Title

The remains of change: how the legacies of shifting disturbance regimes impact the resilience of contemporary coral reefs

Author

Kopecky, Kai Logan

Publication Date

2024

UNIVERSITY OF CALIFORNIA

Santa Barbara

The remains of change: how the legacies of shifting disturbance regimes impact the resilience of contemporary coral reefs

A dissertation submitted in partial satisfaction of the
requirements for the degree Doctor of Philosophy
in Ecology, Evolution, and Marine Biology

by

Kai Logan Kopecky

Committee in charge:
Professor Russell J. Schmitt, Co-chair
Professor Adrian C. Stier, Co-chair
Professor Holly V. Moeller
Professor Deron E. Burkepile

June 2024

The dissertation of Kai Logan Kopecky is approved.

Holly V. Moeller

Deron E. Burkepile

Adrian C. Stier, Committee Co-chair

Russell J. Schmitt, Committee Co-chair

May 2024

The remains of change: how the legacies of shifting disturbance regimes impact the resilience of contemporary coral reefs

by

Kai Logan Kopecky

ACKNOWLEDGEMENTS

I would like to thank a number of people for helping and enabling me to complete the work included in this dissertation. First of all, I would like to thank my academic committee in providing invaluable insight and support throughout my graduate career. Additionally, I would like to thank Dana Cook, Randi Honeycutt, Jordan Gallagher, Lauren Enright, Emalia Partlow, and Maddie Cunningham for consistent and crucial assistance with fieldwork., without which my dissertation research would not have been possible. I would further like to thank Andy Brooks, Tom Adam, and Scott Miller for continuous statistical consultation over the last several years. I would like to give a huge thanks to Tony Yousing, Jacques Yousing, Irma Yousing, and Valentine Brotherson, as well as the entire staff of the UC Berkeley Gump Research Station in Mo’orea, French Polynesia for phenomenal logistical support while I conducted the fieldwork for my dissertation. Lastly, I would like to thank the Mā’ohi people of Mo’orea for the warmth and hospitality they gave me while I visited their island home.

VITA OF KAI LOGAN KOPECKY
May 2024

EDUCATION

2021	**M.A., Ecology, Evolution, and Marine Biology** University of California, Santa Barbara
2015	**B.S., Ecology and Evolutionary Biology**, *Honors* University of California, Santa Cruz

PEER-REVIEWED PUBLICATIONS

In prep.	**Kopecky, K. L**., Pavoni, G., Corsini, M., Nocerino, E., Menna, F. Clearing a path to resilience: removal of dead coral skeletons mitigates impacts of coral bleaching.
In review	**Kopecky, K. L**., Partlow, E., Cunningham, M., Holbrook, S. J., Schmitt, R. J. Changing disturbance regimes, material legacies, and stabilizing feedbacks: dead coral skeletons impair key recovery processes following coral bleaching. *Global Change Biology*.
2023	**Kopecky, K. L**., Pavoni, G., Nocerino, E.; Brooks, A. J., Corsini, M., Menna, F., Gallagher, J. P., Capra, A., Castagnetti, C., Rossi, P., et al. Quantifying the Loss of Coral from a Bleaching Event Using Underwater Photogrammetry and AI-Assisted Image Segmentation. *Remote Sensing*. 2023, *15*, 4077. https://doi.org/10.3390/rs15164077.
2023	**Kopecky, K. L.,** Stier, A. C., Schmitt, R. J., Holbrook, S. J., & Moeller, H. V. (2023). Material legacies can degrade resilience: Structure-retaining disturbances promote regime shifts on coral reefs. *Ecology*, e4006. https://doi.org/10.1002/ecy.4006.
2022	Ingeman, K. E., Zhao, L. Z., Wolf C., Williams, D. R., Ritger, A. L., Ripple, W. J., **Kopecky, K. L.,** Dillon, E. M., DiFiore, B. P., Curtis, J. S., Csik, S. R., Bui, A., Stier, A. C. Glimmers of hope in global apex predator recoveries. *Scientific Reports*, 12(1), 10005. https://doi.org/10.1038/s41598-022-13671-7.
2021	**Kopecky, K. L.,** Cook, D. T., Schmitt, R. J., & Stier, A. C. (2021). Effects of corallivory and coral colony density on coral growth and survival. *Coral Reefs*, 40, 283-288. https://doi.org/10.1007/s00338-021-02076-z

GRANTS AND FELLOWSHIPS

2023	**Graduate Division Dissertation Fellowship.** Funding for advanced doctoral students to complete dissertation work at UC Santa Barbara ($10,800)
2023	**Storke Graduate Fellowship.** Funding for advanced doctoral students to complete dissertation work at UC Santa Barbara ($2,500)
2022	**Worster Research Award.** Funding for a graduate and undergraduate student pair to conduct field research ($7,000)
2021	**Schmidt Family Foundation Graduate Student Accelerator Award**. Funding to perform summer field work for PhD dissertation research ($8,000)
2019, 2020	**Departmental Fellowship**. To perform graduate studies at UC Santa Barbara in the department of Ecology, Evolution, and Marine Biology ($13,500)

PROFESSIONAL EXPERIENCE

2018 - 2024	**Graduate Student Researcher |** NSF Moorea Coral Reef Long Term Ecological Research site
2021 - 2023	**Instructor of record** | UC Santa Barbara, Dept. of Ecology, Evolution, and Marine Biology
2018-2023	**Teaching Assistant** | UC Santa Barbara, Dept. of Ecology, Evolution, and Marine Biology

RESEARCH COMMUNICATIONS

Contributed talks and invited seminars

2024	The roles of dead coral skeletons under changing disturbance regimes. *Applied Marine Ecology, Bren department of Environmental Science.*
2023	Understanding the role of material legacies in conservation and restoration. *Institute for Conservation Research and Education Expert Talk Series.*
2023	Skeletons in the closet: How dead coral skeletons shape the potential for recovery on coral reefs in a changing world. *Science by the Pint.*
2022	Material legacies, disturbance, and resilience. *University of Sassari, Sardinia, Italy.*
2022	Material legacies can degrade resilience: Structure-retaining disturbances promote regime shifts on coral reefs. *Western Society of Naturalists.*
2021	Effects of disturbance type on coral reef resilience. *Graduate Student Symposium, department of Ecology, Evolution, and Marine Biology, UCSB.*
2020	Use of automated segmentation software for 3D measurement and change detection of coral reefs. *Moorea Coral Reef Long Term Ecological Research Site All-Investigators Meeting.*
2019	Effects of disturbance type on benthic community assembly. *Moorea Coral Reef Long Term Ecological Research Site All-Investigators Meeting.*

ABSTRACT

The remains of change: how the legacies of shifting disturbance regimes impact the resilience of contemporary coral reefs

by

Kai Logan Kopecky

Global conditions are changing, leading to novel settings in which ecosystems must operate. In particular, ecological disturbances that were once rare are becoming commonplace, like heatwaves both on land and in the ocean that cause widespread mortality of species and leave behind legacies that pose new challenges to the resilience of contemporary ecosystems. Coral reefs, for example, have historically been afflicted mainly by tropical storms that create reef-scouring waves, but in recent decades, episodes of coral bleaching caused by marine heatwaves have become an additional, prevalent source of mass coral mortality. Tropical storms tend to remove corals from the reef entirely, whereas marine heatwaves that cause coral bleaching kill corals but leave their stony skeletons intact – a type of *material legacy*. When these structures are left in place, this creates a fundamentally different post-disturbance environment in which reef recovery must take place and poses an uncertain future for these incredibly important ecosystems.

In my dissertation research, I explored how shifting disturbance regimes on coral reefs affect the capacity for these ecosystems to rebound from disturbance and regain their pre-disturbance identity, structure, and function. Through a combination of mathematical modeling, remote sensing, and field experimentation, I compared the impacts of tropical storms and coral bleaching on reef resilience, investigating how dead coral skeletons modify key ecological processes and influence trajectories of community assembly after disturbance. I found that dead coral skeletons impair key ecological processes that underpin coral resilience, like top-down control of macroalgae (spatial competitors of coral) by herbivores, and the successful recruitment of new coral colonies. The impairment of these two critical processes can erode coral resilience and ultimately increase the occurrence of transitions from reefs dominated by corals to those dominated by macroalgae. More encouragingly, however, I found that removing dead skeletons after bleaching can mitigate these negative impacts, offering a promising avenue to explore for the management of coral reefs that have been perturbed by disturbances that leave in place large standing stocks of dead coral skeleton. As material legacies become more prominent ecological features, a critical need emerges to understand the powerful roles they play in altering ecosystem resilience, as well as the roles we may be able to play in leveraging these legacies for desirable management outcomes.

TABLE OF CONTENTS

Chapter I. Material legacies can degrade resilience: Structure-retaining disturbances promote regime shifts on coral reefs

ABSTRACT

Standing dead structures of habitat-forming organisms (e.g., dead trees, coral skeletons, oyster shells) killed by a disturbance are material legacies that can affect ecosystem recovery processes. Many ecosystems are subject to different types of disturbance that either remove biogenic structure or leave it intact. Here, we use a mathematical model to quantify how the resilience of coral reef ecosystems may be differentially affected following structure-removing and structure-retaining disturbance events, focusing in particular on the potential for regime shifts from coral to macroalgae. We found that dead coral skeletons can substantially diminish coral resilience if they provide macroalgae refuge from herbivory, a key feedback associated with recovery of coral populations. Our model shows that the material legacy of dead skeletons broadens the range of herbivore biomass over which coral and macroalgae states are bi-stable. Hence, material legacies can alter resilience by modifying the underlying relationship between a system driver (herbivory) and a state variable (coral cover).

INTRODUCTION

Major disturbances such as fire, drought, storms, and heat waves can abruptly kill the structure-forming species that create the foundations of ecosystems. When the dead structures of these organisms are left behind, these material legacies can alter recolonization rates and interactions between species in the recovering system (Johnstone et al. 2016). For example, standing or fallen dead trees can affect establishment success of new colonizing individuals in forests (Johnstone et al. 2016), shells of dead oysters can provide substrate for new settling larvae to facilitate recoveries on oyster reefs (Lenihan & Peterson 1998), and skeletons of dead corals can either serve as settlement substrate or harbor macroalgae that compete with live corals for attachment space on coral reefs (Vieira 2020). Because material legacies can have powerful effects on ecological processes, they have the potential to also alter how ecosystems resist and recover from disturbance—i.e., ecosystem resilience. For example, if dead structures occupy significant amounts of habitat space for extended durations, these legacies can prolong the time for new colonists to re-seed a disturbed area and for that ecosystem to regain its pre-disturbance condition. Alternatively, if dead structures facilitate colonization by a functionally different guild of organisms, these structures may facilitate a regime shift in ecosystem state.

To better understand the role of material legacies, we can directly compare how disturbances that either remove or leave in place dead biogenic structures affect resilience. Some disturbances both kill structure-forming organisms and remove their biogenic structure, opening up unoccupied habitat spaces between surviving individuals (hereafter, *structure-removing* disturbances). Examples include intense fires, floods, storms (Fukami 2015), deforestation, landslides, avalanches (Swanson et al. 2011), dredging, and ice scour (Lenihan & Peterson 1998). By contrast, other disturbances kill structure-forming organisms but leave their structures intact, resulting in patchworks of live and dead organisms or dense stands of dead individuals that can restrict the amount of unoccupied space for new colonists and surviving individuals (hereafter, *structure-retaining* disturbances). Examples include drought, disease, predator or pest outbreaks (Johnstone et al. 2016), thermal stress (e.g., heat waves; Folke et al. 2004), and hypoxic events (Lenihan & Peterson 1998). In this study, we use a model to quantify how the resilience of coral reef ecosystems may be differentially affected following structure-removing and structure-retaining disturbance events.

Coral reefs serve as a timely model system to explore the effects of material legacies on resilience. Disturbance regimes are changing such that acute events that either remove or retain structure are changing in frequency, severity, or both (Uthicke et al. 2015; Oliver et al. 2018; Wehner et al. 2018). For example, structure-removing events (e.g., tropical storms) appear to be increasing in intensity (Vecchi et al. 2021), while structure-retaining events (e.g., marine heat waves that cause coral bleaching, predator/disease outbreaks) are becoming more widespread, frequent, and severe (Pratchett et al. 2013; Hughes et al. 2017; Lough et al. 2018). Storm disturbances can remove the entire coral colony, creating planar reef surfaces (Gardner et al. 2005), whereas structure-retaining disturbances kill the soft tissue of corals while leaving their skeletons intact (Baker et al. 2008; Pratchett et al. 2013). Coral taxa that are most sensitive to both disturbance types tend to have higher structural complexity (e.g., branching, corymbose, and tabular colony morphologies), but how their dead structures influence the recovery potential of reefs remains poorly resolved. Some disturbances can tip a coral reef ecosystem from a coral-dominated state to one where macroalgae or other benthic taxa are the more common space holder (Schmitt et al. 2022). There is mounting empirical and theoretical support that these can be alternative basins of attraction (alternative stable states in models) when hysteresis creates a region of bi-stability that includes the ambient environmental conditions (Folke et al. 2004; Schröder et al. 2005; Mumby 2006; Mumby et al. 2013; Muthukrishnan et al. 2016; Briggs et al. 2018; McManus et al. 2019; Schmitt et al. 2019). Yet resilience of coral to disturbance is tremendously variable across coral reef ecosystems, with rapid recovery in some reefs and continued coral decline or shifts to macroalgae in others (Holbrook et al. 2018; Baumann et al. 2022). The presence or type of material legacies has the potential to account for some of the observed variability in resilience of coral following a disturbance.

Competing hypotheses exist regarding the role of dead coral structures in fostering return of coral on disturbed tropical reefs. High structural complexity can promote faster or more successful recovery of corals if it provides habitat for coral-associated organisms that benefit coral growth and/or settlement substrate with refuge spaces for colonizing corals that would otherwise be consumed by predators (Graham et al. 2015). Alternatively, retention of dead coral skeletons may diminish coral resilience if skeletons facilitate the establishment of macroalgae—major competitors of coral for attachment space on the reef—by, for example, creating physical refugia from herbivores for vulnerable, early life-stage macroalgae (Bennett et al. 2010; Puk et al. 2020). Indeed, flat reef surfaces are readily grazed by herbivorous fish and sea urchins, preventing establishment of macroalgae (Bellwood et al. 2006; Adam et al. 2011; 2015; Holbrook et al. 2016). This grazing helps maintain reef surfaces in a suitable condition for the settlement of new coral colonies, and thus can be a crucial stabilizing feedback during periods of coral reef recovery (Adam et al. 2015; Holbrook et al. 2016; Schmitt et al. 2022). Following reductions in herbivory, some coral reefs have transitioned to a degraded ecosystem state in which macroalgae become the dominant space holder (Hughes

1994; Mumby et al. 2013; Vieira 2020). Once mature, macroalgae can become physically and/or chemically defended against herbivory (Davis 2018) and compete directly with corals for reef space by overgrowing live colonies and preempting settlement space for coral larvae (McCook et al. 2001; Vieira 2020). This suggests that macroalgae that are initially protected by dead coral structures could persist on the reef well after the dead structures have completely eroded away, potentially trapping the system in the alternative, macroalgae-dominated state.

Here, we integrate herbivory and retention of biogenic structure using a conceptual framework derived from catastrophe theory (Jones 1977; Loehle 1989) to explore how material legacies could act to modify the coral reef resilience landscape (Fig. 1). At low amounts of algal refugia, the coral-dominated state is resilient to disturbances that do not increase algal refugia (i.e., structure-removing disturbances). However, disturbances that substantially decrease coral abundance and simultaneously increase the level of algal refugia (i.e., structure-retaining disturbances) can move the system to a region of state space in which coral and macroalgal states become bi-stable, thus triggering shifts from coral- to macroalgae-dominance (Fig. 1, red line & bottom right). Material legacies of structure-retaining disturbances may act to modify the resilience landscape and change the underlying relationship between herbivores (a biological driver) and equilibrium coral abundance (a state variable) by increasing the degree of hysteresis (Fig. 1, blue dashed arrow). Importantly, the material legacy in this case causes an effective reduction in the capacity of herbivores to control macroalgae (i.e., the rate of herbivory) without actually changing the biomass of herbivores present in the system.

To investigate the effect of material legacies on coral reef resilience, we explored the consequences of structure-removing and structure-retaining disturbances using a model that simulated how the fraction of reef space occupied by key interacting benthic space-holders (corals, macroalgae) changes following these two types of disturbance events. We address three main questions. 1) How do the material legacies of structure-retaining disturbances affect the presence of alternate states? 2) What disturbance conditions (i.e., intensity and type) are required to trigger shifts between coral and macroalgae states? 3) Do structure-retaining disturbances speed or slow shifts to alternate states or recoveries to the pre-disturbance state?

METHODS

Model description

To quantify the effects of disturbance type on coral reef community structure, we developed a model that describes how benthic cover changes over time. Building on previous work (Mumby 2006; Briggs et al. 2018), we divided benthic cover on hard substrate into a set of classes representing the fraction of reef space occupied by coral C, macroalgae M, and 'empty' space S. In this model, empty reef space is functionally equivalent to hard substrates occupied by a thin layer of turf or crustose coralline algae, which can be colonized or overgrown by either coral or macroalgae (Birrell et al. 2005; O'Brien & Scheibling 2018; Schmitt et al. 2022). To compare structure-removing and structure-retaining disturbances and model the effects of the dead skeleton legacy, we further subdivided the coral cover class into live colonies growing on primary reef substrate (C_L), live colonies growing on dead colonies (C_P), and standing dead skeletons (C_D). Similarly, because dead skeletons may influence herbivory rates on macroalgae (Bennett et al. 2010; Puk et al. 2020), we partitioned macroalgal cover into two classes that differ in the substrate they occupy: macroalgae that grow on open reef spaces and are fully exposed to herbivory (M_E), and macroalgae that grow amidst the branches of dead coral colonies and are protected to some degree from herbivory (M_P).

We described changes in the proportions of the biotic cover classes (corals and macroalgae) using a system of five differential equations that capture transitions between empty space, live and dead branching coral cover, and macroalgal cover on the reef (Fig. 2). First, live coral (C_L) grows onto empty reef spaces at rate g_c. Our model also allows for open recruitment, with coral settlers arriving into empty space at rate γ_c. Live coral can die in two ways: it can experience natural mortality at a rate d_c, which causes transitions from live to dead coral, or it can be overgrown by either exposed or protected macroalgae at rate g_{mc}, which causes transitions directly from live coral to protected macroalgae. The balance of these gain and loss processes gives the change in proportional live coral on the reef over time:

$$\frac{dC_L}{dt} = g_c C_L S + \gamma_c S - g_{mc} C_L (M_E + M_P) - d_c C_L \qquad (1)$$

When corals die naturally, their skeletal structures remain on the reef and continue to occupy benthic space as they gradually erode over several years (Adam et al. 2014). We represented this as C_D, or the fraction of reef space occupied by standing dead coral skeleton. Transitions from live coral to dead coral result from natural mortality of live coral ($d_c C_L$). Further, herbivores can remove macroalgae from dead coral structure, but at a reduced rate $h(1-p)$ compared to herbivory on exposed macroalgae, representing the product of the ambient rate of herbivory h scaled by the degree of protection afforded by a dead coral skeleton (p), resulting in a transition from protected macroalgae to dead coral. Dead coral is lost in three ways: it is removed via erosion at a fixed rate, e; it can be settled and grown on by live coral at rates γ_c and g_c, respectively; and it can be settled onto or overgrown by macroalgae at rates γ_m and g_m, respectively. We thus describe the change in proportional cover of standing dead coral over time as:

$$\frac{dC_D}{dt} = d_c(C_L + C_P) + M_P(h(1-p) + d_m) - g_c C_P C_D - s\gamma_c C_D - g_m C_D(M_E + M_P) - \gamma_m C_D - eC_D \quad (2)$$

Standing dead coral provides a secondary substrate on which corals can settle and grow, and we represented this in our model as C_P, or live coral that grows specifically on dead coral structure. Corals of this class arise only as a result of settlement (γ_c) and subsequent growth (g_c); lateral overgrowth by mature colonies does not tend to occur in structure-forming coral species, so we did not include this process in our model. We included a multiplier, s, for the rate of settlement of live coral onto dead coral relative to open substrate, where values less than one correspond to reduced settlement, and values greater than one correspond to increased settlement relative to that on open substrate. As a default, we set the settlement rate onto dead coral equal to that on open substrate (i.e., $s = 1$). Similar to live coral that grows on primary reef substrate, live coral that grows on dead coral can be lost via ambient mortality, at rate d_c, as well as overgrowth by macroalgae, at rate g_{mc}. This class of coral can also be lost via erosion, at rate e, to capture the transient nature of standing dead coral as a substrate. We thus describe the change in proportional cover of live coral growing on dead coral over time as:

$$\frac{dC_P}{dt} = g_c C_P C_D + s\gamma_c C_D - g_{mc} C_P(M_E + M_P) - d_c C_P - eC_P \quad (3)$$

We tested the sensitivity of our model's predictions to coral settlement on dead structure by varying the parameter s.

Macroalgae growing within or beneath complex structures—such as the skeletons of dead corals—tend to have reduced rates of herbivory relative to more planar, exposed reef surfaces (Bennett et al. 2010). To capture this, we subjected the exposed and protected macroalgae classes to different levels of herbivory. Exposed macroalgae (M_E) are removed at the ambient rate of herbivory, h. Protected macroalgae (M_P), by contrast, experience reduced herbivory pressure, $h(1 - p)$, where p is a value between 0 and 1 that decreases the ambient level of herbivory by a designated amount (hereafter, referred to as *algal protection*). Both exposed and protected macroalgae can grow (at rate g_m) and settle (at rate γ_m) into empty space (S), which increases exposed macroalgae (M_E), and onto dead coral, which increases protected macroalgae (M_P). Both classes of macroalgae can overgrow either class of live coral, but at a slower rate, g_{mc}, resulting in a transition from live coral to protected macroalgae. Finally, both classes of macroalgae are lost via senescence (i.e., natural mortality) at a fixed rate, d_m. The rates of change in proportional cover for these two classes of macroalgae are given by the equations:

$$\frac{dM_E}{dt} = g_m M_E S + g_m M_P S + \gamma_m S - M_E(h + d_m) \qquad (4)$$

$$\frac{dM_P}{dt} = g_m M_P C_D + g_m M_E C_D + g_{mc} C_L(M_E + M_P) + g_{mc} C_P(M_E + M_P) + \gamma_m C_D - M_P(h(1-p) + d_m + e) \quad (5)$$

Finally, because our state variables represent the fraction of space occupied by any given class, we note that the fraction of empty space can be described as:

$$S = 1 - C_L - C_D - C_P - M_E - M_P \qquad (6)$$

Disturbance

To model an acute disturbance, such as a storm event (structure-removing disturbance) or bleaching episode (structure-retaining disturbance), we used a kick-flow approach in which the ‘flow’ of the system described by equations (1) to (6) is paused, the system is instantaneously perturbed by a ‘kick’ (e.g., an acute mortality event), and then the simulation is resumed. During these perturbations, the fraction of reef occupied by each space holder is either reduced, increased, or unchanged to simulate pulse disturbance events of each type.

Specifically, structure-removing disturbances reduce all space holders to a designated percentage of their pre-disturbance levels (increasing empty space), where the percentage represents the intensity of the disturbance. Structure-retaining disturbances affect only the three coral classes (i.e., live coral on open substrate or on dead coral, and standing dead coral). In these instances, both classes of live coral are reduced by a fixed proportion (again, representative of disturbance intensity), and dead coral increases by the amount that live coral is reduced.

Model parameterization and analysis

We parameterized the model following ranges of parameters published by Fung et al. (2011) for reef systems not subjected to anthropogenic stressors (e.g., overfishing and sedimentation) and default values used by Briggs et al. (2018) (Table 1). We modified some of the parameters and added additional ones to account for the addition of the new state variable representing dead coral skeletons. In particular, we reduced the coral mortality rate (production of dead skeletons) and estimated a new parameter, the erosion rate of dead coral skeletons, as ten times greater than the mortality rate of live corals to ensure that the abundance of dead skeletons remained within a range typically observed in nature (see Appendix S1). Our estimated erosion rate of 1% per year falls within published estimates of bioerosion of calcium carbonate structures on reefs of 0 to 5% per year (Silbiger et al. 2014). Importantly, these published rates estimate annual volumetric loss, not two-dimensional surface loss, as modeled here. Nonetheless, a volumetric loss of this magnitude translates to a comparable loss of two-dimensional area (see Appendix S1). Because this lower coral mortality rate resulted in a reduced rate of production of empty space, we increased macroalgal growth and settlement rates to allow macroalgae to colonize this reduced open space efficiently.

We first explored the sensitivity of equilibrium conditions to variation in key parameters without disturbance using bifurcation diagrams. For this analysis, we solved for the equilibria of our model equations numerically (using MATLAB version R2016a) and assessed the equilibrium cover of each class of space holder across selected ranges in key parameters. This analysis focused on how variation in algal protection from herbivory (p) affected equilibrium values of live coral and total macroalgae (M_E + M_P) cover. Independent simulations were run for values of algal protection ranging between 0 and 1 (i.e., from no protection to complete protection for M_P). Further, we analyzed the model's sensitivity to variation in algal protection for starting conditions that reflect either a coral-dominated or macroalgae-dominated equilibrium to test for bi-stability between these two ecosystem states (i.e., hysteresis). We then explored equilibrium conditions of coral cover as a response surface determined by the degree of algal protection, p, and the ambient level of herbivory, h. For this analysis, we constrained the maximum level of herbivory to 0.4 to represent a realistic range in this parameter (Mumby 2007). Lastly, we conducted a sensitivity analysis in similar fashion to explore equilibrium conditions of coral and macroalgae cover as a function of the erosion rate of dead coral (e) and coral mortality rate (d_c) (see Appendix S1).

Over the range in algal protection that produced alternative stable states, we used numerical simulations (in R version 4.0.0) to explore how the model responded to structure-removing and structure-retaining disturbances of various intensities (fractional mortality of the affected space holders). Beginning with a coral-dominated state, we simulated the fraction of space occupied through time by each space holder following single disturbances that ranged in intensity from no mortality to complete mortality of the affected space holders (i.e., 0 to 1). We evaluated the equilibrium cover of each class of space holder via simulation by determining proportional cover after disturbance once the rates of change all reached zero. We then designated the state of the system as either a coral or macroalgae equilibrium based on which organisms were the predominant space holders (a low equilibrium cover of coral always corresponded with a high equilibrium cover of macroalgae). We identified the intensity of each disturbance type that was required to trigger a shift from a coral to macroalgal state for each value of algal protection. This analysis was repeated for an ecosystem state that initially was dominated by macroalgae such that the initial cover of each space holder reflected that of a macroalgae equilibrium. Finally, we quantified the time taken to reach equilibrium for each combination of algal protection and disturbance intensity. All analyses and figures were produced using R (version 4.0.0; R Core Team, 2020), RStudio (version 1.2.5042; RStudio Team, 2020), the fields package (Nychka et al. 2021), colors from Manu: NZ Bird Colour Palettes (Thomson 2022), and MATLAB (version R2016a). All model code is permanently archived on Zenodo (Kopecky 2023): https://doi.org/10.5281/zenodo.7556007.

RESULTS

Algal protection creates alternative stable states

As is common among models of benthic cover on coral reefs (Mumby 2006; Fung et al. 2011; Sandin & McNamara 2012; Muthukrishnan et al. 2016; Briggs et al. 2018; McManus et al. 2019), our model predicted the existence of alternative stable states dominated by either coral or macroalgae (Fig. 3). The magnitude of hysteresis between these states depended both on the amount of herbivory and the strength of algal protection (Fig. 3c). A sensitivity analysis of equilibrium coral cover as a function of the erosion rate of dead coral (*e*) and coral mortality rate (d_c) revealed that bi-stability between the coral and macroalgae states exists when erosion occurs relatively slowly (i.e., the material legacy is more persistent), but only the coral state exists at higher rates of erosion when the material legacy becomes more ephemeral. Additionally, this analysis also showed that higher erosion rates allow the system to tolerate higher rates of coral mortality without transitioning to dominance by macroalgae (Appendix S1).

Structure-retaining disturbances promote and maintain shifts from coral to macroalgal states

Overall, structure-retaining disturbances were more likely to drive transitions to and maintain the macroalgae-dominated state (Fig. 4 & 5). For example, coral-dominated systems that were perturbed by a structure-removing disturbance with an intensity of 0.6 (i.e., all space holders instantaneously reduced by 60%) rapidly regained pre-disturbance levels of live coral and macroalgae cover (Fig. 4a & c). By contrast, a structure-retaining disturbance of the same intensity (i.e., where 60% of space occupied by live coral on open substrate and on dead coral was converted to standing dead coral) triggered persistent shifts to the macroalgal state (Fig. 4b & d). In this case, live coral cover continued to drop after the disturbance and eventually stabilized far below its pre-disturbance equilibrium cover. Both exposed and protected macroalgae sharply increased after the disturbance and achieved an equilibrium cover substantially higher than their pre-disturbance levels, surpassing coral as the dominant space holders on the reef (Fig. 4b & d). When varying the rate of live coral settlement onto dead coral, we found that this outcome held when settlement onto dead coral was less than or equal to the rate of settlement on open substrate (i.e., when $s \leq 1$)(Fig. 4a-d). However, when settlement on dead coral was doubled relative to open substrate, the system was able to recover from structure-retaining disturbance at this intensity, though at a slower rate than when structure was removed (Fig. 4e & f).

Across the range of algal protection that created bi-stability, the thresholds for state shifts from coral- to macroalgae-dominated reefs were lower for structure-retaining disturbances relative to structure-removing disturbances. When the initial state was dominated by coral, the system returned to coral dominance following nearly all intensities of a structure-removing disturbance. However, when algal protection was sufficiently high, large structure-removing disturbances tipped the reef into macroalgal dominance (Fig. 5a). By contrast, much lower intensities of structure-retaining disturbance were needed to tip the system from coral- to macroalgal-dominance, and the intensity required to do so was inversely related to the strength of algal protection offered by the dead skeletons (black line, Figure 5b). When the system was instead initially dominated by macroalgae (Fig. 5, bottom row), only high intensity structure-removing disturbances at low levels of algal protection resulted in shifts to coral dominance (Fig. 5c). The tipping point in disturbance intensity required to do so increased with increasing algal protection (Fig. 5c, black line). Importantly, the macroalgal state was maintained following all intensities of structure-retaining disturbance and at all values of algal protection, revealing that shifts from the macroalgal to the coral state were not possible with disturbances that leave dead structure in place across this range of algal protection (Fig. 5d).

Equilibration times varied with disturbance intensity and level of algal protection

Generally, rapid returns to a coral equilibrium occurred following most intensities of disturbance and at most values of algal protection. However, some slower return times resulted from disturbances near the threshold value of disturbance intensity and at higher values of algal protection (Fig. 5a & 5b). In these situations, macroalgae temporarily achieved a higher cover post-disturbance and thus delayed slightly the return to a coral equilibrium. By contrast, systems that shifted to the macroalgal state had longer equilibration times overall, the longest of which followed the most intense disturbances (Fig. 5b). This reflects the time taken for macroalgae to take up the newly available substrate (i.e., dead skeletons). When shifts from macroalgae to coral took place, equilibration times were also generally longer for systems near the tipping point of disturbance intensity (Fig. 5c). When the system returned to macroalgal dominance after disturbance, the time to reach equilibrium was generally longer following higher intensity disturbances of both types (Fig. 5d).

DISCUSSION

Material legacies shape the resilience landscape

Globally, ecosystems are increasingly crossing tipping points, in many cases to degraded states that offer diminished ecosystem services (Scheffer et al. 2001; Millennium Ecosystem Assessment Program 2005; Fagre et al. 2009). Knowledge of the factors that either enhance resilience and foster recoveries or reduce resilience and promote shifts to alternative states is central to our ability to understand resilience now and forecast trajectories of community re-assembly as disturbance regimes change in the future. Here, we showed that disturbances that leave dead skeletons (material legacies) can erode coral resilience, either prolonging the return to a coral dominated state or causing a regime shift from a coral to a macroalgae community. Our findings suggest that better integration of material legacies into studies of resilience may offer key insight into when and where ecosystems that are dominated by structure-forming organisms will cross tipping points.

Disturbance-driven shifts between alternative ecosystem states (i.e., those that occur without changes to underlying drivers) have traditionally been thought to depend on whether the intensity of a disturbance is sufficient to push the system across the unstable equilibrium value of a state variable (Beisner et al. 2003; Scheffer & Carpenter 2003; Suding & Hobbs 2009; Fabina et al. 2015). Our findings add nuance to this, showing that even at the same intensity, different disturbance types can lead to divergent outcomes (i.e., recovery versus regime shift) if there is differential production of a material legacy that modifies a stabilizing feedback. Our model exhibited high resilience to structure-removing disturbances, showing very low hysteresis (Fig. 1, blue lines). Non-linear systems with little (or no) hysteresis tend to be resilient to disturbance, and abrupt shifts between ecological states occur only if the threshold value of a system driver is crossed (Beisner et al. 2003; Suding & Hobbs 2009). By contrast, our model suggests that coral-dominated reefs were resilient only to low intensities of structure-retaining disturbance, while moderate to intense disturbances caused shifts from coral to macroalgae because of the great increase in the amount of algal protection afforded by the dead skeletons. When bi-stability exists across a wide range of the driver in this fashion (Fig. 1, red lines), an abrupt shift in ecosystem state is possible with a disturbance that displaces the system across a tipping point without any change to the underlying driver (e.g., herbivore biomass). Consistent with the dynamics we hypothesized in Figure 1, our results suggest that material legacies hold the capacity to shape the landscape of resilience in which a system operates by determining the magnitude of hysteresis between a system variable and its driver.

The importance of material legacies in preventing or driving regime shifts is likely to depend on the type of stabilizing feedback that promotes recovery in a given system. For our coral reef example, the material legacy (dead coral skeletons) acts to weaken a stabilizing feedback (the rate of herbivory), but the possibility also exists that a material legacy could instead strengthen a stabilizing feedback. For example, oyster reefs provide a soft sediment analog to coral reefs, as oysters are structure-forming organisms that are periodically killed by disturbances that either remove shell structures (e.g., dredging) or leave shell structures intact (e.g., hypoxic events). Disturbances that leave shells intact may in fact promote recoveries on oyster reefs, as oyster shells provide substrate for larvae to settle on and reduce impacts from seafloor sediments that can smother young oysters (Lenihan & Peterson 1998). This contrasts with coral reefs where coral larvae that recruit to dead skeletons may be doomed to early death by erosion of their dead host structure (Swanson 2016). In our model, high recruitment of coral onto dead structure could prevent tipping into the macroalgal state by pre-empting algal settlement (Fig. 4f). However, it is important to note that, in our model, this high recruitment does not come at a cost to coral settlement in empty space: in other words, dead coral does not act as an “ecological trap” for larvae (Battin 2004). If a settlement tradeoff did exist, dead coral could act as a “sink” for larval propagules and erode coral persistence (see Kopecky et al. 2021). In forests, the removal of tree roots during disturbance can increase the erosion of topsoil and destabilize the forested ecosystem state. If tree roots are instead retained through a disturbance, topsoil persists afterward and can increase colonization success of new trees (Flores et al. 2020). However, there is evidence that standing or fallen dead trees can potentially decrease resilience by negatively affecting the establishment of new individuals (Swanson et al. 2011; Johnstone et al. 2016). These examples illustrate the importance of considering context dependency in assessing how a material legacy may affect the stabilizing and destabilizing feedbacks that govern alternative states of an ecosystem.

The dead coral skeleton legacy decreases recovery potential on coral reefs

Building on previous models of alternative stable states in coral reefs (e.g., Mumby 2006; Briggs et al. 2018), we explored the effects of disturbances that either remove or leave in place dead coral skeletons on resilience by incorporating three novel components: 1) the occupation of space by dead coral skeletons (i.e., a material legacy); 2) the (transient) substrate these dead structures provide for corals and macroalgae; and 3) the protection from herbivores that these dead coral structures provide for macroalgae. The dead skeleton legacy produced by structure-retaining disturbance effectively reduced the strength of herbivory and produced a relatively high degree of hysteresis in our coral-macroalgae system, compared to a relatively low degree of hysteresis when this legacy was removed by disturbance. The retention of this structure created a higher incidence of coral-macroalgae shifts (lower chance of recovery) when the dead skeleton legacy was in place to inhibit herbivory. These results indicate that coral-dominated reefs are likely to be more resilient to disturbances that remove dead skeletons (e.g., storm-generated waves), while disturbances that leave dead skeletons intact (e.g., predator outbreaks or bleaching) greatly lower the threshold of disturbance intensity required to trigger a regime shift to macroalgae dominance. We note that our model does not account for dynamical responses by herbivores that could result from changes in the amount of complex reef structure that provides habitat. Indeed, the degree of habitat complexity has been found to positively affect abundances of reef fishes, including herbivores (Holbrook et al. 2003; Blackwood et al. 2011; Bozec et al. 2013); however, increases in herbivore abundance associated with higher habitat complexity may not directly translate to increased rates of herbivory if the habitat provides a high degree of protection for macroalgae. Nevertheless, future investigations into the role of the dead coral skeleton legacy on coral-algae dynamics could consider dynamical responses by herbivores to the removal or retention of dead coral skeletons with varying degrees of algal protection.

Our results suggest that the degree of hysteresis in the relationship between coral cover (the state variable) and herbivory (a system driver) depended on the type of disturbance that occurred. More specifically, the amount of macroalgal refugia generated during a disturbance event (via coral skeletons that are left on the reef) determined the degree of bi-stability between coral-dominated and macroalgae-dominated reef states. In turn, the amount of spatial refugia generated depends on the intensity of the disturbance, while the strength of protection offered by the skeletons likely depends on morphological traits of the affected coral species, such as the 3-dimensional structural characteristics of the coral skeleton. The genera of coral that are most sensitive to bleaching mortality from marine heatwaves tend to be those with higher structural complexity (e.g., branching, corymbose, and tabular colony morphologies). These growth forms are also preferred by Crown-of-Thorns Seastars (Acanthaster planci)(COTS), a coral predator that similarly leaves behind intact coral skeletons by removing coral tissue. Populations of this predator can exhibit ‘boom-and-bust’ outbreaks that periodically cause widespread mortality of coral tissue over landscape scales (Pratchett et al. 2013; 2017).

The findings described above are likely most representative of reefs dominated by complex, branching coral morphologies. Reefs dominated by massive or mounding coral morphologies have skeletons which may not provide as much protection for algae. Massive and mounding corals tend to be less susceptible to disturbance in general (Zawada et al. 2019), and therefore were not the main focus of our model. Nonetheless, these reef types were captured in our sensitivity analysis of algal protection, *p*, when *p* was set to extremely low levels (Figure 3c). Further, we parameterized our model to the level of dead coral cover observed in natural systems (i.e., < 10% for a coral-dominated reef state). Although our estimated rate falls within observed bioerosion rates (Silbiger et al. 2014), erosion of dead coral likely varies widely with flow rates, wave exposure, coral skeleton morphology/structural composition, and the presence of bio-eroding organisms. Indeed, when erosive forces such as storms act to rapidly remove coral skeletons, reef recovery to coral-dominated states can be rapid (Holbrook et al. 2018). Additionally, we found that the rate at which coral skeletons are produced via mortality can be counteracted by the rate at which these skeletons are removed via erosion (i.e., higher erosion allows for higher coral mortality without a transition to macroalgal dominance; Appendix S1). This underscores the importance of considering how multiple processes could interact to modify the strength of the material legacy effect, and thereby, equilibrium conditions.

Theoretical and empirical work support the notion that the skeletons of dead branching corals could facilitate the proliferation of macroalgae. Many primary producers (both terrestrial and marine) show stage-dependent vulnerability to herbivory, where early life-stages are palatable to herbivores but become physically and/or chemically defended as they mature or increase in size (Cronin & Hay 1996; Barton & Koricheva 2010; Davis 2018). On coral reefs, this well-known life history trait of macroalgae has been posited as a mechanism that contributes to shifts from coral to macroalgal states (e.g., Davis 2018). Theory shows not only that stage-dependent vulnerability in macroalgae can produce alternative stable states between coral and macroalgae, but also that the rate of maturation from the vulnerable to invulnerable stage influences the magnitude of hysteresis between herbivory and coral cover (Briggs et al. 2018). Further, empirical studies have revealed that vulnerable (juvenile) macroalgae escape herbivory by receiving associational refuge from unpalatable adults (Davis 2018) or reef structures that hinder herbivore access (Puk et al. 2020), both of which can lead to multi-generational persistence of stands of macroalgae (Schmitt et al. 2019, 2022). Thus, dead coral skeletons could provide a key spatial refuge for vulnerable life history stages of macroalgae and could be a critical element contributing to transitions to macroalgae-dominated reef states. This is highly problematic for conservation and restoration because reversing shifts when hysteresis exists requires either a large relaxation of the underlying driver, or a subsequent large disturbance to reset the system (Beisner et al. 2003). Further, structure-retaining disturbances—particularly coral bleaching events—are increasing in prevalence and severity due to elevated sea temperatures associated with global climate change (Uthicke et al. 2015; Pratchett et al. 2017; Hughes et al. 2018; Hughes et al. 2019; Lough et al. 2018; Donovan et al. 2021). This changing disturbance regime may lead to more reefs becoming trapped in the macroalgae state (Fabina et al. 2015), which has potentially far-reaching consequences for human populations who rely directly on coral reefs for a wide array of ecosystem services.

REFERENCES

Adam, T.C., Brooks, A.J., Holbrook, S.J., Schmitt, R.J., Washburn, L. & Bernardi, G. (2014). “How will coral reef fish communities respond to climate-driven disturbances? Insight from landscape-scale perturbations.” *Oecologia*, 176, 285–296.

Adam, Thomas C., Deron E. Burkepile, Benjamin I. Ruttenberg, and Michelle J. Paddack. 2015. “Herbivory and the Resilience of Caribbean Coral Reefs: Knowledge Gaps and Implications for Management.” *Marine Ecology Progress Series* 520 (February): 1–20. https://doi.org/10.3354/meps11170.

Adam, Thomas C., Russell J. Schmitt, Sally J. Holbrook, Andrew J. Brooks, Peter J. Edmunds, Robert C. Carpenter, and Giacomo Bernardi. 2011. “Herbivory, Connectivity, and Ecosystem Resilience: Response of a Coral Reef to a Large-Scale Perturbation.” Edited by Julian Clifton. *PLoS ONE* 6 (8): e23717. https://doi.org/10.1371/journal.pone.0023717.

Baker, Andrew C., Peter W. Glynn, and Bernhard Riegl. 2008. “Climate Change and Coral Reef Bleaching: An Ecological Assessment of Long-Term Impacts, Recovery Trends and Future Outlook.” *Estuarine, Coastal and Shelf Science* 80 (4): 435–71. https://doi.org/10.1016/j.ecss.2008.09.003.

Barton, Kasey E., and Julia Koricheva. 2010. “The Ontogeny of Plant Defense and Herbivory: Characterizing General Patterns Using Meta-Analysis.” *The American Naturalist* 175 (4): 481–93. https://doi.org/10.1086/650722.

Battin, James. 2004. “When Good Animals Love Bad Habitats: Ecological Traps and the Conservation of Animal Populations.” *Conservation Biology* 18 (6): 1482–91. https://doi.org/10.1111/j.1523-1739.2004.00417.x.

Baumann, Justin H., Lily Z. Zhao, Adrian C. Stier, and John F. Bruno. 2022. “Remoteness Does Not Enhance Coral Reef Resilience.” *Global Change Biology* 28 (2): 417–28. https://doi.org/10.1111/gcb.15904.

Beisner, Be, Dt Haydon, and K. Cuddington. 2003. “Alternative Stable States in Ecology.” *Frontiers in Ecology and the Environment* 1 (7): 376–82. https://doi.org/10.1890/1540-9295(2003)001[0376:ASSIE]2.0.CO;2.

Bellwood, David R., Terry P. Hughes, and Andrew S. Hoey. 2006. “Sleeping Functional Group Drives Coral-Reef Recovery.” *Current biology* 16 (24): 2434–39. https://doi.org/10.1016/j.cub.2006.10.030.

Bennett, S., A. Vergés, and D. R. Bellwood. 2010. “Branching Coral as a Macroalgal Refuge in a Marginal Coral Reef System.” *Coral Reefs* 29 (2): 471–80. https://doi.org/10.1007/s00338-010-0594-5.

Birrell, Chico L., Laurence J. McCook, and Bette L. Willis. 2005. “Effects of Algal Turfs and Sediment on Coral Settlement.” *Marine Pollution Bulletin* 51 (1–4): 408–14.

Blackwood, Julie C., Alan Hastings, and Peter J. Mumby. 2011. “A Model-Based Approach to Determine the Long-Term Effects of Multiple Interacting Stressors on Coral Reefs.” *Ecological Applications* 21 (7): 2722–33. https://doi.org/10.1890/10-2195.1.

Bozec, Yves-Marie, Laith Yakob, Sonia Bejarano, and Peter J. Mumby. 2013. “Reciprocal Facilitation and Non-Linearity Maintain Habitat Engineering on Coral Reefs.” *Oikos* 122 (3): 428–40. https://doi.org/10.1111/j.1600-0706.2012.20576.x.

Briggs, Cheryl J., Thomas C. Adam, Sally J. Holbrook, and Russell J. Schmitt. 2018. “Macroalgae Size Refuge from Herbivory Promotes Alternative Stable States on

Coral Reefs." Edited by Geerat J. Vermeij. *PLoS ONE* 13 (9): e0202273. https://doi.org/10.1371/journal.pone.0202273.

Cronin, Greg, and Mark E. Hay. 1996. "Within-Plant Variation in Seaweed Palatability and Chemical Defenses: Optimal Defense Theory versus the Growth-Differentiation Balance Hypothesis." *Oecologia* 105 (3): 361–68. https://doi.org/10.1007/BF00328739.

Davis, Samantha L. 2018. "Associational Refuge Facilitates Phase Shifts to Macroalgae in a Coral Reef Ecosystem." *Ecosphere* 9 (5): e02272. https://doi.org/10.1002/ecs2.2272.

Donovan, Mary K., Deron E. Burkepile, Chelsey Kratochwill, Tom Shlesinger, Shannon Sully, Thomas A. Oliver, Gregor Hodgson, Jan Freiwald, and Robert van Woesik. 2021. "Local Conditions Magnify Coral Loss after Marine Heatwaves." *Science* 372 (6545): 977–80. https://doi.org/10.1126/science.abd9464.

Fabina, Nicholas S., Marissa L. Baskett, and Kevin Gross. 2015. "The Differential Effects of Increasing Frequency and Magnitude of Extreme Events on Coral Populations." *Ecological Applications* 25 (6): 1534–45. https://doi.org/10.1890/14-0273.1.

Fagre, D. B., C. W. Charles, C. D. Allen, C. Birkeland, F. S, Chapin III, P. M. Groffman, G. R. Guntenspergen, A. K. Knapp, A. D. McGuire, and P. J. Mulholland. 2009. "CCSP: Thresholds of Climate Change in Ecosystems." *A Report by the US Climate Change Science Program and the Subcommittee and Global Change Research*.

Flores, Bernardo M., Arie Staal, Catarina C. Jakovac, Marina Hirota, Milena Holmgren, and Rafael S. Oliveira. 2020. "Soil Erosion as a Resilience Drain in Disturbed Tropical Forests." *Plant and Soil* 450 (1–2): 11–25. https://doi.org/10.1007/s11104-019-04097-8.

Folke, Carl, Steve Carpenter, Brian Walker, Marten Scheffer, Thomas Elmqvist, Lance Gunderson, and C.S. Holling. 2004. "Regime Shifts, Resilience, and Biodiversity in Ecosystem Management." *Annual Review of Ecology, Evolution, and Systematics* 35 (1): 557–81. https://doi.org/10.1146/annurev.ecolsys.35.021103.105711.

Fukami, Tadashi. 2015. "Historical Contingency in Community Assembly: Integrating Niches, Species Pools, and Priority Effects." *Annual Review of Ecology, Evolution, and Systematics* 46 (1): 1–23. https://doi.org/10.1146/annurev-ecolsys-110411-160340.

Fung, Tak, Robert M. Seymour, and Craig R. Johnson. 2011. "Alternative Stable States and Phase Shifts in Coral Reefs under Anthropogenic Stress." *Ecology* 92 (4): 967–82. https://doi.org/10.1890/10-0378.1.

Gardner, Toby A., Isabelle M. Côté, Jennifer A. Gill, Alastair Grant, and Andrew R. Watkinson. 2005. "Hurricanes and Caribbean coral reefs: impacts, recovery patterns, and role in long-term decline." *Ecology* 86 (1): 174–84. https://doi.org/10.1890/04-0141.

Graham, Nicholas A. J., Simon Jennings, M. Aaron MacNeil, David Mouillot, and Shaun K. Wilson. 2015. "Predicting Climate-Driven Regime Shifts versus Rebound Potential in Coral Reefs." *Nature* 518 (7537): 94–97. https://doi.org/10.1038/nature14140.

Holbrook, Sally J., Thomas C. Adam, Peter J. Edmunds, Russell J. Schmitt, Robert C. Carpenter, Andrew J. Brooks, Hunter S. Lenihan, and Cheryl J. Briggs. 2018. "Recruitment Drives Spatial Variation in Recovery Rates of Resilient Coral Reefs." *Scientific Reports* 8 (1). https://doi.org/10.1038/s41598-018-25414-8.

Holbrook, Sally J., Andrew J. Brooks, and Russell J. Schmitt. 2003. “Variation in Structural Attributes of Patch-Forming Corals and in Patterns of Abundance of Associated Fishes.” *Marine and Freshwater Research* 53 (7): 1045–53. https://doi.org/10.1071/mf02063.

Holbrook, Sally J., Russell J. Schmitt, Thomas C. Adam, and Andrew J. Brooks. 2016. “Coral Reef Resilience, Tipping Points and the Strength of Herbivory.” *Scientific Reports* 6 (1): 35817. https://doi.org/10.1038/srep35817.

Hughes, Terry P., J. T. Kerry, and T. Simpson. 2018. “Large-Scale Bleaching of Corals on the Great Barrier Reef.” *Ecology* 99 (2): 501–501. https://doi.org/10.1002/ecy.2092.

Hughes, Terence P. 1994. “Catastrophes, Phase Shifts, and Large-Scale Degradation of a Caribbean Coral Reef.” *Science* 265 (5178): 1547–51.

Hughes, Terry P., James T. Kerry, Mariana Álvarez-Noriega, Jorge G. Álvarez-Romero, Kristen D. Anderson, Andrew H. Baird, Russell C. Babcock, et al. 2017. “Global Warming and Recurrent Mass Bleaching of Corals.” *Nature* 543 (7645): 373–77. https://doi.org/10.1038/nature21707.

Hughes, Terry P., James T. Kerry, Sean R. Connolly, Andrew H. Baird, C. Mark Eakin, Scott F. Heron, Andrew S. Hoey, et al. 2019. “Ecological Memory Modifies the Cumulative Impact of Recurrent Climate Extremes.” *Nature Climate Change* 9 (1): 40–43. https://doi.org/10.1038/s41558-018-0351-2.

Johnstone, Jill F, Craig D Allen, Jerry F Franklin, Lee E Frelich, Brian J Harvey, Philip E Higuera, Michelle C Mack, et al. 2016. “Changing Disturbance Regimes, Ecological Memory, and Forest Resilience.” *Frontiers in Ecology and the Environment* 14 (7): 369–78. https://doi.org/10.1002/fee.1311.

Jones, Dixon D. 1977. “Catastrophe Theory Applied to Ecological Systems.” *Simulation* 29 (1): 1–15. https://doi.org/10.1177/003754977702900102.

Kopecky, Kai L., Dana T. Cook, Russell J. Schmitt, and Adrian C. Stier. 2021. “Effects of Corallivory and Coral Colony Density on Coral Growth and Survival.” *Coral Reefs* 40 (2): 283–88.

Kai Kopecky. (2023). kkopecky711/Material-legacy-disturbance-type-model: v1.0 (v1.0). Zenodo. https://doi.org/10.5281/zenodo.7556007

Lenihan, Hunter S., and Charles H. Peterson. 1998. “How Habitat Degradation through Fishery Disturbance Enhances Impacts of Hypoxia on Oyster Reefs.” *Ecological Applications* 8 (1): 128–40.

Loehle, Craig. 1989. “Catastrophe Theory in Ecology: A Critical Review and an Example of the Butterfly Catastrophe.” *Ecological Modelling* 49 (1–2): 125–52. https://doi.org/10.1016/0304-3800(89)90047-1.

Lough, J. M., K. D. Anderson, and T. P. Hughes. 2018. “Increasing Thermal Stress for Tropical Coral Reefs: 1871–2017.” *Scientific Reports* 8 (1): 6079. https://doi.org/10.1038/s41598-018-24530-9.

McCook, L., J. Jompa, and G. Diaz-Pulido. 2001. “Competition between Corals and Algae on Coral Reefs: A Review of Evidence and Mechanisms.” *Coral Reefs* 19 (4): 400–417. https://doi.org/10.1007/s003380000129.

McManus, Lisa C., James R. Watson, Vítor V. Vasconcelos, and Simon A. Levin. 2019. “Stability and Recovery of Coral-Algae Systems: The Importance of Recruitment Seasonality and Grazing Influence.” *Theoretical Ecology* 12 (1): 61–72. https://doi.org/10.1007/s12080-018-0388-x.

Millennium Ecosystem Assessment (Program), ed. 2005. *Ecosystems and Human Well-Being: Wetlands and Water Synthesis: A Report of the Millennium Ecosystem Assessment*. Washington, DC: World Resources Institute.

Mumby, P. J. 2006. “Fishing, Trophic Cascades, and the Process of Grazing on Coral Reefs.” *Science* 311 (5757): 98–101. https://doi.org/10.1126/science.1121129.

Mumby, Peter J., Alan Hastings, and Helen J. Edwards. 2007. “Thresholds and the Resilience of Caribbean Coral Reefs.” *Nature* 450 (7166): 98–101. https://doi.org/10.1038/nature06252.

Mumby, Peter J., Robert S. Steneck, and Alan Hastings. 2013. “Evidence for and against the Existence of Alternate Attractors on Coral Reefs.” *Oikos* 122 (4): 481–91. https://doi.org/10.1111/j.1600-0706.2012.00262.x.

Muthukrishnan, Ranjan, James O. Lloyd-Smith, and Peggy Fong. 2016. “Mechanisms of Resilience: Empirically Quantified Positive Feedbacks Produce Alternate Stable States Dynamics in a Model of a Tropical Reef.” *Journal of Ecology* 104 (6): 1662–72. https://doi.org/10.1111/1365-2745.12631.

O’Brien, John M., and Robert E. Scheibling. 2018. “Turf Wars: Competition between Foundation and Turf-Forming Species on Temperate and Tropical Reefs and Its Role in Regime Shifts.” *Marine Ecology Progress Series* 590: 1–17.

Oliver, Eric C. J., Markus G. Donat, Michael T. Burrows, Pippa J. Moore, Dan A. Smale, Lisa V. Alexander, Jessica A. Benthuysen, et al. 2018. “Longer and More Frequent Marine Heatwaves over the Past Century.” *Nature Communications* 9 (1): 1324. https://doi.org/10.1038/s41467-018-03732-9.

Pratchett, Morgan S., Ciemon F. Caballes, Jennifer C. Wilmes, Samuel Matthews, Camille Mellin, Hugh P. A. Sweatman, Lauren E. Nadler, et al. 2017. “Thirty Years of Research on Crown-of-Thorns Starfish (1986–2016): Scientific Advances and Emerging Opportunities.” *Diversity* 9 (4): 41. https://doi.org/10.3390/d9040041.

Pratchett, Morgan S., Dominique McCowan, Jeffrey A. Maynard, and Scott F. Heron. 2013. “Changes in Bleaching Susceptibility among Corals Subject to Ocean Warming and Recurrent Bleaching in Moorea, French Polynesia.” *PLoS ONE* 8 (7): e70443. https://doi.org/10.1371/journal.pone.0070443.

Puk, Laura D., Alyssa Marshell, John Dwyer, Nicolas R. Evensen, and Peter J. Mumby. 2020. “Refuge-Dependent Herbivory Controls a Key Macroalga on Coral Reefs.” *Coral Reefs*, March. https://doi.org/10.1007/s00338-020-01915-9.

R Core Team (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

RStudio Team (2020). RStudio: Integrated Development for R. RStudio, Inc., Boston, MA URL http://www.rstudio.com/.

Sandin, Stuart A., and Dylan E. McNamara. 2012. “Spatial Dynamics of Benthic Competition on Coral Reefs.” *Oecologia* 168 (4): 1079–90. https://doi.org/10.1007/s00442-011-2156-0.

Scheffer, Marten, and Steve R. Carpenter. 2003. “Catastrophic Regime Shifts in Ecosystems: Linking Theory to Observation.” *Trends in Ecology & Evolution* 18 (12): 648–56. https://doi.org/10.1016/j.tree.2003.09.002.

Scheffer, Marten, Steve Carpenter, Jonathan A. Foley, Carl Folke, and Brian Walker. 2001. “Catastrophic Shifts in Ecosystems.” *Nature* 413 (6856): 591–96. https://doi.org/10.1038/35098000.

Schmitt, Russell J., Sally J. Holbrook, Andrew J. Brooks, and Thomas C. Adam. 2022. “Evaluating the Precariousness of Coral Recovery When Coral and Macroalgae Are Alternative Basins of Attraction.” *Limnology and Oceanography*, lno.11929. https://doi.org/10.1002/lno.11929.

Schmitt, Russell J., Sally J. Holbrook, Samantha L. Davis, Andrew J. Brooks, and Thomas C. Adam. 2019. “Experimental Support for Alternative Attractors on Coral Reefs.” *Proceedings of the National Academy of Sciences* 116 (10): 4372–81. https://doi.org/10.1073/pnas.1812412116.

Schröder, Arne, Lennart Persson, and André M. De Roos. 2005. “Direct Experimental Evidence for Alternative Stable States: A Review.” *Oikos* 110 (1): 3–19. https://doi.org/10.1111/j.0030-1299.2005.13962.x.

Silbiger, Nyssa J., Òscar Guadayol, Florence I. M. Thomas, and Megan J. Donahue. 2014. “Reefs Shift from Net Accretion to Net Erosion along a Natural Environmental Gradient.” *Marine Ecology Progress Series* 515 (November): 33–44. https://doi.org/10.3354/meps10999.

Swanson, Stella A. 2016. “Echinoid Herbivores and Coral Reef Resilience.” Dissertation, UC Santa Barbara.

Suding, Katharine N., and Richard J. Hobbs. 2009. “Threshold Models in Restoration and Conservation: A Developing Framework.” *Trends in Ecology & Evolution* 24 (5): 271–79. https://doi.org/10.1016/j.tree.2008.11.012.

Swanson, Mark E, Jerry F Franklin, Robert L Beschta, Charles M Crisafulli, Dominick A DellaSala, Richard L Hutto, David B Lindenmayer, and Frederick J Swanson. 2011. “The Forgotten Stage of Forest Succession: Early-Successional Ecosystems on Forest Sites.” *Frontiers in Ecology and the Environment* 9 (2): 117–25. https://doi.org/10.1890/090157.

Thomson, G. 2022. Manu: NZ Bird Colour Palettes. R package version 0.0.2, https://github.com/G-Thomson/Manu.

Uthicke, S., M. Logan, M. Liddy, D. Francis, N. Hardy, and M. Lamare. 2015. “Climate Change as an Unexpected Co-Factor Promoting Coral Eating Seastar (*Acanthaster planci*) Outbreaks.” *Scientific Reports* 5 (1): 8402. https://doi.org/10.1038/srep08402.

Vecchi, Gabriel A., Christopher Landsea, Wei Zhang, Gabriele Villarini, and Thomas Knutson. 2021. “Changes in Atlantic Major Hurricane Frequency since the Late-19th Century.” *Nature Communications* 12 (1): 4054. https://doi.org/10.1038/s41467-021-24268-5.

Vieira, Christophe. 2020. “Lobophora–Coral Interactions and Phase Shifts: Summary of Current Knowledge and Future Directions.” *Aquatic Ecology* 54 (1): 1–20. https://doi.org/10.1007/s10452-019-09723-2.

Wehner, Michael F., Kevin A. Reed, Burlen Loring, Dáithí Stone, and Harinarayan Krishnan. 2018. “Changes in Tropical Cyclones under Stabilized 1.5 and 2.0 °C Global Warming Scenarios as Simulated by the Community Atmospheric Model under the HAPPI Protocols.” *Earth System Dynamics* 9 (1): 187–95. https://doi.org/10.5194/esd-9-187-2018.

Zawada, Kyle J. A., Joshua S. Madin, Andrew H. Baird, Tom C. L. Bridge, and Maria Dornelas. 2019. “Morphological Traits Can Track Coral Reef Responses to the Anthropocene.” *Functional Ecology* 33 (6): 962–75. https://doi.org/10.1111/1365-2435.13358.

FIGURES

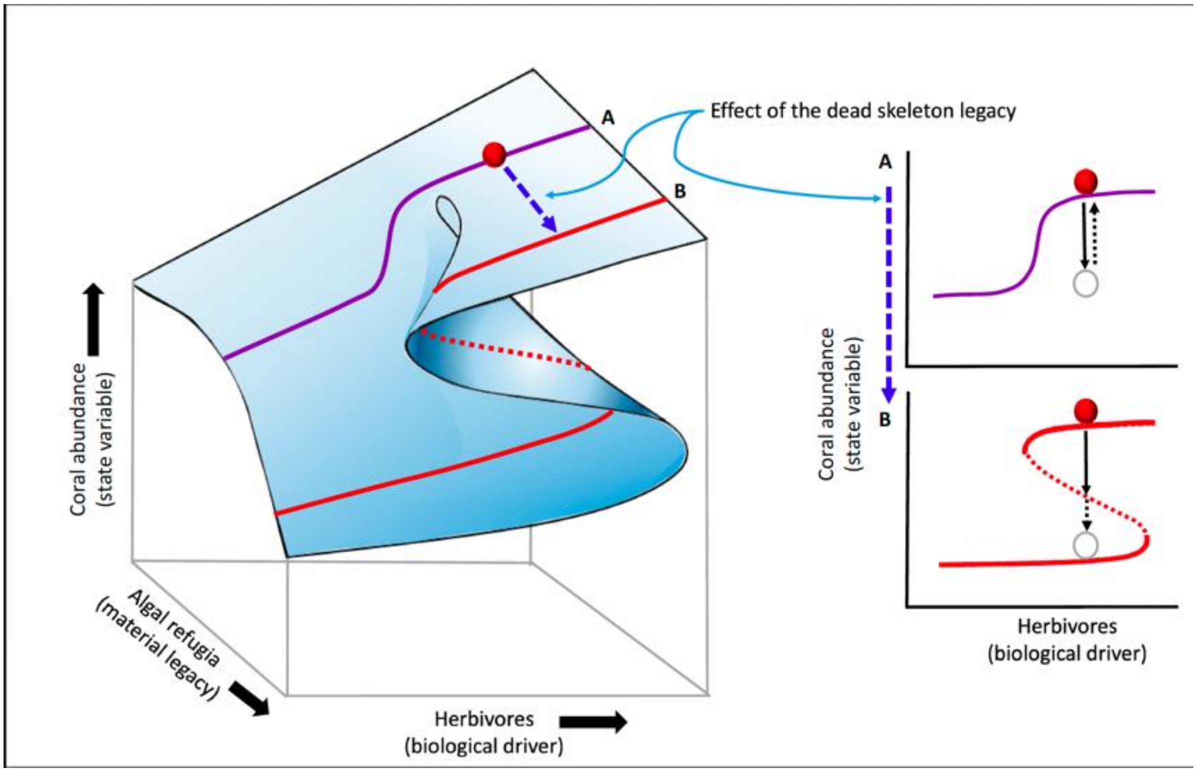


Figure 1. (Left) A hypothetical response surface showing how the equilibrium abundance of coral might vary as a function of herbivory and the amount of physical refugia in the environment that facilitate the proliferation of macroalgae; for heuristic purposes, we assume the response surface for macroalgae is the inverse of that shown for coral. The material legacies of structure-retaining disturbances (dead coral skeletons) provide vulnerable stages of macroalgae with refuge space from herbivores, potentially moving the system into a region of state space where hysteresis exists in the relationship with herbivory (blue dashed arrows). Such hysteresis promotes bi-stability of coral and macroalgae for some range of herbivory. (Top right) In regions of state space without hysteresis, coral would return to its pre-disturbance state (upward dotted black arrow) after a high intensity disturbance (downward solid black arrow). (Bottom right) By contrast, for regions of state space with hysteresis, the same intensity of disturbance could flip the system to a macroalgae stable state without any change in herbivory.

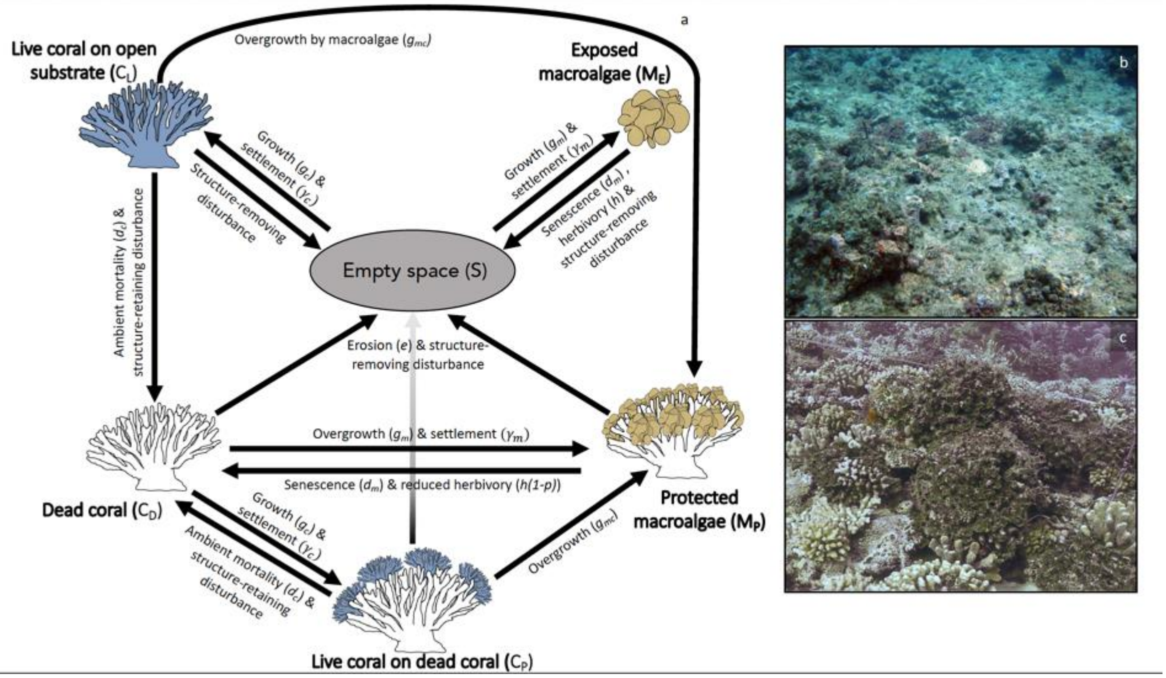


Figure 2. (a) Graphical depiction of interactions among state variables via model parameters (shown in parentheses). Arrows indicate the transfer of spatial occupation from one state variable to another by the associated process (e.g., dead coral transitions to open space via erosion). (b) Photograph of a coral reef following a structure-removing disturbance event (cyclone) that created bare, unoccupied reef space (photo credit: Russ Schmitt). (c) Photograph of a coral reef following a structure-retaining disturbance event (coral bleaching) that left in place dead coral skeletons (a material legacy) that are being overgrown by macroalgae (photo credit: Kai Kopecky).

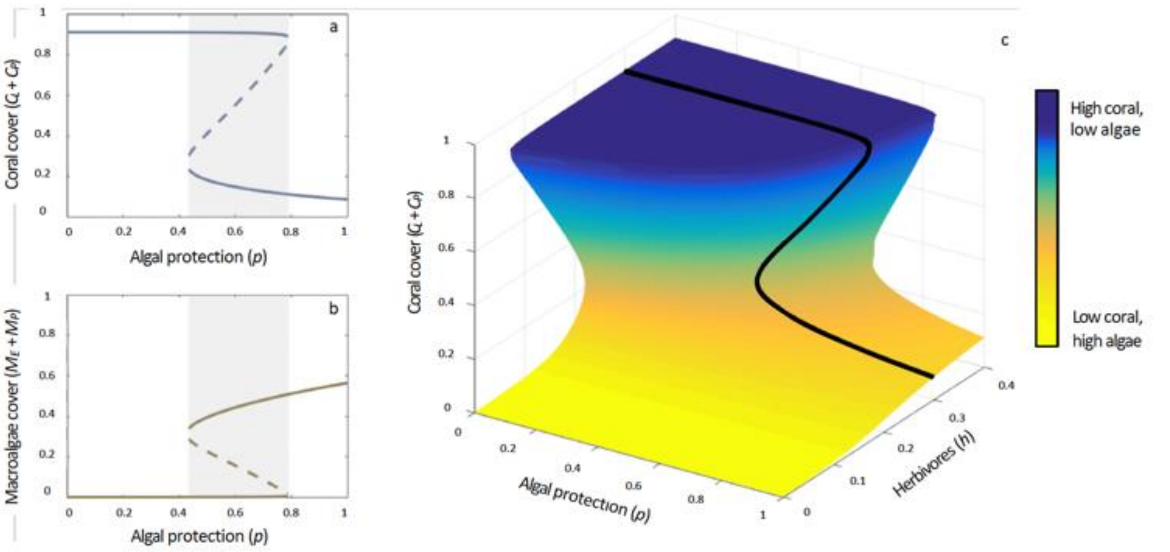


Figure 3. (a & b) Bifurcation diagrams showing (a) equilibrium cover of total live coral (C_L + C_P) and (b) total macroalgae (M_E + M_P) as a function of algal protection from herbivory. Solid lines indicate stable equilibria (i.e., values of the state variable to which the system will return after perturbations in either direction), and dotted lines indicate unstable equilibria (i.e., values of the state variable from which the system will diverge if perturbed). Equilibria were determined via numerical solving of our model equations. Shaded portions of each plot illustrate the regions of bi-stability (the range of algal protection over which coral and macroalgae are alternative stable states). (c) Response surface displaying the resultant equilibrium cover of coral at varying values of both algal protection, p, and herbivores, h. Blue shading represents high-coral equilibria, and yellow represents low-coral equilibria. The black line indicates equilibrium coral cover at the default value of herbivores but across the range of algal protection.

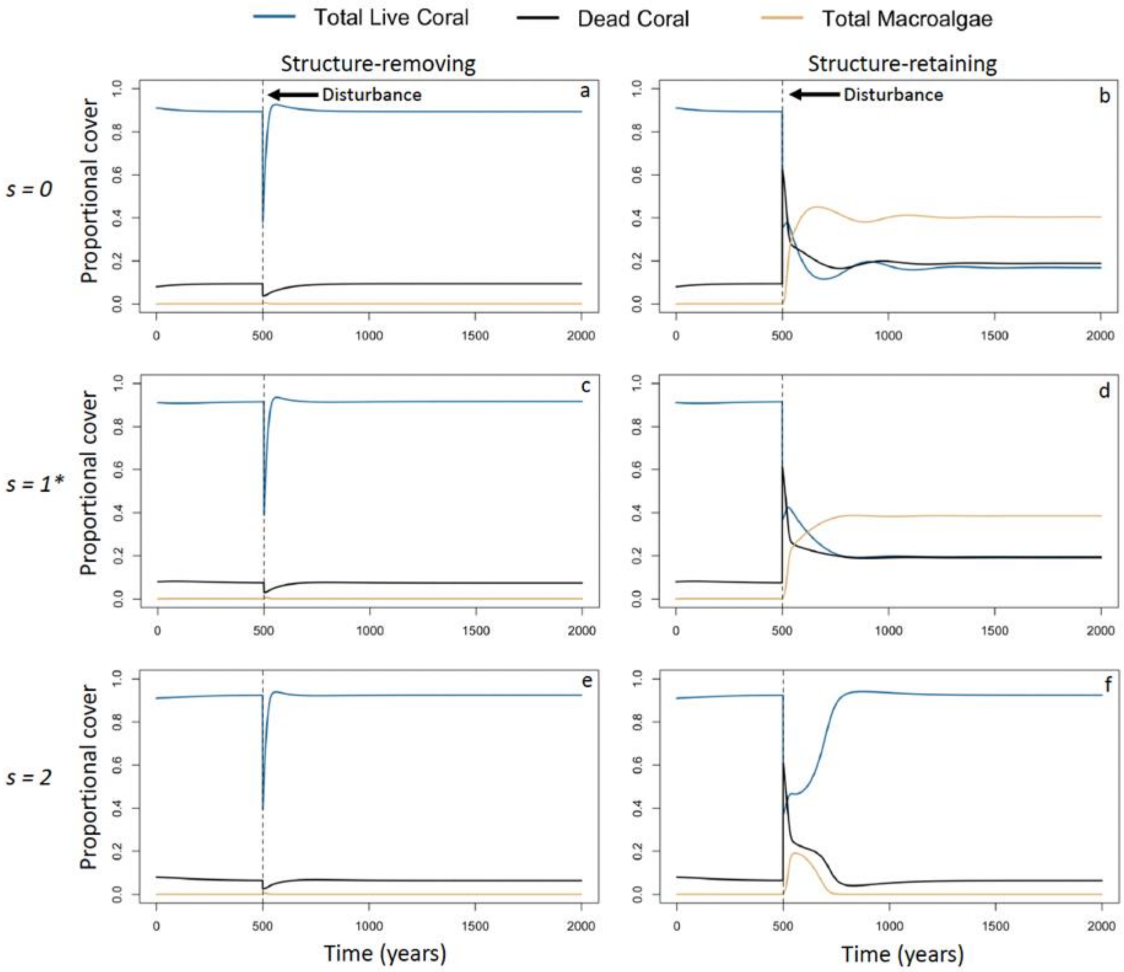


Figure 4. Time series of an initially coral-dominated community subjected to either a moderate structure-removing disturbance (a, c, e) or a moderate structure-retaining disturbance (b, d, f). Results are shown for settlement rates onto dead coral that were either to 0, 1, or 2 times the rate of settlement on open substrate (i.e., $s = 0$, 1, or 2; asterisk indicates default value). Blue lines (Total Live Coral) show combined proportional cover of live coral that grows on open substrate and dead coral ($C_L + C_P$), while brown lines (Total Macroalgae) show combined proportional cover of macroalgae that grow on open substrate and dead coral ($M_E + M_P$). In both cases, the model system was subjected to a 60% intensity disturbance (indicated by dashed vertical black lines), where 60% of all space holders were removed in (a, c, & e), and 60% of each class of live coral cover was converted to dead coral in (b, d, & f) at the time of disturbance.

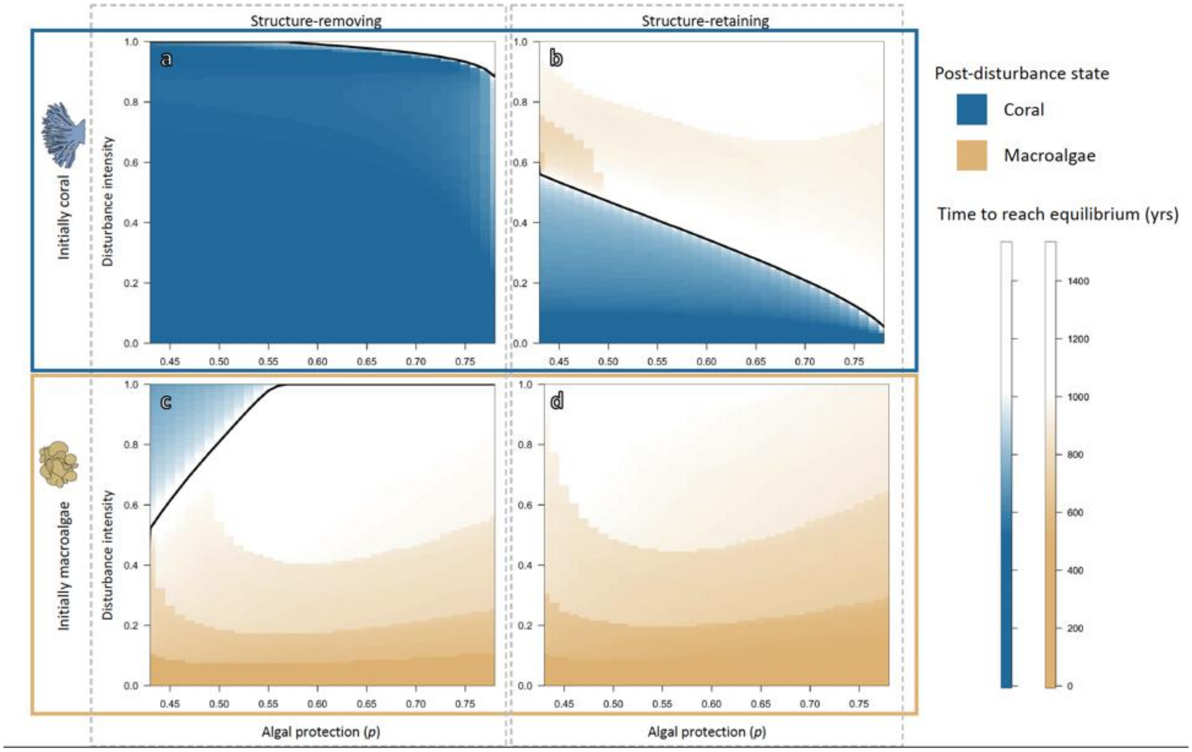


Figure 5. Equilibrium community states following structure-removing (a) and (c) and structure-retaining (b) and (d) disturbances plotted across a range of algal protection and disturbance intensity. Model outputs for initial conditions that reflect a coral-dominated state are shown in (a) and (b), while (c) and (d) show outputs for an initially macroalgae-dominated state. Blue shading depicts a coral equilibrium after disturbance and brown depicts a macroalgae equilibrium. Black lines indicate the level of disturbance required to trigger a state shift at the respective level of algal protection (the tipping point). The saturation of each color represents the time taken for the system to reach equilibrium at a given value of algal protection and disturbance intensity. The range of macroalgal protection from herbivory shown is the region of bi-stability (the range in values over which alternative stable states exist, indicated by the shaded regions in Figure 3). Output is shown for all intensities of disturbance (i.e., from no disturbance to complete mortality).

Tables

Table 1. Variable and parameter symbols, descriptions, and default values. Units for all parameters are change in proportional cover per year. Values in parentheses indicate the ranges used for sensitivity analyses.

Symbol	Description	Default value (range)
Variable		
C_L	Live coral on open substrate	
C_D	Dead coral	
C_P	Live coral on dead coral	
M_E	Exposed macroalgae	
M_P	Protected macroalgae	
S	Empty space; colonizable by coral or macroalgae	
Parameter		
g_c	Growth rate of coral	0.1 y^{-1}
g_m	Growth rate of macroalgae	0.6 y^{-1}
g_{mc}	Overgrowth rate of macroalgae onto live coral	0.06 y^{-1}
d_c	Death rate of coral	0.001 y^{-1}
d_m	Senescence rate of macroalgae	0.05 y^{-1}
e	Erosion rate of dead coral	0.01 y^{-1}
γ_c	Open settlement rate of coral	0.001 y^{-1}
s	Multiplier for rate of coral settlement onto dead coral	1 (0 – 2)
γ_m	Open settlement rate of macroalgae	0.001 y^{-1}
h	Ambient herbivory rate	0.3 (0 – 0.4) y^{-1}
p	Algal protection; degree to which ambient herbivory is reduced for protected macroalgae	0.5 (0 – 1)

SUPPLEMENTARY MATERIALS: Appendix S1

Field observations to corroborate model predictions and parameter values

Here, we show a time series of coral and macroalgae cover (Fig. S1) from the Moorea Coral Reef Long Term Ecological Research site (http://mcr.lternet.edu/) for the fore reef on the northern shore of Moorea that shows divergent recovery patterns following a cyclone (in 2010), and more recently, a mass coral bleaching event (in 2019). Following the cyclone, we observed a marked recovery of coral in which pre-disturbance coral cover was regained 5 years after the disturbance, then far exceeded pre-disturbance levels in the following years before the bleaching event. A similar trajectory is shown by our theoretical time series plot for a reef subjected to a severe structure-removing disturbance (Fig. 4a). By contrast, following the recent bleaching event, coral cover has continued to decline and macroalgae have shown a marked increase, primarily growing within dead coral structures. These patterns are consistent with our model's predictions for a reef subjected to a severe structure-retaining disturbance event (Fig. 4b).

Because previous models did not explicitly simulate cover of dead coral or integrate it as a separate substrate, we felt that the coral mortality rates used in these models were not appropriate for our model. We instead adjusted our rate for coral mortality to create a realistic amount of dead coral in our system (<10%), that is, the amount that would be present at 'equilibrium' or pre-disturbance. This value of dead coral cover is corroborated by field data from the Moorea Coral Reef Long Term Ecological Research project, which show the areal coverage of dead coral during four different years in the time series. In 2006 (the only year in the 4-year dataset before the outbreak of the Crown-of-Thorns Seastar), the island-wide mean percent cover of dead coral (i.e., across all 6 fore reef sites) was 7.1 ± 3.1%

(mean ± SD; Table S1; Adam et al. 2012). With the default value we chose for coral mortality, the percent cover of dead coral at equilibrium (in the coral-dominated state) in our model system is 7.6%, and thus closely aligns with these field observations.

Translating volumetric loss to areal loss for carbonate structures

Our estimated erosion rate of 1% per year falls within published estimates of bioerosion of calcium carbonate structures on reefs of 0 to 5% per year (Silbiger et al. 2014); however, these published rates estimate annual volumetric loss, not two-dimensional surface loss, as modeled here. We made a simple calculation (see 1-5 below) to compare how the reduction in volume of a hemisphere (a commonly used shape to estimate the volume of a coral colony; e.g., see Konh and Parry 2019, Shlesinger and van Woesik 2021) relates to a reduction in the area of a circle - the two-dimensional footprint of a hemisphere - using the change in radii from the hemisphere. We found that a 0-5% reduction in hemispheric volume translates roughly to a 0-3.3% reduction in the area of a circle with the same changes in radii:

1) Volume of a hemisphere: $100cm^3 = \frac{2\pi r^3}{3}$, radius = $3.63cm$
2) Initial, circular footprint of $100cm^3$ hemisphere: $\pi(3.63cm)^2 = 41.40cm^2$
3) Volume of hemisphere, reduced by 5%: $95cm^3 = \frac{2\pi r^3}{3}$, radius = $3.57cm$
4) Circular footprint of reduced, $95cm^3$ hemisphere: $\pi(3.57cm)^2 = 40.04cm^2$
5) % reduction of circular footprint: $\frac{Final\ - initial\ area}{initial\ area} = \frac{40.04cm^2 - 41.40cm^2}{41.40cm^2} = -0.033$,

$$-0.033 * 100 = 3.3\%$$

Thus, our estimate of a 1% annual loss in two-dimensional area of dead coral skeletons via erosion fits within the range of 0-5% found by Silbiger et al. (2014) for volumetric losses of carbonate structures.

Sensitivity analyses of other parameters – erosion rate and coral mortality

To understand how the erosion rate of dead corals interacts with the mortality rate of live corals to affect equilibrium conditions, we created response surfaces (Fig. S2) to explore the sensitivity of equilibrium coral and macroalgae cover to variation in the erosion rate of dead coral (e) and coral mortality rate (d_c). For coral mortality, we explored a range from 0 to 0.02, the lowest value that has been used in previous models. Not unexpectedly, higher erosion rates allow the system to tolerate higher rates of coral mortality. Generally, high erosion rates tend to produce coral-dominated reefs. This is because only dead coral skeletons (populated by macroalgae or not) erode, and when they erode quickly enough, the effect of this material legacy (i.e., protecting macroalgae from herbivory) is not sufficiently strong to facilitate the proliferation of macroalgae. Specifically, higher rates of erosion reduce the abundance of protected macroalgae, thereby reducing the overgrowth of live coral by that macroalgae. Importantly, this response surface shows that our model still exhibits bi-stability between coral and algae at a coral mortality rate > 10x our default rate (~0.015), or within an order of magnitude of the lowest rate used in previous models.

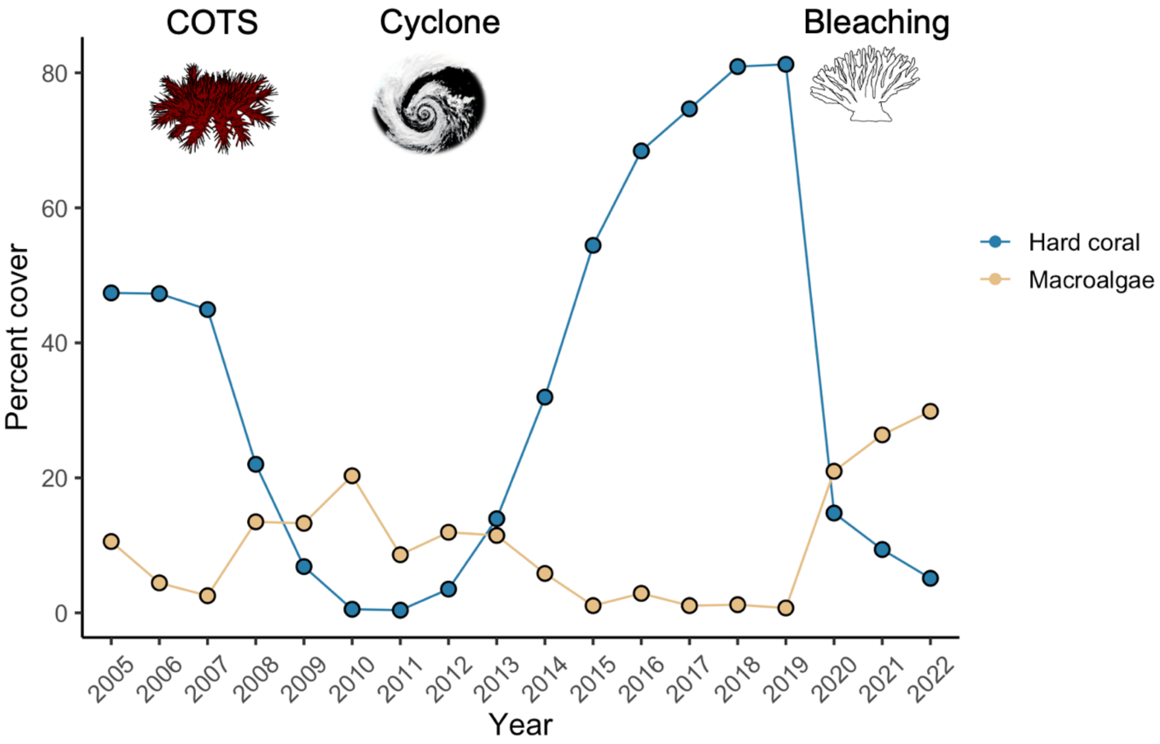


Figure S1. Time series of live coral cover (blue dots) and macroalgae cover (brown dots) following different disturbance types on the north shore fore reef of Moorea, French Polynesia. An outbreak of predatory Crown-of-Thorns Seastars occurred from 2007-2009, followed by a powerful cyclone that removed nearly all live and dead coral structure at these sites in 2010. In 2019, a marine heat wave triggered a coral bleaching event that resulted in significant coral mortality, leaving the dead skeletons intact.

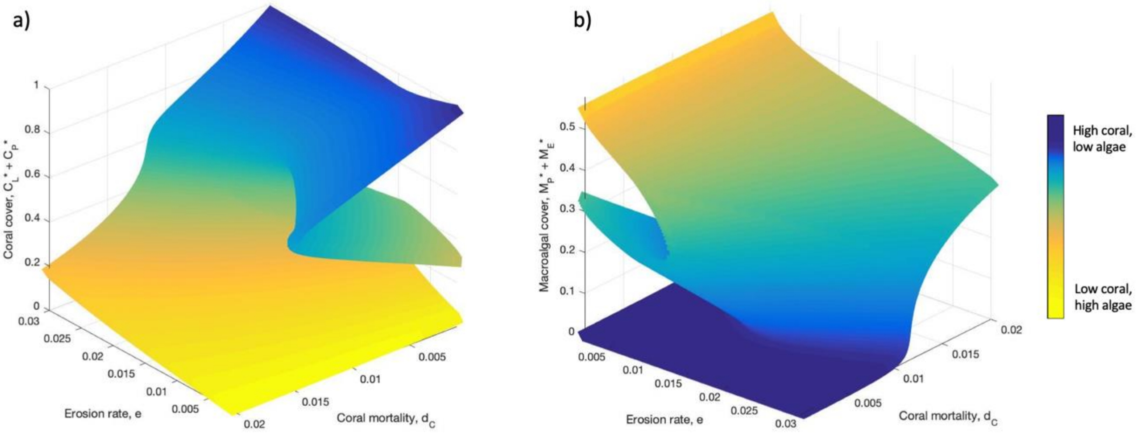
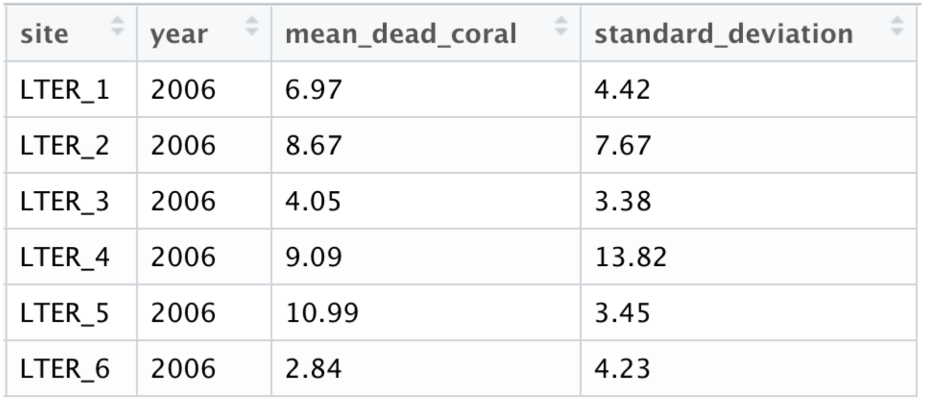


Figure S2. Response surface displaying the resultant equilibrium cover of a) live coral and b) macroalgae and at varying values of both the erosion rate of dead corals, *e*, and coral mortality, d_C. Blue shading represents high-coral, low-macroalgae equilibria, and yellow represents low-coral high, macroalgae equilibria.

Table S1. Mean cover (and standard deviation) of dead coral at 6 long term monitoring sites for the year 2006 (the only year with data on dead coral cover prior to the outbreak of predatory seastars and subsequent coral mortality).



site	year	mean_dead_coral	standard_deviation
LTER_1	2006	6.97	4.42
LTER_2	2006	8.67	7.67
LTER_3	2006	4.05	3.38
LTER_4	2006	9.09	13.82
LTER_5	2006	10.99	3.45
LTER_6	2006	2.84	4.23

SUPPLEMENTAL REFERENCES

Adam, T., A. Brooks, R. Schmitt and S. Holbrook of Moorea Coral Reef LTER. 2012. MCR LTER: Coral Reef Resilience: Live and Dead *Pocillopora* and *Acropora* Coral Colony Time Series from 2006 to 2011. knb-lter-mcr.7010.2 doi:10.6073/pasta/23157cfdedcc6522c999e593d83007c9

Carpenter, R of Environmental Data Initiative. 2022. MCR LTER: Coral Reef: Long-term Population and Community Dynamics: Benthic Algae and Other Community Components, ongoing since 2005. knb-lter-mcr.8.33 doi:doi:10.6073/pasta/69b6927cca72a5893573276c9b0dc2a0

Konh, B., and M. Parry. 2019. Design, fabrication, installation, and population of a novel fiberglass reinforced plastic coral nursery structure off the south shore of O’ahu, Hawaii. Frontiers in Marine Science 6:569.

Edmunds, P of Moorea Coral Reef LTER. 2022. MCR LTER: Coral Reef: Long-term Population and Community Dynamics: Corals, ongoing since 2005. knb-lter-mcr.4.39 doi:doi:10.6073/pasta/913b1532594fcaf02de7671ed940b4c5

Shlesinger, T., and R. van Woesik. 2021. Different population trajectories of two reef-building corals with similar life-history traits. Journal of Animal Ecology 90:1379–1389.

Silbiger, N. J., Ò. Guadayol, F. I. M. Thomas, and M. J. Donahue. 2014. Reefs shift from net accretion to net erosion along a natural environmental gradient. Marine Ecology Progress Series 515:33–44.

Chapter II. Changing disturbance regimes, material legacies, and stabilizing feedbacks: dead coral skeletons impair key recovery processes following coral bleaching

ABSTRACT

As patterns of disturbance become progressively modified by climate change, ecosystem dynamics are increasingly influenced by novel legacies left by emerging disturbance regimes. Ecosystem responses to disturbance depend on the nature of the perturbation and the ecological legacies left behind, making it critical to understand how climate-driven changes in disturbance regimes modify resilience properties of ecosystems. For coral reefs, the recent increase in marine heat waves that bleach and kill corals but leave their skeletons intact now co-occur with the historic agent of disturbance, powerful storms that kill coral and remove their skeletons. Here, we explored how the material legacy of dead coral skeletons modifies two key ecological processes that underpin coral reef resilience: the ability of herbivores to control macroalgae (spatial competitors of corals), and the replenishment of new coral colonies. Our findings revealed that the presence of structurally complex dead skeletons reduced herbivory on less preferred (unpalatable) macroalgal taxa by > 40%, but only by 10% on more preferred algae, allowing unpalatable macroalgae to reach ~ 45% cover in 2 years, whereas herbivores were able to prevent macroalgae from becoming established on adjacent reefs that lacked skeletons. Manipulation of unpalatable macroalgae cover revealed that the cover reached after one year (~ 21%) reduced recruitment of corals by 50%. The effect of skeletons on juvenile coral growth after settlement was contingent on the timing of settlement relative to the disturbance. If corals settled directly after bleaching (before macroalgae colonized), dead skeletons enhanced colony growth by 34%, but this benefit was lost if corals colonized dead skeletons a year after the disturbance once macroalgae had proliferated. These findings underscore how a material

legacy from a changing disturbance regime can alter ecosystem resilience properties by disrupting key trophic and competitive interactions that shape post-disturbance community dynamics.

INTRODUCTION

Global climate change is modifying the disturbance regimes ecosystems have historically experienced. Heightened global temperatures have brought new and more extreme forms of disturbance to the forefront, such as unprecedented droughts in terrestrial ecosystems (Dai 2013) and increasingly frequent and intense thermal stress events (marine heat waves) in marine systems (Hughes et al. 2018, Oliver et al. 2018). In turn, these are creating novel environmental settings in which ecosystem recovery trajectories take place (Ingeman et al. 2019). Both ecological theory and empirical evidence indicate that, following disturbance, community recovery is facilitated by stabilizing feedbacks from suites of ecological processes that act to maintain an ecosystem within a given state or on a given trajectory (Suding et al. 2004, Suding and Hobbs 2009, Nyström et al. 2012, Schmitt et al. 2019). However, the emergence of new disturbance regimes and the novel environmental and physical legacies they leave behind may disrupt or break these feedbacks, potentially setting in place alternative feedbacks that could erode ecosystem resilience (Kopecky et al. 2023a).

Ecological memory refers to the capacity of past events to influence current and future trajectories in ecosystems (Johnstone et al. 2016, Hughes et al. 2019, Walker et al. 2024). Material legacies, or biological materials that persist in an environment after disturbance, are a type of ecological memory that can shape post-disturbance trajectories and other resilience properties (Franklin et al. 2000, Johnstone et al. 2016, Hughes et al. 2019, Kopecky et al.

2023a, Saldaña et al. 2023). Material legacies from foundation organisms (i.e., habitat-providing species that dominate in abundance or biomass; Ellison 2019) in particular can have profound effects on important ecosystem functions and processes (Saldaña et al. 2023). For example, the leftover shells of dead bivalves can provide substrate for recruitment of new bivalves (Lenihan and Peterson 1998), while fallen tree trunks can hamper the establishment of new saplings (Swanson et al. 2011). What is less clear, however, is the degree to which material legacies of dead foundation organisms influence trophic and competitive interactions surrounding living foundation organisms, especially when those biotic interactions constitute the stabilizing feedbacks that promote the recovery of an ecosystem from a disturbance. In coral reefs, for example, top-down control of macroalgae that are superior spatial competitors of coral underpins resilience of the coral state (Holbrook et al. 2016, Adam et al. 2022) and the consumer-resource and competitive interactions involved could operate quite differently depending on whether material legacies are left in the reef environment following a disturbance. Specifically, these trophic interactions could potentially be disrupted by disturbances such as marine heat waves that kill coral colonies but leave the material legacy of intact coral skeletons (Kopecky et al. 2023b). As such, coral reefs provide an opportunity to explore how changing disturbance regimes might increase the role of material legacies and thereby modify stabilizing feedbacks that affect coral resilience (Cheal et al. 2017, Vercelloni et al. 2020, Cheung et al. 2021).

Historically, coral reefs primarily have been disturbed by wave-scouring from powerful cyclonic storms – hydrodynamic events that dislodge reef-building corals and pulverize their skeletons into rubble – that leave behind a landscape with relatively low structural complexity (Gardner et al. 2005). More recently, marine heat waves that cause coral tissues to bleach and die have increased in frequency and intensity to become major agents of mass mortality for reef-forming corals (Hughes et al. 2017, Pratchett et al. 2017, Lough et al. 2018, Vercelloni et al. 2019). On some tropical reefs, periodic boom-and-bust outbreaks of coral predators (e.g., Crown-of-Thorns Seastars, COTS) also can act as pulse disturbances that kill coral over landscape scales (Vercelloni et al. 2017). Importantly, heat waves and predator outbreaks kill corals in place and leave their structurally complex calcium carbonate skeletons intact, thus creating a fundamentally different reef landscape compared to that left by a powerful storm disturbance. Recent theory and empirical work suggest that the material legacy of a structurally complex landscape of intact dead skeletons is likely to alter key ecological processes that influence the community trajectory and functioning of the reef, and possibly the rate and extent of coral recovery (Adam et al. 2011, Kopecky et al. 2023a).

Recovery of corals following a major disturbance event is influenced by two major ecological processes: herbivory that prevents the establishment of macroalgae, and the recruitment of new coral colonies to the reef (Connell et al. 1997, Hughes et al. 2007, Ledlie et al. 2007, Adam et al. 2011, 2015, Hoey et al. 2011, Holbrook et al. 2016, 2018, Nash et al. 2016, Schmitt et al. 2022). Typically, herbivorous fishes and/or sea urchins prevent the establishment of macroalgae, a spatial competitor of coral, and maintain reef surfaces in a grazed condition suitable for coral settlement (Carpenter and Edmunds 2006, Hoey et al. 2007, Adam et al. 2015, Holbrook et al. 2016). Then, coral larvae settle on these grazed reef surfaces, grow, and ultimately replenish depleted coral populations (Connell et al. 1997, Holbrook et al. 2018). Previous studies have shown that heterogeneity of the reef substrate (e.g., cracks and crevices) and emergent, structurally complex features (e.g., coral colonies, manmade structures) can favor recruitment of coral colonists by providing shelter from predators

(Vermeij 2005, Bennett et al. 2010, Kopecky et al. 2021, Rivas et al. 2021). Similarly, these features can also protect macroalgae from herbivores (Puk et al. 2020), and therefore a tradeoff may exist where, after a disturbance, complex reef features either promote a return to the coral state or preclude coral recovery by fostering a benthic community dominated by macroalgae. The dead skeletons of branching corals likely play a similar – and possibly stronger – role as a physical refuge for young, highly vulnerable life stages of both coral and macroalgae that affords protection from consumers, but the strength and consequences of such a sheltering effect have not yet been adequately explored. As a result, the circumstances under which dead coral skeletons differentially modify key trophic (herbivory, corallivory) and competitive (coral-algae competition) interactions to promote alternative post-disturbance trajectories are not well resolved.

Here, we explored the extent, mechanisms, and contexts under which the post-disturbance material legacy of dead coral skeletons alters key ecological processes (herbivory, recruitment) and thereby disrupts the stabilizing feedbacks vital for recovery of coral following a mass coral mortality event. Using field experiments, we sought to answer a set of questions related to how dead skeletons may alter resilience of the coral state. First, we quantified how dead coral skeletons affected the removal rate of macroalgae by herbivores, including whether the level of protection afforded by skeletons varied among species of macroalgae based on their palatability / preference. Second, we assessed the capacity for dead coral skeletons to facilitate the development of macroalgal communities, and in turn, impact the initial input of coral colonists and their subsequent growth and survivorship. Further, we explored whether the timing of a coral recruitment pulse after a disturbance event influenced the effect of dead skeletons on the performance of young coral. Mechanistic knowledge of when and how dead coral skeletons alter key ecological processes will strengthen our understanding of how changing global conditions are likely to alter coral reef resilience to disturbances in the future, as well as provide useful insight for developing more effective management strategies.

METHODS

Site description

We conducted a series of field assays and experiments in the Maharepa lagoon on the north shore of Moorea, French Polynesia (17.5388° S, 149.8295° W). Moorea's shallow lagoons (1-4m depth) are characterized by patch reefs formed by live and dead colonies of mounding coral species (*Porites*) interspersed with sand and coral rubble. These patch reefs typically serve as attachment substrate for a variety of taxa of branching coral and macroalgae.

Effect of dead skeletons on removal of macroalgae by herbivorous fishes

Dead coral skeletons could physically restrict access of herbivorous fishes to macroalgae growing on the adjacent reef substrate. To assess how the presence of dead coral skeletons affected the rate at which macroalgae are removed by browsing herbivores, we deployed *in situ* a series of paired assays in which macroalgae were presented on 30 x 30 cm assay trays (made from PVC-coated, 2.5 cm^2 metal mesh fencing material) and were either fully exposed or nestled between dead coral skeletons (Fig. 1a, b). We conducted all assays on a fringing reef in the Maharepa lagoon at ~ 3 m depth. On one assay tray per pair, we attached 10 dead skeletons of similar-sized branching coral in the genus *Pocillopora* that ranged from 8-14 cm in longest diameter and 7-10 cm in height; all skeletons were sourced from specimens that were cleaned and archived in 2013 following the termination of a prior experiment where coral spat was transplanted to tiles and grown in cages for two years (see Adam et al. 2022). The dead skeletons on each tray were spaced to create 50% cover, which was the average coral cover on the fore reef of Moorea prior to a massive bleaching event in 2019 (Moorea Coral Reef LTER and Edmunds 2024) (Fig. 1a). Five small clothes pins were attached to each tray between the dead skeletons to hold the macroalgae in place below the dead coral canopy. The alternative assay tray design (Fig. 1a) simulated reef patches scoured by storm waves (i.e., had no dead skeletons), and for these we simply attached clothespins holding macroalgae to the trays in spatial layouts identical to those on the trays with dead skeletons (Fig. 1a).

The assays tested the consumption of six of the most common macroalgal taxa found in Moorea (Moorea Coral Reef LTER, and Carpenter 2023): *Dictyota* spp., *Turbinaria ornata*, *Lobophora variegata*, *Amansia* spp., *Sargassum pacificum*, and *Padina* spp. We used juvenile individuals of *Turbinaria*, as these are less physically and chemically defended than adult plants that are much less vulnerable to herbivory (Stiger et al. 2004, Davis 2018). Because the consumption of macroalgae species can vary based on herbivore communities (Sura et al. 2021) and structural and/or chemical defenses (Duffy and Hay 1994, Ryznar et al. 2023), we utilized the consumption (biomass removed) of the six taxa over 5 days in the open assays (dead skeletons absent) to identify their relative preferences by browsing herbivores.

Macroalgae used in the assays were collected from nearby lagoon sites, apart from *Lobophora*, which was collected from the adjacent fore reef where it grew in higher abundance. After collection, macroalgae were brought to a water table at the laboratory, then divided into roughly equal clumps to be distributed across the replicate assay trays. Each clump was spun in a salad spinner for 30 seconds to remove excess seawater, weighed (g), and then divided evenly amongst the five clothespins on each tray. For a single trial, we collected and deployed only a single macroalgal taxon, and we conducted two trials for each taxon (n = 8 replicate assays per taxon per treatment across two trials). During each trial, we deployed four assay trays with dead skeletons and four without, pairing each dead skeleton tray with an open tray. After five days, assays were retrieved and any algae remaining in the clothespins were re-weighed after removing excess seawater in the same manner as before. Due to variation in thallus size and density of the macroalgae we used, there were differences in initial masses across taxa. Thus, to better be able to compare among the taxa, we calculated the proportion of macroalgal biomass that was removed in each assay tray during each trial. Based on the proportion of algae removed in the open treatment, we categorized each taxon into either a More Preferred (> 90% removed) or Less Preferred (< 70% removed) group. For each taxon, we then calculated the log difference in the remaining algal biomass between dead skeleton and open assay trays for each pair (considering pairs as replicates). We used this variate in a nested ANOVA, with algal taxa nested within preference group (n = 8 pairs per taxon, n = 3 taxa per preference group), to evaluate whether the magnitude of difference in algal removal between skeleton treatments differed significantly between the More and Less Preferred algal groups (total of n = 24 pairs per preference group).

Establishment of macroalgae in the presence or absence of dead coral skeletons

To assess whether reef surfaces covered in dead coral skeletons following a mass coral bleaching event (or COTS outbreak) promote a shift to dominance by macroalgae compared to more planar, open reef surfaces that result from a powerful storm, we quantified the accumulation of macroalgae over a 2-year period on a set of paired patch reefs where we added dead coral skeletons to one member of the pair. At a mid-lagoon site ~ 400 m offshore of the site where herbivore assays described above were conducted, we selected patch reefs similar in size, depth, and height off the seafloor, then scraped any existing macroalgae off their surfaces. A 0.25 m^2 area devoid of coral (and cleared of macroalgae) was demarcated on the top surface of each patch reef. For the Open treatment (n = 10 replicate patch reefs), no further manipulation was done. For the Dead Skeleton treatment (n = 10 replicate patch reefs), we attached six dead *Pocillopora* spp. skeletons (similar in size to those used for the herbivory assays described above) to the top of each experimental patch reef with marine epoxy (Z-Spar A-788 Splash Zone Epoxy), making a ring of five skeletons encircling a central one (Fig. 1d). Skeletons had been sterilized in bleach, sun-dried and then stored protected in the dark for several years before deployment to ensure no macroalgal spores were present. Then, over a period of two years, we periodically identified and visually estimated the percent cover of all macroalgae within the demarcated 0.25 m^2 area on each of the 20 experimental patch reefs. To evaluate differences in algal coverage between Dead Skeleton and Open treatments over time, we built a general linear mixed effects model using the lme4 package in R (Bates et al. 2014) of macroalgal cover over time with structure treatment as a fixed effect and time as a random effect, using a Gaussian distribution; data were log-transformed (log(x + 1)) to increase homogeneity of variances. We then we ran a Type II Wald chi-square Analysis of Deviance test using the car package in R (Fox and Weisberg 2018) to test for a treatment effect on macroalgae cover between reefs with dead skeletons and open reef surfaces.

Effect of macroalgae on early colonization of coral

Coral recruitment overall was too low during the two-year duration of the macroalgae accumulation experiment described above to conduct quantitative statistics on recruitment patterns as a function of macroalgal cover. Therefore, to quantify how variation in the cover of macroalgal species influences early colonization of sexually-produced coral in our lagoon system, we assessed coral recruitment annually on 60 patch reefs during a 7-year-long experiment (2016-2022) conducted in the mid-lagoon ~ 300 m southwest of the site used to quantify macroalgae accumulation rates. Initially, all 60 patch reefs, which had similar surface areas (mean ± SE: 1.36 m^2 ± 0.07), were dominated by the unpalatable alga *Turbinaria ornata* (pre-manipulation mean cover ± SE cover: 43.5% ± 2.1). In July 2015, different amounts of *Turbinaria* were removed from the patch reefs as follows: (1) complete removal on 30 haphazardly-selected patch reefs, (2) 50% removal on 15 additional haphazardly-selected patch reefs, and (3) no removal (i.e., *Turbinaria* left intact) on the remaining 15 patch reefs. Cover of macroalgae was quantified on the patch reefs annually.

In addition to quantifying the cover of macroalgae in annual surveys, all living and dead coral colonies present were counted, identified to genus, and sized (diameter). Virtually all encountered colonies were species of branching coral (primarily *Pocillopora* spp. and *Acropora* spp.). Live colonies that were ≤ 4 cm in diameter in a yearly survey were considered a new recruit provided they could not be accounted for in the previous year; the ≤ 4 cm cut-off was based on measured rates of growth of branching corals in this system (Kopecky et al. 2021, Adam et al. 2022, Schmitt et al. 2022). At the initial survey in 2015, colonies ≤ 4 cm were uncommon (mean: 0.23 m^{-2}). To account for variation in surface area among the patch reefs, we analyzed the density of coral recruits (number m^{-2}) and tested whether cumulative coral recruitment differed among the three categories of macroalgal cover (Low, Medium, High) using an ANOVA; data were log-transformed (log(x+1)) to achieve homogeneity of variances.

Statistical differences among the three levels of macroalgae cover were assessed using a Tukey HSD pairwise comparison post-hoc test.

Context-dependent effects of dead skeletons on performance of coral recruits

We assessed whether the presence of dead skeletons altered growth and mortality of coral recruits relative to when skeletons were absent, and also whether any impact on performance depended on the length of time after disturbance the colonization event occurred. This exploration of the timing of coral recruitment relative to the disturbance event was based on our expectation that dead skeletons are likely to foster a more rapid development of a benthic community in which macroalgae are a major space holder (see Kopecky et al. 2023a), which would likely suppress coral performance. We conducted two consecutive experiments, each lasting one year, in which juvenile branching corals (*Pocillopora* spp.) were deployed inside the fixed arrays of dead branching coral skeletons or onto the exposed (open) reef surfaces described above. To hold juvenile corals in place, we attached five threaded bases (Falcon Tube™ caps) in a circle onto the surface of each replicate reef, either within the arrays of dead skeletons or on the exposed reef surface (Fig. 1c-f). We drilled holes into the reef, filled them with marine epoxy, and inserted a screw through the cap and into the drilled, epoxy-filled hole.

We collected juvenile colonies of *Pocillopora* spp. with a mean (± SE) diameter of 2.0 (± 0.3) cm from reefs near our experimental site. In the laboratory, corals were measured and staged for deployment while continuously immersed in seawater. Using marine epoxy, each juvenile coral was mounted on a threaded, upside-down polypropylene cylinder (cut from a 15 ml Falcon™ conical centrifuge tube that later was screwed into the threaded tube cap base affixed on the experimental reef), and labeled each cylinder with a uniquely numbered tag. We measured the longest diameter (*L*), the perpendicular diameter (*W*), and height (excluding the threaded base; *H*) of each coral, then estimated each coral's volume as an irregular hemisphere with the following formula:

$$V = \frac{2}{3}\pi\left[\left(\frac{L}{2}\right) * \left(\frac{W}{2}\right) * H\right]$$

Note that L and W in this formula are divided by two to obtain radii, while H already represents a radius and therefore is not divided by two. This metric of growth is appropriate because the shape of *Pocillopora* throughout our year-long experiments was approximately hemispherical with little to no branch development (Fig. S1). We then weighed the corals with their bases in air on a digital scale after removing excess seawater by shaking each coral 30 times by hand (each coral was out of the water for less than one minute during weighing). Corals were randomly assigned to treatments and patch reefs, transported (continuously submerged in seawater) to the field and screwed onto the threaded bases. Installing the corals in this way ensured they would be stable for the duration of the experimental period and allowed us to non-destructively retrieve them for re-measurement of individual colonies. Any coral that died within 48 hours after deployment was deemed to have done so due to handling stress, and was therefore replaced.

We tested whether the effect of dead skeletons on post-settlement performance (growth and mortality) of coral recruits depended on the elapsed time of the colonization event after the disturbance. We evaluated two post-disturbance time periods of coral recruitment: very shortly after the disturbance and prior to establishment of macroalgae (Immediate Recruitment), and 1 year later, after macroalgae had become established (Delayed Recruitment). To assess the effect of skeletons under the Immediate Recruitment scenario, we deployed the first cohort of *Pocillopora* recruits within two days of thoroughly clearing macroalgae from the patch reefs and installing the clean dead coral skeletons as described above, which ensured that neither the Open or Dead Skeleton treatments had macroalgae at the start (Fig. 1c, d). Individually numbered coral recruits were assigned haphazardly among patch reefs (50 per treatment). After one year, we retrieved the corals and measured them as described above, assessed each for signs of coral predation (i.e., excavation of the coral skeleton) and quantified the amount of live (surviving) tissue remaining on the colony. To assess if the impacts of dead skeletons differed for a 'delayed' recruitment event that occurred 1 year after a disturbance, we initiated the second experiment right after the first was terminated, with a new cohort of similarly sized *Pocillopora* recruits deployed in the same positions as in the first trial. We left intact the benthic communities that had developed naturally during the previous year (i.e., no macroalgae were cleared and no experimental plot was manipulated in any other way; Fig. 1e, f). After one year, this second cohort of coral recruits was retrieved, remeasured, assessed for signs of predation, and the amount of live tissue remaining per colony was visually estimated as before.

To ensure there was not a biased distribution of coral recruit sizes between the experimental treatments or years, we ran a two-factor ANOVA of initial coral size as a function of treatment and patch reef for each experimental year, which revealed that no main effect or interaction term was statistically significant. At the end of each 12-month experimental period, we designated only coral colonies that had > 5% living tissue remaining as having survived in order to account for a narrow band of tissue near the base of a colony that was protected from corallivory by our method of attachment. For corals designated as survivors of the cohort, we calculated two metrics of growth – change in volume and change in mass as described above – then calculated proportional changes in volume and mass to account for variation in initial coral sizes. Because of highly variable numbers of survivors (0 to 5) among patch reefs within a treatment, we found that using patch reefs as the replicate yielded unreliable values of mean colony growth because the variate (i.e., average growth of coral on a patch reef) was poorly estimated. As a consequence, we used survivors of the cohort as the replicates in two-sample t-tests to compare mean growth metrics of corals between the Dead Skeleton and Open treatments for each experiment.

For corals that did not survive the experiment (i.e., had ≤ 5% live tissue remaining), we compared the proportions of colonies that fell into two categories of mortality: those that exhibited skeletal growth before dying (positive change in volume and mass; referred to as 'dead in place'), and those that exhibited skeletal loss before dying (negative change in volume and mass; referred to as 'removal'). These categories likely reflect different agents of mortality, such as death from excavating corallivores (i.e., removal) versus death from altered local environmental conditions (i.e., dead in place) such as those arising from competition with macroalgae growing nearby. To test whether mortality type depended on the structure treatment a coral was assigned to, we ran a Pearson's Chi-square test for the (first) Immediate Recruitment trial, but, due to a relatively low number of dead colonies we used a Fisher's exact test for the (second) Delayed Recruitment trial. All statistics were conducted and visualizations were created in R (Version 4.2.3; R Core Team 2023) and R Studio (Version 2023.12.1.402; Posit Team 2024) using the Tidyverse package (Wickham et al. 2019) and color palettes from the Manu: NZ Bird Colour Palettes (Thomson 2022).

RESULTS

Effect of dead skeletons on removal of macroalgae by browsing fishes

Based on our standardized assay metric, the six taxa of macroalgae fell into two distinct groups of consumption preference by herbivores. Three taxa (*Amansia, Sargassum,* and *Padina*) had > 90% of their mass removed when presented alone and unprotected for 5 days, whereas the percentage removed for the three other taxa (*Dictyota, Turbinaria,* and *Lobophora*) was substantially lower, ranging from 59 – 67% (Fig. S2). We therefore categorized these two groups as 'More Preferred' and 'Less Preferred' macroalgae respectively.

Although the presence of dead coral skeletons reduced the average proportion of biomass removed for both More Preferred and Less Preferred macroalgae (Fig. 2a), the presumptive protection effect of skeletons differed substantially between the two groups. The relative difference in algal biomass that remained between the Dead Skeleton and Open treatments (dashed lines and double-ended arrows in Fig. 2b) was significantly greater for Less Preferred macroalgae compared to the More Preferred group (nested ANOVA: $F_{1,42} = 8.32$, $p = 0.006$; Fig. 2b). The individual taxa nested within preference groups did not differ significantly from one another ($F_{4,42} = 2.48$, $p = 0.06$). For Less Preferred algae, skeletons reduced removal on average by 43%, whereas skeletons reduced the removal of More Preferred macroalgae by only 10% (Fig. 2b), suggesting that herbivores were far less inclined or able to consume as much of a macroalga growing among coral skeletons when it was not a preferred food item.

Establishment of macroalgae in the presence or absence of dead coral skeletons

When the 2-year long benthic community development experiment was initiated, patch reefs in the Dead Skeleton and Open treatments were all devoid of macroalgae (Fig. 3a). Over the two years, reefs in the Open treatment remained almost entirely free of macroalgae (mean <

2% coverage), while those where we had affixed dead coral skeletons continuously accumulated macroalgae (effect of structure treatment: X^2 (1) = 194.71, $p < 0.001$; Fig. 3a). The mean (± SE) cover of macroalgae on reefs in the Dead Skeleton treatment was 21% (± 3%) a year after initiation of the experiment, growing to 45% cover (± 7%) two years after the simulated structure-retaining (e.g., coral bleaching) disturbance (Fig. 3a, c). As predicted from the results of our herbivore-structure assays, the composition of the macroalgal assemblage that developed at every time point in the Dead Skeleton treatment was heavily dominated by less preferred taxa (primarily *Dictyota* spp. and *Turbinaria*; Fig. 3b).

Effect of macroalgae on early colonization of coral

The 7-year long macroalgae-reduction experiment explored the effects of macroalgae – primarily unpalatable *Turbinaria* – on early colonization of coral to patch reefs. Annual quantification of macroalgae on the reefs revealed that cover on some 'thinned' and 'unmanipulated' patch reefs declined early in the 7-year period, ultimately resulting in 33 patch reefs that we classified as having low macroalgae cover throughout the study period (range: 0 – 7.5% cover), 14 categorized as having medium cover (range: 12 - 30%) and 13 designated as having high cover (range: 37 - 59%). The time-averaged mean (± SE) cover of macroalgae was 1.7% (± 0.3%) on patch reefs considered as having low algae cover, 23.3% (± 1.8%) for reefs with medium cover, and 46.4% (± 2.0%) high cover (Fig. 4). These time-averaged covers of less preferred macroalgae corresponded closely to those observed in the Dead Skeleton treatment of our macroalgae establishment experiment at the start, after 1 year, and after 2 years, respectively, whereas the Low cover treatment corresponded to the Open treatment in that experiment at all time points (Fig. 3a).

Increases in cover of less preferred macroalgae had a profoundly negative influence on early colonization (i.e., larval settlement plus early post-settlement mortality) of sexually-produced coral colonies (Fig. 4). The cumulative density of coral recruits varied significantly across the three levels of algal cover ($F_{2,57} = 13.5$; $p < 0.001$). A *post hoc* Tukey HSD pairwise comparison indicated that recruit density was significantly greater on reefs with low algal cover (4.8 ± 0.5 recruits m^{-2}) than on those with medium algal cover (2.4 ± 0.3 recruits m^{-2}) or high algal cover (1.8 ± 0.5 recruits m^{-2}), but reefs with medium and high cover were not significantly different from one another (low-high: $p < 0.001$; low-medium: $p = 0.008$; medium-high: $p = 0.256$). Thus, the recruitment rate of young coral was suppressed by 50% to 62.5% at covers of less preferred macroalgae that we observed after 1 and 2 years respectively in the Dead Skeleton treatment of our benthic development experiment.

Context-dependent effects of dead skeletons on performance of coral recruits

The effect of dead skeletons on the post-recruitment performance of young coral depended on when colonization occurred relative to the disturbance event. When coral recruitment was simulated to occur very soon after a bleaching or other skeleton-retaining disturbance event, volumetric colony growth was substantially and statistically greater for individuals that were among dead skeletons compared to recruits on open surfaces ($t_{37.5} = 2.26$, $p = 0.03$; Fig. 5a, left panel: Immediate Recruitment). Changes in mass followed a similar pattern during this experiment and were at the margin of statistical significance ($t_{41.8} = 1.92$, $p = 0.06$). In the first year when less preferred macroalgae grew in cover from 0 to ~ 21% in the Dead Skeleton treatment, corals in that treatment increased an average of 34% in volume and 24% in mass relative to corals in the Open treatment where macroalgae cover remained exceedingly low.

By contrast, this positive effect of dead skeletons on growth of young coral recruits was lost during the second year when macroalgae increased from ~ 21 to ~ 45% in the Dead Skeleton treatment. During this simulated 1-year delay in recruitment of coral (i.e., 1 year after a disturbance), changes in volume (and mass) of young coral colonies did not differ between Dead Skeleton and Open treatments (volume change: $t_{68.1} = 0.61$, $p = 0.55$; mass change: $t_{59.3} = 0.85$, $p = 0.4$; Fig. 5a, right panel: Delayed Recruitment). Furthermore, while growth of colonies in the Open treatment was similar between the Immediate Recruitment and Delayed Recruitment cohorts, colony growth in the Dead Skeleton treatment was impaired when recruitment was delayed (Fig. 5a).

The total number of corals that underwent whole-colony mortality (i.e., had ≤ 5% live tissue remaining at the end of the experiment) was nearly identical between treatments for both experiments (Fig. 5b). However, the nature of coral mortality differed by treatment consistently across the two years. In both years, a significantly higher proportion of corals that died in the Open treatment exhibited negative volume change (partial or complete skeletal removal) before dying (Pearson's Chi-square tests, Immediate Recruitment: X^2 (1) = 7.71, $p = 0.005$; Delayed Recruitment: X^2 (1) = 5.53, $p = 0.02$). This suggests a high proportion of deaths in this treatment were attributable to excavating corallivores. By contrast, the majority of corals that died in the Dead Skeleton treatment showed positive volume change before they died ('Dead in place'), with relatively few showing signs of skeletal removal (< 10% in each year; Fig. 5b).

DISCUSSION

In coral reef ecosystems, the recent rise of marine heat waves that cause massive bleaching mortality of reef-forming corals now occur along with powerful cyclonic storms that historically have been the major source of disturbance (Halford and Caley 2009, Hughes et al. 2017, 2019, Vercelloni et al. 2020, González-Barrios et al. 2023). While both of these perturbations kill coral tissue at landscape scales, intense marine heat waves leave behind a 'forest' of intact dead coral skeletons, whereas powerful cyclonic storms pulverize and remove coral skeletons to yield a more open, planar reef surface. Thus, the disturbance regime to coral reefs that began emerging in the past few decades is increasingly resulting in post-disturbance landscapes where the high structural complexity provided by the calcium carbonate skeletons of dead coral is retained until they gradually erode away (Adam et al. 2014, Hughes et al. 2017, Lough et al. 2018, Speare et al. 2022). Here, we show that two key ecological processes that influence the recovery of the coral state after a mass disturbance event – herbivory (Johns et al. 2018) and coral recruitment (Holbrook et al. 2018) – are altered by the material legacy of dead skeletons in a manner that weakens the resilience of the coral state. These findings have profound general and practical implications.

Our herbivory assays revealed two important mechanistic insights regarding how dead skeleton legacies can reduce coral resilience and promote a regime shift to macroalgae. First, dead coral skeletons reduced rates of herbivory on macroalgae, which are superior space competitors to corals (Kuffner et al. 2006, Johns et al. 2018), presumably by lowering encounter and/or consumption rates. This is similar to other studies that found macroalgae can receive protection from structurally complex reef features like cracks and crevices (Puk et al. 2020), or by growing beneath live branching coral colonies (Bennett et al. 2010). Second, we found that the protective effect of dead coral skeletons was > 4 times greater for less preferred macroalgae relative to more favored taxa, which to our knowledge, has not been explored in other systems but may be a relatively general phenomenon. This pattern, where the protection effect of a physical refuge varies with consumer preference, suggests that herbivores were far less able or inclined to consume as much of a macroalga growing between dead skeletons when the alga was a less preferred food item, which generally are less palatable taxa due to the onset of chemical and physical defenses as plants develop (Cook 2023, Cook et al. 2024). While the foraging mechanisms underlying this preference-related difference in protective effect of skeletons remains to be explored, the dynamical implications are clear: dead skeletons not only promote the establishment of macroalgae as major space holders, but they also favor a macroalgal assemblage that is more resistant to control by herbivores. This prediction was supported by our field experiment where dead coral skeletons fostered the proliferation of unpalatable taxa of macroalgae that are less vulnerable to herbivory, whereas in adjacent experimental plots that lacked skeletons, herbivores were able to keep macroalgae suppressed and maintain the reef substrate in a condition that is invasible by coral (i.e., closely cropped turf algae).

Results of our community trajectory experiment align with recently developed theory that suggests when herbivory is sufficiently impaired by dead coral, a skeleton-retaining disturbance can both shift the system to a region of state space where bistability of coral and macroalgae is possible, as well as flip the community into the macroalgae stability basin without crossing a bifurcation tipping point in the level of herbivory (Kopecky et al. 2023a). Models of disturbance to coral reefs that did not explicitly consider the influence of material legacies (Briggs et al. 2018) revealed that when more vulnerable, young stages of macroalgae can grow to the less vulnerable adult stage, a mass coral mortality event or change in herbivory can trigger a regime shift to macroalgae because stage-structured vulnerability of macroalgae promotes hysteresis in the underlying relationship between herbivore biomass and macroalgae. Theoretical explorations of the effects of fishing of herbivores in this model system revealed that harvesting patterns can further trap the benthic community in a macroalgal state, either from the movement pattern of fishers across the reefscape (Rassweiler et al. 2022) or by fisher selectivity of browsers that consume mature macroalgae relative to grazers that do not (Cook 2023). With respect to models that compared structure-removing and structure-retaining disturbances on coral reefs, Kopecky et al. (2023a) found that the physical refuge afforded by dead skeletons increased the probability of an abrupt shift to a macroalgal stability basin by lowering the consumption rate on vulnerable stages for a given biomass of herbivores. Results of our skeleton manipulation experiment conformed with the dynamical prediction of the Kopecky et al. (2023a) model, while our herbivore assays provided mechanistic support that the outcome of the model and our experiment arose from macroalgae gaining an added measure of protection from dead skeletons.

Our findings also suggest that, in addition to enhancing throughput of vulnerable life stages of macroalgae that can trigger and help maintain a regime shift to macroalgae, dead skeleton legacies can generate another stabilizing feedback that can strengthen resilience of the macroalgal state once it arises, even after skeletons eventually erode away. In our study system, dead skeletons altered herbivore foraging behavior in a manner that promoted the establishment of less preferred macroalgal taxa. In general, herbivore preference commonly reflects palatability, where reduced palatability typically is achieved by a proportionately greater investment by a plant in metabolically expensive defenses that deter herbivores at the cost of competitive ability (Hems and Mattson 1992). Cook (2023) found that this tradeoff paradigm applied to the algae in our Moorea study system. Adults of less preferred macroalgae such as *Turbinaria*, which develop effective chemical and structural defenses as they mature, often provide an associational defense for more vulnerable life stages and taxa (Duffy and Hay 1994, Roff et al. 2015, Davis 2018, Sura et al. 2021, Ryznar et al. 2023). Field studies have shown that once established, the associational refuge that adults provide younger, more vulnerable life stages creates a positive feedback that reinforces a highly resilient community of unpalatable macroalgae over multiple population turnovers (Davis 2018, Schmitt et al. 2019, 2022). Thus, our mechanistic findings suggest that compared to a cyclonic storm, the material legacy of dead coral skeletons left by a marine heat wave can generate multiple feedbacks that both increase the probability of a coral-to-macroalgae regime shift and reduce the likelihood it can be readily reversed.

With respect to the recruitment of coral to a benthic community where macroalgae is a major space holder, results of our *Turbinaria* removal experiment were similar to those reported by several others, namely that macroalgae can greatly suppress settlement and early recruitment of corals (Kuffner et al. 2006, Vermeij et al. 2009, Johns et al. 2018, Bulleri et al. 2018, Adam et al. 2022). However, our work here adds an important new dimension. We found that compared to open reef surfaces left by a skeleton-removing disturbance, reefs where dead coral skeletons remained after a disturbance were rapidly colonized by macroalgae and reached a cover that substantially suppressed coral recruitment in about a year. In our experiment, cover of (unpalatable) macroalgae in plots with dead skeletons increased from 0 to ~ 21% in 1 year, reaching ~ 45% after 2 years, whereas macroalgae were unable to colonize and proliferate on adjacent cleared plots that lacked skeletons. Our coral recruitment experiment revealed that patch reefs with the cover of macroalgae attained in just 12 months after a skeleton-retaining disturbance (i.e., ~21%) reduced colonization of sexually-produced coral by half relative to experimental patch reefs with little or no macroalgae (also see Schmitt et al. 2022). Following a simulated storm disturbance to patch reefs in Moorea, Schmitt et al. (2022) quantified how close ambient herbivory was to the level where control of macroalgae was lost. They found that ambient herbivory prevented the establishment of macroalgae on their (skeleton-free) plots over the 5-year duration of their study, and that ambient herbivory had to be reduced by > 50% before macroalgae was able to proliferate (Schmitt et al. 2022). Here we also found that ambient herbivory was sufficient to prevent macroalgae from becoming established on plots in our Open (no dead coral) disturbance treatment for the 2-year duration of our study; by contrast, that same ambient biomass of grazing and browsing herbivores was not sufficient to prevent the rapid establishment and proliferation of macroalgae in our Dead Skeleton treatment. This indicates that the dead skeleton legacy did not just increase the precariousness of the coral-invasible state, it moved the system past the herbivory switch-point to macroalgae. Thus, unlike after a storm disturbance, there likely will be a much shorter time window for coral to recruit after a mass bleaching mortality event before priority effects from macroalgae greatly impede the input rate of coral propagules.

Our exploration of how the timing of coral recruitment following a disturbance event influenced post-recruitment performance of young coral revealed two important insights. First, the effect of dead skeletons on young coral performance depended on the timing of arrival of coral recruits, that is, whether or not it occurred very soon after the disturbance in the relatively short period before macroalgae had become firmly established. Coral recruits that were associated with dead skeletons before macroalgae became a major space holder had a substantial (~ 24-34%) colony growth advantage over recruits on adjacent, cleared surfaces, which likely arose from a protective effect of dead skeletons shielding young corals from predators. However, there was not a positive effect of skeletons on colony growth when coral recruitment occurred a year after a disturbance when macroalgae had become established, likely because any protective advantage was offset by competition with established macroalgae. Herbivores typically mitigate coral-algae competition, but in the absence of such top-down control, priority effects can result in alternate community pathways depending on the sequence of arrival of corals and macroalgae (Adam et al. 2022). Our findings suggest that the effect of dead skeletons in hindering top-down control of macroalgae produces a condition where priority effects between corals and macroalgae could result in alternative trajectories of the benthic community. As such, this adds an element of stochastic uncertainty in the recovery of coral following a mass bleaching mortality event that is much less likely after a storm disturbance.

The second important insight regarding the effect of the material legacy on post-recruitment performance was that the major agent of mortality likely differed for coral growing among relative to far away from dead skeletons. Compared to recruits associated with dead skeletons, young corals that died on fully exposed reef surfaces more commonly had pieces of their skeletons missing in a manner characteristic of excavating corallivory (Rotjan and Lewis 2008). This contrasted with the pattern for young corals associated with dead skeletons; nearly all recruits that failed to survive the year within the Dead Skeleton treatment had gained colony volume and mass before dying, suggesting their mortality might be due to some form of neighborhood competition with the macroalgae growing within and between the dead skeletons. Taken together, our results suggest that if corals recruit in the short window after a marine heat wave leaves behind dead skeletons and before macroalgae begins to proliferate, the recruits may be able to more quickly grow to sizes at which they are much less vulnerable to predation and can better compete with or perhaps suppress macroalgae (Adam et al. 2022). On the whole, however, our findings revealed that the material legacy of dead skeletons tends to alter trophic and competitive interactions in a manner that weakens resilience of the coral state and promotes a persistent regime shift to macroalgae.

Material legacies need not weaken resilience of the original community. Indeed, the disturbance legacy of dead foundation organisms can bolster resilience and give rise to stabilizing feedbacks following a mass mortality event. For example, after boom-and-bust pest outbreaks and drought, intact dead tree roots act to stabilize soils, prevent erosion, and facilitate the establishment of new saplings. When trees are instead uprooted, erosivity of soils increases, setting in place an alternate feedback that degrades soil conditions such that new trees cannot colonize (Flores et al. 2020). Similarly, dredging events that remove oyster shells from oyster reefs or storms that rip away the rhizomes of seagrass beds can render the seabed loose and unstable, preventing recolonization by the respective foundation organisms and trapping the system in a degraded state (Lenihan and Peterson 1998, Oprandi et al. 2020). These examples, along with the findings we present here, underscore the powerful influence material legacies of foundation organisms can have on ecosystem stability following disturbance, but also highlight the stark context-dependency of their roles across disparate ecosystems.

In both terrestrial and marine systems, altered trophic interactions such as between herbivores and vegetation can lead to novel feedbacks that suppress recovery and trigger shifts to alternative, degraded ecosystem states that are highly resistant to restoration efforts (Suding et al. 2004). For example, top-down release of herbivores can lead to unconstrained grazing, like deer that selectively consume saplings in woody riparian systems (Opperman and Merenlender 2000) or herbivorous urchins that decimate kelp forests (Filbee-Dexter and Scheibling 2014), in either case locking these systems in a degraded state. Our study is, to the best of our knowledge, one of the first to show the potential for this phenomenon to be driven by the presence of a material legacy, illustrating the mechanisms and feedbacks that weaken resilience of the coral state and strengthen that of macroalgae. When alternative stable domains exist in an environment, identifying the mechanisms that maintain alternative states provides vital knowledge of the specific feedbacks that need to be broken to elicit favorable outcomes from conservation or other management efforts (Suding et al. 2004, Briggs et al. 2018). As new disturbance regimes emerge from globally changing climate conditions, it is imperative that we more fully understand how novel material and information legacies they produce modify ecosystem dynamics and resilience properties (Franklin et al. 2000, Graham and Nash 2013, Johnstone et al. 2016, Hughes et al. 2019, Turner et al. 2020, Saldaña et al. 2023).

REFERENCES

Adam, T. C., A. J. Brooks, S. J. Holbrook, R. J. Schmitt, P. J. Edmunds, L. Washburn, and G. Bernardi. 2014. How will coral reef fish communities respond to climate-driven disturbances? Insight from landscape-scale perturbations. Oecologia 176:285–296.

Adam, T. C., D. E. Burkepile, B. I. Ruttenberg, and M. J. Paddack. 2015. Herbivory and the resilience of Caribbean coral reefs: knowledge gaps and implications for management. Marine Ecology Progress Series 520:1–20.

Adam, T. C., S. J. Holbrook, D. E. Burkepile, K. E. Speare, A. J. Brooks, M. C. Ladd, A. A. Shantz, R. Vega Thurber, and R. J. Schmitt. 2022. Priority effects in coral–macroalgae interactions can drive alternate community paths in the absence of top-down control. Ecology 103:e3831.

Adam, T. C., R. J. Schmitt, S. J. Holbrook, A. J. Brooks, P. J. Edmunds, R. C. Carpenter, and G. Bernardi. 2011. Herbivory, connectivity, and ecosystem resilience: Response of a coral reef to a large-scale perturbation. PLoS ONE 6:e23717.

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2014. Fitting linear mixed-effects models using lme4. arXiv. arXiv preprint arXiv:1406.5823.

Bennett, S., A. Vergés, and D. R. Bellwood. 2010. Branching coral as a macroalgal refuge in a marginal coral reef system. Coral Reefs 29:471–480.

Briggs, C. J., T. C. Adam, S. J. Holbrook, and R. J. Schmitt. 2018. Macroalgae size refuge from herbivory promotes alternative stable states on coral reefs. PLoS ONE 13:e0202273.

Bulleri, F., L. Thiault, S. C. Mills, M. M. Nugues, E. M. Eckert, G. Corno, and J. Claudet. 2018. Erect macroalgae influence epilithic bacterial assemblages and reduce coral recruitment. Marine Ecology Progress Series 597:65–77.

Carpenter, R. C., and P. J. Edmunds. 2006. Local and regional scale recovery of *Diadema* promotes recruitment of scleractinian corals. Ecology Letters 9:271–280.

Cheal, A.J., MacNeil, M.A., Emslie, M.J. and Sweatman, H., 2017. The threat to coral reefs from more intense cyclones under climate change. Global Change Biology 23: 1511-1524.

Cheung, M.W., Hock, K., Skirving, W. and Mumby, P.J., 2021. Cumulative bleaching undermines systemic resilience of the Great Barrier Reef. Current biology 31: 5385-5392.

Connell, J. H., T. P. Hughes, and C. C. Wallace. 1997. A 30-year study of coral abundance, recruitment, and disturbance at several scales in space and time. Ecological Monographs 67:461–488.

Cook, D. T. 2023. Processes that promote resilience of coral reef systems: How dynamics of fishing and herbivory alter coral-algal interactions. Ph.D. dissertation, University of California Santa Barbara, CA.

Cook, D. T., R. J. Schmitt, S. J. Holbrook, and H. V. Moeller. 2024. Modeling the effects of selectively fishing key functional groups of herbivores on coral resilience. Ecosphere 15(1): e4749.

Dai, A. 2013. Increasing drought under global warming in observations and models. Nature Climate Change 3:52–58.

Davis, S. L. 2018. Associational refuge facilitates phase shifts to macroalgae in a coral reef ecosystem. Ecosphere 9:e02272.

Duffy, J. E., and M. E. Hay. 1994. Herbivore resistance to seaweed chemical defense: The roles of mobility and predation risk. Ecology 75:1304–1319.

Ellison, A. M. 2019. Foundation species, non-trophic interactions, and the value of being common. iScience 13:254–268.

Filbee-Dexter, K., and R. E. Scheibling. 2014. Sea urchin barrens as alternative stable states of collapsed kelp ecosystems. Marine Ecology Progress Series 495:1–25.

Flores, B. M., A. Staal, C. C. Jakovac, M. Hirota, M. Holmgren, and R. S. Oliveira. 2020. Soil erosion as a resilience drain in disturbed tropical forests. Plant and Soil 450:11–25.

Fox, J., and S. Weisberg. 2018. An R Companion to Applied Regression. Sage Publications, Inc. Los Angeles CA. 608 p.

Franklin, J. F., D. Lindenmayer, J. A. MacMahon, A. McKee, J. Magnuson, D. A. Perry, R. Waide, and D. Foster. 2000. Threads of continuity: There are immense differences between even-aged silvicultural disturbances (especially clearcutting) and natural disturbances, such as windthrow, wildfire, and even volcanic eruptions. Conservation in Practice 1:8–17.

Gardner, T. A., I. M. Côté, J. A. Gill, A. Grant, and A. R. Watkinson. 2005. Hurricanes and Caribbean coral reefs: impacts, recovery patterns, and role in long-term decline. Ecology 86:174–184.

Graham, N. A. J., and K. L. Nash. 2013. The importance of structural complexity in coral reef ecosystems. Coral Reefs 32:315-326.

González-Barrios, F.J., Estrada-Saldívar, N., Pérez-Cervantes, E., Secaira-Fajardo, F. and Álvarez-Filip, L., 2023. Legacy effects of anthropogenic disturbances modulate dynamics in the world's coral reefs. Global Change Biology 29:3285-3303.

Halford, A.R. and Caley, M.J., 2009. Towards an understanding of resilience in isolated coral reefs. Global Change Biology 15: 3031-3045.

Herms, D. A., and W. J. Mattson. 1992. The dilemma of plants: To grow or defend. The Quarterly Review of Biology 67:283–335.

Hoey, A. S., M. S. Pratchett, and C. Cvitanovic. 2011. High macroalgal cover and low coral recruitment undermines the potential resilience of the world's southernmost coral reef assemblages. PLoS ONE 6(10):e25824.

Holbrook, S. J., T. C. Adam, P. J. Edmunds, R. J. Schmitt, R. C. Carpenter, A. J. Brooks, H. S. Lenihan, and C. J. Briggs. 2018. Recruitment drives spatial variation in recovery rates of resilient coral reefs. Scientific Reports 8:7338.

Holbrook, S. J., R. J. Schmitt, T. C. Adam, and A. J. Brooks. 2016. Coral reef resilience, tipping points and the strength of herbivory. Scientific Reports 6:35817.

Hughes, T. P., M. J. Rodrigues, D. R. Bellwood, D. Ceccarelli, O. Hoegh-Guldberg, L. McCook, N. Moltschaniwskyj, M. S. Pratchett, R. S. Steneck, and B. Willis. 2007. Phase shifts, herbivory, and the resilience of coral reefs to climate change. Current Biology 17:360–365.

Hughes, T. P., J. T. Kerry, M. Álvarez-Noriega, J. G. Álvarez-Romero, K. D. Anderson, A. H. Baird, R. C. Babcock, M. Beger, D. R. Bellwood, R. Berkelmans, T. C. Bridge, I. R. Butler, M. Byrne, N. E. Cantin, S. Comeau, S. R. Connolly, G. S. Cumming, S. J. Dalton, G. Diaz-Pulido, C. M. Eakin, W. F. Figueira, J. P. Gilmour, H. B. Harrison, S. F. Heron, A. S. Hoey, J.-P. A. Hobbs, M. O. Hoogenboom, E. V. Kennedy, C. Kuo, J. M. Lough, R. J. Lowe, G. Liu, M. T. McCulloch, H. A. Malcolm, M. J. McWilliam, J. M. Pandolfi, R. J. Pears, M. S. Pratchett, V. Schoepf, T. Simpson, W. J. Skirving, B.

Sommer, G. Torda, D. R. Wachenfeld, B. L. Willis, and S. K. Wilson. 2017. Global warming and recurrent mass bleaching of corals. Nature 543:373–377.

Hughes, T. P., J. T. Kerry, A. H. Baird, S. R. Connolly, A. Dietzel, C. M. Eakin, S. F. Heron, A. S. Hoey, M. O. Hoogenboom, G. Liu, M. J. McWilliam, R. J. Pears, M. S. Pratchett, W. J. Skirving, J. S. Stella, and G. Torda. 2018. Global warming transforms coral reef assemblages. Nature 556:492–496.

Hughes, T. P., J. T. Kerry, S. R. Connolly, A. H. Baird, C. M. Eakin, S. F. Heron, A. S. Hoey, M. O. Hoogenboom, M. Jacobson, G. Liu, M. S. Pratchett, W. Skirving, and G. Torda. 2019. Ecological memory modifies the cumulative impact of recurrent climate extremes. Nature Climate Change 9:40–43.

Ingeman, K. E., J. F. Samhouri, and A. C. Stier. 2019. Ocean recoveries for tomorrow's Earth: Hitting a moving target. Science 363:eaav1004.

Johns, K. A., M. J. Emslie, A. S. Hoey, K. Osborne, M. J. Jonker, and A. J. Cheal. 2018. Macroalgal feedbacks and substrate properties maintain a coral reef regime shift. Ecosphere 9:e02349.

Johnstone, J. F., C. D. Allen, J. F. Franklin, L. E. Frelich, B. J. Harvey, P. E. Higuera, M. C. Mack, R. K. Meentemeyer, M. R. Metz, G. L. Perry, T. Schoennagel, and M. G. Turner. 2016. Changing disturbance regimes, ecological memory, and forest resilience. Frontiers in Ecology and the Environment 14:369–378.

Kopecky, K. L., D. T. Cook, R. J. Schmitt, and A. C. Stier. 2021. Effects of corallivory and coral colony density on coral growth and survival. Coral Reefs 40:283–288.

Kopecky, K. L., A. C. Stier, R. J. Schmitt, S. J. Holbrook, and H. V. Moeller. 2023a. Material legacies can degrade resilience: Structure-retaining disturbances promote regime shifts on coral reefs. Ecology 104:e4006.

Kopecky, K. L., G. Pavoni, E. Nocerino, A. J. Brooks, M. Corsini, F. Menna, J. P. Gallagher, A. Capra, C. Castagnetti, P. Rossi, A. Gruen, F. Neyer, A. Muntoni, F. Ponchio, P. Cignoni, M. Troyer, S. J. Holbrook, and R. J. Schmitt. 2023b. Quantifying the loss of coral from a bleaching event using underwater photogrammetry and AI-assisted image segmentation. Remote Sensing 15:4077.

Kuffner, I. B., L. J. Walters, M. A. Becerro, V. J. Paul, R. Ritson-Williams, and K. S. Beach. 2006. Inhibition of coral recruitment by macroalgae and cyanobacteria. Marine Ecology Progress Series 323:107–117.

Ledlie, M. H., N. A. J. Graham, J. C. Bythell, S. K. Wilson, S. Jennnings, N. V. C. Polunin, and J. Hardcastle. 2007. Phase shifts and the role of herbivory in the resilience of coral reefs. Coral Reefs 26:641–653.

Lenihan, H. S., and C. H. Peterson. 1998. How habitat degradation through fishery disturbance enhances impacts of hypoxia on oyster reefs. Ecological Applications 8:128–140.

Lough, J. M., K. D. Anderson, and T. P. Hughes. 2018. Increasing thermal stress for tropical coral reefs: 1871–2017. Scientific Reports 8:6079.

Moorea Coral Reef LTER, and P. Edmunds. 2024. MCR LTER: Coral Reef: Long-term population and community dynamics: Corals, ongoing since 2005 ver 40. Environmental Data Initiative.

Moorea Coral Reef LTER, and R. Carpenter. 2023. MCR LTER: Coral reef: Long-term population and community dynamics: Benthic algae and other community components, ongoing since 2005 ver 36. Environmental Data Initiative.

Nash, K. L., N. A. J. Graham, S. Jennings, S. K. Wilson, and D. R. Bellwood. 2016. Herbivore cross-scale redundancy supports response diversity and promotes coral reef resilience. Journal of Applied Ecology 53:646-655.

Nyström, M., A. V. Norström, T. Blenckner, M. de la Torre-Castro, J. S. Eklöf, C. Folke, H. Österblom, R. S. Steneck, M. Thyresson, and M. Troell. 2012. Confronting feedbacks of degraded marine ecosystems. Ecosystems 15:695–710.

Oliver, E. C. J., M. G. Donat, M. T. Burrows, P. J. Moore, D. A. Smale, L. V. Alexander, J. A. Benthuysen, M. Feng, A. Sen Gupta, A. J. Hobday, N. J. Holbrook, S. E. Perkins-Kirkpatrick, H. A. Scannell, S. C. Straub, and T. Wernberg. 2018. Longer and more frequent marine heatwaves over the past century. Nature Communications 9:1324.

Opperman, J. J., and A. M. Merenlender. 2000. Deer herbivory as an ecological constraint to restoration of degraded riparian corridors. Restoration Ecology 8:41–47.

Oprandi, A., L. Mucerino, F. De Leo, C. N. Bianchi, C. Morri, A. Azzola, F. Benelli, G. Besio, M. Ferrari, and M. Montefalcone. 2020. Effects of a severe storm on seagrass meadows. Science of The Total Environment 748:141373.

Posit Team. 2024. RStudio: Integrated Development Environment for R. Posit Software, PBC, Boston, MA.

Pratchett, M. S., C. F. Caballes, J. C. Wilmes, S. Matthews, C. Mellin, H. P. A. Sweatman, L. E. Nadler, J. Brodie, C. A. Thompson, J. Hoey, A. R. Bos, M. Byrne, V. Messmer, S. A. V. Fortunato, C. C. M. Chen, A. C. E. Buck, R. C. Babcock, and S. Uthicke. 2017. Thirty years of research on Crown-of-Thorns Starfish (1986–2016): Scientific advances and emerging opportunities. Diversity 9:41.

Puk, L. D., A. Marshell, J. Dwyer, N. R. Evensen, and P. J. Mumby. 2020. Refuge-dependent herbivory controls a key macroalga on coral reefs. Coral Reefs 39:953-965.

R Core Team. 2023. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rassweiler, A., S. D. Miller, S. J. Holbrook, M. Lauer, M. A. Strother, S. E. Lester, T. C. Adam, J. Wencélius, and R. J. Schmitt. 2022. How do fisher responses to macroalgal overgrowth influence the resilience of coral reefs? Limnolology and Oceanography 67:S365-S377.

Rivas, N., D. Hesley, M. Kaufman, J. Unsworth, M. D'Alessandro, and D. Lirman. 2021. Developing best practices for the restoration of massive corals and the mitigation of predation impacts: influences of physical protection, colony size, and genotype on outplant mortality. Coral Reefs 40:1227–1241.

Roff, G., C. Doropoulos, M. Zupan, A. Rogers, R. S. Steneck, Y. Golbuu, and P. J. Mumby. 2015. Phase shift facilitation following cyclone disturbance on coral reefs. Oecologia 178:1193–1203.

Rotjan, R. D., and S. M. Lewis. 2008. Impact of coral predators on tropical reefs. Marine Ecology Progress Series 367:73–91.

Ryznar, E. R., L. L. Smith, B. A. Hà, S. R. Grier, and P. Fong. 2023. Functional trait variability supports the use of mean trait values and identifies resistance trade-offs for marine macroalgae. Journal of Ecology 111:2049–2063.

Saldaña, P. H., C. Angelini, M. D. Bertness, and A. H. Altieri. 2023. Dead foundation species drive ecosystem dynamics. Trends in Ecology & Evolution 39:294-305.

Schmitt, R. J., S. J. Holbrook, A. J. Brooks, and T. C. Adam. 2022. Evaluating the precariousness of coral recovery when coral and macroalgae are alternative basins of attraction. Limnology and Oceanography 67:S285–S297.

Schmitt, R. J., S. J. Holbrook, S. L. Davis, A. J. Brooks, and T. C. Adam. 2019. Experimental support for alternative attractors on coral reefs. Proceedings of the National Academy of Sciences 116:4372–4381.

Speare, K. E., T. C. Adam, E. M. Winslow, H. S. Lenihan, and D. E. Burkepile. 2022. Size-dependent mortality of corals during marine heatwave erodes recovery capacity of a coral reef. Global Change Biology 28:1342–1358.

Stiger, V., E. Deslandes, and C. E. Payri. 2004. Phenolic contents of two brown algae, *Turbinaria ornata* and *Sargassum mangarevense* on Tahiti (French Polynesia): interspecific, ontogenic and spatio-temporal variations. Botanica Marina 47:402–409.

Suding, K. N., K. L. Gross, and G. R. Houseman. 2004. Alternative states and positive feedbacks in restoration ecology. Trends in Ecology & Evolution 19:46–53.

Suding, K. N., and R. J. Hobbs. 2009. Threshold models in restoration and conservation: a developing framework. Trends in Ecology & Evolution 24:271–279.

Sura, S. A., N. E. Molina, D. T. Blumstein, and P. Fong. 2021. Selective consumption of macroalgal species by herbivorous fishes suggests reduced functional complementarity on a fringing reef in Moorea, French Polynesia. Journal of Experimental Marine Biology and Ecology 536:151508.

Swanson, M. E., J. F. Franklin, R. L. Beschta, C. M. Crisafulli, D. A. DellaSala, R. L. Hutto, D. B. Lindenmayer, and F. J. Swanson. 2011. The forgotten stage of forest succession: early-successional ecosystems on forest sites. Frontiers in Ecology and the Environment 9:117–125.

Thomson, G. 2022. Manu: NZ Bird Colour Palettes. R package version 0.0.2, https://github.com/G-Thomson/Manu.

Turner, M. G., W. J. Calder, G. S. Cumming, T. P. Hughes, A. Jentsch, S. LaDeau, T. M. Lenton, B. N. Shuman, M. R. Turetsky, Z. Ratajczak, J. W. Williams, A. P. Williams, and S. R. Carpenter. 2020. Climate change, ecosystems and abrupt change: science priorities. Philosophical Transactions of the Royal Society B 375:20190105.

Vercelloni, J., M. J. Caley, and K. Mengersen. 2017. Crown-of-thorns starfish undermine the resilience of coral populations on the Great Barrier Reef. Global Ecology and Biogeography 26: 846–853.

Vercelloni, J., Kayal, M., Chancerelle, Y. and Planes, S., 2019. Exposure, vulnerability, and resiliency of French Polynesian coral reefs to environmental disturbances. Scientific Reports 9: 1027.

Vercelloni, J., Liquet, B., Kennedy, E.V., González-Rivero, M., Caley, M.J., Peterson, E.E., Puotinen, M., Hoegh-Guldberg, O. and Mengersen, K., 2020. Forecasting intensifying disturbance effects on coral reefs. Global Change Biology 26: 2785-2797.

Vermeij, M. J. A. 2005. Substrate composition and adult distribution determine recruitment patterns in a Caribbean brooding coral. Marine Ecology Progress Series 295:123–133.

Vermeij, M. J. A., J. E. Smith, C. M. Smith, R. Vega Thurber, and S. A. Sandin. 2009. Survival and settlement success of coral planulae: independent and synergistic effects of macroalgae and microbes. Oecologia 159:325–336.

Walker, A.S., Kratochwill, C.A. and van Woesik, R., 2024. Past disturbances and local conditions influence the recovery rates of coral reefs. Global Change Biology 30: 17112.

Wickham, H., M. Averick, J. Bryan, W. Chang, L. D. McGowan, R. François, G. Grolemund, A. Hayes, L. Henry, J. Hester, M. Kuhn, T. L. Pedersen, E. Miller, S. M. Bache, K. Müller, J. Ooms, D. Robinson, D. P. Seidel, V. Spinu, K. Takahashi, D. Vaughan, C. Wilke, K. Woo, and H. Yutani. 2019. Welcome to the Tidyverse. Journal of Open Source Software 4:1686.

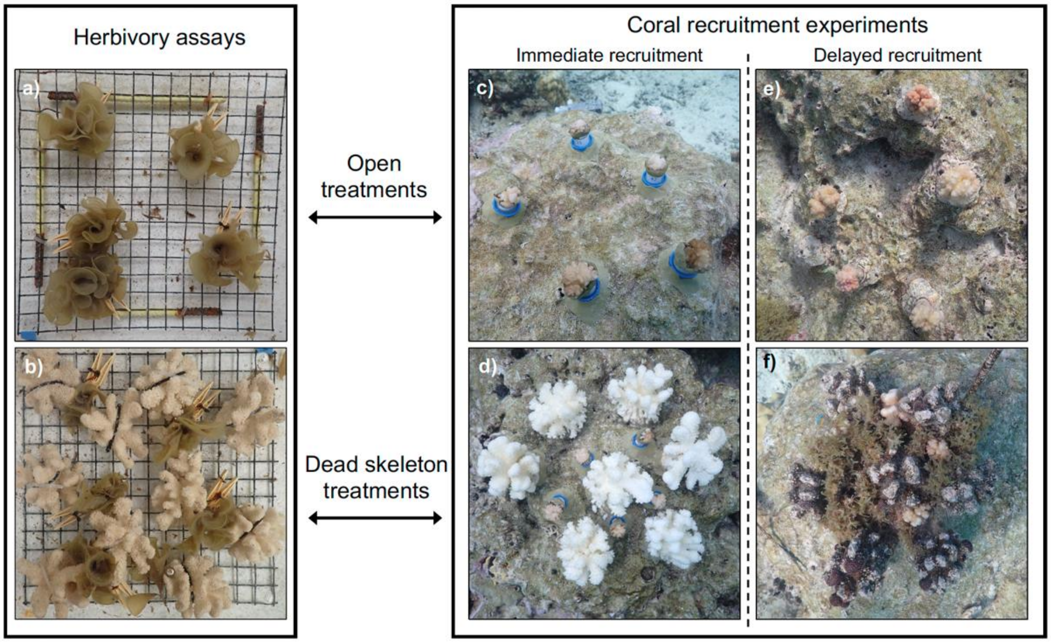


Figure 1. Photographs of experimental designs (PC: K.L. Kopecky). a-b) Example of a pair of herbivory assay trays before deployment in the field; c-d) Recruitment experiment with live corals deployed immediately after manipulations (removal of algae and outplanting of dead coral skeletons); e-f) Recruitment experiment with corals deployed one year after manipulations (note macroalgae on dead skeletons in panel f). Top row (panels a, c, and e) shows the Open treatment (simulated storm wave scouring disturbance) for all experiments, and bottom row shows the Dead Skeleton treatment (simulated coral bleaching).

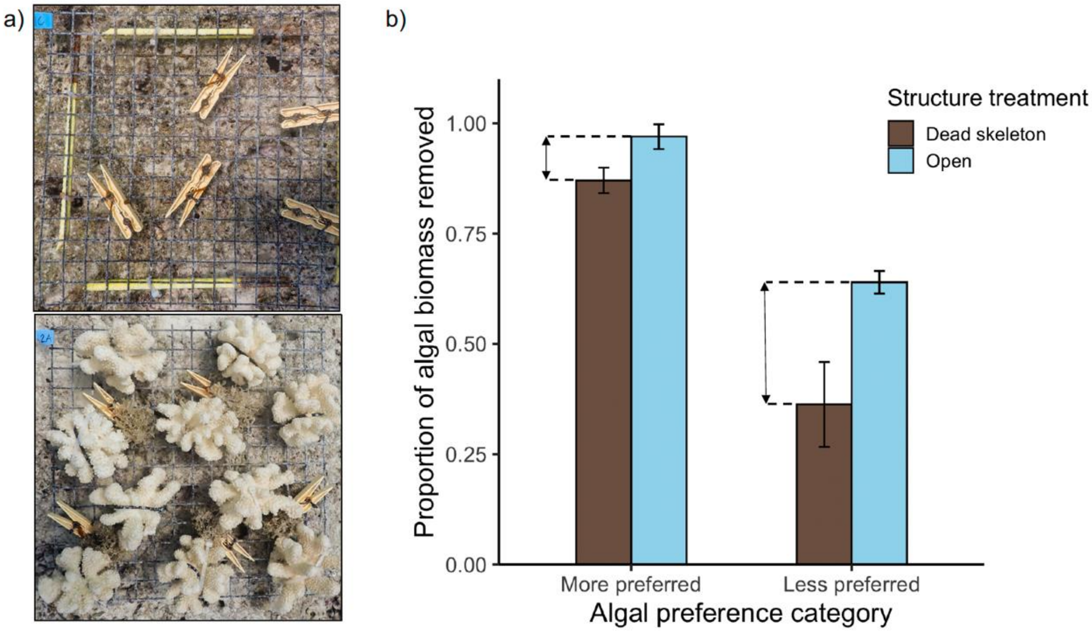


Figure 2. a) Example photographs of a paired herbivory assay (Open treatment top, Dead Skeleton treatment bottom) using a Less Preferred algal taxon after five days (note higher remaining biomass in Dead Skeleton assay) (PC: K.L. Kopecky). b) Mean (± 1 SE) proportion of algal biomass removed after five days in Dead Skeleton (brown bars) and Open (blue bars) assay treatments as a function of algal preference category (More or Less Preferred taxa). Dashed lines and double-ended arrows represent the difference in algal removal between Dead Skeleton and Open treatments, or the degree of protection for macroalgae afforded by dead skeletons.

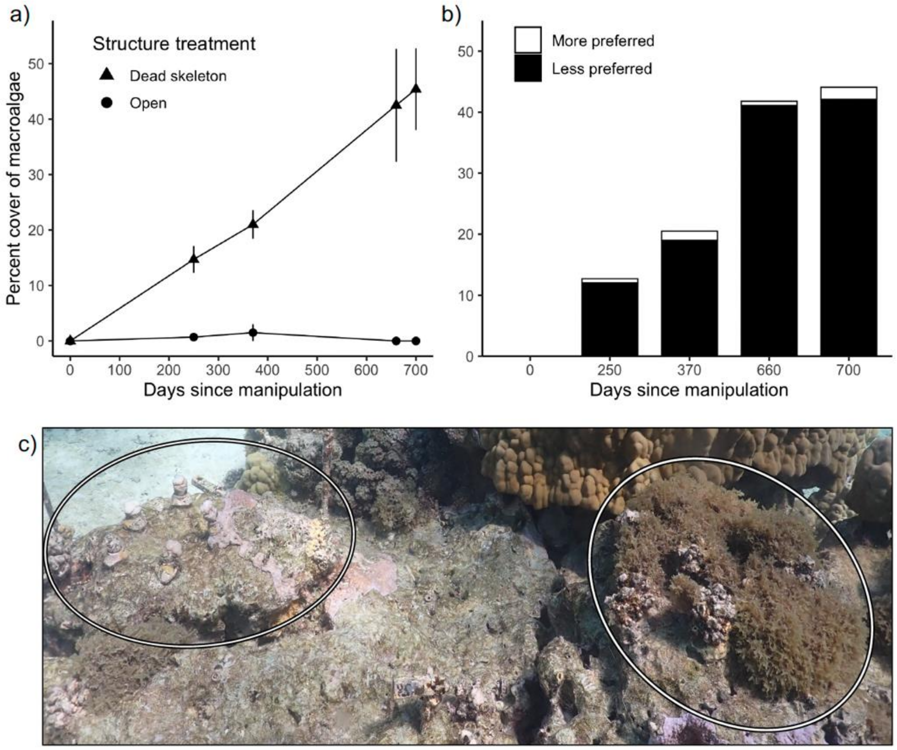


Figure 3. a) Time series of macroalgae cover (mean % cover ± 1 SE) on experimental patch reefs over two years, beginning immediately after manipulation (either simulated storm-wave scour or simulated bleaching). Triangles show algae coverage on patch reefs affixed with dead skeletons (simulated bleaching), circles show coverage on open patch reefs (no skeletons; simulated storm-wave scour). b) The percentage of macroalgae across reefs with dead skeletons at each time point that were More Preferred (white) or Less Preferred (black) taxa. c) Photograph showing a patch reef in the Open treatment free of macroalgae (left ellipse) and a patch reef in the Dead Skeleton treatment with high macroalgal cover (right ellipse) after two years (PC: K.L. Kopecky).

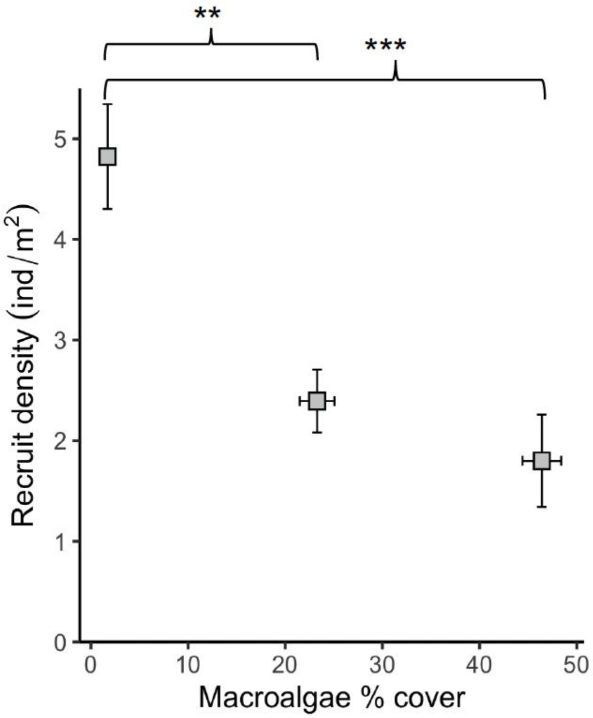


Figure 4. Density of coral recruits (individuals m^{-2}) as a function of macroalgae cover in the algae-reduction experiment. Values from left to right represent mean cumulative recruit densities as a function of time-averaged macroalgae cover on reefs where macroalgae were completely removed, partially removed, and not removed at the beginning of the experiment. Values displayed are means ± 1 SE, and asterisks and brackets denote significant differences between groups.

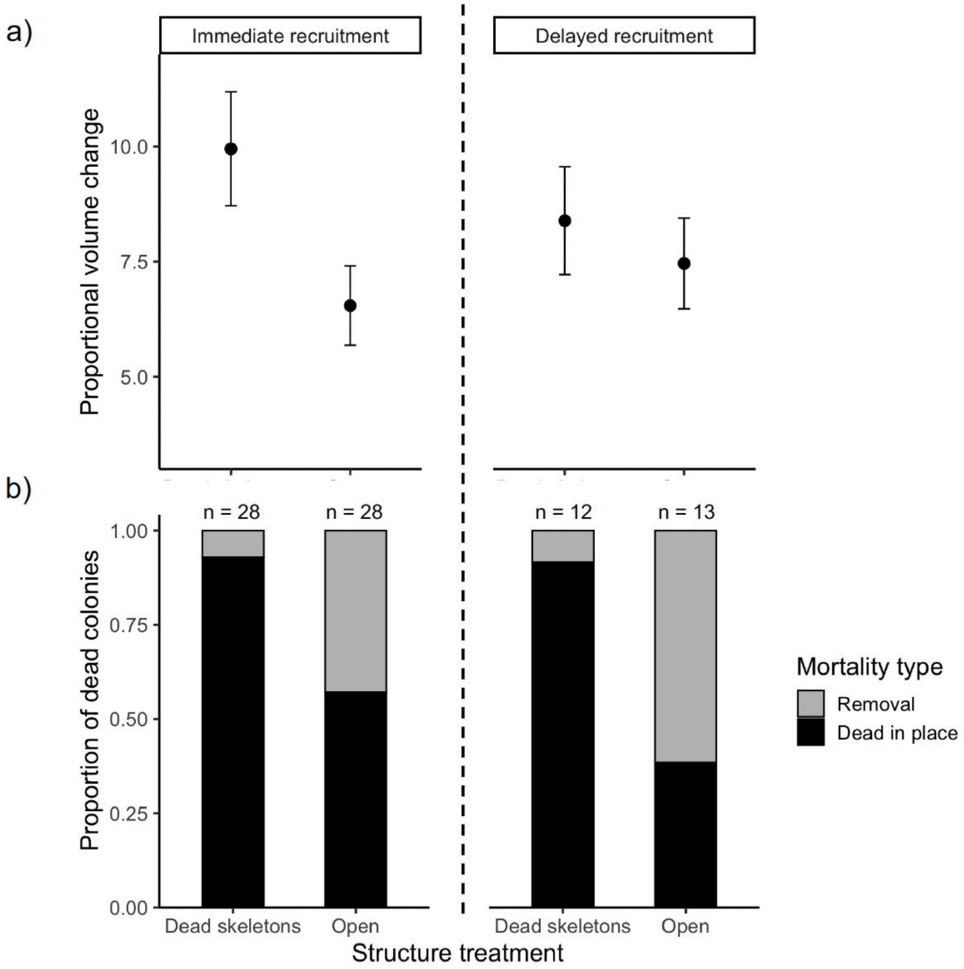


Figure 5. Coral recruit performance metrics. a) Proportional change in volume (mean ± 1 SE) of coral recruits during each recruitment experiment. Immediate Recruitment refers to deployment of corals immediately after the simulated disturbance (either storm-wave scour or bleaching), while Delayed Recruitment refers to deployment of corals one year after simulated disturbance. b) The proportion of colonies that died (i.e., had < 5% live tissue remaining after one year) in the Dead Skeleton and Open treatments for the Immediate Recruitment and Delayed Recruitment experiments. Grey shading indicates corals that underwent skeletal removal (negative volume change before dying), black shading indicates corals that died in place (positive volume change before dying). Sample sizes indicate the total number of corals that died in each treatment in each experiment.

SUPPLEMENTAL FIGURES

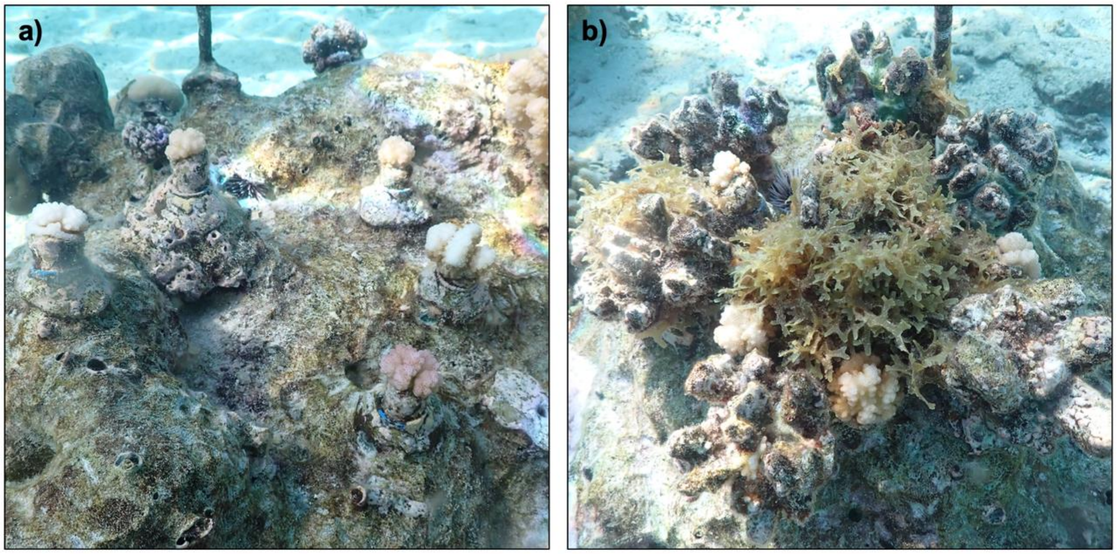


Figure S1. Experimental coral recruits after one year of growth in a) an Open treatment reef and b) a Dead Skeleton treatment reef, all of which show a largely hemispherical growth pattern with minimal branching.

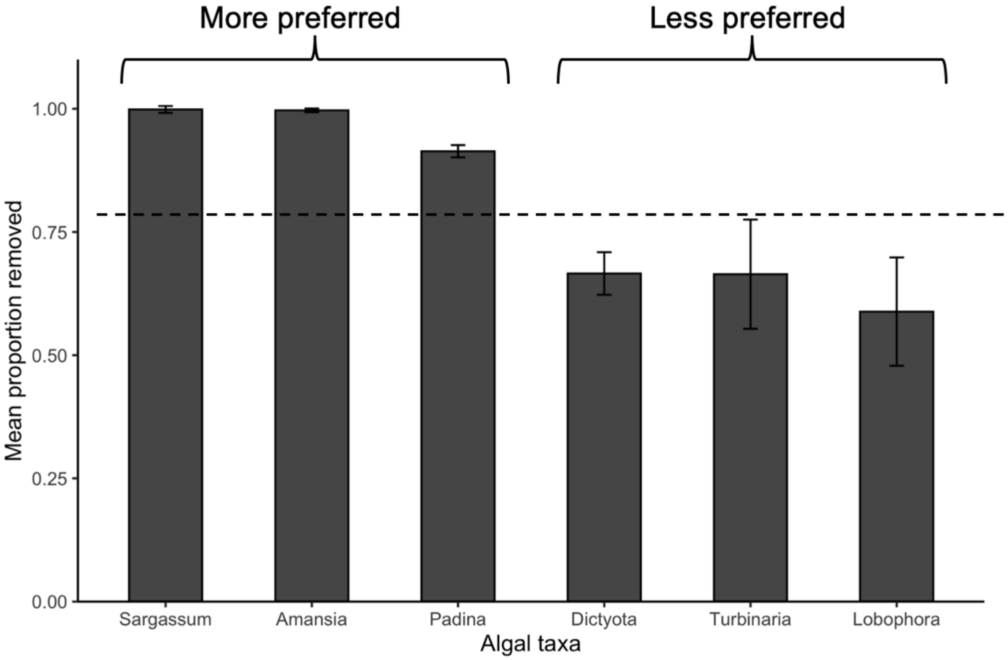


Figure S2. Proportional removal of macroalgae by taxa. Bars are means ± 1 SE. Dashed horizontal line indicates break in mean values used to group taxa into More and Less Preferred categories.

Chapter III. Quantifying the Loss of Coral from a Bleaching Event Using Underwater Photogrammetry and AI-assisted Image Segmentation

ABSTRACT

Detecting impacts of natural and anthropogenic disturbances that cause declines in organisms or changes in community composition has long been a focus of ecology, but a tradeoff often exists between the spatial extent over which relevant data can be collected, and the resolution of those data. Recent advances in underwater photogrammetry, as well as computer vision and machine learning tools that employ artificial intelligence (AI), offer a potential solution to resolve this tradeoff. Here, we coupled a rigorous photogrammetric survey method with novel AI-assisted image segmentation software to quantify the impact of a coral bleaching event on a tropical reef, both at an ecologically meaningful spatial scale and with high spatial resolution. In addition to outlining our workflow, we highlight three key results: 1) dramatic changes in the three-dimensional surface areas of live and dead coral, as well as the ratio of live to dead colonies before and after bleaching, 2) a size-dependent pattern of mortality in bleached corals, where the largest corals were disproportionately affected, and 3) a significantly greater decline in the surface area of live coral as revealed by our approximation of the 3D shape compared to the more standard planar area (2D) approach. The technique of photogrammetry allows us to turn 2D images into approximate 3D models in a flexible and efficient way. Increasing the resolution, accuracy, spatial extent, and efficiency with which we can quantify effects of disturbances will improve our ability to understand the ecological consequences that cascade from small to large scales, as well as allow more informed decisions regarding mitigation of undesired impacts.

INTRODUCTION

Natural and anthropogenic disturbance events can cause mass declines in the foundation species of ecosystems. Detecting and quantifying the impacts of these events is a critical focus of ecology (Osenberg and Schmitt 1996), but doing so can be difficult to achieve at ecologically meaningful scales (Solow 2017). The effort required to collect high resolution data constrains the areal and temporal extent that can feasibly be surveyed, limiting our ability to fully assess the ecological consequences of disturbance. This is especially the case for shallow marine ecosystems (Miller et al. 2023). Fortunately, advances in underwater photogrammetry techniques and computer vision tools assisted by artificial intelligence (AI) provide solutions to resolve this tradeoff.

Coral reef ecosystems illustrate the need for and challenges associated with high resolution change detection. These highly productive systems host a staggering level of biodiversity that relies on reef-building corals (Knowlton et al. 2010). The benthic communities of tropical reefs are difficult to quantify at all relevant spatial and temporal scales. *In situ* visual surveys can be relatively rapid and cost-effective, but they often yield coarse estimates of organismal cover, while manual annotation of images can produce high resolution data but is comparatively time and labor intensive (Couch et al. 2021, Urbina-Barreto et al. 2021). This is a growing issue because coral reefs are increasingly threatened by disturbances that cause persistent and expansive declines in reef-building corals, the organisms that form the structural foundations of these ecosystems (Hoegh-Guldberg et al. 2007). Specifically, episodes of coral bleaching associated with periods of elevated ocean temperatures can kill corals on landscape scales, and these events are increasing both in intensity and frequency on a global scale (Hughes et al. 2018, 2019, Lough et al. 2018, Donovan et al. 2020, 2021). This underscores the importance of developing methods that can be used to accurately and efficiently assess the severity of disturbances that kill coral so that we may better understand their cascading impacts (Holbrook et al. 2008, 2015, Messmer et al. 2011, Adam et al. 2014, Han et al. 2016, Schmitt et al. 2019, Kopecky et al. 2023).

A suite of innovative tools and technologies has been utilized to map coral reef communities. Underwater photogrammetry, for example, is increasingly used to quantify the structural attributes of coral reefs. Large scale efforts have been undertaken to create extensive maps of these ecosystems at high spatial resolution using photogrammetry (Leon et al. 2015, Casella et al. 2017, Urbina-Barreto et al. 2021). Generally, extracting metrics of the physical attributes of a reef (e.g., surface rugosity or roughness) from these maps is relatively straightforward, while efficiently extracting biological metrics, such as the cover of benthic organisms (e.g., coral or algae), can be more complicated and time-consuming (Couch et al. 2021). A widely implemented approach is image segmentation – the scaled measurement and annotation of objects within an image (Lirman et al. 2007, Kikuzawa et al. 2018, El-Khaled et al. 2022, Rich et al. 2022). This form of image analysis is generally used to estimate metrics including percent cover of benthic flora and fauna via the 2D areal footprint of organisms in a given area. Although image segmentation has been used on orthophotomosaics (Burns et al. 2015, Sandin et al. 2020), the effort to do so manually constrains the ability to scale up in space and time. Thus, a bottleneck exists that prevents the extraction of biological metrics like growth and survival of individual coral colonies both at large spatial scales and with high temporal resolution (Couch et al. 2021). This limits our ability to track meaningful changes in benthic community composition on coral reefs over time and thereby inhibits our understanding of how fine scale changes in the populations or communities of benthic organisms might translate to landscape scale impacts. Fortunately, innovations in machine learning provide a promising solution to this challenge.

Through AI-assisted image segmentation, the labor required to measure and identify ecologically relevant objects such as the sizes and identities of coral colonies can be automated, decreasing the time required for this task and increasing the amount of information that potentially can be acquired. Deep-learning methods have been implemented to greatly increase the efficiency with which complex or irregular objects, such as coral colonies, can be segmented from images (Zhang et al. 2022a, Zhong et al. 2023) and reef scale changes in rugosity and structure can be detected over time (Zhang et al. 2022b). We build on this work here, outlining a framework that combines a rigorous underwater photogrammetry technique (Nocerino et al. 2020) with novel, AI-assisted image segmentation software, TagLab (Pavoni et al. 2022), to quantify the impact of a major coral bleaching event on a South Pacific coral reef with high spatial resolution over an ecologically meaningful tract of reef. Specifically, we aimed to: 1) quantify the amount of live coral loss that resulted from the bleaching event with higher accuracy and precision; 2) explore size-dependent patterns of coral mortality; and 3) compare the estimates from our approach with more widely used methods for quantifying changes in coral cover. Using the workflow outlined in Figure 2, we detected a dramatic loss in the amount of live coral on the reef and a reorganization in the size structure of an important coral population through size-dependent mortality of bleached corals. Lastly, we found that using approximated 3D surface area as a metric to estimate coral cover enabled us to capture a significantly greater loss of live coral compared to using 2D planar area, a metric that has been widely used to measure coral size in images.

METHODS

Site description

We conducted our study on Moorea, French Polynesia (17.5388° S, 149.8295° W), a high volcanic island in the South Pacific with steep fore reef slopes that extend offshore of a barrier reef that surrounds the island's ~ 60 km perimeter (Fig. 1a,b). The Moorea Coral Reef Long Term Ecological Research program (MCR LTER, https://mcr.lternet.edu) has been collecting time series data on coral reef communities of Moorea since 2005, including photogrammetric surveys of several reef tracts at about 10 m depth on the north shore fore reef annually since 2017. In April 2019, a prolonged period of elevated sea surface temperatures triggered a major coral bleaching event that resulted in significant coral mortality on the fore reef (Moorea Coral Reef LTER and Edmunds 2024; Fig. 1c). Our photogrammetric surveys spanned this major disturbance, providing an opportunity to evaluate the utility of our AI-assisted approach to quantify change. We focused our analyses on two time points (photogrammetric epochs): August 2018 (epoch 1), about 8 months before the bleaching event when live coral cover was at an all-time high, and August 2019 (epoch 2), about 4 months after the bleaching event once significant mortality of live coral had taken place.

Reference network establishment, image acquisition, and orthophotomosaic generation

The first step in the workflow (Fig. 2) is to establish a series of geodetic networks, that is, permanent, fixed reference points in the reef substrate from which the reference network can be measured. Creating a permanent and reliable reference network is critical both for scaling the photogrammetric models and registering multiple models in space and time. For our network, the reference points were established by SCUBA divers who drilled holes into the primary reef substrate and affixed anchors (using underwater epoxy) into which specially designed photogrammetry targets could be installed and then removed during each sampling event (Fig. 2a). The horizontal and vertical distances between all targets are then measured with sub-centimeter precision (see Nocerino et al. 2020, Rossi et al. 2020). The 5 reef plots used in this study each have a footprint of about 25 m^2 (5 x 5 m), and all had a geodetic reference network that was established in 2017. From the reference network measurements for each plot, we estimate a set of coordinates that are used to establish a temporally stable reference system, which allows us to co-register the photogrammetric surveys and products from the different epochs (see Nocerino et al. 2020).

Once the reference network is in place, SCUBA divers systematically photograph the reef (Fig. 2b). As the diver swims, downward-pointing and oblique photographs are taken at a fixed distance above the reef (1-2 m) and at a consistent rate so as to achieve at least 80% overlap (but generally > 90%) between consecutive images. Divers were able to maintain a consistent distance above the reef while acquiring images using the depth gauge on their dive computers (Nocerino et al. 2020, Rossi et al. 2020). The diver completes a series of parallel passes along the length of a reef plot, then a series of passes perpendicular to the first. Finally, a series of oblique (45-degree angle to the reef) photographs are taken around the perimeter of the plot. To minimize temporal and environmentally-caused variation in light incidence on the reef, we photographed our plots during the same time of year (August, the austral winter) and during the same time of day (between late morning and early afternoon). In total, 500-800 images were taken of each plot (see Nocerino et al. 2020). Images were acquired in raw format and white balance adjustment was performed using color checkers distributed in the measurement area before converting the images to the highest quality JPG format to reproduce a more accurate color spectrum (Nocerino et al. 2020). This allows us to extensively adjust the lighting and color of the acquired images, despite environmental conditions (e.g., cloud cover, water turbidity, depth, etc.) that might cause variation in these attributes. This step is fundamental in our protocol as color-fidelity is critical for human identification of marine organisms, as well as facilitation of the training and implementation of the automated semantic segmentation process described below.

The final step of our photogrammetric process is constructing Digital Elevation Models (DEMs) and orthorectified photomosaics (orthophotomosaics, for short) of each plot (Fig. 3). We would like to clarify, however, that the three dimensional information obtained from DEMs is of the single valued form, z = f(x,y), and hence is an approximation (i.e., '2.5D') of the true three-dimensional shape of the reef. All photogrammetric models and orthophotomosaics were generated using Agisoft Metashape (version 2.0), with an average ground resolution of less than 1 mm (i.e., pixel size: < 1 x 1 mm), and a discrepancy among reference coordinates of a few millimeters (Nocerino et al. 2020, Rossi et al. 2020)

AI-assisted image segmentation and manual validation and editing

Semantic segmentation involves the detection and partitioning of an image into different subdivisions based on their class. We employed TagLab (https://taglab.isti.cnr.it; Pavoni et al. 2022), an open-source, AI-powered, interactive image segmentation software designed for coral reef habitats to annotate and measure corals in our orthophotomosaics (Fig. 2d, 4). TagLab enables pixel-wise accurate, scale-aware labeling and analysis of orthophotomosaics. This software also facilitates time series analysis when multiple images of a site are available from different epochs. For example, it is possible to automatically track temporal changes of individual objects (e.g., growth, shrinkage, or death of coral colonies) in sequential orthophotomosaics of the same site when the objects are co-registered (Fig. 4, inset panels). Further, TagLab enables a user to create custom classifiers for automatic recognition of objects of interest via creation of a training dataset. Building the training dataset utilizes semi-automatic segmentation, in which a human operator manually identifies and labels colonies using AI-assisted tools to outline coral colony borders. For example, the user only needs to indicate the four most extreme points of a colony border, rather than tracing the entire colony. This and other semi-automatic segmentation tools greatly expedite creation of the training dataset, after which fully automatic segmentation can be used. In this study, two of the ten orthophotomosaics (the same plot from both epochs) we produced were annotated semi-automatically to build the training dataset for the fully automatic classifier, which was then used to segment the remaining eight orthophotomosaics. TagLab is available to download from Github: https://github.com/cnr-isti-vclab/TagLab (see Pavoni et al. 2022 for more detail on the software's mechanics).

A human operator should always validate the automatic segmentations visually (Fig. 2e). Then, depending on the desired metric or level of accuracy, the operator can correct mistakes made during the automatic classification by manually correcting any poorly predicted colony borders or mislabeled objects. This will require additional human labor and processing time. In this study, once the training dataset had been used to build the fully automatic classifier, we took further action to validate the accuracy of the automatic classifier and improve the quality of the automatic segmentations. Because we were interested in exploring patterns based on individual coral colony size, we manually divided segmentations that enclosed multiple, overlapping or adjacent coral colonies of the same taxon. However, if a user is interested solely in the total areal coverage by different types of objects (e.g., live and dead corals), minimal further editing would likely be required. Lastly, we modified the TagLab software for this study in order to approximate 3D metrics of reef organisms. Previously, TagLab did not support the loading or analysis of DEMs, but only three-channel (RGB) images. The software was modified to be able to layer the RGB images on their respective DEMs in order to extract 3D approximations of coral colony (and other) surface areas.

Analyses and impact assessment

Due to the dominance of corals in the genus *Pocillopora* inhabiting the reefs we studied (> 90% of coral colonies present), and the relative scarcity of other taxa, we focused our analyses on changes in *Pocillopora* corals. Using the automatically generated, manually corrected segmentations, we analyzed several metrics of live and dead coral cover to estimate changes driven by the bleaching event (Fig. 2f). First, we excluded all segmentations < 2 cm^2, as these were too small for a human observer to reliably identify. Next, we calculated the total proportion of colonies that were alive or dead before and after the bleaching event to understand how the ratio of live to dead colonies changed in response to this disturbance. To quantify the magnitude of change in live and dead coral area from before to after bleaching, we summed the total 3D surface areas (estimated from Digital Elevation Models (DEMs) of the photogrammetric models) of live and dead colonies for all 5 plots in each epoch (pre-bleaching: 2018, post-bleaching: 2019), then averaged across replicate plots within an epoch.

To explore patterns of size-dependent mortality after bleaching, we sorted the live and dead colonies by size classes (based on the approximated 3D surface area of a coral colony) and compared abundances of these classes before and after the bleaching event. Thresholds for the size classes were based on the quartiles of colony sizes for live corals before the bleaching event (i.e., the size structure of the pre-bleaching population). We rounded the size thresholds slightly to create clean cut-offs between classes. To create just three size classes (Small, Medium, and Large), the middle two quartiles were combined for the Medium size class, as these two quartiles behaved similarly to one another through time. The final size classes used were: < 100 cm^2 (Small), 100 - 400 cm^2 (Medium), and > 400 cm^2 (Large). Because larger colonies were more scarce than smaller ones, the 'Large' class contained a much wider range in sizes (401 - 3,487 cm^2) than the two smaller classes. Lastly, we applied these size classes to the dead coral colonies to assess mortality of corals based on colony size.

Finally, we compared estimated loss of live coral cover after the bleaching event using two different metrics of coral surface area: approximated 3D surface area derived from the DEMs, and 2D planar area derived from the areas enclosed by the perimeters of segmented regions. 2D planar area is commonly used in studies of coral reefs to estimate the areal footprints of corals and other organisms within an image, which are then used as a proxy for coral colony size. To test whether the approximated 3D metric captured a greater magnitude of coral decline after bleaching compared to the 2D metric, we ran an Analysis of Covariance (ANCOVA) on live coral surface area as a function of area metric (approximated 3D or 2D) and epoch (pre-bleaching: 2018, post-bleaching: 2019). All analyses were performed in R (version 4.0.0; R Core Team 2023) and RStudio (version 2022.12.0.353; Posit team 2024) using the Tidyverse package (Wickham et al. 2019), and visualizations utilized colors from Manu: NZ Bird Colour Palettes (Thomson 2022).

RESULTS

Automatic segmentation and manual validation/improvement

After training a custom classifier on two orthophotomosaics of the same plot (one image from epoch 1 pre-bleaching: 2018; one from epoch 2 post-bleaching: 2019), the fully automatic classification correctly classified 93% of pixels (each ~ 1 mm) for living *Pocillopora,* which is comparable to the performance of a human operator and is the maximum accuracy generally achievable (Pavoni et al. 2022). The classification accuracy for dead coral, however, was lower, with 70% of pixels correctly classified. There were two reasons for this. First, dead coral often resembles the primary reef substrate and therefore was sometimes mis-classified as background reef. Second, there was a relatively low representation of dead coral in the two orthophotomosaics used for the training dataset, as dead corals were prevalent only in the post-bleaching image, which could be rectified by additional training. Nonetheless, the automatic classifier was able to segment the corals in an entire orthophotomosaic in a matter of minutes, a task that would have taken a human operator tens of hours to complete manually.

While the automatic classifier was highly accurate in classifying pixels as live or dead coral, it does not yet have the ability to distinguish well between colonies that have abutting borders. Therefore, to obtain information on sizes and numbers of colonies, further manual division of the segmentations by a human was required. Before cropping our orthophotomosaics down to designated working areas (to standardize the areas surveyed), and before removing segmentations < 2 cm^2 in area, 2060 segmentations of live coral were completed automatically for the orthophotomosaics of the pre-bleaching epoch. These segmentations were further divided manually by a human observer into 4366 live colonies. For the post-bleaching epoch, 2426 segmentations were completed automatically but were then manually divided further into 3181 live colonies. The number of dead coral colonies was nearly identical between the automatic and manual segmentations for the pre-bleaching epoch (1288 compared to 1289, respectively), but for the 2019 epoch, manual division increased the number of dead colonies from 1471 to 2077. After manually correcting all segmentations, removing segmentations < 2 cm^2, and standardizing to the designated working areas for the plots, the total number of corals (live + dead) was 4,306 in the pre-bleaching epoch and 4,015 in the post-bleaching epoch. Manually dividing the automatically segmented colonies added only about one hour per orthophotomosaic to the overall time required for processing the images.

Changes in colony numbers, approximated 3D surface areas, and size structure of corals

As expected, the proportions of live and dead coral colonies changed substantially from before to after the bleaching event (Fig. 5a). Of the 4,306 colonies measured across all 5 plots before bleaching (within designated working areas), roughly 21% (904) of these were dead. However, this proportion nearly doubled following the bleaching event, after which 41% (1,646) of the 4,015 colonies measured were classified as dead. Our assessment of changes in the approximated 3D surface areas of live and dead corals at the plot scale (~ 25 m^2) before and after bleaching revealed even more dramatic changes (Fig. 5b). After bleaching, the approximated 3D surface area of live coral decreased by more than half, from 26.7 (± 2.4) m^2 to 12.5 (± 1.0) m^2 (means ± SE), respectively. By contrast, the total surface area of dead coral increased by over eight-fold, from 1.9 ± 0.3 m^2 to 16.6 ± 1.6 m^2 and surpassed the total amount of coral surface area that remained alive after the bleaching event.

We explored size-dependent relationships of coral mortality and found striking differences among size classes in their response to bleaching (Fig. 6). The number of colonies in the largest size class of dead coral (> 400 cm^2) increased by 24-fold after the bleaching event, from 5.6 (± 1.3) dead colonies per plot (mean ± SE) before bleaching to 133.8 (± 16.0) dead colonies afterward. The medium size class (100 - 400 cm^2) showed a much more modest increase of 1.3-fold, from 60.4 (± 8.7) colonies before bleaching to 89.4 (± 15.4) colonies after. Lastly, the smallest size class showed no statistical differences in mean number of dead corals per plot from before to after the bleaching event. This size-dependent pattern in mortality corroborates our observation that the change in surface area of live and dead coral was markedly higher than the change in the proportion of live and dead colonies, as larger colonies contribute disproportionately more to reef coverage than do smaller colonies.

Comparison of approximated 3D surface area with 2D planar area

Our comparison of the approximated 3D surface area estimates with 2D planar area estimates of live corals showed, unsurprisingly, that the 3D metric estimated far greater amounts of live coral area within a time period than the 2D metric (triangles compared to squares in Fig. 7). More importantly, the approximated 3D metric revealed a significantly greater loss rate of live coral than the 2D metric (slopes of the relationships in Fig. 7 differ; ANCOVA: $F_{1,0.05} = 5.05$, $p = 0.03$; see Appendix A, Table A1).

DISCUSSION

Quantification of the coral bleaching event

Assessing the ecological impacts of natural and anthropogenic disturbances is increasingly important as these events become more common and severe. Therefore, innovative tools and reliable methods are needed to accurately quantify changes in populations and communities of organisms affected by these disturbances. This is especially important for shallow subtidal ecosystems such as coral reefs, which are becoming increasingly threatened by more frequent and severe bleaching events (Hughes et al. 2018, 2019, Lough et al. 2018, Donovan et al. 2020, 2021). Here, we outlined a novel method that combined underwater photogrammetry with AI-assisted image segmentation software to rapidly and accurately quantify the impact of a major coral bleaching event on a tropical reef. We showed significant changes to the composition of this reef both at the coral colony and the landscape scale. Use of an approximated 3D metric to quantify coral, as facilitated by the tools and techniques we described, provided a more accurate estimate of the amount of coral present and the rate of loss due to a coral mortality event compared to the more commonly used 2D metric.

The workflow described here not only enables a more accurate quantification of coral loss over ecologically meaningful spatial scales (Fig. 5), it also provides the ability to characterize a colony size-specific pattern of mortality. For *Pocillopora*, the prominent taxon of coral in the system, the largest colonies were disproportionately affected by the bleaching event, where the number of dead colonies in the largest size class increased by an order of magnitude more than for smaller sized colonies (Fig. 6). This pattern aligns with other field studies of coral bleaching in Moorea (Burgess et al. 2021, Speare et al. 2022, Honeycutt et al. 2023) and energetic modeling of corals (Cunning et al. 2017) that have all found size-specific variation in susceptibility of *Pocillopora* colonies to bleaching and subsequent mortality. The disproportionate loss of larger *Pocillopora* colonies also explains the greater effect we observed on the change in coral cover (Fig. 5b) compared to the smaller change in proportions of live and dead colonies (Fig. 5a).

Many studies of coral reefs have implemented manual tracing of coral colonies to estimate their areal footprint as a 2D surface, which is used as a proxy for colony size (Connell et al. 1997, Lirman et al. 2007, Kikuzawa et al. 2018, El-Khaled et al. 2022, Rich et al. 2022). By approximating the 3D surface areas of corals, we captured a loss rate of live coral that was significantly greater than that estimated by 2D planar area (Fig. 7). A previous study (House et al. 2018) that explored the relationship between 2D and 3D estimates of total surface area of single coral colonies revealed scaling relationships that depended on coral morphology, leading the authors to conclude that the labor-intensive nature of measuring corals in 3D may be avoided by converting 2D measurements into 3D metrics to quantify change over ecologically meaningful spatial scales in the field. Our coupling of a rigorous photogrammetric survey method with novel, open-access AI-assisted image segmentation software (TagLab) enables direct 3D approximation of both the surface area of coral skeletons and semantic segmentation of co-located coral colonies with high resolution over large scales. This AI-assisted approach enabled us to estimate absolute changes in live and dead coral cover on the reef with a realistic level of effort. In turn, this could improve estimates of how disturbance will modify important ecological processes and services that corals provide, such as reef metabolism and habitat provisioning (Moberg and Folke 1999, Holbrook et al. 2011), enabling ecologists to better predict cascading ecological consequences of disturbance (Holbrook et al. 2008, 2015, Messmer et al. 2011, Adam et al. 2014, Han et al. 2016, Schmitt et al. 2019, Kopecky et al. 2023).

Advantages to our approach

Our photogrammetric approach allowed us to quantify changes in live and dead coral cover over spatial scales of tens of square meters with sub-centimeter resolution and accuracy (Nocerino et al. 2020, Pavoni et al. 2022). From an ecological standpoint, the use of a fixed geodetic reference network as we described here provides several benefits compared to more commonly used photogrammetric survey techniques. First, the reference network acts to set a robust, three-dimensional scale for measuring objects (such as coral colonies) within an orthophotomosaic. Second, the reference network enables users to georeference their orthophotomosaics and therefore align multiple orthophotomosaics of the same site taken at different times (epochs). This facilitates highly precise spatiotemporal comparisons that can yield highly accurate time series estimations of important biological variables. Third, the reference network provides users a means of estimating the error margins of their measurements, allowing the assessment of whether changes in biological variables through time (such as growth or loss of corals) are statistically significant (Nocerino et al. 2020, Pavoni et al. 2022).

When coupled with AI, the high volumes of information contained in large orthophotomosaics can be processed efficiently. With the use of TagLab, we were able to rapidly extract large amounts of high spatial resolution data from the orthophotomosaics produced by our photogrammetric approach (Fig. 4). Automating the annotation of these orthophotomosaics substantially reduced the processing time compared to annotations completed manually (Pavoni et al. 2022, Miller et al. 2023). Not only were the automated annotations highly accurate compared to those completed by humans, they can be improved through manually editing or additional data and training. Further, once a desired level of accuracy is achieved in training the program, the process of extracting data from orthophotomosaics can be completed by personnel with less taxonomic or ecological expertise. Automating the highly time-intensive task of measuring corals within photographs, such as we have shown here, can boost our capabilities to monitor and detect changes in highly threatened ecosystems like coral reefs.

Caveats to our approach

Several opportunities exist for improvement of our workflow. With regard to the photogrammetric process, the establishment of an underwater fixed reference network can be a challenging and labor-intensive task. New tools based on the integration of Inertial Measurement Unit (IMU) and depth sensors (Menna et al. 2021, Nocerino and Menna 2023), however, are being developed to reduce the number of measurements needed between fixed reference points – in particular, the vertical distances between fixed reference points, which are the most difficult to measure. With regard to the AI-assisted segmentation process, a few issues arose that required manual intervention. First, while the automatic classifier was highly accurate in classifying live coral and reasonably accurate in classifying dead coral, it had difficulty differentiating between colonies in the same semantic category when they shared borders or overlapped one another. This is understandable, as this task was difficult even for human observers due to the high density of abutting, congeneric coral colonies on the reefs we studied. If a user is interested in colony-level changes (as opposed to total, reef-scale changes in coral cover), some additional labor may be required to manually separate colonies if colony density is high on the reef being studied. Second, the automatic classifier failed to classify live and dead coral in a small minority of cases (< 10%), which could be attributable to the image quality for those particular colonies, or the relatively small training dataset we used (the program was trained on only two orthophotomosaics, one of which contained relatively few dead coral colonies). Nonetheless, TagLab performed impressively with respect to quantifying live and dead coral cover, its automatic segmentations can be continually improved with further training or manual editing, and it will likely become a widely used tool in the study and monitoring of coral reef ecosystems.

Future directions

There are several avenues to build on the work we have presented here, some of which are already underway. First, researchers in our group are currently developing techniques to perform segmentation on 3D point clouds, which will further enhance the accuracy of measuring the 3D surface areas of complex structures like coral colonies using photogrammetric methods. Additionally, we are exploring the incorporation of multispectral sensors affixed to underwater drones to facilitate the acquisition and processing of underwater images used for underwater photogrammetry. As for developments regarding TagLab, there are several in progress. First, data from subsequent years following those presented in this study can be used to further train the automatic classifier, making it more robust. We plan to release this trained model to be publicly available. We are also currently refining methods and algorithms to easily track individual objects as they transition between classes, such as a live coral colony that dies wholly or partially between epochs. Further, we are developing an AI-assisted point classification tool that can be used to estimate the cover of organisms and objects that are difficult to measure via currently available tools (e.g., patches of algae). Lastly, the architecture of TagLab will soon transition from using semantic segmentation to panoptic segmentation, which will allow for the quantification of amorphous or indistinct components of the benthos, such as reef substrate or coral rubble.

CONCLUSIONS

The pace of changing global conditions warrants development of sophisticated methods and tools that can be used to make informed decisions for management of threatened ecosystems. Here, we have described an integrated underwater photogrammetry and AI-assisted image segmentation methodology for robustly and efficiently quantifying change in coral, the foundation species of tropical reefs. The insights that can be gleaned from this technique are numerous and could enable ecologists to answer questions that may not feasibly be addressed with traditional methods. Further, robust change detection as we have demonstrated could prove highly valuable for ecological monitoring efforts by reducing the tradeoff between the areal extent that can be feasibly surveyed and the spatial resolution that can be achieved. Enhancing both the spatial extent and resolution of ecological monitoring will strengthen our ability to forecast how the functioning of vulnerable ecosystems, such as coral reefs, will change in an uncertain future, helping us to mitigate undesired impacts of disturbance.

REFERENCES

Adam, T.C.; Brooks, A.J.; Holbrook, S.J.; Schmitt, R.J.; Washburn, L.; Bernardi, G. How Will Coral Reef Fish Communities Respond to Climate-Driven Disturbances? Insight from Landscape-Scale Perturbations. *Oecologia* **2014**, *176*, 285–296, doi:10.1007/s00442-014-3011-x.

Burgess, S.C.; Johnston, E.C.; Wyatt, A.S.J.; Leichter, J.J.; Edmunds, P.J. Hidden Differences in Bleaching Among Cryptic Coral Species. *Bull. Ecol. Soc. Am.* **2021**, *102*, 1–7.

Burns, J.H.R.; Delparte, D.; Gates, R.D.; Takabayashi, M. Integrating Structure-from-Motion Photogrammetry with Geospatial Software as a Novel Technique for Quantifying 3D Ecological Characteristics of Coral Reefs. *PeerJ* **2015**, *3*, e1077, doi:10.7717/peerj.1077.

Casella, E.; Collin, A.; Harris, D.; Ferse, S.; Bejarano, S.; Parravicini, V.; Hench, J.L.; Rovere, A. Mapping Coral Reefs Using Consumer-Grade Drones and Structure from Motion Photogrammetry Techniques. *Coral Reefs* **2017**, *36*, 269–275, doi:10.1007/s00338-016-1522-0.

Connell, J.H.; Hughes, T.P.; Wallace, C.C. A 30-Year Study of Coral Abundance, Recruitment, and Disturbance at Several Scales in Space and Time. *Ecol. Monogr.* **1997**, *67*, 461–488, doi:10.1890/0012-9615(1997)067[0461:AYSOCA]2.0.CO;2.

Couch, C.S.; Oliver, T.A.; Suka, R.; Lamirand, M.; Asbury, M.; Amir, C.; Vargas-Ángel, B.; Winston, M.; Huntington, B.; Lichowski, F.; et al. Comparing Coral Colony Surveys From In-Water Observations and Structure-From-Motion Imagery Shows Low Methodological Bias. *Front. Mar. Sci.* **2021**, *8*.

Cunning, R.; Muller, E.B.; Gates, R.D.; Nisbet, R.M. A Dynamic Bioenergetic Model for Coral-Symbiodinium Symbioses and Coral Bleaching as an Alternate Stable State. *J. Theor. Biol.* **2017**, *431*, 49–62, doi:10.1016/j.jtbi.2017.08.003.

Donovan, M.K.; Adam, T.C.; Shantz, A.A.; Speare, K.E.; Munsterman, K.S.; Rice, M.M.; Schmitt, R.J.; Holbrook, S.J.; Burkepile, D.E. Nitrogen Pollution Interacts with Heat Stress to Increase Coral Bleaching across the Seascape. *Proc. Natl. Acad. Sci.* **2020**, *117*, 5351–5357, doi:10.1073/pnas.1915395117.

Donovan, M.K.; Burkepile, D.E.; Kratochwill, C.; Shlesinger, T.; Sully, S.; Oliver, T.A.; Hodgson, G.; Freiwald, J.; van Woesik, R. Local Conditions Magnify Coral Loss after Marine Heatwaves. *Science* **2021**, *372*, 977–980, doi:10.1126/science.abd9464.

El-Khaled, Y.C.; Kler Lago, A.; Mezger, S.D.; Wild, C. Comparative Evaluation of Free Web Tools ImageJ and Photopea for the Surface Area Quantification of Planar Substrates and Organisms. *Diversity* **2022**, *14*, 272, doi:10.3390/d14040272.

Han, X.; Adam, T.C.; Schmitt, R.J.; Brooks, A.J.; Holbrook, S.J. Response of Herbivore Functional Groups to Sequential Perturbations in Moorea, French Polynesia. *Coral Reefs* **2016**, *35*, 999–1009, doi:10.1007/s00338-016-1423-2.

Hoegh-Guldberg, O.; Mumby, P.J.; Hooten, A.J.; Steneck, R.S.; Greenfield, P.; Gomez, E.; Harvell, C.D.; Sale, P.F.; Edwards, A.J.; Caldeira, K.; et al. Coral Reefs Under Rapid Climate Change and Ocean Acidification. *Science* **2007**, *318*, 1737–1742, doi:10.1126/science.1152509.

Holbrook, S.J.; Schmitt, R.J.; Brooks, A.J. Indirect Effects of Species Interactions on Habitat Provisioning. *Oecologia* **2011**, *166*, 739–749, doi:10.1007/s00442-011-1912-5.

Holbrook, S.J.; Schmitt, R.J.; Brooks, A.J. Resistance and Resilience of a Coral Reef Fish Community to Changes in Coral Cover. *Mar. Ecol. Prog. Ser.* **2008**, *371*, 263–271, doi:10.3354/meps07690.

Holbrook, S.J.; Schmitt, R.J.; Messmer, V.; Brooks, A.J.; Srinivasan, M.; Munday, P.L.; Jones, G.P. Reef Fishes in Biodiversity Hotspots Are at Greatest Risk from Loss of Coral Species. *PLOS ONE* **2015**, *10*, e0124054, doi:10.1371/journal.pone.0124054.

Honeycutt, R.N.; Holbrook, S.J.; Brooks, A.J.; Schmitt, R.J. Farmerfish Gardens Help Buffer Stony Corals against Marine Heat Waves. *PLOS ONE* **2023**, *18*, e0282572, doi:10.1371/journal.pone.0282572.

House, J.E.; Brambilla, V.; Bidaut, L.M.; Christie, A.P.; Pizarro, O.; Madin, J.S.; Dornelas, M. Moving to 3D: Relationships between Coral Planar Area, Surface Area and Volume. *PeerJ* **2018**, *6*, e4280, doi:10.7717/peerj.4280.

Hughes, T.P.; Kerry, J.T.; Connolly, S.R.; Baird, A.H.; Eakin, C.M.; Heron, S.F.; Hoey, A.S.; Hoogenboom, M.O.; Jacobson, M.; Liu, G.; et al. Ecological Memory Modifies the Cumulative Impact of Recurrent Climate Extremes. *Nat. Clim. Change* **2019**, *9*, 40–43, doi:10.1038/s41558-018-0351-2.

Hughes, T.P.; Kerry, J.T.; Simpson, T. Large-Scale Bleaching of Corals on the Great Barrier Reef. *Ecology* **2018**, *99*, 501–501, doi:10.1002/ecy.2092.

Kikuzawa, Y.P.; Toh, T.C.; Ng, C.S.L.; Sam, S.Q.; Taira, D.; Afiq-Rosli, L.; Chou, L.M. Quantifying Growth in Maricultured Corals Using Photogrammetry. *Aquac. Res.* **2018**, *49*, 2249–2255, doi:10.1111/are.13683.

Knowlton, N.; Brainard, R.E.; Fisher, R.; Moews, M.; Plaisance, L.; Caley, M.J. Coral Reef Biodiversity. In *Life in the World's Oceans*; McIntyre, A.D., Ed.; Wiley-Blackwell: Oxford, UK, 2010; pp. 65–78 ISBN 978-1-4443-2550-8.

Kopecky, K.L.; Stier, A.C.; Schmitt, R.J.; Holbrook, S.J.; Moeller, H.V. Material Legacies Can Degrade Resilience: Structure-Retaining Disturbances Promote Regime Shifts on Coral Reefs. *Ecology* **2023**, *104*, e4006, doi:10.1002/ecy.4006.

Leon, J.X.; Roelfsema, C.M.; Saunders, M.I.; Phinn, S.R. Measuring Coral Reef Terrain Roughness Using 'Structure-from-Motion' Close-Range Photogrammetry. *Geomorphology* **2015**, *242*, 21–28, doi:10.1016/j.geomorph.2015.01.030.

Lirman, D.; Gracias, N.R.; Gintert, B.E.; Gleason, A.C.R.; Reid, R.P.; Negahdaripour, S.; Kramer, P. Development and Application of a Video-Mosaic Survey Technology to Document the Status of Coral Reef Communities. *Environ. Monit. Assess.* **2007**, *125*, 59–73, doi:10.1007/s10661-006-9239-0.

Lough, J.M.; Anderson, K.D.; Hughes, T.P. Increasing Thermal Stress for Tropical Coral Reefs: 1871–2017. *Sci. Rep.* **2018**, *8*, 6079, doi:10.1038/s41598-018-24530-9.

Menna, F.; Nocerino, E. PRINSY: A Low-Cost Pressure Inertial System for Underwater Photogrammetry. **In prep.**

Menna, F.; Nocerino, E.; Chemisky, B.; Remondino, F.; Drap, P. Accurate Scaling and Leveling in Underwater Photogrammetry with a Pressure Sensor. *Int. Arch. Photogramm. Remote Sens. Spat. Inf. Sci.* **2021**, *XLIII-B2-2021*, 667–672, doi:10.5194/isprs-archives-XLIII-B2-2021-667-2021.

Messmer, V.; Jones, G.P.; Munday, P.L.; Holbrook, S.J.; Schmitt, R.J.; Brooks, A.J. Habitat Biodiversity as a Determinant of Fish Community Structure on Coral Reefs. *Ecology* **2011**, *92*, 2285–2298, doi:10.1890/11-0037.1.

Miller, S.D.; Dubel, A.K.; Adam, T.C.; Cook, D.T.; Holbrook, S.J.; Schmitt, R.J.; Rassweiler, A. Using Machine Learning to Achieve Simultaneous, Georeferenced Surveys of Fish and Benthic Communities on Shallow Coral Reefs. *Limnol. Oceanogr. Methods* **2023**, *n/a*, doi:10.1002/lom3.10557.

Moberg, F.; Folke, C. Ecological Goods and Services of Coral Reef Ecosystems. *Ecol. Econ.* **1999**, *29*, 215–233, doi:10.1016/S0921-8009(99)00009-9.

Nocerino, E.; Menna, F. In-Camera IMU Angular Data for Orthophoto Projection in Underwater Photogrammetry. *ISPRS Open J. Photogramm. Remote Sens.* **2023**, *7*, 100027, doi:10.1016/j.ophoto.2022.100027.

Nocerino, E.; Menna, F.; Gruen, A.; Troyer, M.; Capra, A.; Castagnetti, C.; Rossi, P.; Brooks, A.J.; Schmitt, R.J.; Holbrook, S.J. Coral Reef Monitoring by Scuba Divers Using Underwater Photogrammetry and Geodetic Surveying. *Remote Sens.* **2020**, *12*, 3036, doi:10.3390/rs12183036.

Osenberg, C.W.; Schmitt, R.J. Chapter 1 - Detecting Ecological Impacts Caused by Human Activities. In *Detecting Ecological Impacts*; Schmitt, R.J., Osenberg, C.W., Eds.; Academic Press: San Diego, 1996; pp. 3–16 ISBN 978-0-12-627255-0.

Pavoni, G.; Corsini, M.; Ponchio, F.; Muntoni, A.; Edwards, C.; Pedersen, N.; Sandin, S.; Cignoni, P. TagLab: AI-Assisted Annotation for the Fast and Accurate Semantic Segmentation of Coral Reef Orthoimages. *J. Field Robot.* **2022**, *39*, 246–262, doi:10.1002/rob.22049.

Peter Edmunds MCR LTER: Coral Reef: Long-Term Population and Community Dynamics: Corals, Ongoing since 2005 2022.

R Core Team (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

RStudio Team (2022). RStudio: Integrated Development for R. RStudio, Inc., Boston, MA URL http://www.rstudio.com/.

Rich, W.A.; Carvalho, S.; Cadiz, R.; Gil, G.; Gonzalez, K.; Berumen, M.L. Size Structure of the Coral Stylophora Pistillata across Reef Flat Zones in the Central Red Sea. *Sci. Rep.* **2022**, *12*, 13979, doi:10.1038/s41598-022-17908-3.

Rossi, P.; Castagnetti, C.; Capra, A.; Brooks, A.J.; Mancini, F. Detecting Change in Coral Reef 3D Structure Using Underwater Photogrammetry: Critical Issues and Performance Metrics. *Appl. Geomat.* **2020**, *12*, 3–17, doi:10.1007/s12518-019-00263-w.

Sandin, S.A.; Edwards, C.B.; Pedersen, N.E.; Petrovic, V.; Pavoni, G.; Alcantar, E.; Chancellor, K.S.; Fox, M.D.; Stallings, B.; Sullivan, C.J.; et al. Chapter Seven - Considering the Rates of Growth in Two Taxa of Coral across Pacific Islands. In *Advances in Marine Biology*; Riegl, B.M., Ed.; Population Dynamics of the Reef Crisis; Academic Press, 2020; Vol. 87, pp. 167–191.

Schmitt, R.J.; Holbrook, S.J.; Davis, S.L.; Brooks, A.J.; Adam, T.C. Experimental Support for Alternative Attractors on Coral Reefs. *Proc. Natl. Acad. Sci.* **2019**, *116*, 4372–4381, doi:10.1073/pnas.1812412116.

Solow, A.R. On Detecting Ecological Impacts of Extreme Climate Events and Why It Matters. *Philos. Trans. R. Soc. B Biol. Sci.* **2017**, *372*, 20160136, doi:10.1098/rstb.2016.0136.

Speare, K.E.; Adam, T.C.; Winslow, E.M.; Lenihan, H.S.; Burkepile, D.E. Size-Dependent Mortality of Corals during Marine Heatwave Erodes Recovery Capacity of a Coral Reef. *Glob. Change Biol.* **2022**, *28*, 1342–1358, doi:10.1111/gcb.16000.

Thomson, G. 2022. Manu: NZ Bird Colour Palettes. R package version 0.0.2, https://github.com/G-Thomson/Manu.

Urbina-Barreto, I.; Garnier, R.; Elise, S.; Pinel, R.; Dumas, P.; Mahamadaly, V.; Facon, M.; Bureau, S.; Peignon, C.; Quod, J.-P.; et al. Which Method for Which Purpose? A Comparison of Line Intercept Transect and Underwater Photogrammetry Methods for Coral Reef Surveys. *Front. Mar. Sci.* **2021**, *8*.

Wickham, H.; Averick, M.; Bryan, J.; Chang, W.; McGowan, L.D.; François, R.; Grolemund, G.; Hayes, A.; Henry, L.; Hester, J.; et al. Welcome to the Tidyverse. *J. Open Source Softw.* **2019**, *4*, 1686, doi:10.21105/joss.01686.

FIGURES

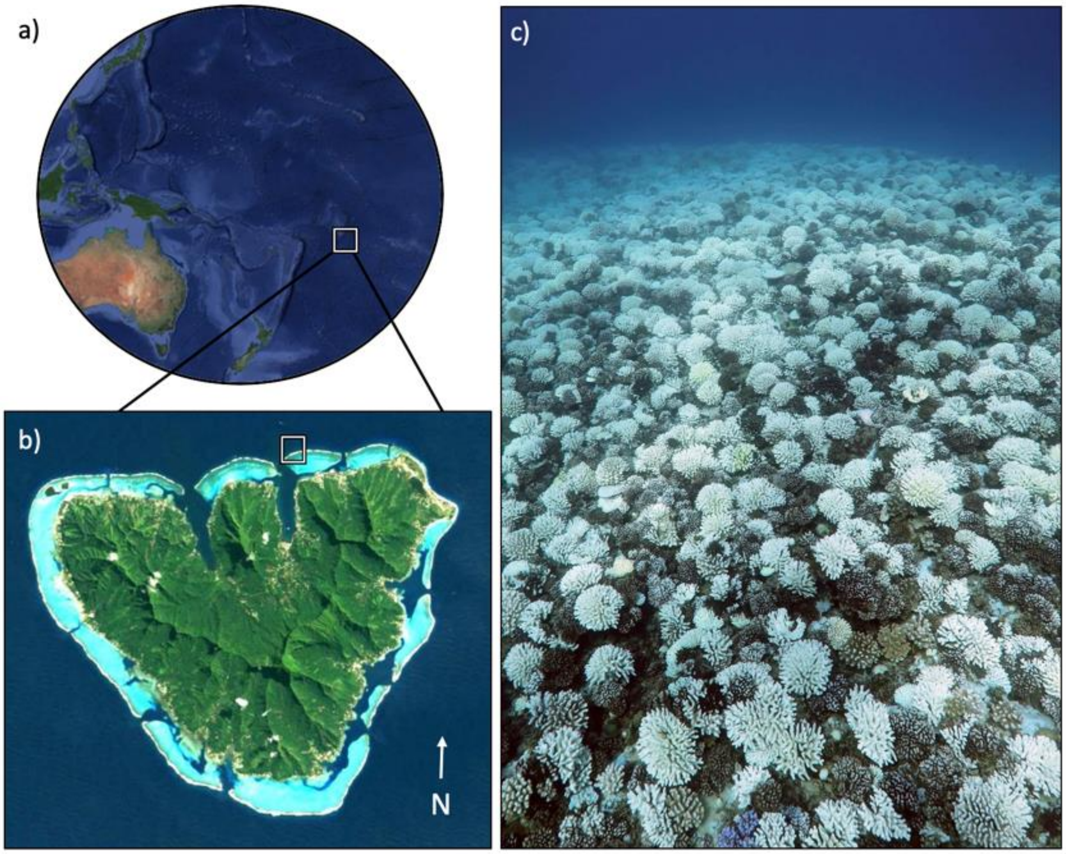


Figure 1. Site location. a) satellite image of geographical location of French Polynesia in the south Pacific Ocean; b) satellite image of Moorea, French Polynesia with a box indicating the location of the study site; c) the fore reef of Moorea near our study site after the bleaching event that occurred in April of 2019 (PC: A. Thurber).

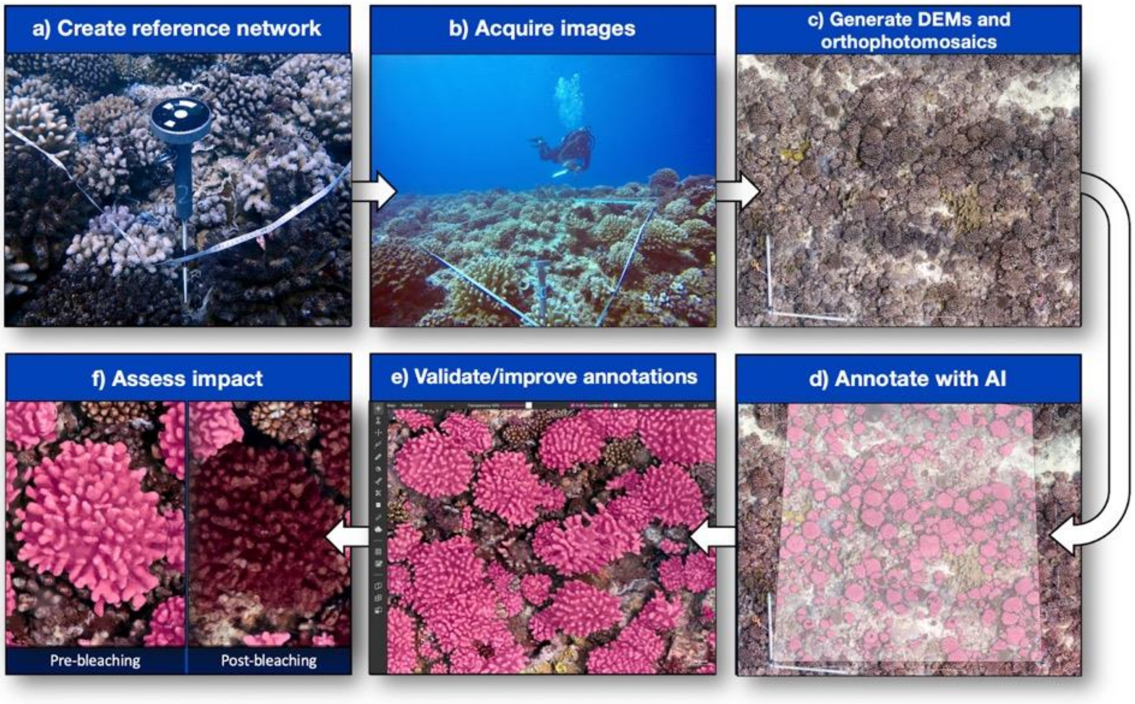


Figure 2. Schematic of workflow: a) custom designed mount for a photogrammetry target that can be screwed into an anchor mounted in the reef substrate (PC: Kai L. Kopecky); b) diver taking photographs of the reef with custom photogrammetry targets in place (PC: Randi N. Honeycutt); c) orthophotomosaic of a single reef plot before the bleaching event; d) automatic segmentations made in TagLab (bright pink shapes) inside of a designated working area (shaded square) on the orthophotomosaic; e) zoomed-in view of annotated live corals in TagLab; f) an example live coral colony (left panel) that died after the bleaching event (right panel).

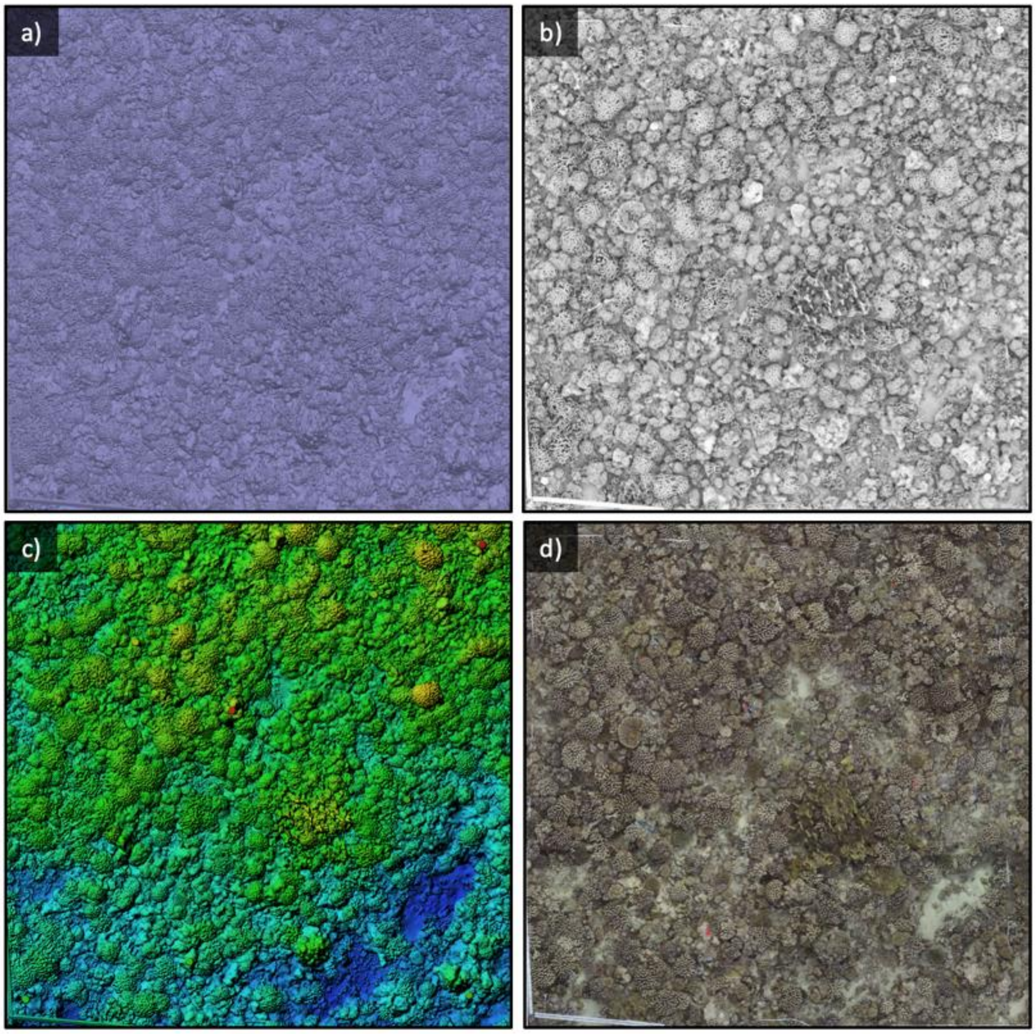
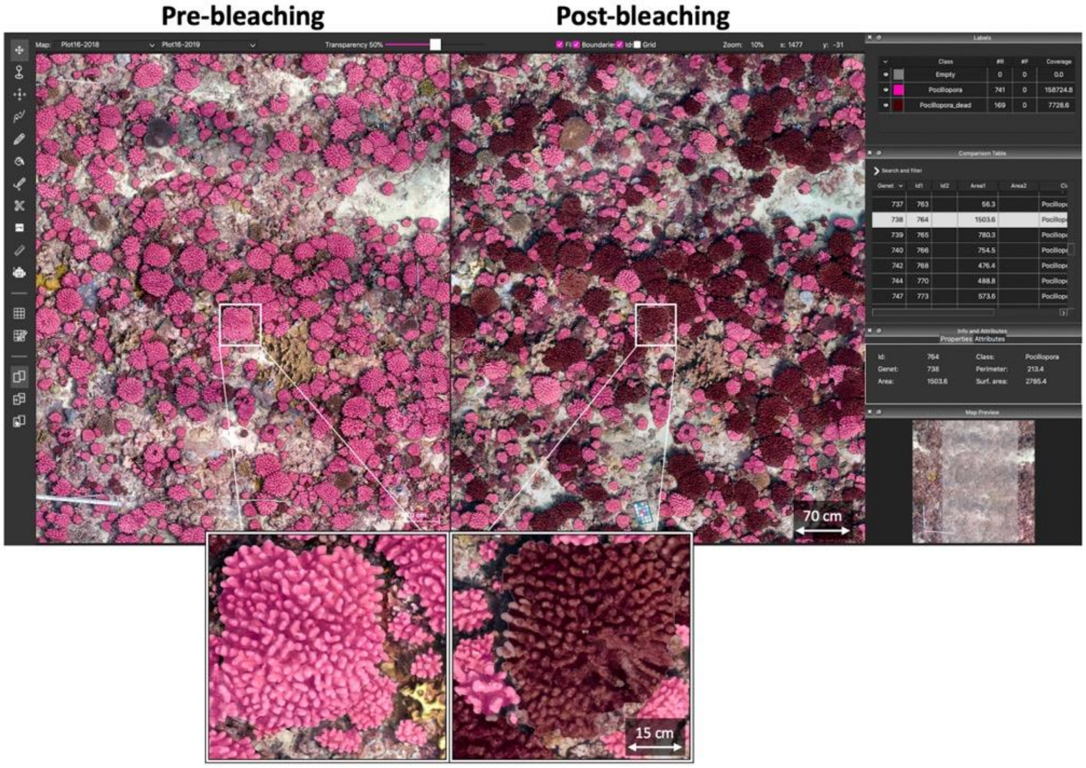


Figure 3. Example of 3D model layers for a single reef plot and epoch. a) 3D mesh model with shaded rendering; b) 3D mesh model with ambient occlusion rendering; c) Digital Elevation Model (DEM); and d) orthorectified photomosaic.



	Class	#R	#P	Coverage
🟫	Empty	0	0	0.0
🟪	Pocillopora	741	0	158724.8
🟥	Pocillopora_dead	169	0	7728.6

Genet	Id1	Id2	Area1	Area2	Cl
737	763		56.3		Pocillop
738	764		1503.6		Pocillop
739	765		780.3		Pocillop
740	766		754.5		Pocillop
742	768		476.4		Pocillop
744	770		488.8		Pocillop
747	773		573.6		Pocillop

Id:	764	Class:	Pocillopora
Genet:	738	Perimeter:	213.4
Area:	1503.6	Surf. area:	2785.4

Figure 4. The TagLab computer interface. A plot with automatic segmentations of live and dead coral before (left) and after (right) the bleaching event. The small images show a live coral colony (left, pink shading) that died as a result of the bleaching event (right, brown shading). White boxes and lines indicate where the example colony is located in each of the larger images. The panels on the far right display various attributes of the plot and the annotated colonies. From top to bottom: total coverage of designated coral classes (i.e., live and dead coral); a data table showing all annotated colonies, co-registered through time; attributes of the selected colony (e.g., 2D planar area, approximated 3D surface area, and perimeter); and a map preview showing the portion of the entire orthophotomosaic that is currently displayed.

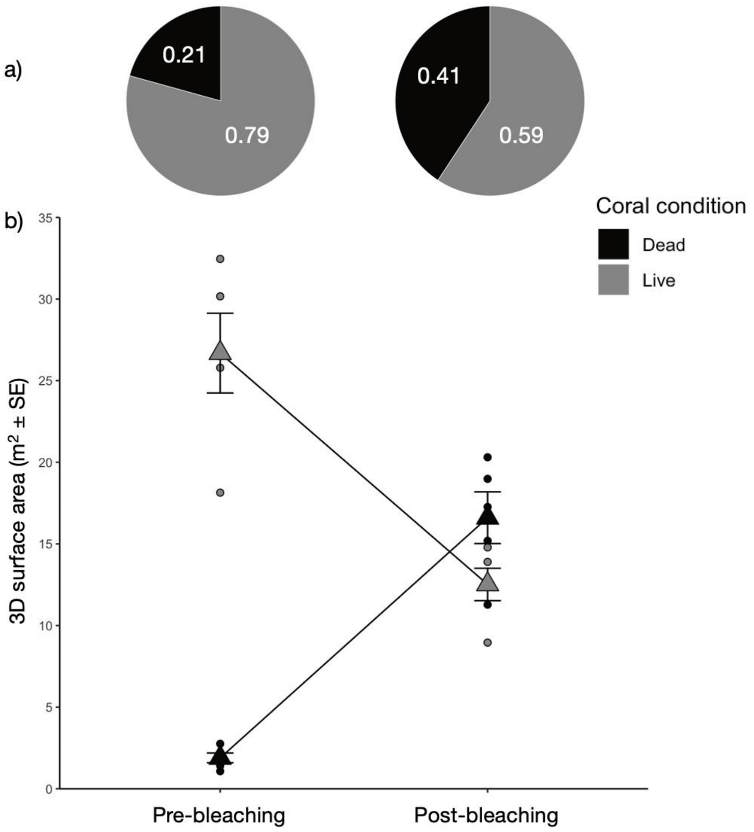


Figure 5. Changes in live and dead coral from before to after bleaching. a) The proportions of the total number of colonies (summed across replicate plots) in each year that were either alive (gray) or dead (black). Total number of colonies before bleaching: N = 4306; total number of colonies after bleaching: N = 4015. b) Total approximated 3D surface areas (m^2) of live coral (gray) and dead coral (black). Triangles indicate means, error bars are ± 1 SE, lines connect means through time, and small dots are plot (replicate) totals.

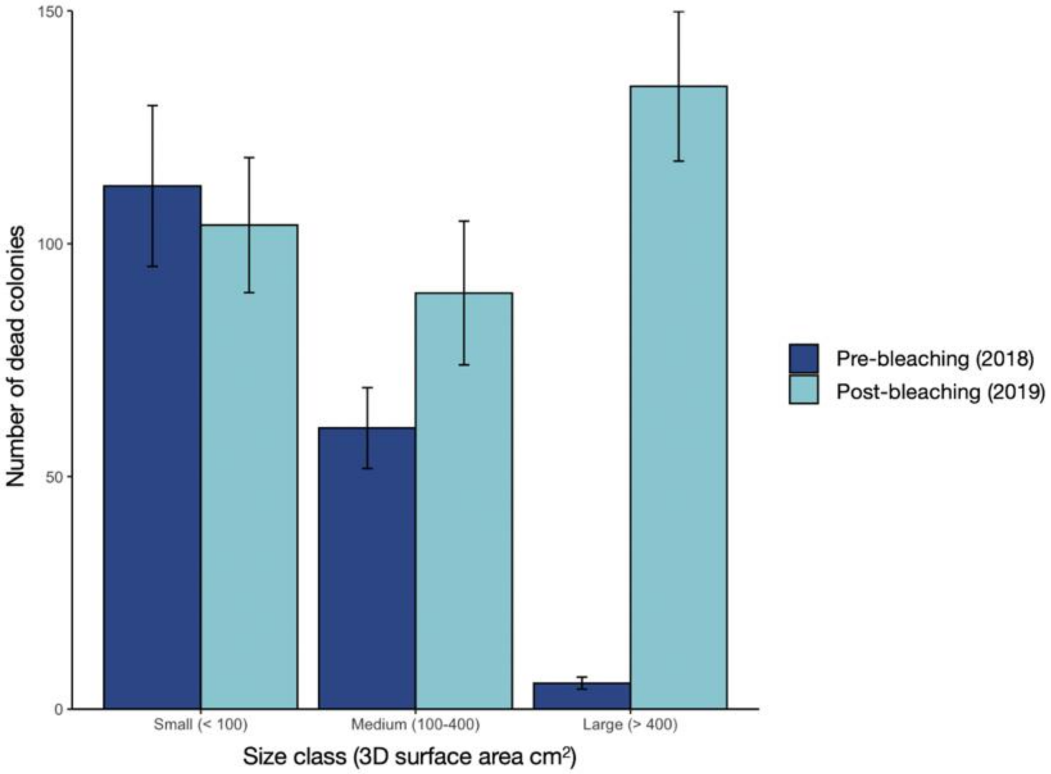


Figure 6. The mean number (± 1 SE; N = 5 plots) of dead coral colonies per plot in three size classes (approximated 3D surface area in cm^2), before (2018, dark blue) and after (2019, light blue) the bleaching event.

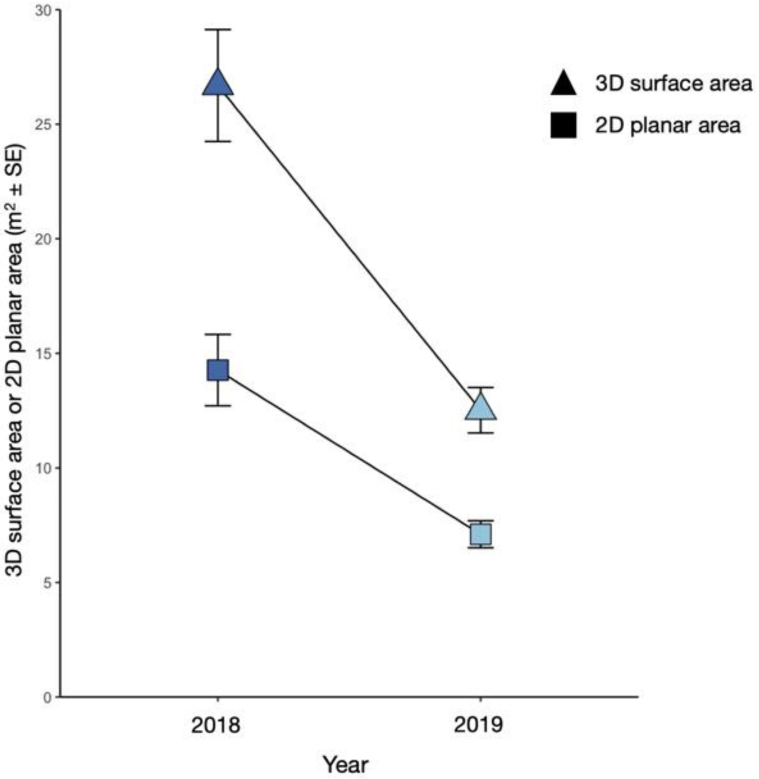
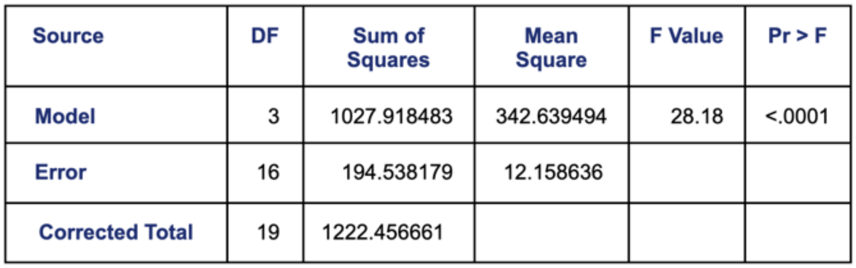


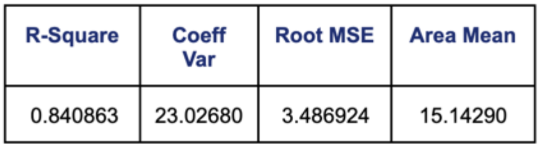
Figure 7. Comparison of estimates of live coral using approximated 3D surface area (m^2, triangles) and 2D planar area (m^2, squares) in 2018 (pre-bleaching, dark blue) and 2019 (post-bleaching, light blue) (plots as replicates). Triangles and squares represent means, error bars are ± 1 SE, and lines connect observations through time.

SUPPLEMENTARY MATERIALS: Appendix A

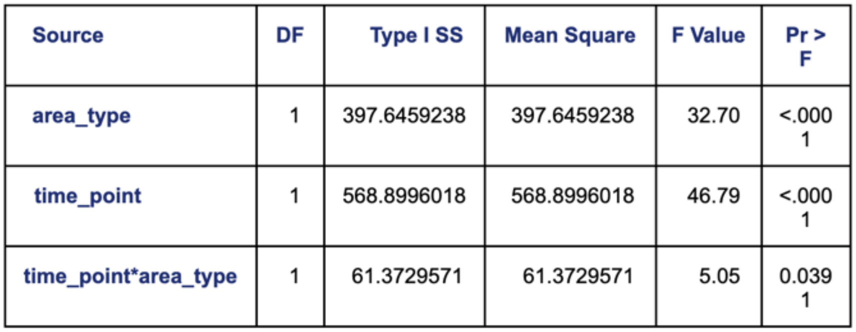
Table A1. Results of Analysis of Covariance (ANCOVA) testing the effect of using 2D vs 3D measures of live coral area to compare changes in cover of live coral before and after a major bleaching event.



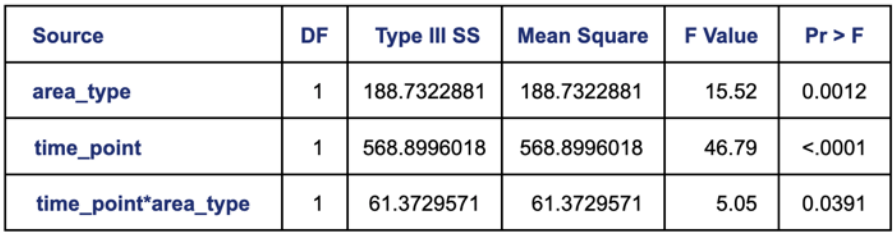
Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	3	1027.918483	342.639494	28.18	<.0001
Error	16	194.538179	12.158636		
Corrected Total	19	1222.456661			



R-Square	Coeff Var	Root MSE	Area Mean
0.840863	23.02680	3.486924	15.14290



Source	DF	Type I SS	Mean Square	F Value	Pr > F
area_type	1	397.6459238	397.6459238	32.70	<.0001
time_point	1	568.8996018	568.8996018	46.79	<.0001
time_point*area_type	1	61.3729571	61.3729571	5.05	0.0391



Source	DF	Type III SS	Mean Square	F Value	Pr > F
area_type	1	188.7322881	188.7322881	15.52	0.0012
time_point	1	568.8996018	568.8996018	46.79	<.0001
time_point*area_type	1	61.3729571	61.3729571	5.05	0.0391

Chapter IV. Clearing a path to resilience: removal of dead coral skeletons mitigates impacts of coral bleaching

ABSTRACT

Ecological disturbance regimes are being modified under global change, and as a consequence, new types of disturbance legacies are arising that pose an uncertain future for contemporary ecosystems. In particular, the standing structures of dead foundation species – a type of *material legacy* – are increasingly prominent in post-disturbance environments and can have lasting effects on ecosystem structure and function, but how these legacies alter ecosystem resilience remains less understood. Here, we explored how the material legacy of an increasingly common disturbance on coral reefs – dead coral skeletons left by heatwave-induced coral bleaching – influences dynamics of spatial competition between corals and macroalgae, relative to when skeletons are removed by cyclonic storms, the historically predominant disturbance type. Shortly after a coral bleaching event in 2019 in Moorea, French Polynesia, we initiated a 4-yr-long pulse field experiment where newly dead coral skeletons were either left intact or manually removed from replicate patches of reef. We then used underwater photogrammetry combined with AI-powered image analysis to quantify subsequent patterns of coral growth and death, as well as proliferation of macroalgae, as a function of the initial presence or absence of intact dead skeletons. Our results provide multiple lines of evidence that dead coral skeletons diminish coral resilience, and that removing them can help mitigate adverse impacts of a coral bleaching event on post-disturbance dynamics. After four years, plots where we had removed dead skeletons had 1.6 times more live coral and less than half the amount of macroalgae compared to plots where skeletons were left in place. Among-plot variation in the abundance of macroalgae was strongly tied to the

prevalence of dead coral skeletons, and in turn, higher cover of macroalgae resulted in a greater reduction of live coral over time. Lastly, removing dead skeletons stimulated four times greater recruitment of corals onto stable, primary reef substrate, relative to when dead coral was not manipulated. These findings highlight promising avenues to explore to manage for resilience of contemporary coral reefs, which increasingly are perturbed by heatwaves, outbreaks of predatory seastars and other such disturbances that generate large standing stocks of dead coral skeletons. As material legacies in general become more prominent under global change, there is an increasing need to understand their emerging ecological roles and integrate this knowledge into current conservation and management of ecosystems.

INTRODUCTION

As ecological disturbance regimes shift under changing global conditions, it becomes increasingly critical to understand how the novel legacies of these shifting regimes will alter the resilience of contemporary ecosystems. Of particular concern are the fates of foundation species, such as trees and corals, which dominate their respective ecosystems in abundance and/or biomass. Due to their pervasiveness, foundation species and the biogenic structures they create confer strong influences over ecological processes tied to resilience (Ellison 2019, Lamy et al. 2020, Kopecky et al. 2023a). These organisms are particularly vulnerable to global change, as historically rare disturbances like episodes of thermal stress and outbreaks of pests or predators that cause mass mortality of these organisms become commonplace (Dai 2013, Hughes et al. 2017, Oliver et al. 2018). The loss of foundation species can have enduring effects on the resilience properties of ecosystems (Ellison et al. 2005), and an emerging focus is to understand how the dead structures of these organisms that remain after disturbance – a type of *material legacy* – affect the capacity for ecosystems to regain their pre-disturbance conditions (Johnstone et al. 2016, Saldaña et al. 2023).

One aspect that hampers the study of material legacies from foundation species is the range of scales and high spatial resolutions required to appropriately explore how they may alter resilience properties of the ecosystem. Recent innovations in tools used for ecological observation enable us to detect changes at unprecedented scales, providing a window to better understand the impacts of disturbance on foundation species across space and through time. Specifically, advances in remote sensing technologies allow us to survey extensive areas at fine-scale resolution both on land (Kerr and Ostrovsky 2003, Lechner et al. 2020, Lee et al. 2020) and underwater (Hedley et al. 2016, McCarthy et al. 2017, Carneiro et al. 2024, Remmers et al. 2024). Further, advances in artificial intelligence (AI) enable us to efficiently extract high volumes of data from remote sensing products (Bjorck et al. 2021, Pavoni et al. 2022), making it possible to do so at ecologically meaningful temporal and spatial scales. This combined approach has been increasingly used to map biological and physical attributes of landscapes to assess levels of environmental quality and monitor changes in species distributions (Shi and Li 2007, Nourani et al. 2020, Burns et al. 2022, Rapinel et al. 2023), but a newer focus is to directly evaluate the impacts of ecological disturbances and track subsequent patterns of recovery or degradation. For instance, remote sensing and AI have been implemented in concert to detect outbreaks of pathogens that cause widespread mortality of trees in forests (Sandino et al. 2018, Iordache et al. 2020, Marvasti-Zadeh et al. 2023), as well as quantify the loss of reef-building corals following episodes of bleaching on coral reefs (Kopecky et al. 2023b).

Coral reefs showcase both the power of combining remote sensing and AI, as well as the critical issue of shifting disturbance regimes. While tropical storms that generate powerful waves were historically the primary agent of disturbance on coral reefs, marine heat waves and outbreaks of coral predators (Crown of Thorns seastars) have become increasingly prominent sources of widespread coral mortality over the last several decades (Hughes et al. 2017, Pratchett et al. 2017, Oliver et al. 2018). Unlike tropical storms which tend to scour coral skeletons from the reef (Harmelin-Vivien 1994, Gardner et al. 2005), thermal stress events and predator outbreaks tend to leave dead coral skeletons intact (Baker et al. 2008, Pratchett et al. 2017), and thus create a fundamentally different benthic environment in which subsequent community reassembly takes place. Recent empirical evidence shows that dead branching coral skeletons can facilitate the development of macroalgae – a spatial competitor of coral –

by impairing the ability of herbivores to forage and limit successful recruitment of new coral colonists (Kopecky et al. *in review*). Additionally, recently developed theory suggests impairment of this nature can cascade into long-term consequences for coral resilience, like shifts from coral to macroalgae-dominated reefscapes (Kopecky et al. 2023a) that can be especially challenging or impractical to reverse (Schmitt et al. 2019, 2022). An important aspect that remains to be more fully explored is how dead skeletons modify spatial interactions between coral and macroalgae in the wake of a disturbance (e.g., coral bleaching or predator outbreaks) and thereby influence the outcomes of coral-algae spatial competition.

To address the open question of how dead skeletons affect competition between coral and macroalgae for reef space, we initiated a long-term field experiment following a moderately severe coral bleaching event on the reefs of Moorea, French Polynesia that caused widespread coral mortality. In the 4 years following this bleaching event, these reefs have shown continued declines in coral and concomitant increases in macroalgae, which stands in sharp contrast to the rapid recovery of coral (~5 years) that took place after a powerful cyclone killed almost all colonies on the same reefs in 2010 (Holbrook et al. 2018). Importantly, dead skeletons were largely removed from these reefs by the cyclone, whereas vast canopies of dead branching coral skeletons have remained following the recent bleaching event. To explore whether the capacity for reef recovery is limited by the retention of dead skeletons after disturbance, we compared trajectories of coral and macroalgae assemblages inside 4 m^2 patches of reef where we manually removed dead skeletons with those inside unmanipulated patches. To track coral growth and death, as well as the development of macroalgae, in these patches at a very high (sub-centimeter) spatial resolution over several years, we implemented a robust workflow that combined underwater photogrammetry with AI-powered image analysis. We tested three central questions regarding the role of dead coral skeletons in post-disturbance benthic dynamics compared to when they are removed: 1) How do dead standing coral skeletons affect the growth and survival of live coral relative to when dead skeletons are removed? 2) How do dead skeletons influence the proliferation of macroalgae through time and across space? and 3) How do dead skeletons affect the distribution pattern of newly settled corals among microhabitats, and therefore their likely fate?

METHODS

Site description

Moorea, French Polynesia (17.5388° S, 149.8295° 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 are typically 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. In April 2019, a moderately severe 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 coral skeletons intact on the reef.

Removal of dead coral skeletons

In August of 2019, four months after bleaching when affected colonies had either died or recovered, we demarcated 20 plots, each roughly 4 m^2 in area and spaced > 1 m from its nearest neighbor, over an area of ~1000 m^2 at a depth of 9 – 11 m on the north shore fore reef. This exact study site was studied extensively following Cyclone Oli in 2010 (Adam et al. 2011, Holbrook et al. 2016, 2018, Schmitt et al. 2019). We used visual estimates to select reef areas that reflected natural variation in the cover of live *Pocillopora* (15-30%; by far the most dominant coral taxon) and dead branching coral (15- 38%). We then identified pairs of these plots with similar amounts of live and dead coral coverage and randomly selected one plot from each pair from which to remove dead branching coral skeletons (i.e., the *Skeleton removal* treatment), then left the other plot unmanipulated. We assigned plots to treatments in this way to ensure that each treatment contained ten plots with similar ranges in live and dead coral before manipulation. Before removing any skeletons, we photographed each plot using our photogrammetric workflow (described in the next section), then in August 2019, we manually removed dead branching coral skeletons from the ten designated plots using hammers and chisels and transported the dead skeletal material to nearby reef grooves well below the plots. Because some corals had undergone only partial mortality, we removed any colonies with > 50% tissue loss, assuming these would soon die completely, but left dead skeleton material in place on colonies with < 50% mortality, meaning the Skeleton removal treatment still contained some dead coral structure (Fig. S1). At the start of the experiment, both treatments had an equivalent amount of live coral (Skeletal removal: 2.41 ± 0.17 m^2; Skeletal retention: 2.47 ± 0.11 m^2; Fig S2). Lastly, we also removed any existing macroalgae from the Skeleton removal plots, assuming that macroalgae would also be dislodged during a wave-scouring disturbance event such as from a powerful cyclonic storm (Harmelin-Vivien 1994). No subsequent manipulations were undertaken for the 4-year duration of this experiment.

Image collection and photogrammetry

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 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 in the center; we used the four corner reference points to delimit the perimeter of each plot. Due to the distribution of suitable substrate into which anchors could permanently be installed in the reef, our plots varied somewhat in shape and size, but the average plot areas were similar between treatments (Skeleton removal mean plot area ± SE: 4.1 ± 0.2 m^2; Skeleton retention: 3.9 ± 0.1 m^2). The measured relative positions among reference points within a plot create what is referred to as a 'geodetic network' (a three-dimensional coordinate system with known dimensions), which allows us to set the scale of our photogrammetric models as well as spatially co-register models of the same plot from different timepoints (Nocerino et al. 2020). To create the geodetic network of each plot, we measured the lateral distances between all five reference points to the nearest millimeter using a metal measuring tape, taking repeated reciprocal measurements (e.g., from point 1 to point 2 and from point 2 to point 1) to obtain an average distance and minimize error; prior quantification of the error in 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). Then, we used a dive computer to measure the depth of each reference point (to the nearest tenth of a meter) to obtain relative elevational differences among the reference points (i.e., the Z-dimension).

We collected images of our plots to build orthophotos using SCUBA in the austral winters of each year from 2019 – 2023, implementing the general protocol described by Nocerino et al. (2020). When photographing a plot, we screwed custom-made, aluminum posts mounted with coded photogrammetry targets (which aid in auto-alignment of images when building photogrammetric models) into each reference point anchor and laid a transect tape around the perimeter of the plot. We then collected images, with ~80% overlap between sequential images, from a top-down perspective by continuously taking photographs in a 'lawnmower pattern', or a series of parallel passes, followed by a second series of passes perpendicular to the first. Finally, we took one series of images from a 45-degree angle relative to the reef plane (referred to as 'oblique') from around the perimeter and pointed toward the center of the plot. Photographing our reef plots from roughly 1 m above the reef yielded a ground sample distance that ranged from 0.3-0.5 mm/pixel. We collected 200-300 images of each plot at each time point using an Olympus Tough TG6 camera inside an Olympus underwater camera housing mounted with a wet dome port lens.

We used Metashape Pro (version 2.0.3) to build 3D models, DEMs, and orthophotos for image analysis. Using the geodetic networks, we created 'reference panes', or sets of X, Y, and Z coordinates for each plot that could be applied to the point cloud of each successive time point to standardize the perspective of the orthophotos through each time point and minimize measurement errors associated with differing angles or points of view. 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 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 general workflow outlined in Kopecky et al. (2023b) to annotate our orthophotos and extract metrics of coral growth and death, as well as the development of macroalgae over time. 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, which 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 and dead coral in the orthophotos from all five timepoints in each of four plots (i.e., 20 orthophotos) using 'semi-automatic' segmentation tools (see Pavoni et al. 2022) to build a training dataset. This dataset was then used to train a fully automated classifier via machine learning (see Pavoni et al. 2022 for more details) to annotate and measure the three-dimensional surface areas of live and dead corals in the remaining (79) orthophotos.

Because branching corals were most impacted by the bleaching event (Speare et al. 2022), we focused on these taxa in this study – specifically *Pocillopora* spp. and *Acropora* spp. To evaluate the effects of dead skeleton removal on live coral cover over time, we calculated the fraction of live branching coral remaining at each time point, standardized to the amount present at the start of the experiment, setting all values equal to one at the initial time point (2019). This standardization did not introduce bias because both treatments began with equivalent amounts of live 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). We then built a generalized linear mixed effects model (package glmmTMB) to test for differences between treatments in the proportions of live coral remaining at each successive time point, testing for an interaction between skeletal treatment and time point. For this model, we used a beta distribution and logit link function and treated time point as a categorical variable. Because we set all values to one for the initial 2019 sampling date, we omitted this time point from the model. For the GLMM analysis, we treated plot identity as a random effect to account for random variation among our replicate plots and for repeated measures through time.

Because macroalgae exhibit highly variable growth morphologies and are moved easily by ocean surge, we could not use the same image segmentation technique as we did for coral to quantify cover of macroalgae. Instead, we used a point classification method to estimate macroalgae cover, 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 taxa. As we did for coral, we built a generalized linear mixed effects model to test for differences between treatments in the cover of macroalgae at each time point and tested for an interaction between skeletal treatment and time point. We used a beta distribution, a logit link function, treated time point as categorical, and set plot identity as a random effect. We again omitted the initial time point from this analysis because algae cover was very low ($\leq 2\%$) in all plots and in both treatments at the start of the experiment. To explore the degree to which macroalgae grew on 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 within each treatment and 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, relative to primary reef substrate and 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 influence the prevalence of macroalgae, we tested the degree to which the amount of dead coral in a plot at a given time point influenced the amount of macroalgae. Because dead coral was present in varying quantities across both treatments and all time points, we did not explicitly consider treatment or time in this analysis, and instead explored the effect of dead coral as a continuous predictor on the amount of macroalgae in each plot x time point combination. We used a generalized linear mixed effects model with a beta distribution and logit link function, but in this case, we set both time point and treatment as random effects. Lastly, we tested whether the mean cover of macroalgae between two sample years (hereafter, a *period*) influenced the proportional change in live coral over the same period. We calculated the mean cover of macroalgae for a period simply by adding the percent cover of macroalgae into successive years and dividing by two for each plot. To calculate the proportional change in live coral over each period, we subtracted the amount of live coral in a year from the amount in the following year, then divided by the earlier year for each plot x period combination. For this analysis, we built a linear mixed effects model of the proportional change in live coral in a period as a function of the average cover of macroalgae in the same period. We used a Gaussian distribution and set time period and plot identity 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). While the high resolution of our orthophotos were able to reliably capture larger juvenile corals (i.e., > 2 years old), corals that settled between 2022 and 2023 would likely have been too small and/or cryptic to be detected with the resolution of our orthophotos. We instead conducted visual counts *in situ* of coral recruits in our experimental plots in August 2023 to assess whether corals preferentially settled on primary reef substrate, standing dead coral, or coral rubble. While on SCUBA, we visually counted *Acropora* spp.*, Pocillopora* spp.*,* and *Porites* spp. recruits ≤ 5cm in diameter, noting which of the three substrate types each recruit had settled on. We used a Chi-squared contingency test to assess whether there were significant associations of recruits to each substrate type, and whether this depended on the skeletal treatment. All analyses were performed and visualizations created in R (Version 4.2.3; R Core Team 2023) and R Studio (Version 2023.12.1.402; Posit team 2024) using the Tidyverse package (Wickham et al. 2019). Visualizations utilized colors from the Manu: NZ Bird Colour Palettes (Thomson 2022) and the California Ecosystems Palettes (calecopal) package (Bui 2024).

RESULTS

Our fully automatic classifier was able to rapidly and accurately detect, measure, and identify live and dead colonies of *Pocillopora* spp. and *Acropora* spp. relative to a human observer, reducing labor time by up to two orders of magnitude. By comparing the human-annotated training dataset with the fully automatic classification of the same images, we found that the accuracy of the automatic classifier in correctly identifying pixels of the various classes was

95.1% for background (i.e., not objects of interest), 92.5% for *Acropora*, 92.1% for *Pocillopora*, and 85% for pixels of dead coral (Fig. S3). The slightly lower accuracy achieved for dead coral is attributable to the automatic classifier (understandably) mistaking this class as background reef substrate (see confusion matrix, Fig. S3), as these two classes appear similar to one another in later years of the experiment as the dead corals break down and disintegrate. Some minor correction of the automatic classifications was therefore needed to resolve mistaken identification of dead coral as background, and vice versa, as well as to manually divide multiple live coral colonies of the same class (taxon) that shared borders and were therefore mistakenly annotated by AI as a single colony.

Our experiment revealed marked effects of removing dead coral on the outcomes of spatial competition following a coral-killing disturbance. While live coral cover declined in both treatments during our four-year experiment, significantly more live coral remained in the Skeleton removal treatment than the retention treatment in all years after 2019 ($p < 0.05$, pairwise contrasts with Bonferroni correction; Fig. 2a). While the amount of live coral was virtually identical at the start of the experiment in 2019, after four years, 1.6 times more live coral remained in plots where we had removed dead coral in 2019 compared to unmanipulated (Skeleton retention) plots. On average, 1.13 ± 0.15 m^2 (mean ± SE) of live coral remained by the final time point in plots where we had removed dead coral, compared to 0.71 ± 0.7 m^2 remaining in the plots where we left dead coral intact (Fig. S2). The percent cover of macroalgae also varied by treatment and through time. At the start of the experiment, macroalgal cover was very low in all plots of both treatments ($\leq 2\%$; Fig. 2b). Apart from this first time point, however, macroalgal cover remained significantly and consistently lower in the Skeleton removal treatment for all subsequent time points ($p < 0.001$, pairwise contrasts with Bonferroni correction; Fig. 2b). One year after the start of our experiment (in 2020), the cover of macroalgae had increased in both treatments, but 3-fold more sharply in plots where dead skeletons were retained, reaching an average of 23.0 ± 2.6% cover (mean ± 95% CI), compared to 8.0 ± 1.0% in plots where Skeletons were removed. After 2020, both treatments decreased somewhat in algae cover and more or less stabilized for the remainder of the experiment, with macroalgae staying at least twice as abundant in plots where skeletons were left intact (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 clear dominant taxon across nearly all time points in both treatments, largely driving the initial spike of macroalgae in 2020 (Fig. 3). The other three taxa contributed relatively less to overall macroalgae cover, increasing in both treatments more gradually throughout the experiment. Notably, these four taxa showed varying degrees of association with dead coral skeleton as a substrate, compared with primary reef (Skeleton removal: χ^2 (3) = 377.27; $p < 0.001$; Skeleton retention: χ^2 (3) = 455.35; $p < 0.001$), but the strength of these associations varied by taxa and by treatment (Fig. 3). Unsurprisingly, all taxa were more often found growing on dead skeletons in the Skeleton retention treatment, where dead skeletons were consistently more abundant, than in the Skeleton removal treatment (pie charts in Fig. 3; Fig. S1). *Asparagopsis* and *Halimeda* seemed to grow on dead skeleton somewhat proportionally to its availability as a substrate: 62% and 56% of points, respectively, fell within regions of dead coral in the retention treatment, and 33% and 22% in the removal treatment. By contrast, the majority of points identified as *Lobophora* fell within regions of dead coral in both treatments: 86% of points in the Skeleton retention treatment, and 69% in the removal treatment. *Turbinaria* showed the opposite association, where only 5% of points in the removal treatment were found on dead skeletons, and 20% in the retention treatment, while the majority in both treatments were found on primary reef. A Chi-squared post-hoc test revealed that all associations to substrates were significant for the four algal taxa ($p < 0.001$ for all).

Due to continued mortality of live coral after the bleaching event, dead coral skeleton continued to accumulate in both skeleton treatments throughout our study. While the amount of dead coral was consistently lower through time in the Skeleton removal treatment over time (Fig. S1), the ranges in dead coral cover for each treatment 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 significantly 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), apart from the initial timepoint when macroalgae were effectively absent in all plots. The change in live coral for a plot between two sample years (i.e., a period) was significantly negatively correlated with the mean cover of macroalgae in that plot over the same period (slope estimate: -0.008 ± 0.002, $p < 0.001$; Fig. 4b). In other words, steeper declines in live coral cover occurred in each period when macroalgae were increasingly abundant during that period. Only two plots showed net positive changes in coral cover between two successive years, both of which were in the Skeleton removal treatment (Fig. 4b).

Our quantification of young coral recruits in the final year of the experiment (2023) revealed clear patterns in coral settlement relative to available substrate types. While we observed roughly similar total numbers of coral recruits in the two treatments (Skeleton removal: n = 44; Skeleton retention: n = 54), the pattern of association between dead skeletons and primary substrate differed significantly between the treatments (χ^2 (1) = 20.8, $p < 0.001$;

Fig. 5a). The proportion of recruits that had settled on primary reef (59%) was nearly four times higher in the Skeleton removal treatment than the retention treatment (15%), whereas settlement onto dead coral was almost 2.5 times higher in the retention treatment (82%) than the removal treatment (34%; Fig. 5a). By 2023 (the last year of the experiment), there was twice as much dead coral on average in the Skeleton retention treatment than the removal treatment ($t_{15.0} = -6.3$, $p < 0.001$; Fig. 5b); this difference was mirrored by the twice as great proportion of coral recruits on skeletons in the retention (82%) relative to the removal (41%) treatment. Together, these data suggest that corals likely do not show settlement preference between dead coral skeletons and primary reef as substrate types, but rather settle roughly in proportion to substrate availability.

DISCUSSION

With the onset of global change, ecosystems increasingly face altered disturbance regimes that pose an uncertain future for the resilience of these systems. In particular, disturbances that leave behind standing structures of dead foundation organisms have been brought to the forefront, and as a consequence, these material legacies are becoming prominent features of contemporary ecosystems (Swanson et al. 2011, Johnstone et al. 2016, Kopecky et al. 2023b, Saldaña et al. 2023). Here, we combined novel techniques in underwater photogrammetry and machine learning (AI) to understand how standing dead coral skeletons produced by coral bleaching – the material legacy of an increasingly common form of disturbance – influence the outcomes of benthic spatial competition between corals and macroalgae on coral reefs. While coral decline was pervasive across space and time in our study, we found that removing dead skeletons soon after a bleaching event substantially reduced this decline and mitigated the development of macroalgae that compete with corals for reef space. The majority of these macroalgae relied on dead coral as a substrate and therefore were more prevalent when dead coral was more abundant. Further, we showed that higher amounts of macroalgae drove steeper declines in live coral cover. Lastly, we found that coral recruits also readily settled on dead skeletons when available, but they did not appear to exhibit a preference for these structures as a settlement substrate relative to primary reef, raising concern for the fates of corals that recruit following disturbances that leave behind large quantities of standing dead coral skeletons.

Dead skeletons influence the outcomes of spatial competition between coral and macroalgae

While the competition for benthic space between coral and macroalgae has been extensively explored (Lirman 2001, McCook et al. 2001, Stiger et al. 2004, Smith et al. 2006, Kuffner et al. 2006, Holbrook et al. 2016, Bulleri et al. 2018, Puk 2020, Adam et al. 2022, Schmitt et al. 2022), we present here the novel contribution that the outcomes of this interaction can be heavily swayed by dead coral skeletons, a material legacy of coral bleaching events. Our four-year experiment showed that dead skeletons acted as substrate that promoted the development and persistence of macroalgae that then drove losses of live coral. Specifically, the dominant algal taxon we observed in our reef plots throughout our experiment, *Lobophora* spp., is well known to aggressively compete with reef-building corals, in some cases helping to drive shifts from coral-dominated to algae-dominated reefscapes (Vieira 2020). This taxon was not only the most abundant among the macroalgae that developed in our experimental plots, but also the most strongly tied to the prevalence of dead coral. Further, when macroalgae were more abundant during a given time period, live coral were lost at a faster rate. Our experiment suggests, therefore, that dead coral skeletons can provide substrate that favors the proliferation of harmful macroalgae that outcompete live coral, thereby swaying the outcomes of coral-algae competition and ultimately undermining coral resilience.

In general, herbivorous fishes are the agents that prevent the colonization of macroalgae after disturbance (Burkepile and Hay 2008, Adam et al. 2011, Holbrook et al. 2016, Schmitt et al. 2019) and remove macroalgae that have become established (Bellwood et al. 2006). However, *Lobophora* and other species of macroalgae are sometimes capable of escaping top-down control, either when herbivore abundance is depleted (e.g., via disease or overfishing; Hughes 1994, Jackson et al. 2014) or by growing within complex reef structures that provide refuge space from herbivores (Bennett et al. 2010, Puk et al. 2020, Kopecky et al. *in review*). Moorea is a relatively isolated island with only a small-scale reef fishery and with no documented disease outbreaks affecting herbivore species (Leenhardt et al. 2016). Further, surges in the biomass and numerical abundance of herbivorous fish species were observed in response to increased algae abundance following a cyclone in 2010 that caused substantial mortality of coral but removed dead coral skeletons, which provided herbivores with an enhanced supply of algal resources (Adam et al. 2011, Han et al. 2016). We therefore posit that the complex structure of the dead branching coral skeletons provided ample refuge space from herbivores for macroalgae, and thereby facilitated their rapid and persistent proliferation in our unmanipulated (Skeleton retention) reef plots, relative to plots where we had removed dead skeletons. This in turn led to greater losses of live coral in reef patches where dead skeletons were more prevalent.

While dead skeletons may be a favorable substrate for macroalgae, the same may not be true for recruiting corals. The dead skeletons of complex coral morphologies have been found to erode over a few years if undisturbed (Ferrari et al. 2017, Morais et al. 2022), including in our fore reef system (Adam et al 2014), becoming brittle and eventually breaking apart into rubble. The survival of coral recruits on dead skeletons and rubble is generally much lower compared to that of recruits on consolidated reef surfaces (Fox et al. 2003, Swanson 2016, Yadav et al. 2016, Kenyon et al. 2023), and the prevalence of both dead coral skeletons and subsequently rubble is expected to increase on contemporary reefs with the projected increase in both tropical storms and thermal stress events (Wehner et al. 2017, Oliver et al. 2018). In our experiment, recruitment of corals onto unstable dead coral skeletons was two and a half times higher when dead skeletons were in place, whereas reducing the standing stock of dead coral skeleton after bleaching increased settlement of coral recruits onto primary reef substrate four-fold. While this poses a concerning future for coral reef recovery, as the increasing prevalence of dead coral skeletons will likely serve as a sink for recruiting corals, our results suggest that removing dead skeletons could stimulate recovery of coral populations by increasing coral recruitment onto stable reef surfaces that enhance the long-term survival of settling corals.

Ecological and technological generality of findings

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 community trajectory, 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 the coral bleaching event created a markedly different set of post-disturbance conditions for recovery to take place in, which likely reduced the effectiveness of vital recovery processes like herbivory and the growth of surviving and newly recruited coral colonies (Kopecky et al. *in review*). The altered post-disturbance conditions brought on by shifting disturbance regimes can therefore create misalignments between historic attributes of ecosystem resilience and contemporary disturbances these ecosystems now face.

To fully understand the impacts and consequences of shifting disturbance regimes on ecological properties, innovative approaches that capture ecologically meaningful scales are needed. Our combined use of underwater photogrammetry and AI to evaluate the effects of dead skeletons on coral reef benthic dynamics provides a useful and widely applicable tool for exploring material legacy effects in other ecosystems. We build on previous tool development and application (Guo et al. 2016, Sandino et al. 2018, Iordache et al. 2020, Nocerino et al. 2020, Burns et al. 2022, Kopecky et al. 2023, Marvasti-Zadeh et al. 2023, Miller et al. 2023) by showing the utility of these tools not just for monitoring purposes, but also for experimentation. This strategy can be especially useful for studies that aim to explore the spatio-temporal dynamics of foundation organisms *in situ* in a non-destructive manner, which is critical as these organisms are increasingly threatened by global change (Ellison et al. 2005, Fraser et al. 2014, Saldaña et al. 2023). Further, because our photogrammetric workflow creates permanent, high-resolution, and spatially co-registered records of the environment, this technique allows for continued data collection and scientific investigation into the future. This greatly enhances the power of time series, as not only is it possible to conduct new analyses on existing data, but it is also possible to extract new data from the past to address entirely new questions. We therefore encourage the expanded use of remote sensing technologies coupled with AI-powered analysis techniques beyond the contexts of ecological monitoring into more experimental and mechanistic applications.

Potential applications for conservation and management

The combined findings from our study reveal promising avenues to explore in the context of managing contemporary coral reefs to enhance resilience. In our experiment, physically removing dead coral skeletons from the reef resulted in multiple benefits from the perspective of mitigating the impacts of coral bleaching, or other disturbances that leave in place large stands of structurally complex dead coral skeletons (e.g., outbreaks of coral predators). Where we had reduced the initial standing stock of dead coral, we saw substantially more live coral remaining after several years, reduced accumulation of macroalgae, and increased recruitment of corals onto stable reef substrate. While coral declined and macroalgae increased even in plots where we had initially removed dead skeletons, we implemented this manipulation only once at the beginning of the experiment. Had we continually removed dead coral skeleton throughout the experiment, the loss of live coral and buildup of macroalgae would likely have been further reduced, as suggested by the strong correlation we observed between these metrics and the amount of dead coral present. We therefore recommend further study centered on the removal of dead coral skeletons as a direct management strategy to foster reef recovery after coral bleaching events or outbreaks of coral predators, like the Crown of Thorns seastar, both of which are increasingly prominent forms of disturbance on coral reefs (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 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 dead coral removal on the abundances and assemblages of coral-associated fishes and invertebrates that may or may not reside in dead branching coral skeletons before attempting to remove dead coral on a large scale.

To date, the roles of dead coral skeletons have received little attention from a conservation and management standpoint. In other ecosystems, however, the important roles material legacies play in ecosystem dynamics have long been integrated into management and restoration practices. On oyster reefs, dredging and overharvesting have extirpated oysters from much of their historical habitats, which as a consequence has left behind enduringly degraded mud flats (Lenihan and Peterson 1998). To foster recovery of oyster reefs, piles of dead oyster shells are often deployed to stabilize the underlying loose sediment and provide settlement substrate for larval oysters (Howie and Bishop 2021). In forests, managers intentionally retain large dead trees (snags) that provide important habitat for forest-dwelling species and enhance forest biodiversity (Swanson et al. 2011, Vítková et al. 2018) but remove smaller dead trees and other woody debris (either mechanically or via prescribed burning) to reduce fuel loads and mitigate the risk of severe wildfire (Shang et al. 2004, Husari et al. 2006). We would be wise to follow the examples offered by these other ecosystems by explicitly considering how dead coral skeletons could be leveraged to achieve desired management goals. 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. As material legacies become more prominent ecological features under global change, our emerging understanding of the strong, yet nuanced ways in which they drive community dynamics may be a vital contribution to the effort of conserving contemporary ecosystems.

REFERENCES

Adam, T. C., A. J. Brooks, S. J. Holbrook, R. J. Schmitt, L. Washburn, and G. Bernardi. 2014. How will coral reef fish communities respond to climate-driven disturbances? Insight from landscape-scale perturbations. Oecologia 176:285–296.

Adam, T. C., S. J. Holbrook, D. E. Burkepile, K. E. Speare, A. J. Brooks, M. C. Ladd, A. A. Shantz, R. Vega Thurber, and R. J. Schmitt. 2022. Priority effects in coral–macroalgae interactions can drive alternate community paths in the absence of top-down control. Ecology 103:e3831.

Adam, T. C., R. J. Schmitt, S. J. Holbrook, A. J. Brooks, P. J. Edmunds, R. C. Carpenter, and G. Bernardi. 2011. Herbivory, Connectivity, and Ecosystem Resilience: Response of a Coral Reef to a Large-Scale Perturbation. PLoS ONE 6:e23717.

Baker, A. C., P. W. Glynn, and B. Riegl. 2008. Climate change and coral reef bleaching: An ecological assessment of long-term impacts, recovery trends and future outlook. Estuarine, Coastal and Shelf Science 80:435–471.

Bellwood, D. R., T. P. Hughes, and A. S. Hoey. 2006. Sleeping functional group drives coral-reef recovery. CURRENT BIOLOGY 16:2434–2439.

Bjorck, J., B. H. Rappazzo, Q. Shi, C. Brown-Lima, J. Dean, A. Fuller, and C. Gomes. 2021. Accelerating Ecological Sciences from Above: Spatial Contrastive Learning for Remote Sensing. Proceedings of the AAAI Conference on Artificial Intelligence 35:14711–14720.

Bui A, Lowman H, Guerra A, Miller-ter Kuile A (2024). calecopal: A California-inspired Package of Color Palettes. R package version 0.1.0.

Bulleri, F., L. Thiault, S. C. Mills, M. M. Nugues, E. M. Eckert, G. Corno, and J. Claudet. 2018. Erect macroalgae influence epilithic bacterial assemblages and reduce coral recruitment. Marine Ecology Progress Series 597:65–77.

Burkepile, D. E., and M. E. Hay. 2008. Herbivore species richness and feeding complementarity affect community structure and function on a coral reef. Proceedings of the National Academy of Sciences 105:16201–16206.

Burns, C., B. Bollard, and A. Narayanan. 2022. Machine-Learning for Mapping and Monitoring Shallow Coral Reef Habitats. Remote Sensing 14:2666.

Carneiro, I. M., J. A. Sá, P. M. Chiroque-Solano, F. C. Cardoso, G. M. Castro, P. S. Salomon, A. C. Bastos, and R. L. Moura. 2024. Precision and accuracy of common coral reef sampling protocols revisited with photogrammetry. Marine Environmental Research 194:106304.

Dai, A. 2013. Increasing drought under global warming in observations and models. Nature Climate Change 3:52–58.

Ellison, A. M. 2019. Foundation Species, Non-trophic Interactions, and the Value of Being Common. iScience 13:254–268.

Ellison, A. M., M. S. Bank, B. D. Clinton, E. A. Colburn, K. Elliott, C. R. Ford, D. R. Foster, B. D. Kloeppel, J. D. Knoepp, G. M. Lovett, J. Mohan, D. A. Orwig, N. L. Rodenhouse, W. V. Sobczak, K. A. Stinson, J. K. Stone, C. M. Swan, J. Thompson, B. Von Holle, and J. R. Webster. 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. Frontiers in Ecology and the Environment 3:479–486.

Ferrari, R., W. F. Figueira, M. S. Pratchett, T. Boube, A. Adam, T. Kobelkowsky-Vidrio, S. S. Doo, T. B. Atwood, and M. Byrne. 2017. 3D photogrammetry quantifies growth and external erosion of individual coral colonies and skeletons. Scientific Reports 7:16737.

Fox, H. E., J. S. Pet, R. Dahuri, and R. L. Caldwell. 2003. Recovery in rubble fields: long-term impacts of blast fishing. Marine Pollution Bulletin 46:1024–1031.

Fraser, M. W., G. A. Kendrick, J. Statton, R. K. Hovey, A. Zavala-Perez, and D. I. Walker. 2014. Extreme climate events lower resilience of foundation seagrass at edge of biogeographical range. Journal of Ecology 102:1528–1536.

Gardner, T., I. Cote, J. Gill, A. Grant, and A. Watkinson. 2005. Hurricanes and Caribbean coral reefs: Impacts, recovery patterns, and role in long-term decline. ECOLOGY 86:174–184.

Guo, T., A. Capra, M. Troyer, A. Grün, A. J. Brooks, J. L. Hench, R. J. Schmitt, S. J. Holbrook, and M. Dubbini. 2016. Accuracy assessment of underwater photogrammetric three dimensional modelling for coral reefs. Pages 821–828 International Archives of the Photogrammetry, Remote Sensing and Spatial Information Sciences. ISPRS.

Han, X., T. C. Adam, R. J. Schmitt, A. J. Brooks, and S. J. Holbrook. 2016. Response of herbivore functional groups to sequential perturbations in Moorea, French Polynesia. Coral Reefs 35:999–1009.

Hedley, J. D., C. M. Roelfsema, I. Chollett, A. R. Harborne, S. F. Heron, S. Weeks, W. J. Skirving, A. E. Strong, C. M. Eakin, T. R. L. Christensen, V. Ticzon, S. Bejarano, and P. J. Mumby. 2016. Remote Sensing of Coral Reefs for Monitoring and Management: A Review. Remote Sensing 8:118.

Holbrook, S. J., T. C. Adam, P. J. Edmunds, R. J. Schmitt, R. C. Carpenter, A. J. Brooks, H. S. Lenihan, and C. J. Briggs. 2018. Recruitment Drives Spatial Variation in Recovery Rates of Resilient Coral Reefs. Scientific Reports 8:7338.

Holbrook, S. J., R. J. Schmitt, T. C. Adam, and A. J. Brooks. 2016. Coral Reef Resilience, Tipping Points and the Strength of Herbivory. Scientific Reports 6:35817.

Howie, A. H., and M. J. Bishop. 2021. Contemporary Oyster Reef Restoration: Responding to a Changing World. Frontiers in Ecology and Evolution 9.

Hughes, T. P. 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. Science 265:1547–1551.

Hughes, T. P., J. T. Kerry, M. Álvarez-Noriega, J. G. Álvarez-Romero, K. D. Anderson, A. H. Baird, R. C. Babcock, M. Beger, D. R. Bellwood, R. Berkelmans, T. C. Bridge, I. R. Butler, M. Byrne, N. E. Cantin, S. Comeau, S. R. Connolly, G. S. Cumming, S. J. Dalton, G. Diaz-Pulido, C. M. Eakin, W. F. Figueira, J. P. Gilmour, H. B. Harrison, S. F. Heron, A. S. Hoey, J.-P. A. Hobbs, M. O. Hoogenboom, E. V. Kennedy, C. Kuo, J. M. Lough, R. J. Lowe, G. Liu, M. T. McCulloch, H. A. Malcolm, M. J. McWilliam, J. M. Pandolfi, R. J. Pears, M. S. Pratchett, V. Schoepf, T. Simpson, W. J. Skirving, B. Sommer, G. Torda, D. R. Wachenfeld, B. L. Willis, and S. K. Wilson. 2017. Global warming and recurrent mass bleaching of corals. Nature 543:373–377.

Husari, S., H. T. Nichols, N. G. Sugihara, and S. L. Stephens. 2006. Fire and Fuel Management. Pages 444–465 in N. Sugihara, editor. Fire in California's Ecosystems. University of California Press.

Iordache, M.-D., V. Mantas, E. Baltazar, K. Pauly, and N. Lewyckyj. 2020. A Machine Learning Approach to Detecting Pine Wilt Disease Using Airborne Spectral Imagery. Remote Sensing 12:2280.

Jackson, J. (ed), M. (ed) Donovan, K. (ed) Cramer, and V. (ed) Lam. 2014. Status and trends of Caribbean coral reefs: 1970-2012. Gland, Switzerland: Global Coral Reef Monitoring Network; International Union for the Conservation of Nature (IUCN).

Johnstone, J. F., C. D. Allen, J. F. Franklin, L. E. Frelich, B. J. Harvey, P. E. Higuera, M. C. Mack, R. K. Meentemeyer, M. R. Metz, G. L. Perry, T. Schoennagel, and M. G. Turner. 2016. Changing disturbance regimes, ecological memory, and forest resilience. Frontiers in Ecology and the Environment 14:369–378.

Kenyon, T. M., C. Doropoulos, K. Wolfe, G. E. Webb, S. Dove, D. Harris, and P. J. Mumby. 2023. Coral rubble dynamics in the Anthropocene and implications for reef recovery. Limnology and Oceanography 68:110–147.

Kerr, J. T., and M. Ostrovsky. 2003. From space to species: ecological applications for remote sensing. Trends in Ecology & Evolution 18:299–305.

Kopecky, K. L., G. Pavoni, E. Nocerino, A. J. Brooks, M. Corsini, F. Menna, J. P. Gallagher, A. Capra, C. Castagnetti, P. Rossi, A. Gruen, F. Neyer, A. Muntoni, F. Ponchio, P. Cignoni, M. Troyer, S. J. Holbrook, and R. J. Schmitt. 2023a. Quantifying the Loss of Coral from a Bleaching Event Using Underwater Photogrammetry and AI-Assisted Image Segmentation. Remote Sensing 15:4077.

Kopecky, K. L., A. C. Stier, R. J. Schmitt, S. J. Holbrook, and H. V. Moeller. 2023b. Material legacies can degrade resilience: Structure-retaining disturbances promote regime shifts on coral reefs. Ecology 104:e4006.

Kuffner, I. B., L. J. Walters, M. A. Becerro, V. J. Paul, R. Ritson-Williams, and K. S. Beach. 2006. Inhibition of coral recruitment by macroalgae and cyanobacteria. Marine Ecology Progress Series 323:107–117.

Lamy, T., C. Koenigs, S. J. Holbrook, R. J. Miller, A. C. Stier, and D. C. Reed. 2020. Foundation species promote community stability by increasing diversity in a giant kelp forest. Ecology 101.

Lechner, A. M., G. M. Foody, and D. S. Boyd. 2020. Applications in Remote Sensing to Forest Ecology and Management. One Earth 2:405–412.

Lee, B., N. Kim, E.-S. Kim, K. Jang, M. Kang, J.-H. Lim, J. Cho, and Y. Lee. 2020. An Artificial Intelligence Approach to Predict Gross Primary Productivity in the Forests of South Korea Using Satellite Remote Sensing Data. Forests 11:1000.

Lenihan, H. S., and C. H. Peterson. 1998. How habitat degradation through fishery disturbance enhances impacts of hypoxia on oyster reefs. Ecological applications 8:128–140.

Lirman, D. 2001. Competition between macroalgae and corals: effects of herbivore exclusion and increased algal biomass on coral survivorship and growth. Coral Reefs 19:392–399.

Marvasti-Zadeh, S. M., D. Goodsman, N. Ray, and N. Erbilgin. 2023. Early Detection of Bark Beetle Attack Using Remote Sensing and Machine Learning: A Review. ACM Computing Surveys 56:97:1-97:40.

McCarthy, M. J., K. E. Colna, M. M. El-Mezayen, A. E. Laureano-Rosario, P. Méndez-Lázaro, D. B. Otis, G. Toro-Farmer, M. Vega-Rodriguez, and F. E. Muller-Karger. 2017. Satellite Remote Sensing for Coastal Management: A Review of Successful Applications. Environmental Management 60:323–339.

McCook, L., J. Jompa, and G. Diaz-Pulido. 2001. Competition between corals and algae on coral reefs: a review of evidence and mechanisms. Coral Reefs 19:400–417.

Miller, A. D., H. Inamine, A. Buckling, S. H. Roxburgh, and K. Shea. 2021. How disturbance history alters invasion success: biotic legacies and regime change. Ecology Letters 24:687–697.

Miller, S. D., A. K. Dubel, T. C. Adam, D. T. Cook, S. J. Holbrook, R. J. Schmitt, and A. Rassweiler. 2023. Using machine learning to achieve simultaneous, georeferenced surveys of fish and benthic communities on shallow coral reefs. Limnology and Oceanography: Methods 21:451–466.

Mireille L. Harmelin-Vivien. 1994. The Effects of Storms and Cyclones on Coral Reefs: A Review:22.

Moorea Coral Reef LTER, and P. Edmunds. 2024. MCR LTER: Coral Reef: Long-term Population and Community Dynamics: Corals, ongoing since 2005. [object Object].

Morais, J., R. Morais, S. B. Tebbett, and D. R. Bellwood. 2022. On the fate of dead coral colonies. Functional Ecology 36:3148–3160.

Nocerino, E., F. Menna, A. Gruen, M. Troyer, A. Capra, C. Castagnetti, P. Rossi, A. J. Brooks, R. J. Schmitt, and S. J. Holbrook. 2020. Coral Reef Monitoring by Scuba Divers Using Underwater Photogrammetry and Geodetic Surveying. Remote Sensing 12:3036.

Nourani, V., E. Foroumandi, E. Sharghi, and D. Dąbrowska. 2020. Ecological-environmental quality estimation using remote sensing and combined artificial intelligence techniques. Journal of Hydroinformatics 23:47–65.

Oliver, E. C. J., M. G. Donat, M. T. Burrows, P. J. Moore, D. A. Smale, L. V. Alexander, J. A. Benthuysen, M. Feng, A. Sen Gupta, A. J. Hobday, N. J. Holbrook, S. E. Perkins-Kirkpatrick, H. A. Scannell, S. C. Straub, and T. Wernberg. 2018. Longer and more frequent marine heatwaves over the past century. Nature Communications 9:1324.

Pavoni, G., M. Corsini, F. Ponchio, A. Muntoni, C. Edwards, N. Pedersen, S. Sandin, and P. Cignoni. 2022. TagLab: AI-assisted annotation for the fast and accurate semantic segmentation of coral reef orthoimages. Journal of Field Robotics 39:246–262.

Posit team. 2024. RStudio: Integrated Development Environment for R. Posit Software, PBC, Boston, MA.

Pratchett, M. S., C. F. Caballes, J. C. Wilmes, S. Matthews, C. Mellin, H. P. A. Sweatman, L. E. Nadler, J. Brodie, C. A. Thompson, J. Hoey, A. R. Bos, M. Byrne, V. Messmer, S. A. V. Fortunato, C. C. M. Chen, A. C. E. Buck, R. C. Babcock, and S. Uthicke. 2017. Thirty Years of Research on Crown-of-Thorns Starfish (1986–2016): Scientific Advances and Emerging Opportunities. Diversity 9:41.

Puk, L. 2020, April 29. Ecological drivers of the brown macroalgal genus Lobophora on Pacific coral reefs. PhD Thesis, The University of Queensland.

R Core Team. 2023. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rapinel, S., L. Panhelleux, G. Gayet, R. Vanacker, B. Lemercier, B. Laroche, F. Chambaud, A. Guelmami, and L. Hubert-Moy. 2023. National wetland mapping using remote-sensing-derived environmental variables, archive field data, and artificial intelligence. Heliyon 9:e13482.

Remmers, T., A. Grech, C. Roelfsema, S. Gordon, M. Lechene, and R. Ferrari. 2024. Close-range underwater photogrammetry for coral reef ecology: a systematic literature review. Coral Reefs 43:35–52.

Rossi, P., C. Castagnetti, A. Capra, A. J. Brooks, and F. Mancini. 2020. Detecting change in coral reef 3D structure using underwater photogrammetry: critical issues and performance metrics. Applied Geomatics 12:3–17.

Saldaña, P. H., C. Angelini, M. D. Bertness, and A. H. Altieri. 2023. Dead foundation species drive ecosystem dynamics. Trends in Ecology & Evolution.

Sandino, J., G. Pegg, F. Gonzalez, and G. Smith. 2018. Aerial Mapping of Forests Affected by Pathogens Using UAVs, Hyperspectral Sensors, and Artificial Intelligence. Sensors 18:944.

Schmitt, R. J., S. J. Holbrook, A. J. Brooks, and T. C. Adam. 2022. Evaluating the precariousness of coral recovery when coral and macroalgae are alternative basins of attraction. Limnology and Oceanography 67:S285–S297.

Schmitt, R. J., S. J. Holbrook, S. L. Davis, A. J. Brooks, and T. C. Adam. 2019. Experimental support for alternative attractors on coral reefs. Proceedings of the National Academy of Sciences 116:4372–4381.

Shang, B. Z., H. S. He, T. R. Crow, and S. R. Shifley. 2004. Fuel load reductions and fire risk in central hardwood forests of the united states: a spatial simulation study. Ecological Modelling 180:89–102.

Shi, Z., and H. Li. 2007. Application of artificial neural network approach and remotely sensed imagery for regional eco-environmental quality evaluation. Environmental Monitoring and Assessment 128:217–229.

Smith, J., M. Shaw, R. Edwards, D. Obura, O. Pantos, E. Sala, S. Sandin, S. Smriga, M. Hatay, and F. Rohwer. 2006. Indirect effects of algae on coral: algae-mediated, microbe-induced coral mortality. ECOLOGY LETTERS 9:835–845.

Stiger, V., E. Deslandes, and C. E. Payri. 2004. Phenolic contents of two brown algae, Turbinaria ornata and Sargassum mangarevense on Tahiti (French Polynesia): interspecific, ontogenic and spatio-temporal variations 47:402–409.

Swanson, M. E., J. F. Franklin, R. L. Beschta, C. M. Crisafulli, D. A. DellaSala, R. L. Hutto, D. B. Lindenmayer, and F. J. Swanson. 2011. The forgotten stage of forest succession: early-successional ecosystems on forest sites. Frontiers in Ecology and the Environment 9:117–125.

Swanson, S. 2016. Echinoid herbivores and coral reef resilience. Dissertation, UC Santa Barbara.

Thomson, G. 2022. Manu: NZ Bird Colour Palettes. R package version 0.0.2, https://github.com/G-Thomson/Manu.

Vieira, C. 2020. Lobophora–coral interactions and phase shifts: summary of current knowledge and future directions. Aquatic Ecology 54:1–20.

Vítková, L., R. Bače, P. Kjučukov, and M. Svoboda. 2018. Deadwood management in Central European forests: Key considerations for practical implementation. Forest Ecology and Management 429:394–405.

Wehner, M. F., K. A. Reed, B. Loring, D. Stone, and H. Krishnan. 2017. Changes in tropical cyclones under stabilized 1.5 °C and 2.0 °C global warming scenarios as simulated by the Community Atmospheric Model under the HAPPI protocols. preprint, Earth system change: climate prediction.

Whitlock, C., D. B. McWethy, A. J. Tepley, T. T. Veblen, A. Holz, M. S. McGlone, G. L. W. Perry, J. M. Wilmshurst, and S. W. Wood. 2015. Past and Present Vulnerability of

Closed-Canopy Temperate Forests to Altered Fire Regimes: A Comparison of the Pacific Northwest, New Zealand, and Patagonia. BioScience 65:151–163.

Wickham, H., M. Averick, J. Bryan, W. Chang, L. D. McGowan, R. François, G. Grolemund, A. Hayes, L. Henry, J. Hester, M. Kuhn, T. L. Pedersen, E. Miller, S. M. Bache, K. Müller, J. Ooms, D. Robinson, D. P. Seidel, V. Spinu, K. Takahashi, D. Vaughan, C. Wilke, K. Woo, and H. Yutani. 2019. Welcome to the Tidyverse. Journal of Open Source Software 4:1686.

Yadav, S., P. Rathod, T. Alcoverro, and R. Arthur. 2016. “Choice” and destiny: the substrate composition and mechanical stability of settlement structures can mediate coral recruit fate in post-bleached reefs. Coral Reefs 35:211–222.

FIGURES

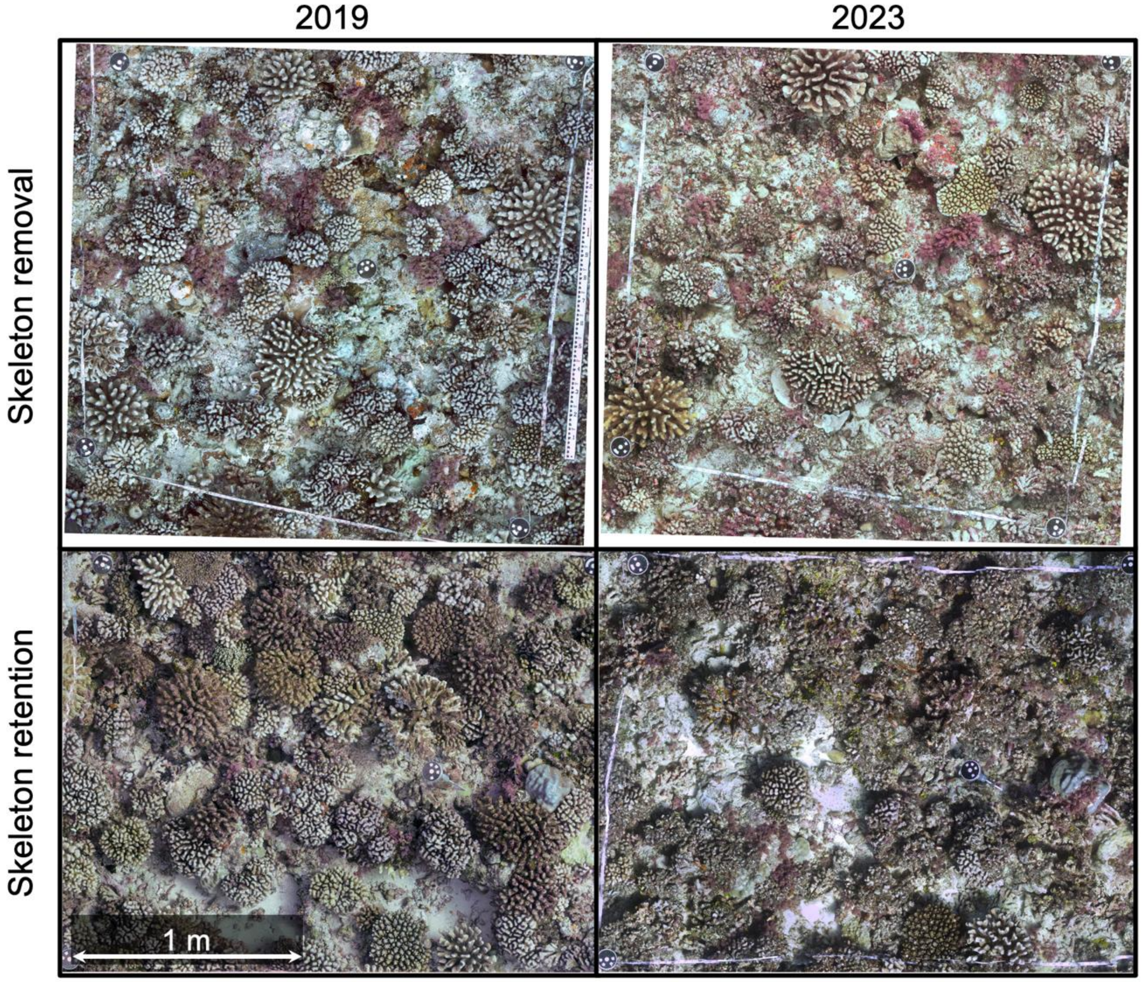


Figure 1. Example orthophotos of experimental plots at the beginning and end of the experiment. Top row shows a plot in 2019 and 2023 that had dead skeletons removed (prior to the image shown), bottom row shows an unmanipulated plot (skeletons left in place) in 2019 and 2023. Black and white coded photogrammetry targets can be seen in the corners and centers of each orthophoto, representing the fixed reference points for each plot.

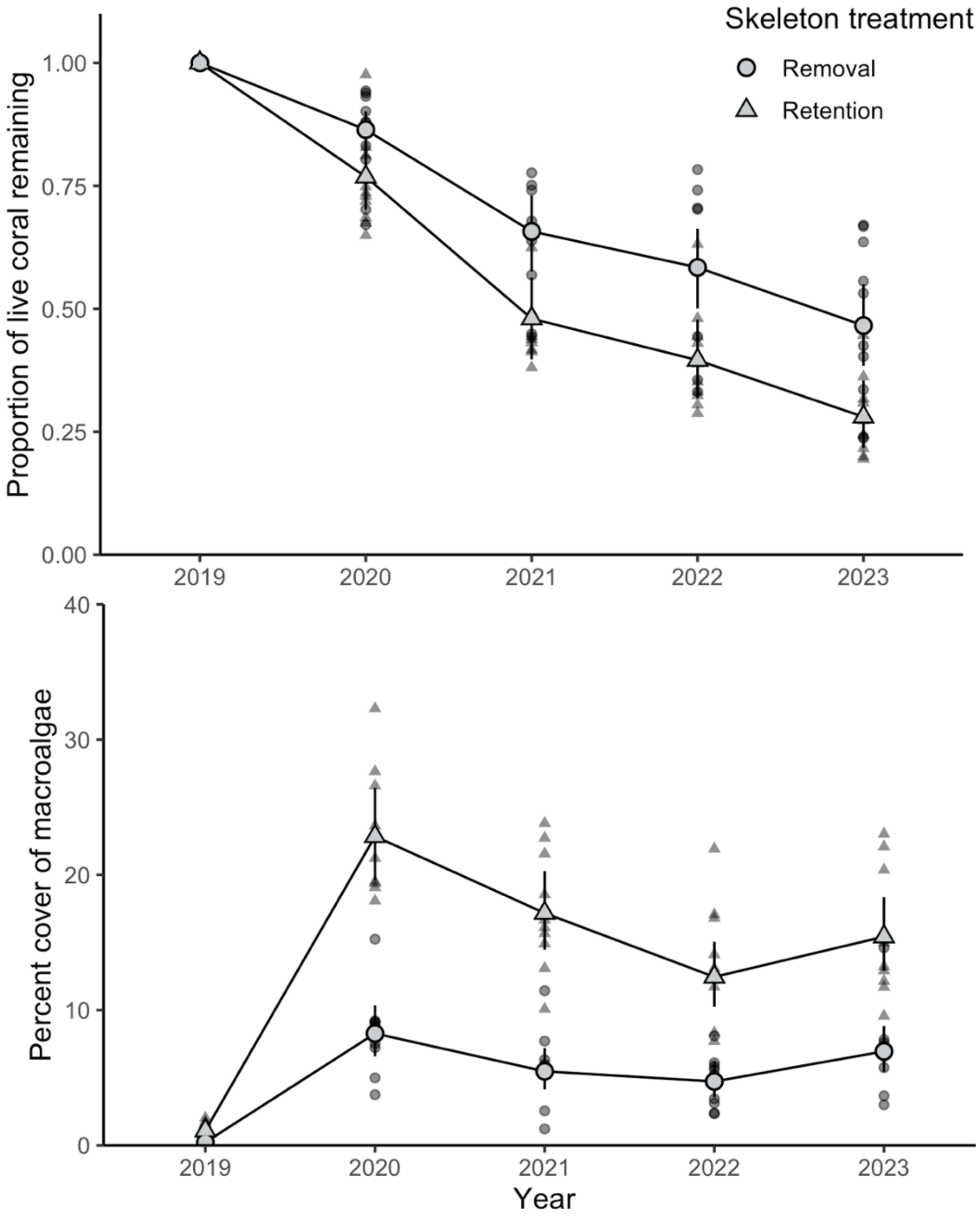


Figure 2. Time series of a) the proportion of live coral remaining in each year, and b) percent cover of macroalgae by treatment. Large shapes show model predicted means ± 95% confidence intervals, and small shapes are raw values of replicate plots.

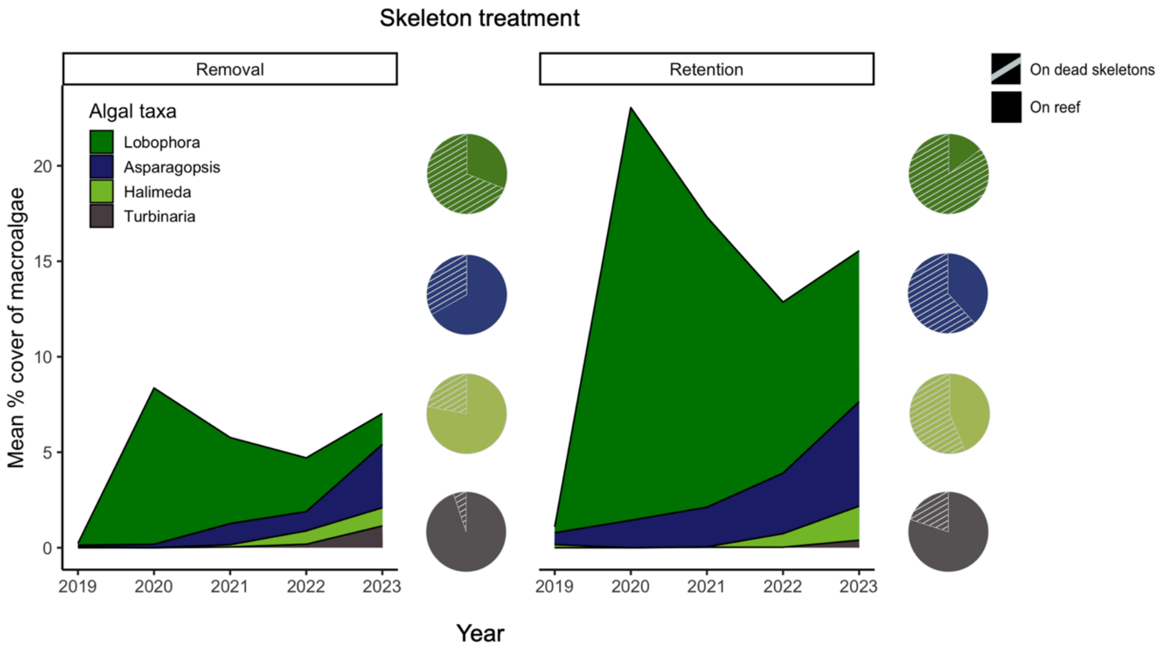


Figure 3. Stacked area chart of mean algae cover at each time point, separated by algal taxa, for each skeletal treatment. Pie charts indicate the proportions of points labelled as each algal taxon that fell within regions of dead coral (stripes) or on primary reef substrate (no stripes).

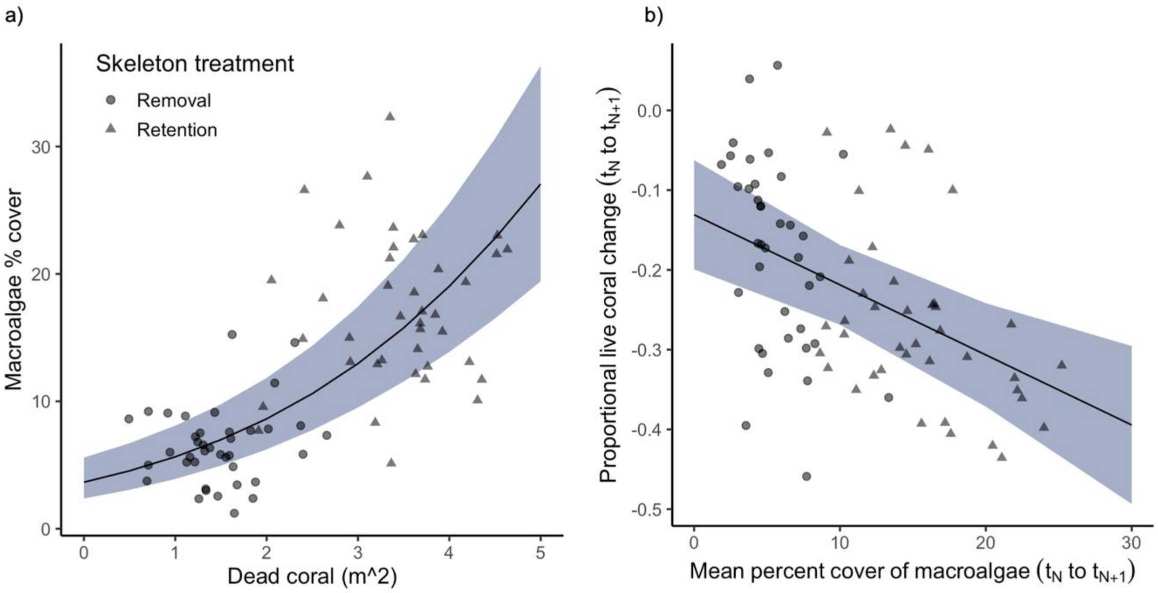


Figure 4. a) Percent cover of macroalgae as a function of the 3D surface area of dead coral (m^2) for each plot in a given year. b) Proportional change in live coral for a given year as a function of the time-averaged percent cover of macroalgae over the same period. Shapes indicate the skeletal treatment of each plot. Trendlines are model predicted means ± 95% confidence intervals.

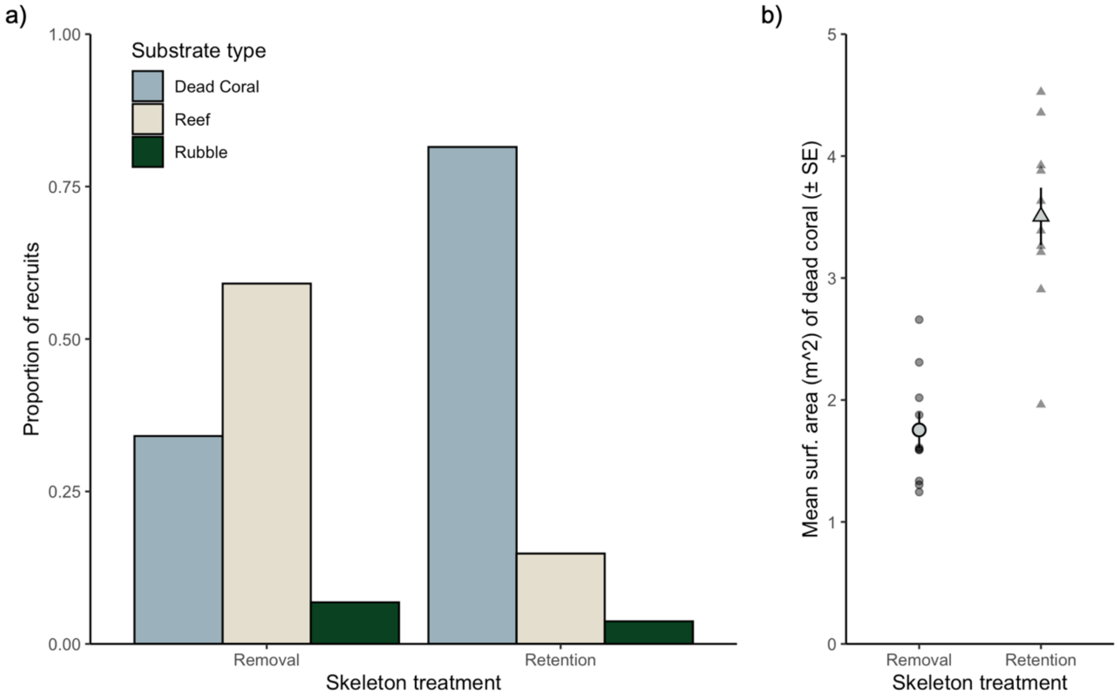


Figure 5. a) Proportion of coral recruits found on each of three substrate types (separated by skeletal treatment) in 2023. b) 3D surface areas of dead coral in each skeletal treatment in 2023. Large shapes indicate treatment means (± SE) and small shapes indicate raw replicate values.

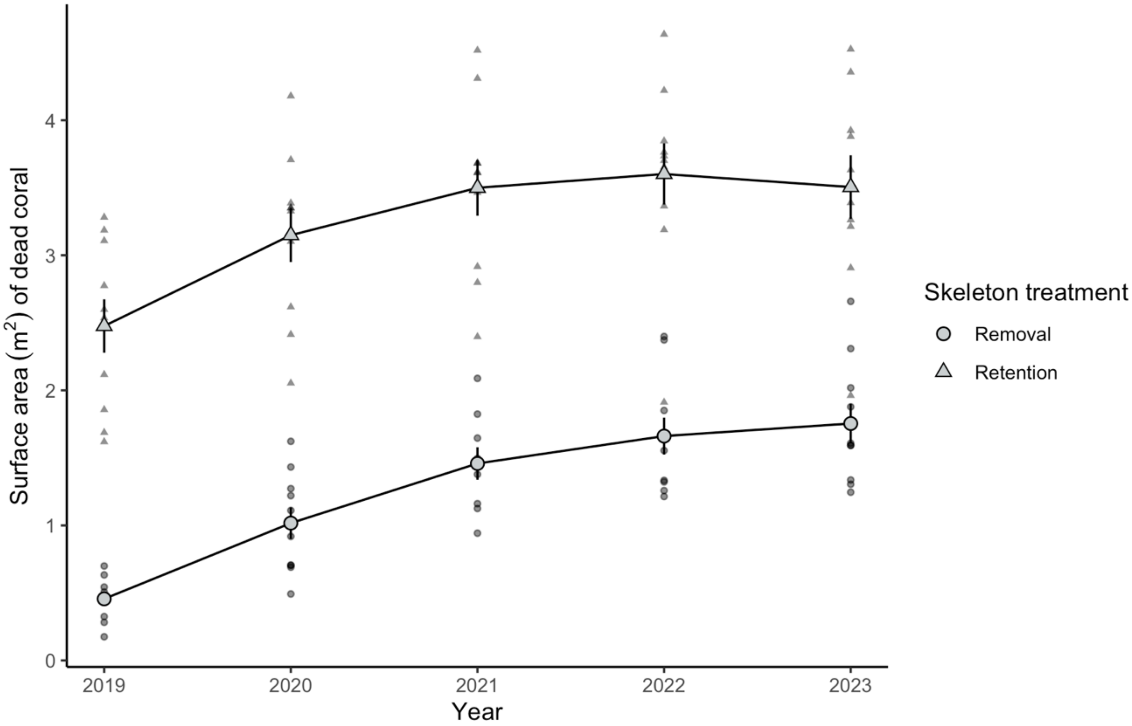


Figure S1. Time series of the 3D surface area of dead coral cover in each skeleton treatment over time. Large shapes are mean values ± SE, and small shapes are raw values of replicate plots.

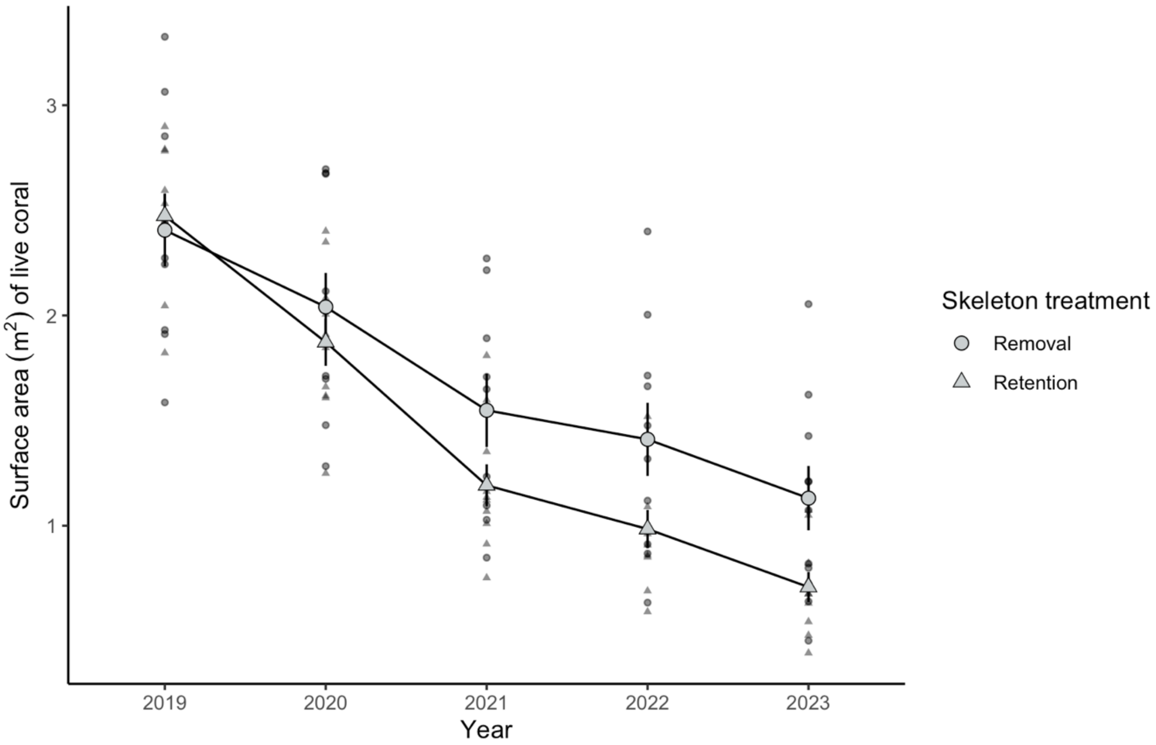


Figure S2. Time series of the 3D surface area of live coral cover in each skeleton treatment over time. Large shapes are mean values ± SE, and small shapes are raw values of replicate plots.

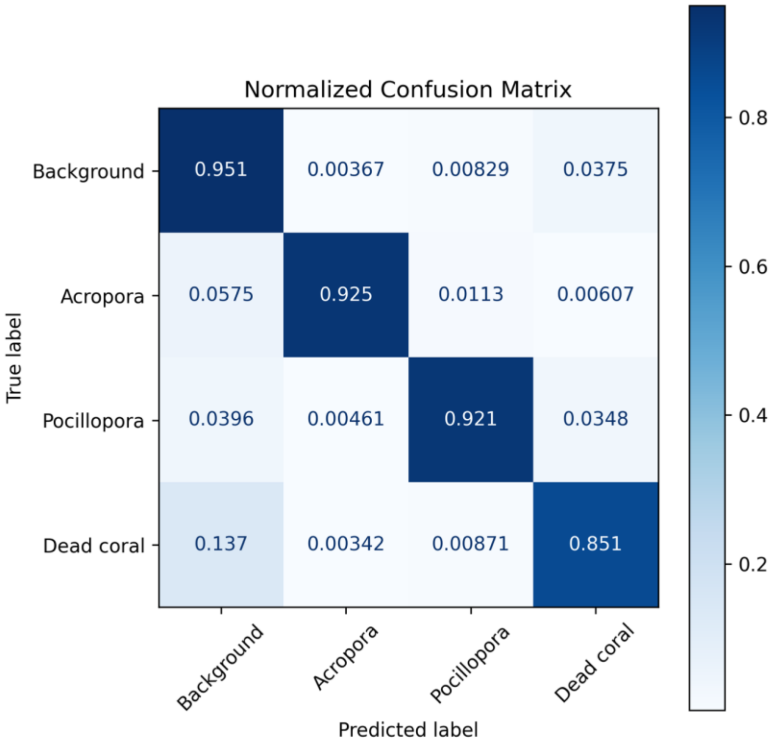


Figure S3. Confusion matrix of the automatic classifier. Diagonal cells from top-left to bottom-right show the proportion of pixels in the training dataset correctly classified by the automatic classifier relative to a human observer (i.e., the accuracy for each class). Other cells show the proportion of pixels incorrectly classified for each class (the ‘True label’), and what the incorrectly classified labels were mistaken as (‘Predicted label’).