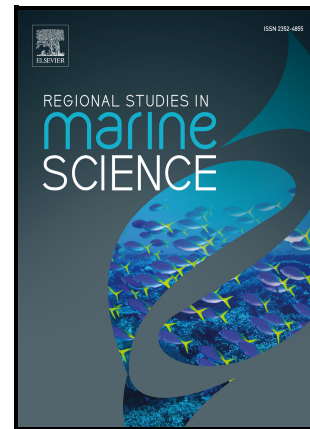


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Complex coral reefs offer hope for management in a Marine Protected Area in Zanzibar

Gudka Mishal^{1,2*}, Samoily Melita^{1,3}, Musembi Peter^{1,4}, Aboud Swaleh A.¹, Grimsditch Gabriel⁵, Mabwa Randall^{1,6}, Yahya Saleh^{7,8}, Osuka Kennedy^{1,9}

¹CORDIO East Africa, Mombasa, Kenya

²University of Melbourne, Melbourne, Victoria, Australia

³Dept Biochemistry & Biotechnology, Pwani University, Kilifi, Kenya

⁴Wildlife Conservation Society, Kenya Marine Program, Mombasa, Kenya

⁵United Nations Environment Programme, UN Avenue, Nairobi, Kenya

⁶Blue Ventures Conservation, East Africa Region - Mombasa, Kenya

⁷Institute of Marine Sciences, University of Dar es Salaam, Zanzibar, Tanzania

⁸Deep Sea Fishing Authority, P.O. Box 56, Fumba, Zanzibar, Tanzania

⁹Department of Earth, Ocean and Ecological Sciences, University of Liverpool, England

**Corresponding author: mgudka@cordioea.net*

Address: Unit 5 492 Barkers Road, Hawthorn East, Victoria, Australia, 3123

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fish, status, assessment, western Indian ocean, east Africa, Pemba Island, bleaching

Abstract

Management of Marine Protected Areas can be supported by a detailed understanding of ecosystem state. We assessed coral reefs within Pemba Channel Conservation Area in 2019 and evaluated changes over the previous decade. In 2019, hard coral cover ranged from 3.5 to 58.4% across sites, while coral recruitment was exceptionally high in places (14 recruits/m²). The highest total fish biomass was ~ 500 kg/ha, which is low compared to forereefs elsewhere in the Western Indian Ocean. Between 2009 and 2019, benthic substrate shifted to higher soft coral and turf algae cover, and mean fish density significantly decreased. This suggests that overfishing is a major threat and some reefs will require restoration to facilitate recovery. However, Pemba's unique geomorphology might offer refuge for corals from future warming and habitat for large, endangered fishes such as

groupers. This could elevate the global significance of Pemba's reefs and should motivate investment in management and conservation of these resources.

Introduction

Coral reefs are vital natural resources that support the livelihoods of millions of vulnerable communities in the Western Indian Ocean (WIO) (Cinner et al., 2009; Obura et al., 2017b). Unfortunately, these benefits are impacted by multiple stressors, including marine heatwaves that cause coral bleaching, destructive fishing and overexploitation (Burke et al., 2011; Halpern et al., 2012; Obura et al., 2021). To safeguard coral reefs and the socio-economic and ecological services they provide, Marine Protected Areas (MPAs) have been established across the WIO. The effectiveness of MPAs in fulfilling their function is dependent on resource availability and institutional commitment (Hattam et al., 2020; Yahya, 2021). The Pemba Channel Conservation Area (PECCA) was established in 2005 and extends over the west coast of Pemba Island, which is part of the Zanzibar Archipelago in Tanzania. The overarching goal of establishing the MPA was to conserve the biological diversity and other natural and cultural values within PECCA in the long term, while providing recreational, social and economic benefits for present and future generations (The Revolutionary Government of Zanzibar (RGoZ), 2021).

Pemba's fringing reefs represent 9% of Tanzania's coral reefs (Klaus, 2014; Levin et al., 2018), and are known for their high coral and fish diversity, large predatory fish and complex reef structures, including steep walls and ledges (United Nations Environment Programme, 2001; Daniels et al., 2003). The island is separated from mainland Tanzania by the deep Pemba Channel, and is the only island in the eastern African coastal reef system with oceanic reefs, which could promote differences in diversity and reef state compared to neighbouring Unguja Island, and Mafia Island further south (Archer and Turner, 1993; Jebri et al., 2020). There are strong currents around the reefs, including upwellings and downwellings (Jebri et al., 2020; Painter et al., 2021), which may confer resilience to coral bleaching by rapidly moving hot surface water away from the reefs. In addition, East Africa, including Pemba Island, is predicted to be a climate refuge in the future, maintaining favourable conditions for coral survival (Beyer et al., 2018; McClanahan, 2020). This makes

local actions around Pemba Island, both positive and threatening, critical to maximising the health and benefits accrued from these natural resources.

The reefs support a recreational diving industry (Johnstone et al., 1998; Muthiga et al., 1998), and are adjacent to important small-scale pelagic fisheries such as tuna (Sekadende et al., 2020; Painter et al., 2021; Kizenga et al., 2021). The significance of the reefs for the coastal people and ecosystems in this area is magnified given the severe damage from dynamite fishing to reefs on the Tanzania mainland side of the Pemba Channel (Wells, 2009; Slade and Kalangahe, 2015). However, despite their reputation, complexity and importance, the reefs remain poorly studied, with the only quantitative information on coral state and structure and fish populations coming from surveys around the Misali islet (Muhando, 2001; Daniels et al., 2003; Muhando, 2009; Jones et al., 2019).

Given the dependence of communities on reef resources for food and income, and the widespread impact of the coral bleaching event in 2016 on most of the WIO (Gudka et al., 2019), it is likely that the condition of reefs in PECCA is declining. Empirical data on the state of marine ecosystems can be used to understand the effect of threatening activities, and the impact of management interventions, allowing MPA managers to make more informed decisions. Collecting data post-2016, can help confirm the impact of the 2016 bleaching event, and act as an important baseline to track changes over time, such as future recovery (Knowlton and Jackson, 2008). The study used a comprehensive and standardised suite of underwater visual survey methods to gather data to examine the state of the coral reefs along Pemba Island's western coastline in 2019. In addition, we evaluated differences in fish, benthic and coral communities between 2009 and 2019. The information can be used to support PECCA achieve its management goals of sustainable utilization of its fisheries and to restore, preserve and maintain a representative area of coral reef communities (Bodiguel and Breuil, 2015; Wanyonyi et al., 2016; Rehren et al., 2020).

Methods

Study sites

The western fringe of Pemba Island has a complex coastline with numerous islets, deep reef passes leading into shallow bays, and a diverse range of marine habitats (United Nations Environment Programme, 1989; McClanahan et al., 2000; United Nations Environment Programme, 2001). The study was situated along Pemba Island's leeward coral reefs in the Pemba Channel Conservation Area (PECCA), which is a marine conservation area covering the entire western coast of the Island (Fig. 1, Table S1). PECCA (area 825.8km²) was established in 2005, replacing the much smaller Misali Island Conservation Area (MICA (1.4km² non-extraction zone within a 21.6km² conservation area), which had been functional since 1998 (Daniels et al., 2003; Yahya, 2021). As with other MPAs in Tanzania, PECCA allows some human activity within its boundaries (such as small-scale fishing and recreational use), with three designated core-zones closed to fishing and other resource exploitation. It is currently managed by the Department of Marine Conservation of The Ministry of Blue Economy and Fisheries. Ecological data on benthic, coral, and fish communities were collected in 2019 at 12 sites using standardized Underwater Visual Census (UVC) methods on SCUBA (Obura, 2014; Obura et al., 2019; Samoily et al., 2019). Each site was surveyed at two dive stations, approximately 500-1000m apart, with one exception where only one station was surveyed (23 dives in total). Of the 12 sites, 9 were repeat sites from a 2009 survey that used similar methods (Table S1).



Figure 1: Monitoring sites surveyed in 2009 and 2019 on the west coast of Pemba Island using underwater visual census methods

Benthic and coral survey methods

Four benthic and coral surveys were conducted by two observers at each station: benthic cover, adult coral size-class distributions, coral condition, and coral recruit density. The surveys were focused on the reef slope or wall, and were concentrated around a 25m-long transect line (Obura, 2014) placed between 8 - 14m, with two shallow exceptions at 4.7 and 5.3m (Table S1).

Benthic photo quadrats were collected from a height of approximately 0.7 -1 m above the substrate at an interval of between 3-5 fin kicks along both sides of the transect line. Between 30 - 111 photo quadrats (mean= 58) were taken at each station, of which 24 were selected at random and annotated using CoralNet to classify the benthic community composition (Bryant et al., 2017). Hard corals were identified to genus level, and other benthic substrata were classified into broad categories (Table S2). We averaged the proportion of points per benthos per photo across 24 replicates for station-level averages

and 48 replicates for site-level averages. We summed the percent cover of all thermally resistant and sensitive corals (refer to Table S2 for thermal classifications) (Cowburn et al., 2019; McClanahan et al., 2020).

Coral recruits, defined as colonies with the longest diameter of <10cm (Cowburn et al., 2018), were counted in six 1m² quadrats along each transect (except PAR_01=4, MIS_02=5) (Obura and Grimsditch, 2009; Obura, 2014). Recruits were classified into three size classes (0-2.5cm, 2.5-5cm, 5-10cm) and identified to genus level. Mean coral recruit density per m² was calculated by averaging total counts across all quadrats at each site.

Adult corals (longest width >10cm) of 23 pre-determined genera within a 25m by 1m belt were classified into six size-categories based on their longest horizontal width (Obura and Grimsditch, 2009; Cowburn et al., 2018; Cowburn et al., 2019). The 23 genera were selected based on their extensive distribution in the region, as well as their gradient of responses to heat stress and diverse functional traits (Table S2). The condition of each coral was recorded as healthy, partially dead, diseased, predated, pale, partially bleached, bleached, sediment on top, mucus sheath, or other (Obura and Grimsditch, 2009).

To estimate coral biomass, we utilised size-class data and assumed an elliptical shape in the calculation of colony area, with the second diameter being half that of the larger diameter (measured length) (Cowburn et al., 2018). For each genus, we applied the following equation:

$$Colony\ Biomass_{genus} = \sum^{i=N} \frac{1}{8} \times \pi \times x_i \times M_i$$

Where; x is the colony count and M is the median length of the size class (for size class >320 cm, we assume a putative median from 320-640 cm), and N is the number of size classes. i represent a particular size-class

Biomass of thermally resistant and sensitive corals was calculated using the same method as for percent cover data, but only considering the focus 23 genera.

Fish community survey methods

Two fish observer divers estimated fish numbers (density) and sizes in 5cm size classes at each site using five replicate 50 x 5 m transects (5 x 250m²). This followed a standard UVC method adopted by the Global Coral Reef Monitoring Network (GCRMN) (English et al.,

1997; Samoily and Carlos, 2000). We made periodic checks using a calibrated slate to ensure accurate visual estimates. Transects were placed haphazardly perpendicular to the reef edge to span the depth range of the reef to a maximum depth of 18m (mean minimum and maximum depths across all sites were 6.8m and 14.2m, respectively) (Samoily et al., 2019). The lead fish observer swam ahead counting the fish while the second diver followed closely behind laying out the tape measure. We surveyed 11 sites (Fundo Gap was excluded), but two sites had only four replicates due to adverse sea conditions.

We counted all fish species from 11 pre-selected families, namely Acanthuridae, Balistidae, Caesionidae, Chaetodontidae, Haemulidae, Lethrinidae, Lutjanidae, Pomacanthidae, Epinephelidae, Scarinae (Labridae), and Siganidae (Samoily et al., 2019)(Table S3). These families span 12 trophic groups: piscivores, omnivores, corallivores, invertivores, planktivores, detritivores, and six sub-groups of herbivores: large excavators, small excavators, scrapers, browsers, grazers, and grazers-detritivores, as defined by Green and Bellwood (2009).

Fish biomass was derived from fish size for each species using published length-weight relationships (Samoily et al., 2018). The dataset was organised into a matrix of density (individuals/hectare) and biomass (kg/hectare) of species and trophic groups across the 22 stations.

Data Analysis

Spatial and temporal variability and patterns were primarily explored at the site level. Pearson correlations were used to test for collinearity between benthic and coral variables to ensure that variables with an $r > 0.7$ were not included in the same analysis (Vatcheva et al., 2016).

To illustrate benthic community composition among sites and stations in 2019, percent cover of all benthic categories except "Other" (excluded due to cover $< 2\%$ at all sites) was plotted using Non-metric Multidimensional Scaling (nMDS) constrained to 2-dimensions with a stress level < 0.15 and Bray-Curtis dissimilarity index (Shafii et al., 2013; Manikandan et al., 2017). The analysis was done in R using the metaMDS function from the Vegan package (Oksanen et al., 2020). Vectors for benthic and coral variables (recruit density, % of

healthy colonies, resistant coral biomass, and sensitive coral biomass) with $p < 0.05$ (calculated using a permutation test) were overlaid over the benthic station distribution using the `envfit` function (`vegan` package).

Five clusters were produced based on benthic cover using the `hclust` function in R and Bray-Curtis dissimilarity matrix at a similarity level of 0.32. Non-parametric ANOSIM (ANalysis Of Similarities) and SIMPER (Similarity Percentage) analyses were used to determine which cluster pairs were statistically different from one another and which benthos are driving the differences, respectively (Clarke, 1993). To determine differences in coral recruit density between sites in 2019, we used a Kruskal-Wallis non-parametric test with Dunn's post-hoc test (McDonald, 2014; Dinno, 2015).

An ANOVA was carried out to test for significant differences in both density and biomass of fish between sites after natural log-transforming the data due to non-normality of variances (Shapiro-Wilk test, $w = 0.88073$, $p < 0.05$). A posthoc multiple pairwise comparison using Tukey HSD was used to check for pairs of sites that were significantly different.

Spatial patterns in fish density and biomass along the coastline in 2019 were assessed using a Ward cluster analysis based on Euclidean distances. This was undertaken at the station level to increase the replication and power in the analysis. A similarity profile analysis (SIMPROF) was then used to test the significance of the posterior clustered groups using the package `Clustsig` in R (Clarke et al., 2008). In most cases, fish biomass data showed stronger patterns than density; therefore, only biomass results are presented. The proportion of the 12 trophic fish groups in each of the two clusters of sites generated by the Ward analysis was compared. A Wilcoxon test was used to compare differences in biomass between the two clusters of two aggregate fish trophic groups: higher trophic level piscivores-omnivores, typical of target fishery species (Samoilys et al., 2019) and lower trophic level herbivores-detritivores (Obura et al., 2017a). The combined biomass of these two indicators represented over 70% of the total fish biomass, therefore providing a robust representation of the entire fish community.

To assess the correlation between fish community assemblage and four benthic variables (rubble, live hard coral, soft coral, and turf algae), we conducted a random permutation test

with 999 permutations. These benthic variables were chosen as they had significant influences on patterns in the reef benthos (Fig. 2).

Changes in benthic, coral and fish communities between 2009 and 2019

We used an nMDS ordination to visually compare benthic community composition between sites in 2009 and 2019, and ANOSIM and SIMPER analyses to test for statistical differences and the contribution of the variables to these differences, respectively. We also tested differences between the two years using bootstrap resampling, with 100,000 iterations and replacement, as it can handle non-normal data (Carpenter and Bithell, 2000; Rowland et al., 2021). The test statistic was the absolute difference in means between the two years, and the null hypothesis was that there is no difference. We used the `two.boot` function in R to calculate a 95% confidence interval for the bootstrapped statistic (2.5th and 97.5th percentiles) (Rowland et al., 2021). To calculate the p-value from bootstrapping, we randomised the samples across both years (the null being they are from the same sample) and calculated the proportion of iterations where the bootstrapped statistic was greater than or equal to the test statistic we got from our sample. We tested select benthic groups that were significant from the SIMPER analysis using data from (a) all sites from each year (n=12) and (b) just the common (re-surveyed) sites (n=9). Both sets of sites produced the same patterns for all variables tested. We also used the bootstrapping approach to compare mean recruit levels and thermally sensitive and resistant corals for the common sites. Additionally, we used nMDS, ANOSIM, and SIMPER analyses to compare hard coral genera across all sites (n=12) (mean percent cover of hard coral genera). *Porites* cover was not disaggregated by growth form for four sites in 2009, therefore we used the ratio of biomass of each growth form to total *Porites* biomass (from size-class data) at each site to split the *Porites* cover (hard coral cover and total biomass are highly correlated ($r=0.81$)). We used the bootstrapping approach to compare fish community density between 2009 and 2019 (no biomass data available for 2009) and used ANOSIM and SIMPER to test for statistical differences and contribution of various trophic groups to the differences.

Results

State of benthic and fish communities in 2019

Reef state, in terms of live coral cover, other benthic communities and fish abundance, varied considerably across Pemba's west coast in 2019. Benthic communities were statistically different between clusters of sites in 2019 (five distinct clusters at a dissimilarity of 0.32 (Table S1), ANOSIM, $R=0.64$, $p=0.001$). Hard coral, soft coral, turf algae, sand, rubble and solid substrate mainly drove these differences (Fig. 2, Table S4). Sites separated along an axis of soft coral and turf algae (y - NMDS2) and hard coral to sand and rubble (x - NMDS1). Mean site hard coral cover varied between 3.5% and 58.4%, while soft coral cover ranged from 3.2% to 45.3%, turf algae cover from 9.0% to 40.2%, and rubble cover from 0.4% to 13.7% (Fig. 2, right). Misali, Njao Coral Garden and Mandela, had the highest hard coral cover, with coral recruit density and sensitive coral biomass correlating with these sites (Fig. 2, left). The three most northern sites, Scorpion Secret, Paradise, and Shimba grouped with higher rubble, soft coral, and sand, though with large variation among them.

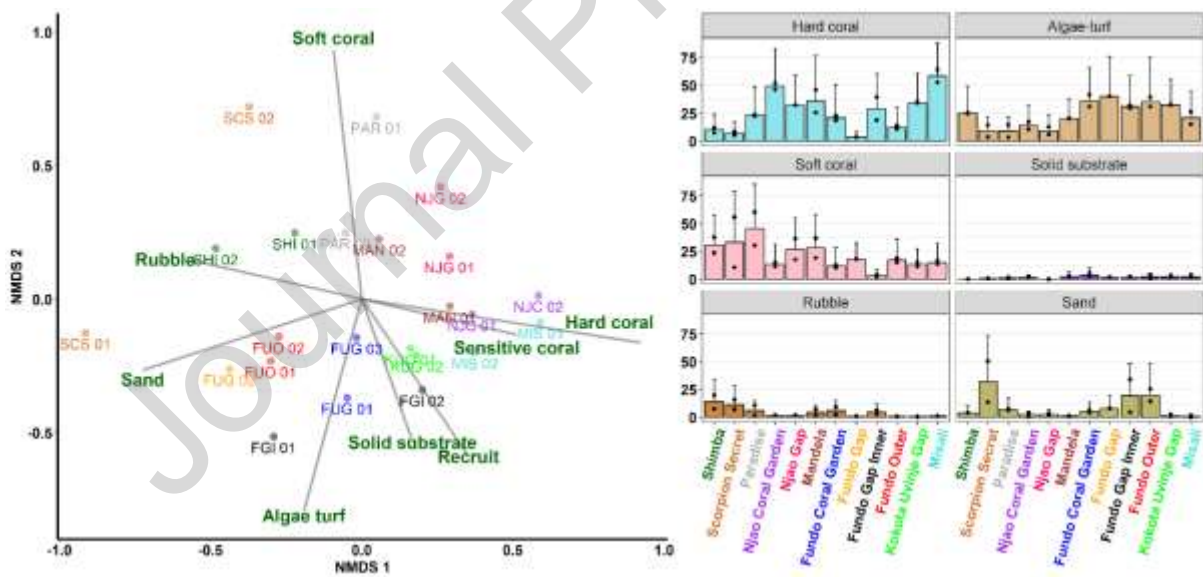


Figure 2: (left) nMDS ordination of stations (colour-coded by site) based on the mean benthic cover (%) in 2019 (stress=0.13) with significant benthic and coral variables overlaid as vector lines (significance levels of $p \leq 0.05$ determined using envfit function in vegan package). Benthic variables included are Hard coral*, Soft coral*, Algae-coralline, Algae-macro/fleshy, Algae-turf*, Algae-Halimeda, Rubble*, Solid-substrate*, Inverts and Sand* (*significant). Coral variables overlaid are recruit density (m^{-2}), and sensitive coral biomass (% of healthy colonies and resistant coral biomass were not statistically significant). (right) Mean % cover of significant benthic variables for each site (bars) and stations (black points) in 2019 (sites arranged from North to South, error bars represent median absolute deviation)

A trend of decreasing hard coral recruit density from south to north was observed in 2019 (Fig. 3, left). The two most southern sites, Misali and Kokota Uvinje Gap, had significantly higher recruitment compared to three of the most northern sites, Scorpion Secret, Paradise and Njao Gap (Fig. 3, left). Mean recruit density ranged from 1.5 recruits per m^2 (Scorpion Secret) to 14.0 recruits per m^2 (Misali).

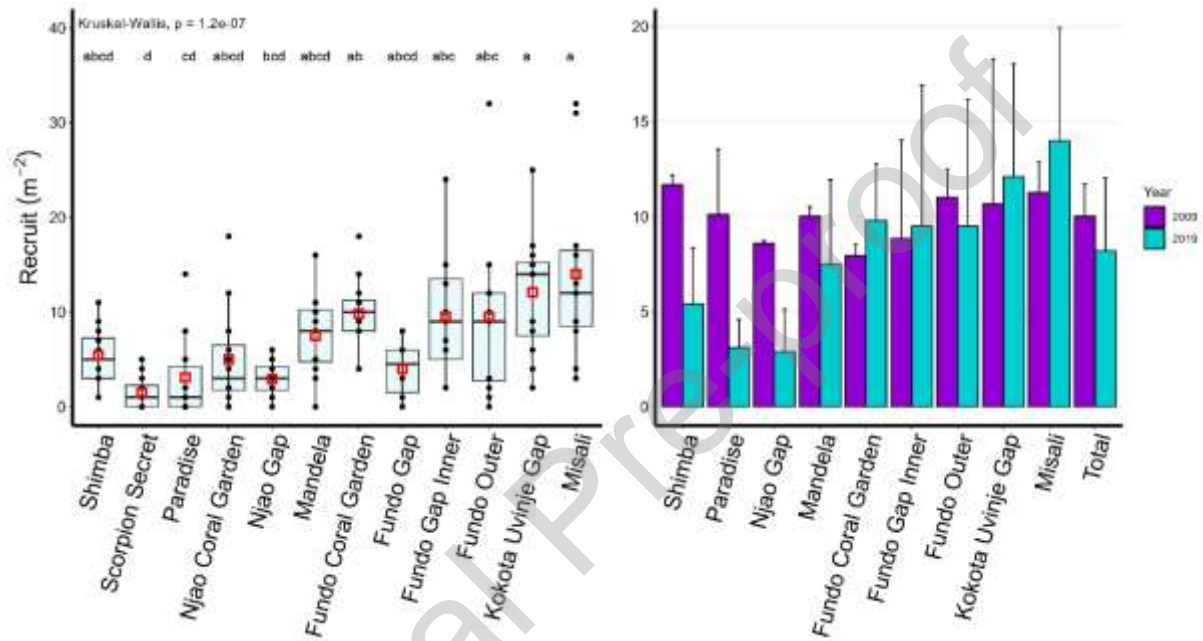


Figure 3: left) Average density of coral recruits $< 5\text{cm}</math> ($m^{-2}</math>) for all sites in 2019 – square red point represents the mean, horizontal bar is the median, black points represent quadrat values and box boundaries represent the quartile range; results of the post-hoc Dunn test is shown by the letter(s) at the top of each box, sites with the same letter are not significantly different; **right)** Average density of coral recruits ($m^{-2}</math>) in 2009 (violet) and 2019 (turquoise) at resurveyed sites ($n=9</math>) - error bars represent median absolute deviation. Sites arranged from north to south.$$$$

There were significant differences in fish density (ANOVA $F = 5.714, p < 0.05</math>) and biomass ($F = 3.295, p = 0.05</math>) between sites in 2019. Using total fish biomass data for each species, stations clustered into two higher-level clusters (Ward cluster analysis, SIMPROF $p < 0.05</math>, Fig. 4), which were significantly different (ANOSIM $R = 0.0937, p = 0.032</math>). Cluster A (red in Fig. 4) consisted of 15 out of the 22 stations with a mean total fish biomass of $215.1 \pm 102.2\text{ kg/ha}</math>, while the remaining seven stations (cluster B) had a mean total biomass of $407 \pm 181\text{ kg/ha}</math>. High intra-site variability was seen in three sites (Fundo Coral Garden, Misali and Njao Coral$$$$$$

Garden), with one station in each cluster. Random permutation tests found no significant relationships between the benthic variables and the fish clusters (Table S8).

The reefs at Fundo Outer recorded the highest fish density while the highest biomass was found at Fundo Coral Garden. Scorpion Secret and Paradise recorded the lowest density and biomass, respectively (Fig. S2). Three pairs of sites were significantly different in total fish biomass i) Paradise and Fundo Coral Garden (ii) Paradise and Fundo Outer (iii) Scorpions Secret and Fundo Outer (Tukey's HSD posthoc pairwise test, Table S7). Moreover, Fundo Outer had significantly higher total density than seven other sites, while Misali had significantly higher biomass than Scorpions Secret but was significantly lower than Njao Coral Garden.

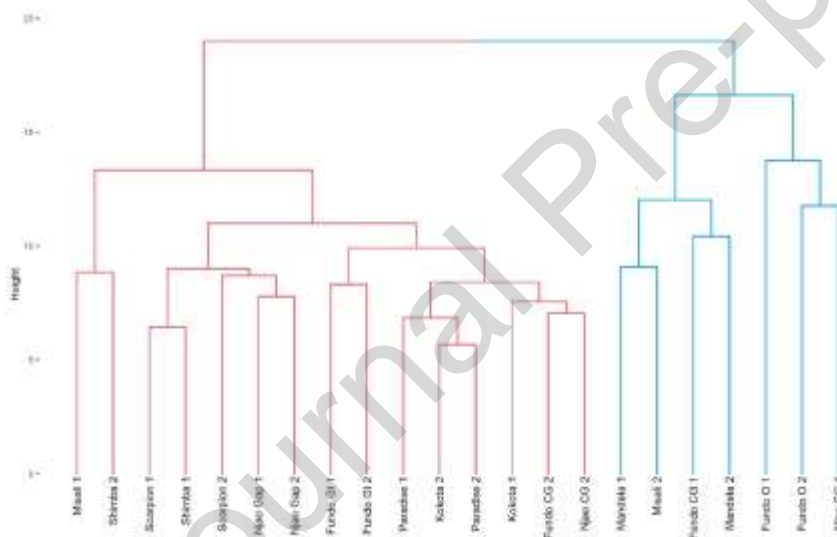


Figure 4. Ward cluster analysis dendrogram showing variation in total fish biomass data (all species) across the 22 stations surveyed in 2019; colours highlight two significantly different clusters

The biomass of the 12 fish trophic groups also differed between the two clusters of stations (Fig. 5a). Sites in cluster B had significantly higher biomass of omnivores, scrapers and small excavators ($p < 0.05$, SIMPER analysis). The biomass of two aggregate indicators, Herbivores-Detritivores and Piscivores-Omnivores, were also both significantly higher in cluster B (Fig. 5b).

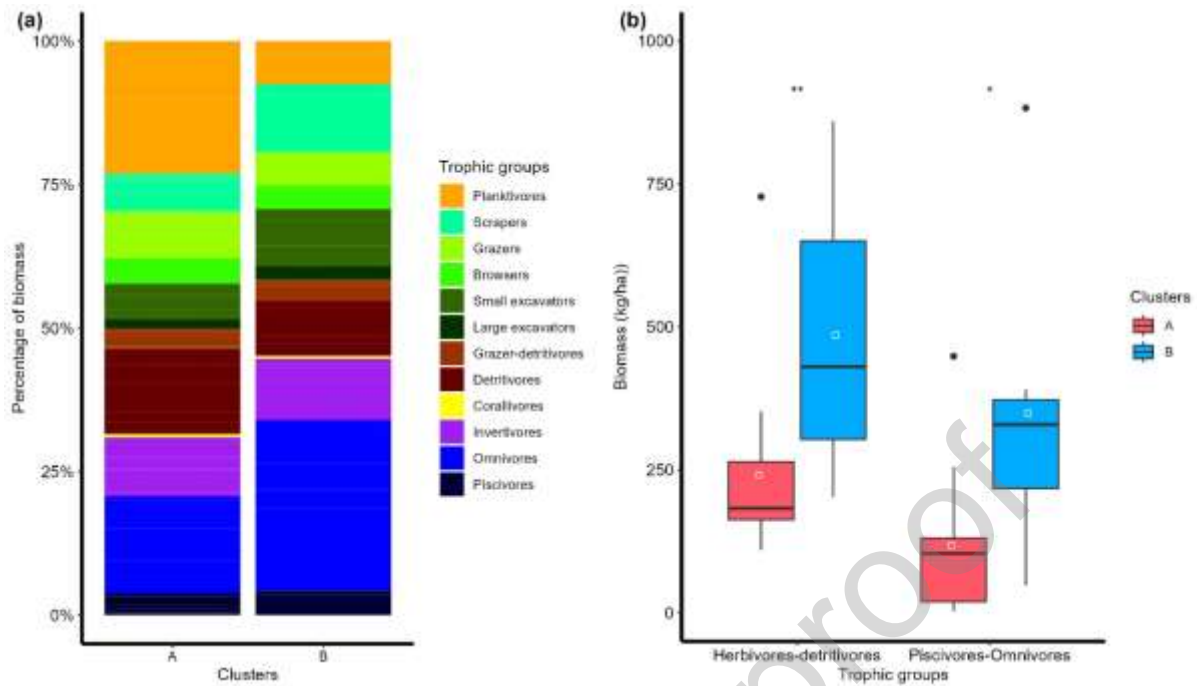


Figure 5: (a) Relative proportion of biomass of 12 fish trophic groups in the two significant clusters (Fig 4): A (high rubble, soft coral) and B (high hard coral, turf); **(b)** biomass of two aggregate trophic groups between the two clusters (Wilcoxon test $p < 0.05^*$ or 0.01^{**}). White, open square represents the mean, horizontal bar is the median, black points represent outliers, upper and lower box boundaries represent the quartile range.

Changes in benthic, coral and fish communities between 2009 and 2019

The benthic community showed significant differences between 2009 and 2019 (ANOSIM, $R=0.33$, $p<0.001$). Soft coral, sand, turf algae, rubble and solid substrate cover were the primary drivers of these differences, accounting for 63% of the overall variance between sites (Table S5). Over the decade, benthic communities have shown a general shift towards higher soft coral and turf algae cover (Fig. 6; bootstrapping results, soft coral: $p=0.0002$, 95% CI for difference in means = 12.0% – 25.1%; turf algae: $p=0.021$, 95% CI = 2.5% – 18.0%). Hard coral contributed the most to the overall variance (21.9%, Table S5), but no significant difference was found between the years (bootstrapping $p=0.49$, 95% CI = -21.1 to 9.3%). This suggests there is considerable variation in the abundance of hard corals between sites within each sampling year, exemplified by the spread of sites along the NMDS 1 axis in Fig. 6, which is parallel to the hard coral vector. Although significant, the differences in rubble (bootstrapping $p=0.017$, 95% CI = -2.5% – -12.9%) and solid substrate cover account for a low contribution to the overall variance (2.3%, Table S5).

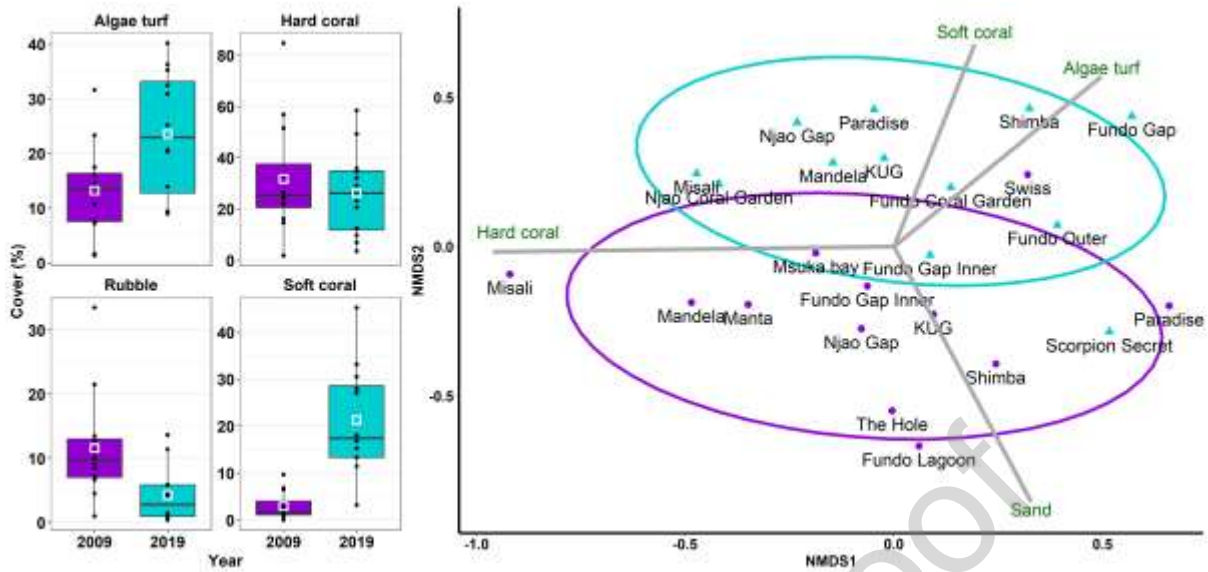


Figure 6: left) percent cover of turf algae, hard coral, rubble and soft coral for all sites surveyed in 2009 and 2019 ($n=12$). White, open square represents the mean, horizontal bar is the median, black points represent site values and upper and lower box boundaries represent the quartile range. **right)** nMDS ordination showing 2009 (violet, circle) and 2019 (turquoise, triangle) sites ($n=12$) ordered by benthic cover (%) with 4 significant benthic variables (vectors). Polygons represent 85% confidence envelopes, and stress=0.172. Significance levels of $p < 0.05$ determined using *envfit* function in *vegan* package. KUG – Kokota Uvinje Gap.

The mean recruit density across all sites in 2009 and 2019 did not differ statistically (8.6 recruits/m² in 2009 and 7.0 recruits/m² in 2019; Bootstrap, $p=0.17$, CI: -0.71 – 4.03).

However, the three northernmost sites (Shimba – Njao Gap) exhibited potentially significant declines in recruitment (Fig. 3, right). Between 2009 and 2019, there were no significant changes in the biomass or cover of thermally sensitive (biomass: $p=0.35$, 95% CI = -0.794 – 2.98 m²/25m²; cover: $p=0.44$, 95% CI = -0.077-0.179%) and resistant (biomass: $p=0.67$, 95% CI = -2.1 – 2.88 m²/25m²; cover: $p=0.30$, 95% CI = -0.107 – 0.033%) corals (the confidence interval represents the difference in means between the years).

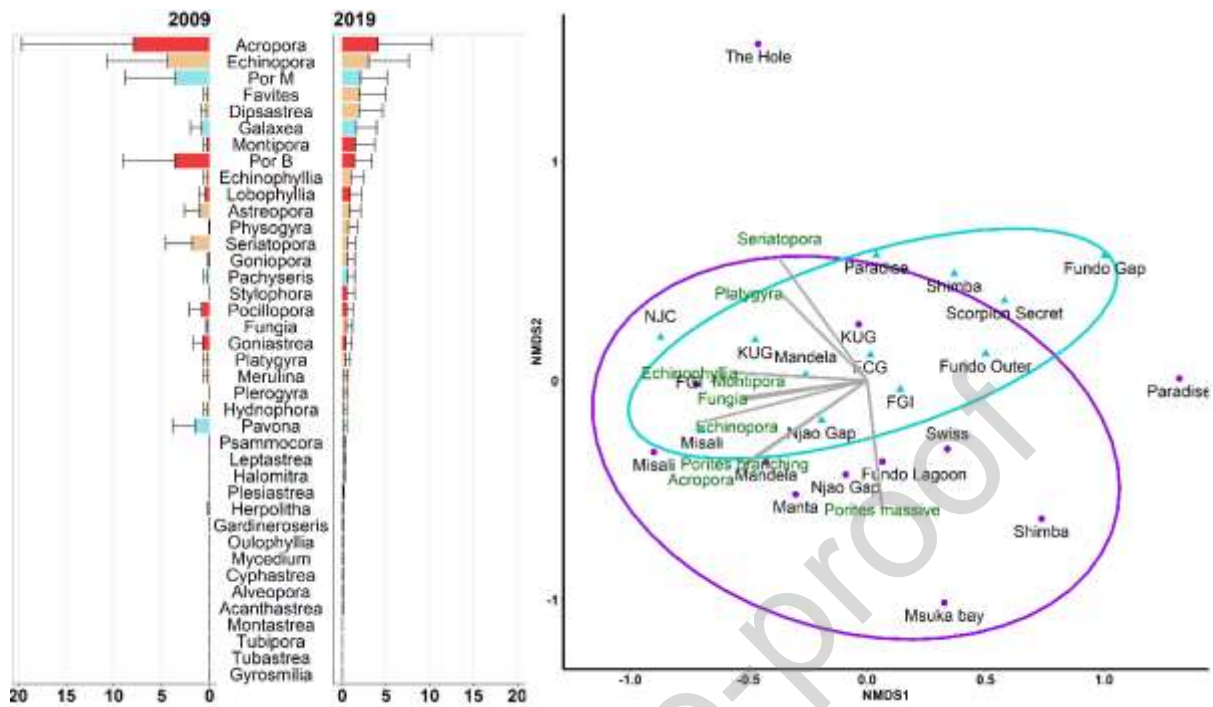


Figure 7: left) Comparison of percent cover of hard coral genera between 2009 and 2019 across all common sites ($n=8$) (colour of bars represents thermal tolerance: red – sensitive, blue – resistant, orange – neutral); **right)** nMDS plot showing 2009 (violet, circle) and 2019 (turquoise, triangles) sites ($n=12$) organised by coral genera cover (vectors show significant genera). Stress=0.178, polygons represent 85% confidence envelopes. Significance levels of $p \leq 0.05$ determined using *envfit* function in *vegan* package.

The coral community composition has changed significantly between 2009 and 2019 (ANOSIM, $R=0.136$, $p=0.02$). Four coral genera showed statistically significant differences (Table S6), with *Porites* branching declining in cover (Fig. 7, left), and *Dipsastrea*, *Favites*, and *Stylophora* increasing. The narrowing of the 2019 ellipse in Figure 7 (right) indicates a less diverse community in 2019 compared to 2009, with 2019 sites primarily varying in levels of *Echinopora*, *Porites* branching, and *Acropora* (*Acropora* remains the most abundant genus) (Fig. 7, right). In 2009, sites were distributed along an axis of *Seriatopora* and *Porites* massive, with The Hole having more than double the *Seriatopora* cover of any other site, explaining its isolated position.

The total fish density in 2019 had significantly declined compared to 2009 (ANOSIM: $R = 0.8363$, $p < 0.05$). The 95% confidence interval for differences in mean density from bootstrapping was between 1545.4 and 3742.7 individuals per hectare. Significant differences were found for four of the re-surveyed sites (Fig. 8). The decrease in density was

primarily driven by five trophic groups: piscivores, browsers, scrapers, grazers and corallivores (Fig. S3, Table S9).

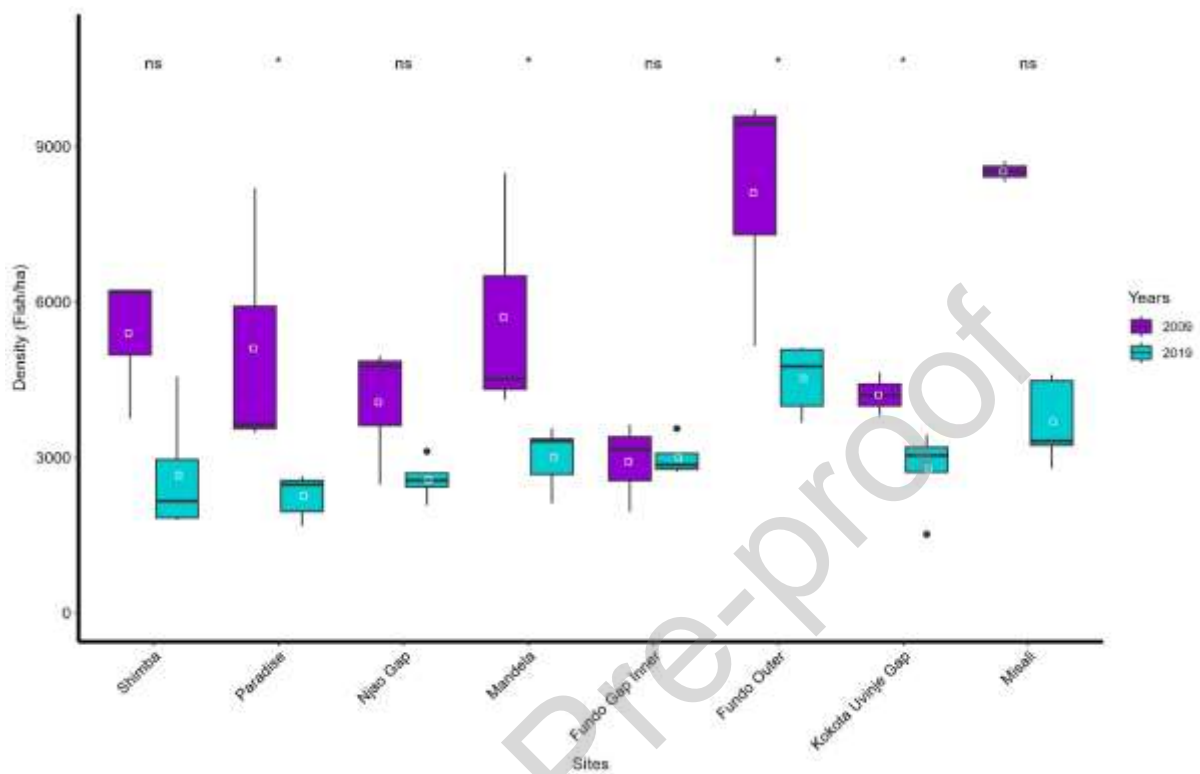


Figure 8: Median total fish density (ind/ha) (from five replicate transects) for sites surveyed in both 2009 and 2019. White, open square represents the mean, horizontal bar is the median, black points represent outliers, upper and lower box boundaries represent the quartile range, and whiskers represent the minimum and maximum values within 1.5x the interquartile range. Significance level of post-hoc Tukey HSD pairwise tests indicated by *, ns=not significant.

Discussion

The coral reefs off the west coast of Pemba Island were in a relatively poor state in 2019. The average hard coral cover was 26%, with only two sites recording a hard coral cover of over 40%, and four sites having less than 15% coral cover. These levels are similar to those observed in 2017 at Unguja Island, Zanzibar, and in 2016 at Moheli, Comoros (Gudka et al., 2018; Cowburn et al., 2018). However, they are lower compared to other areas in Tanzania, such as Tanga, Mafia Island, and Songosongo, and significantly lower than estimates of 40-50% coral cover on healthy Tanzanian reefs prior to the 1998 bleaching (Gudka et al., 2023). The highest total fish biomass recorded at a site was ~ 500 kg/ha, which is approximately half the fish biomass levels reported from forereefs elsewhere in the western Indian Ocean (Samoilys et al., 2019). Further, several sites had total biomass values of <250 kg/ha. These

results suggest that Pemba's forereefs have suffered severe coral mortality in some locations and have been inadequately protected from heavy fishing pressure.

There was a notable difference in the state of the reefs from north to south. The northern reefs were highly degraded, dominated by rubble, soft coral and sand. Additionally, the lowest fish biomass was measured at two sites in the north. These rubble-dominated reefs are likely having a negative impact on fish species that require complex reef structures for survival (Bellwood et al., 2004; McCauley et al., 2012; Frisch et al., 2014), and the absence of live coral is likely causing declines in obligate corallivores (Munday et al., 2008). As a result, these northern reefs are unlikely to provide much potential for the recovery of a healthy fish community, though they may still benefit predatory pelagic fish (Morais and Bellwood, 2019; Osuka et al., 2022). In contrast, the south had healthier coral communities, with moderate to high hard coral cover and high coral recruitment levels. This corresponded to healthier fish communities in the south, particularly omnivores (largely snapper) and scrapers and small excavators (both parrotfish), indicating that an intact and live reef structure is an important habitat for these trophic groups. Interestingly, two sites with low coral covers of 12% and 21%, had the highest fish biomass. This variability suggests factors operating at localised spatial scales, such as management and fishing pressure (Jones et al., 2019; Rehren et al., 2020), and currents, depth, and upwelling (Jebri et al., 2020; Painter et al., 2021; Osuka et al., 2022), may be driving these patterns.

Coral recruitment and survival play a crucial role in determining the recovery potential of reefs (Shlesinger and Loya, 2016; Manikandan et al., 2017; Harvey et al., 2018). Sufficient recruitment is needed to maintain coral levels during normal mortality regimes, and it is becoming increasingly important to repopulate communities following mass mortality events (Maynard et al., 2010; Mumby et al., 2014; Chung et al., 2019). Between 2009 and 2019, coral recruitment levels have remained remarkably high, with an average of 7 recruits/m² in 2019. This is similar or exceeds the levels required to increase coral coverage found in French Polynesia, Palau, the Great Barrier Reef and Seychelles (Connell et al., 1997; Graham et al., 2015; Adjeroud et al., 2018; Gouezo et al., 2020). Misali averaged 14 recruits/m², suggesting a high recovery potential. Therefore, local management can play a crucial role in maintaining the site by enforcing measures to avoid direct physical damage to corals, such as strict anchoring prohibition and regulations around purse-seine fishing. The local

purse seines (“ring-nets”) use sacks filled with sand which are dropped onto the reef and then the sacks emptied in situ when the net is removed. Despite the high coral recruitment in the south, there seems to be a trend of decreasing coral recruit density from south to north, consistent with the northernmost sites being more degraded and having loose substrate. Tanzania has a history of widespread dynamite fishing reducing thriving corals to rubble, notably across the Pemba Channel in Tanga (Wells, 2009; Slade and Kalangahe, 2015). This practice was reported as ongoing in 2015 on the northwest coast of Pemba (Braulik et al., 2015), and in other areas of Tanzania as recently as 2018-2019 (Braulik et al., 2020). This would explain the extensive rubble found at sites in the north.

Our surveys provide a decade-long assessment of the trajectory of Pemba's coral reefs, including their response to the global bleaching event in 2016 (Hughes et al., 2018; Eakin et al., 2019). On average, hard coral cover has remained stable over the past 10 years. The overall thermal sensitivity of the coral community has also remained relatively stable, with only branching *Porites* experiencing a significant decline. *Acropora* remains the most common genus, even though over 80% of *Acropora* corals perished at Misali during the 2016 bleaching event (Ussi et al., 2019). Massive *Porites* is the second most abundant genus, creating a good balance of competitive and resistant species that can maintain a robust reef framework (Darling et al., 2013; Darling et al., 2019). Turf algae has increased, but this could be due to colonising what was classified as rubble in 2009, or because of declines in herbivorous fish. This colonisation by turf algae rather than substrate-cementing crustose coralline algae is not ideal, as solidifying the reef framework would have longer-term benefits for coral settlement and recovery (O’Leary et al., 2012). Macro-algae is generally considered to be the main competitor for space for hard corals in the WIO. When established, it can be difficult to outcompete (Jompa and McCook, 2003; Obura et al., 2021), particularly when herbivorous fish that graze on macro-algae are heavily overfished (Clements et al., 2016; Bellwood et al., 2019). Critically, we found that macro-algae cover levels remain low, with levels below 10% across all sites (Fig. S4). This, along with the stable hard coral cover, suggests that Pemba’s reefs are not yet moving towards a phase-shift. To maintain this balance, it is crucial to maximize top-down control of algae by protecting specific grazer parrotfish (*Calotomus* spp., *Leptoscarus* spp.), macro-algal browsers such as rabbitfish (*Siganus* spp.), and surgeonfish (*Zebbrasoma* spp. and small *Acanthurus* species)

(Bellwood et al., 2019; Samoilys et al., 2019). However, substantial declines in fish density were observed between 2009 and 2019 in half the re-surveyed sites (Fundo Outer, Kokota, Mandela, and Paradise). Herbivorous browsers, scrapers and grazers declined by 95%, 84% and 69%, respectively, while piscivores and corallivores declined by 96% and 75%, respectively. These taxa are commonly caught in local fisheries (Rehren et al., 2020), with the exception of the corallivores which are likely responding to any loss of live coral (Munday et al., 2008).

It is apparent overfishing remains a major threat to Pemba's coral reefs, indicating that the management approaches to achieve sustainable utilisation of fisheries have not been effective. Compliance to regulations, has proven challenging due to limited resources hindering enforcement (e.g. funding and staff) and a heavy reliance of communities on natural resources with inadequate livelihood alternatives (Jones et al., 2019). This is further supported by the lack of shark sightings during dives and Baited Remote Underwater Video surveys (only 1 individual recorded) (Osuka et al., 2022). In addition there was frequent presence of small purse-seine ("ring-net") fishing boats which are highly destructive when used near coral reefs (Thoya et al., 2020). Understanding feasible opportunities to improve management and attain more sustainable fishing levels is crucial, particularly considering the socio-economic reliance on fishing by coastal communities (Rehren et al., 2020).

Given the patterns in reef state and the favourable warming projections for East Africa (Beyer et al., 2018), effective local management can have a significant impact on ecosystem resilience (Steneck et al., 2019; Abelson, 2020; Obura et al., 2021). Pemba Island's unique features, such as its steep drop-offs, upwelling from deep channel water (Semba et al., 2019; Osuka et al., 2021; Painter et al., 2021), and unique gaps between reefs, offer potential refuges for corals from future warming, and ideal habitats for endangered species such as groupers and sharks. The gaps may also be important sites for fish spawning aggregations (Colin, 2012). The implementation of strategic no-take zones that are co-managed with communities and resorts are an ideal approach to protect both coral habitat and fish populations (Kawaka et al., 2017; Estradivari et al., 2022).

This study has filled critical knowledge gaps to support local management of a regionally significant coral reef system. Although the condition of Pemba's west coast reefs has declined over the last 10 years, there is still potential for recovery in the south due to high

coral recruitment levels. However, the northern reefs are severely degraded and will require artificial interventions to facilitate recovery, such as coral restoration or substrate stabilisation, along with control of destructive fishing practices such as ring-netting and dynamite fishing. A review and implementation of management strategies within PECCA, with a strong focus on patrolling and enforcement of fishing regulations is recommended. PECCA boasts diverse and potentially resilient marine ecosystems, upon which communities are heavily dependent. As such, it should attract investment to improve the management and conservation of these natural resources to enhance the societal, economic, and ecological benefits derived from them.

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Author contributions

Author	CRedit roles
Gudka Mishal	Conceptualization; Data curation; Formal analysis; Methodology; Project administration; Investigation; Writing - original draft
Samoiyls Melita	Conceptualization; Funding acquisition; Methodology; Project administration; Investigation; Writing - original draft

Musembi Peter	Data curation; Formal analysis; Investigation; Writing - review & editing.
Aboud Swaleh A.	Data curation; Formal analysis; Writing - original draft
Grimsditch Gabriel	Data curation; Project administration; Investigation; Writing - review & editing
Mabwa Randall	Data curation; Investigation; Writing - review & editing
Yahya Saleh	Project administration; Writing - review & editing
Osuka Kennedy	Formal analysis; Writing - review & editing

Highlights

- Evidence is required to support management of Marine Protected Areas
- Fish populations at reefs in Pemba Channel Conservation Area are low compared to elsewhere in the Western Indian Ocean
- Coral reef condition has declined between 2009 and 2019,
- Pemba's unique and complex reef structure offers a potential refuge for corals from future warming and habitat for endangered fishes