Journal name: *Ecological Applications*

Manuscript type: Article

Manuscript title: Removing dead coral after marine heatwaves can mitigate coral-algae competition and increase viable coral recruitment

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Data Availability Statement: All data and code used that support this manuscript can be accessed at https://github.com/kkopecky711/Dead-coral-removal-experiment.git. Additionally, all data and code will be permanently archived in a publicly accessible repository via the Environmental Data Initiative (EDI) upon acceptance of this manuscript.

Keywords: Material legacies, resilience, disturbance, competition, global change, marine heatwaves, foundation species, coral reefs, macroalgae, underwater photogrammetry, artificial intelligence

ABSTRACT

Ecological disturbance regimes are shifting and leaving behind novel legacies, like the remnant structures of dead foundation species, which have poorly known impacts on ecosystem resilience. We explored how dead coral skeletons produced by marine heatwaves–material legacies of increasingly common disturbances on coral reefs–influence spatial competition between corals and macroalgae, focusing on whether removing dead branching skeletons stimulates recovery of coral after disturbance. Following a marine heatwave, we removed dead skeletons from reef patches then used underwater photogrammetry and AI-powered image analysis to quantify trajectories of coral and macroalgae. After four years, removal of dead skeletons resulted in 1.6 times more live coral remaining and reduced development of macroalgae by half, relative to patches where skeletons were left intact. Dead skeletons acted as an alternate substrate type that facilitated macroalgae development, and greater macroalgal abundance caused steeper declines in live coral. Lastly, removal of dead skeletons led to five times greater densities of coral recruits on stable (primary) reef substrate. Our findings identify a promising avenue to manage for coral resilience (on reefs where carbonate budgets are not in a deficit) and reveal how material legacies of changing disturbance regimes can alter physical environments to sway the outcomes of spatial competition.

INTRODUCTION

As regimes of ecological disturbance shift under global change, it becomes critical to understand how the legacies of these novel regimes alter the resilience of contemporary ecosystems. A major concern are the fates of foundation species, such as trees and corals, which dominate their respective ecosystems in abundance and/or biomass, and thereby confer strong influences over ecological processes that are tied to resilience (Ellison 2019, Lamy et al. 2020, Kopecky et al. 2023a). Due to their pervasiveness, foundation species are particularly vulnerable to changing disturbance regimes, and the loss of these organisms can have enduring effects on the resilience properties of ecosystems (Ellison et al. 2005). An emerging focus is to understand how the dead structures of these organisms that remain after disturbance—a type of *material legacy* (Franklin et al. 2000)—affect the capacity for ecosystems to regain their pre-disturbance community structures (Johnstone et al. 2016, Saldaña et al. 2023).

Material legacies of foundation species, in some cases, are known to influence important ecological processes, such as dead standing trees, oyster shells, or coral skeletons that affect performance of surviving individuals and success of new, recruiting individuals (Lenihan and Peterson 1998, Swanson et al. 2011, Johnstone et al. 2016, Kopecky et al. 2024). Under global change, historically rare disturbances that generate large standing stocks of these legacies are becoming commonplace, like terrestrial and marine heatwaves or outbreaks of pests and predators that cause mass mortality of foundation species (Dai 2013, Hughes et al. 2017, Oliver et al. 2018, Jaime et al. 2024). The heightened prevalence of material legacies that results from altered disturbance regimes is modifying the physical environments in which species interact and communities reassemble after disturbance. This raises a clear and critical question of how these novel environmental settings will influence the outcomes of species interactions that cascade to ultimately drive post-disturbance community assembly.

Coral reefs are an ecosystem that face the pressing issue of shifting disturbance regimes that produce and leave novel legacies. Historically, tropical storms that generate powerful waves were the primary type of disturbance in these systems (Harmelin-Vivien 1994, Gardner et al. 2005), but in recent decades marine heatwaves and outbreaks of coral predators (Crown of Thorns seastars) have become increasingly prominent sources of coral mortality (Hughes et al. 2017, Pratchett et al. 2017, Oliver et al. 2018). Unlike tropical storms which tend to pulverize and scour coral skeletons from the reef (Harmelin-Vivien 1994, Connell et al. 1997, Connell 1997, Gardner et al. 2005, Kenyon et al. 2023), heatwaves and predator outbreaks tend to leave standing dead coral skeletons in place–i.e., a material legacy–which creates a fundamentally different physical template on which post-disturbance community assembly takes place (Baker et al. 2008, Pratchett et al. 2017). Specifically, heatwaves and predator outbreaks produce structurally complex and unstable reefscapes (Swanson 2016, Morais et al. 2022, Kenyon et al. 2023) that can hamper important ecological processes that underpin coral reef recovery. Specifically, standing dead skeletons of branching corals can inhibit removal of macroalgal competitors by herbivores, and once broken down into rubble, dead skeletons reduce successful coral recruitment but continue to allow colonization by macroalgae (Kenyon et al. 2023, Kopecky et al. 2024). This, in theory, can lead to long-term consequences for coral resilience, such as shifts from coral- to macroalgae-dominated reefs (Kopecky et al. 2023a). A logical follow-on question that remains to be explored, however, is whether manipulation (removal) of standing dead coral skeletons after a disturbance could reduce the competitive advantages for macroalgae and improve recovery of coral populations.

Despite the rising prevalence of dead coral skeletons on tropical reefs, these structures have received little attention from a management standpoint, such as whether manipulating them could mediate more desirable post-disturbance trajectories on tropical reefs. In other ecosystems, however, the important roles that material legacies play in ecosystem dynamics have long been integrated into management and restoration, such that legacies are often manipulated to enhance desired outcomes. On oyster reefs, ecosystem managers deploy dead oyster shells to stabilize unconsolidated sediments, provide settlement substrate for larval oysters, and foster recovery of oyster beds (Howie and Bishop 2021). In forests, managers retain large standing dead trees (snags) that enhance forest biodiversity by providing important habitat for forest-dwelling species (Swanson et al. 2011, Vítková et al. 2018) but remove smaller dead trees and woody debris (mechanically or via prescribed burning) to reduce fuel loads and mitigate the risk of severe wildfires (Husari et al. 2006). We would be wise to follow the examples exercised in these other ecosystems by exploring how manipulation of dead coral skeletons after disturbance could help achieve desired management outcomes on tropical reefs.

To investigate this open question, we initiated a long-term field experiment to track benthic community trajectories following a severe marine heatwave on the reefs of Moorea, French Polynesia that caused widespread coral mortality. We explored the extent to which coral and macroalgae utilized dead branching coral skeletons as substrate and whether physically removing dead skeletons from the reef benefitted the recovery of branching coral. We used a novel technological approach that combines underwater photogrammetry with AI-powered image analysis (Kopecky et al. 2023b) to quantify trajectories of coral and macroalgae assemblages at high spatial resolution (sub-centimeter) over several years. With this approach, we tested two related hypotheses: 1) dead branching coral skeletons act as a substrate that favors the proliferation of an alternate competitive dominant, fleshy macroalgae; and 2) removing dead skeletons after a disturbance reduces this competitive advantage for macroalgae and increases the survival of live branching coral.

METHODS

Site description

Moorea, French Polynesia (17°30′S, 149°50′W) is a high-lying volcanic island with a barrier reef enclosing a shallow lagoon around the entirety of the island's roughly 60 km perimeter. Beyond the barrier reef lie fore reef slopes that extend from the surface (reef crest) down to 50+ m, and these are characterized by reef spurs separated by grooves that typically are filled with sand and coral rubble. Many taxa of scleractinian (stony) corals grow on the reef spurs, including branching, tabling, corymbose, encrusting, and mounding morphologies (Moorea Coral Reef LTER and Edmunds 2024). In April 2019, a thermal anomaly elevated sea temperatures that caused a mass episode of coral bleaching, ultimately resulting in > 50% mortality of corals in some areas and disproportionately affecting the more structurally complex morphologies (i.e., branching, tabling, and corymbose; Speare et al. 2022). As a result, this event left large amounts of structurally complex, dead branching coral skeletons intact on the reef.

Removal of dead branching coral skeletons

Because heat stress disproportionately impacts branching coral morphologies, and because the structural complexity of their skeletons is known to hamper important recovery processes on coral reefs (compared to mounding and encrusting morphologies with low structural complexity), we chose to focus our study on branching coral taxa. At our research site, *Pocillopora* spp. were by far the dominant taxon of branching coral prior to and during our study, *Acropora* spp. were present but not common, and other taxa were very rare by comparison (Appendix S1, Fig. S1; Moorea Coral Reef LTER and Edmunds 2024). Thus, by quantifying patterns in cover of *Pocillopora* and *Acropora*, we captured the predominant dynamics of branching coral cover.

In August of 2019 (four months after the marine heat wave event) when most affected colonies had either died or recovered, we demarcated 20 reef plots that captured natural variation in the cover of live and dead branching coral (*Pocillopora* and *Acropora*), each roughly 4 m^2 in area and spaced > 1 m from one another. These plots were distributed over an area of ~1000 m^2 on the north shore fore reef and ranged in depth from 9 – 11 m at a site that was studied extensively following Cyclone Oli in 2010 (Adam et al. 2011, Holbrook et al. 2016, 2018, Schmitt et al. 2019). We conducted visual estimates of live and dead branching coral (*Pocillopora* and *Acropora*) cover within single images of each plot using ImageJ to identify pairs of plots with similar cover of each. One plot from each pair was then assigned at random to have dead skeletons removed (hereafter, the *Skeleton Removal* treatment). The other plot in each pair was left unmanipulated (hereafter, the *Skeleton Retention* treatment). We assigned plots to treatments in this way to ensure that each treatment contained similar ranges in cover of live branching coral (primarily Pocillopora;15-30%) and dead branching coral (15-38%) before manipulation.

From August 5th to August 19th, 2019, we manually removed dead branching coral skeletons from the ten designated plots using hammers and chisels and transported the dead skeleton material to nearby reef grooves well below the experimental plots. Because some corals had undergone only partial mortality at the time of manipulation, we removed any colonies with

> 50% tissue loss, assuming these would soon die completely (Speare et al. 2022). Similarly, we left dead skeleton material in place on colonies with < 50% mortality, meaning the Skeleton Removal treatment still contained some dead coral at the start of the experiment (Appendix S1, Fig. S2, S3). Both treatments began with a roughly equivalent amount of live coral (mean surface area ± 1 SE, Skeleton Removal: 2.41 ± 0.17 m^2; Skeleton Retention: 2.47 ± 0.11 m^2; Fig S2). While macroalgae were relatively rare across all plots at the start of the experiment (< 2% cover in all), we removed any existing macroalgae from the Skeleton Removal plots, assuming that macroalgae would also be dislodged during a wave-scouring disturbance event, such as a powerful cyclonic storm (Harmelin-Vivien 1994). By contrast, we left in place any macroalgae in the Skeleton Retention treatment present at the start of the experiment, assuming that a marine heatwave would not mechanically remove macroalgae as would a wave-scouring disturbance. No subsequent manipulations were undertaken for the 4-year duration of this experiment. The aim of our study was to capture post-disturbance benthic dynamics of coral-algal spatial competition within a window that was comparable to the previous coral recovery seen on Moorea, wherein long-term monitoring sites near the location of our experiment regained their pre-disturbance coral cover in 4-5 years (Holbrook et al. 2018). Therefore, we chose to end our study four and a half years after the marine heatwave took place, on September 2nd, 2023.

Photogrammetry and image analysis

We followed the photogrammetric workflow developed by Nocerino et al. (2020) to create a time-series of Digital Elevations Models (DEMs) and orthorectified photomosaics (hereafter, *orthophotos*) of our experimental plots that were spatially co-registered (i.e., aligned) through time (Fig. 1). We established five fixed reference (ground control) points in each plot by drilling holes into the primary reef substrate and installing a threaded anchor into each hole with marine epoxy (Z-Spar A-788 Splash Zone Epoxy). A reference point was installed in all four corners of each plot, and the fifth was placed somewhere near the center. Due to the distribution of suitable substrate into which anchors could be permanently installed in the reef, our plots varied somewhat in shape and size, but the average plot area was similar between treatments (mean ± SE, Skeleton Removal: 4.1 ± 0.2 m^2; Skeleton Retention: 3.9 ± 0.1 m^2; Welch's two-sample t-test: $t_{13.5} = 0.93$, $p = 0.37$). To create a 'geodetic network' of each plot (used for scaling and alignment of photogrammetric models; Nocerino et al. 2020), we measured the distances between all five reference points with sub-centimeter precision using a metal measuring tape and taking redundant measurements between points (e.g., from point 1 to 2 and from 2 to 1). Prior quantification of the error in sub-centimeter planimetry associated with this XY measurement technique in our fore reef system yielded a standard error of under 3 mm for our plot size (Nocerino et al. 2020). We used a dive computer to measure the depth of each reference point (with sub-meter accuracy) to obtain relative elevational differences among the reference points (i.e., the Z-dimension) and provide vertical references to the XY measurements.

We used the protocol described by Nocerino et al. (2020) to construct orthophotos from 200-300 images of each plot collected in the austral winter each year from 2019 – 2023 using an Olympus Tough TG-6 camera inside an Olympus underwater camera housing equipped with a Backscatter wet dome port lens. Photographing our reef plots from roughly 1 m above the reef yielded a ground image resolution (or ground sample distance, GSD) that ranged from 0.3-0.5 mm/pixel. We used Metashape Pro (version 2.0.3) to build all 3D models, DEMs, and orthophotos for subsequent image analysis. The 3D coordinates of the reference points constituting the geodetic networks were used to reference the photogrammetric models from different time points to the same coordinate system during photogrammetric processing. This allowed us to generate orthophotos from different time points that are projected onto a consistent reference plane and minimize measurement errors associated with variation in spatial orientation across different models (i.e., from different time points) of the same plot. We built DEMs and orthophotos for 5 time points of each plot (aside from one plot which we were not able to photograph in 2021), totaling 99 DEMs and 99 orthophotos at a specified resolution of 0.5mm/pixel to standardize our image analysis across all plots and time points.

Image and data analysis

We employed the AI-powered image segmentation software, TagLab (Pavoni et al. 2022), and the general workflow outlined in Kopecky et al. (2023b) to annotate our orthophotos (both interactively and automatically) and extract metrics of branching coral growth and death, as well as the development of macroalgae over time. TagLab enables users to create a single project containing all time points related to a plot and automates the calculation of growth, erosion, mortality, and recruitment of individual coral colonies. By layering each orthophoto atop its respective DEM, TagLab allows for measuring a three-dimensional approximation (‘2.5D’) of the surface areas of objects within an image. This enables more accurate change detection than traditional, two-dimensional image segmentation methods that yield only planar area (Kopecky et al. 2023b). We first annotated live colonies of *Pocillopora* and *Acropora*, as well as dead branching coral skeletons in the orthophotos from all five timepoints in each of four plots (i.e., 20 orthophotos) using AI-interactive segmentation tools to build a training dataset. We then utilized TagLab's built-in training pipeline to train a fully automated classifier (see Pavoni et al. 2022 for more details) to annotate the remaining (79) orthophotos. We quantified dead coral skeletons that appeared (within our photomosaics) to be branching in nature, which may have included skeletons of some additional, rare coral taxa. However, based on the estimates of live coral before the heat wave took place (Appendix S1, Fig. S1), the vast majority of dead skeletons in our estimates were likely those of *Pocillopora* and *Acropora* colonies, and other (rarer) taxa likely contributed very little to our estimates of dead coral cover. Additionally, we largely quantified only standing dead skeletons, as well as branches that had recently broken off, as highly degraded patches of rubble can be difficult for the automatic algorithms (and for human observers) to reliably discern from background reef substrate. See Appendix S1 for details on accuracy of the automatic classifiers for live and dead coral colonies.

Finally, we quantified the cover of macroalgae over time in our experimental plots. However, because macroalgae exhibit highly variable growth morphologies and are moved easily by ocean surge, we could not quantify macroalgal cover with the same image segmentation technique that we used to quantify coral cover. Instead, we used a point classification method, in which we laid a grid of 750 – 900 points in each image (the number of points that fell within the plot boundaries varied due to variation in plot shape and size) and classified whether each point was macroalgae, and if so, the algal taxon. To estimate macroalgae coverage within our experimental plots, we divided the number of points classified as macroalgae (or as a certain macroalgal taxon) by the total number of points to obtain an estimate of the percent cover of macroalgae. While this point contact method is, by nature, a coarser method than our image segmentation method for measuring coral, it has been used extensively to quantify benthic cover of both coral and macroalgae in many coral reef studies (e.g., Dumas et al. 2009, Jokiel et al. 2015, González-Rivero et al. 2020), including at our research site (e.g., Bramanti and Edmunds 2016).

Statistical analyses

To evaluate the effects of dead skeleton removal on live coral cover over time, we calculated the proportion of live branching coral (*Pocillopora* and *Acropora*) remaining at each time point relative to the amount present at the start of the experiment. We set the initial value in 2019 equal to one, because both treatments began with roughly equivalent amounts of live branching coral at the initial sampling date in 2019 (means ± SE; Skeleton Removal: 2.41 ± 0.17 m^2; Skeleton Retention: 2.47 ± 0.11 m^2; Fig. S4). We built generalized linear mixed effects models (package glmmTMB; Brooks et al. 2017) to test for differences over time in both the proportion of live coral remaining and the amount of macroalgae between the treatments. Specifically, we tested for an interaction between treatment (e.g. Removal vs. Retention) and time point (a categorical predictor for sampling year). We assumed beta distributions and logit link functions because these response variables were both continuous proportions (Douma and Weedon 2019). We omitted the initial, 2019 sampling point from both models because we set all values of coral cover to one for this time point, and because macroalgal cover was very low in all 20 plots at the start of the experiment. We treated plot identity as a random effect to account for plot-specific variation that was not due to our predictor variables. Finally, we conducted *post hoc* pairwise comparisons between treatments for each year (with Bonferroni correction for multiple comparisons) using the emmeans package (Lenth 2023).

To explore the degree to which macroalgae associated with dead coral skeletons as a substrate, we calculated the proportions of points classified as macroalgae that fell within regions classified as dead coral. For this analysis, we pooled all points across years and treatments for each algal taxon we observed. We then used a Chi-squared contingency test to determine whether each macroalgal taxon we observed was disproportionately found on dead coral skeleton compared to primary reef substrate. Finally, we used a Chi-squared *post hoc* test to identify which taxa, if any, had significant associations to dead coral vs primary reef.

To explore how dead coral influences the prevalence of macroalgae, we explored the relationship between the amount of dead coral and the cover of macroalgae in each plot x year combination. Because dead coral was present in varying quantities in both treatments and across all time points, we did not explicitly consider treatment or time in this analysis. Instead, we modeled macroalgae cover as a continuous function of dead coral cover, including both year and treatment as random effects in a similar GLMM. Finally, we tested whether the macroalgae cover at the end of a year was correlated with the change in live coral in the same year. To calculate the change in live coral over each year, we simply subtracted the amount of live coral in a given year from the amount in the previous year. For this analysis, we built a linear mixed effects model of the change in live coral during a year as a function of the macroalgae cover at the end of the same year. We used a Gaussian distribution and set year and plot ID as random effects.

Quantifying coral recruits

Between our 2022 and 2023 sample points, a large coral recruitment event took place (Moorea Coral Reef LTER and Edmunds 2024). Given the resolution of our orthophotos, corals that had recruited between 2022 and 2023 would likely have been too small and/or cryptic to be reliably detected in our images. We instead conducted visual counts *in situ* of coral recruits in our experimental plots in August 2023 to assess whether these recruits were found disproportionately on primary reef substrate or dead coral (standing and rubble). While on SCUBA, we visually counted recruits of *Acropora* spp.*,* *Pocillopora* spp.*,* and *Porites* spp. that were > 1 cm and ≤ 5 cm in diameter, noting which of the three substrate types each recruit had settled on. We included *Porites* spp. in these counts because this is an important reef-building taxon, and its long-term survival would likely be influenced by whether it settled on dead branching skeleton or primary reef. We excluded this taxon from other parts of the experiment, however, as *Porites* spp. in Moorea typically exhibit a mounding morphology and therefore would leave behind a structurally different type of dead skeleton compared to *Pocillopra* and *Acropora*. To analyze whether coral recruit densities differed between substrate types (primary reef or dead branching coral + rubble), and whether this relationship depended on the skeleton treatment, we built a GLMM of recruit density as a function of substrate and treatment with an interaction term. We used a log-transformation for recruit density, assumed a Gaussian distribution, and designated the plot ID as a random effect. We then performed *post hoc* tests for differences between substrates within treatments, and vice versa, with Tukey adjustments.

All statistics and visualizations for this study were done in R (Version 4.2.3; R Core Team 2023) and RStudio (Version 2023.12.1.402; Posit team 2024).Visualizations utilized colors from the Manu New Zealand Bird Colour Palettes (Thomson 2022) package and the California Ecosystems Palette (calecopal) package (Bui 2024).

RESULTS

Our experiment revealed marked effects of removing dead branching coral skeletons on the outcomes of coral-algae spatial competition following a coral-killing disturbance. While live branching coral cover (*Pocillopora* + *Acropora*) declined in both treatments during our four-year experiment, significantly more live coral remained in the Skeleton Removal treatment than the

Skeleton Retention treatment in all years after 2019 ($p < 0.05$, pairwise contrasts with Bonferroni correction; Fig. 1,2a). In the final year of the experiment, there was on average 46% of the initial live coral remaining in the Removal treatment (95% CI: 38-55%), compared to 28% remaining in the Retention treatment (95% CI: 22-35%). In terms of raw surface area, 1.1 ± 0.2 m^2 (mean ± SE) of live coral remained in the Removal treatment, compared to 0.7 ± 0.1 m^2 in the Retention treatment (Appendix S1, Figure S4).

Abundance of macroalgae also varied by treatment and through time. Macroalgal cover remained significantly and consistently lower in the Skeleton Removal treatment for all time points, apart from the initial time point ($p < 0.001$, pairwise contrasts with Bonferroni correction; Fig. 2b). One year after the start of our experiment, the cover of macroalgae increased in both treatments, but three times more sharply in plots where dead skeletons were left in place, reaching an average of 23.0% cover (95% CI: 19.6% - 26.4%), compared to 8.0% (95% CI: 6.6 - 20.4%) in plots where skeletons were removed. After 2020, both treatments decreased somewhat in macroalgae cover; however, the Retention plots maintained at least twice as much macroalgae for all successive time points (Fig. 2b).

We observed four taxa of macroalgae in our experiment that showed variable patterns over time: *Lobophora* sp., *Asparagopsis taxiformis, Halimeda* spp., and *Turbinaria ornata*. *Lobophora* was the dominant taxon across nearly all time points in both treatments, driving the initial spike of macroalgae in 2020 (Fig. 2b,3). The other three taxa initially contributed relatively little to overall macroalgae cover but increased in abundance gradually throughout the experiment (Fig. 3). Notably, *Lobophora* was found disproportionately growing on dead coral skeletons (χ^2 (3) = 1007.1, $p < 0.001$), while the other three taxa showed weaker associations to this substrate type relative to primary reef (pie charts in Fig. 3).

Due to continued mortality of live coral after the bleaching event, dead coral skeletons continued to accumulate in both treatments throughout our study. While the amount of dead coral consistently was lower in the Removal treatment (Fig. S2), the ranges in dead coral cover for each treatment over time overlapped one another and created a continuous gradient across treatments (Removal: 0.17 – 2.66 m^2, Retention: 1.62 – 4.64 m^2; Fig. 4a). The cover of macroalgae was positively correlated with the amount of dead coral present in any given plot across both treatments (slope estimate: 0.46 ± 0.05, $p < 0.001$; Fig. 4a). Further, the change in live coral over a given year was negatively correlated with the macroalgae cover in the same year (slope estimate ± SE: -1.2 ± 0.3 $p < 0.001$; Fig. 4b). In other words, macroalgae were more abundant when dead skeletons were also more abundant, and more abundant macroalgae led to steeper annual declines in live coral. Only two plots showed net positive changes in coral cover between two successive years, both of which were in the Removal treatment (Fig. 4b).

Our quantification of young coral recruits in the final year of the experiment (2023) revealed clear patterns in recruitment to available substrate types (i.e., dead branching coral or primary reef). We observed roughly similar total numbers of coral recruits across the two experimental treatments (Removal: $n = 44$; Retention: $n = 54$). However, the density of coral recruits on a given substrate depended on whether dead skeletons were removed or retained (substrate–treatment interaction: $p < 0.01$; Fig. 5). The average density of recruits found on primary reef was five-times higher in plots where dead corals were removed (0.7 recruits/m^2, 95% CI: 0.4-1.2) compared to plots where skeletons were left intact (0.14 recruits/m^2, 95% CI: 0.04-0.5; *post hoc* comparison with Tukey adjustment: $p = 0.02$). Within the Retention treatment, the average recruit density on primary reef was only 15% of that found on dead skeletons ($p < 0.01$). Together, these data show that coral recruits are found more often on dead skeletons when dead skeletons are more abundant as a substrate, but removing skeletons can increase recruitment onto primary reef substrate.

DISCUSSION

The dead, remnant structures of foundation species (a form of material legacies) are becoming prominent fixtures in contemporary ecosystems but have largely unknown effects on ecosystem resilience. Here, we found that the material legacy of an increasingly common form of disturbance (dead coral skeletons produced during marine heatwaves) influences the outcomes of spatial competition between alternative competitive dominants (corals and macroalgae). We showed that these structures act as a novel substrate that favors the establishment of macroalgae, which can then likely drive continued declines in live coral after the disturbance has subsided. Encouragingly, we found that removing dead skeletons substantially mitigated these declines and increased the assumed viability of new, recruiting corals, revealing a promising strategy to manage for coral reef resilience (in some contexts). More generally, the dynamics we observed illustrate that material legacies of novel disturbance regimes can alter physical environments in ways that modify species interactions and shape post-disturbance community assembly.

When disturbance regimes change, the disturbance legacies of the emerging regime can render processes that historically fostered resilience in an ecosystem ineffective (Johnstone et al. 2016). As a result, changes in material legacies that coincide with shifting disturbance regimes can increase invasion success by competing organisms and undermine the potential for the ecosystem to return to its pre-disturbance community condition. For example, Miller et al. (2021) found that invasion success in plants, and thereby the trajectory of a plant community, can be determined solely by variation in disturbance history that leaves behind differing biotic legacies (seed banks), in some cases favoring the establishment and persistence of novel, exotic species guilds. Similarly, historic New Zealand forests underwent a vast transformation with the anthropogenic introduction of fire disturbance, which acted to remove topsoils necessary for native plant regeneration and allowed invasion by more opportunistic non-natives (Whitlock et al. 2015). In our system, the dead skeletons left by a marine heatwave created a novel physical environment for the system to reassemble within, which in turn diminished the effectiveness of vital processes such as herbivory and the growth of live coral colonies that are necessary for coral recovery (Kopecky et al. 2024). While bioeroding organisms (such as large-bodied parrotfishes and sea urchins) are typically able to break down dead coral, the high volume of skeletons produced over the short time frame of a heat-induced coral mortality event would likely dilute the strength of this process as well. Consequently, this facilitated establishment of macroalgae, an alternative competitive dominant (McManus and Polsenberg 2004, Bellwood et al. 2004, Schmitt et al. 2019, Kopecky et al. 2023a). Novel disturbance regimes can thus alter post-disturbance landscapes and disrupt important processes needed for ecosystem recovery, thereby creating misalignments between historic attributes of ecosystem resilience and the disturbances ecosystems now face.

While competition for benthic space between corals and macroalgae has been explored extensively (McCook et al. 2001, Kuffner et al. 2006, Holbrook et al. 2016, Adam et al. 2022, Schmitt et al. 2022), we present novel evidence that the outcomes of this interaction can be heavily swayed by the presence of dead coral skeletons. Our four-year experiment showed that standing dead skeletons promoted the development and persistence of macroalgae that then likely contributed to continued losses of surviving coral colonies, well after the heat-stress event had subsided. Additionally, the branches of standing dead corals may protect vulnerable, earlylife stage macroalgae from herbivory and facilitate development of mature, herbivore-resistant macroalgal stands that are self-reinforcing (Davis 2018, Briggs et al. 2018, Kopecky et al. 2024). Thus, removing dead coral relatively soon after a skeleton-producing disturbance will likely have the greatest benefit, as dead standing skeletons can negatively affect live coral before breaking down into rubble.

The dominant algal taxon we observed in our experiment, *Lobophora* sp., is well known to aggressively compete with and overgrow live coral, in some cases driving shifts from coral-dominated to algae-dominated reefscapes (Vieira 2020). This taxon was not only the most abundant among the macroalgae we observed, but also the most strongly associated with dead skeletons. Further, when macroalgae were more abundant during a given time period, live coral was lost at a faster rate. Our experiment suggests, therefore, that standing skeletons of dead branching corals can act as an alternate substrate type that favors the proliferation of aggressive macroalgae and thereby confer a competitive advantage for macroalgae in the wake of skeleton-producing disturbances on coral reefs.

Dead branching coral skeletons can be a favorable substrate for macroalgae, even after the skeletons are mechanically broken down into coral rubble. For corals, however, rubble tends to be an ill-suited substrate and reduces long-term survival (Yadav et al. 2016, Johns et al. 2018). The dead skeletons of complex, branching coral morphologies have been found to erode and break down into rubble over time (Fox et al. 2003, Ferrari et al. 2017, Morais et al. 2022), including in our fore reef system (Adam et al. 2014). In our experiment, the density of coral recruits on dead branching coral skeletons was substantially higher when dead skeletons were left in place, whereas reducing the standing stock of dead coral skeletons significantly increased recruit density on primary reef, which is a relatively more stable substrate. This suggests that removing dead skeletons increases coral settlement onto reef substrate that is more viable for the long-term survival of coral recruits. The prevalence of both dead coral skeletons and rubble is expected to increase on contemporary reefs with the projected rise of both tropical storms and thermal stress events (Wehner et al. 2018, Oliver et al. 2018, Kenyon et al. 2023)(Wehner et al. 2017; Oliver et al. 2018; Kenyon et al. 2023), which will likely serve as a major sink for recruiting corals that will impede reef recovery. Our results suggest, however, that removing dead branching skeletons that will eventually become rubble could help facilitate recovery of coral populations by increasing coral recruitment onto stable reef surfaces where long-term survival is improved.

While we found marked benefits of removing dead coral skeletons on coral resilience at our site in the South Pacific, the same benefits may not occur across tropical reefs globally. For example, on reefs with high water flow that rapidly erodes dead skeletons in place or high wave exposure that mechanically breaks skeletons apart into rubble, skeleton removal may not be necessary. Instead, efforts on these reefs may be better focused on removing or stabilizing unconsolidated coral rubble after it is produced (Fox et al. 2019). In addition, we anticipate the negative effects of dead skeletons will be minimal when dead skeletons are rare or sparse following a disturbance, for instance after only a minor heatwave or on reefs with little live coral cover prior to a disturbance. Additionally, regions that support low cover of reef-building corals—the Caribbean, for example—may exist in calcification deficits, where reef erosion outweighs reef accretion (Perry et al. 2013, Hubbard and Dullo 2016, Toth et al. 2018). Removing dead skeletons on these reefs may in fact be more detrimental than beneficial, and would therefore be ill-advised. We recommend consideration of factors such as these before implementing dead skeleton removal as a management strategy.

Our study demonstrated that physically removing dead skeletons from the reef resulted in multiple long-term benefits that support coral resilience: more surviving coral, lower macroalgal abundance, and increased densities of coral recruits on stable reef substrate. While coral declined and macroalgae increased even in plots where we had removed dead skeletons, we conducted these removals only once (at the beginning of the experiment). Continually removing dead skeletons may further mitigate the loss of live coral and buildup of macroalgae over time, potentially sustaining higher coral cover that would facilitate coral recovery. We therefore recommend further study on the removal of dead skeletons as a direct management strategy to strengthen coral resilience after marine heatwaves or outbreaks of coral predators, like the Crown of Thorns seastar, both of which are becoming more prevalent (Hughes et al. 2017, Pratchett et al. 2017). It would be particularly valuable to explore how both the frequency and amount of dead coral removal (i.e., the degree of thinning) influence the survival of live corals, colonization by macroalgae, and settlement patterns of recruiting corals. Further, it will be prudent to assess the implications of removing dead skeletons on the abundances and assemblages of coral-associated fishes and invertebrates that may or may not reside in dead branching coral skeletons before conducting large scale removals. While there would certainly be logistical challenges associated with scaling up dead skeleton removal on coral reefs, we feel the potential benefits this could offer as a management strategy are well worth exploring.

ACKNOWLEDGEMENTS

We thank L. Enright, J. Gallagher, E. Partlow, M. Cunningham, D. Cook, and R. Honeycutt for invaluable assistance with fieldwork, the staff of the University of California Gump Research Station, and the Moorea Coral Reef Long Term Ecological Research site personnel for logistical support. Field research was executed under permits issued by the French Polynesian Government (Délégation à la Recherche) and the Haut-Commissariat de la République en Polynésie Francaise (DTRT) (Protocoled'Accueil 2005–2023); we thank them for their continued support.

AUTHOR CONTRIBUTIONS

KLK conceived the study question; KLK, AJB, FM, and EN designed the field experiment and methods; KLK, FM, and EN designed the photogrammetric protocols; KLK built all photogrammetric products; GP and MC designed the software used for image classification; KLK, GP, and MC extracted data from the photogrammetric products and trained the automatic image classification system; KLK and BPD analyzed the data and built the statistical models; KLK wrote the first draft of the manuscript; all authors revised the manuscript.

CONFLICT OF INTEREST STATEMENT

All authors state no conflict of interest.

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FIGURES

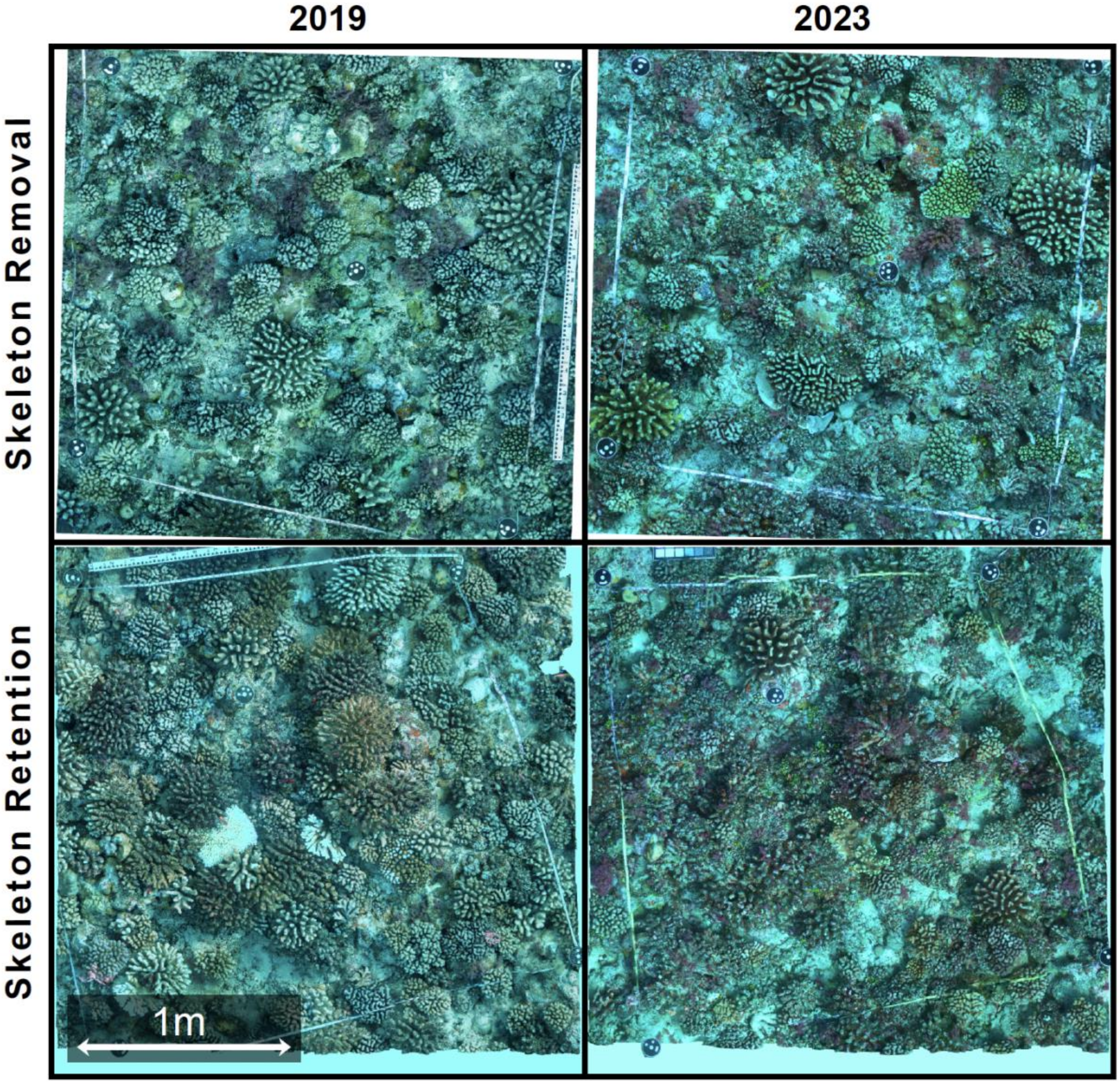

Figure 1. Example orthophotos of experimental plots at the beginning (2019, left) and end (2023, right) of the experiment. Top row shows a Skeleton Removal plot (the 2019 image shows the plot post-manipulation), bottom row shows a Skeleton Retention plot. Black and white coded photogrammetry targets that represent fixed reference points can be seen in the corners and centers of each orthophoto.

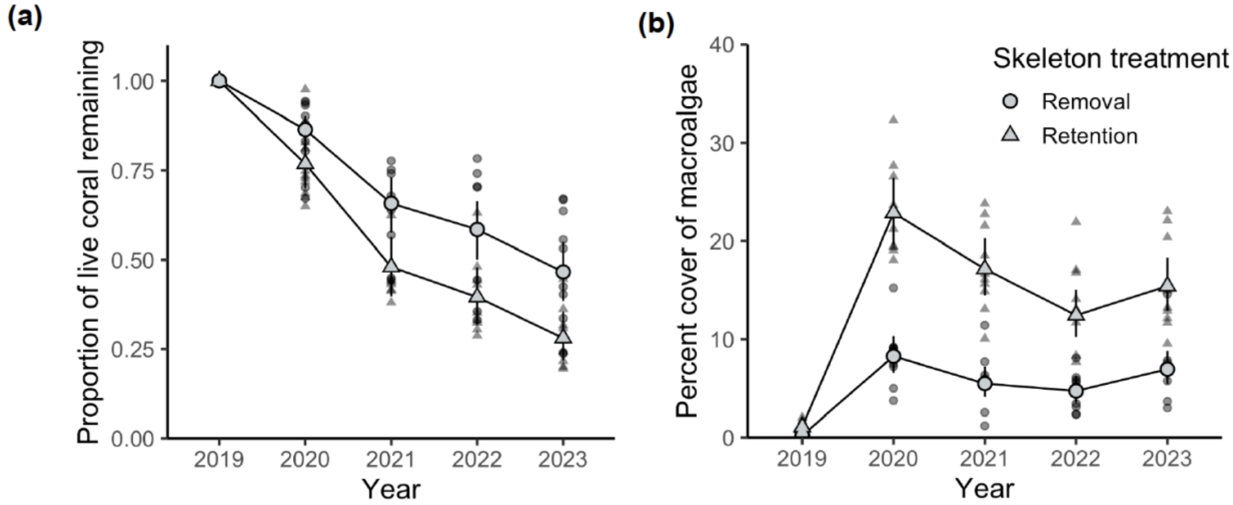

Figure 2. Time series of a) the proportion of live branching coral cover (*Pocillopora* + *Acropora*) remaining and b) percent cover of macroalgae in each year, separated by skeleton treatment. Points represent the observed data, while large shapes show predicted means ± 95% confidence intervals from generalized linear mixed effects models.

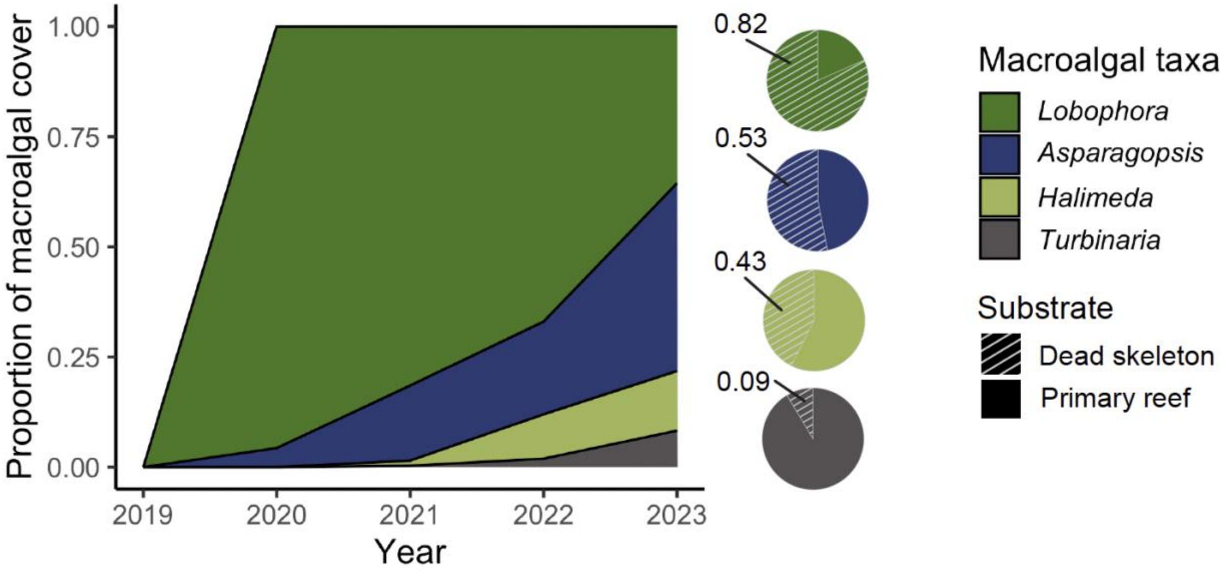

Figure 3. Stacked area chart showing the proportion of macroalgae cover at each timepoint, separated by algal taxa. Pie charts indicate the proportions of points identified as each algal taxon that fell within regions of dead coral (stripes) or on primary reef substrate (no stripes).

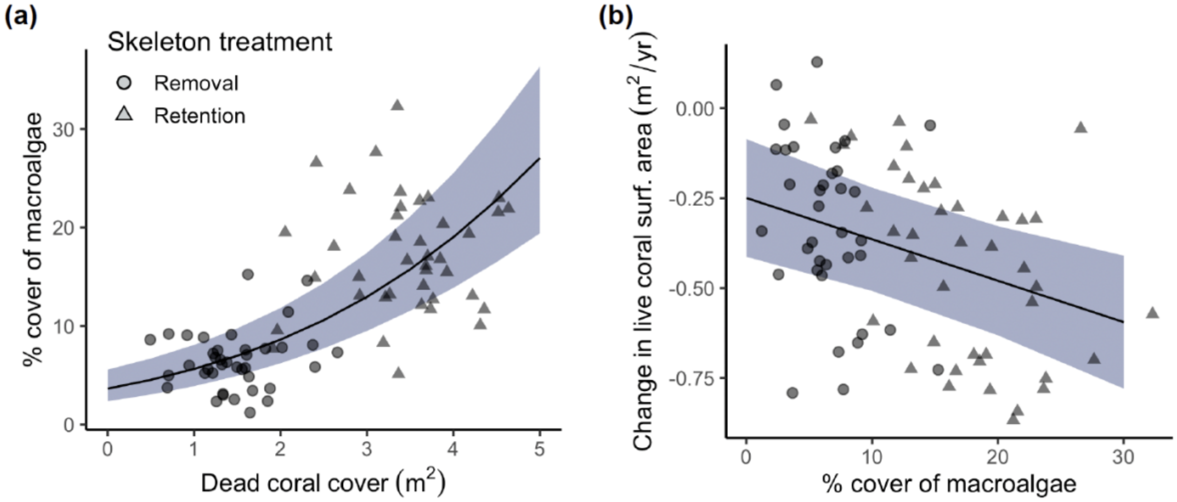

Figure 4. a) Percent cover of macroalgae as a function of the surface area of dead branching coral (m^2) for each plot x year combination. b) Change in surface area of live branching coral (*Pocillopora* + *Acropora*) cover from year$_n$ to year$_{n+1}$ as a function of the percent cover of macroalgae in year$_{n+1}$ for each plot. Lines and surrounding shading are predicted means ± 95% confidence intervals from generalized linear mixed effects models.

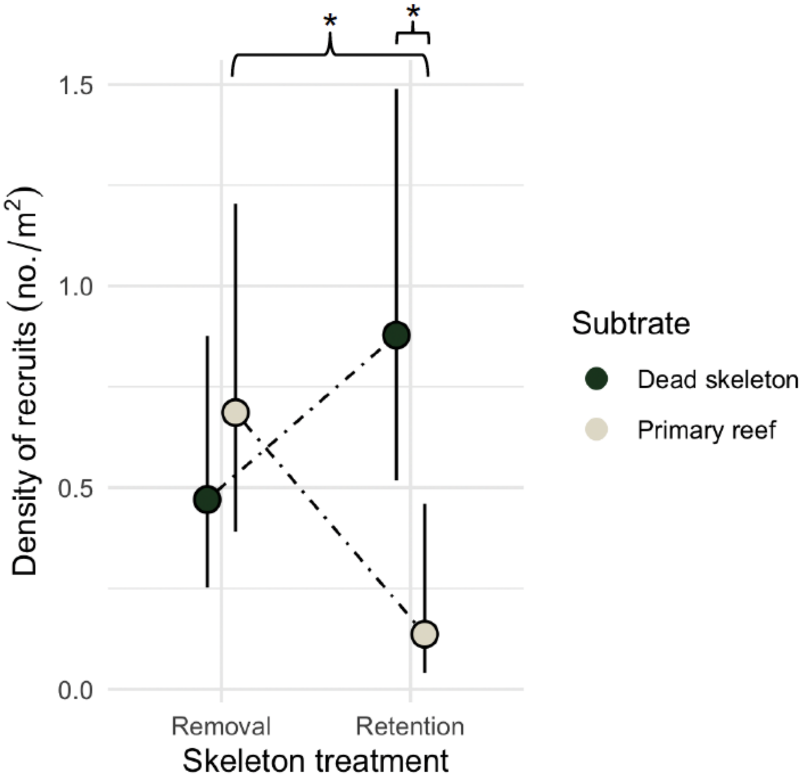

Figure 5. Density of coral recruits (*Pocillopora, Acropora,* and *Porites*) found on primary reef and on dead branching coral skeleton (standing + rubble) in each experimental treatment in the final year of the study (2023). Dots indicate predicted means ± 95% confidence intervals from a generalized linear mixed effects model.