Regional Studies in Marine Science 48 (2021) 102037

Contents lists available at ScienceDirect

Regional Studies in Marine Science

journal homepage: www.elsevier.com/locate/rsma

Uncharted coral reefs from the Inhambane Province, Mozambique

Cesar A.M.M. Cordeiro [a,b,*], Marcos B. Lucena [a,b], Fenias Muhate [c], Kátia C.C. Capel [d]

[a] *Universidade Federal do Rio de Janeiro, Rio de Janeiro, RJ, Brazil*
[b] *Universidade Federal Fluminense, Niterói, RJ, Brazil*
[c] *Universidade Pedagógica de Maputo, Maputo, Mozambique*
[d] *Centro de Biologia Marinha, Universidade de São Paulo, São Sebastião, SP, Brazil*

ARTICLE INFO

Article history:
Received 1 July 2021
Received in revised form 3 October 2021
Accepted 5 October 2021
Available online 12 October 2021

Keywords:
Fish assemblages
Benthic cover
Invertebrate megafauna
Diversity
Mozambique Channel

ABSTRACT

Mozambique has the third-largest coastline in the western Indian Ocean with a large and diverse reef area. Those reefs provide food and income for a large proportion of coastal communities but remain scarcely studied. As a baseline assessment, we sampled four uncharted shallow reefs (Baixo Africa, Baixo Zambia, Pomene and Baixo Silvia) within a 56 km stretch line from 5 to 32 meters deep. The fish abundance and assemblage composition were assessed by underwater visual census (25x2m, n = 112). The benthic community was characterized by digital images (0.5x0.5m, n = 164) and the invertebrate megafauna by direct counting (25x2m, n = 52). A total of 209 reef fish species was observed, with similar mean richness (22.4 ± 7.2 species.100 m^{-2}) at all reefs. Invertivorous (n = 79) and planktivorous fish species (n = 36) represented 55% of species total. Trophic composition was similar among sites and with large contribution of planktivores. The presence of large shoals (>100 ind.100 m^{-2}, e.g., surgeonfish, fusiliers, snappers) and large-bodied fishes (>90 cm) (e.g., groupers) was a clear indication of local productivity and health conditions of reefs. Seventy-nine taxa were observed on the benthic cover with the largest richness found at Baixo Silvia (28.5 ± 7.4, species.100m^{-2}, mean ± SD). Turf algae dominated the benthos (31.5% ± 16.4) at all sampled reefs. Coral cover was variable between sites (9.3 – 25.8%), dominated by branching and plate corals, and <1% of colonies showed signs of diseases/bleaching. The baseline assessment indicated large biomass of fishes and negligible evidence of large impacts on coral formations which indicated a good conservation status of those areas. Based on these findings, a marine protected area is proposed for establishment in collaboration with environmental authorities and the local community.

1. Introduction

Mozambique has the third-largest coastline in the Western Indian Ocean (WIO), about 2515 km in total length (FAO, 2017) which bears a variety of ecosystems, from estuaries to sandy beaches, rocky shores, mangroves, seagrasses, and coral reefs (Rodrigues et al., 2000; Hoguane, 2007). Coral reefs in Mozambique have an estimated area of 1290 km^2 (Motta, 2000), exhibiting great biodiversity (e.g., Riegl, 1996; Pereira, 2000; Benayahu et al., 2003). Reef ecosystems are the primary source of food and income for a large proportion of the country's coastal communities, which compose more than 45% of the Mozambican population (INE, 2019). Mozambican reefs shelter more than 320 species of scleractinian corals, around 790 reef associated fish species (Pereira, 2000), and many taxa yet to be investigated.

Despite the key role of coral reef environments to the coastal communities and the national economy (Rodrigues et al., 1999), scientific studies about the Mozambican reefs remain scarce because of complex logistics. Still, many threats such as repeated events of bleaching in the Western Indian Ocean (Gudka et al., 2020), growing fishing pressure (artisanal and commercial - Samoilys et al., 2019), and ongoing exploration of fossil fuels along the Mozambican coast (Salazar et al., 2013; Andreasson, 2018) has been reported. The reefs from Inhambane Province are known for sheltering large and iconic species such as whale sharks and giant manta rays (Rohner et al., 2013), and also for touristic diving activities, mostly in Tofu and the Bazaruto National Park (Haskell et al., 2013) regions. Because of better local infrastructure and accessibility those areas have the most studied reefs in the region, with occasional efforts in reefs adjacent to the Pomene National Reserve (see Louro et al., 2017; Pereira et al., 2018).

Conservation efforts largely rely on composition and community structure data to evaluate the conservation status of established protected areas (Noss, 1990; Tucker et al., 2017) and for prioritization of new efforts (Harris et al., 2017). Integrated assessments of a variety of marine organisms have the potential

---

[*] Corresponding author at: Universidade Federal do Rio de Janeiro, Rio de Janeiro, RJ, Brazil.
E-mail address: cammcordeiro@id.uff.br (C.A.M.M. Cordeiro).

https://doi.org/10.1016/j.rsma.2021.102037
2352-4855/

to greatly help understanding the relative contribution of anthropogenic and natural disturbances to community patterns, aiding direct conservation efforts (Friedlander et al., 2014; Meirelles et al., 2015). In this context, our efforts aimed to fulfill the urgent need of primary information to establish a baseline and support the monitoring of reef sites along the coast of Inhambane focusing on future conservation actions. Our specific aims were to (1) describe the relative cover and composition of benthic communities and (2) characterize the reef fish assemblages indicating dominant species and functional groups of shallow-water reef formations (up to 30 m deep) between the southern limits of the Santuário Bravio de Vilanculos (VCWS) and the Pomene National Reserve. There are no reports of large anthropogenic pressures, and the sampled reefs are accessed mainly by artisanal fishermen and few recreational fishing boats, thus we expected to find no signs of overfishing (e.g., presence of large carnivores and top predators). Regarding the benthic communities, even considering the widespread recent bleaching events reported to other WIO countries (Gudka et al., 2020), we expected to find a healthy coral community with very low to no signs of bleaching or pathogenic diseases usually associated with the pollution of coastal waters.

2. Material and methods

2.1. Study site

The surveyed area is located in the central region of the Inhambane Province and included a 56 km stretch of coastline with four shallow reef structures (Baixo Africa, Baixo Zambia, Pomene, and Baixo Silvia). Some of those reefs are already mapped on navigation charts, but others are only known by local fishermen communities and diving operators. All reef formations are located between 0.5 to 6.5 km from the shore (Fig. 1) and within a depth range from 5 to 32 m. Ponta Pomene (herein called Pomene) and Baixo Zambia are sites previously known for diving activities (Pereira et al., 2018), while the reefs of Baixo Silvia and Baixo Africa had only recently been visited by recreational divers, as reported by local fishermen. Previous to this study, there was no record or official registers considering those reefs (Baixo Africa and Baixo Silvia) in scientific surveys.

Baixo Silvia is composed of three main reef structures connected by shallower flat areas located around 6 km from the shore and extending for 5.5 km, with reef formations found between 8 to 28 m. Pomene reefs are located on the coast of the Reserva Nacional do Pomene — RNP (MTADR, 2006), with reef formations located from 500 to 1000 m off the coast within depths from 15 to 40 m. Baixo Zambia reefs are formed by a group of moderately complex reefs located at 6.5 km from the shoreline, with depths ranging from 7 to 24 m. Lastly, the Baixo Africa reefs are grouped in a narrow formation following the coastline approximately 5 km distant from the shore and within a depth range from 7 to 24 m. Detailed reef's general morphology is described in the supplementary material.

2.2. Benthic cover and invertebrate megafauna

Estimates of cover were based on non-destructive sampling. The benthic community associated with reef areas was characterized by counting all large mobile invertebrates (> 5 cm) observed up to one meter from both sides along a transect line (25 m), and taking digital images (50 × 50 cm) at two meters intervals on the way back. Transects were haphazardly distributed along the reef slope in parallel to the sea bottom with at least 20 m from each ending point of one transect and the starting point of the next, and a minimum of 11 transects (10 images per transect) at each reef site (table 1s). Transects sampling was performed at similar depths for all sites (12.6 ± 2.3 m, mean ± SD; details in table 1s — supplementary material). Each image was analyzed for relative cover with the *photoQuad* software (Trygonis and Sini, 2012) by overlaying 50 random points on each image. Benthic cover organisms were identified at the lowest taxonomic level possible, and then assigned to the following categories for analysis purposes: turf algae, macroalgae, coral, zoanthid, crustose coralline algae (CCA), suspension/filter feeders, other invertebrates, and cyanobacteria. Lost information due to edges, shade or undefined features in images comprised less than 1% of total cover and was not included in the analysis.

2.3. Reef fish surveys

Fish abundance and assemblage composition were assessed by underwater visual census (UVC) along 25 × 2 m belt transects. This method consists of identifying, counting, and estimating the size (total length in cm) of all fish species observed in a determinate area (Brock, 1982). Swimming along the transect, the divers registered all fishes > 10 cm on the way out, and cryptic species and fish < 10 cm were registered on the way back. Transects were haphazardly placed along the reefs from depths between 7 to 16 m at accessible areas with a minimum number of 20 replicates at each site (see table 1s for detailed information).

2.4. Data analysis

The richness, diversity, evenness of taxa from the benthic cover, the invertebrate megafauna and fish species were tested for normality (Shapiro Wilks test) and homogeneity of variance (Levene's test) before subject to the analysis of variance (ANOVA). The same procedure was applied to the density of fishes and invertebrate megafauna. When necessary, data was square root transformed to attain ANOVA premises (Underwood, 1996). Reef site was used as a fixed factor and samples (transects or quadrats) were used as replicates in analysis. The same structure of analysis was applied for Permutational Multivariate Analysis of Variance (PERMANOVA) both for fish assemblage and invertebrate megafauna data using transects as replicates. In the case of benthic communities, transects were treated as random factors nested within reef sites, using quadrats as replicates. Multivariate homogeneity of groups dispersions was evaluated prior to PERMANOVA analysis and, when heterogeneity was found samples were pooled as averages of samples for analysis. When differences were found between levels of the tested factor, a Tukey test was applied a posteriori to identify differences between levels. When differences were found between levels of tested factor, a Tukey test was applied *a posteriori* to identify differences between levels.

The composition of the benthic cover was investigated using metric multidimensional scaling, while the invertebrate megafauna and fish assemblages were analyzed using non-metric multidimensional scaling because of differences in variables' distribution nature. The benthic cover data was transformed using the arscin square root of relative cover before calculating distance among replicates (Euclidian distance). Fish and megafauna data were transformed using the Hellinger method prior to calculate dissimilarities (Bray–Curtis distance). Only taxa with ≥ 1% in average cover (taxa), and fish species with ≥ 1% of total abundance (81 species) were included in ordination analysis. Finally, similarities between sampled assemblages were tested for each group of data using the Mantel test with Ward's agglomeration method using average values for sampled sites. Cophenetic distances of Ward's cluster were all > 55%. All analyzes were done using R language (R Core Team, 2020). Univariate analyzes were applied using *stats* package (R Core Team, 2020) and lmer4 package (Bates et al., 2015), and multivariate analysis used functions from *vegan* (Oksanen et al., 2019) and *ape* packages (Paradis and Schliep, 2018).

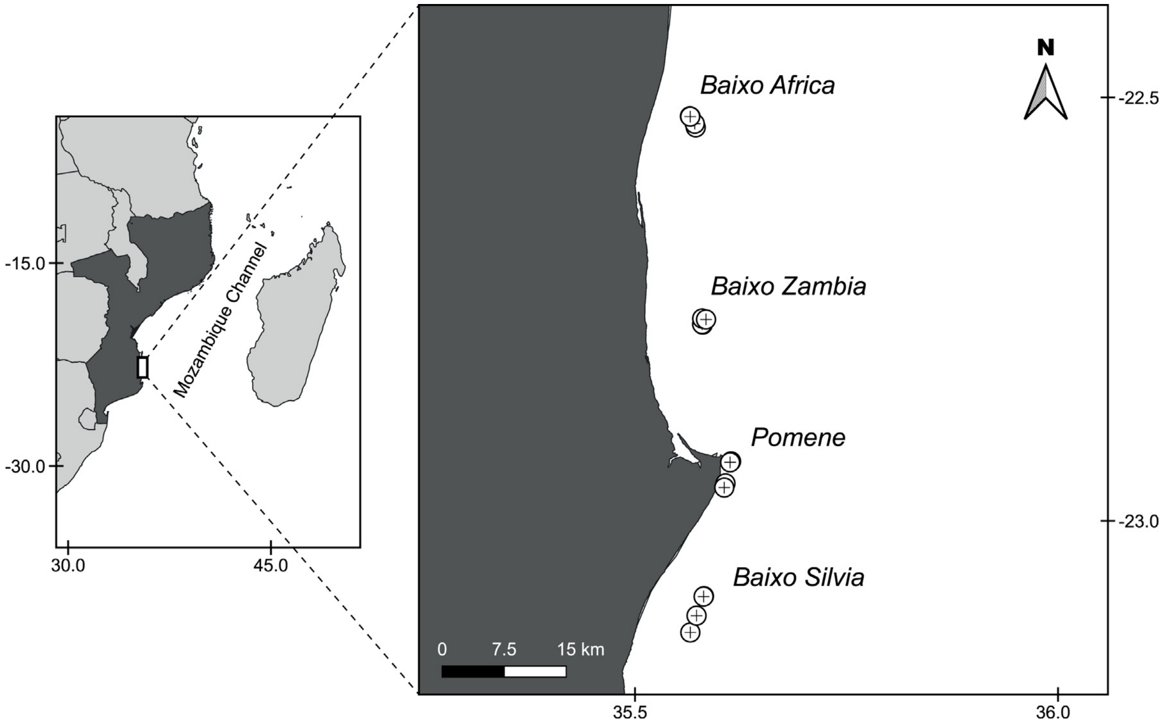

Fig. 1. Surveyed reefs along the coastline between São Sebastião Lighthouse and south of the Reserva Nacional de Pomene in Inhambane Province (Mozambique). Circular markers indicate sampled points in each of the reef formations indicated.

3. Results

3.1. Benthic cover and invertebrate megafauna

Most of the reef formations were parallel to the coastline with a steeper seaward side, a low relief plateau, and a gradual depth range on the leeward side. Few partially dead corals were observed, and only a few colonies of *Porites* spp. and *Astreopora myriophthalma* showed signs of disease in surveyed areas. The shallow reef flat areas usually had lower coral cover (Fig. 1s), and deeper interface zones were dominated by coral rubble and broken coral colonies (Fig. 2s), with few coral recruits (defined as colonies with less than 3 cm). Spur and groove formations were common to the seaward side of reefs with a dominance of coral rubble and sand (Fig. 2s). Higher coral cover was observed at intermediate depths (12–18 m) with a dominance of branching, arborescent, and plate corals at reef slopes (figure 2s). Fishing lines, pieces of rope, and nets were observed entangled with corals at Pomene and Baixo Zambia (figure 3s), mainly on *Acropora*, *Pocillopora*, and *Tubastraea* colonies. Fish and benthic surveys were concentrated at reef slope and reef flat habitats.

Regarding the benthic cover composition, 46 species of Scleractinia, three Zoantharia, nine Alcyonacea, four Ascidiacea, two Arthropoda, ten Mollusca, and nine Echinodermata were identified on studied reefs Table 2 (Table 1), with the majority of the species being found in, at least, two sites (Table 2s). Reef areas differed on the benthic cover taxa richness (ANOVA, *F-value* $_{3,465} = 28.02$, $p < 0.001$), taxa diversity (*F-value* $_{3,523} = 7.25$, $p < 0.001$), and evenness (*F-value* $_{3,523} = 5.29$, $p < 0.001$), with Pomene having the lowest values for all variables (Fig. 2). In a first approach, multivariate groups dispersions of benthic communities' composition were heterogeneous (F-value $_{3,531} = 10.1$, $p < 0.001$), thus we averaged quadrat samples to transect level for a second test. No differences were found in multivariate groups dispersions this time (*F value*$_{3,44} = 2.61$, $p = 0.06$) neither between benthic taxa composition (PERMANOVA: pseudo-*F value* $_{3,47} = 3.43$, $p = 0.19$) of reef areas.

An average, sponges, turf algae, and substrate (rock, sand, or coral rubble) were the dominant groups at all sampled reefs (Fig. 3). Turf algae was the most abundant at Pomene (32.0 ± 17.4, mean ± SD) and Baixo Zambia (30.6 ± 18.1), and the second most abundant at Baixo Africa (22.9 ± 18.7) and Baixo Silvia (17.2 ± 11.4). Sponges (18.5 ± 10.9) and other invertebrates (25.8 ± 35.1) were dominant in Baixo Silvia and Baixo Africa reefs, respectively (Fig. 2). The high cover of other invertebrates found at Baixo Africa was related to the large aggregations of the sea anemone *Heteractis magnifica* observed in a few areas (Table 2s). Among scleractinian corals, plate growth forms were the most abundant in all reefs, especially in Baixo Africa (19.8 ± 21.4, mean ± SD) followed by Baixo Zambia (18.9 ± 21.8), Baixo Silvia (14.0 ± 16.9), and Pomene (13.5 ± 13.7) (Fig. 3). Total coral cover was higher at Baixo Zambia (25.8%) and Baixo Africa (23.9%), followed by Baixo Silvia (13.8%) and Pomene (9.3%). Coral recruits were observed only at Baixo Silvia and Pomene, and solitary corals were observed at all sites but Baixo Zambia (Table 2s). Recently dead colonies were observed at all sites but summed $< 1\%$ of total cover (Fig. 3). The species *Acropora* cf. *branchi* was the most frequent plate coral at all reef sites, and the branching *Pocillopora* sp. was abundant only at Baixo Zambia (Table 2s).

A total of 26 taxa from five phyla of mobile and sedentary macro-invertebrates were identified for all sampled sites (Table 1), with Echinodermata and Mollusca beingthe most frequent groups on all sites except for Baixo Africa, where cnidarians were dominant (Fig. 4). Total macrofauna density (Fig. 4) was similar at all surveyed reefs (ANOVA, *F-value* $_{3,48} = 1.24$, $p = 0.31$), and the same was found for ecological indexes (Fig. 2) of richness (*F-value* $_{3,48} = 2.32$, $p = 0.08$), diversity (*F-value* $_{3,48} = 1.65$, $p = 0.19$), and evenness (*F-value* $_{3,40} = 1.86$, $p = 0.15$). The slightly lower evenness observed at Baixo Africa was associated with the local dominance of the anemone *Heteractis magnifica*, which was the most common macroinvertebrate species observed, together with the sea star *Linckia* sp., the sea urchin *Echinothrix calamaris*, and the bivalve *Hyotissa* sp. (Table 3s). Multivariate groups dispersions were heterogeneous for the megafauna (*F value* $_{3,48}$ =

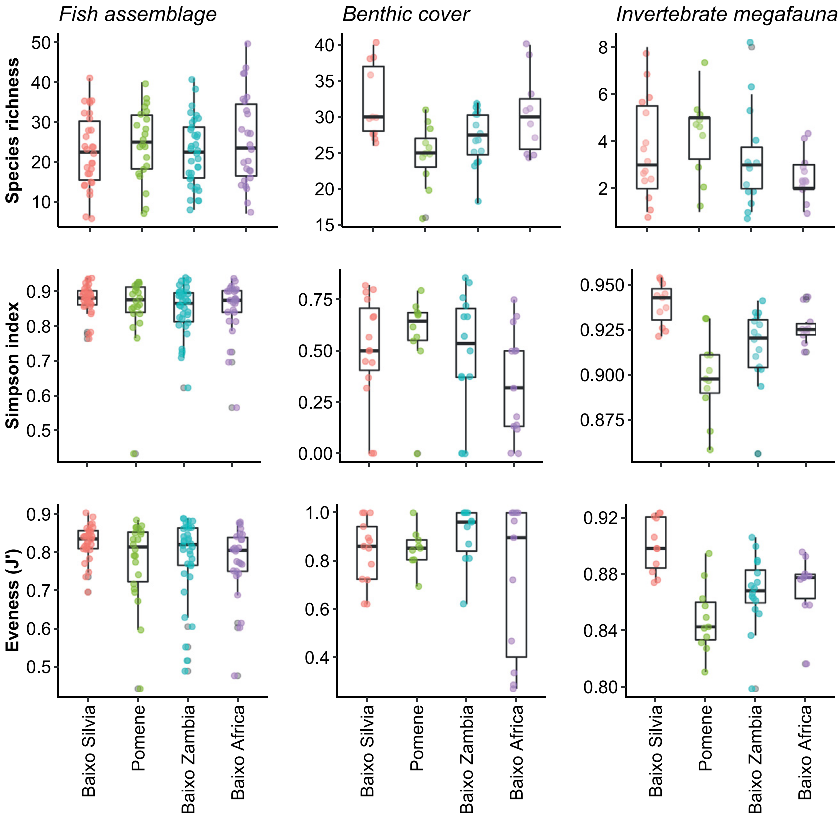

Fig. 2. Species richness, diversity (Simpson index), and evenness (per 100 m^2) of the benthic cover, macrofauna, and fish assemblage of reefs along the coastline between São Sebastião Lighthouse and south of the Reserva Nacional de Pomene in Inhambane Province (Mozambique). Colored dots indicate samples, vertical bars represent the median, boxes indicate first and third quantiles, and whiskers indicate 1.5*IQR (inter-quantile range). Note that *y*-axis scales are different in each panel.

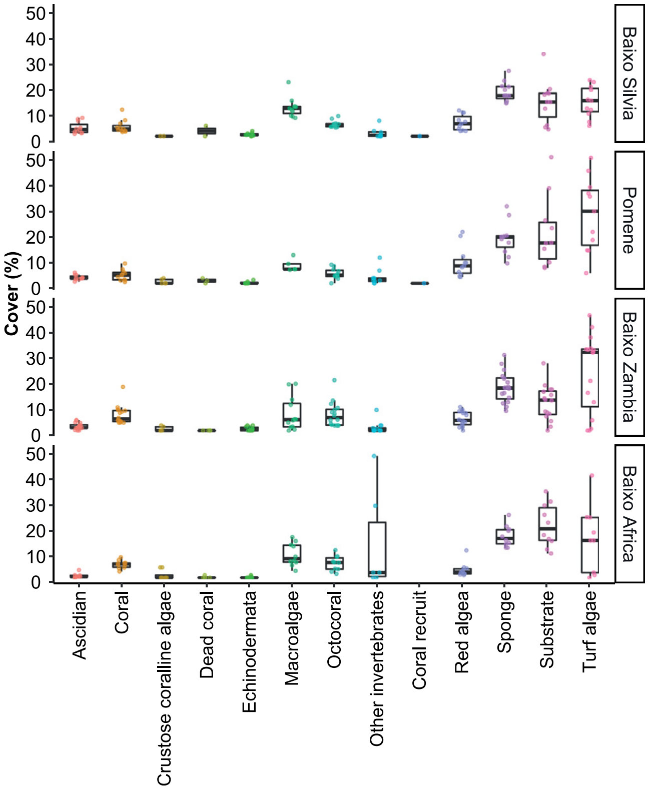

Fig. 3. Relative cover of benthic groups observed on four reef areas along the coastline between São Sebastião Lighthouse and south of the Reserva Nacional de Pomene in Inhambane Province (Mozambique). Dots represent individual values, and boxes define the interquartile range, with whiskers limiting the 1.5*IQR (inter-quantile range).

3.23, $p = 0.03$) with differences between Pomene and Baixo Africa (Tukey test, $p = 0.03$). Because differences were small, the PERMANOVA analysis showed no differences in megafauna composition (PERMANOVA: pseudo-*F value* $_{3,51} = 2.03$, $p = 0.99$) of reef areas.

3.2. Reef fish assemblages

A total of 209 different fish taxa was observed along all sampled sites (Table 2), with Baixo Zambia showing the highest richness ($n = 136$), followed by Baixo Silvia and Baixo Africa ($n = 132$), and Pomene ($n = 116$). No difference was found between sampled reefs (Fig. 2), either for fish density (*F-value* $_{3,108} = 0.98$, $p = 0.40$), fish species richness (*F-value* $_{3,108} = 0.69$, $p = 0.56$), diversity (*F-value* $_{3,108} = 0.94$, $p = 0.43$) or evenness (ANOVA: *F-value* $_{3,108} = 1.86$, $p = 0.14$).

The reef fish species assemblage's composition was similar among sampled reefs (Fig. 5; PERMANOVA: pseudo-*F value* $_{3,111} = 0.07$, $p = 0.9$) irrespective of differences in sampling effort (Fig. 4s) and multivariate variance of groups was homogeneous (*F value* $_{3,108} = 0.12$, $p = 0.95$). Most of the species found were common to all reef sites and with similar contributions (Table 4s in supplementary material), which explains the large overlap observed in ordination analysis (Fig. 5).

Reef fish trophic structures had higher numbers of planktivorous ($n = 110$) and invertivorous species ($n = 70$), and the remaining trophic groups accounted for 40% of species total (Table 4s). The relative contribution of species for each trophic group was also similar among all sites (Fig. 4). The mean size of individuals from the same trophic group did not differ between reef formations ($p > 0.05$), except for mobile invertebrate feeders (*F value* $_{3,553} = 3.77$, $p = 0.01$) that were larger at Pomene

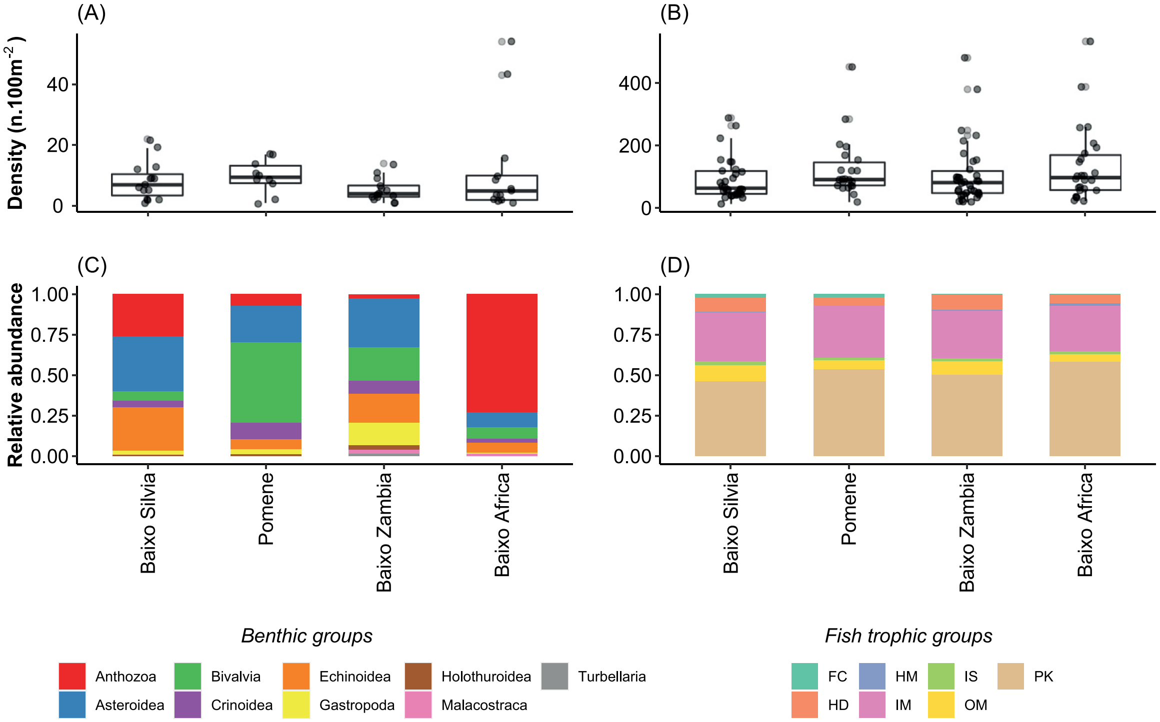

Fig. 4. Density of benthic macrofauna (A) and reef fish species (B), and relative frequency of macrofauna classes (C) and reef fish trophic groups (D) observed in four reef areas along the coastline between São Sebastião Lighthouse and south of the Reserva Nacional de Pomene in Inhambane Province (Mozambique). FC — piscivore, HD — herbivore–detritivore, HM — macroalgivore, IM — mobile invertebrate feeder, IS — sessile invertebrate feeder, OM — omnivore, PK — planktivore. Dots represent individual values, and boxes define the interquartile range, with whiskers limiting the 1.5*IQR (inter-quantile range).

than Baixo Zambia and similar between other reefs (Fig. 6). However, the size of macroalgivores was larger at Baixo Africa and Baixo Silvia, and the opposite pattern was observed for sessile invertebrate feeders (Fig. 6). Piscivores had the largest mean (36.8 ± 34.8 cm, mean ± SD) and range (6–230 cm) in body size.

Several planktivores (e.g., large unicorn-fish from *Naso* genus, and fusiliers from *Caesio* genus), carnivores (e.g., snappers, Lutjanidae family), and piscivore (e.g., jacks, Carangidae family) species were commonly found forming large shoals ($>$ 100 individuals), especially at Pomene where reefs run deeper. Chondrichthyes species were not abundant but observed in all reefs despite not being recorded inside transects. Gray reef shark (*Carcharhinus amblyrhynchos*), whitetip reef shark (*Triaenodon obesus*), and blacktip reef shark (*Carcharhinus melanopterus*) were observed at Pomene, Baixo Silvia, and Baixo Zambia, respectively. One female (∼4 m wide) giant manta ray (*Mobula birostris*) and one juvenile whale shark (∼4 m long) of the observed at Baixo Africa, and another two species of rays (blue-spotted ray *Taeniura lymma* and a large unidentified *Dasyatidae*, Fig. 5s) were observed at Baixo Zambia.

No correlations were found between the benthic cover and the fish assemblage compositions (Mantel test, $Z = 22.1$, $p = 0.13$), the invertebrate megafauna and the fish assemblage compositions ($Z = 68.7$, $p = 0.08$), or the benthic cover and megafauna compositions ($Z = 29.4$, $p = 0.34$).

4. Discussion

Our study presents the first large assessment of fish and benthic biodiversity of four uncharted shallow reefs of the Mozambique Channel, a poorly studied area from the Western Indian Ocean where more than 200 fish species and 84 species of benthic invertebrates were identified. In general, the studied reefs showed similar richness to those found for other reefs of the Mozambican Channel (Motta et al., 2000; Gudka et al., 2020; Samoilys et al., 2019). Nevertheless, the present findings add valuable information to this understudied region. The abundance of fish and the prevailing of healthy corals may be signs of low human impacts to the sampled reefs. We did not stratify sampling according to classical reef features (back reef, fore reef, platform) because of logistic and access restrictions, but we observed very low coral cover at the reef flat areas. The Mozambican coast has a high potential for the formation of cyclones (Malan et al., 2013), and several strong cyclones have indeed hit its coastal zone in the last 25 years (Chikoore et al., 2015; Bié et al., 2017). Negative impacts on shallow reefs caused by cyclones (e.g., breakage and dislodgment of corals) are expected (Cheal et al., 2017) but it is not possible to confirm if those events, such as the tropical cyclone Eline in 2000 (Reason and Keibel, 2004), had contributed to the low coral cover observed at Inhambane reefs, since they are historically more frequent in the northern part of Mozambique (Chikoore et al., 2015).

4.1. Benthic cover and invertebrate megafauna

The benthic cover taxa had large differences in ecological indicators (taxa richness, diversity, and evenness) between sampled reefs, but those differences were not reflected on the assemblage's composition. The coral fauna in the area was composed of several common and widely distributed species, including species from of the genera *Acropora*, *Pocillopora*, and *Porites*, which can be found throughout the whole Indo-Pacific region (Veron et al., 2016), and a few rare and uncommon species, such as *Gyrosmillia interrupta* and *Horastrea indica*, both restricted to the Western Indian Ocean (Veron et al., 2016). *Horastrea indica* is currently classified as vulnerable by the IUCN Red List (Sheppard et al., 2008) and was observed only at Baixo Silvia and Baixo Africa, the two sites with the highest diversity of benthic species. The most abundant plate coral observed at all sites was *Acropora* cf.

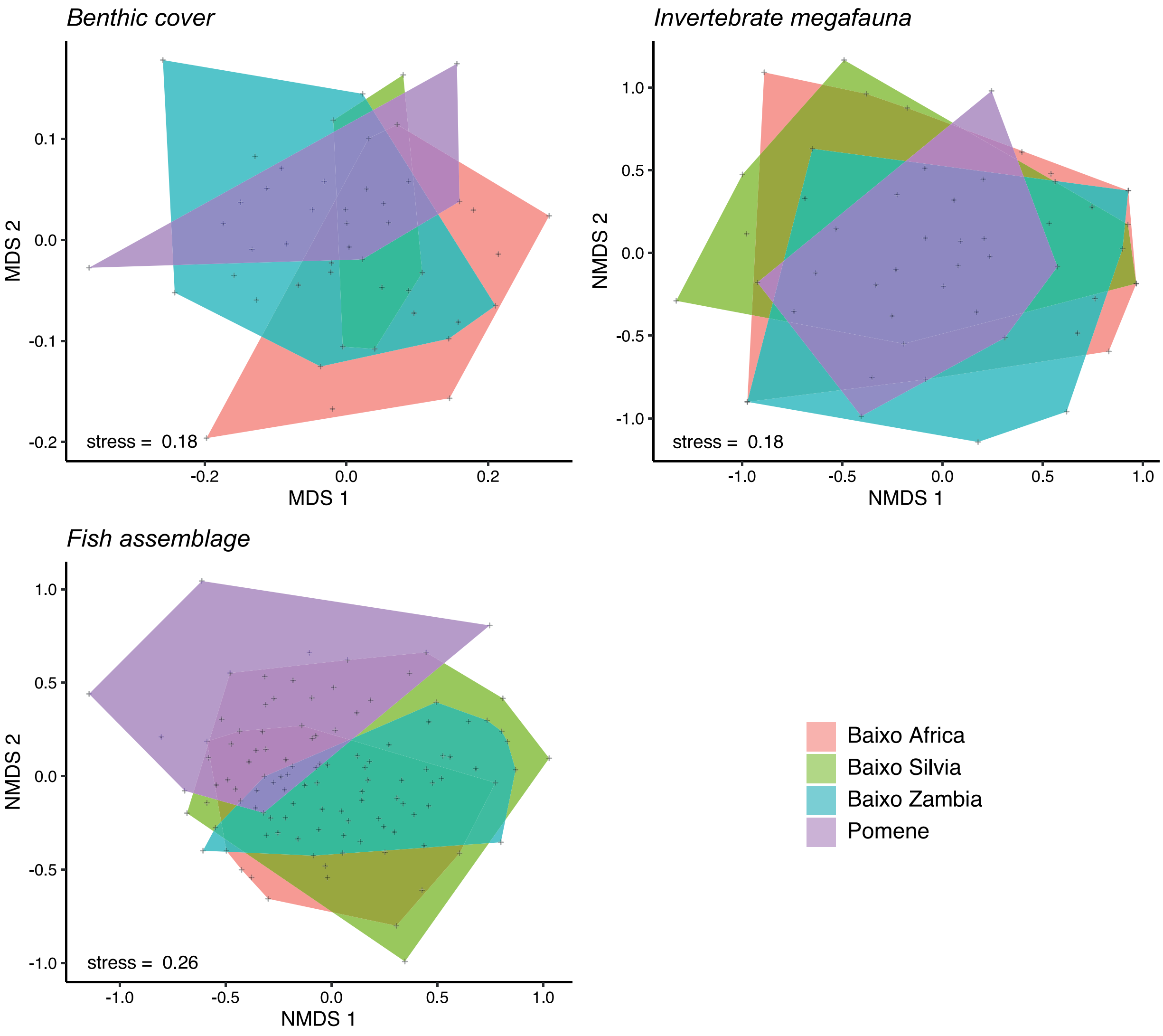

Fig. 5. Ordination plot (nMDS) of reef fish assemblage from four reefs along the coastline between São Sebastião Lighthouse and south of the Reserva Nacional de Pomene in Inhambane Province (Mozambique). Dots indicate transect level samples, and polygons delimitate each reef assemblage multivariate space.

branchi, an endemic species of the Western Indian Ocean, widely distributed, and a key species that creates structural complexity on Mozambican reefs (Veron et al., 2016). It is important to highlight that the species list presented here represents only the species that could be clearly identified from images. Thus, a detailed assessment including morphological and molecular analyzes is recommended for a complete description of the local coral biodiversity.

Both coral species diversity and cover are important proxies to the health of the local environment as they are positively correlated to reef fish diversity and abundance (Komyakova et al., 2013, 2018). The tridimensional environment created by corals, especially those with branching growth forms such as *Acropora*, generates structural complexity that provides shelter for several species of fishes and invertebrates (Nanami et al., 2013; Darling et al., 2017; Rogers et al., 2018), which constitute the basis of coral reef communities. When reef formations are damaged, the environment loses diversity and complexity, with negative impacts on reef biodiversity (Graham and Nash, 2013; Komyakova et al., 2018). The survey showed a large contribution of branching and plate corals, mainly fast-growing species from the genus *Acropora*, providing higher structural complexity. Nevertheless, despite the key role of branching species in enhancing structural complexity – consequently higher biodiversity – recent studies have shown that coral species diversity is also a relevant factor in maintaining reef fish diversity (Komyakova et al., 2013, 2018). Here, we did not find any relationships between the benthic cover and the fish assemblage, or invertebrate megafauna compositions which may indicate that further processes, such as planktonic primary production inputs, may regulate species interactions besides structural complexity. Coral assemblages of Baixo Silvia and Baixo Zambia showed higher coral cover with dominance of *Acropora*, *Alveopora allingi, Pocillopora* spp. and *Astreopora myriophthalma* which conferred a more complex reef structure to these reefs. Interestingly, despite having the highest mean density of fish and mean diversity of macroinvertebrates, Pomene reefs showed the lowest values of mean richness and diversity of benthic organisms and lowest coral cover. However, Pomene reefs are surrounded by deeper waters and have a high primary structural complexity which may compensate for refugees and attraction of fishes. The mean coral cover of all surveyed reefs was lower than that observed in other areas in the northern portion of Mozambique but higher than the observed at Tofo (Inhambane), also dominated by turf algae (Costa et al., 2005). Although the observed mean coral cover was lower than 10% for all four sites, the standard deviation was high, indicating that the surveyed areas are heterogeneous and composed of patches with distinct coral cover.

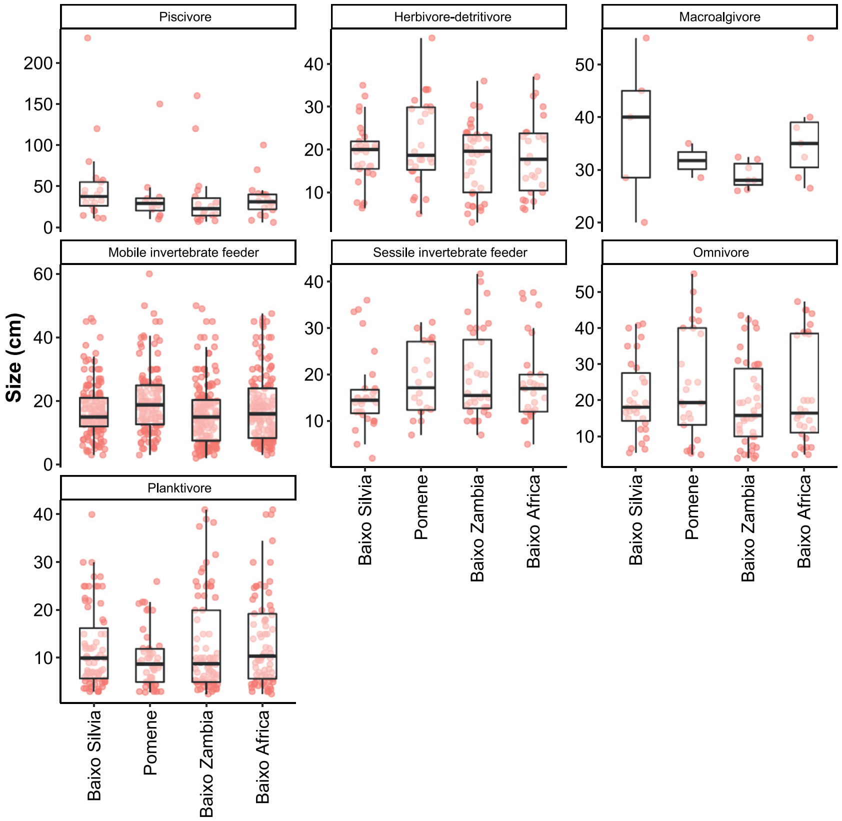

Fig. 6. Estimated size of reef fishes according to trophic groups observed on four reefs along the coastline between São Sebastião Lighthouse and south of the Reserva Nacional de Pomene in Inhambane Province (Mozambique). FC — piscivore, HD — herbivore–detritivore, HM — macroalgivore, IM — mobile invertebrate feeder, IS — sessile invertebrate feeder, OM — omnivore, PK — planktivore. Dots represent individual values, and boxes define the interquartile range, with whiskers limiting the 95% quantile interval.

All surveyed reefs had no signs of bleached colonies, with few observations of recently dead or partially dead colonies, mainly at Pomene. The average water temperature (∼22 °C) observed was below extreme limits (> 30 °C) that induce bleaching by overheating, indicating that other factors may have caused the death of these isolated corals in these colonies. Most of the partially dead colonies were found isolated and should not be considered a sign of poor water condition (e.g., eutrophication) or presence of chronic stressors, such as high temperatures. Only few entirely dead colonies were observed in Pomene, which might be a result of predation by the crown-of-thorns starfish. There were also only a few signs of disease affecting the zooxanthellate species *Astreopora myriophthalma* and *Porites* sp..

The invertebrate megafauna was heterogeneous among sampled reefs, and different groups were abundant in each reef (e.g., sea urchins at Baixo Silvia, sea anemones at Baixo Africa), but some were conspicuous to all reefs such as the giant clam (*Tridacna* spp.) and sea cucumbers (*Holothuria* cf. *nobilis*). *Tridacna* populations in the WIO have suffered severe declines associated with direct extraction (Ramah et al., 2018), and sea cucumbers have been especially targeted in northern Mozambique (Conand, 2008). However, although the frequency of occurrence of the giant clams and sea cucumbers might indicate low or null extraction of those species in surveyed reefs, our data is not sufficient to confirm that. Large crustaceans (e.g., lobsters) were seldom observed and were observed only out of the transects at Baixo Africa and Baixo Silvia. Similarly, that low representativeness should not be interpreted directly as a result of extraction pressure, despite this being of large concern along the Eastern African coast (Obura et al., 2019). Most marine invertebrates have cryptical or nocturnal behavior (Glynn and Echochs, 2011), being underestimated in diurnal surveys. Thus, the data presented here is a baseline for local reef communities, and the lack of previous data or the evaluation of local invertebrates harvesting activities precludes conclusions about the general 'health' of invertebrate megafauna communities or the influence of human exploitation.

4.2. Reef fish assemblages

The reef fish assemblages of surveyed reefs were similar in terms of mean size of individuals, average density, and species composition. Planktivorous fish species were the most abundant at all sites, which is expected for areas under a high influence of currents (Hobson, 1991). This high productivity associated with particulate material and plankton carried by coastal tidal currents, sustains a large number of small fish species and also attracts large filter-feeding species such as giant manta rays and whale sharks (Rohner et al., 2013). Schools of large and mid-size planktivores (e.g., surgeonfish, fusiliers, and unicorn fishes) but also mesopredators (snappers and jacks) were commonly observed at sampled reefs, which is an indication of local high productivity (Duffy and Wissel, 1988), and healthy conditions of reef communities (Shantz et al., 2015). However, most fish species from higher trophic levels were mesopredators, and large groupers and sharks (top predators) were only seldom observed. Although occasional, small sharks were observed at all reefs, including the gray reef shark (*Carcharhinus amblyrhynchos*), whitetip reef sharks (*Triaenodon obesus*), and blacktip reef sharks (*Carcharhinus melanopterus*). The presence of top predators in the reef environment is critical for the resilience of these ecosystems (Roff et al., 2016), and fishing activities focused on these species can quickly collapse local shark populations over a short period

(Heupel et al., 2009). Along the surveyed area, fishermen were observed throwing chunks of red meat to the sea, suggesting a directed fishing practice targeting sharks in the region.

Individuals from the family Epinephelidae (i.e., Groupers) were common at all sampled reefs in considerable shallow depths when compared to reefs where they are the focus of fishing activities (Sadovy et al., 2013). Large groupers and large jacks (Carangidae) are usually found in deeper reefs because of diving and fishing activities in shallow areas (Lindfield et al., 2016). Although all surveyed reefs were shallow (up to 30 m deep), the presence of large-bodied fishes at these depths may indicate that these species suffer low fishing pressure locally. However, the presence of broken fishing lines, ropes, and net pieces in the surveyed reefs, especially at Baixo Silvia, Baixo Zambia, and Pomene reefs, are clear signs of fishing pressure. The observation of large groupers in Baixo Africa, as well as other small and medium fish species that did not seem disturbed by divers are probably associated with the low disturbance by human activities, which is probably related to the difficult access to the reefs. Despite differences in dimensions, benthic cover, and structural complexity among sampled reefs, the similarity of fish assemblages' composition suggests high connectivity between those reef groups, which may be tested in further studies.

Table 1
Taxa richness of invertebrate megafauna and benthic cover observed in four reefs along the coastline between São Sebastião Lighthouse and south of the Reserva Nacional de Pomene in Inhambane Province (Mozambique).

Method	Taxon	Reef site			
		Baixo Silvia	Pomene	Baixo Zambia	Baixo Africa
Invertebrate megafauna	Platyhelminthes	1	1	1	–
	Cnidaria	1	2	1	2
	Mollusca	4	4	4	3
	Arthropoda	–	–	1	1
	Echinodermata	12	8	9	6
Benthic cover	Algae	4	4	4	4
	Porifera	2	2	2	1
	Hydrozoa	1	1	1	1
	Actiniaria	2	2	2	1
	Octocorallia	8	8	7	8
	Zoantharia	2	2	2	1
	Scleractinia	35	26	25	28
	Mollusca	1	–	–	1
	Echinodermata	3	2	1	1
	Ascidiacea	4	3	3	3

Table 2
Reef fish species richness according to trophic groups and reef sites along the coastline between São Sebastião Lighthouse and south of the Reserva Nacional de Pomene in Inhambane Province (Mozambique).

Reef site	Trophic group						
	FC	HD	HM	IM	IS	OM	PK
Baixo Silvia	15	8	3	54	12	11	25
Pomene	8	10	1	52	11	10	21
Baixo Zambia	9	11	2	56	13	14	25
Baixo Africa	12	9	4	51	15	11	25

FC — piscivore, HD — herbivore–detritivore, HM — macroalgivore, IM — mobile invertebrate feeder, IS — sessile invertebrate feeder, OM — omnivore, PK — planktivore.

4.3. Conservation and monitoring

Synergistic pressures such as overfishing, pollution, and climate change have been affecting coral reefs worldwide (Halpern et al., 2008; Hoegh-Guldberg and Bruno, 2010). Extreme climatic events have been responsible for the intense bleaching of coral reefs in the Western Indian Ocean (WIO), from Kenya to Mozambique (Rodrigues et al., 1999; Scheyler et al., 1999; Motta et al., 2000; Gudka et al., 2020). Mozambican reefs have suffered declines in cover during the massive bleaching event of 1998 and 2016 (Scheyler et al., 1999; Motta et al., 2000), but were less affected than other regions of the Western Indian Ocean (Gudka et al., 2020). However, the reef formations sampled here were not included in these studies, and up to date, there was virtually no data on these reef formations. Considering the local biodiversity and the importance of coral reef formations to the Mozambican economy and livelihood (Pereira et al., 2018; Obura et al., 2019), conservation efforts should focus on monitoring and protecting reef areas, especially understudied reef structures. Efforts could be focused on the participation of local communities in programs including local ecological knowledge and the training of locals to help in monitoring efforts, participative management, and enforcement.

Due to the scarcity of knowledge about this important region of the Mozambican coast, the data obtained here represents a baseline for future monitoring activities in coral reefs of Inhambane Province, which require further conservation efforts. This first assessment of fish and benthic diversities and composition will help future actions focused on sustainable use of coral reef resources and maintenance of ecosystem services, especially related to local food security, low impact tourism activities and biodiversity conservation.

5. Conclusions

- Reef fish species diversity of the four reef formations surveyed (Baixo Silvia, Pomene, Baixo Zambia and Baixo Africa) had similar values to other reefs in the Western Indian Ocean;
- Coral cover was low, with very few dead colonies, few signs of diseases, and no sign of recent bleaching;
- Reef formations had few signs of fishing pressure, and Baixo Africa – the most isolated reef – resembled an unfished reef;
- The conservation status of sampled reefs is worth noting, and conservation action is recommended to maintain such conditions.

CRediT authorship contribution statement

Cesar A.M.M. Cordeiro: Conceptualization, Formal analysis, Writing – original draft, Revision & editing. **Marcos B. Lucena:** Writing – original draft, Revision & editing. **Fenias Muhate:** Writing – original draft & editing. **Kátia C.C. Capel:** Formal analysis, Writing – original draft, Revision & editing.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Cesar A M M Cordeiro reports financial support was provided by WIORI (Western Indian Ocean Research Initiative), NATURA and AVM Consultores Lda. Cesar A M M Cordeiro reports a relationship with WIORI that includes: consulting or advisory.

Acknowledgments

The authors are thankful to the Universidade Pedagógica de Maputo, especially to the Faculdade de Ciências Naturais e Matemática and the rector Dr. Jorge Ferrão for the support and partnership in this project. We are also thankful to WIORI (Western Indian Ocean Research Initiative), NATURA and AVM Consultores Lda for funding the expedition, and to Instituto Nacional de Investigação Pesqueira for the research permit. We are also grateful to The Santuário Bravio de Vilanculos, the Msasa House (VCWS - Mr. Hugh Brown), Mr. Grenville Wilson and the crew of HQ2 for their support. Also, we acknowledge Mr. Augusto Nhampossa for his great assistance with all scientific activities.

Appendix A. Supplementary data

Supplementary material related to this article can be found online at https://doi.org/10.1016/j.rsma.2021.102037.

References

Andreasson, S., 2018. Emerging frontiers of energy exploration in post-boom africa. In: S., Raszewski (Ed.), The International Political Economy of Oil and Gas. pp. 195–208. http://dx.doi.org/10.1007/978-3-319-62557-7.

Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67 (1), 1–48.

Benayahu, Y., Shlagma, A., Scleyer, M.H., 2003. Corals of the south-west Indian ocean: VI. The Alcyonacea (Octocorallia) of Mozambique, with a discussion on soft coral distribution on south equatorial East African reefs. Zool. Verh. 345, 49–57.

Bié, A.J., Camargo, R., Mavume, A.F., Harari, J., 2017. Numerical modeling of storm surges in the coast of Mozambique: the cases of tropical cyclones Bonita 1996 and Lisette 1997. Ocean Dyn. 67, 1443–1459.

Brock, R.E., 1982. A critique of the visual census method for assessing coral reef fish populations. Bull. Mar. Sci. 32 (1), 269–276.

Cheal, A.J., MacNeil, M.A., Emslie, M.J., Sweatman, H., 2017. The threat to coral reefs from more intense cyclones under climate change. Global Change Biol. 23 (4), 1511–1524.

Chikoore, H., Vermeulen, J.H., Jury, MR., 2015. Tropical cyclones in the Mozambique channel: January–2012. Nat. Hazards 77, 2081–2095.

Conand, C., 2008. Population status, fisheries and trade of sea cucumbers in Africa and the Indian Ocean. In: Toral-Granda, V., Lovatelli, A., Vasconcellos, M. (Eds.), Sea Cucumbers. a Global Review of Fisheries and Trade. FAO Fisheries and Aquaculture Technical Paper. 516, Rome, Italy, pp. 143–193, 318pp..

Costa, A., Pereira, M.A.M., Motta, H., Schleyer, M., 2005. Status of coral reefs of mozambique: 2004. In: D, Souter, O., Lindén (Eds.), Coral Reef Degradation in the Indian Ocean Status Report 2005. pp. 54–60.

Darling, E.S., Graham, N.A.J., Januchowski-Hartley, F.A., Nash, K.L., Prachett, M.S., Wilson, S.K., 2017. Relationships between structural complexity, coral traits, and reef fish assemblages. Coral Reefs 36 (2), 561–575.

Duffy, D.C., Wissel, C., 1988. Models of fish school size in relation to environmental productivity. Ecol. Model. 40, 201–211.

FAO, 2017. Country profile – Mozambique. Available at http://www.fao.org/3/i9805en/I9805EN.pdf, (accessed in 02 2020).

Friedlander, A.M., Caselle, J.F., Ballesteros, E., Brown, E.K., Turchik, A., Sala, E., 2014. The real bounty: Marine biodiversity in the pitcairn islands. PLoS One 9 (6), e100142.

Glynn, P.W., Echochs, I.C., 2011. Invertebrates and their roles in coral reef ecosystems. In: Dubinsky, Z., Stambler, N. (Eds.), Coral Reefs: An Ecosystem in Transition. Springer Science+Business Media, London, UK, pp. 273–325.

Graham, N.A.J., Nash, K.L., 2013. The importance of structural complexity in coral reef ecosystems. Coral Reefs 32, 315–326.

Gudka, M., Obura, D., Mbugua, J., Ahamada, S., Kloiber, U., Holter, T., 2020. Participatory reporting of the 2016 bleaching event in the Western Indian Ocean. Coral Reefs 39, 11. http://dx.doi.org/10.1007/s00338-019-01851-3.

Halpern, B.S., Walbridge, S., Selkoe, K.A., Kappel, C.V., et al., 2008. A global map of human impact on marine ecosystems. Science 319, 948–952.

Harris, J.L., Estradivari, E., Fox, H.E., McCarthy, O.S., Ahmandia, G.N., 2017. Planning for the future: Incorporating global and local data to prioritize coral reef conservation. Aquat. Conserv. Mar. Freshw. Ecosyst. 27 (S1), 65–77.

Haskell, P.J., McGowan, A., Show, A.N., Pierce, S.J., et al., 2013. Monitoring the effects of tourism on whale shark *Rhincodon typus* behaviour in Mozambique. Oryx 43 (3), 492–499.

Heupel, M.R., Williams, A.J., Welch, D.J., Ballagh, A., Mapstone, B.D., Carlos, G., Davies, C., Simpfendorfer, ., 2009. Effects of fishing on tropical reef associated shark populations on the Great Barrier Reef. Fish. Res. 95 (2–3), 350–361.

Hobson, E.S., 1991. Trophic relationships of fishes specialized to feed on zooplankters above coral reefs. In: Sale, PF. (Ed.), The Ecology of Fishes on Coral Reefs. Academic Press, San Diego, pp. 69–95.

Hoegh-Guldberg, O., Bruno, J.F., 2010. The impact of climate change on the world's marine ecosystems. Science 328, 1523–1528.

Hoguane, A.M., 2007. Perfil diagnóstico da zona costeira de moçambique. Rev. Gest. Costeira Integr. 7 (1), 69–82.

INE - Instituto Nacional de Estatística, 2019. Projecções de População. Available at: http://www.ine.gov.mz/estatisticas/estatisticas-demograficas-e-indicadores-sociais/populacao/projeccoes-da-populacao/projeccoes-2007-2040-inhambane.pdf - (access in 5th December 2019).

Komyakova, V., Jones, G.P., Munday, P.L., 2018. Strong effects of coral species on the diversity and structure of reef fish communities: A multi-scale analysis. PLoS One 13 (8), e0202206.

Komyakova, V., Munday, P.L., Jones, G.P., 2013. Relative importance of coral cover, habitat complexity and diversity in determining the structure of reef fish communities. PLoS One 8 (12), e83178, pmid:24349455.

Lindfield, S.J., Harvey, E.S., Halford, A.R., McIlwain, J.L., 2016. Mesophotic depths as refuge areas for fishery-targeted species on coral reefs. Coral Reefs 35 (1), 125–157.

Louro, C.M.M., Litulo, C., Pereira, M.A.M., Pereira, T.I.F.C., 2017. Investigação e Monitoria de Espécies e Ecossistemas Nas áreas de Conservação Marinhas Em Moçambique: Reserva Nacional do Pomene 2016. Centro Terra Viva, Maputo, p. 38 pp.

Malan, C., Reason, C.J., Loveday, B.R., 2013. Variability in tropical cyclone heat potential over the Southwest Indian Ocean. J. Geophys. Res. Oceans 118, 6734–6746.

Meirelles, P.M., Amado-Filho, G.M., Pereira-Filho, G.H., Pinheiro, H.T., de Moura, R.L., Joyeux, J-C., et al., 2015. Baseline assessment of mesophotic reefs of the Vitória-Trindade seamount chain based on water quality, microbial diversity, benthic cover and fish biomass data. PLoS One 10 (6), e0130084.

Motta, H., 2000. Status of the Protected Coral Reefs of Mozambique. A Report to ICRAN, p. 18 pp.

Motta, H., Rodrigues, M.J., Schleyer, M.H., 2000. Coral reef monitoring and management in Mozambique. In: Souter, D., Obura, D., Lindén, O. (Eds.), Coral Reef Degradation in the Indian Ocean. Status report 2000, Cordio.

MTADR – Ministério da Terra, 2006. Ambiente e desenvolvimento rural 2006 plano de maneio da reserva nacional de pomene. Volume I – plano de maneio. Available only in Portuguese at: http://anac.gov.mz/wp-content/uploads/2017/07/Plano-Maneio-Pomene.pdf (Accessed in: 21 2021).

Nanami, A., Sato, T., Takebe, T., Teruya, K., Soyano, K., 2013. Microhabitat association in white-streaked grouper epinephelus ongus: importance of Acropora spp. Mar. Biol. 160, 1511–1517.

Noss, R.F., 1990. Indicators for monitoring biodiversity: A hierarchical approach. Conserv. Biol. 4 (4), 355–364.

Obura, D.O., Bandeira, S.O., Bodin, N., Burgener, V., Braulik, G., Chassot, E., …, Ternon, J.-F., 2019. The northern mozambique channel. In: World Seas: An Environmental Evaluation. pp. 75–99.

Oksanen, J., Blanchet, J.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., 2019. Vegan: Community Ecology. R package version 2.5-6.

Paradis, E., Schliep, K., 2018. Ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. Bioinformatics 35, 526–528.

Pereira, M.A.M., 2000. Preliminary Checklist of Reef-Associated Fishes of Mozambique. UGC/MICOA, Maputo, p. 21 pp.

Pereira, M.A.M., Louro, C.M.M., Litulo, C., Fernandes, R.S., 2018. Levantamento Ecológico de Base Sobre Recifes de Coral e Florestas de Mangal Dentro ou Próximo de Cinco áreas de Pesca de Gestão Comunitária. IDEPA, Centro Terra Viva & RARE, Maputo, p. 108 pp.

R Core Team, 2020. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria, URL https://www.R-project.org/.

Ramah, S., Taleb-Hossenkhan, N., Todd, P.A., et al., 2018. Drastic decline in giant clams (Bivalvia: Tridacninae) around Mauritius Island, Western Indian Ocean: implications for conservation and management. Mar. Biodivers. 49, 815–823.

Reason, C.J.C., Keibel, A., 2004. Tropical cyclone eline and its unusual penetration and impacts over the southern african mainland. Weather Forecast. 19, 789–805.

Riegl, B., 1996. Hermatypic coral fauna of subtropical south-east Africa – a check-list. Pac. Sci. 50, 404–414.

Rodrigues, M.J., Motta, H., Pereira, M.A.M., Gon̨ calves, M., Carvalho, M., Schleyer, M., 1999. Reef Monitoring in Mozambique. I: The Monitoring Programme and 1999 Report. MICOA/IIP, Maputo, p. 57 pp.

Rodrigues, M.J., Motta, H., Whittington, M.W., Schleyer, M.H., 2000. Coral reefs of mozambique. In: McClanahan, T., Sheppard, C., Obura, D. (Eds.), Coral Reefs of the Western Indian Ocean: Their Ecology and Conservation. Oxford University Press, Oxford, U.K, pp. 112–132.

Roff, G., Doropoulos, C., Rogers, A., Bozec, Y-M., Krueck, N.C., Aurellado, E., Priest, M., Birrell, C., Mumby, P.J., 2016. The ecological role of sharks on coral reefs. Trends Ecol. Evol. 31 (5), 395–407.

Rogers, A., Blanchard, J.L., Newman, S.P., Dryden, C.S., Mumby, P.J., 2018. High refuge availability on coral reefs increases the vulnerability of reef-associated predators to overexploitation. Ecology 99 (2), 450–463.

Rohner, C.A., Pierce, S.J., Marshall, A.D., Weeks, S.J., Bennett, M.B., Richardson, A.J., 2013. Trends in sightings and environmental influences on a coastal aggregation of manta rays and whale sharks. Mar. Ecol. Prog. Ser. 482, 153–168.

Sadovy, Y., Graig, M.T., Bertoncini, A., et al., 2013. Fishing groupers towards extinction: a global assessment of threats and extinction risks in a billion-dollar fishery. Fish Fish. 14, 119–136.

Salazar, M.U., Baker, D., Francis, M., Kornpihl, D., West, T., 2013. Frontier exploration offshore the Zambezi Delta, Mozambique. First Break 31 (6), 135–144.

Samoilys, M.A., Osuka, K., Mussab, J., Rosendoc, S., Riddell, M., Diade, M., Mbugua, J., Kawaka, J., Hill, N., Koldewey, H., 2019. An integrated assessment of coastal fisheries in Mozambique for conservation planning. Ocean Coast. Manag. 182 (1), 104924.

Scheyler, M., Obura, D., Rodrigues, M.J., 1999. A Preliminary Assessment of Coral Bleaching in Mozambique: Coral Reef Degradation in Indian Ocean: Status reports and project presentations. CORDIO, Stockholm (Sweden), pp. 37–42.

Shantz, A.A., Ladd, M.C., Schrack, E., Burkepile, D.E., 2015. Fish-derived nutrient hotspots shape coral reef benthic communities. Ecol. Appl. 25 (8), 2142–2152.

Sheppard, C., Turak, E., Wood, E., 2008. *HOrastrea indica*. In: The IUCN Red List of Threatened Species 2008. e.T133529A3788398. http://dx.doi.org/10.2305/IUCN/.UK.2008.RLTS.T133529A3788398.en, Downloaded on 08 2020.

Trygonis, V., Sini, M., 2012. Photoquad: a dedicated seabed image processing software, and a comparative error analysis of four photoquadrat methods. J. Exp. Mar. Biol. Ecol. 424–425, 99–108.

Tucker, C.M., Cadotte, M.W., Carvalho, S.B., Davies, T.J., Ferrier, S., Fritz, A.S., Grenyer, R., Helmus, M.R., Jin, L.S., Mooers, A.O., Pavoine, S., Purschke, O., Redding, D.W., Rosauer, D.F., Winter, M., Mazel, F., 2017. A guide to phylogenetic metrics for conservation, community ecology and macroecology. Biological Rev. 92, 698–715. http://dx.doi.org/10.1111/brv.12252.

Underwood, A.J., 1996. Experiments in Ecology. Cambridge University Press, UK, p. 524pp.

Veron, J.E.N., Stafford-Smith, M.G., Turak, E., DeVantier, L.M., 2016. Corals of the World. version 0.01, http://www.coralsoftheworld.org/page/home/?version=0.01 (Accessed 28 2020).