



When coral dies but fish remain: limits of local restoration under climate pressure (Bora Bora, French Polynesia)

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Abstract While global change presents significant threats to all environments, local scale conservation efforts such as coral restoration may help mitigate reef degradation. Our study investigates the combined effects of local coral restoration versus a coral bleaching event on coral health and fish assemblages. Between January and April 2024, approximately 60–70 marine heatwave days occurred across the Bora Bora region (French Polynesia). Two experiments were conducted on the fringing reef of Bora Bora: the first surveyed coral and reef fish communities in two

biotopes (shallow fringing reefs and a deeper “reef drop”) before and after the 2024 bleaching event; the second assessed fish communities at restoration sites managed by high school children (citizen science) at three time points: (i) before restoration, (ii) after restoration, and (iii) after bleaching. Our results show a significant decline in live coral on the shallow fringing reef (with or without reef restoration) after the 2024 bleaching event, whereas the deeper reef drop exhibited minimal change, highlighting a depth-related difference in reef vulnerability to thermal stress. Despite these changes in coral cover, fish abundance and richness remained relatively stable across

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time (before and after the bleaching event). Overall, our findings highlight the lack of resilience of coral reefs under heatwaves and provide useful insights into the limitations of small-scale restoration when faced with large-scale thermal stress. This underscores the urgent need to design local-scale restoration strategies that are better aligned with addressing global change, particularly in regions where healthy reefs are vital for the survival of local human communities.

Keywords Fish communities · Restoration efforts · Marine educational area · Coral health · Bleaching event

Introduction

To limit global warming to around 2 °C, global greenhouse gas emissions must peak before 2026 and then decline by approximately 25% by 2030, an objective that requires far more ambitious commitments and actions from the international community (IPCC 2022) than those being seen today. Despite some global attempts to limit the level of global warming, current efforts remain insufficient to meet the IPCC's climate targets (IPCC 2022). Despite often being far from the world's major capitals, coral reefs are heavily impacted by global change, as well as by local stressors (Hughes et al. 2017; Morrison et al. 2019; Mulà et al. 2025). For example, a long-term monitoring program of the Great Barrier Reef has revealed a gradual and widespread decline in coral cover attributed to increased cyclone frequency, bleaching events, and *Acanthaster planci* (crown-of-thorns starfish) proliferations (De'ath et al. 2012). Yet, coral reefs are among the most biologically diverse and complex marine ecosystems on Earth, and they support a variety of essential socioeconomic and physical processes including food production, tourism, biotechnology, and coastal protection (Costanza et al. 2014). Thus, many island nations, such as those within the South Pacific, are strongly dependent on these processes for socio-economic and food security (Moritz et al. 2018).

Alongside global activities, efforts are being made to build positive relationships with local communities to improve management at the local scale (e.g., Almany et al. 2010; Dunlap et al. 2021). McLeold et al. (2019) and Good and Bahr (2021)

highlighted the importance of reducing CO₂ emissions in combination with implementing local management actions to protect reefs that are resilient to extreme events and/or to establish reef zoning regulations to enhance larval connectivity. Local restoration and protection initiatives should be aligned with the realities of climate change (McLeold et al. 2019). For example, in Hawai'i, regional management of multiple stressors can enhance coral resistance to elevated temperatures (Bahr et al. 2017; Coles et al. 2018). With the involvement of local populations, it is possible to reduce terrestrial nutrient pollution (Fabricius 2011), limit overfishing of herbivores (Steneck et al. 2019), and remove coral predators (Shaver et al. 2018), all of which are actions that often support resilience by enhancing coral growth and survival. Other local actions may include establishing marine protected areas (through integrated land-to-sea models, ecosystem-based management at larger scales, and resilience-based management to foster social adaptive capacity), regulating fisheries, improving water quality; and implementing marine bioengineering approaches such as coral gardening, selective breeding, microbiome manipulation in the holobiont, and assisted migration (McLeod et al. 2019; Morrison et al. 2020; Good and Bahr 2021).

The Pacific Island communities often engage in local-scale initiatives, tackling issues such as managing overfishing so as to ensure the security of their food resources for future generations (Bambridge 2019). Moreover, numerous coral restoration programs are conducted by local actors, high school children, or NGOs, which employ active physical and biological restoration methods such as coral gardening, direct transplantation, coral micro-fragmentation, coral larvae reseeding, and the re-introduction of herbivorous species, with the aim of repairing degraded or damaged reefs (e.g., Raick et al. 2024; Suggett et al. 2024). Lastly, local actions such as reducing algal abundance (e.g., protecting herbivores and limiting terrestrial pollutants that promote algal growth) can greatly enhance the recovery potential of corals (Bellwood et al. 2004; Steneck et al. 2019). However, the success of these restoration efforts is most often measured solely in terms of coral survival and growth (e.g., Boström-Einarsson et al. 2020; Hughes et al. 2023), yet it is equally important to monitor how the key functionalities of the damaged reefs are restored.

In this context, monitoring the fish community dynamics is essential for comprehensive evaluation of restoration progress (e.g., Zakaria et al. 2020; Hein et al. 2020). For example, Krimou et al. (2024) investigated the short-term effects of coral restoration on fish assemblages at Bora Bora over a period of 28 days. They observed a rapid shift in certain adult fish assemblages with coral restoration, although species richness, diversity, and abundance remained unchanged. Importantly, the effect of coral restoration on fish assemblages can differ substantially between short (within the first month) and long term (>1 year) periods (e.g., Fadli et al. 2012; Hein et al. 2020). Thus, despite numerous coral restoration initiatives around the world (e.g., Anthony et al. 2020; Morrison et al. 2020), knowledge regarding their impact on fish assemblages remains limited (e.g., Sangil et al. 2024; Krimou et al. 2024). Moreover, the debate concerning the resilience of coral reefs and fish populations to climate change, with or without conservation actions by island communities, is still ongoing (e.g., IPBES 2019; Donovan et al. 2023). Harris et al. (2017) underlined the need to co-design conservation interventions with expert knowledge from local resource users and Indigenous peoples, thereby ensuring that global and local knowledge are effectively integrated into reef conservation strategies.

In Bora Bora (French Polynesia, South Pacific), a program of coral restoration was initiated in 2022 by high school children with the support of scientists representing a local conservation effort to restore a degraded reef. Unfortunately, in 2024, the selected site experienced severe coral bleaching due to abnormally high seawater temperatures in the South Pacific (LeGendre et al. 2024). Our study aims to assess the influence of local conservation efforts (coral restoration) versus global changes (seawater warming) on coral health and fish assemblages in the Bora Bora reefs. To achieve this, two experiments were conducted: (1) a comparison of substrate and fish assemblages over time (September 2022, 2023, and 2024) and across biotopes (*Experiment 1*: visual underwater surveys in September 2022, 2023, and 2024 used to examine changes in coral and fish communities from before to after the bleaching event), followed by (2), a three-phase analysis of fish assemblages: before coral restoration, after coral restoration (but before the 2024 bleaching event), and after the 2024 bleaching event (*Experiment 2*). Thus, the study will provide an

interesting look at the limitations of local reef restoration in the face of global-scale stressors and will add to the literature concerning short-term impacts of coral mortality on reef fish communities.

Materials and methods

The study was conducted at the Marine Educational Area (MEA) of Bora Bora (16° 1' 29" S, 151° 44' 20" W) (French Polynesia). An MEA is a small coastal marine area managed in a participatory manner by one or several schools. The Bora Bora MEA is managed by high school children aged 11 to 18 and represents a 40,000 m² area located on the west coast of the southern part of the main island (Fig. 1—16° 31' 29" S, 151° 44' 20" W). The MEA, with depths ranging from 0 to 16 m, can be separated into four different biotopes: muddy habitat close to the coastline; sandy habitat with few coral colonies (mostly dead colonies); the fringing reef with many small reef patches; and finally, a reef drop from 2 to 16 m depth (Fig. 2).

Experiment 1

To raise children's awareness of environmental monitoring and illustrate the spatio-temporal variations in coral reef communities, CRIOBE (Centre de Recherches Insulaires et Observatoire de l'Environnement) established an annual monitoring program in 2022. The results of this monitoring (focusing on coral and fish density and diversity) are analyzed each year with high school students. In the present study, the biodiversity monitoring survey utilized data collected in September 2022, 2023, and 2024 from the fringing reef and reef drop of the MEA. The muddy and sandy habitats were excluded from the survey as they are inhabited by very few fish or living corals. For each biotope (fringing reef and reef drop), three transect replicates were set up (0.5–1 m depth for the fringing reef and 2–2.5 m depth for the reef drop). The transects were positioned randomly but always parallel to the shoreline and spaced 26 m apart. On each transect (25 m length×5 m wide), the substrate types (i.e., living coral, dead coral with macroalgae, coral rubble, and sand) were recorded every meter using the line intercept transect method. The statistical difference in substrate composition for

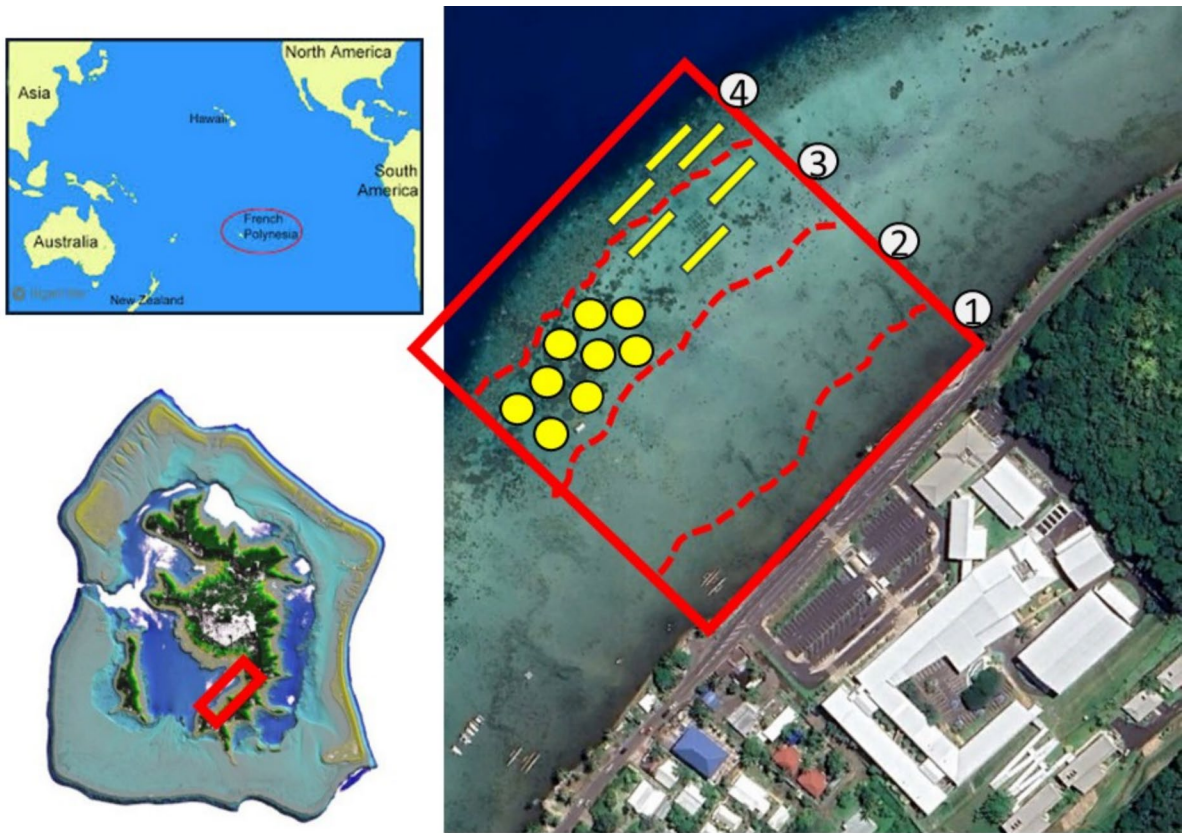


Fig. 1 Location of the Marine Educational Area (MEA—red rectangle), in front of the high school at Bora Bora (bottom-left image) localized in the Pacific (top-left image). The MEA is characterized by four biotopes: muddy habitat close to the coastline (1), sandy habitat (2), fringing reef (3), and the reef

drop (4). The transects for Experiment 1 were set up on the fringing reef and the reef drop of the MEA (yellow rectangles). The nine reef patches for Experiment 2 were set up on the fringing reef (yellow spots). The imagery used was generated by Airbus and has been modified from Google Earth

both the fringing reef and the reef drop between the years was assessed by means of χ^2 tests.

The fishes (all species except small cryptic species such as Blenniidae and Gobiidae Lecchini and Galzin 2005; Lecchini et al. 2021) were recorded (data collected: the number of individuals per species, not accounting for size, to calculate fish abundance and species richness) by underwater visual surveys along the given transects (25 m length \times 5 m wide = 125 m²) and over two successive passes. On the first transect pass, the observer recorded highly mobile fishes that entered the transect but usually fled at a diver's approach. On the second pass, less mobile and site-attached species were recorded. David Lecchini conducted all fish surveys in Experiment 1.

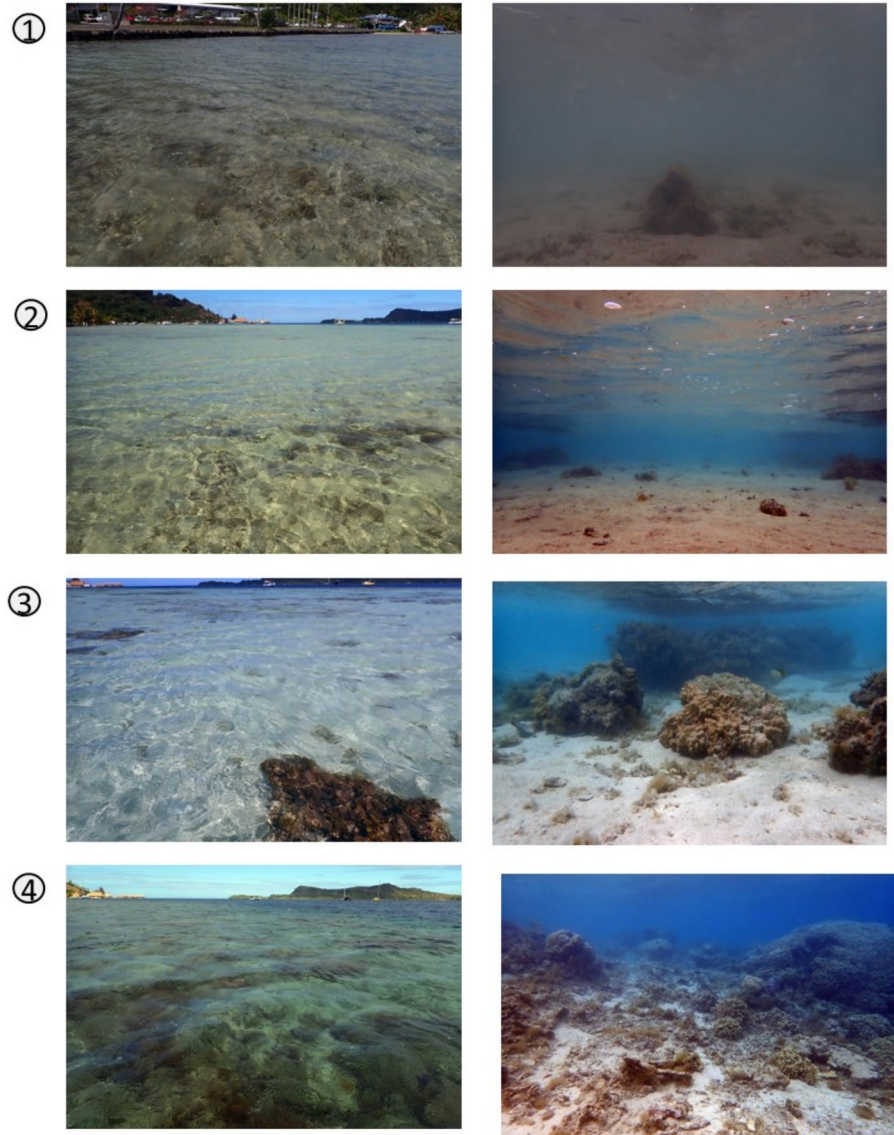
First, fish abundance and richness were compared between 2022 and 2024 (all years are compared with

each other) on each biotope separately (fringing reef and reef drop) with Friedman Anovas. Second, total fish abundance and richness were compared between the two biotopes (fringing reef vs. reef drop) with Wilcoxon-Mann-Whitney tests.

Experiment 2

In 2022, the high school children and the CRIOBE researchers restored the fringing reef of the MEA by coral transplantation. The restored reefs were not on the biodiversity survey transects (Fig. 1). To conduct Experiment 2, sixteen dead reef patches (spaced at least 2 m apart) with a size range from 5 to 12 m² were selected (see method in Krimou et al. 2024). Prior to the restoration efforts, the selected reef patches showed less than 1% living coral cover and

Fig. 2 Photos of the Marine Educational Area (MEA) of Bora Bora that visually depict the differences between the four biotopes: (1) muddy habitat near the coastline; (2) sandy habitat with few, generally dead, coral colonies; (3) fringing reef with many small reef patches; and (4) reef drop ranging from 2 to 16 m depth



were dominated by over 85% macroalgae (*Dictyota* spp., *Halimeda* spp., *Padina boryana*, and *Turbina-ria ornata*). The percentage of substrate cover was visually quantified by choosing 10 random visual intercept points on each of the four sides and on the top of the coral patches present at different points (50 sampling points per coral patch—method adapted from Dethier et al. 1993; Krimou et al. 2023). To restore them, the macroalgae were first removed by hand and healthy coral fragments were then transplanted on the reef patch (size between 10×5×5 cm and 15×30×10 cm) in keeping with the relative abundance occurring in reefs near the MEA (70%

Acropora spp., 18% *Porites rus*, and 12% *Porites lobata*—Lecchini et al. 2021, Krimou et al. 2024). The reef patches were grouped according to four conditions: four were non-restored (control condition), four were restored to 25% living coral cover (25% condition), four were restored to 50% living coral cover (50% condition), and four were restored to 75% living coral cover (75% condition). The abundance of fish was assessed before the coral restoration and again after 28 days (see results in Krimou et al. 2024). Fish surveys were conducted using the fixed-point method, with each of the 16 reef patches observed for a period of 5 min.

From January to April 2024, French Polynesia underwent a heatwave which generated abnormally high seawater temperatures. In the Bora Bora lagoon, this increase led to an important coral bleaching event with seawater temperature remaining above 30 °C for several weeks (Reimer et al. 2024). In September–October 2024, after bleaching, we recorded fish abundance and diversity in 9 of the 16 dead reef areas. These 9 reef areas consisted of dead colonies of *Porites rus* which measured 5–10 m², were cylindrical in shape, wider than they were tall, and which were spaced at least 2 m apart. The fixed-point method was used for a period of 5 min on each reef patch (as described in Krimou et al. 2024). The remaining patches ($n=7$) could either not be found or could not be identified with certainty and were therefore excluded from this study.

Thus, the nine patches included three reef patches of control condition, three of 50% condition and three of 75% condition. For each reef condition, we compared the fish assemblages before the coral restoration (three visual survey replicates in 2022), after the coral restoration (three visual survey replicates after the restoration in 2022), and after the bleaching event (three visual survey replicates in 2024: three separate 5 min surveys conducted at each of the nine reef patches) with Friedman Anovas followed by Nemenyi post-hoc tests. The same analysis was performed at the trophic guilds level by comparing the assemblages of omnivores, herbivores, piscivores, corallivores and planktivores prior to coral restoration, after coral restoration, and after the bleaching event. SK conducted all fish surveys in Exp. 2.

Satellite temperature data

To contextualize the 2024 heatwave (as continuous in-situ temperature data for the Bora Bora MEA were not available), we used satellite sea surface temperature (SST) from NOAA Coral Reef Watch (CRW) v3.1 at 5 km resolution (Skirving et al. 2020) along with a standard marine heatwave (MHW) detection method (Hobday et al. 2016). For each calendar day, we computed a 90th-percentile climatological threshold over the baseline period 1995–2024, with a moving 11-day window to ensure enough daily SST samples for a robust 90th-percentile estimate. A 30-day smoothing filter was then applied to remove high-frequency noise. An MHW was identified when SST

exceeded this 90th percentile threshold for ≥ 5 consecutive days. We applied the MHW detection pixelwise to the CRW 5-km SST field over the Society Islands (which include Bora Bora); the total number of MHW days is mapped in Fig. 3.

For the period spanning January to April 2024, approximately 60–70 days have been detected as MHW days around the Bora Bora region. Although CRW SST data alone does not fully resolve fine-scale lagoon conditions in the Bora Bora MEA, these results support our conclusion that the MEA experienced a pronounced MHW period during this time. Whether this reflects a single prolonged event or multiple successive episodes, and whether MHW characteristics varied among the different MEA biotopes (Fig. 1), cannot be determined here. Resolving these questions would require higher-frequency in situ measurements, which lie beyond the scope of this study.

Results

At the MEA of Bora Bora (Experiment 1), the substrate composition of the fringing reef showed significant changes from 2022 to 2024 ($\text{Chi}^2=108.8$, $P<0.001$), with an increase in the proportion of dead coral/macroalgae between 2023 (before the bleaching event) and 2024 (following the bleaching event), and a decrease of the live coral proportion between 2022/2023 and 2024 (Fig. 4). On the reef drop, while a significant difference was detected in the substrate composition between 2022, 2023, and 2024 ($\text{Chi}^2=1579$, $P<0.001$), the 2024 bleaching event had little negative effect on the proportion of live coral (93% in 2022 vs. 89% in 2024). In contrast, the proportion of live coral on the fringing reef deteriorated from 22% in 2022 to 0% in 2024.

In the Experiment 1 surveys, neither the abundance nor the richness of fishes showed significant differences from 2022 to 2024 for both the fringing reef (Friedman Anova, abundance: $\text{Chi}^2=2$, $P=0.37$; richness: $\text{Chi}^2=1.63$, $P=0.44$) and the reef drop (Friedman Anova, abundance: $\text{Chi}^2=0.67$, $P=0.71$; richness: $\text{Chi}^2=3$, $P=0.22$). Nevertheless, we observed a weak, non-statistically supported decrease of fish abundance on the fringing reef between 2022 (mean \pm SD per transect = 65 ± 18) and 2024 (50 ± 9),

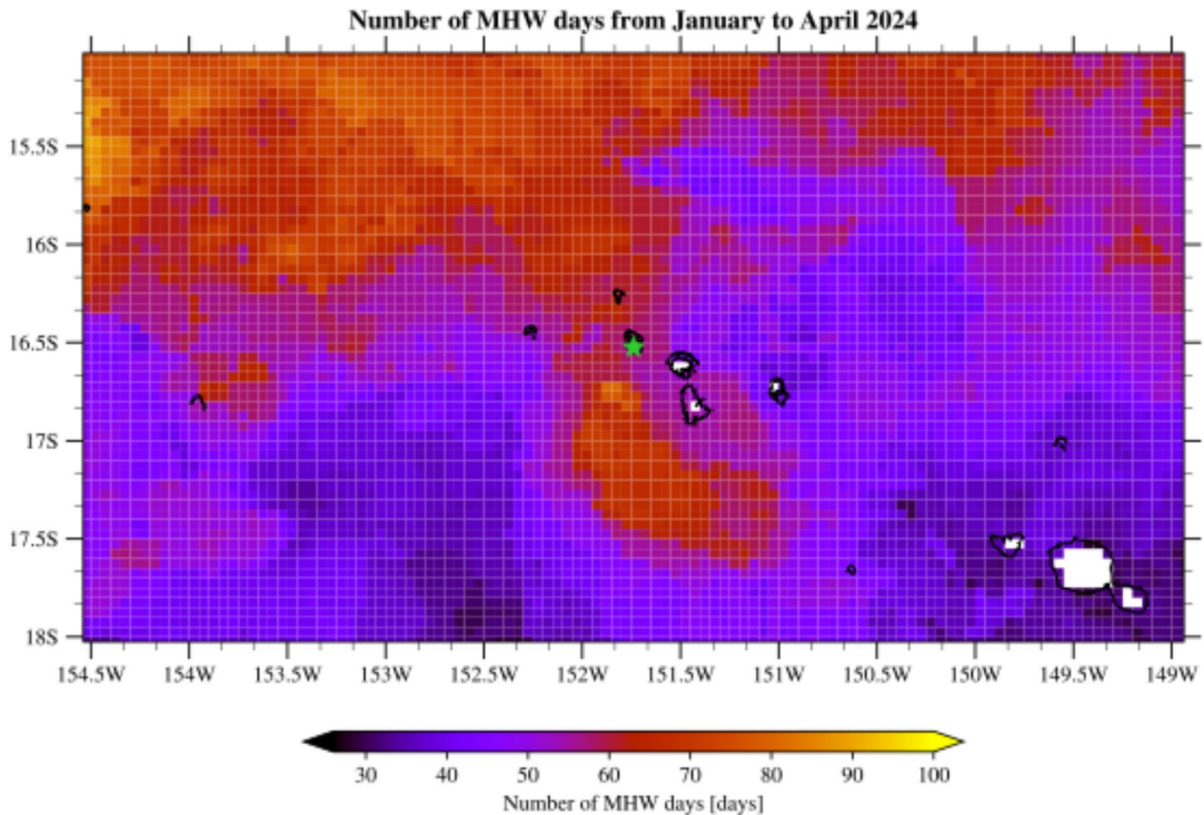


Fig. 3 Number of MHW days detected over the Society Archipelago using CRW SST at 5 km resolution, from 1 January to 30 April 2024. The green star indicates the location of the Bora Bora MEA. The baseline period used for MHW detection is 1995–2024

and a weak increase of fish abundance on the reef drop between 2022 (105 ± 7) and 2024 (117 ± 6).

From 2022 to 2024, fish abundance was significantly higher on the reef drop (109 ± 14) than on the fringing reef (61 ± 32) (Mann–Whitney test, $W=6.5$, $P=0.003$) (Fig. 5a), but no difference was observed for species richness (reef drop = 12 ± 2 ; fringing reef = 9 ± 2) (Mann–Whitney test, $W=20$, $P=0.07$) (Fig. 5b).

In Experiment 2, all the corals restored in the MEA in 2022 were found dead in 2024 following the bleaching event, with live coral cover on the reef patches declining from 50% or 75% in 2022 to 0% in 2024. We also observed a decrease in turf algae proportion and an increase in macroalgae proportion, leading to a new cover of macroalgae (*Dictyota* spp., *Halimeda* spp., *Padina boryana*, *Turbinaria ornata*, and *Sargassum* sp.) by up to 45%. On reef patches with 75% living coral originally restored, the remaining 25% turf algae cover was replaced by 12% to 20%

of macroalgae (Fig. 6a). On reefs with 50% living coral, the turf was replaced by 20% to 45% of macroalgae (Fig. 6b). On reef patches having undergone no restoration, macroalgae were also dominant, covering 40–100% of the area of the patches (Fig. 6c).

In Experiment 2, fish abundance did not vary significantly after the 2024 bleaching event compared with observations made in 2022, both before and after restoration on unrestored reef patches (Friedman Anova, $\text{Chi}^2=1.56$, $P=0.46$) or on patches restored to 50% (Friedman Anova, $\text{Chi}^2=3.83$, $P=0.15$). However, a significant change was observed on patches restored to 75% (Friedman Anova, $\text{Chi}^2=6.59$, $P=0.04$), with a significant decrease between abundance after restoration in 2022 (24 ± 7 individuals) and in 2024 (11 ± 8 individuals). (Nemenyi test, critical diff = 3.33, $P=0.048$) (Fig. 7a). Species richness did not differ between 2022 and 2024 on patches with 0% or 50% restoration (Friedman Anova, no restoration:

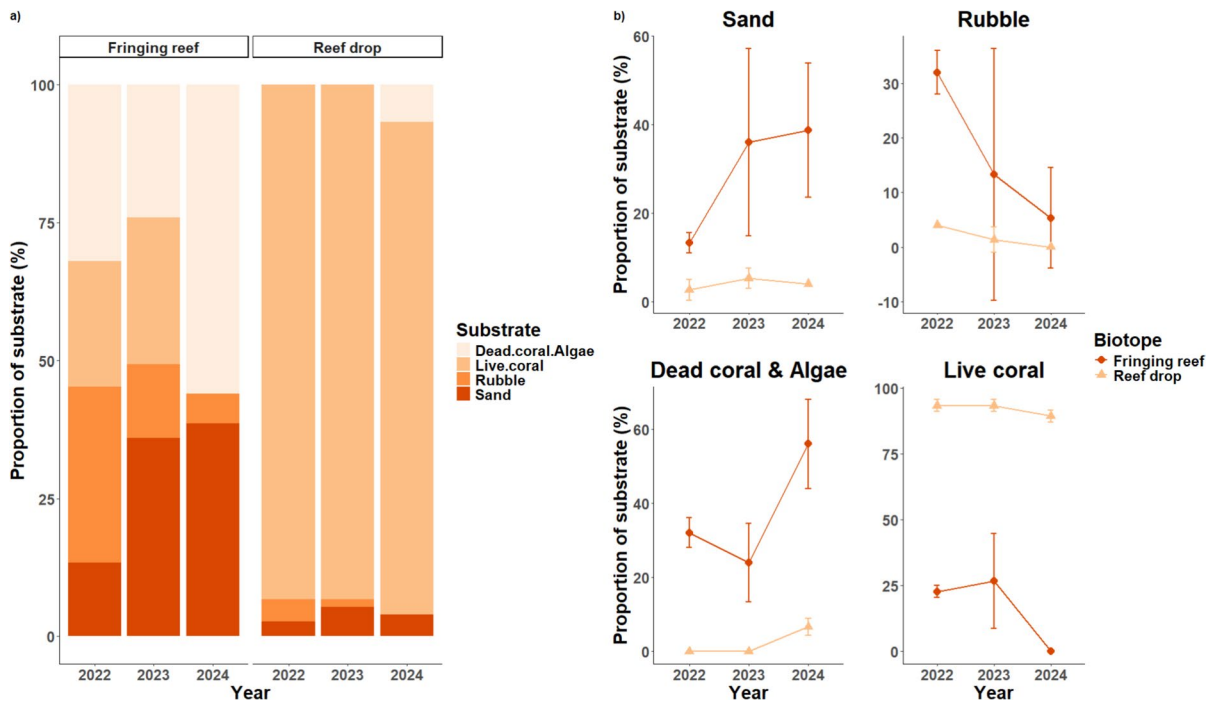


Fig. 4 Composition of the substrate on the fringing reef and the reef drop in 2022, 2023, and 2024. **a** Percent stacked bar plot showing the proportion of dead coral with macroalgae,

live coral, rubble and sand covering the substrate. **b** Relative percentage of each type of substrate. Values are mean \pm SD

$\text{Chi}^2 = 5.51$, $P = 0.06$; 50% restoration: $\text{Chi}^2 = 1.65$, $P = 0.44$). In contrast, species richness significantly decreased on patches with 75% restoration (Friedman test, $\text{Chi}^2 = 9.94$, $P = 0.007$), with fewer species in 2024 (5 ± 2 species) compared to 2022 after restoration (10 ± 2 species) (Nemenyi test, critical diff = 4.33, $P = 0.006$) (Fig. 7b). When examining the different diets (Fig. 8), no significant differences were found in the abundance of omnivores before and after restoration, for any restoration levels (Friedman Anovas, unrestored sites: $\text{Chi}^2 = 6$, $P = 0.05$; 50%: $\text{Chi}^2 = 5.54$, $P = 0.06$; 75%: $\text{Chi}^2 = 4.17$, $P = 0.12$). Omnivore richness differed only on reefs restored to 75% (Friedman Anova, $\text{Chi}^2 = 6.22$, $P = 0.04$), with a significant decrease between 2022 after restoration and 2024 (Nemenyi test, critical diff = 3.33, $P = 0.048$). For herbivores, abundance was significantly lower in 2024 compared to 2022 before restoration on both unrestored sites (Friedman Anova, $\text{Chi}^2 = 8.47$, $P = 0.014$; Nemenyi test, critical diff = 4, $P = 0.013$) and sites restored to 75% (Friedman Anova, $\text{Chi}^2 = 10.34$, $P = 0.006$; Nemenyi test, critical diff = 4.33,

$P = 0.006$). No significant differences were observed in herbivore richness (Friedman Anovas, unrestored sites: $\text{Chi}^2 = 0.75$, $P = 0.68$; 50%: $\text{Chi}^2 = 6.08$, $P = 0.05$; 75%: $\text{Chi}^2 = 4.2$, $P = 0.12$). Piscivore abundance did not differ significantly (Friedman Anovas, unrestored sites: $\text{Chi}^2 = 4.93$, $P = 0.08$; 50%: $\text{Chi}^2 = 4$, $P = 0.13$; 75%: no piscivore), nor did their richness (Friedman Anova, unrestored sites: $\text{Chi}^2 = 6.61$, $P = 0.04$ but not detected by Nemenyi tests; 50%: $\text{Chi}^2 = 4$, $P = 0.13$; 75%: no piscivore;). Corallivores were significantly more abundant in 2022 after restoration on sites restored to 75% (Friedman Anova, $\text{Chi}^2 = 9.5$, $P = 0.009$; Nemenyi test, critical diff = 3.67, $P = 0.026$), as well as higher richness (Friedman Anova, $\text{Chi}^2 = 11.38$, $P = 0.003$; Nemenyi test, critical diff = 3.67, $P = 0.026$). Finally, planktivores exhibited a significant increase in both abundance (Friedman Anova, $\text{Chi}^2 = 8.59$, $P = 0.01$) and richness (Friedman Anova, $\text{Chi}^2 = 7.6$, $P = 0.02$) between time periods on sites restored to 75%, although these differences were not confirmed by Nemenyi tests (all $P > 0.05$).

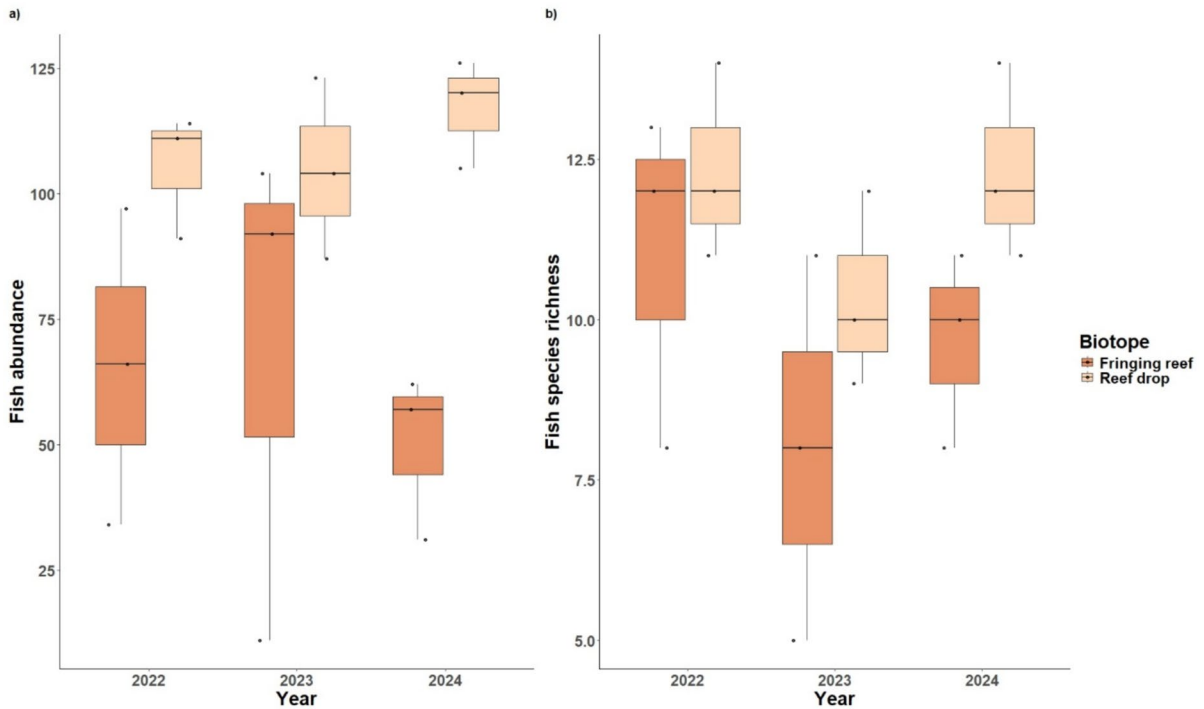


Fig. 5 Fish abundance (a) and fish species richness (b) on the fringing reef and the reef drop in 2022, 2023 and 2024. Boxes represent the first and third quartiles, the middle horizontal

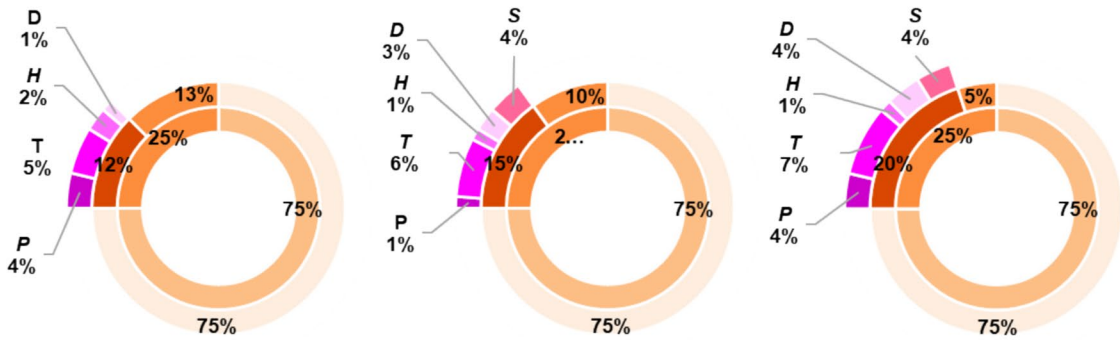
bars represent the median (second quartile), whiskers correspond to the range of values, and dots are individual observations

Discussion

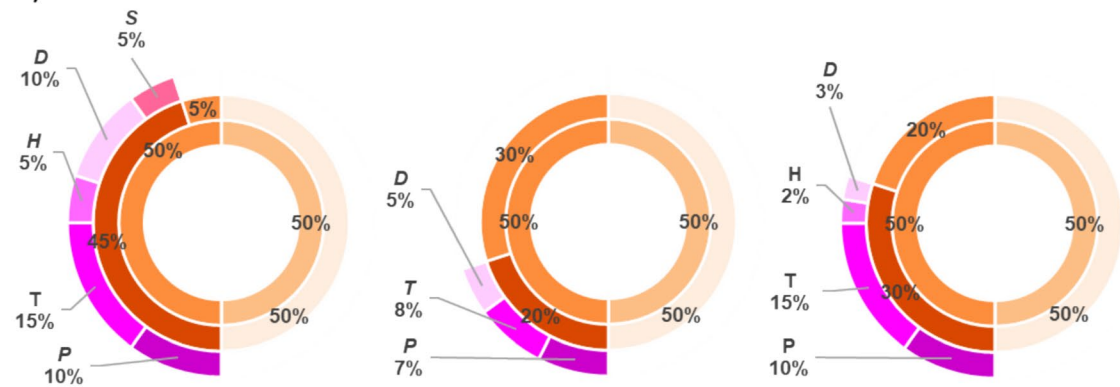
Coral reefs, among the most productive and biodiverse ecosystems in the world, are also highly impacted by local and global anthropogenic stressors which can cause significant environmental changes, including shifts from coral- to algal-dominated communities (Bellwood et al. 2019). In addition to corals, fishes are particularly vulnerable to global warming because, as ectotherms, their physiology is strongly influenced by the temperature of the surrounding water (McKenzie et al. 2020). Thus, loss of marine biodiversity on coral reefs constitutes a global crisis which is caused mainly by impacts of anthropogenic activities such as land-use change, overexploitation of commercial species, and climate change (e.g., Hoegh-Guldberg 2011; Hughes et al. 2018). To counterbalance the detrimental effects which are often global in origin, local coral reef restoration programs can be undertaken by scientists with the help of members of the local community including high school children, and NGOs (e.g., Jaap 2000; Suggett et al. 2024).

Our study aims to explore the limits of local reef restoration as conducted by high school children with the support of scientists, under climate pressure and specifically during a marine heat wave. Between January and April 2024, approximately 60–70 MHW days occurred around the Bora Bora region. Our results from Bora Bora (Fig. 4) indicate that the effect of bleaching is highly variable depending on the depth and current of the restored corals. Coral bleaching is a stress phenomenon as corals expel their photosynthetic endosymbiotic algae (zooxanthellae), essential for their nutrition and coloration. It is mainly caused by an increase in water temperature, but also by high light levels, pollution, or ocean acidification (Hoegh-Guldberg et al. 2007). The loss of zooxanthellae turns the corals white and severely weakens their metabolism. If the stress persists, the coral may die, but recovery is possible when conditions become favorable again. Over the past few decades, this phenomenon has become a major threat to coral reefs worldwide (Hoegh-Guldberg et al. 2007; Mellin et al. 2024). However, our finding corroborates results from other recent studies about the spatial

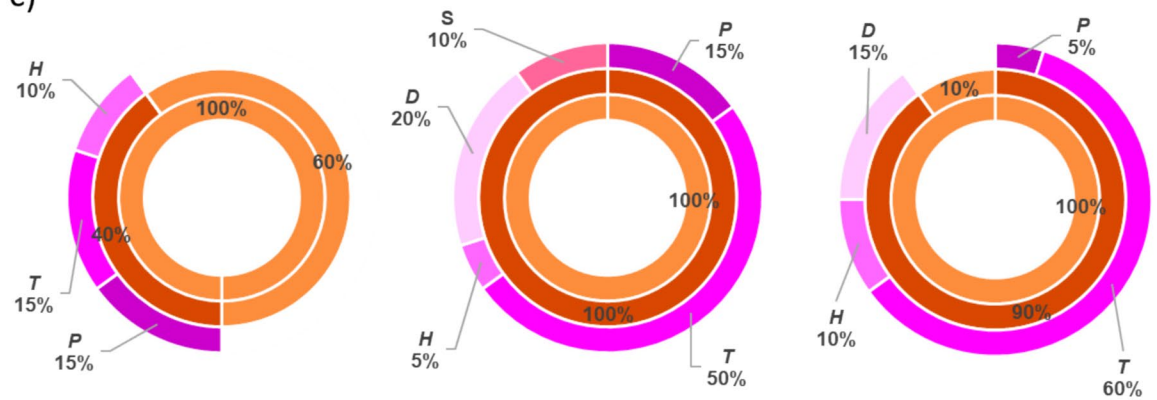
a)



b)



c)



◀**Fig. 6** Percentage of substrate type covering the three reef patches for the following conditions: **a** 75% restored living coral, **b** 50% restored living coral, and **c** control condition. Inner circles refer to 2022 (after the restoration), middle circles represent 2024 (after bleaching) and outer circles show the composition in macroalgae observed in 2024. S, *Sargassum*; D, *Dictyota*; H, *Halimeda*; T, *Turbinaria*; and P, *Padina*

variability of bleaching event (e.g., Pérez-Rosales et al. 2021; Shlesinger and van Woesik 2023; Winslow et al. 2024). At small spatial scale, hydrodynamics (currents, waves), depth, sunlight exposure, pollution, and water turbidity can alter the stress conditions experienced by corals and create mosaics of spatial vulnerability even within the same reef (Coulibaly et al. 2025). In addition, the specific composition of corals and their algal symbionts, influenced by evolutionary history and past disturbances, also plays an important role in differential responses to thermal stress at fine spatial scale. The difference of bleaching between corals on the reef drop and the fringing reef at Bora Bora could be explained by the depth and the currents that are slightly different

between the two biotopes, even if we did not have any water parameters to validate this hypothesis. Thus, the interactions between the climatic, oceanographic, and ecological factors often explain the complex spatial variability of bleaching events observed around the world (Winslow et al. 2024). Rising ocean temperatures therefore pose major risks to coral reefs worldwide, with the increasing frequency of mass coral bleaching events compromising ecosystem resilience (Riegl et al. 2009; Mellin et al. 2024).

Following bleaching events, Magel et al. (2020) first found that reef fish biomass and abundance declined by over 50% during heat stress due to a vertical (downward) displacement of fish to cooler waters. However, they then observed a rebound in reef fish abundance to pre-stress levels, a result that appears more relevant to our Bora Bora findings. In our study, despite some changes in coral cover in the MEA, the total fish abundance and richness remained relatively stable across time (before and after the bleaching event). The short observation period after the bleaching event may explain why we did not detect

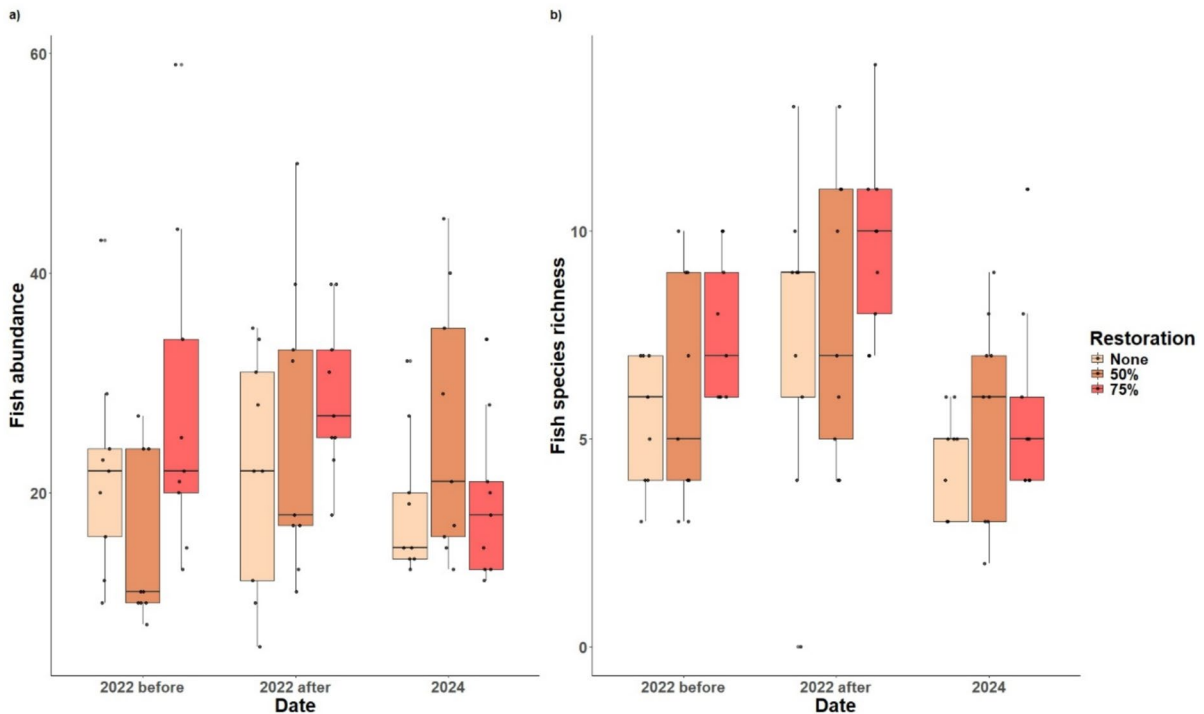


Fig. 7 Fish abundance (a) and fish species richness (b) on the coral reef patches in 2022 before restoration, in 2022 after restoration (control=no restoration, 50% and 75% of restoration) and in 2024 after the bleaching event. Boxes represent the first

and third quartiles, middle horizontal bars are the median (second quartile), whiskers correspond to the range of values, and dots are individual observations

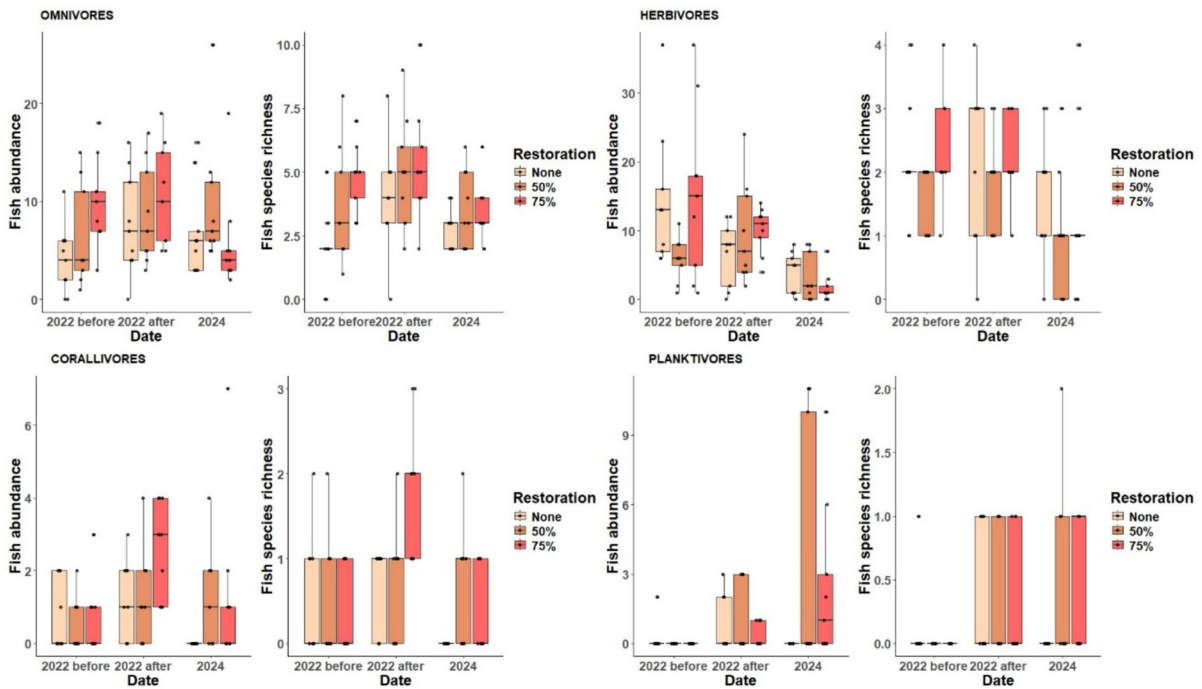


Fig. 8 Fish abundance and fish species richness of omnivores, herbivores, corallivores, and planktivores on coral reef patches in 2022 before restoration, in 2022 after restoration (control=no restoration, 50% and 75% of restoration) and in 2024 after the bleaching event. Piscivores are not shown due to

low numbers. Boxes represent the first and third quartiles, the middle horizontal bars indicate the median (second quartile), whiskers show the range of values, and dots represent individual observations

significant trends in fish population in Bora Bora. Magel et al. (2020) suggest that the relatively short time frame in which fish populations could decline and subsequently recover after a bleaching event is likely due to spatial shifts in reef fish distribution, rather than negative impacts on reef fish fitness. Other studies showed that coral bleaching can lead to shifts in reef fish community structure but over a longer observation period than our study (Graham et al. 2015; Robinson et al. 2019). For example, Stuart-Smith et al. (2018) reported declines in corallivore abundance and decreased fish species richness on the Great Barrier Reef (Australia) 8–12 months after coral bleaching. Thus, our short observation period after the bleaching event at Bora Bora may explain why no significant trends were detected in fish populations. Reef fish assemblages are strongly influenced by interannual fluctuations in larval recruitment, which are highly dependent on oceanographic conditions such as temperature anomalies, currents, and larval supply (Lecchini and Galzin 2003; Sale 2010). In addition, the effects of disturbances such as coral bleaching, habitat degradation, or fishing pressure may manifest

themselves with a time lag, particularly for long-lived or sedentary species (Graham et al. 2007). Several long-term studies of coral reefs have shown that short-term surveys may fail to detect population declines or recovery trajectories that only become apparent on a decadal timescale (Hughes et al. 2018). Therefore, the absence of significant trends in our study may reflect limited temporal resolution rather than true stability in reef fish populations.

However, at the scale of fish diet, our data suggests that a decrease in omnivorous and herbivorous species may explain the reduction in abundance and richness observed after the 2024 bleaching event compared to 2022 on reefs restored to 75%. On Jarvis Island, Brainard et al. (2018) found that the loss of over 95% live coral cover resulted in substantial declines in total reef fish biomass, while warming-induced changes in primary productivity negatively affected planktivores. Based on previous literature on fish assemblage modifications following coral restoration, significant differences have been reported for adult fish at Bora Bora (Krimou et al. 2024). In

addition, some species are known to be more strongly associated with highly restored patches (e.g., *Chaetodon citrinellus*, *Halichoeres trimaculatus*, and *Zanclus cornutus*). In our study, a significant decrease in fish species richness was observed on patches with 75% restoration. This may be related to the fact that greatest differences in the mean number of individuals are known to occur at 75% restoration for certain trophic groups, such as piscivores. Lastly, some direct physiological effects on fish cannot be ruled out. Indeed, numerous studies have shown such impacts, including oxygen limitation of thermal tolerance (Farrell 2016; Comte and Olden 2017).

Conclusion

Our results suggest that heat waves seem to provoke a more pronounced negative impact on the shallow coral reefs of Bora Bora compared to deeper reef zones. However, no significant changes were observed in fish abundance or species richness across depths, neither prior to nor after the bleaching. The implications of the small sample sizes could partly explain the absence of significant difference in the fish population across time. As seen in Fig. 5, only three data points were collected per year in each biotope for Experiment 1, resulting in large variation in the results on the fringing reef and likely significantly limiting the power of statistical tests. Nevertheless, our findings underscore, despite some local-scale restoration efforts, that large-scale stressors such as heat waves, which trigger coral bleaching events, can significantly undermine restoration activities led both by scientists (e.g., CRI-OBE) and by community members (e.g., high school children). Yet far from calling for the abandonment of local-scale initiatives, these findings highlight the necessity of aligning such actions with the realities of climate change, following the concept of resilience assessments which prioritize management actions to support coral reef resilience (McClanahan et al. 2012; McLeold et al. 2019). Moreover, an outcome of our study, conducted with high school children since 2021 and still ongoing as an awareness-raising activity, is that both children and their parents have recognized the importance of transitioning to more environmentally friendly energy sources. Such measures are essential if local conservation efforts are to meaningfully contribute to the health of coral reefs which are heavily relied

upon by Pacific communities for food and tourism. Thus, local restoration strategies must be informed by the latest scientific advances if they are to limit the impact of climate change (e.g., the depth-related difference in coral responses to thermal stress) and must be implemented in accordance with global scale pressures (Anthony et al. 2020; Good and Bahr 2021).

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Author contribution All authors gave final approval to publish the present study. Conceptualization: David Lecchini, Stéphanie Krimou, Jérôme Sowinski, Vincent Sturny, Tehani Maueau. Methodology: David Lecchini, Stéphanie Krimou, Laura Gautrand, Bastien Pagli, Jérôme Sowinski. Formal analysis: Xavier Raick, Bastien Pagli, Matthieu Juncker and Frédéric Bertucci. Writing – original draft: David Lecchini, Frédéric Bertucci, Xavier Raick, and Stéphanie Krimou. Writing – review & editing: all authors

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Data availability The sampling, analysis and data generated in this study are available from the corresponding author on reasonable request. The NOAA Coral Reef Watch (CRW) v3.1 SST dataset can be found at <https://www.ncei.noaa.gov/data/oceans/crw/5km/v3.1/nc/v1.0/daily/sst/>.

Declarations

Ethics approval No ethical approval was required for this study, although the research was guided by the ethical code of conduct in place at the CRIOBE.

Conflict of interest The authors declare no competing interests.

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