDAs, based on the percentage of explained variation (R²). If any of the MEMs were found to be significant, the tbrDA was reconstructed using the MEMs as additional spatial predictors. As no MEM was selected for either the benthic or the fish tbrDA, however, we concluded that spatial autocorrelation was negligible in the dataset, and that no additional modifications were needed for the models⁸⁰. The association of biotic components (benthos or fish) to any given reef or subset of reefs (i.e., all possible sets containing between one and eight reefs) was assessed using the indicator value index (IndVal)⁸⁰.

We then ran a predictive Co-Correspondence Analysis, CoCA⁸¹ to investigate the relationship between benthic and fish species composition. Although similar to Canonical Correspondence Analysis (CCA), CoCA is specifically designed to predict the structure of one biological community based on another, making it particularly effective for examining inter-community relationships and accounting for biological variables (84). All statistical analyses were performed in R 4.2.0, using the packages ‘vegan’, ‘indicpecies’, ‘spdep’, ‘adespatial’, and ‘cocorresp’ packages.

Data availability

The datasets used and/or analysed during the current study are available from the corresponding author upon reasonable request.

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Declarations

Competing interests

The author declare no competing interests.

Additional information

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