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Reef Check chronicles: A comprehensive analysis of 19 Years of Maldives coral reef history and impacts response

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ARTICLE INFO

Keywords: Maldives Reef check Island management Global warming Anthropic impacts Indian ocean

ABSTRACT

The synergic effect of temperature anomalies and anthropogenic pressure has amplified the negative effects of climate change all around the world. Over an 19-year period, comprehensive coral reef monitoring was conducted throughout the Maldivian central atolls using the Reef Check protocol. The study aims to explore the combined impact of varying degrees of human pressures with climate change effects, and their implications for reef recovery. By categorising reefs based on island management, inhabited, uninhabited, and resort, we examined the benthic community composition and the fish and macro-invertebrate communities, revealing significantly different environmental responses between oceanic and lagoon reefs. Reefs near inhabited and resort islands, subject to higher human pressures, exhibited greater impacts during the 2016 bleaching event. However, some oceanic reefs demonstrated notable post-bleaching recovery. Uninhabited islands, with lower human impact, showed faster post-bleaching recovery. Recognising these distinctions at the reef management level can inform policymakers in crafting targeted management and regulation for safeguarding natural environments, particularly amidst climate change-induced threats.

1. Introduction

Over the past two decades, the synergistic effects of climate change and escalating pressure from human activities have posed severe threats to coral reefs globally, intensifying concerns about their sustainability and resilience (Ateweberhan et al., 2013; He and Silliman, 2019; O'Hara et al., 2021; Pancrazi et al., 2020). Coral reefs, recognised as among the most productive and economically valuable ecosystems on earth, provide a habitat for approximately 25 % of all oceanic species (Shaver and Silliman, 2017). Despite their immense value, coral reefs are inherently susceptible to environmental change and over-exploitation. In 2020, the global average hard coral cover declined by 13.5 %, marking a significant loss from 33.3 % to 28.8 % (Souter et al., 2021). The ENSO phenomenon, which is a natural periodic fluctuation in sea surface temperature (El Niño), is intensifying (Herbert and Dixon, 2002). Rising seawater temperatures, exacerbated by phenomena like the ENSO, have

triggered widespread coral bleaching and mass mortality events, compromising the long-term stability of coral ecosystems and hampering their resilience to local human pressure (Wang, 2018; Hughes et al., 2018; Pancrazi et al., 2020). The third global coral bleaching event was the most severe, widespread, and prolonged bleaching event ever recorded. Beginning in 2014–2015 and lasting until 2016–2017, it led to extensive coral mortality on many reefs, rapid degradation of reef structures, and widespread environmental consequences (Hughes et al., 2018; Eakin et al., 2019).

In numerous developing small island nations, the demand for land coupled with limited space has prompted land reclamation works, which involve transforming sea areas for human use (Bertaud, 2002; Nepote et al., 2016; Heery et al., 2018; Bisaro et al., 2020). Dredging, a central component of these initiatives, directly impacts the natural environment by depositing sand, rock and cement on reefs (Jaap, 2000; Manap and Voulvoulis, 2015; Miller et al., 2016). Another substantial anthropic

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impact is associated with the growth of mass tourism, where ecological threats primarily stem from the built infrastructure, preference for local reef fish (e.g. Serranidae, Lutjanidae and Haemulidae), and transportation required to sustain increased demand. The physical development of resorts and pollution from sewage and waste production collectively contribute to considerable, often irreversible, environmental degradation (Davenport and Davenport, 2006). In tropical regions, recreational diving on coral reefs has witnessed a rapid surge in popularity and participation, and the potential impact of diving activities on coral reefs raises concerns, especially in heavily dived locations (Roche et al., 2016). In these sites, reefs frequently suffer from skeletal breakage, higher incidence of coral diseases and lower coral cover (Tratalos and Austin, 2001; Marshall and Schuttenberg, 2006; Carilli et al., 2010; Guzner et al., 2010; Hasler and Ott, 2008; Lamb et al., 2014). Addressing the escalating anthropogenic pressures on ocean ecosystems is crucial for halting and reversing biodiversity decline. Long-term ecological monitoring plays a pivotal role in identifying stressors, quantifying their impacts, and enhancing our comprehension of ecosystem resilience (Obura et al., 2019; Montefalcone et al., 2020; Andrello et al., 2021; Gonzalez et al., 2024).

In this context, citizen science projects have emerged as powerful tools, fostering public engagement and providing cost-effective means to collect extensive spatiotemporal datasets (Witt et al., 2012; Bonney et al., 2016; Cowburn et al., 2019; Earp and Liconti, 2020). This study focuses on the Republic of Maldives, an archipelago uniquely vulnerable to environmental change due to its small (<1 km), low-lying (~2.5m above the sea level), unconsolidated islands (Woodroffe, 2008; Dhunya et al., 2017). The country experienced marine heatwaves in 1998, 2010 and 2016, with consequential coral bleaching events. While the 2010 bleaching event resulted in minor bleaching (Guest et al., 2012), in 1998 and 2016 the heat waves triggered mass mortality in the country, resulting in respectively $\sim\!95$ % and $\sim\!70$ % of the hard coral cover loss in shallow waters (Morri et al., 2015; Montefalcone et al., 2018; Montefalcone et al., 2020). Furthermore, escalating background local anthropic pressures pose an increasing synergistic threat: tourism, a significant economic driver in the archipelago, has surged over the last 20 years, contributing nearly 30 % to the country's GDP in 2011 and attracting almost 2,000,000 visitors in 2023 (Scheyvens et al., 2011; Ministry of Tourism, Republic of Maldives). Concurrently, dredging activities and land reclamation, especially in the central atolls, have intensified since the 1970s, posing additional challenges to the delicate balance of marine ecosystems (Fallati et al., 2017; Hassan Ahmed, pers.

Against this backdrop, we examined an extensive 19-year dataset (2005–2023) from the Maldives, encompassing periods before, during, and after the major 2016 bleaching event (Montefalcone et al., 2018). The aim of the study is to investigate how varying degrees of human pressures influence Maldivian coral reefs, their capacity to withstand disturbances caused by climate change, and their subsequent recovery. To examine the effects of different degrees of human pressures, the surveyed sites were categorised into distinct levels of management: inhabited islands, which include reefs surrounding cities or villages; uninhabited islands, covering submerged reef formations (giri and thila), lagoons, and reefs around uninhabited islands; and resort islands, encompassing all reefs surrounding resort islands (Moritz et al., 2017). Determining the exact average population on inhabited islands in the Maldives is challenging. However, the 2022 census (Maldives Bureau of Statistics, 2022) reported that out of 187 inhabited islands, 20 administrative islands have a population above 2,000, while the capital, Malé, alone has 212,138 residents. Inhabited islands are expected to experience the highest human pressure due to coastal modifications and direct anthropogenic impacts (Moritz et al., 2017). In contrast, uninhabited islands generally experience the lowest human impact, though many are frequently visited for recreational diving activities. Resort islands represent a unique case of anthropogenic influence. In the Maldives, the tourism industry began in 1972 with just two hotels. Since then, it has expanded rapidly, with over 100 operational resorts occupying entire islands, and many more still under construction. While they are often designed to maintain a natural aesthetic and have ownership over their house reefs, they undergo significant coastal modifications due to construction and infrastructure development. Additionally, inadequate waste management practices can exacerbate environmental impacts (Scheyvens, 2011). A notable practice on these islands is 'fish feeding,' which attracts marine species for tourism purposes but can disrupt fish behaviour, alter species distribution, increase predation on certain species, and pose risks to both marine life and tourists (Moritz et al., 2017; Patroni et al., 2018).

Beyond coastal modifications, the expansion of mass tourism has significantly increased the demand for reef fish to supply resorts and restaurants, leading to the daily harvest of large numbers of Serranidae, Lutjanidae, and Haemulidae (Chang, 2020). Additionally, reef fish consumption has risen among local populations, with a growing preference for these species over the last generation (Yadav et al., 2021). The Maldives Ministry of Fisheries and Ocean Resources estimates the annual reef fish harvest to be between 18,000 and 23,400 tonnes, but specific data on fishing pressure across island management types is lacking. Local communities often travel to nearby uninhabited or resort islands (when permitted) to fish using handlines and fishing poles. The most targeted reef fish groups include groupers (Serranidae), snappers (Lutjanidae), and live bait fish (e.g., certain species of mackerel, fusiliers, and triggerfish). Macro-invertebrate fishing pressure is even harder to assess due to limited data. While some information exists on exported species, such as sea cucumbers (Ministry of Fisheries, Marine Resources and Agriculture, 2020), there is even less data on locally consumed species like lobsters.

To conduct a thorough analysis of the reef community, we carried out Reef Check benthic community, fish and macro-invertebrate surveys. Historically, benthic community indicators have served as crucial tools for assessing coral health and characterising coral reefs (Morri et al., 1995; Bianchi et al., 1997; Morri et al., 2015; Morri et al., 2017; Montefalcone et al., 2018; Montefalcone et al., 2020). In addition, fish and macro-invertebrate communities provide essential information regarding local pressures, such as overfishing and sedimentation, as well as changes in substrate composition, and the abundance of important herbivores (e.g. Scaridae) in degraded reefs (Harding et al., 2003; Hodgson et al., 2006; Purcell et al., 2016; Habibi et al., 2007; Shantz et al., 2020). Due to their varying sensitivities to environmental impacts, these three indicator groups have been assessed and analysed separately. This approach allows for a more nuanced understanding of the complexities within the reef ecosystem.

This research endeavours to offer valuable insights into the resilience dynamics of Maldivian coral reefs, considering the diverse impacts that stem from human activities. Such an assessment holds the potential to inform the development and implementation of conservation and management strategies aimed at safeguarding these vital ecosystems.

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 covered with water (Dhunya et al., 2017). The climate and oceanographic conditions of the Maldives are primarily shaped by the seasonally reversing Indian monsoon system (Tomczak and Godfrey, 2003). During the northern hemisphere summer (April–November), southwestern winds prevail (*Hulanghu* season), while northeastern winds dominate during winter (December–March, *Iruvaai* season). These wind patterns generate ocean currents that flow westward in winter and eastward in summer (Betzler et al., 2013).

However, the current dynamics within the Maldives are complex, influenced by factors such as tides, wind patterns, atoll geography, and equatorial currents. Due to the archipelago's geographical intricacies and data limitations, providing a comprehensive description of Maldivian currents remains challenging.

From 2005 to 2023, annual research expeditions and local community programs were conducted, gathering data across the central atolls of North Malé, South Malé, Ari, Rasdhoo, Felidhoo, Mulaku, and Vattaru (Fig. 1, Table S1). Tables S2 and S3 summarise the number of reefs surveyed for management type and time period for both ocean and lagoon reefs. Each year, an equal number of ocean reef sites, situated on the outer edges of the atoll rims, and lagoon reef sites, including lagoon patch reefs or the lagoon-facing sides of the atoll rim, were sampled (Lasagna et al., 2008, 2014). Geographical coordinates for each site were recorded using a portable GPS (Table S1). SCUBA diving at depths of 5 and 10 m was employed to apply the international monitoring protocol Reef Check at each site. A total of 387 survey dives covered 108 dive sites, many revisited over the years, primarily focusing on the central atolls due to logistical constraints.

2.2. Thermal stress

During the study period (2005–2023), the average sea surface temperature (SST) in the Maldives was 29.38 ± 0.007 °C (mean \pm SE, NOAA Coral Reef Watch). Seasonal fluctuations were modest, with the coolest months (January–March and July–December, SSTmin) averaging 28.29 \pm 0.007 °C and the warmest months (April–June, SSTmax) reaching

 29.98 ± 0.010 °C, with a typical seasonal deviation of just ±1.69 °C. The third global coral bleaching event began in the Maldives in April 2016, when SST peaked at 31.55 °C. Elevated temperatures persisted until April–May 2018, with SST remaining as high as 31.29 °C.

The 2016-2018 bleaching event coincided with an unprecedented marine heatwave, reaching a record 31.63 °C in May 2016 and producing the highest Degree Heating Weeks (DHWs) ever recorded in the Maldives, 11 DHWs, reflecting extreme and prolonged thermal stress. DHWs, a metric developed by NOAA, measure accumulated heat stress over 12 weeks and are a critical indicator of bleaching risk. Compared to the 19-year study average, the 2016 peak SST represented a $+2.25~^{\circ}\text{C}$ deviation, an exceptional anomaly, given that the Maldives' typical seasonal range is only $\pm 1.69\,^{\circ}\text{C}$ and its climate lacks pronounced variability. SST in the Maldives follows a broad latitudinal gradient, with northern and southern atolls occasionally experiencing different thermal anomalies (Moritz et al., 2017; Cowburn et al., 2019). However, within the central archipelago, where the study sites are located, SST anomalies are relatively homogeneous, and NOAA Coral Reef Watch data have been widely used to represent regional thermal stress in Maldivian studies (Moritz et al., 2017; Cowburn et al., 2019; Chaudhuri et al., 2021).

2.3. Reef Check protocol and field activities

To encompass the diverse range of coral reef indicators, spanning from the benthic community to the fish and macro-invertebrate communities, the Reef Check protocol was selected. Developed in 1997, the

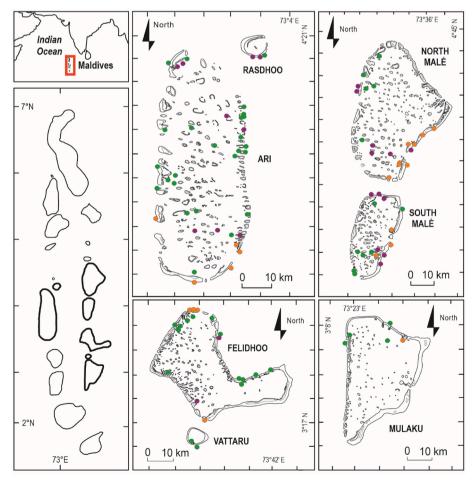


Fig. 1. Map of the Maldives Archipelago with a focus on Ari, Rasdhoo, North Malé, South Malé, Felidhoo, Vattaru and Mulaku atolls. The dots represent surveyed sites: green for uninhabited islands, orange for inhabited islands, and purple for resort islands. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Reef Check protocol aimed to provide a rapid 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, it is ascribed to "citizen science" programmes, relying on 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 surveys, develop a sense of stewardship toward the monitored reefs, leading to an ideological transformation from foreign-influenced organisation to local ownership and coordination (Hodgson, 2001). Reef Check monitoring is conducted exclusively by certified volunteers who complete a standardised 5-day training program. This training ensures that participants can accurately identify the broad taxonomic categories outlined in the protocol. Each site was surveyed via SCUBA diving at 5 m and 10 m depths, employing four 20 m replicate transects parallel to the reef. Transect start and end points were spaced by 5m, 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. Reef Check teams collect four types of data: (1) site description, (2) benthic community cover using the Point Intercept Transect (PIT) method, where data points are recorded every 0.5 m along the transect, and (3) fish and (4) macro-invertebrate abundances, both assessed through visual census along a belt transect measuring 20 m in length and 5 m in width.

Over the 19 years of surveys, certified observers included university students, local community members, and tourists who completed the Reef Check training program. Given this diversity of participants, it was not possible to retrospectively quantify inter-observer variability across years. However, the Reef Check methodology is explicitly designed to minimise observer error by focusing on broad, easily recognisable indicators and by providing standardised global training and certification (Hodgson et al., 1998; Done et al., 2017). In addition, data consistency was supported by the use of replicate transects, exclusion of rare taxa with high identification uncertainty, and the long-term application of the same monitoring protocol.

Indicators were selected based on their economic and ecological value, sensitivity to human impacts, and ease of identification. Categories included in the protocol range from individual species to families (Hodgson et al., 2006). As a citizen science methodology, Reef Check relies on easily recognisable groups rather than species-level identification, with exceptions made only for highly distinctive species. The benthic community composition was assessed using 10 indicators: hard coral (HC), soft coral (SC), recently killed coral (RKC), nutrient indicator algae (NIA), sponge (SP), rock (RC), rubble (RB), sand (SD), silt/clay (SI), and other (OT) (Table S4). The fish community was categorised primarily at the family level, with one exception at the species level, and included grouper (Serranidae), butterflyfish (Chaetodontidae), Humphead Napoleon wrasse (Cheilinus undulatus), sweetlips (Haemulidae), parrotfish (Scaridae), snapper (Lutjanidae), and moray eel (Muraenidae) (Table S5). Similarly, the macro-invertebrate community was described using the following indicators: giant clams (Tridacna spp.), sea cucumbers (Thelenota ananas, Stichopus chloronotus and Holothuria edulis), Triton shell (Charonia tritonis), crown-of-thorns sea star (Acanthaster planci), Diadema urchin (Diadema spp.), pencil urchin (Heterocentrotus mamillatus), and collector urchin (Tripneustes spp.) (Table S6).

2.4. Data management and analysis

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/). Substrate, fish, and macro-invertebrate indicators were analysed separately between lagoon and ocean reefs due to their distinct environmental conditions, including differences in

geomorphology, reef profile, exposure to currents, and hydrodynamics (Gischler et al., 2014). Data collected at depths of 5 and 10 m were analysed together due to the absence of significant differences between these two depths.

To assess the impacts of the 2016 bleaching event and anthropogenic pressures, data were organised into two fixed and crossed factors: 'time period', including pre-bleaching (2005–2015), bleaching (2016–2018), and post-bleaching (2019–2023); and 'management type', inhabited, uninhabited, and resort. Being the Reef Check, a citizen science program, the obtained dataset was highly unbalanced (Tables S2 and S3), with unequal numbers of observations across factors. This imbalance reduces the power of statistical tests and can bias Type I error rates if not explicitly accounted for. To minimise these risks, analyses specifically designed to handle unbalanced data were employed: PERMANOVA was run with Type III sums of squares, which partitions variance independently of sample size; permutation tests were used instead of parametric assumptions, ensuring that p-values remain valid despite unequal replication; and pairwise comparisons were corrected for multiple testing. To avoid pseudo-replication, transects were treated as independent sampling units, and permutations were constrained within the relevant strata (time period \times management type). This approach ensures that differences are tested against the correct null model, despite the uneven sample distribution.

For the simple interpretation of the results, the indicators of rock (RC), rubble (RB), sand (SD), and silt (SI) have been grouped under the indicator 'abiotic' (AB). The indicator hard coral (HC) was 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. Due to their high variation in values, the macro-invertebrate data were transformed with $\log_{10}~(x+1)$ prior to graphical representation and statistical analysis.

Before conducting statistical analyses, the normality of the data was assessed using the Shapiro-Wilk test for each variable. As the data did not follow a normal distribution (p < 0.05 for most variables), and transformation attempts were unsuccessful (Shapiro-Wilk, p < 0.05), non-parametric tests were employed. Additionally, Levene's test was used to assess the homogeneity of variances across groups, indicating unequal variances in most groups (p < 0.05). For multivariate analyses, the homogeneity of multivariate dispersions was tested using PERMDISP for benthic, fish, and macro-invertebrate communities, revealing significant differences in dispersion across groups (p < 0.05).

To visualise patterns in community composition across time periods and management types, Non-Metric Multidimensional Scaling (NMDS) was performed using Bray-Curtis dissimilarity. Changes in benthic, fish, and macro-invertebrate communities were also illustrated with stacked bar plots, including both ocean and lagoon reefs. Standard errors (SE) for each indicator are provided in Table S7–S9, offering further insight into the precision of the representation.

Differences in community composition were then analysed using a two-way Permutational Multivariate Analysis of Variance (PERMA-NOVA) with Type III Sum of Squares (SS) to account for the unbalanced design (Anderson et al., 2001). PERMANOVA was based on a Euclidean distance matrix for substrate composition and a Bray-Curtis dissimilarity matrix for fish and macro-invertebrate communities. In addition, permutation-based two-way ANOVA tests were applied to each individual indicator to assess univariate responses, followed by pairwise comparisons using the pairwiseAdonis method, which tests for group differences based on dissimilarity matrices. Bonferroni-adjusted p-values were used to account for multiple testing (Table S10–S15). The factors 'time period' (pre-bleaching, bleaching, post-bleaching) and 'management type' (inhabited, uninhabited, resort) were treated as

fixed and crossed for both analyses.

Data analyses were conducted using RStudio (R Core Team, 2024). To assess homogeneity of variances, Levene's test was performed using the 'car' package (Fox et al., 2019). The 'vegan' package (Oksanen et al., 2019) was used to calculate the Bray-Curtis dissimilarity matrix, the Euclidean distance matrix, to perform the PERMANOVA analysis, and to test for homogeneity of multivariate dispersions (PERMDISP). The permutation-based two-way ANOVA tests were conducted using the 'permuco' package (Frossard and Renaud, 2022). The 'pairwiseAdonis' package (Martínez Arbizu, 2020) was used for conducting pairwise comparisons. The 'ggplot2' package (Wickham, 2016) was used to create NMDS plots. All statistical tests were performed using 999 permutations to assess the significance of the effects (Anderson et al., 2001).

3. Results

3.1. Substrate characterisation

Oceanic reefs revealed a predominance of the indicator abiotic (AB) across all three periods (Fig. 2). However, hard coral cover recovered significantly after the 2016 bleaching event. Standard errors (SE) for all benthic indicators are provided in Supplementary Table S7.

The PERMANOVA analysis highlighted a significant interaction between the management levels and the three periods (p=0.001, Table 1), indicating an overall different response to the bleaching event according to management type, in particular between resort and uninhabited reefs. Permutation ANOVA tests highlighted how the hard coral (HC) cover drives the main differences over time, exhibiting significant changes across the three periods, varying among the three management types (p)

Table 1

Results of two-way PERMANOVA (Type III sum of squares) and pairwise tests with Bonferroni-adjusted p-values applied to ocean reefs in the benthic community. Type = Inhabited (H), Resort (R), and Uninhabited (U); year = prebleaching, bleaching, and post-bleaching. The bold values indicate significance (p < 0.05).

PERMANOVA						
Source	Df	SS	R^2	F	P	
Туре	2	6317	0.053	5.677	0.001	
Year	2	1591	0.013	1.430	0.203	
Type X Time	4	1056	0.088	4.746	0.001	
Residual	181	1007	0.845			
Total	189	1192	1.000			
PAIRWISE test						
	H≠R		H≠U		R≠U	
Pre-bleaching	1.000		0.468		1.000	
Bleaching	1.000		0.648		0.036	
Post-bleaching	0.064		0.535		0.144	

< 0.001, Table S10). Reefs surrounding inhabited and resort islands experienced a decrease in HC cover during the heat wave, failing to return to the original coral cover post-bleaching. In contrast, reefs surrounding uninhabited islands did not display coral loss.

Permutation ANOVA showed significant differences in the recently killed corals (RKC) cover between the three management types and the time periods (p=0.006, Table S10). Inhabited islands showed an 11 % increase in RKC cover between the pre- and bleaching periods, while uninhabited islands displayed a 4 % increase during the same period. RKC cover decreased in both management types during the post-bleaching.

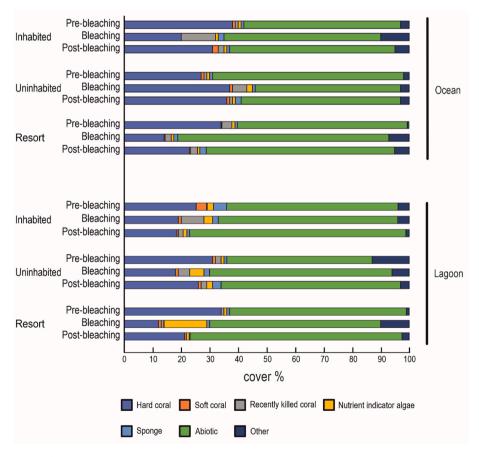


Fig. 2. Percent cover (%) of the benthic community composition for ocean and lagoon reefs in the three reef management types: Inhabited, Uninhabited and Resort; for the three periods: pre-bleaching, bleaching and post-bleaching. Standard errors (SE) for all indicators are provided in Supplementary Table S7.

Lagoon reefs exhibited a higher overall impact compared to oceanic reefs (Fig. 2). The AB category was predominant throughout all the time periods. However, except for inhabited islands, both uninhabited and resort islands showed signs of recovery in the post-bleaching period, although the HC cover did not return to pre-bleaching values. Standard errors (SE) for all benthic indicators are provided in Supplementary Table S7. The PERMANOVA analysis showed a significant interaction between the types of management and through the three periods (p=0.001, Table 2), but pairwise test showed differences in the benthic communities between inhabited and resort reefs only in the prebleaching period.

Permutation ANOVA showed a significant variation in the HC cover through the three periods (p=0.003, Table S11). Reefs surrounding resort islands were the most impacted, followed by the reefs surrounding uninhabited islands. Inhabited islands maintained a low coral cover of approximately 20 ± 2.3 % throughout the three time periods, with no significant differences recorded. This typology of reefs neither recorded impacts nor recovery in subsequent years.

Permutation ANOVA showed significant variations in RKC cover in the different levels of the island's management (p=0.008, Table S11) and over the three periods (p=0.032, Table S11). Inhabited islands' reefs displayed the highest increase in RKC cover (25 % increase) during the bleaching period, and coral cover lowered in the post-bleaching period.

The high coral loss was followed by an increase in NIA cover during the bleaching period. Permutation ANOVA showed a significant interaction between the island's management and the three periods of time (p=0.004, Table S11). Resort island reefs recorded the highest increase in NIA cover (14 % increase), which subsequently decreased, returning to pre-bleaching levels.

To explore differences in community composition, NMDS was performed separately for ocean and lagoon sites (Fig. 5a and b). In ocean sites (Fig. 5a, stress =0.11), the ordination shows substantial overlap among points, indicating no clear separation between groups. However, a few sites from uninhabited and inhabited reefs during the bleaching and post-bleaching periods deviate from this trend. Similarly, in lagoon sites (Fig. 5b, stress =0.08), most points overlap, but inhabited sites in the pre-bleaching period show some differences from the rest. The stress values for both ordinations are below 0.2, which is generally considered acceptable, though they still indicate some level of uncertainty in the ordination.

3.2. Fish community

The fish community on oceanic reefs showed a significant difference in the interaction between the time periods and the management types

Table 2 Results of two-way PERMANOVA (Type III sum of squares) and pairwise tests with Bonferroni-adjusted p-values applied to lagoon reefs in the benthic community. Type = Inhabited (H), Resort (R), and Uninhabited (U); year = prebleaching, bleaching, and post-bleaching. The bold values indicate significance (p < 0.05).

PERMANOVA					
Source	Df	Ss	R^2	F	P
Туре	2	4952	0.023	2.669	0.017
Year	2	2008	0.092	10.82	0.001
Type X Year	4	1204	0.055	3.245	0.001
Residual	195	1209	0.830		
Total	203	2180	1.000		
PAIRWISE test					
		H≠R	H≠	U	R≠U
Pre-bleaching	0.036		0.324		0.144
Bleaching	1.000		1.000		1.000
Post-bleaching		1.000	0.1	44	0.612

(p = 0.005, Table 3), and it was dominated by butterflyfish (Chaetodontidae) across all sites and periods (Fig. 3).

Standard errors (SE) for all fish indicators are provided in Supplementary Table S8. Permutation ANOVA showed a significant difference in the abundance of butterfly fish between the different site management typologies and the three time periods (p < 0.001, Table S12). The abundance of butterfly fish dropped in inhabited islands in the bleaching period (2016–2018) and did not recover in the following years, indicating not only an impact on the community during the warming event but also a lack of recovery post-bleaching. In contrast, permutation ANOVA showed that parrotfish (Scaridae) abundance significantly increased throughout the three periods (p = 0.048, Table S12); the increase is particularly evident in uninhabited and resort island reefs (Fig. 3).

In lagoon reefs, the fish community is predominantly composed of butterflyfish, except for the resort islands in the post-bleaching period (Fig. 3). Standard errors (SE) for all fish indicators are provided in Supplementary Table S8. PERMANOVA revealed a significant difference in the interaction between management types and time periods (p=0.001, Table 4), with resort reefs significantly different from the other two types in the post-bleaching period. The permutation ANOVA showed a significant difference in the Parrotfish (Scaridae) abundance in the different management types and between the three periods (p=0.003, Table S13), with uninhabited and resort islands recording the highest increases in parrotfish abundance in the post-bleaching.

Furthermore, permutation ANOVA showed a significant difference in the snapper (Lutjanidae) abundance among the three time periods and different reef typologies (p < 0.001, Table S13), especially at resort islands that had the highest change in snapper numbers from prebleaching to the bleaching time (Fig. 3).

The NMDS for oceanic reefs (Fig. 5c, stress = 0.11) indicates a certain degree of variability within management types and time periods, though the points are mostly overlapping. Fish community composition appears relatively similar across groups, except for inhabited islands postbleaching, where some points are more distinct, suggesting changes in community structure. In contrast, the NMDS ordination for lagoon reefs (Fig. 5d, stress = 0.17) shows a higher degree of variability, with points more broadly spread within the ordination space. However, reefs from resorts and uninhabited islands during the bleaching and post-bleaching periods show some separation from the rest while occupying a similar ordination space, indicating similarity in their community composition. The stress values for both ordinations are below 0.2, which is typically regarded as acceptable, although they still suggest a degree of uncertainty in the ordination.

Table 3 Results of two-way PERMANOVA (Type III sum of squares) and pairwise tests with Bonferroni-adjusted p-values applied to oceanic reef fish community. Type = Inhabited (H), Resort (R), and Uninhabited (U); year = pre-bleaching, bleaching, and post-bleaching. The bold values indicate significance (p < 0.05).

PERMANOVA					
Source	Df	Ss	R ²	F	P
Type Year Type X Year Residual Total	2 2 4 171 179	0.564 0.619 1.212 20.224 22.619	0.025 0.027 0.053 0.894 1.000	2.383 2.616 2.562	0.028 0.013 0.005
PAIRWISE test					
		H≠R	H≠U		R≠U
Pre-bleaching Bleaching Post-bleaching		0.144 1.000 1.000	.000 1.000		1.000 1.000 1.000

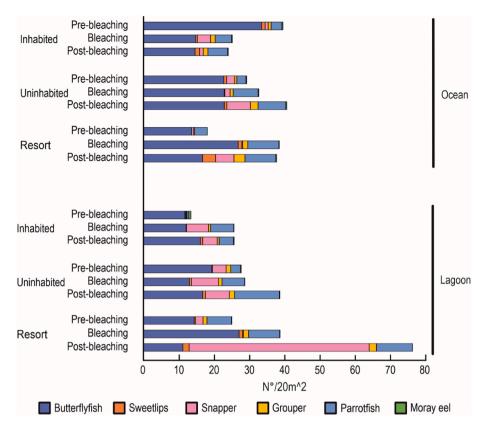


Fig. 3. Average abundance (N°/20 m2) of the fish community for ocean and lagoon reefs in the three reef management types: Inhabited, Uninhabited and Resort; for the three periods: pre-bleaching, bleaching and post-bleaching. Standard errors (SE) for all indicators are provided in Supplementary Table S8.

Table 4 Results of two-way PERMANOVA (Type III sum of squares) and pairwise tests with Bonferroni-adjusted p-values applied to lagoon reefs fish community. Type = Inhabited (H), Resort (R), and Uninhabited (U); year = pre-bleaching, bleaching, and post-bleaching. The bold values indicate significance (p < 0.05).

PERMANOVA					
Source	Df	Ss	R^2	F	P
Туре	2	0.810	0.034	3.752	0.001
Year	2	2.314	0.096	10.725	0.001
Type X Year	4	1.810	0.075	4.194	0.001
Residual	177	19.097	0.795		
Total	185	24.031	1.000		
PAIRWISE test					
		H≠R	H≠U		R≠U
Pre-bleaching		0.036	0.036		0.180
Bleaching		1.000	1.000		0.108
Post-bleaching		0.036	1.000		0.036

3.3. Macro-invertebrates community

In ocean reefs, macro-invertebrates exhibited generally low abundance across all reef managements and time frames, with sea cucumbers and *Diadema* urchins being notable exceptions. The sea cucumbers, specifically the species *Thelenota ananas, Stichopus chloronotus* and *Holothuria edulis*, reached abundances of up to 10 individuals per 20 m², while *Diadema* urchins were found in abundance exceeding 300 individuals per 20 m² (Fig. 4). Standard errors (SE) for all macro-invertebrate indicators are provided in Supplementary Table S9. PERMANOVA showed a significant difference in the abundance of the macro-invertebrates in the interaction between three time periods and among the different reef management (p = 0.001, Table 5), with resort reefs significantly differing from the other types in the post-bleaching

period. In particular, Diadema urchins showed significant variation in abundance in the interaction between different management types and over different time periods (p=<0.001, Table S14). Inhabited islands experienced the highest change in Diadema urchins, followed by resort island reefs. Sea cucumbers showed a decrease in abundance in all the sites from the bleaching to the post-bleaching periods, although not significant.

At lagoon reefs, macro-invertebrate abundance was generally low across all periods and management types, except for Diadema urchins at resort islands in the post-bleaching period, which showed the highest abundance (Fig. 4). Standard errors (SE) for all macro-invertebrate indicators are provided in Supplementary Table S9. The PERMANOVA showed significant variations in the interaction between site management types and time periods (p = 0.001, Table 6), also in this case highlighting differences between resort reefs and the others in the postbleaching period. Permutation ANOVA highlighted a significant interaction between the three time periods and reef management types for the Diadema urchin abundance (p < 0.001, Table S15). An increase in urchin numbers was particularly evident in resort islands, where the average abundance increased from 0.7 \pm 0.2 to 239 \pm 98.5 N° 20m2 from the bleaching to the post-bleaching period. Finally, permutation ANOVA highlighted a significant difference in the abundance of the Crown of Thorns (Acanthaster planci) over the three periods and in the three management types (p = 0.043, Table S15), with an increase during the bleaching period, especially in resort islands and a decrease during the post-bleaching period.

The NMDS dispersion for oceanic reefs (Fig. 5e, stress = 0.13) shows high variability among management types and time periods, with a stress value considered acceptable, indicating a reasonably reliable representation of community composition. However, inhabited sites in the pre-bleaching period are strongly clustered together, while uninhabited sites during the bleaching and post-bleaching periods are distanced from the other points, indicating a different macro-

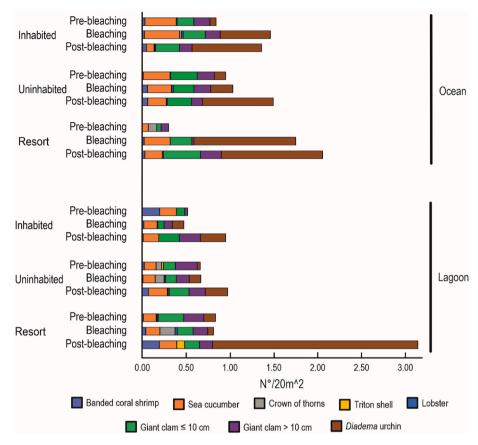


Fig. 4. Average abundance ($N^{\circ}/20$ m²) of the macro-invertebrates community for ocean and lagoon reefs in the three reef management types: Inhabited, Uninhabited and Resort; for the three periods: pre-bleaching, bleaching and post-bleaching. Standard errors (SE) for all macro-invertebrate indicators are provided in Supplementary Table S9.

invertebrate composition. Similarly, for lagoon reefs (Fig. 5f, stress = 0.20), the points are widely spread across the ordination space, highlighting high variability. However, some uninhabited sites during the bleaching period are distanced from the rest, suggesting distinct community composition. The higher stress value of 0.20 suggests some uncertainty in the ordination, indicating that the representation of the community composition may be less precise.

4. Discussion

This study provides a comprehensive 19-year analysis (2005–2023) using the Reef Check protocol to examine coral reef responses in the Maldives under varying levels of anthropogenic pressure. The 2016 bleaching event resulted in severe coral mortality across the archipelago (Montefalcone et al., 2018), with sea surface temperatures peaking at 31.63 °C for several weeks (NOAA Coral Reef Watch 2024). In this context, the use of NOAA Coral Reef Watch (CRW) SST values is appropriate for characterising the thermal stress experienced by the study sites in the central Maldives, where SST anomalies are relatively homogeneous (Chaudhuri et al., 2021). Differences in bleaching severity and recovery among sites are more likely attributable to local geomorphological, hydrodynamic, or anthropic factors rather than to major differences in thermal stress. By encompassing this catastrophic event, the study period offers valuable insights into the resistance and resilience of Maldivian reefs over time. Consistent with findings from other studies (Montefalcone et al., 2018, 2020), it was noted that oceanic reefs displayed lower susceptibility to bleaching caused by the 2016 heat wave in comparison to lagoon reefs. Nonetheless, although the hard coral (HC) cover of oceanic reefs remained relatively stable across the three time periods, suggesting resilience to bleaching events, these sites

did not exhibit substantial post-bleaching recovery, with coral cover consistently remaining below 40 %. Conversely, lagoon reefs exhibited a lower overall coral cover, recording less than 30 % in the post-bleaching period. However, a slight trend of recovery in the post-bleaching was observed, albeit not returning to pre-bleaching levels (Cowburn et al., 2019).

Despite high spatial variability, oceanic reefs are predominantly composed of more resistant coral genera, such as massive *Porites* and encrusting corals, whereas lagoon reefs are dominated by the more sensitive yet resilient genus *Acropora*, which exhibits various growth forms, including branching, digitate, and tabular morphologies (Morri et al., 2015; Montefalcone et al., 2020). Although the Reef Check protocol records hard coral as a broad category (HC), our interpretation of resilience patterns is consistent with previous Maldivian studies that identified resistant taxa such as massive *Porites* and *Pocillopora*, and more vulnerable taxa such as *Acropora* (Morri et al., 2015; Montefalcone et al., 2018, 2020). These differences in benthic composition likely influenced both the extent of bleaching impact experienced by the two reef types (lagoon and oceanic) and their respective recovery trajectories in the post-bleaching period.

Considering the different reef management typologies for ocean reefs, both inhabited and resort islands experienced the highest overall impacts during the 2016 heat wave, with promising signs of recovery in the post-bleaching period. Inhabited oceanic reefs not only experienced a 50 % coral loss and an 11 % increase in RKC, but the impact also extended to the fish communities, resulting in a significant reduction in fish abundance, notably halving the population of butterflyfish (Chaetodontidae). This could be linked to the loss of coral cover, which led to a reduction in habitat complexity in the post-bleaching period, a critical factor that influences fish abundance and biodiversity on coral reefs

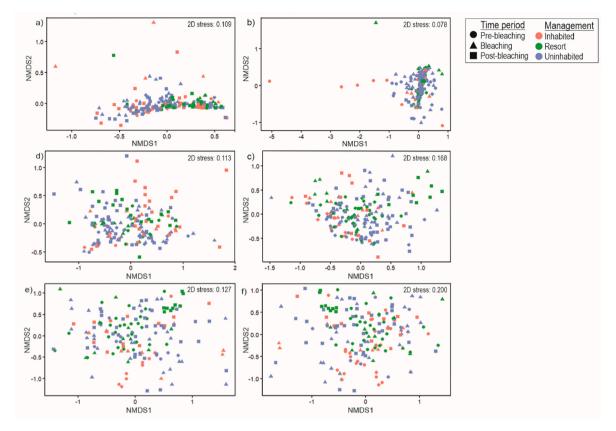


Fig. 5. Non-metric multidimensional scaling (NMDS) plots depicting community dissimilarity for: (a) ocean substrate, (b) lagoon substrate, (c) ocean fish community, (d) lagoon fish community, (e) ocean macro-invertebrate community, and (f) lagoon macro-invertebrate community. Dissimilarity is based on three management types (inhabited, resort, and uninhabited) and three time periods (pre-bleaching, bleaching, and post-bleaching). Points are color-coded by management type (red for inhabited, green for resort, and blue for uninhabited) and shaped by time period (round for pre-bleaching, triangle for bleaching, and square for post-bleaching). The stress value for each NMDS plot is indicated on the respective panel. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Table 5 Results of two-way PERMANOVA (Type III sum of squares) and pairwise tests with Bonferroni-adjusted p-values applied to the oceanic macro-invertebrates' community. Type = Inhabited (H), Resort (R), and Uninhabited (U); year = prebleaching, bleaching, and post-bleaching. The bold values indicate significance (p < 0.05).

PERMANOVA					
Source	Df	Ss	R ²	F	P
Туре	2	0.937	0.022	2.1676	0.018
Year	2	2.324	0.055	5.3746	0.001
Type X Year	4	4.008	0.095	4.6341	0.001
Residual	161	34.814	0.827		
Total	169	42.084	1.000		
PAIRWISE test					
		H≠R	H≠U		R≠U
Pre-bleaching		0.036	0.0	36	1.000
Bleaching		1.000	1.00	00	1.000
Post-bleaching		0.036	1.00	00	0.036
Post-bleaching		0.036	1.00	00	0.036

(González-Rivero et al., 2017; Ferrari et al., 2018). Furthermore, butterflyfish face local removal for the aquarium trade, particularly prevalent on inhabited islands where reef access is easier. However, a species-specific study would be needed to confirm these hypotheses. Similarly, the increase in *Diadema* urchins and sea cucumbers, specifically *Thelenota ananas, Stichopus chloronotus and Holothuria edulis*, post-bleaching may be connected to substrate modification. *Diadema* urchins are significant herbivores, playing a pivotal ecological role in controlling algal populations (Precht and Precht, 2015). Their numbers

Table 6 Results of two-way PERMANOVA (Type III sum of squares) and pairwise tests with Bonferroni-adjusted p-values applied to the lagoon reefs macro-invertebrates' community. Type = Inhabited (H), Resort (R), and Uninhabited (U); year = pre-bleaching, bleaching, and post-bleaching. The bold values indicate significance (p < 0.05).

PERMANOVA						
Source	Df	Ss	\mathbb{R}^2	F	P	
Туре	2	0.919	0.020	1.975	0.034	
Year	2	2.181	0.047	4.686	0.001	
Type X Year	4	3.369	0.073	3.619	0.001	
Residual	171	39.8	0.860			
Total	179	46.27	1.000			
PAIRWISE test						
		H≠R	H≠I	U	R≠U	
Pre-bleaching		0.252	1.000		1.000	
Bleaching		1.000	1.000		1.000	
Post-bleaching		0.036	1.000		0.036	

surged during the bleaching period, probably due to coral loss-induced proliferation of the algal community (NIA). Similarly, sea cucumbers, essential for substrate oxygenation and nutrient cycling in the ocean (Purcell et al., 2016), found a favourable environment in the post-bleaching period. The increase in sand and rubble, which previous studies have shown to support higher sea cucumber populations (Purcell et al., 2016; Lee et al., 2017), likely contributed to their abundance.

Ocean resort reefs experienced 53 % coral loss and an increase in parrotfish (Scaridae) and *Diadema* urchins' abundance post-bleaching.

Parrotfish are essential for both sediment production and removal of excess algae due to their scraping-herbivorous nature, and their increased abundance during and immediately post-bleaching may be linked to macro-algae proliferation and their protection from fishing by national regulation: the 2020 Maldives General Fisheries Regulation (2020/R-75), prohibits the catch, killing, or retention of all parrotfish species. The impacts on the ecosystem from resort islands stem primarily from the construction phase of the resort itself (Scheyvens, 2011), which represents a chronic disturbance often involving dredging and sand-spilling activities over a period of 18 months to 3 years (Erftemeijer et al., 2012). Subsequent construction phases, such as jetties and water villas, further contribute to habitat alteration. Following completion, the influx of tourists exerts substantial local pressure through recreational diving, snorkelling activities and waste production. Waste management practices vary, with some waste managed on the islands, some used for fish-feeding, or illegally dumped into the ocean. There is also an increased demand for reef fish for resort visitors, driving the reduction in local reef grouper (Serranidae), trevally (Carangidae), larger snapper (Lutjanidae) and emperor fish (Lethrinidae) populations. All of these impacts collectively diminish the resilience of reefs associated with resort islands, reducing their capacity to withstand global impacts stemming from climate change (Scheyvens, 2011).

The oceanic reefs of uninhabited islands offered better conditions to buffer climate impacts, especially in terms of coral cover (Cowburn et al., 2019; Moritz et al., 2017). Reefs of uninhabited islands exhibited resilience, experiencing a consistent increase in coral cover across all three periods, dominated by massive and robust coral genera (such as massive *Porites* and *Pocillopora*) that are more resistant to bleaching than susceptible species of the *Acropora* genus that have traditionally dominated more sheltered inshore reefs.

Taking into account the indicators for the ocean reefs, the reef management most significantly affected by bleaching and with the lowest recovery was associated with inhabited islands. These findings highlight how anthropogenic pressures (i.e. coastal modification, over tourism, improper waste disposal, and overfishing) exacerbate the impacts of climate change, compromising reefs' resilience and affecting coral cover, fish, and macro-invertebrate communities. Conversely, for lagoon reefs, inhabited islands showed no significant differences in coral cover or fish and macro-invertebrate abundances. These reefs were already highly impacted before the 2016 bleaching event, with a low average of hard coral cover (25 \pm 5.5 %) and low average fish abundance (14 \pm 2 organisms 20m2). The absence of recovery in the postbleaching period underscores how the degradation of reefs, coupled with increasing local and global pressures, is likely to hinder natural recovery (Nepote et al., 2016). In this context, active coral restoration measures play a crucial role in regenerating reef ecosystems, particularly on inhabited islands. Here, community involvement can enhance restoration success, as local residents can take ownership of their house reefs, actively outplant corals, and regularly maintain the site. In contrast, passive conservation strategies, such as the establishment of Marine Protected Areas (MPAs), may be more effective on uninhabited islands, and at a greater scale by reducing diving pressure and promoting natural recovery with more natural assemblages of keystone species such as herbivorous fish. On resort islands, limiting construction and fishing activities could further support reef regeneration and long-term resilience (Montefalcone et al., 2020). Moreover, the disparities observed between oceanic and lagoon reefs, particularly on inhabited islands, are linked to varying degrees of local human impact. Lagoon reefs face intensified pressures due to land reclamation activities (Duvat, 2020) and more limited water exchange. These actions (overfishing and damage to the coral framework through inappropriate development) undermine the ability of the 'self-maintaining' reef-island system to adapt to sea-level rise through natural vertical growth (Temmerman et al., 2013), necessitating reliance on costly engineering solutions (Duvat and Magnan, 2019). Consequently, these factors exacerbate global impacts, amplifying negative effects in lagoon areas

and impeding natural recovery efforts. Resort islands' lagoon reefs were the most impacted, with a coral loss of 65 % over the 19 years, compounded by a subsequent proliferation of macro-algae (NIA). This change in community character coincided with an increased abundance of parrotfish and sea urchins during and after the bleaching period, perhaps due to an increased availability of food. These results suggest a correlation between coral cover loss, high temperatures, organic waste from fish-feeding practices, and macro-algae growth. Unlike inhabited islands, resort reefs are relatively protected from fishery pressures, as commercial fishing is typically prohibited in the surrounding reefs owned by the resorts (McClanahan, 2011). This protection seems to be reflected in the significant increase in the abundance of butterflyfish (Chaetodontidae) and snapper (Lutjanidae), as both species are targeted for aquarium trade and fishing purposes, respectively. Moreover, the surge in snapper (Lutjanidae) abundance may also be influenced by fish-feeding practices by resorts, as observed already by Moritz et al. (2017). Given their carnivorous nature and tendency to form large schools in the water column, they could be more attracted by food waste inputs from the surface compared to other more benthic carnivorous fishes, such as groupers (Serranidae). Furthermore, mid-level carnivores recorded by Reef Check (snappers and sweetlips) are known to exhibit site fidelity (Vignon et al., 2008). Additional comprehensive studies are warranted to definitively link their abundance to resort island fish-feeding practices. These findings affirm the 'resort effect' theory proposed by Moritz et al. (2017), suggesting that resorts that operate environmentally sensitive and sustainable practices can offer a degree of biodiversity protection, particularly concerning the diversity and abundance of fish species. This underscores the potential for resorts to serve as sanctuaries for fished, rare, or endangered species. Nevertheless, the impact on benthic communities is notably severe, particularly during the initial building development, often accompanied by limited awareness of the significant environmental consequences and an absence of effective monitoring. As a result, the 'positive' effects of resorts on biodiversity only become apparent once the reef recovers from the initial build phase, typically occurring several years later (Nepote et al., 2016).

Lagoon reefs of uninhabited islands were the only ones to recover to pre-bleaching hard coral cover after experiencing 42 % coral loss during the bleaching period. Consistent with broader patterns, uninhabited lagoon reefs also witnessed a post-bleaching increase in parrotfish (Scaridae) and butterflyfish (Chaetodontidae) abundances, affirming a positive trajectory towards conditions necessary to facilitate recovery and restoration of coral cover and habitat complexity. This is likely due to the reduced levels of pollution and physical damage.

However, overall coral cover recorded using the Reef Check protocol exhibited lower values compared to other studies conducted in the same years and areas (i.e. Montefalcone et al., 2018; Montefalcone et al., 2020) using a different assessment method. This disparity could potentially be attributed to the unique characteristics of Maldivian reefs, where site selection seems to play a fundamental role. Furthermore, following the impact of the 2016 marine heat wave and the general increase in sea surface temperatures, several reefs today exhibit higher coral cover around 15 m, a depth not reached by the Reef Check protocol (maximum depth for Reef Check dives is 12m).

In addition, the Reef Check protocol relies on recreational divers to collect data. Although they undergo a 5-day training course, this may lead to potential discrepancies compared to data collected by professional researchers. Finally, the selected indicators are broad, and this limitation is particularly evident with the HC (Hard Coral) indicator, which does not differentiate between genera or growth forms, hindering the ability to identify the most fragile or resilient corals or assess potential biodiversity trade-offs during recovery.

However, the 'generic' indicator HC has been widely used to assess the impact, the recovery and the resilience of coral reefs (Nepote et al., 2016; Montefalcone et al., 2020; Amir, 2022; Zampa et al., 2023; Pancrazi et al., 2025). Therefore, the Reef Check protocol emerges as a

reliable data collection instrument across expansive reef regions for benthic habitats, owing to its simplicity and ease of implementation (e.g. Done et al., 2017). Its capacity to engage local communities and foster interest and respect for the underwater world underscores its indispensable role in driving conservation initiatives forward (Hodgson, 2001).

The findings of this study hold profound significance for local governments and policymakers, serving as a comprehensive guide on where and how to prioritise reef conservation efforts within management and regulatory plans. By meticulously identifying and addressing the diverse array of local pressures, including both anthropogenic impacts and climatic stressors highlighted in this research, policymakers and managers are empowered to formulate informed strategies aimed at safeguarding these invaluable ecosystems for the benefit of present and future generations. Such strategies may include implementing targeted conservation measures, establishing marine protected areas, regulating coastal development activities, promoting sustainable tourism practices, and investing in ecosystem restoration initiatives. Through proactive and evidence-based policy delivery and management aligned with a true understanding of the value of healthy coral reefs, it will be possible to ensure the long-term resilience and vitality of the Maldives, preserving their ecological, economic, and cultural services for years to come.

CRediT authorship contribution statement

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

Funding

Project partially funded under the National Recovery and Resilience Plan (NRRP), Mission 4 Component 2 Investment 1.4—Call for tender No. 3138 of December 16, 2021, rectified by Decree n.3175 of December 18, 2021, of Italian Ministry of University and Research funded by the European Union—NextGenerationEU; Award Number: Project code CN_00000033, Concession Decree No. 1034 of June 17, 2022, adopted by the Italian Ministry of University and Research, CUP D33C22000960007, Project title "National Biodiversity Future Center—NBFC."

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.

Acknowledgements

Thanks to the joint effort of the Scientific Cruise Expedition, organised by the ISSD (International School for Scientific Diving) in partnership with the University of Genoa (Italy) and the tour operator Albatross Top Boat (Verbania, Milan and Malé); Biosphere Expeditions in partnership with the dive operator Dune Maldives; and the Maldivian non-

governmental organisation Save the Beach Maldives, Reef Check Maldives and LaMer Group. Thanks to our volunteer contributors and Maldivian Reef Check expedition participants.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2025.107664.

Data availability

Data will be made available on request.

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