



A remote coral reef shows macroalgal succession following a mass bleaching event

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ABSTRACT

Coral reefs worldwide are exposed to increased levels of thermal stress due to global warming. A coral reef at the remote island of Kapou (Lisianski) in Papahānaumokuākea experienced an unprecedented level of heat stress in 2014, which resulted in coral bleaching and subsequent mass mortality that resulted in nearly 100 % loss of live coral cover. Here, we describe successional changes in benthic communities occurring on the reef from 2014 to 2021 based on our surveys utilizing underwater photogrammetric techniques. Despite having > 85 % *Montipora* live coral cover before the bleaching event, the newly available substrata created by the loss of coral were quickly colonized by the green macroalga *Halimeda*, along with an ephemeral bloom of the green macroalga *Boodlea* in 2016. While *Halimeda* continued to increase in benthic cover, other algae (*Neomeris*, *Asparagopsis* and unidentified filamentous red and green algae) also started colonizing the reef between 2017 and 2021. Erosion of the reef substrata was evident in both in-situ and three-dimensional surveys in 2015 following the bleaching event and has continued to progress through time. The high abundance of *Halimeda* may indicate a slow process of coral recovery, but the overall benthic diversity increased in 2021 due to the presence of other algae and an increase in hard substrata and turf algal cover. New colonies of *Montipora* coral were also observed during annual surveys following the bleaching-induced mortality. Future monitoring efforts should continue to track coral and algal communities and survey herbivorous fish and reef binders that play important ecological roles in algal control, reef erosion and sediment binding. Such efforts should reveal interactions among these different ecological processes that enable reef succession following mass coral mortality.

1. Introduction

Coral reefs worldwide are under increased levels of thermal stress due to global warming resulting from climate change (Hughes et al., 2017). Increases in seawater temperature can result in bleaching and mortality, which in turn cause extensive losses in coral cover. These intensifying losses of live coral can alter benthic community structure and diversity and transform the reefs into degraded systems (Hughes et al., 2018; Couch et al., 2017). While relatively quick recovery of coral cover was reported following the global coral bleaching event of 1997/1998 through regeneration from surviving cryptic tissues (Roff et al., 2014) and the growth of remnant corals followed by a rapid increase in recruitment (Gilmour et al., 2013), the possibility of recurrent bleaching

events due to rising global temperature makes full recovery of reefs to the original states uncertain (Hughes et al., 2017).

The ecological impacts of mass coral bleaching include loss of live coral cover, changes in the structure of reef communities and architectural complexity, increases in macroalgal abundance, potential local extinction of coral and reef-associated organisms and loss of reef structure through bioerosion (Baker et al., 2008; Glynn, 2011; Loya et al., 2001). Recovery of coral reefs following mass bleaching events is highly variable among reefs, and neither the extent of the impacts sustained by reef ecosystems nor the amount of remaining live coral seems to be a sole determinant of the rate of recovery (Baker et al., 2008). Interactions among multiple stressors may also result in synergistic, not simply additive, effects (Ban et al., 2014), and the presence of chronic

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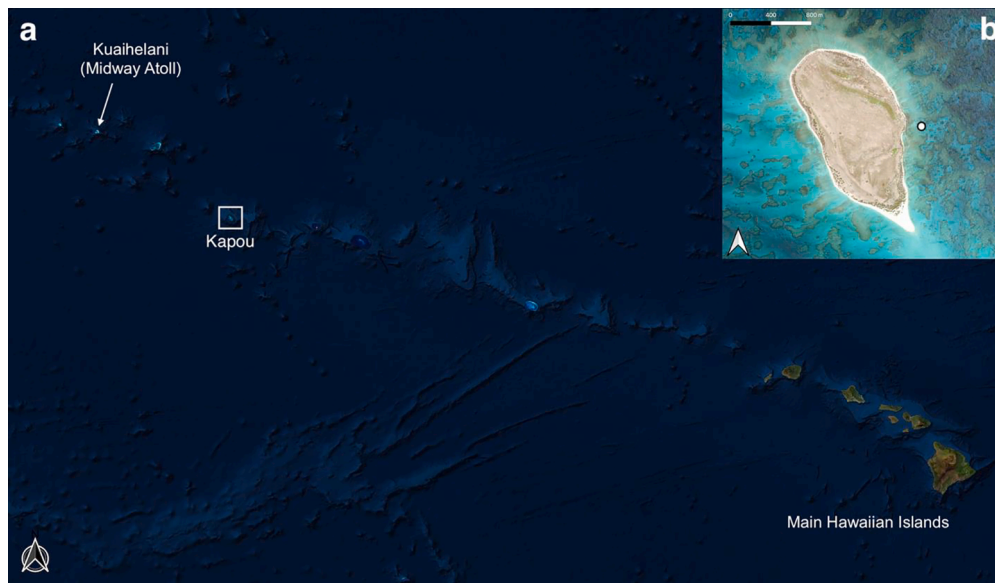


Fig. 1. Map of the Hawaiian Archipelago showing the locations of (a) Kapou and (b) and the study site (white dot in inset) at Kapou.

anthropogenic stressors can hinder the recovery of coral reefs after a bleaching event (Carilli et al., 2009).

Papahānaumokuākea Marine National Monument is a fully protected marine conservation area that encompasses uninhabited remote islands and atolls of the Northwestern Hawaiian Islands (Fig. 1a). Coral reefs in Papahānaumokuākea experienced an unprecedented level of heat stress in 2014, which resulted in coral bleaching and subsequent mortality especially on the island of Kapou, also referred to as Lisianski (Couch et al., 2017). This study describes a survey effort using photogrammetric techniques to monitor changes in the benthic cover at a reef site at Kapou following the mass bleaching event. Our study presents a rare scenario of reef succession after mass coral mortality at a site that is removed from direct local anthropogenic impacts (e.g., fishing, anthropogenic nutrient/contaminant input) due to the remoteness and fully protected status of Papahānaumokuākea. The use of photogrammetric techniques allows for three-dimensional (3D) reconstructions and quantitative assessments of the same reef area over time and is particularly useful when tracking the location, morphology and volumetric properties of coral colonies and other benthic features on a reef. Our approach reveals detailed successional stages following coral mortality and offers important insights into factors affecting reef resilience.

2. Material and methods

2.1. Photogrammetry surveys

The study site (26.0638° N, 173.9593° W) is located on the east side of Kapou at approximately 3-m depth (Fig. 1b). This location experienced the most severe coral bleaching among those surveyed during the 2014 mass bleaching event in Papahānaumokuākea (Couch et al., 2017). Permanent markers (pins) were installed at the site in 2015 to align transects for future surveys to facilitate temporal monitoring of the site. Prior to the bleaching event in 2014, the site had >85% *Montipora* coral cover (Couch et al., 2017).

Benthic surveys of the site were conducted in summer (late May – September) 2014, 2015, 2016, 2017, 2019 and 2021 during National Oceanic and Atmospheric Administration's research expeditions to Papahānaumokuākea using photogrammetric techniques. Two 10-m transect tapes were laid along the permanent pins, with the first transect (T1) located on top of a reef and the second one (T2) at the edge of the same reef along a relatively large sand patch. Due to an error in recording of the compass heading of T1, the T1 in 2014 did not align

with the T1s from all other years. In addition, due to a thick growth of macroalgae, the permanent pins for T1 could not be located in 2019. Thus, the T1 data consist of four time points (2015, 2016, 2017 and 2021), while the T2 data contain all survey years.

For each transect, a diver collected a sequence of overlapping photographs while swimming approximately 1 m above the transect in a lawn-mower pattern with 70–80% overlap between the images. All photographs were taken using either a Canon 5D Mark III digital SLR camera (2014–2017) or a Sony α7rIII mirrorless camera (2019 and 2021) with a 24–70 mm lens in an underwater housing with an 8-inch hemispheric dome port. The focal length of the lens was set to 24 mm and ISO fluctuated automatically to maintain standardized exposure throughout the imagery collection. Ground control points (e.g., scale bars) were placed around the transect tape prior to the imagery collection to scale the resulting 3D model.

2.2. Generation and processing of orthophotomosaics

Three-dimensional models were built from the acquired images using the software Agisoft PhotoScan/Metashape Professional (Agisoft LLC., St. Petersburg, Russia). A sparse point cloud was generated for each survey plot through the photo-alignment process. After optimizing the alignment and scaling the resulting model using the ground control points, a dense point cloud was rendered. An orthophotomosaic and an associated 2.5-dimensional digital elevation model (DEM) were then generated from a single-projection overhead angle and exported as GeoTIFF data files for analysis in the open-source geographic information system software QGIS (<https://qgis.org/>).

Orthophotomosaics from different years were aligned separately for the two transects, and the same 30-m² areas (10-m long × 3-m wide) were identified and used for benthic characterization using digital annotation points. A thousand random points were generated within each of the 30-m² plots and biotic/abiotic benthic features under the points were identified to the lowest possible taxonomic level to calculate benthic cover of different organisms and abiotic features. Live coral colonies were also digitized as polygons to track changes in percent coral cover and spatial location of the colonies over time.

2.3. Reef fish surveys

Fish visual surveys were conducted at the study site in 2021 by a diver who had been formally trained to conduct in-situ fish surveys in

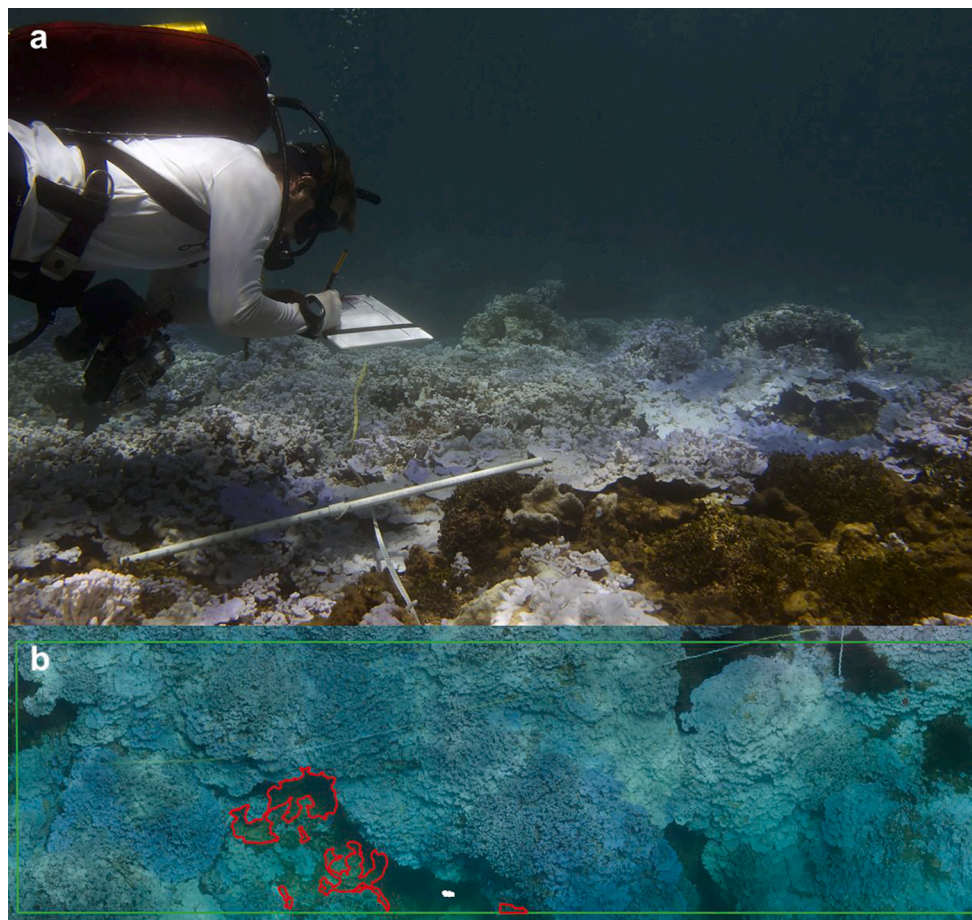


Fig. 2. Photograph from 2014, showing (a) bleached *Montipora* coral at the reef site (photo credit: NOAA/Courtney Couch), and (b) an orthophotomosaic with digitization of live (non- bleached) *Montipora* colonies in red at the edge of the reef (T2) in 2014. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

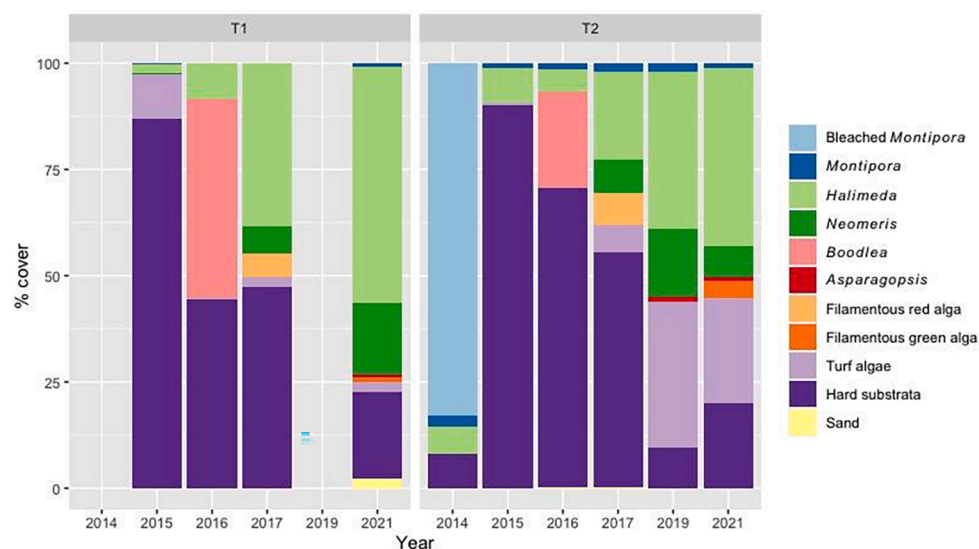


Fig. 3. Changes in benthic cover on top of the reef (T1) and at the edge of the reef (T2) from 2014 to 2021. No data is available for T1 from either 2014 or 2019.

Hawaiian waters. Prior to the photogrammetry surveys of T1 and T2, the diver swam along the 10-m transect tapes identifying, sizing and enumerating all reef fishes within 2.5 m on either side of the transect tapes. Reef fishes were categorized into five trophic habits (herbivore, invertivore, planktivore, omnivore and apex predator) based on

FishBase (<https://www.fishbase.org>), Hiatt and Strasburg (1960), Hobson (1974) and Hoover (1993).

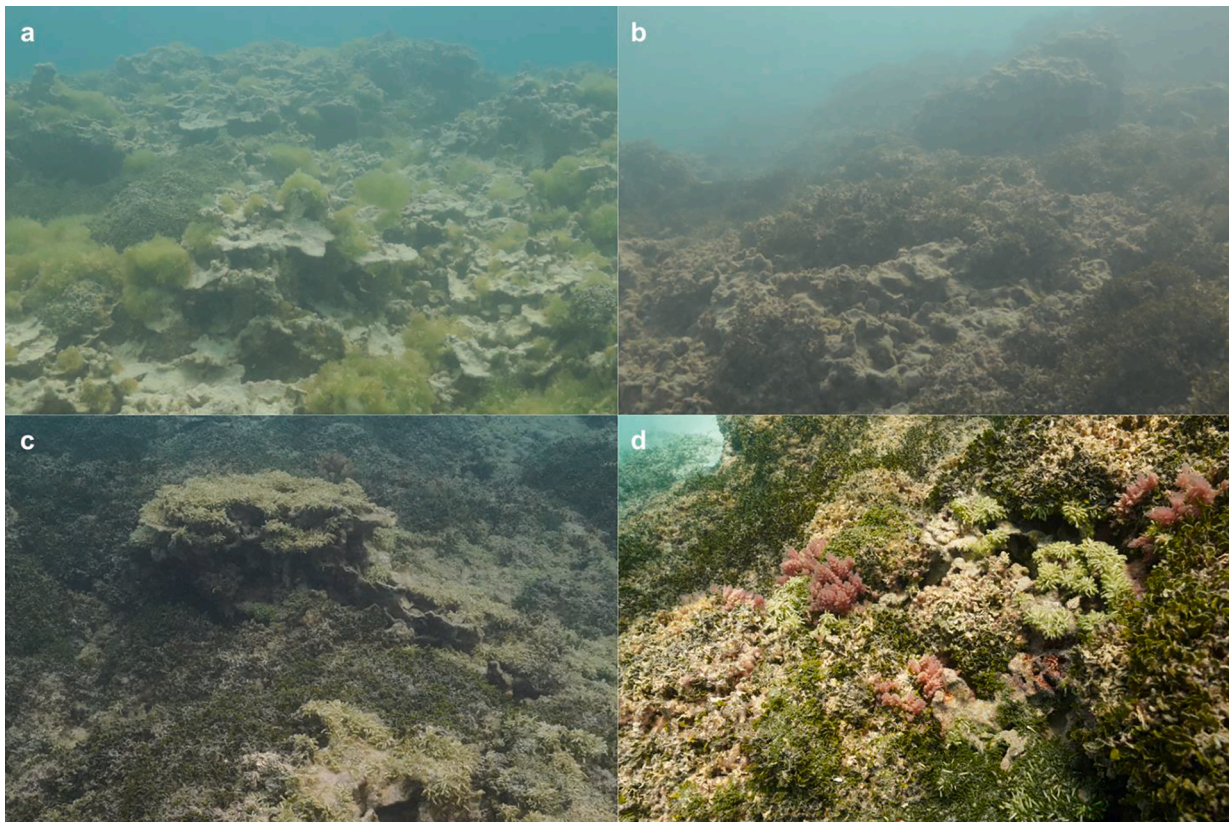


Fig. 4. Site photos from (a) 2016, (b) 2017, (c) 2019 and (d) 2021, showing changes in macroalgal cover and composition.

3. Results and discussion

Following the mass bleaching event in 2014, *Montipora* coral exhibited nearly 100 % mortality (Fig. 2), and the study site was primarily covered by hard substrata (i.e., dead coral), turf algae and the green macroalga *Halimeda* on top of the reef (T1) and at the edge of the reef (T2) in 2015 (Fig. 3). In 2016, there was a *Boodlea* bloom at the site (Fig. 4a), which resulted in the green macroalga covering approximately 50 % of the benthos on top of the reef and approximately 25 % at the edge of the reef (Fig. 3). This *Boodlea* bloom was similar to the one observed on shallow reefs of Midway Atoll and Kure Atoll in Papahānaumokuākea in summer 2008, in that the bloom conditions dissipated relatively quickly by the following summer (Vroom et al., 2009). *Boodlea* was not observed in 2017, but there was a large increase in the percent cover of *Halimeda* and the green macroalga *Neomeris* (Fig. 3). These green macroalgae formed relatively thick mats (Fig. 4b) that continued to grow and covered approximately 75 % of benthos on top of the reef in 2021 and approximately 50 % at the edge of the reef in 2019 and 2021 (Figs. 3 & 4c). Small amounts of growth of the red macroalga *Asparagopsis* were observed in 2019 and 2021 (Figs. 3 & 4d) and unidentified filamentous red and green algae were also observed in 2017 and 2021, respectively.

Live *Montipora* cover on top of the reef (T1) was reduced to 0.29 % in 2015 after the bleaching event and remained low in 2016 (0.06 %) and 2017 (0.12 %). Some of the coral colonies that survived the bleaching event disappeared by 2016 (Fig. 5a, b), but new colonies were detected in 2017 (Fig. 5c), which resulted in a slight increase in *Montipora* cover from 2016 to 2017. Growths of these colonies, as well as new colonization, were visible in 2021 (Fig. 5d) and live *Montipora* cover increased to 0.69 %. Reef erosion was also observed through volumetric analysis in 2015 (Couch et al., 2017) and loss of habitat was continually observed; in the 2021 survey, the loss of reef substratum from erosion was observed through our in-situ survey and 3D reconstruction of the reef

using the photogrammetric techniques, and a new small patch of sand became visible in the orthophotomosaic in the area adjacent to the starting point of T1 (Fig. 5d, left side of the figure). These visual observations were numerically corroborated by an increase in the percent cover of sand for T1 in 2021 (Fig. 3).

Live *Montipora* cover at the edge of the reef (T2) was 1.03 % after the bleaching, being higher than live coral cover on top of the reef (T1). The surviving colonies grew, and new colonies appeared by 2016 (Fig. 6a, b), which produced a total of 1.29 % coral cover. Although some colonies were outcompeted by *Halimeda* (Fig. 6c, d), live *Montipora* cover continued to increase to 1.51 % in 2017 and 1.84 % in 2019. This positive trend ended in 2021 as erosion of the reef became visible (Fig. 6e, at the bottom of the figure) and live *Montipora* cover decreased to 0.87 %. Note that due to the orthophotomosaics being generated from the overhead angle, any colonies on the side of or under the eroding reef could not be captured during the digitization, so this might have resulted in an underestimation of coral cover in 2021.

Montipora coral at the reef site prior to the bleaching included *Montipora dilatata/flabellata*, *Montipora patula* and *Montipora capitata* (Couch et al., 2017), but all live coral colonies that were observed in situ during our surveys and identified in the orthophotomosaics between 2015 and 2021 (Figs. 5 & 6) were *M. capitata*. While non-bleached *M. capitata* exhibits relatively low contribution of heterotrophy to daily respiration, bleached and recovering *M. capitata* can meet their metabolic energy requirement by increasing heterotrophic feeding rates and replenish their energy reserve (Grottoli et al., 2006). This switch to heterotrophy potentially explains why *M. capitata* is the only species that have returned to the site so far.

The increase in *Halimeda* cover and reef erosion at the site is consistent with what was observed on remote Maldivian reefs after a bleaching event in 2016 (Perry et al., 2020). On the Maldivian reefs, sediment generation increased due to increases in the abundances of two sediment generators, *Halimeda* and parrotfish through bioerosion (Perry

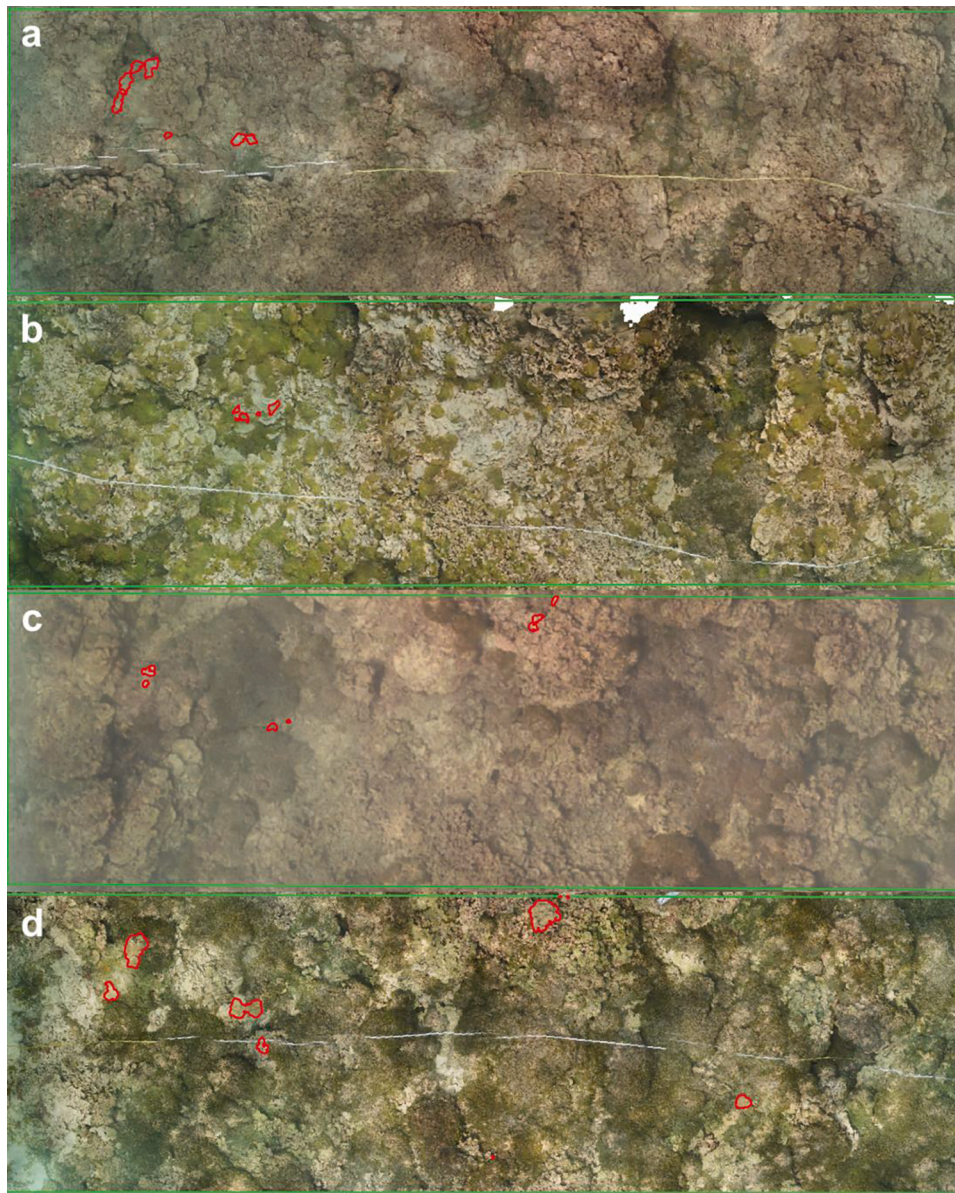


Fig. 5. Orthophotomosaics with digitization of live *Montipora* colonies on top of the reef (T1) in (a) 2015, (b) 2016, (c) 2017 and (d) 2021. *Montipora* colonies are digitized in red. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

et al., 2020). Increases in the abundances of macroalgae (largely *Halimeda*) and parrotfish (mostly *Chlorurus sordidus*¹ and *Scarus psittacus*) were also observed on coral reefs in Moorea following near-complete loss of coral due to a crown-of-thorns starfish outbreak (Adam et al., 2011). In the present study, fish surveys were not conducted until 2021, so it is not possible to examine whether the abundance of parrotfish increased on the reef over time. In 2021, two species of parrotfish, *Chlorurus perspicillatus* and *S. psittacus*, were recorded on the reef (Table S1): seven individuals of *C. perspicillatus* ranging from 25 to 40 cm and 14 individuals of *S. psittacus* ranging from 14 to 19 cm. In a study in Hanauma Bay, which is a no-take marine protected area on the island of O'ahu, two species of parrotfish, *C. perspicillatus* (excavator) and *Scarus rubroviolaceus* (scraper) were estimated to remove 60 % of the gross carbonate production on the reefs of Hanauma Bay (Ong and Holland, 2010), indicating the potentially important role of parrotfish in reef

¹ *Chlorurus sordidus* occurs in the Indian Ocean, so this species was likely *Chlorurus spilurus* (Randall, 2007).

erosion in Hawai'i.

Herbivorous fish affect algal succession on coral reefs and thus play an important role in regulating algal abundance in coral-reef ecosystems (Hixon and Brostoff, 1996). In the present study, the percent cover of the green calcareous macroalga *Halimeda* increased over the years following the bleaching event and was highest in 2021 (Fig. 3). This increase in algal cover at the remote reef site contradicts findings from previous studies where herbivorous fish could suppress macroalgal growth in the absence of overfishing (Adam et al., 2011; Gilmour et al., 2013). In the study in Moorea, the increase in parrotfish abundance was approximately 4-fold on the forereefs following the loss of coral, but their size distribution indicated the fish primarily settling into the lagoon and moving to the forereef later in life (Adam et al., 2011). Kapou lacks fully protected lagoon habitats (Fig. 1b), thus the parrotfish population could be limited by the availability of juvenile habitat, which may be reducing their capacity to control macroalgal growth. Furthermore, Kapou supports a large population of seabirds despite being a remote island (Office of National Marine Sanctuaries, 2009). The high abundance of seabirds could stimulate macroalgal growth by causing high nutrient loading into

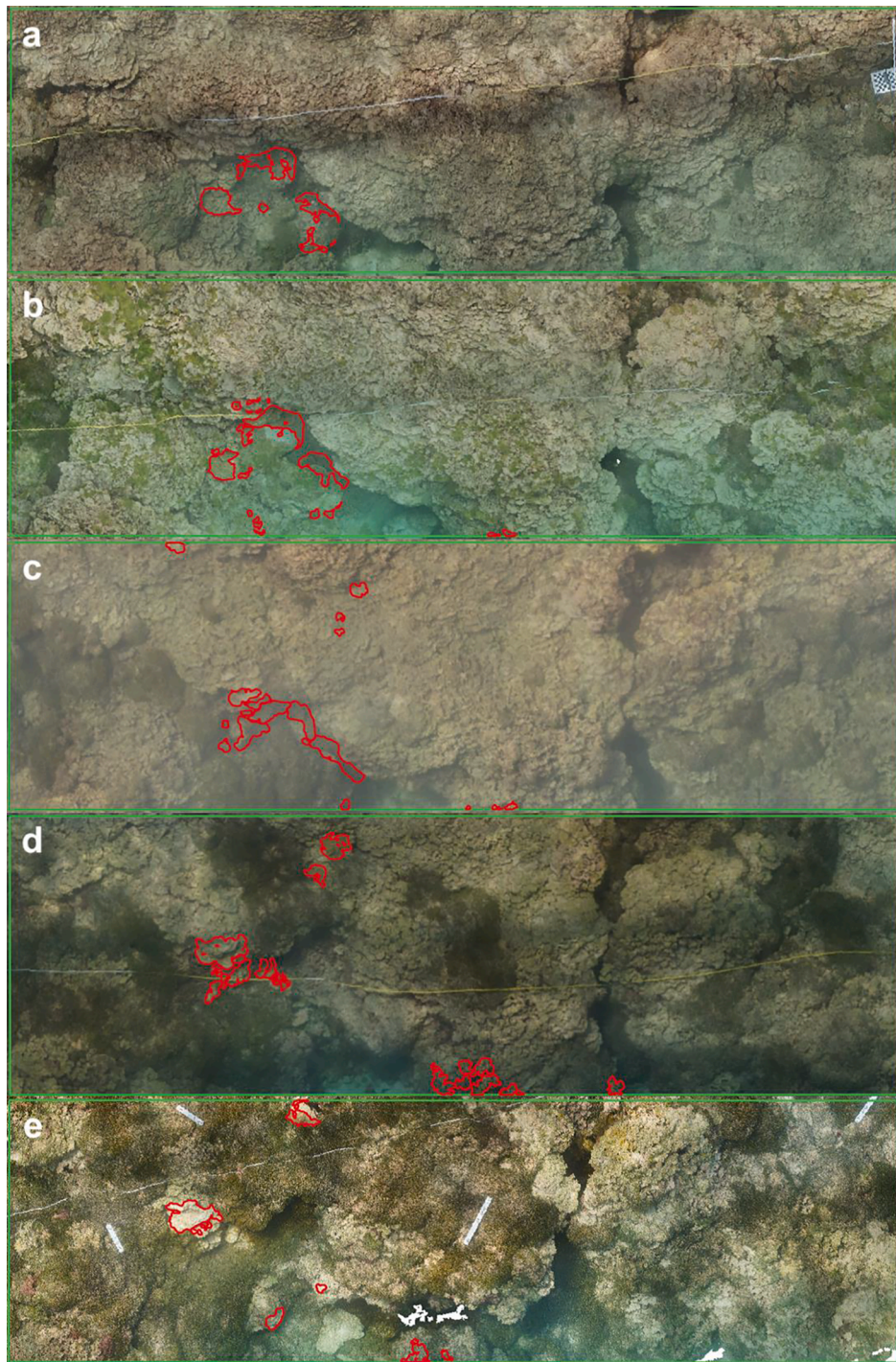


Fig. 6. Orthophotomosaics with digitization of live *Montipora* colonies at the edge of the reef (T2) in (a) 2015, (b) 2016, (c) 2017, (d) 2019 and (e) 2021. *Montipora* colonies are digitized in red. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

shallow-water reef habitats surrounding the island.

While the abundance of *Halimeda* is concerning, especially due to their chemical and structural protection from predation and the ability to propagate through vegetative fragmentation (Walters et al., 2002), there were patches of *Halimeda* mats turning white in the area (A.F. and K.H.P. personal observation) in 2021. The benthic cover of hard substrata and turf algae also increased at the edge of the reef in 2021, causing an increase in overall benthic diversity (Fig. 3). Although slow growing, new colonies of *M. capitata* coral were also confirmed on the reef resulting in a small increase in live coral cover (Figs. 5 & 6). Reef erosion observed in the present study indicates the important roles of

reef binders, such as crustose coralline algae and sponges, in supporting reef resilience as these organisms stabilize sediment on coral reefs (Ceccarelli et al., 2020). Reef binders are often overlooked with focus of monitoring efforts being placed on enumerating the abundance and diversity of coral and fish. While these organisms may play critical roles in coral reef ecology, the lack of attention on studying binding organisms may impair our ability to identify species that are important for sustaining reef structure and support recruitment and regrowth of calcifying corals. Future monitoring at Kapou should continue to track both coral and algal community composition and potential reef erosion with further attention to reef binders. An annual fish survey to

enumerate herbivore abundance and diversity will be a critical component in future monitoring, as herbivorous fishes play important roles in algal control and reef erosion. Such efforts should reveal how different, yet interacting, ecological processes of herbivory, reef erosion and sediment binding contribute to reef resiliency.

Declaration of Competing Interest

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

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2022.109175>.

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