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Coral resilience in a changing climate: A site-specific analysis of Maldivian reefs over 19 years

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ABSTRACT

The Maldives Archipelago faces significant environmental vulnerabilities, primarily from rising sea surface temperatures and local human pressures, which result in coral bleaching and mortality, and local declines in biodiversity. This study analyses nineteen years (2005–2023) of data across four reefs under varying conditions to examine disturbance and recovery patterns, with a focus on spatial variability and site-specific influence. Using the Reef Check protocol, surveys assessed benthic composition, fish, and macro-invertebrate abundance in North Malé, Ari, and Rasdhoo atolls. Results highlight distinct site responses: Rasdhoo Madivaru, an oceanic site, maintained stable coral cover, while lagoon sites showed varied post-bleaching recovery trajectories. Reefs with minimal human impact had higher recovery rates, unlike heavily frequented sites, like Dhega Thila, where benthic composition shifted. These findings underscore the need for localised, adaptive conservation strategies to preserve Maldivian reef ecosystems in a changing climate.

1. Introduction

The Republic of Maldives, an archipelago uniquely vulnerable to environmental changes due to its small (<1 km^2), low-lying (~2.5 m above sea level), and unconsolidated islands, faces distinct challenges across its vast expanse of over 90,000 km^2. Despite its equatorial location providing warm, stable temperatures and relative protection from cyclones, specific conditions vary by atoll (Chaudhuri et al., 2021).

The most pressing environmental threat is the increase in sea surface temperature (Pisapia et al., 2016, 2019), which has triggered widespread coral bleaching and mass mortality events during ENSO (El Niño Southern Oscillation) events in 1998, 2010, and 2016. While the bleaching event of 2010 had minor consequences (Guest et al., 2012); 1998 and 2016 saw severe heat waves causing mass coral mortality, with nearly 95 % and 70 % loss of shallow and deeper reef hard coral cover, respectively (Montefalcone et al., 2018, 2020). Notably, after the 2016 bleaching, several 'hope spots' were identified where bleaching affected only 25 % or less of coral colonies, indicating diverse influences beyond biological factors alone (De Falco et al., 2020). Additionally, escalating human impact, particularly from 'mass' tourism, poses a growing threat.

Tourism, a vital economic driver, contributed nearly 30 % to the country's GDP in 2011 and attracted almost 2,000,000 visitors in 2023 (Scheyvens, 2011; Ministry of Tourism of Maldives, 2024). However, 'luxury' tourism that is predominantly marketed in the Maldives brings significant ecological threats due to the infrastructure, transportation, water usage, and pollution it necessitates (Davenport and Davenport, 2006). Heavily recreational diving can cause coral damage, lower hard coral cover and spreading of disease (Tratalos and Austin, 2001; Marshall and Schuttenberg, 2006; Carilli et al., 2010 ; Guzner et al., 2010; Hasler and Ott, 2008; Lamb et al., 2014; Roche et al., 2016). Dredging activities and land reclamation, particularly in the central atolls, have intensified since the 1970s, exacerbating challenges to the balance of marine ecosystems, already upset by overfishing (Fallati et al., 2017; Hassan Ahmed, personal communication).

The demand for land, coupled with limited space, has prompted a considerable increase in these activities since the 1990s, which involve transforming sea areas for human use (Bisaro et al., 2020; Pancrazi et al.,

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2020), with the creation of artificial headlands, airports (Nepote et al., 2016; Heery et al., 2018), and harbours (Bertaud, 2002). Dredging, a central component of these initiatives, directly impacts the natural environment, increasing turbidity and adversely affecting coral health (Jaap, 2000; Manap and Voulvoulis, 2015; Miller et al., 2016). Although global El-Niño-related temperature increases lead to mass bleaching events, the extent of impact on individual reefs depends on local biological and physical processes (Carilli et al., 2012). Corals exhibit varying abilities to resist and recover from severe thermal stress, particularly in ocean regions characterised by high-frequency variability and temperature fluctuations (Thompson and Van Woesik, 2009; Carilli et al., 2012; Cowburn et al., 2019; Montefalcone et al., 2020).

Conversely, reefs subjected to anthropogenic stressors such as overfishing, intense SCUBA diving activities and pollution tend to have diminished recovery capabilities (Wooldridge, 2009; Richmond et al., 2018; Montefalcone et al., 2020).

This study draws on a 19-year dataset (2005–2023) from the Maldives to assess disturbance and recovery processes across four dive sites with distinct environmental characteristics and patterns of use. The aim is to explore spatial variability in post-disturbance responses, focusing on site-specific resilience, defined here as the community's ability to recover to pre-bleaching conditions, and associated recovery trends. By examining benthic, fish, and macro-invertebrate communities, the study provides essential insights to inform targeted conservation strategies under ongoing climate change.

2. Materials and methods

2.1. Study area

Situated in the heart of the central Indian Ocean, the Maldives comprise 26 natural atolls and around 1120 islands, forming the central part of the Laccadive-Maldives-Chagos ridge. Spanning from approximately 7°07′ N to 0°40′ S in latitude and 72°33′ E to 73°45′ E in longitude, 99 % of this archipelago is seawater (Dhunya et al., 2017). From 2005 to 2023, annual research expeditions and local community programs were conducted, gathering data across the atolls of the Maldives, specifically North Malé, Ari and Rasdhoo atolls (Fig. 1). In terms of spatial distribution, North Malé Atoll lies along the central-eastern rim of the Maldivian archipelago, while Ari and Rasdhoo atolls are positioned on the central western side. This geographical distinction entails varying exposure to monsoon winds and currents (Chaudhuri et al., 2021). Furthermore, North Malé Atoll experiences the highest levels of human activity, hosting nearly half of the Maldives' population (Maldives Bureau of Statistics, 2024) and serving as the location of the capital city, Malé. Conversely, Ari and Rasdhoo atolls are renowned as popular tourist destinations, featuring numerous guest houses and resorts, and serving as sought-after destinations for safari boats. Specifically, four dive sites have been revisited through the years: Dhega Thila, Kuda Falhu, Banana Reef and Rasdhoo Madivaru (Fig. 2, Table 1). Each of these sites is distinguished by unique geographical characteristics and varying degrees of human influence.

Through the years, these sites have been revisited and data have been collected through SCUBA diving at depths of 3–5 (shallow) and 7–10 m (deep), applying the international protocol Reef Check. Geographical coordinates for each site were recorded using a portable GPS and confirmed before starting the monitoring.

2.2. Reef Check protocol and field activities

The Reef Check protocol was selected as survey methodology to encompass a diverse range of reef indicators, spanning from the benthic community to the fish and macro-invertebrate communities. Developed in 1997, the Reef Check protocol aimed to provide a rapid and robust method to capture a snapshot of reef health, recording the abundance of specific organisms crucial for determining the ecosystem conditions and easily recognisable to the general public (Hodgson et al., 1998). Today, the protocol is ascribed to "citizen science" programs, relying on scientifically trained volunteer input that facilitates surveys on a large temporal and spatial scale. Furthermore, Reef Check aims to cultivate community support for coral reef monitoring and management programs: community members, through participation in training and

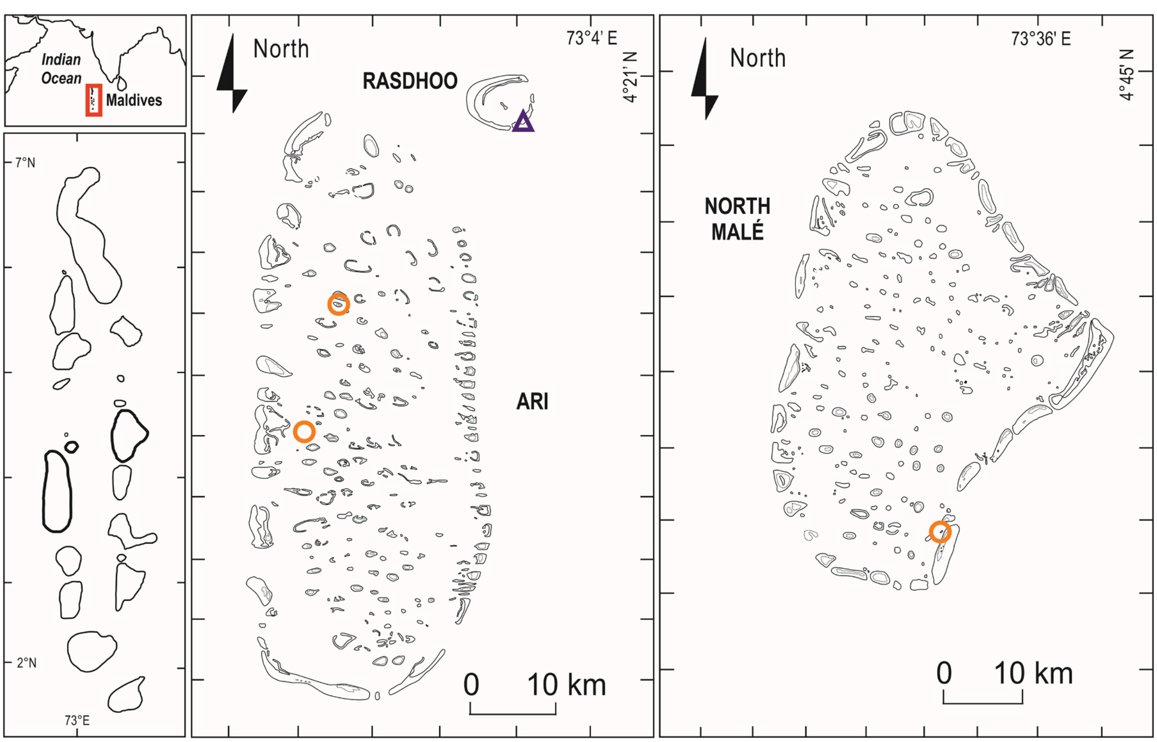

Fig. 1. Map of the Maldives Archipelago with a focus on Ari, Rasdhoo and North Malé atolls. **Orange** circles indicate the lagoon-sheltered sites, while the **purple** triangle indicates the ocean-exposed site at Rasdhoo Madivaru.

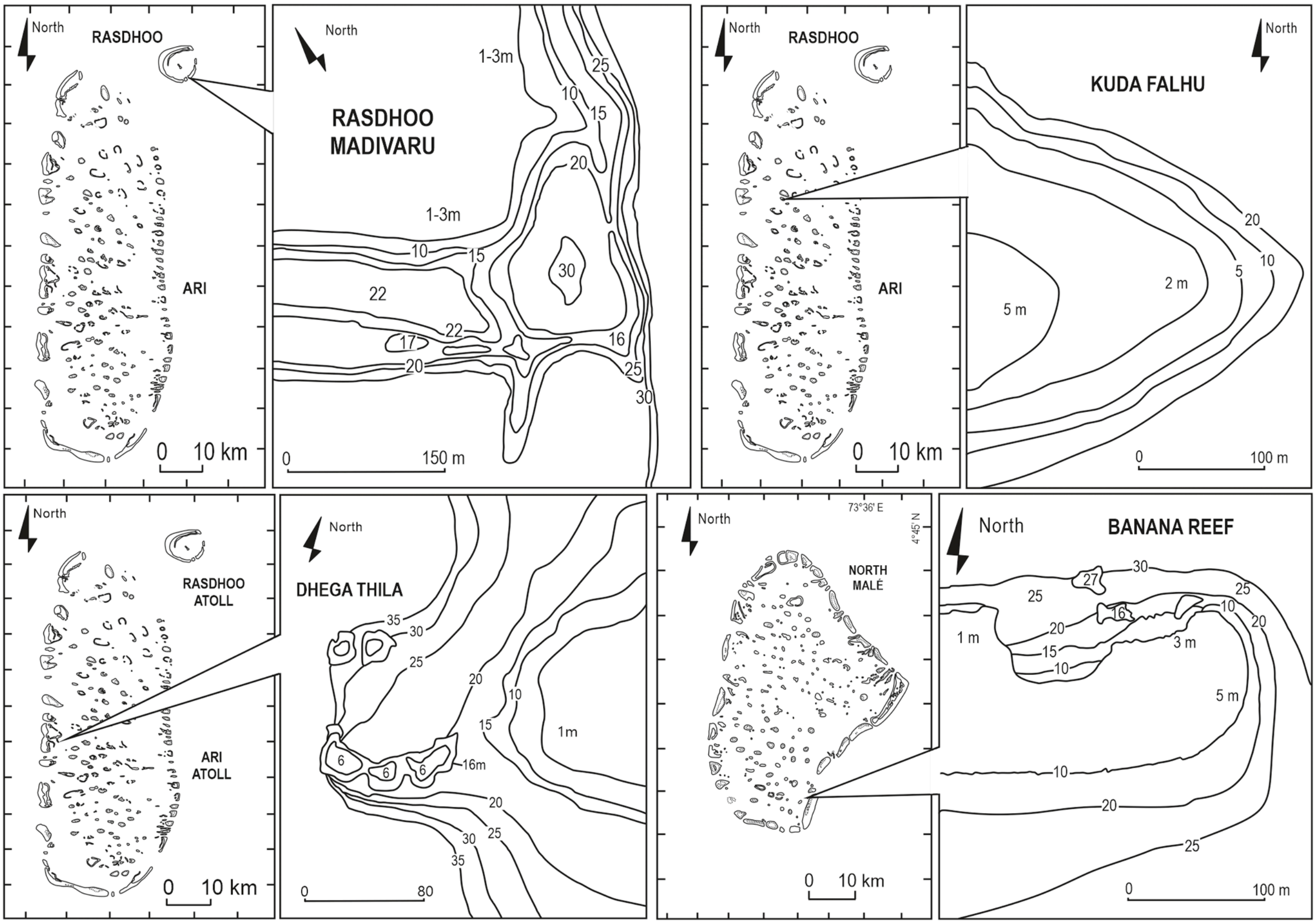

Fig. 2. Bathymetric maps of the four reefs of Rasdhoo Madivaru, Kuda Falhu, Dhega Thila and Banana Reef.

Table 1
Summary of the main characteristics of the four monitored dive sites: Rasdhoo Madivaru, Kuda Falhu, Dhega Thila and Banana Reef. The table includes site name, reef typology, atoll name, geographic coordinates, protection status, and primary use. Usage refers to the predominant human activities associated with each site. Information on protection status was obtained from the 'Maldives Protected Areas' database.

Site name	Typology	Atoll	Coordinates	Protection Status	Primary Usage
Rasdhoo Madivaru	Ocean	North Ari	4°15'51.84" N 73° 0'1.04" E	Protected area since 2018 (WDPA ID 555697560)	Tourism
Kuda Falhu	Lagoon	North Ari	4°1.052' N 72°48.311' E	No	Local fishing
Dhega Thila	Lagoon	Central Ari	3°50.663' N 72°45.028' E	No	Tourism
Banana Reef	Lagoon	North Malé	4°14'2.00" N 73°32'0.66" E	Protected area since 1995 (WDPA ID 81034)	Tourism

surveys, develop a sense of stewardship toward the monitored reefs, leading to an ideological transformation from a foreign-influenced organisation to local ownership and coordination. Reef Check monitoring is exclusively conducted by certified volunteers who undergo standardised training by local reef scientists. Each site was surveyed via SCUBA diving at between 3–5 m (shallow) and 7–10 m (deep) depths, employing four 20 m replicate transects parallel to the reef. Transect start and end points were spaced by 5 m, providing four independent replicated transects per site (Done et al., 2017) at each depth. A measuring tape marks the surveyed area, and pre-printed PVC slates with pencils are used to record underwater data. Indicators are selected based on economic and ecological value, sensitivity to human impacts, and ease of identification (S1, S2, S3 Tables). Reef Check teams collect four types of data: (1) site descriptions, (2) benthic community cover using the Point Intercept Transect (PIT) method, (3) fish abundances, and (4) macro-invertebrate abundances, both recorded through visual census along belt transects. Indicators range from individual species to family identification to assess the impacts on the reefs (Hodgson et al., 2006).

2.3. Data management and analysis

Over a 19-year period (2005–2023), a total of 288 transects were surveyed across four reef sites (Rasdhoo Madivaru, Kuda Falhu, Dhega Thila, and Banana Reef) and three distinct time periods: pre-bleaching, bleaching, and post-bleaching. The number of transects varied slightly among sites and time periods, reflecting the typical variation found in long-term ecological monitoring, due to factors such as logistical limitations, environmental conditions, and fieldwork constraints. Data collected underwater were transcribed from Reef Check data sheets into Excel spreadsheets designed by the international Reef Check Program and subsequently sent to the Reef Check Foundation (https://www.reefcheck.org/). Benthic community, fish and macro-invertebrate indicators were analysed separately between lagoon and ocean reefs due to their different environmental conditions (Gischler et al., 2014). Data collected at depths of shallow and deep transects were analysed together due to the absence of significant differences between these two depth ranges.

For a simple interpretation of the results, the indicators of rock (RC), rubble (RB), sand (SD) and silt (SI) have been grouped in the indicator abiotic (AB). The indicator hard coral (HC) has been used as the main index to determine the health state of the reef (Lasagna et al., 2010; Montefalcone et al., 2018), while the recently killed coral (RKC) was considered for evaluating recent impacts on the reefs (Montefalcone et al., 2020). For the fish and macro-invertebrate communities, indicators with very low occurrence, such as the Napoleon wrasse, pencil urchin and collector urchin, were excluded. Additionally, giant clams were categorised based on size into two groups: $\leq$10 cm and >10 cm. The fish data have been $\sqrt{x}$ transformed while the macro-invertebrates data have been $\log_{10}(x+1)$ transformed before statistical analysis (Zar, 1999; Clarke and Warwick, 2001).

To assess the ecological impacts of the 2016 mass bleaching event, data were grouped into three temporal phases: pre-bleaching (2005–2015), bleaching (2016–2018), and post-bleaching (2019–2023).

Patterns in benthic, fish, and macro-invertebrate community composition across sites and time were examined using non-metric multidimensional scaling (NMDS) based on Bray–Curtis dissimilarities, computed with the metaMDS function in the vegan package (Oksanen et al., 2020). A two-way permutational multivariate analysis of variance (PERMANOVA) was then applied using the adonis2 function to test for differences among the factors time (three levels: pre-bleaching, bleaching, post-bleaching), site (four locations), and their interaction. Bray–Curtis dissimilarities were calculated from benthic cover data and fish and macro-invertebrate abundances. Although PERMANOVA does not accommodate random effects, Site was treated as a fixed factor to allow for inference on group-level differences. Assumptions of homogeneity of multivariate dispersion were assessed using the betadisper function. For the most represented indicators within each community, linear mixed-effects models (LMMs) were fitted using the lmer function from the lme4 package (Bates et al., 2015). In these models, time was included as a fixed factor and site as a random intercept to account for spatial variation. The time variable was treated as categorical and re-leveled to use the pre-bleaching period as the reference level. Degrees of freedom and p-values were calculated using Satterthwaite's approximation, as implemented in the lmerTest package (Kuznetsova et al., 2017). For the benthic community, the analysed indicators included hard coral cover (HC), a combined abiotic category (AB) comprising rock (RC), rubble (RB), sand (SD), and silt (SI), as well as other cover (OT). For the fish community, the indicators included butterflyfish, snappers, sweetlips, and groupers. For the macro-invertebrates, the selected groups were Diadema urchins, crown-of-thorns starfish, and giant clams, categorised into individuals with a shell length $\leq$10 cm and >10 cm. All analyses were performed in R version 4.4.2 (R Core Team, 2021).

3. Results

3.1. Substrate characterisation

The non-metric multidimensional scaling (NMDS) ordination (2D, stress = 0.148; Fig. 3) revealed moderate differentiation in substrate composition across periods and sites. Rasdhoo Madivaru, the only oceanic reef in the dataset, displayed tightly clustered points across all time periods, suggesting a relatively consistent benthic composition over time. In contrast, lagoon sites Kuda Falhu, Dhega Thila and Banana Reef displayed broader spread and clearer separation across the NMDS space, particularly during and after the bleaching period. These spatial patterns may reflect differences in reef type and exposure, with lagoonal reefs appearing more responsive to bleaching disturbances and their subsequent recovery trajectories.

PERMANOVA indicated significant effects of period (R^2 = 0.063, p = 0.001), site (R^2 = 0.169, p = 0.001), and their interaction (R^2 = 0.077, p = 0.001) on community composition (Table 2). However, the assumption of homogeneity of dispersion was violated (betadisper F = 17.96, p < 0.001), indicating significant differences in within-group variability. Notably, the pre-bleaching condition exhibited lower

Table 2
Results of the PERMANOVA test applied to the benthic community. Site = Dhega Thila (DT), Rasdhoo Madivaru (RM), Kuda Falhu (KF) and Banana Reef (BR); period = pre-bleaching, bleaching, and post-bleaching. The bold values indicate significance (p < 0.05).

PERMANOVA					
Source	**Df**	**Ss**	**R^2**	**F**	***p***
Period (p)	2	2.704	0.063	12.629	**0.001**
Site (s)	3	7.238	0.169	22.540	**0.001**
Period × Site (p × s)	6	3.288	0.077	5.119	**0.001**
Residual	276	29.543	0.690		
Total	287	42.772	1.000		

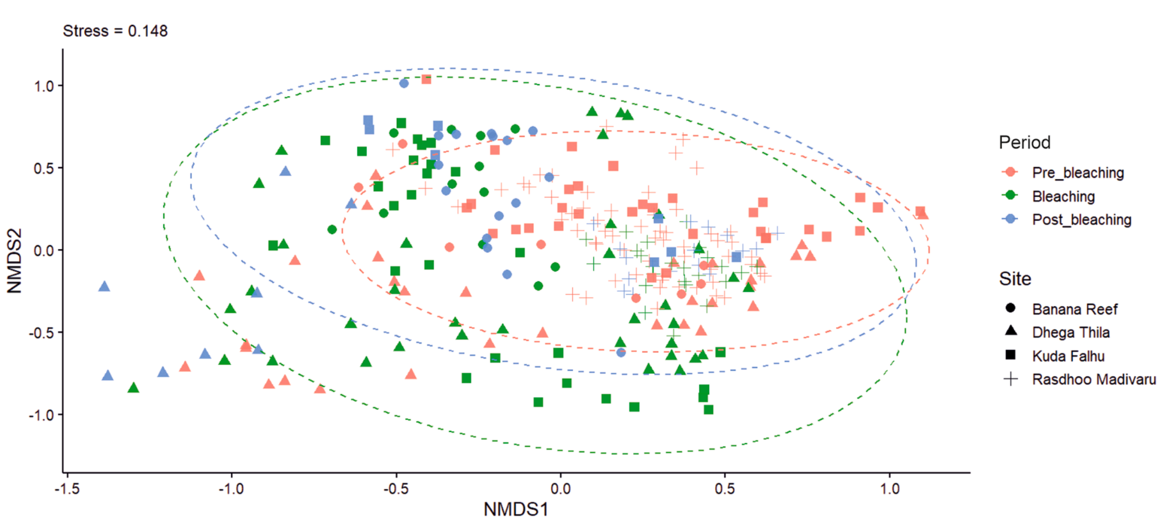

Fig. 3. Non-metric multidimensional scaling (NMDS) plot based on Bray–Curtis dissimilarities showing variation in substrate composition across different time periods and sites. Each point represents a replicate transect, with shapes indicating different sites (Banana Reef = circles, Dhega Thila = triangles, Kuda Falhu = squares, Rasdhoo Madivaru = crosses) and colours indicating time periods (pre_bleaching = red, bleaching = green, post_bleaching = blue). Ellipses represent 95 % confidence intervals for each time period. The stress value of 0.148 indicates a reasonable two-dimensional representation of the community structure.

dispersion, suggesting a more stable and homogeneous community structure before the disturbance.

Linear mixed-effects models (Table 3) revealed significant temporal changes in specific benthic components. For hard coral cover (HC), the model indicated a significant decline during the bleaching period (estimate = -15.26 ± 2.22, $p < 0.001$) and a partial recovery post-bleaching (estimate = -8.87 ± 2.92, $p = 0.003$) relative to the pre-bleaching baseline. For the category 'abiotic' (AB), the model showed a significant increase during the bleaching period (estimate = 12.39 ± 2.47, $p < 0.001$), followed by a non-significant increase post-bleaching (estimate = 4.96 ± 3.25, $p = 0.128$) compared to the baseline. In the case of 'other' (OT), the baseline cover was low (8.66 ± 7.22) and changes over time were not statistically significant, with a slight non-significant increase during bleaching and post bleaching (respectively estimate = 1.33 ± 2.23, $p = 0.553$ and estimate = 5.25 ± 2.94, $p = 0.075$). Fig. 4 shows trends over time for the substrate indicators in the four dive sites. The oceanic reef Rasdhoo Madivaru showed the least impact, maintaining 30–50 % HC cover throughout. Sites Kuda Falhu and Dhega Thila experienced the greatest declines, with Dhega Thila showing no significant post-bleaching recovery and HC dropping to 4.4 ± 1.9 %. AB substrate dominated at Kuda Falhu and Banana Reef, particularly post-bleaching. Recently killed corals (RKC) peaked at Dhega Thila and Kuda Falhu during the bleaching event. The OT category, including mainly the carpet corallimorph *Discosoma* sp., was notably prevalent post-bleaching at Dhega Thila, recovering after declines during bleaching.

Table 3
Summary of linear mixed-effects models (LMMs) assessing the effect of time period (Pre-bleaching, Bleaching, Post-bleaching) on the most represented benthic indicators: 'HC' hard coral, 'AB' abiotic and 'OT' other. Models include site as a random effect to account for spatial variability. Fixed effects report estimates, standard errors, degrees of freedom, t-values, and p-values. Random effects include variance and standard deviation for site and residuals. Significant *p*-values are shown in bold ($p < 0.05$).

HC	**Fixed Effects**	**Estimate**	**Std. Error**	**df**	**t value**	***p*-value**
	(Intercept) Pre_bleaching	31.63	4.51	3.38	7.01	**0.004**
	Time Bleaching	−15.26	2.22	283.3	−6.88	**<0.001**
	Time Post_bleaching	−8.87	2.92	284.7	−3.04	**0.003**
	Random effects	**Variance**	**Std. Dev.**			
	Site	71.5	8.46			
	Residual	276.8	16.64			
AB	**Fixed Effects**	**Estimate**	**Std. Error**	**df**	**t value**	**p-value**
	(Intercept) Pre_bleaching	53.75	7.48	3.14	7.19	**0.005**
	Time Bleaching	12.39	2.47	282.6	5.03	**<0.001**
	Time Post_bleaching	4.96	3.25	283.6	1.53	0.128
	Random effects	**Variance**	**Std. Dev.**			
	Site	211.3	14.54			
	Residual	341.2	18.47			
OT	**Fixed Effects**	**Estimate**	**Std. Error**	**df**	**t value**	**p-value**
	(Intercept) Pre_bleaching	8.66	7.22	3.18	1.2	0.312
	Time Bleaching	1.33	2.23	282.5	0.59	0.553
	Time Post_bleaching	5.25	2.94	283.4	1.79	0.075
	Random effects	**Variance**	**Std. Dev.**			
	Site	198.1	14.08			
	Residual	279.3	16.71			

3.2. Fish community

Non-metric multidimensional scaling (2D, stress = 0.209, Fig. 5) based on Bray-Curtis dissimilarities revealed a small temporal shift in fish community composition across the three survey periods (pre-bleaching, bleaching, post-bleaching), although the moderate stress value suggests the pattern should be interpreted cautiously. Permutational multivariate analysis of variance (PERMANOVA) showed significant effects of period ($R^2 = 0.042$, $p = 0.001$), site ($R^2 = 0.060$, $p = 0.001$), and their interaction ($R^2 = 0.044$, $p = 0.001$) on fish assemblages (Table 4). However, tests for homogeneity of multivariate dispersions (betadisper) revealed significant differences among groups for both period and site ($F = 4.98$, $p < 0.05$), indicating that unequal group variances may influence PERMANOVA results. Notably, the pre-bleaching condition showed lower dispersion, indicating a more stable and homogeneous community structure prior to the bleaching event.

Linear mixed-effects models revealed significant temporal variation in the abundance of the most represented fish indicators (Table 5). Butterflyfish abundance declined significantly during the bleaching period compared to pre-bleaching conditions (estimate = -0.78 ± 0.29, $p = 0.007$). Still, it recovered to levels not significantly different from pre-bleaching in the post-bleaching period ($p = 0.36$). Sweetlips showed a significant increase in abundance post-bleaching relative to pre-bleaching (estimate = 0.39 ± 0.13, $p = 0.002$), with no significant change during bleaching ($p = 0.26$). Snapper abundance increased significantly both during bleaching (estimate = 0.65 ± 0.28, $p = 0.021$) and post-bleaching periods (estimate = 1.36 ± 0.38, $p < 0.001$), indicating a strong positive temporal trend. In contrast, grouper abundance did not vary significantly in the three periods, maintaining stable levels. The factor site was modelled as a random intercept in all cases to account for spatial variation. Fig. 6 illustrates temporal trends in fish abundance across the three survey periods at the four dive sites.

3.3. Macro-invertebrates community

Non-metric multidimensional scaling (NMDS; 2D solution, stress = 0.139; Fig. 7) based on Bray-Curtis dissimilarities revealed a moderate temporal shift in macro-invertebrate community composition across the three survey periods (pre-bleaching, bleaching, and post-bleaching). Overlapping confidence ellipses suggest partial separation among periods, with a noticeable shift in community structure during the bleaching period. Among the four dive sites, Rasdhoo Madivaru exhibited the least variation in macro-invertebrate community composition across the survey periods. Its central clustering in the NMDS space suggests a relatively stable assemblage over time, contrasting with sites like Kuda Falhu, which showed greater temporal shifts, particularly during the bleaching period.

These patterns were supported by PERMANOVA results, which showed significant differences in community composition across period ($R^2 = 0.035$, $p = 0.005$), site ($R^2 = 0.165$, $p = 0.001$), and their interaction ($R^2 = 0.071$, $p = 0.001$) (Table 6).

Tests for homogeneity of multivariate dispersion (betadisper) showed no significant differences in dispersion among sites ($p = 0.21$), confirming that PERMANOVA results were not driven by heterogeneity in spread. However, dispersion varied significantly among time periods ($F = 4.06$, $p = 0.018$), indicating a temporal shift in assemblage variability, particularly during and after the bleaching event.

Linear mixed-effects models (LMMs, Table 7) revealed that *Diadema* urchins significantly declined during the bleaching period (estimate = -0.06 ± 0.03, $p = 0.018$) and did not recover post-bleaching. Crown-of-thorns sea stars (COT, *Acanthaster planci*) also declined during bleaching (estimate = -0.06 ± 0.02, $p = 0.013$) but significantly increased in abundance post-bleaching compared to pre-bleaching levels (estimate = 0.10 ± 0.02, $p < 0.001$). Giant clams ≤10 cm showed a delayed decline, with significantly lower abundance post-bleaching (estimate = -0.08 ± 0.03, $p = 0.002$). In contrast, giant clams >10 cm did not exhibit any

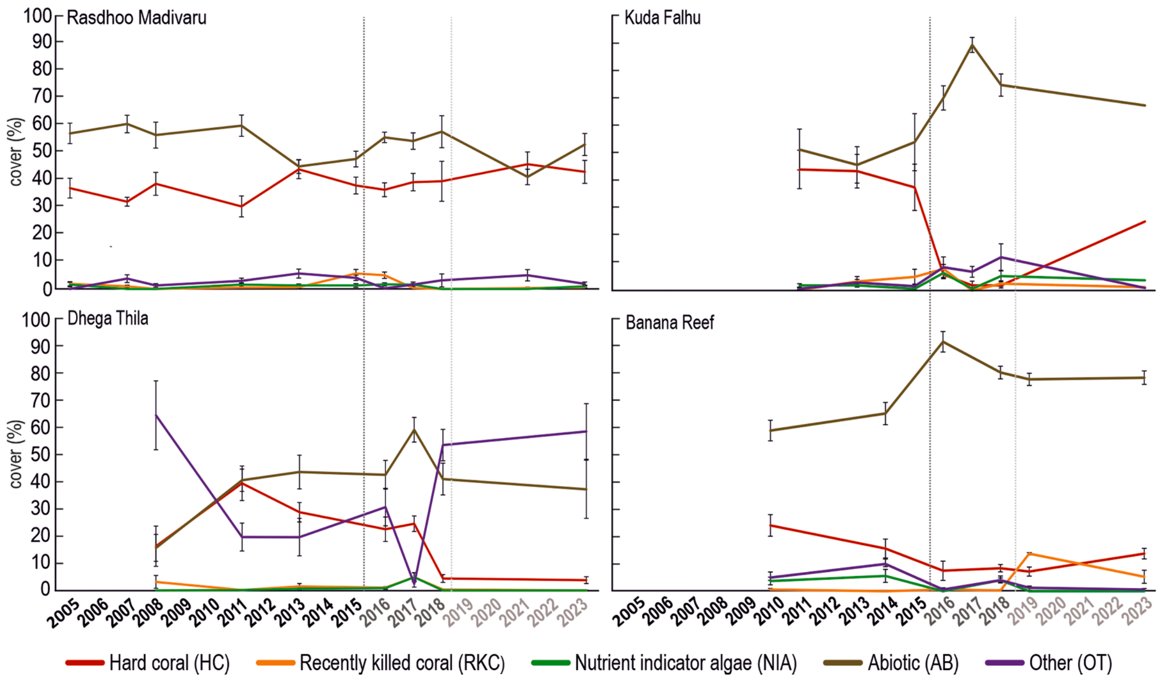

Fig. 4. Percent cover (%) of benthic community composition at the four dive sites over time: Rasdhoo Madivaru (oceanic reef) and Kuda Falhu, Dhega Thila, and Banana Reef (lagoonal reefs). To improve readability, three different shades are used in the x-axis to indicate the time periods considered: pre-bleaching (2005–2015, black), bleaching (2016–2018, dark grey), and post-bleaching (2019–2023, light grey). Two dotted vertical lines indicate the onset of the bleaching (2016) and post-bleaching (2019) periods. Data are presented as mean abundance ± standard error (SE).

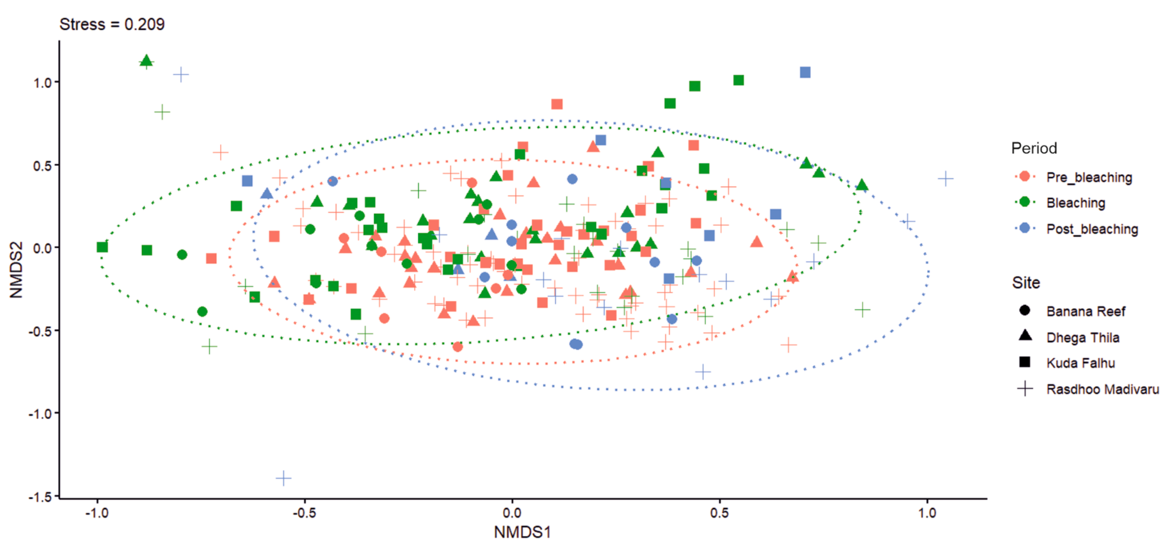

Fig. 5. Non-metric multidimensional scaling (NMDS) plot based on Bray–Curtis dissimilarities showing variation in fish abundance across different periods and sites. Each point represents a replicate transect, with shapes indicating different sites (Banana Reef = circles, Dhega Thila = triangles, Kuda Falhu = squares, Rasdhoo Madivaru = crosses) and colours indicating periods (pre_bleaching = red, bleaching = green, post_bleaching = blue). Ellipses represent 95 % confidence intervals for each period. The stress value of 0.209 indicates a low to moderate fit; the two-dimensional solution provides a marginally acceptable representation of the community structure.

significant temporal trend (all $p > 0.1$). Fig. 8 illustrates temporal trends in fish abundance across the three survey periods at the four dive sites.

4. Discussion

This longitudinal study across four dive sites over 19 years has illuminated the varied responses exhibited by Maldivian reefs in the face of both global and local pressures. The Republic of Maldives, characterised by its scattered and dispersed archipelago (Dunhya et al., 2017), experiences spatial physical variability that intersects with localised anthropogenic influences (Nepote et al., 2016; Pancrazi et al., 2020). This combination of factors leads to varying responses to global stressors, thereby challenging the prediction of future trends at a national level.

Rasdhoo Madivaru, the only oceanic (outer ridge) reef included in this study, exhibited a pattern consistent with trends previously reported for exposed reefs in the Maldives (Cowburn et al., 2019; Montefalcone et al., 2018, 2020). Remarkably, this site exhibited resistance during the 2016 bleaching event, with no observable coral loss and hard coral (HC) cover remaining stable at approximately 40–45 %. However, despite

Table 4
Results of the PERMANOVA test applied to the fish community. Site = Dhega Thila (DT), Rasdhoo Madivaru (RM), Kuda Falhu (KF) and Banana Reef (BR); period = pre-bleaching, bleaching, and post-bleaching. The bold values indicate significance ($p < 0.05$).

PERMANOVA					
Source	**Df**	**Ss**	**R^2**	**F**	***p***
Period (p)	2	1.181	0.042	6.322	**0.001**
Site (s)	3	1.717	0.060	6.125	**0.001**
Site × Period (s × p)	6	1.247	0.044	2.224	**0.001**
Residual	257	24.016	0.853		
Total	268	28.161	1.000		

this apparent stability, no substantial increase in coral cover has been recorded since 2016, suggesting that other factors, such as frequent visitation by divers and snorkelers (Roche et al., 2016), may be limiting further growth. Reducing site use intensity and enhancing conservation education could help promote coral recovery, potentially increasing both ecological value and tourist satisfaction (Sorice et al., 2007).

The only detectable sign of disturbance during the bleaching period was a temporary increase in recently killed corals (RKC) in 2015 and 2016. The fish community remained stable, with moderate overall abundance and a consistent presence of butterflyfish, snappers, and parrotfish as key indicators of the impact on the reefs. Macro-invertebrate abundance also remained low but was well distributed among indicator taxa. Notably, the presence of giant clams (both ≤10 cm and >10 cm) and sea cucumbers is of interest, as these species are often depleted in areas with high fishing pressure. Their presence at Rasdhoo Madivaru may indicate indirect protective effects from the tourism sector, which, by prioritising the site's aesthetic and ecological quality for divers, could limit extractive uses such as local fisheries. Such outcomes underscore the positive influence of tourism, a phenomenon primarily studied around resort islands (Domroes, 2001; Moritz et al., 2017) but potentially applicable to local islands where the community recognises the value of a healthy reef. These findings suggest that long-term monitoring can help disentangle the combined effects of disturbance, natural resilience, and local human pressures.

Conversely, the three lagoon (sheltered) dive sites presented a markedly contrasting narrative. These sites experienced more pronounced effects from the 2016 bleaching event compared to the oceanic site, aligning with broader trends (Montefalcone et al., 2018, 2020). Their geomorphological characteristics, distinguished by reduced currents and limited water exchange, resulted in elevated temperatures and diminished mixing layers (De Falco et al., 2020). However, the distinct geographical positions and varying levels of local human influence at each of these sites yielded disparate responses in terms of impact severity and subsequent recovery trajectories.

Dhega Thila showcased a distinctive trajectory characterised by a notable increase of the indicator other (OT), identified as *Discosoma* sp. corallimorpharians (Fig. 9a). This particularly increased at the shallow-water survey station between 3 and 4 m that had historically (before the 2016 bleaching event) been characterised by over 70 % coral cover (principally of branching and table *Acropora* spp.) (Fig. 9b) .

The shift in benthic composition from scleractinian corals to corallimorph-dominated benthos, became particularly pronounced following the 2016 bleaching event, although signs of this shift were evident at deeper depth (>7 m) as early as the years following the 1998 bleaching event, as the site was first dived by one of the authors in 2005 (JLS). Despite a positive recovery following 1998, the 2016 bleaching event determined a subsequent decline in HC cover in shallow depths, coinciding with a peak in OT cover. This trend highlighted the final steps of a phase shift happening on the site (Norström et al., 2009; Alvin et al., 2021). While conventional understanding associates phase shifts with macroalgae overgrowth, other types of phase shifts involving cnidarians, such as anemones and corallimorphs, are underreported (Work et al., 2008). The exact mechanisms driving these transitions remain poorly understood, with factors such as bleaching, typhoons, overfishing, nutrient influx, coastal development, and tourism implicated in some studies (Chen and Dai, 2004, Kuguru et al., 2004). Notably, Dhega Thila's popularity among divers, coupled with sustained human

Table 5
Summary of linear mixed-effects models (LMMs) examining the effect of Time on the abundance of key macro-invertebrate indicators. Models included Time as a fixed factor, with Pre_bleaching set as the reference level, and Site as a random intercept to account for repeated measures. Significant *p*-values are shown in bold ($p < 0.05$).

Butterflyfish	**Fixed Effects**	**Estimate**	**Std. Error**	**df**	**t value**	**p-value**
	(Intercept) Pre_bleaching	4.446	0.35	4.57	12.69	**<0.001**
	Time Bleaching	−0.775	0.29	265.59	−2.7	**0.007**
	Time Post_bleaching	0.356	0.4	264.07	0.91	0.362
	Random effects	**Variance**	**Std. Dev.**			
	Site	0.33	0.58			
	Residual	4.43	2.11			
Sweetlips	**Fixed Effects**	**Estimate**	**Std. Error**	**df**	**t value**	**p-value**
	(Intercept) Pre_bleaching	0.22	0.1	4.96	2.23	0.076
	Time Bleaching	−0.1	0.09	265.91	−1.12	0.262
	Time Post_bleaching	0.39	0.13	260.97	3.08	**0.002**
	Random effects	**Variance**	**Std. Dev.**			
	Site	0.02	0.16			
	Residual	0.47	0.68			
Snapper	**Fixed Effects**	**Estimate**	**Std. Error**	**df**	**t value**	**p-value**
	(Intercept) Pre_bleaching	0.69	0.4	3.54	1.7	0.173
	Time Bleaching	0.65	0.28	264.88	2.32	**0.021**
	Time Post_bleaching	1.36	0.38	265.68	3.55	**0.000**
	Random effects	**Variance**	**Std. Dev.**			
	Site	0.51	0.71			
	Residual	4.24	2.06			
Grouper	**Fixed Effects**	**Estimate**	**Std. Error**	**df**	**t value**	**p-value**
	(Intercept) Pre_bleaching	0.65	0.12	3.69	5.64	**0.006**
	Time Bleaching	−0.14	0.1	265.68	−1.35	0.177
	Time Post_bleaching	−0.05	0.14	261.91	−0.41	0.681
	Random effects	**Variance**	**Std. Dev.**			
	Site	0.03	0.19			
	Residual	0.54	0.74			

Fig. 6. Average abundance (N°/20 m^2) of the fish community for the four dive sites over time: Rasdhoo Madivaru (oceanic reef) and Kuda Falhu, Dhega Thila, and Banana Reef (lagoonal reefs). To improve readability, three different shades are used in the x-axis to indicate the time periods considered: pre-bleaching (2005–2015, black), bleaching (2016–2018, dark grey), and post-bleaching (2019–2023, light grey). Two dotted vertical lines indicate the onset of the bleaching (2016) and post-bleaching (2019) periods. Data are presented as mean abundance ± standard error (SE).

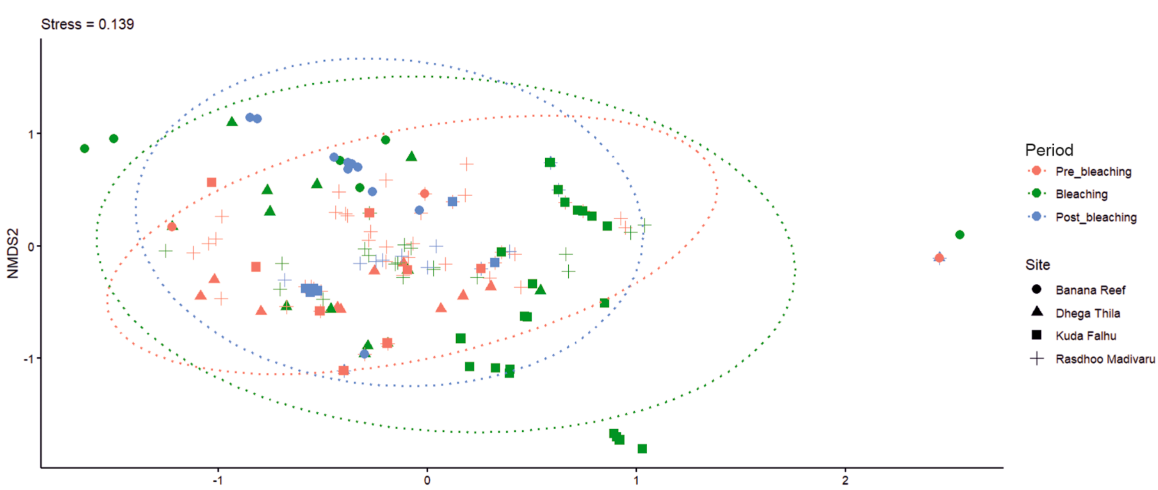

Fig. 7. Non-metric multidimensional scaling (NMDS) plot based on Bray–Curtis dissimilarities showing variation in macro-invertebrates abundance across different periods and sites. Each point represents a replicate transect, with shapes indicating different sites (Banana Reef = circles, Dhega Thila = triangles, Kuda Falhu = squares, Rasdhoo Madivaru = crosses) and colours indicating periods (pre_bleaching = red, bleaching = green, post_bleaching = blue). Ellipses represent 95 % confidence intervals for each period. The stress value of 0.209 indicates a low to moderate fit; the two-dimensional solution provides a marginally acceptable representation of the community structure.

pressure (e.g. nearby dredging activities), likely exacerbates the hindrance to recovery. Similar instances of phase shifting towards corallimorph-dominated reefs have been documented in the Pacific (Carter et al., 2019; Jacobs et al., 2021). Dhega Thila's fish abundance inversely mirrored fluctuations in OT cover. The decline post-2016 bleaching is likely attributed to the loss of coral complexity (González-Rivero et al., 2017; Ferrari et al., 2018) and the proliferation of Corallimorpharia. Conversely, macro-invertebrate abundance remained consistently low, especially post-2008, due to the competition for the substrate with the Corallimorpharia, where other organisms such

Table 6
Results of the PERMANOVA and PAIRWISE tests applied to the macro-invertebrates' community. Site = Dhega Thila (DT), Rasdhoo Madivaru (RM), Kuda Falhu (KF) and Banana Reef (BR); period = pre-bleaching, bleaching, and post-bleaching. The bold values indicate significance ($p < 0.05$).

PERMANOVA					
Source	**Df**	**Ss**	**R^2**	**F**	***p***
Period (p)	2	2.151	0.035	4.980	**0.001**
Site (s)	3	10.158	0.165	15.670	**0.001**
Site × Period (s × p)	6	4.385	0.071	3.382	**0.001**
Residual	208	44.946	0.729		
Total	219	61.640	1.000		

as sea cucumbers, giant clams and urchins remain inhibited from thriving (limited shelter and food availability). This case study presents a rare opportunity to examine the ecological trajectory of a reef undergoing a non-algal phase shift under moderate anthropogenic pressure. When a reef fails to recover its scleractinian coral, fish, and macro-invertebrate communities, it may instead facilitate the dominance of opportunistic species such as those within Corallimorpharia. Dhega Thila thus provides a valuable model for understanding the long-term consequences of compounded disturbances (e.g. bleaching events) and human activities (e.g. tourism), and for identifying thresholds beyond which passive recovery is unlikely. This information is critical for anticipating alternative stable states and for guiding active intervention and management in similarly impacted reef systems.

Kuda Falhu diverges from the aforementioned sites due to its distinct local usage. Unlike recreational dive sites, this location is primarily utilised for fishing, with additional human impact coming from sedimentation from dredging activities, but probably low as the nearest resort is 1 km distant from the site, and long established. However, despite experiencing a considerable decline in HC cover from 2016 to 2018 (from 70 % cover to 1 % cover in the shallow transect), Kuda Falhu demonstrated a notable recovery by 2023 (back to 40 % cover of *Acropora* corals at the shallow transect), confirming that with lower local impacts the recovery process can be significant.

On a broader scale, Kuda Falhu provides valuable insight into coral reef resilience under low anthropogenic pressure. Its trajectory suggests that even reefs subjected to extractive use, such as small-scale fisheries, may retain substantial recovery potential if direct habitat degradation (e.g., dredging activities or overcrowding) is limited. As such, Kuda Falhu's recovery trajectory may serve as a baseline for identifying thresholds of impact beyond which natural recovery becomes compromised, and for prioritising management actions in similar reef settings across the region.

Banana Reef presents a contrasting scenario. Despite being designated as a marine protected area (MPA) since 1998, the site has shown no signs of ecological recovery following the 2016 bleaching event. As one of the most frequently visited dive sites in the region, popular for check dives and snorkelling, it experiences intense tourism pressure. This is further compounded by its proximity to Hulhumalé Island, the second most populous island in the Maldives, which continues to undergo large-scale dredging and land reclamation (Maldives Republic, 2024).

These overlapping human pressures appear to have hindered coral regrowth, suggesting that protection in name alone is insufficient. Without effective management, regulation, and enforcement, MPAs may fail to deliver conservation outcomes, particularly in urban-adjacent or heavily trafficked areas (Montefalcone et al., 2020; Pancrazi et al., 2020; Relano and Pauly, 2023).

Banana Reef underscores the limitations of passive protection in high-use zones and highlights the need for integrated, enforceable management frameworks that address both direct and indirect human impacts. This case also illustrates the critical importance of aligning MPA designation with realistic, site-specific enforcement capacity, particularly in reef systems located near expanding urban centers.

Kuda Falhu and Banana Reef exhibited contrasting trends in fish and macro-invertebrate communities. Kuda Falhu demonstrated higher fish abundance and diversity, even with fishing pressure, while Banana Reef, although a marine protected area, had lower fish abundance and

Table 7
Summary of linear mixed-effects models (LMMs) examining the effect of Time on the abundance of key macro-invertebrate indicators. Models included Time as a fixed factor, with Pre_bleaching set as the reference level, and Site as a random intercept to account for repeated measures. Significant *p*-values are shown in bold ($p < 0.05$).

***Diadema* urchin**	**Fixed Effects**	**Estimate**	**Std. Error**	**df**	**t value**	***p*-value**
	(Intercept) Pre_bleaching	0.25	0.15	2.97	1.64	0.201
	Time Bleaching	−0.06	0.03	214.95	−2.39	**0.018**
	Time Post_bleaching	−0.01	0.03	214.33	−0.28	0.778
	Random effects	**Variance**	**Std. Dev.**			
	Site	0.09	0.30			
	Residual	0.07	0.27			
Crown of thorns	**Fixed Effects**	**Estimate**	**Std. Error**	**df**	**t value**	**p-value**
	(Intercept) Pre_bleaching	0.06	0.06	3.06	1.04	0.371
	Time Bleaching	−0.06	0.02	216.87	−2.50	**0.013**
	Time Post_bleaching	0.10	0.02	215.47	4.36	**< 0.001**
	Random effects	**Variance**	**Std. Dev.**			
	Site	0.01	0.12			
	Residual	0.05	0.23			
Giant clam < 10	**Fixed Effects**	**Estimate**	**Std. Error**	**df**	**t value**	**p-value**
	(Intercept) Pre_bleaching	0.19	0.05	3.36	3.98	**0.023**
	Time Bleaching	−0.01	0.03	216.20	−0.09	0.928
	Time Post_bleaching	−0.08	0.03	216.50	−3.19	**0.002**
	Random effects	**Variance**	**Std. Dev.**			
	Site	0.01	0.09			
	Residual	0.07	0.27			
Giant clam > 10	**Fixed Effects**	**Estimate**	**Std. Error**	**df**	**t value**	**p-value**
	(Intercept) Pre_bleaching	0.24	0.08	2.86	3.04	0.059
	Time Bleaching	−0.04	0.03	216.62	−1.30	0.194
	Time Post_bleaching	−0.02	0.03	215.13	−0.87	0.387
	Random effects	**Variance**	**Std. Dev.**			
	Site	0.02	0.15			
	Residual	0.08	0.28			

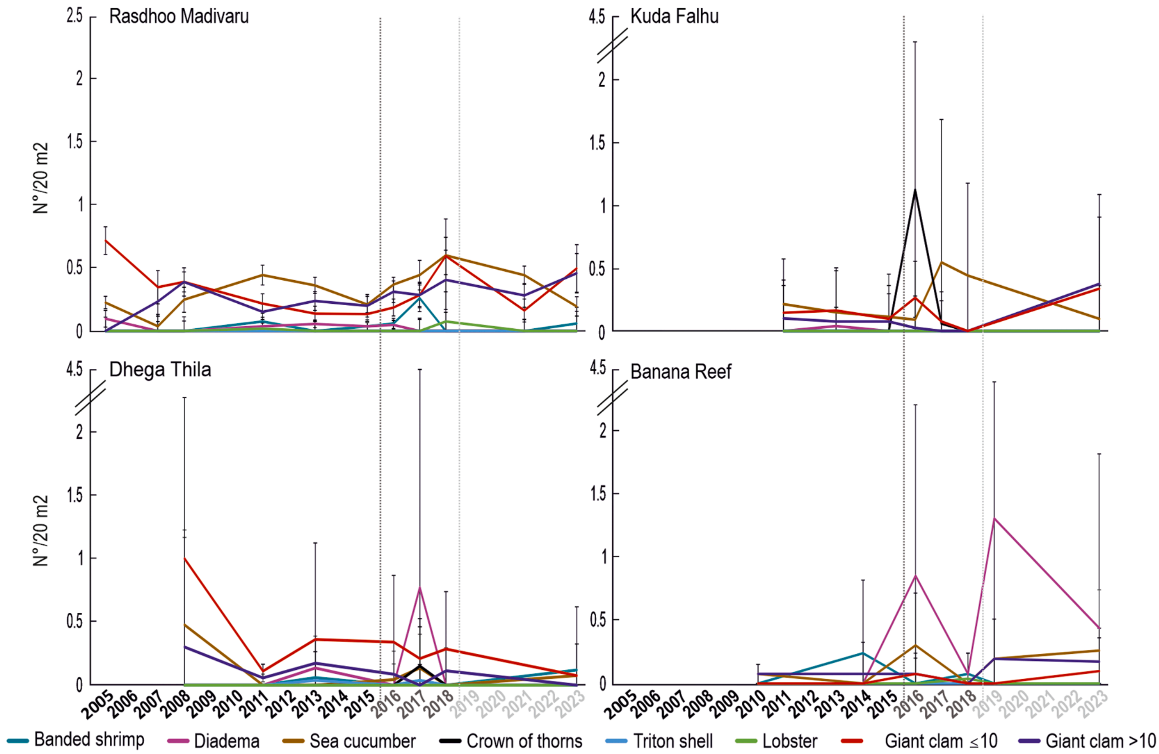

Fig. 8. Average abundance (N°/20 m^2) of the macro-invertebrate community for the four dive sites over time: Rasdhoo Madivaru (oceanic reef) and Kuda Falhu, Dhega Thila, and Banana Reef (lagoonal reefs). To improve readability, three different shades are used on the x-axis to indicate the time periods considered: pre-bleaching (2005–2015, black), bleaching (2016–2018, dark grey), and post-bleaching (2019–2023, light grey). Two dotted vertical lines indicate the onset of the bleaching (2016) and post-bleaching (2019) periods. For Kuda Falhu, Dhega Thila, and Banana Reef, the y-axes are cut to extend the maximum value to 4.5 (instead of 2.5) to accommodate high standard errors. Data are presented as mean abundance ± standard error (SE).

diversity. The macro-invertebrate abundance was higher at Banana Reef compared to Kuda Falhu, especially for the sea cucumber in the pre-bleaching period and the *Diadema* urchins in the post-bleaching period. Both sites recorded the presence of crown-of-thorns (COT) sea stars. Known for their voracious corallivorous nature, COT outbreaks have contributed to coral reef crises in the Indo-Pacific region (Uthicke et al., 2024), with heightened incidence recorded in the Maldives during 2015 and 2016 (Saponari et al., 2018), likely exacerbated by coral bleaching-induced stress.

These results highlight once again how improper management has left Maldivian MPAs in a ’paper park’ status, legally designated but entirely ineffective (Relano and Pauly, 2023). In the Maldives, there are 93 established marine protected areas and 3 UNESCO Biosphere Reserves. However, due to the scattered nature of these areas, enforcement and control are often weak. The case of Addu Atoll exemplifies this issue: despite being a UNESCO Biosphere Reserve since 2018 (WDPA 555576570), large-scale land reclamation (a total of 190 ha) and dredging activities have been approved by the Ministry of National Planning, Housing, and Infrastructure (MNPHI) as part of the Addu Development Project (2023) in June 2022.

The considerable variability observed among the four study sites underscores the potential for significant fluctuations even within the smallest spatial scales. It is evident that the assessment of the overall health status of Maldivian coral reefs is no longer feasible; instead, a nuanced approach that considers reef classification based on location and local management practices is imperative. Given the escalating frequency and severity of coral bleaching events (Hughes et al., 2018), it is paramount to comprehensively evaluate spatial variability alongside varying levels of reef usage to gain a comprehensive understanding of the trends shaping Maldivian coral reefs and where to apply limited resources to protect healthy reefs. Particularly noteworthy is the disparity in live hard coral cover following bleaching events between sites with comparatively lower human pressure (Rasdhoo Madivaru and Kuda Falhu) and those where human activity is notably intense (Dhega Thila and Banana Reef).

While addressing climate-induced stressors necessitates international cooperation, regional management strategies hold promise in mitigating local human pressures (Lasagna et al., 2014; Dhunya et al., 2017). By implementing targeted measures at the regional level, such as sustainable fishing practices, controlled tourism influx and coastal development regulations, it is possible to alleviate the strain on coral reefs and foster their resilience in the face of ongoing environmental challenges.

In conclusion, the longitudinal study of dive sites across the Maldives has unveiled the intricate dynamics of reef responses to global and local stressors. The observed spatial variability, compounded by localised anthropogenic impacts, underscores the need for context-specific management strategies that account for the unique ecological and socio-economic characteristics of each site. Moving forward, concerted efforts to integrate scientific research, stakeholder engagement, and adaptive management are imperative to safeguarding the resilience and sustainability of Maldivian reefs in the face of ongoing environmental change.

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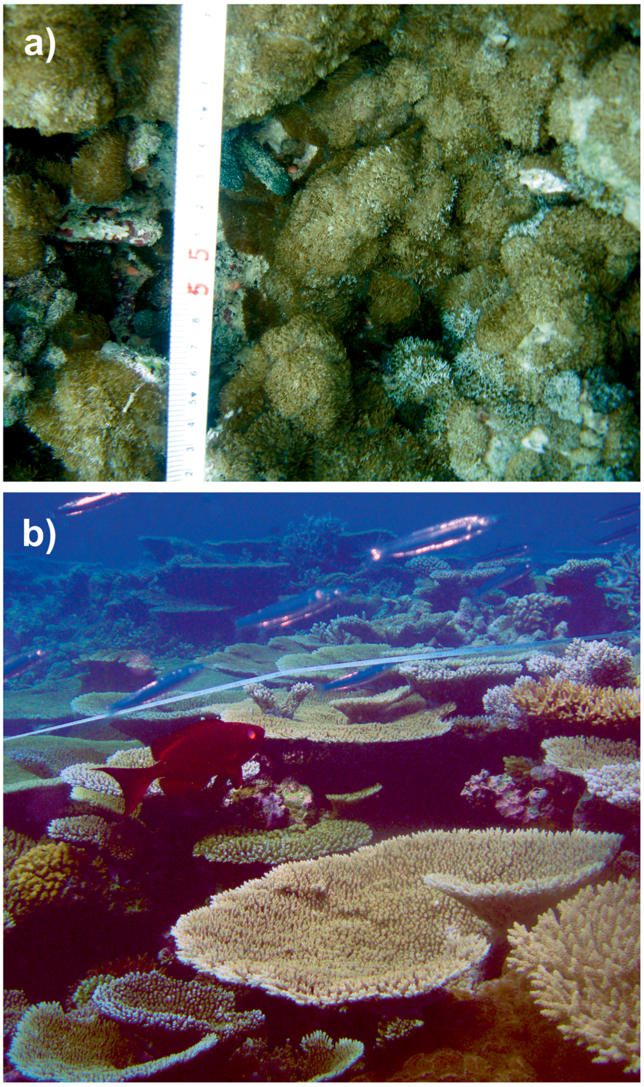

Fig. 9. a) Carpet corallimorph, *Discosoma* sp. dominating the shallow reef habitat (3 m depth) at Dhega Thilla after 2016, b) Dhega Thilla at 3 m displaying over 70 % coral cover before the 2016 bleaching event (photo from 2011). photos: JL Solandt.

CRediT authorship contribution statement

Jean-Luc Solandt: Writing – review & editing, Methodology, Investigation. **Valentina Asnaghi:** Validation, Supervision, Formal analysis, Data curation. **Matthias Hammer:** Writing – review & editing, Methodology, Investigation. **Monica Montefalcone:** Writing – review & editing, Visualization, Validation, Supervision, Resources, Conceptualization. **Irene Sibille:** Writing – review & editing, Investigation, Formal analysis, Data curation, Conceptualization. **Irene Pancrazi:** Writing – review & editing, Writing – original draft, Visualization, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Hassan Ahmed:** Writing – review & editing, Methodology, Investigation. **Arianna Verardo:** Writing – review & editing, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

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.

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Conflicts of interest

The authors declare no conflicts of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript; or in the decision to publish the results.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.rsma.2025.104417.

Data availability

Data will be made available on request.

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