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Post-bleaching alterations in coral reef communities

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ABSTRACT

We explored the extent of post-bleaching impacts, caused by the 2014–2016 El Niño Southern Oscillation (ENSO) event, on benthic community structure (BCS) and herbivores (fish and sea urchins) on seven fringing reefs, with differing protection levels, in Zanzibar, Tanzania. Results showed post-bleaching alterations in BCS, with up to 68 % coral mortality and up to 48 % increase in turf algae cover in all reef sites. Herbivorous fish biomass increased after bleaching and was correlated with turf algae increase in some reefs, while the opposite was found for sea urchin densities, with significant declines and complete absence. The severity of the impact varied across individual reefs, with larger impact on the protected reefs, compared to the unprotected reefs. Our study provides a highly relevant reference point to guide future research and contributes to our understanding of post-bleaching impacts, trends, and evaluation of coral reef health and resilience in the region.

1. Introduction

The world's tropical coral reefs are undergoing a crisis due to pressure from direct (e.g., pollution, overfishing) and indirect (e.g., cyclones, ocean acidification and climate change) human impacts (Jackson et al., 2001; Hoegh-Guldberg et al., 2007; Cheal et al., 2017; Hughes et al., 2017a; Zhao et al., 2021). As coral reefs provide ecosystem goods and services to millions of people living in tropical coastal areas (Moberg and Folke, 1999; Woodhead et al., 2019), the accelerating loss of corals and associated degradation of reef systems caused by climate change and ocean warming is a cause for global concern (Hoegh-Guldberg, 1999; Heron et al., 2016; Lough et al., 2018).

Of particular worry are recurrent and amplified El Niño Southern Oscillation (ENSO) episodes associated with elevated sea surface temperature (SST), which can induce mass coral bleaching events (Glynn, 1984; Wilkinson et al., 1999; Spencer et al., 2000; Hughes et al., 2018). If elevated SST persists over a period of weeks, bleaching events can be followed by mass coral mortality (Glynn and D'Croz, 1990). This results in substantial decline in coral cover and structural complexity, causing alterations in benthic community structure (Pisapia et al., 2019; Magel

et al., 2019), and associated reef fish composition (Lindahl et al., 2001; Graham et al., 2006; Pratchett et al., 2018). Moreover, increasing intensity and frequency of periodic marine heatwaves (Cai et al., 2014; Oliver et al., 2018), and in turn, shortened intervals for recovery between recurrent mass coral bleaching events (Hughes et al., 2017b), may erode reef resilience – that is, the ability of a reef community to maintain its processes, structure, and function after disturbance, without shifting from a coral-dominated state to another ecological state (e.g., macroalgae-dominated) (Nyström et al., 2000; Nyström and Folke, 2001; Norström et al., 2009).

Herbivory (e.g., by fish and sea urchins) is a key process that underpins resilience in coral reefs by keeping algal growth and recruitment in check, and by providing open space for coral recruits, which allow for reefs to remain in a coral-dominated state (Bellwood et al., 2004; Graham et al., 2013; Dajka et al., 2019; Nozawa et al., 2020). Capturing information on such processes and on how they influence reef community response to mass coral bleaching episodes is therefore important to elucidate the dynamics and interactions between altered benthic communities and key ecosystem functions. Such information will enable us to evaluate influences of future pulse perturbations to predict the health

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and resilience of coral reef ecosystems and may aid management and conservation decision-making to counteract reef degradation.

The global-scale coral bleaching event (GCBE) induced by the 2014–2016 ENSO has led to unprecedented coral mortality across regions throughout the tropical belt (Eakin et al., 2019 and references therein). During this period, the Western Indian Ocean (WIO) experienced its largest coral bleaching since the first global event was reported in 1998 (Obura et al., 2017; Gudka et al., 2018).

Of the sites investigated in the WIO region, 37 % experienced high or extreme bleaching, causing an average coral mortality of 60 %. The Seychelles suffered the most, with up to 90 % of the reefs affected by high or extreme bleaching, which was followed by Tanzania with up to 56 % of the reefs severely affected (Wilson et al., 2019; Gudka et al., 2020). While some regional-scale bleaching studies are existent for the Western Indian Ocean region (Gudka et al., 2018; Gudka et al., 2020; Cerutti et al., 2020), few studies have documented post-bleaching alterations and impacts of the 2014–2016 GCBE on individual local reef communities and beyond coral mortality.

Here, we explored the impacts of the 2014–2016 ENSO event and associated bleaching on coral reefs in Zanzibar, Tanzania. More specifically, our main objectives were to: (1) investigate post-bleaching alterations in reef benthic assemblages, and (2) assess changes in the herbivore community structure. Findings are used to identify potential phase shifts and to discuss reef recovery in the context of reef resilience.

2. Materials and methods

2.1. Study site

Zanzibar is an archipelago consisting of two main islands (Unguja and Pemba) and numerous smaller islands, located 25–50 km off the Tanzanian coast in the Indian Ocean. Unguja Island is surrounded by islets and sand banks with fringing reefs configured around these. Field surveys for sea urchin densities were carried out in September–October 2013 and 2016 on seven fringing reefs across the west coast of Unguja Island (Fig. 1). Benthic community structure (BCS) was surveyed over the same period (September–October) for both years. Fish counts were performed from July–October in 2013 and 2016.

2.2. Bleaching impacts

During the 2014–2016 ENSO event, Tanzania experienced up to 5 weeks of peaked SST anomalies in March and April 2016 (Fig. 2). Coral reefs around Zanzibar suffered severe coral bleaching, which resulted in significant coral mortality (Obura et al., 2017; Staehr et al., 2018). The three years prior to the 2014–2016 ENSO event, including the date of the first field surveys (September 2013), did not show any major indications of SST anomalies above the local bleaching threshold (Fig. 2).

2.3. Levels of protection

Seven reef sites were investigated each of which had different levels of protection. During the 2013 survey, Changuu, Bawe, Pange, and Nyange reefs were unprotected with no restrictions relating to fisheries and tourism. In 2014, these reefs were declared protected under the Changuu-Bawe Marine Conservation Area (CHABAMCA). At the time of the 2016 survey, the protected status was hence new with low management effectiveness, and we assume that the initiated protection level did not influence the results. Therefore, these reefs are referred to as unprotected in this study. Chumbe Island Coral Park (CHICOP) is a privately managed no-take Marine Protected Area (MPA) established in the early 1990s and is considered to be one of the most well-protected coral islands in the region (Chumbe Island Coral Park (CHICOP), 2017). Tele and Kwale reefs are located to the south. All three lie within the Menai Bay Conservation Area (MBCA), which was established in 1997 (Tobey and Torell, 2006) and expanded in 2014, however, CHICOP continues to be managed separately and privately.

2.4. Benthic surveys

Field surveys were carried out by the same surveyor (E. Elma) during daytime (between 09:00 and 16:00) at a depth range of 3–6 m using SCUBA and Underwater Visual Census (UVC). Benthic community structure was surveyed using the line-intercept method (English et al., 1997), with 50 m long transects ($n = 10$) set randomly and parallel to the reef crest on each reef site across the entire reef. The benthic assemblage was classified into 10 substrate categories (after Lokrantz et al., 2010):

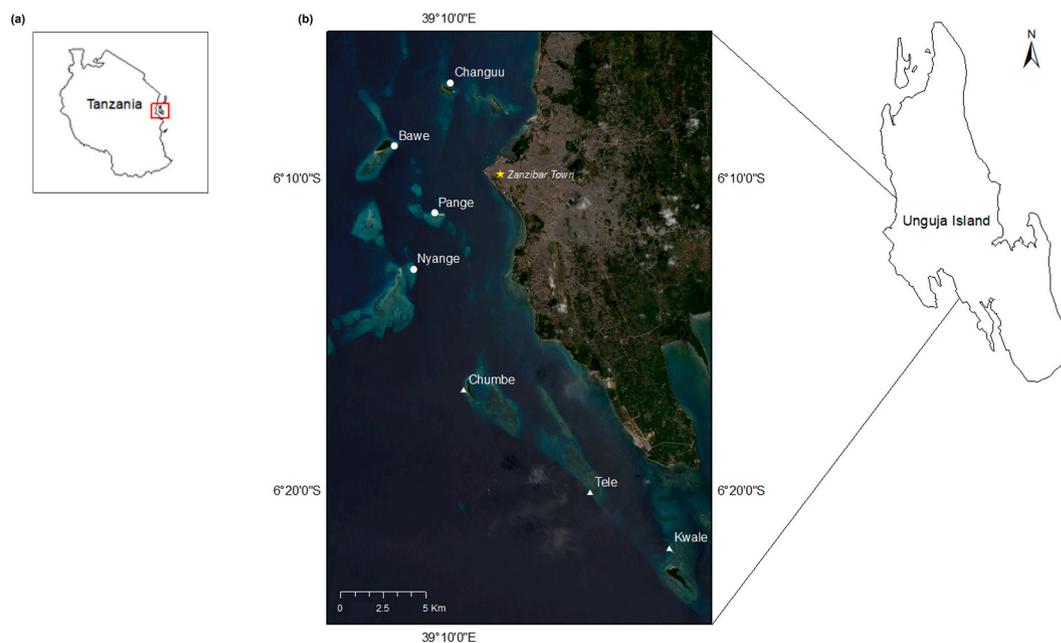


Fig. 1. (a) Map of Tanzania showing the location of Unguja Island off the Tanzanian coast (red square) (b) Unguja Island showing the seven reef sites investigated in this study. Levels of protection are indicated by circles (unprotected) and triangles (protected). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

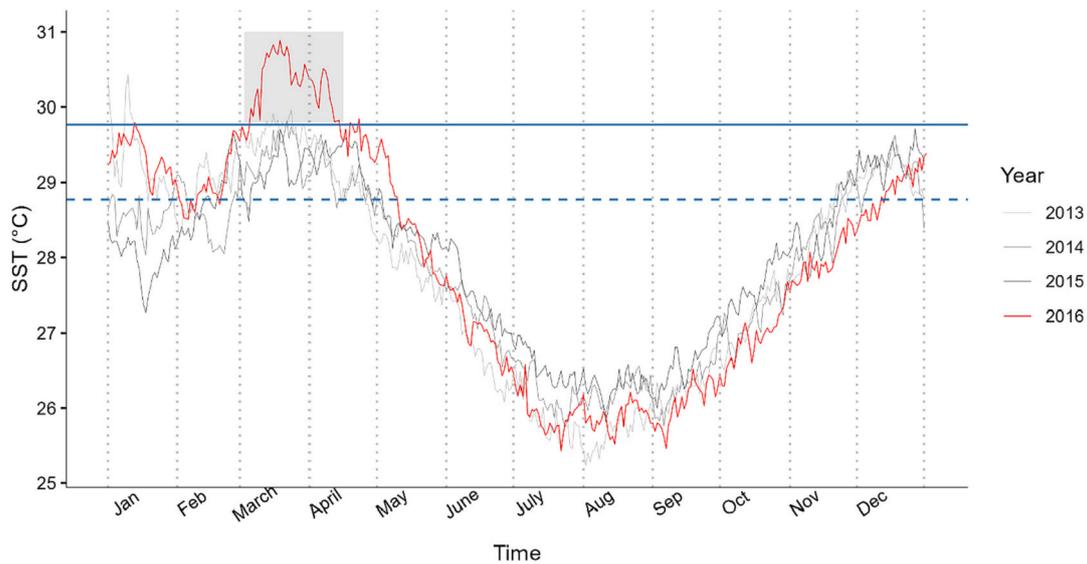


Fig. 2. Daily SST ($^{\circ}\text{C}$) from January to December for multiple years (2013, 2014, 2015 and 2016) for Tanzania. The dashed blue line indicates maximum monthly mean SST, and the solid blue line indicates the bleaching threshold for the Western Indian Ocean region. The grey shadowed area marks the peak SST above the local coral bleaching threshold. Source of data: NOAA Coral Reef Watch (2019). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

live coral, dead coral, turf algae, macroalgae, coralline algae, corallimorpharia, soft coral, sediment (i.e., sediment covering substratum), sand (i.e., patches of bottom sediment in the intercept), and others (including ascidians and sponges). Along each transect, these substrate categories were recorded to the nearest centimetre and percentage cover of each category was then calculated and averaged for each site.

2.5. Herbivore surveys

Species richness, abundance, and total length of herbivorous fish within the families Acanthuridae, Scaridae, Ephippidae, Kyphosidae, and Siganidae were recorded to the nearest 5 cm (Green and Bellwood, 2009). Belt transects of 50×5 m (English et al., 1997) were applied for the reefs located further north, including Changuu, Bawe, Pange, Nyange and Chumbe, while a Stationary Visual Census method (SVC) of 5 m radius (Bohnsack and Bannerot, 1986) was employed for the reefs at Tele and Kwale, located further south. For each site, ten replicates ($n = 10$ transects or SVCs, respectively) were randomly set on the reef flat across the entire reef. Tele and Kwale reefs were added to the survey retrospectively (i.e., after the bleaching had occurred). Existing 2013 surveys conducted at these reefs used the SVC method, hence, we also employed this method in 2016 in order to allow pre/post bleaching comparisons. While this allows pre/post comparisons for each reef, the disparity of methods restricts comparisons between Tele and Kwale and the other survey sites. Fish biomass for each species was estimated using length-weight relationship equations obtained from the literature (Electronic Supplementary Material, Table 1). Sea urchins were surveyed randomly on each reef for abundance and species richness using 10 m^2 plots ($n = 20$) (Lokrantz et al., 2010).

2.6. Data analysis

2.6.1. Multivariate analysis

Principal Component Analysis (PCA) was used to investigate temporal changes in benthic community composition (pre/post bleaching). The analysis was based on the percentage cover of each substratum type on transects in each reef site ($n = 10$) using a correlation matrix

computed on scaled and centred data. Where a substrate category was absent (i.e., macroalgae in Bawe and Nyange, and sediment in Kwale), it was removed from the analysis.

Non-metric multidimensional scaling (nMDS) analysis based on a Bray-Curtis similarity matrix of square-root-transformed fish biomass data was performed to visualize temporal dissimilarities in herbivorous fish community composition. To assess the relationships between fish communities and benthic substrate variables, nMDS ordination plots were fitted with vectors using the 'Envfit' function from the *Vegan* R package (Oksanen et al., 2017). A one-way analysis of similarity (ANOSIM) was applied to the Bray-Curtis dissimilarity matrices to test significant differences in benthic community composition (PCA) and herbivorous fish assemblage composition (nMDS) between years (Clarke and Green, 1988; Clarke, 1993). A similarity percentage (SIMPER) analysis was conducted to determine the contribution of each habitat substrate category to the observed temporal dissimilarities (Clarke, 1993).

2.6.2. Univariate analysis

Two-way repeated measures analysis of variance (ANOVA) tests were run to determine the effects of year (pre/post bleaching) and reef site on different variables, including, live coral, turf algae, fish biomass and sea urchin densities. Two separate analyses were run for fish surveys to consider the different sampling methods across reefs. Mauchly's Test was used to test for sphericity and where data did not meet the requirement of sphericity, the Greenhouse-Geisser correction was used (Greenhouse and Geisser, 1959). To compare between years for each site and among reef sites within each year, significant test results were followed by a post-hoc multiple pairwise comparison using a Bonferroni corrected paired *t*-test. Prior to analysis, all data were checked for homogeneity of variances and normal distribution. To meet assumptions, fish biomass data were $\log(\chi + 1)$ transformed and sea urchin abundance data were square root transformed. Post-bleaching events are often marked by rapid colonization of turf algae on dead coral (Adjeroud et al., 2009). We used a Pearson's product-moment correlation to examine the relationship between live coral and turf algae in the region to investigate ENSO induced impacts. All analyses were performed using

the statistical software R version 4.0.5.

3. Results

3.1. Benthic community structure

All PCAs showed a distinct separation of benthic assemblages between data collected in 2013 and 2016 (Fig. 3). The first 2 axes in the PCAs explained a total temporal variation in benthic assemblage composition ranging from 40 % to 62 % across reef sites. Live coral and turf algae vector arrows are consistently pulling in opposite directions (Fig. 3). ANOSIM analysis showed significant differences in benthic community composition among years for All Sites (ANOSIM_{2013–2016}; $R = 0.47$, $p = 0.01$) and for each reef site, with greatest dissimilarities found in Chumbe and Kwale (ANOSIM_{2013–2016}; $R = 0.99$, $p = 0.001$, for both reefs), and least dissimilarity in Nyange (ANOSIM_{2013–2016}; $R = 0.22$, $p = 0.003$). All other reefs showed strong significant difference in dissimilarities between years (ANOSIM_{2013–2016}; $R =$ between 0.4 and 0.7, $p < 0.01$). The benthic substratum categories that contributed most to the observed differences in benthic community composition between years were live coral (all individual reefs, All Sites), dead coral (all individual reefs), turf algae (Changuu, Nyange, Chumbe, Tele, Kwale, All Sites), macroalgae (Changuu), sand (Pange, Nyange, Tele, Kwale, All Sites), and coralline algae (Nyange) (Table 1).

A significant negative relationship was found between live coral and turf algae (Pearson's correlation coefficient; $r = -0.64$, $p < 0.001$) (Fig. 4), with significant differences in mean cover observed for both variables between years (ANOVA, $F(1,9)_{\text{live coral}} = 580.2$, $p < 0.001$; $F(1,9)_{\text{turf algae}} = 379.1$, $p < 0.001$), and among reef sites (ANOVA, $F(6,54)_{\text{live coral}} = 11.0$, $p < 0.001$; $F(6,54)_{\text{turf algae}} = 43.1$, $p < 0.001$) (Fig. 5).

Live coral was found to be the dominant benthic substratum in All Sites before the bleaching event (57.6 ± 4.1 %). Nyange reef exhibited the lowest mean percent cover (38.0 ± 3.5 %), while all other reefs showed a mean live coral cover of >50 %, with Chumbe reef having the highest mean cover (86.0 ± 2.0 %), which was significantly higher than all other reefs (all Paired t -tests: $p < 0.05$). Pre-bleaching turf algae observations showed low cover (< 4 %) in all individual reefs, except in Kwale reef which had a significantly higher mean cover (12.6 ± 1.8 %) than the other reefs (all Paired t -tests: $p \leq 0.01$) (Fig. 5).

Post-bleaching surveys revealed up to 68 % decline in live coral cover and up to 48 % increase in turf algae cover across the surveyed reefs with a regional average (All Sites) of 37 % and 21 %, respectively (Fig. 6). These findings were supported by Paired t -test comparisons between years, which indicated significant decline in mean live coral with < 28 % cover remaining (all Paired t -tests: $p \leq 0.05$), and a concurrent significant increase in mean turf algae ranging between 6 and 61 % cover (all Paired t -tests: $p \leq 0.001$) across all reefs (Fig. 5). The largest loss in live coral was found on the protected reefs, including Chumbe (-68 %; Paired t -test, $t_9 = 26.08$, $p < 0.001$), Kwale (-48 %; Paired t -test, $t_9 = 11.20$, $p < 0.001$) and Tele reef (-42 %; Paired t -test, $t_9 = 11.20$, $p < 0.001$). Both Chumbe and Kwale reef also exhibited the largest increase in turf algae cover (41 %, Paired t -test, $t_9 = -8.63$, $p < 0.001$; 48 %, Paired t -test, $t_9 = -12.97$, $p < 0.001$) (Figs. 5 and 6).

Other benthic categories that showed a notable increase in cover after the bleaching event included dead coral (Bawe 16 %, Chumbe 17 %, and Tele 13 %), sand (Pange 27 %, Nyange 8 %, and Tele 11 %) and macroalgae (Changuu 12 %). Benthic categories such as soft coral, corallimorpharia, sponges and ascidians showed low cover change in all reef sites (Fig. 6).

3.2. Herbivores

A total of 5049 individual herbivorous fish counts, representing 34 species were recorded during the surveys (Electronic Supplementary Material, Table 1). Comparison of herbivorous fish assemblages, pre/

post bleaching for all sites combined showed weak dissimilarity. At individual reef level, strong significant temporal dissimilarities in herbivorous fish assemblages were found on the reefs of Kwale and Chumbe, followed by significant dissimilarities for Bawe, Nyange and Tele reefs. No significant dissimilarities in fish assemblages were found for Changuu and Pange reef between the two investigated years (Fig. 7). In the reefs of Kwale and Chumbe, fish biomass assemblage correlated well with live coral (Envfit, $r^2_{\text{Chumbe}} = 0.68$, $p = 0.001$; $r^2_{\text{Kwale}} = 0.76$, $p = 0.001$) and turf algae (Envfit, $r^2_{\text{Chumbe}} = 0.44$, $p = 0.007$; $r^2_{\text{Kwale}} = 0.82$, $p = 0.001$), with the vectors pulling in the opposite directions. Among the other benthic substrate variables, dead coral cover had a significant positive correlation with fish biomass assemblages in the reefs of Pange (Envfit, $r^2 = 0.62$, $p = 0.002$) and Chumbe (Envfit $r^2 = 0.66$, $p = 0.001$). On Kwale reef a weak correlation was found between fish biomass assemblages and sand ($r^2 = 0.32$, $p = 0.004$), and a strong correlation was found between fish biomass assemblages and coralline algae (Envfit, $r^2 = 0.54$, $p = 0.004$) (Fig. 7).

Significant differences in fish biomass were found between 2013 and 2016 for All Sites with an average increase of 62 % after bleaching (Fig. 8), including the reefs where the belt-transect method was used (Changuu, Bawe, Pange, Nyange and Chumbe; ANOVA, $F(1, 9) = 4.9$, $p < 0.05$) and those where the SVC method was used (Tele and Kwale; ANOVA, $F(1, 9) = 28.9$, $p < 0.001$).

Post-bleaching observations indicated significant increases in fish biomass on the protected reefs, i.e., Chumbe (Paired t -test, $t_9 = -2.33$, $p = 0.05$), Tele (Paired t -test, $t_9 = -2.39$, $p = 0.04$) and Kwale (Paired t -test, $t_9 = -9.82$, $p < 0.001$). Significant differences in fish biomass were found between reef sites for the reefs surveyed using the belt transect method (ANOVA, $F(4, 36) = 24.1$, $p < 0.001$), whereby the reefs at Chumbe and Nyange exhibited higher post-bleaching fish biomass than the other reefs (all Paired t -tests: $p < 0.05$). No significant differences in fish biomass were found between the reef sites Tele and Kwale (Fig. 8).

In total, four sea urchin species were recorded on the reef sites. *Diadema setosum* was the most dominant species on all reefs before and after bleaching, with the exception of Kwale reef in 2013, where *Echinometra mathaei* was the most abundant species (Fig. 9). Sea urchin densities declined significantly by an average of 32 % in 2016 compared to 2013 for All Sites (ANOVA, $F(1, 19) = 22.3$, $p = 0.001$) and between reef sites (ANOVA, $F(6, 54) = 3.1$, $p < 0.001$), with five investigated reefs having lower mean sea urchin densities after the bleaching event (Fig. 9). There was no major difference in sea urchin densities among sites before the bleaching event, with only Chumbe reef indicating significantly lower densities in comparison to Changuu (Paired t -test, $t_{19} = 4.1$, $p = 0.01$), Bawe (Paired t -test, $t_{19} = 7.5$, $p < 0.001$) and Nyange reef (Paired t -test, $t_{19} = 6.3$, $p < 0.001$). After bleaching, the protected reefs, i.e., Chumbe, Kwale and Tele, showed lower sea urchin densities in comparison to other reefs (all Paired t -tests: $p < 0.01$). Post-bleaching observations for individual reefs showed significant decrease in sea urchin density of up to 57 % for Changuu (Paired t -test, $t_{19} = 2.47$, $p = 0.02$), Bawe (Paired t -test, $t_{19} = 2.30$, $p = 0.03$) and Tele reef (Paired t -test, $t_{19} = 2.26$, $p = 0.04$), and up to 81 % for Kwale reef, with no sea urchins found on Chumbe reef (Paired t -test, $t_{19} = 3.16$, $p = 0.005$). Pange reef was the only reef that showed a significant increase in sea urchin density before and after bleaching (Paired t -test, $t_{19} = -2.78$, $p = 0.01$), while Nyange reef showed no significant difference in sea urchin density (Fig. 9).

4. Discussion

This study shows that coral reefs in Unguja Island have been significantly affected by the 2014–2016 ENSO event, with post-bleaching alterations in benthic community structure, herbivorous reef fish and sea urchin communities. Changes in benthic community structure were marked by extensive loss of coral and increase in turf algae. Furthermore, the results revealed a general pattern of post-bleaching increase in herbivorous fish, often correlated with turf algae increase, and a decline

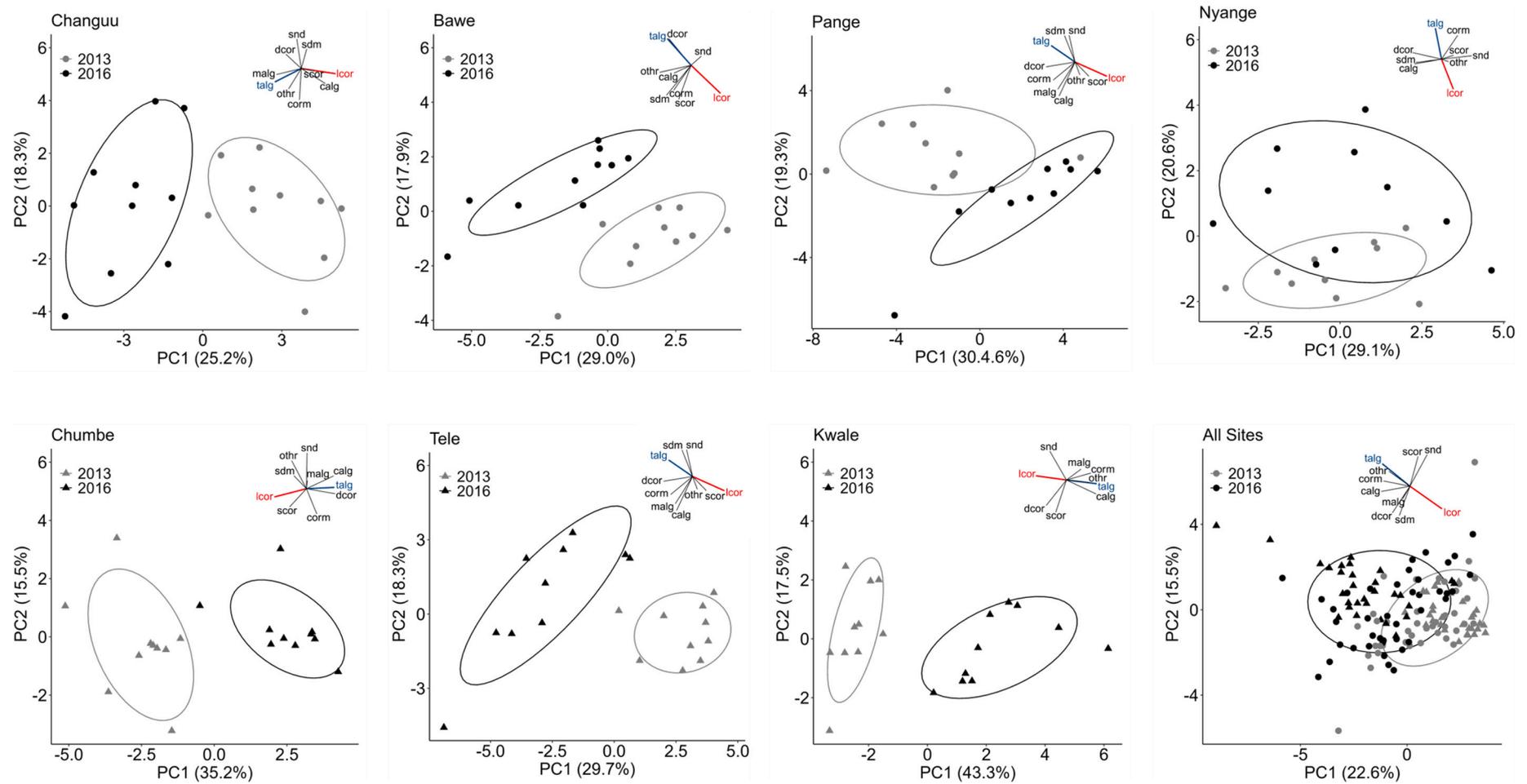


Fig. 3. Principal Component Analyses (PCA) of benthic community composition in each reef site and All Sites before (2013) and after (2016) bleaching. A biplot (top right of the PCA plots) of habitat substrate variable vectors is included to aid interpretation of year groupings (indicated by 95 % confidence ellipses) and contribution of benthic substrate variables to the variation between years. The smaller the angle between two variable vectors, the stronger the correlation. Live coral and turf algae vectors are indicated in red and blue, respectively. Levels of protection are indicated by circles (unprotected) and triangles (protected). Benthic substrates are abbreviated as follows: lcor (live coral), dcor (dead coral), scor (soft coral), corm (corallimorpharia), talg (turf algae), malg (macroalgae), calg (coralline algae), snd (sand), sdm (sediment), and othr (others). Plots are ordered according to their geographical location (from north to south; see Fig. 1): Changuu, Bawe, Pange, Nyange, Chumbe, Tele, and Kwale (consistent with all figures hereafter). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
SIMPER results showing the cumulative contribution (%) of the most influential benthic categories to observed pre/post dissimilarities in benthic community structure for each reef site.

	Live coral (lcor)	Turf algae (talg)	Macroalgae (malg)	Dead coral (dcor)	Sand (snd)	Coralline algae (calg)
Changuu	33 %	13 %	15 %	13 %	-	-
Bawe	36 %	-	-	20 %	18 %	-
Pange	34 %	-	-	14 %	34 %	-
Nyange	23 %	13 %	-	15 %	19 %	10 %
Chumbe	47 %	29 %	-	-	-	-
Tele	43 %	16 %	-	-	17 %	-
Kwale	34 %	34 %	-	-	9 %	-
All Sites	35 %	19 %	-	-	16 %	-

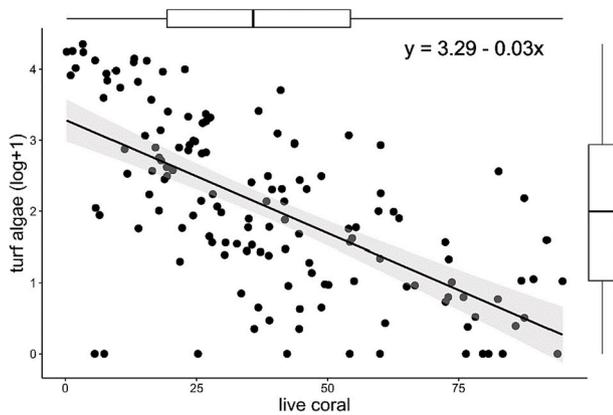


Fig. 4. The relationship between live coral and turf algae cover in the investigated area, including data from 2013 and 2016. Each data point represents the mean percent cover of the substrate variables based on one transect ($n = 140$). Shaded area represents a 95 % confidence interval.

in sea urchin density across reef sites. Overall, the severity of the impact varied across individual reefs, with larger impact on the protected reefs (Chumbe, Tele and Kwale) compared to the unprotected reefs (Changuu, Bawe, Pange and Nyange). The observed shifts from coral dominance to algal dominance in some reefs, highlight the need for resilience-based management practices that can promote moderate grazing levels and help recovery towards coral-dominated states.

4.1. Influence on benthic community structure

The adverse impacts of ENSO-related mass bleaching episodes on the structure and composition of reef habitats are well known and have been reported several times since the 1980s (e.g., Glynn, 1984; Bruno et al., 2001; Atweberhan and McClanahan, 2010; Eakin et al., 2019). The Western Indian Ocean has suffered several previous mass bleaching episodes, such as in 1997/1998, 2010, and 2014–2016 ENSO events, with studies reporting over 80 % coral mortality in Tanzanian reefs (e.g., Wilkinson et al., 1999; Öhman et al., 1999; Spencer et al., 2000; McClanahan et al., 2001; Obura et al., 2017; Gudka et al., 2020). Similar levels of post-bleaching coral mortality were observed in this study. Prior to bleaching, all reefs were dominated by mean live coral cover (between 38 % and 86 %). Shortly after changes in sea surface temperature (SST) were reported for Tanzania, results showed a significant decrease with <28 % in mean live coral cover across all reef sites. Consistent with past studies (McClanahan et al., 2001; Adjeroud et al., 2009; Cerutti et al., 2020), our study found significant post-bleaching increases in turf algae.

In addition to natural pulse perturbations such as mass bleaching events, direct human impacts (Hughes et al., 2010), such as fishing and tourism, can also lead to coral mortality and the alteration of benthic assemblages (Hughes, 1994; Jackson et al., 2001). In Zanzibar, tourism and fishing practices have increased in the past few decades with destructive fishing practices impacting reef habitat structure (Jiddawi and Öhman, 2002). However, it is reasonable to infer that the 2014–2016 ENSO induced elevated SST, was the major cause of the

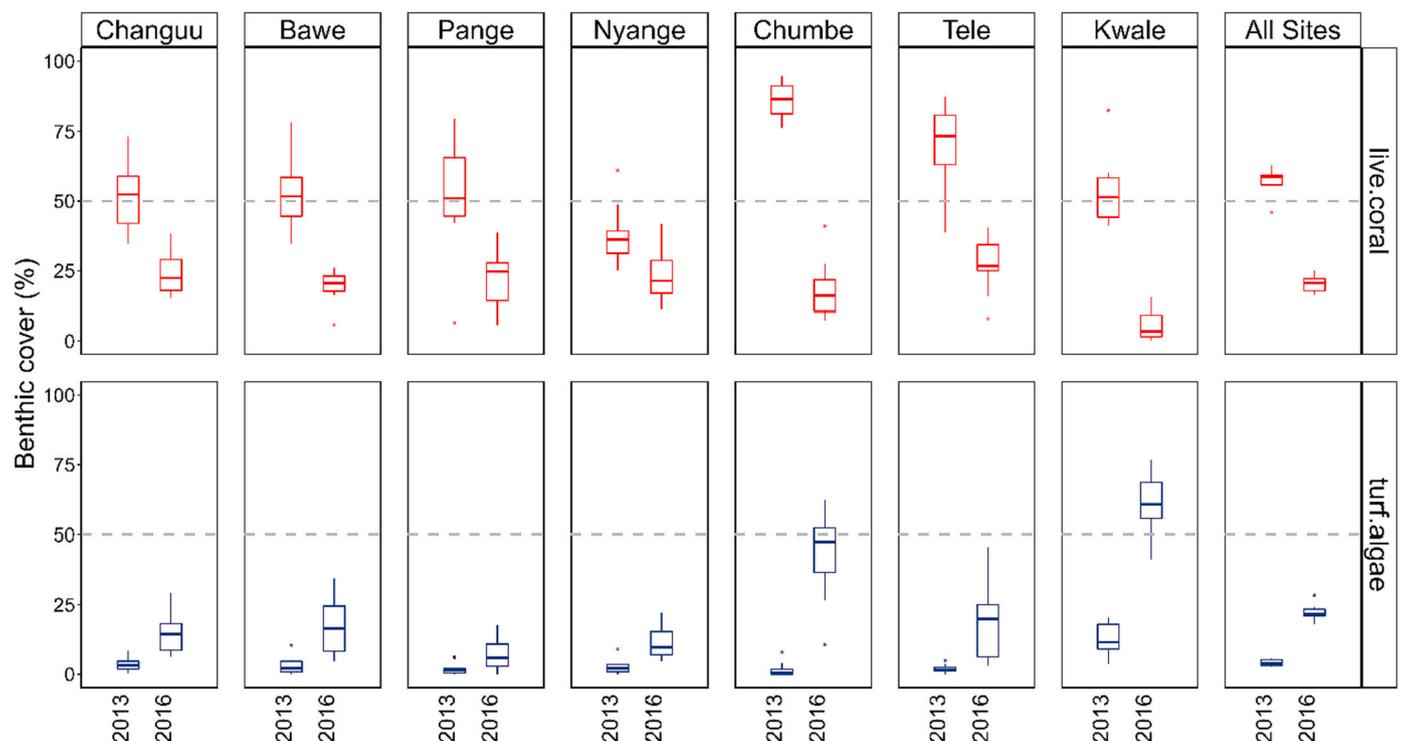


Fig. 5. Boxplots showing medians and quartiles, including outliers, of mean percent cover of live coral and turf algae on each reef site and All Sites before (2013) and after (2016) bleaching. A dashed line at 50 % benthic cover is included to aid orientation.

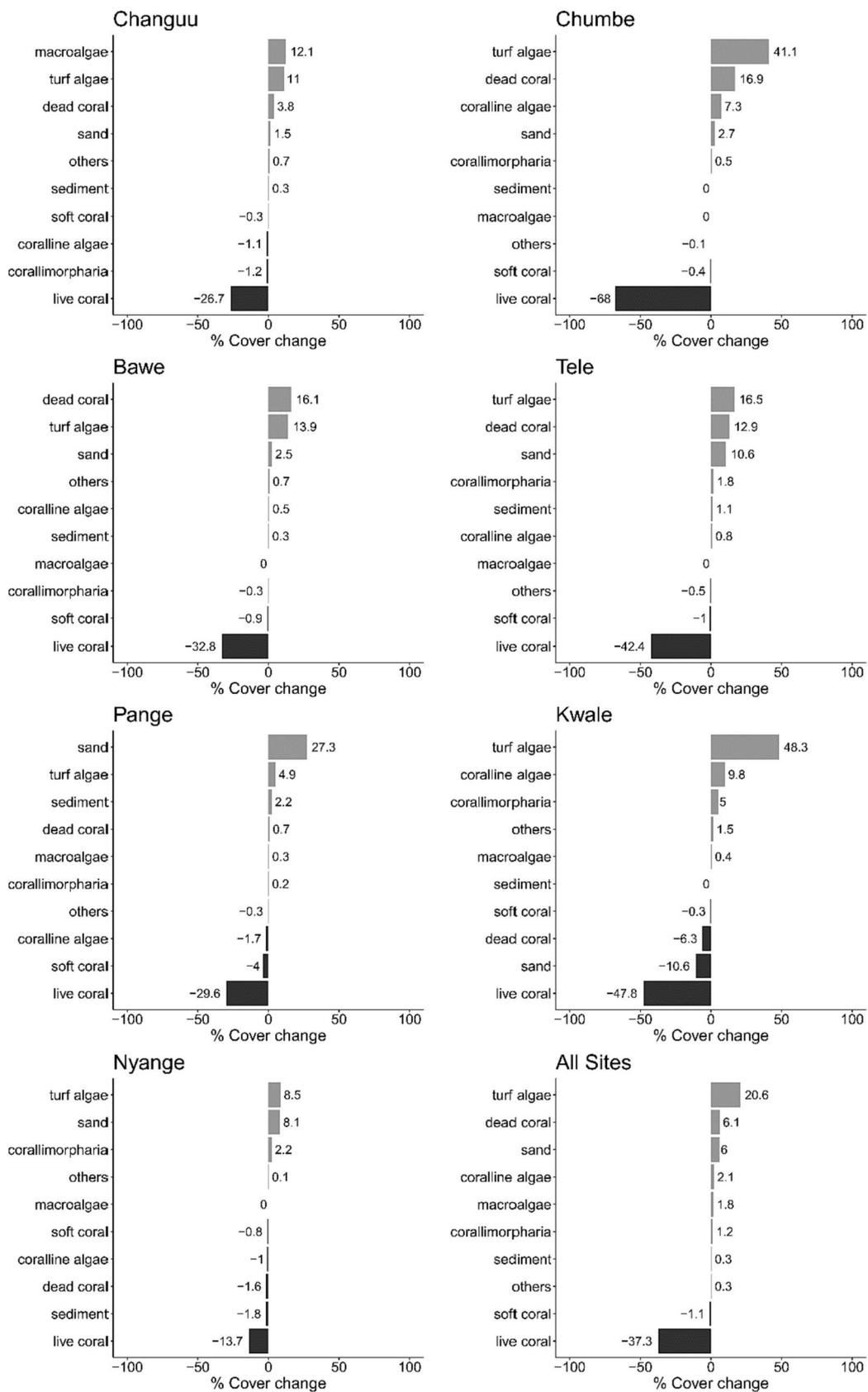


Fig. 6. Post-bleaching percentage increase (grey) and decrease (black) of benthic substrates from 2013 to 2016.

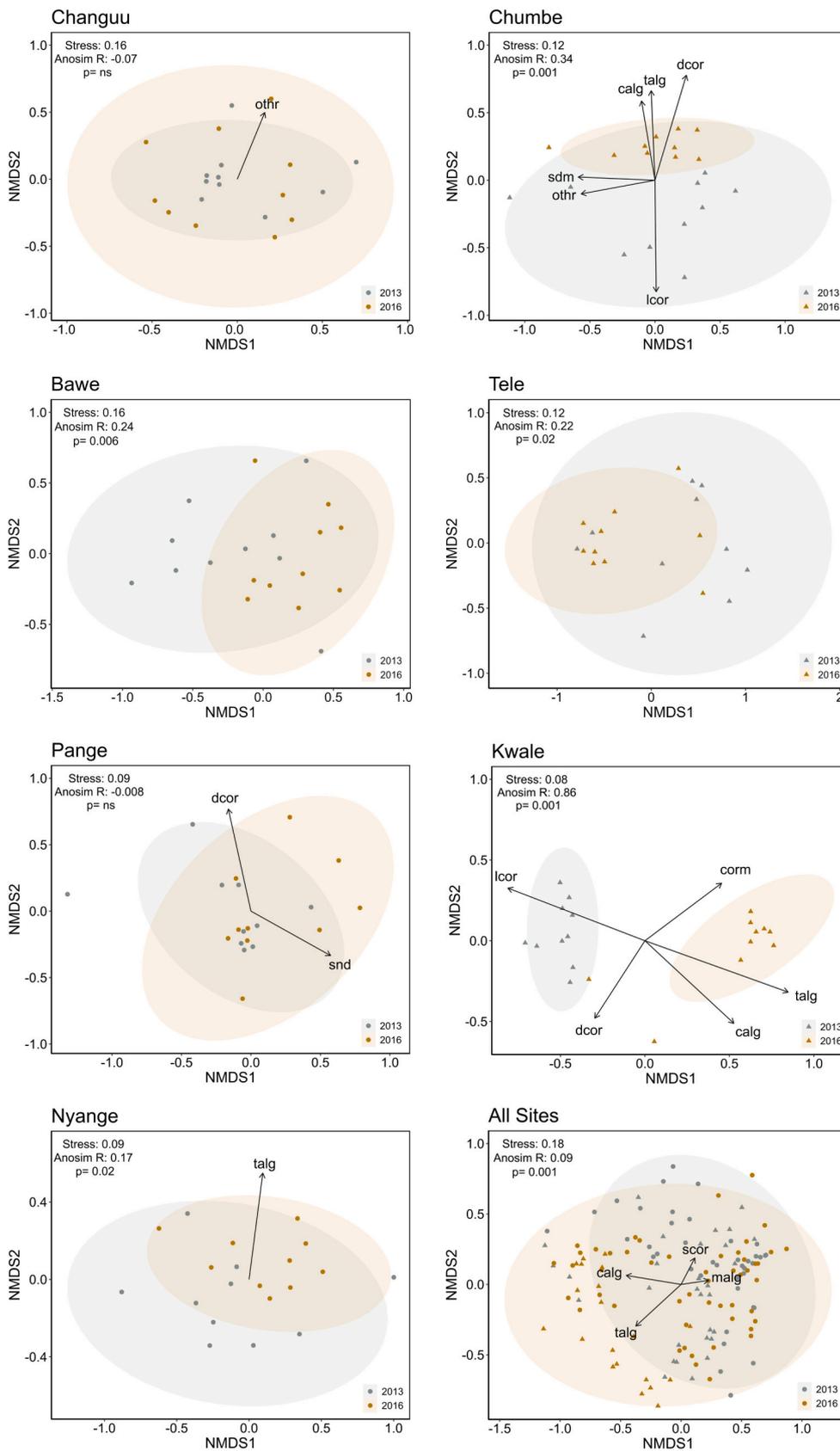


Fig. 7. NMDS ordination plots of temporal dissimilarities in herbivorous fish assemblage composition in each reef site between 2013 (grey) and 2016 (brown). Corresponding stress value of nMDS and ANOSIM test results are shown in the top left corner of each plot. Only benthic variables significantly correlating with the ordination ($p < 0.05$, as determined by 'Envfit' analysis) are represented through vectors. Year groupings are indicated by 95 % confidence ellipses. Levels of protection are indicated by circles (unprotected) and triangles (protected). Benthic substrates are abbreviated as follows: lcor (live coral), dcor (dead coral), corm (corallimorpharia), talg (turf algae), calg (coral-line algae), sdm (sediment), and othr (others). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

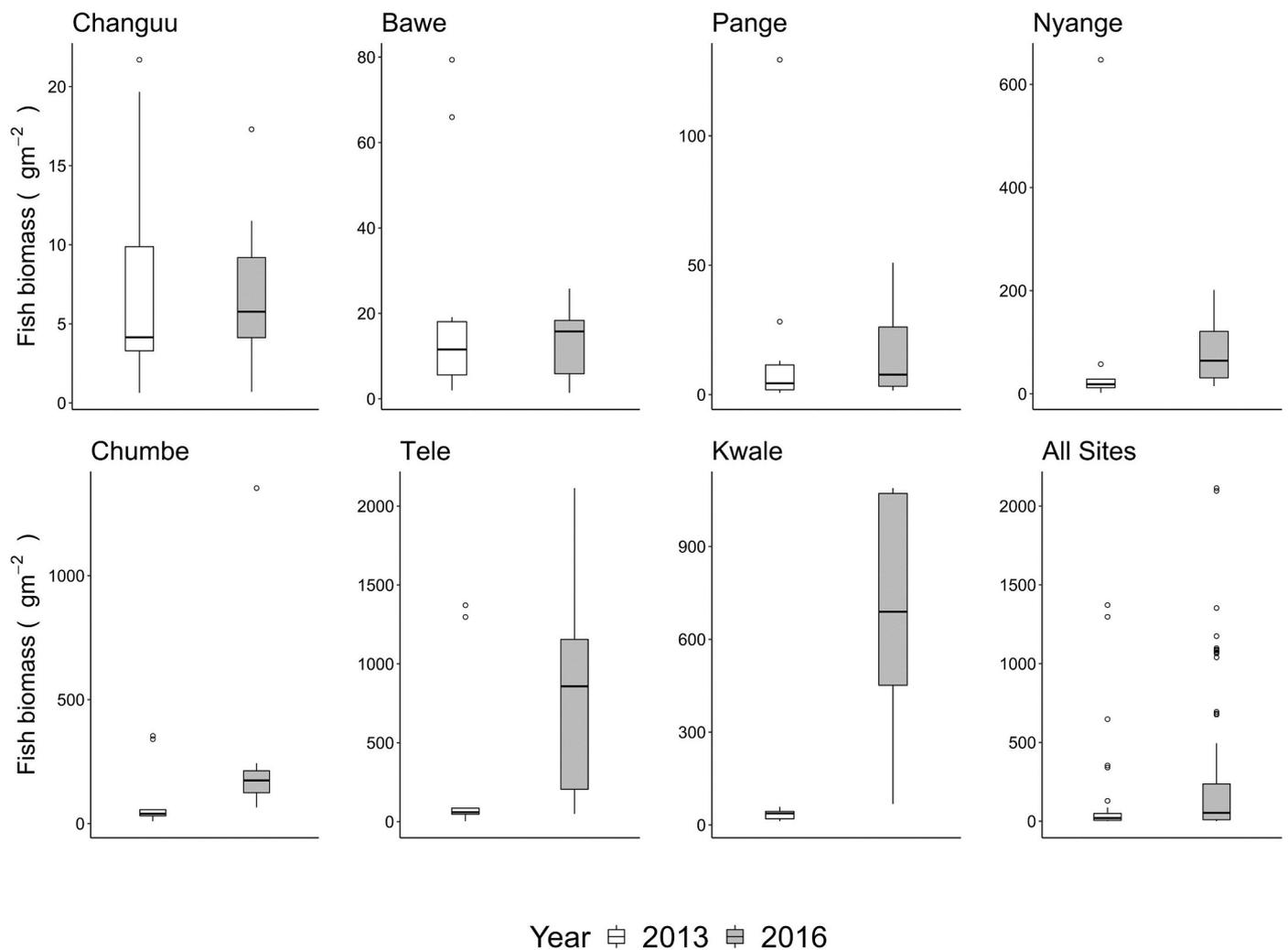


Fig. 8. Boxplots showing medians and quartile, including outliers, of total herbivorous fish biomass (g m^{-2}) for each of the studied reefs between 2013 and 2016. Note, that graphs are based on two different sampling methods, including belt-transect for Changuu, Bawe, Pange, Nyange, Chumbe and the SVC method for Tele and Kwale.

observed mass coral mortality in the area. Notably, the Chumbe reef exhibited significant decrease in live coral cover and increase in turf algae cover, despite its location within a well-enforced no-take reserve sheltered from direct local human impacts. Moreover, when comparing live coral and turf algae cover in the year 2013 (pre-bleaching) for the reefs of Changuu, Bawe, Pange, Nyange and Chumbe, with a study conducted in the year 2004 by Lokrantz et al. (2010), the mean percent live coral cover ($\geq 45\%$ in 2004; $\geq 38\%$ in 2013) and mean turf algae cover ($< 9\%$ in 2004; $< 4\%$ in 2013) appear to be of the same order of magnitude. This relative stability in cover between 2004 and 2013 suggests that the observed drastic changes in benthic community structure found in the present study were likely to have been caused primarily by the 2014–2016 ENSO event.

The extent and intensity of coral bleaching can be spatially discontinuous, producing variability between habitats. Such variability in bleaching patterns can depend on variation in e.g., depth, cloud cover, turbidity, currents and habitat heterogeneity (Penin et al., 2007; Baker et al., 2008; Bayraktarov et al., 2013; Sully and van Woesik, 2020; Gonzalez-Espinosa and Donner, 2021). For instance, reef flats with lower water depths are more likely to be prone to bleaching and among coral taxa, branching corals (taxa: *Acropora*) are more sensitive to elevated SST (Loya et al., 2001; Bridge et al., 2014; Pisapia et al., 2019). A cumulative effect of these two factors may account for the high coral mortality observed in the protected reefs of Chumbe and Kwale, which

feature shallower reef flats with dominating branching corals (Obura et al., 2017; Bravo et al., 2021). The lower coral mortality observed in the unprotected reefs may be attributed to the fact that these reefs are already eroded to the level that more resilient coral species with higher thermal tolerance are likely present. Moreover, a deeper reef flat with increased exposure to surface currents (e.g., Nyange reef, pers. obs.) may also have contributed to the lower bleaching impact observed on these reefs. Therefore, this spatial variation of impact is likely driven by ecological and physical conditions rather than protection status.

4.2. Influence on herbivores

While it is evident that loss of coral cover and the degradation of topographic and structural complexity can influence coral reef fish abundance and biodiversity (Jones et al., 2004; Pratchett et al., 2011, 2018; Newman et al., 2015; Robinson et al., 2019), susceptibility and response to disturbance can vary among species and trophic groups (Pratchett et al., 2011; Stuart-Smith et al., 2018). Obligate coral-dwelling or coral-feeding fish species are more vulnerable to loss of coral, often with immediate effects (Kokita and Nakazono, 2001; Graham et al., 2009; Wilson et al., 2019), whereas herbivorous fish, which are predominantly roving species (Green and Bellwood, 2009), are less vulnerable in the short term (Garpe et al., 2006). Studies have demonstrated increases in herbivorous fish densities after mass coral

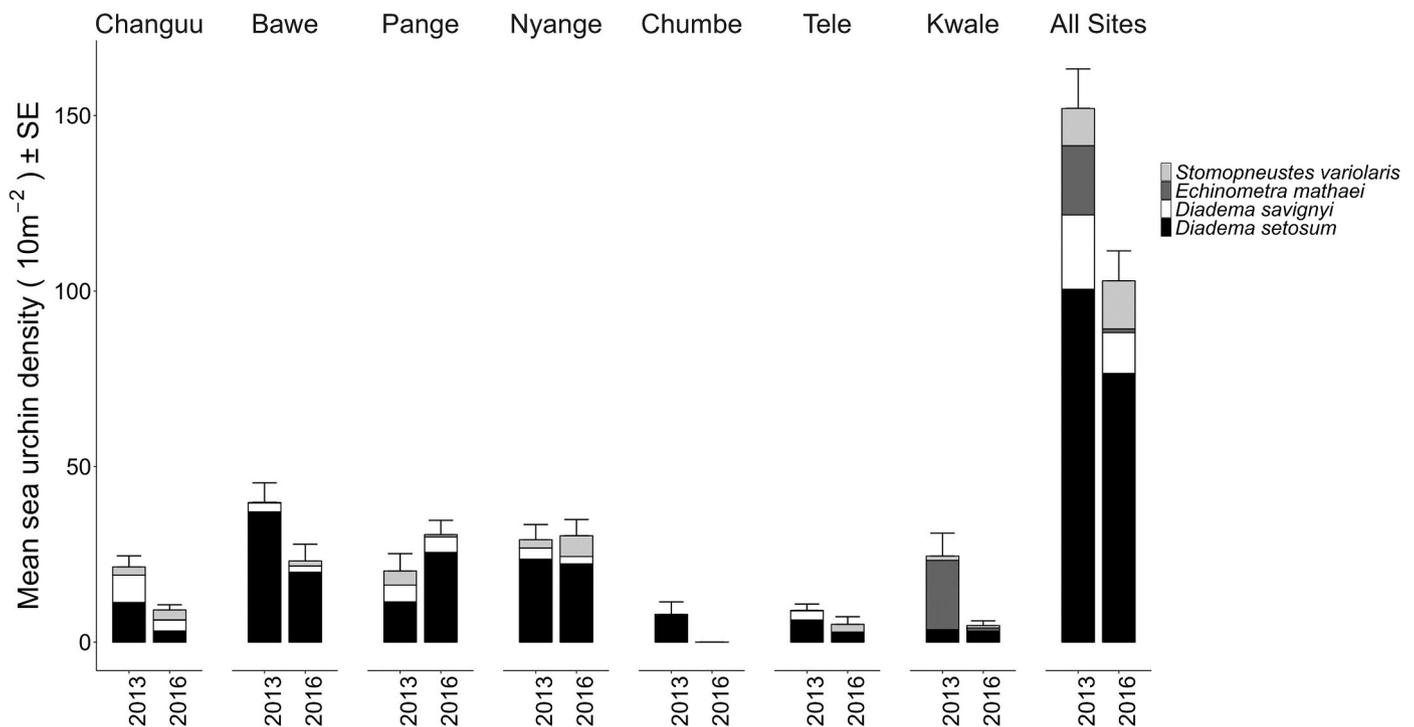


Fig. 9. Mean (\pm SE) density of sea urchin species in the investigated reefs. Error bars show SE and are based on total abundance.

mortalities, which is widely argued to be related to algal overgrowth and increased food availability attracting herbivorous fish species (Lindahl et al., 2001; Garpe et al., 2006; Khalil et al., 2013). This may explain the observed post-bleaching increase in fish biomass in this study, particularly for Chumbe and Kwale reefs. However, with persistent decline of live coral and associated loss of structural complexity, herbivorous fish abundances are likely to decline in the long term (Garpe et al., 2006; Graham et al., 2006). Studies have shown that coral cover below 10 % can lead to a significant decline in coral reef fish densities across trophic groups (Wilson et al., 2006; Beldade et al., 2015; Lamy et al., 2016).

While post-bleaching grazing intensity by herbivorous fish is vital for recovery processes, the presence of fish herbivores alone may not be sufficient. In moderate numbers, sea urchins also play a key functional role in maintaining levels of algal growth and can substitute for fish when these are reduced or absent (Bellwood et al., 2004; Graham et al., 2013). Their effective grazing has particularly been highlighted to facilitate coral recovery following disturbances, by promoting coral recruitment and reef resilience (Carpenter and Edmunds, 2006; Dang et al., 2020a; Dang et al., 2020b; Nozawa et al., 2020). Contrary to expectation, the majority of the investigated reefs, particularly those with the greatest coral mortality, showed a decline in sea urchin densities. However, this significant decline may have only been a short-term observation. For instance, sea urchins may have migrated to adjacent more structurally complex habitats, such as seagrass beds, due to the post-bleaching loss of topographic complexity coupled with predatory pressure (Mcclanahan and Muthiga, 2007). This could explain the significant decline of *E. mathaei* in Kwale reef, which were observed to be found in between branching corals before the mass bleaching event (pers. obs.). On Chumbe reef, the observed absence of sea urchins may be linked to its high level of reef protection and higher densities of fish predators. For example, sea urchin densities across the Chumbe Reef Sanctuary have been gradually declining, while fish densities have been gradually increasing between the years 2006 and 2015 (Kloiber, 2015). Another plausible explanation for observed low post-bleaching densities may be recruitment failure, arising from elevated SST on fertilization success, and also the development of larvae and juvenile sea urchins (Pereira et al., 2020; Gall et al., 2021; Leach et al., 2021).

4.3. Potential phase shifts

Pulse perturbations, such as hurricanes and disease outbreaks, can trigger abrupt shifts in community structure, so-called phase shifts (or regime shifts) (Hughes, 1994). Coral reefs are particularly vulnerable to phase shifts when resilience has been eroded due, for example, to overharvesting (e.g., decline in herbivorous fish abundance) and reduced water quality (e.g., increasing nutrient load) (Nyström et al., 2000; Mumby et al., 2007; Hughes et al., 2010). Among benthic organisms that can dominate in a reef system after disturbances, shifts to fleshy macroalgae are the most reported (e.g., Bruno et al., 2009; Graham et al., 2015). However, post-disturbance macroalgae succession, which showed low cover (≤ 12 %) in the reefs in this study, represents only one of many alternate degraded states. Benthic organisms, including turf algae, soft coral, corallimorpharia, sponges and ascidians, have also been documented as potential organisms that could dominate in a reef system and induce a phase shift (Norström et al., 2009). Among these reported potential phase shifts, turf algae appeared to have become a dominating benthic organism in some of the investigated reefs.

Although it is questionable whether turf algae could persist as a stable state, its prolonged overgrowth has been discussed as a transitional stage towards a fleshy macroalgae establishment, if succession is not checked by herbivores to promote recovery (Paddack et al., 2006; Mumby et al., 2007; Jouffray et al., 2015). Muhando and Mohammed (2002) reported that Chumbe and Kwale reef experienced a macroalgae cover increase after the bleaching event in 1998. Though none of the reefs investigated have shifted towards a macroalgal dominance to date (S. Yahya pers. obs., unpublished data), they could be on course for such changes, if current climate change induced environmental changes persist or worsen. For example, while corallimorpharia cover was considered insignificant in Zanzibar's reefs prior to 1996, it has now increased and spread to most of the reefs off Zanzibar Town (Muhando and Kuguru, 2002; Kuguru et al., 2004; Obura et al., 2017).

Reversal of phase shifts (e.g., turf algae) after disturbance towards a coral-dominated state is possible. This process can take several years to decades (e.g., Baker et al., 2008; Guzman and Cortés, 2007; Adjerdou

et al., 2009; Graham et al., 2015) and primarily depends on grazing activity by herbivores (e.g., Idjadi et al., 2010; Graham et al., 2013; Nozawa et al., 2020). Although it is difficult to evaluate the positive impact of herbivores in individual reefs based on this study, current monitoring programmes have for example, observed high densities of juvenile corals in the protected reefs, particularly Kwale and Chumbe reef (S. Yahya pers. obs., unpublished data).

To promote recovery in the face of future bleaching episodes, building resilience in coral reefs through management practices is imperative (Nyström et al., 2008; Maynard et al., 2010; Mcleod et al., 2019). Although global drivers, such as human-induced climate change (i.e., elevated seawater temperature and ocean acidification), remain outside the control of local managers, managing coral reef resilience at a local scale offers a promising prospect to prevent further degradation of these fragile ecosystems (Graham et al., 2013; Ladd and Collado-Vides, 2013; Mumby et al., 2014; Ford et al., 2018; Donovan et al., 2021). Design of such resilience-based frameworks and their implementation may include local-specific regulation and enforcement. To enforce regulation and management of human pressure on coastal waters around Zanzibar, it is recommended to extend existing coral reef monitoring (which currently focus on recording benthic cover, coral recruits, abundance and diversity of fish and macroinvertebrates) and management (which currently focus on marine protected areas (MPAs), gear control, catch monitoring, temporal closure on some reefs) programmes, by integrating resilience-based management (RBM) practices and strategies to enhance recovery and reef resilience in the region (McClanahan et al., 2012; Anthony et al., 2015; Mcleod et al., 2019). Such implementations, for example, may focus on: (1) management and reduction of major local stressors, such as fishing pressure, tourism, sedimentation, and nutrient input which stimulate turf algae growth; (2) enhance biodiversity and functional redundancy by prioritising the protection of functional groups rather than species of commercial importance; (3) include management of cross-scale dynamics and corridors between habitats to promote ecological connectivity (prevalent in the tropical seascape of Zanzibar), and spatial resilience to foster reef fish replenishment; (4) extend coral reef monitoring programmes beyond ecological surveys, by integrating fisheries data assessment, resource use and user information; (5) an extension beyond ecosystem-based management by considering socio-ecological systems and developing MPA co-management initiatives that involve the participation of stakeholders in decision-making, to encourage learning and understanding of system dynamics and preparation for unforeseen bleaching events, by establishing sustainable resource use, thus promote resilient and healthy reefs.

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CRedit authorship contribution statement

Eylem Elma: Conceptualization, Methodology, Data curation, Investigation, Formal analysis, Visualization, Writing – original draft. **Martin Gullström:** Supervision, Funding acquisition, Project administration, Validation, Writing – review & editing. **Saleh A.S. Yahya:** Funding acquisition, Investigation, Resources, Writing – review & editing. **Jean-Baptiste Jouffray:** Conceptualization, Visualization, Writing – review & editing. **Holly K. East:** Writing – review & editing. **Magnus Nyström:** Supervision, Project administration, Conceptualization, Methodology, Validation, Writing – review & editing.

Declaration of competing interest

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

Data availability

Data will be made available on request.

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