PROJECT SUMMARY

Overview:
For the past 18 years, the Moorea Coral Reef (MCR) LTER program has sought to understand the long-term dynamics of oceanic coral reef ecosystems. Coral reefs have extraordinary biodiversity and provide profoundly important ecosystem services. Yet, reefs worldwide are faced with degradation by local human activities, a warming, rising and slowly acidifying ocean, and a changing disturbance regime. While cyclones have impacted coral reefs throughout their geological history, the first major episodes of coral 'bleaching' mortality caused by anomalously warm water occurred in the early 1980's. Episodes of mass bleaching from marine heat waves now occur on reefs worldwide and are growing in frequency and severity as mean ocean temperature continues to rise. Thus, the disturbance regime of coral reefs now includes recurrent heat waves in addition to powerful storms. Our new research is motivated by a recent heat wave that caused more coral bleaching mortality at our site than any other heat wave in recent decades, and it builds on our long-term measurements and accumulated knowledge, including dynamical responses after a powerful cyclone in 2010. The proposed research centers on how the changing disturbance regime is altering the dynamics, function, and resilience of coral reefs, and is organized around three core questions:

- *How do material legacies from different disturbance types affect community dynamics, changes in state and resilience?*
- *How do local stressors interact with new disturbance regimes to drive spatial heterogeneity in community dynamics, ecosystem processes, and spatial resilience?*
- *How do disturbances generate information legacies in corals and coral reef communities that influence their resilience under current and future environmental conditions?*

Our research integrates the collection and analysis of long-term data, process studies, long-term field experiments, analytical and statistical modeling, cross-LTER site integration, and ecological synthesis.

Intellectual Merit:
The recent coral bleaching event on the fore reef, whose recovery from a cyclone that removed coral skeletons a decade earlier was intensely studied by the MCR, provides the opportunity to understand the causes and consequences of ecological responses to the two major disturbance types that are impacting coral reefs worldwide. Disturbances can trigger abrupt and persistent change in ecosystem state, and we are uniquely positioned to understand whether and why the coral state is more or less resilient to a mass coral mortality event that removes coral skeletons (cyclones) compared to a disturbance that leaves dead skeletons intact (severe heat waves). Further, our site is a model system for understanding how the impact of a disturbance is modulated by interactions among multiple local stressors (e.g., nutrient enrichment, fishing) that might amplify or lessen ecosystem responses, as well as for examining how spatial structure influences system dynamics, function and resilience. Finally, we will also explore whether repeated heat waves and warming water select for species or traits of corals that 'prime' them to respond in beneficial ways to further climate change effects as well as ocean acidification.

Broader Impacts:
Degradation of coral reefs commands substantial public attention. This provides an effective platform for our findings to inform management actions to strengthen resilience of coral reefs in our rapidly changing world. MCR will continue to work with government entities, resource managers, fishers, and other stakeholders concerned with the health of coral reef ecosystems. MCR's education, training, and outreach efforts emphasize broadening participation in STEM fields and strengthening STEM literacy, particularly from groups historically underrepresented in marine field sciences. In addition to our ongoing Schoolyard and other efforts to promote diversity and inclusivity in science, we have initiated 2 new MCR IV activities to: (1) address barriers hindering underrepresented groups becoming scientific SCUBA divers (UCSB *DIVErsity in Diving Program*) and (2) enhance our multi-lingual, media-based outreach and education efforts to disseminate MCR findings to Pacific Islanders in Hawaii, American Samoa, Guam, Palau, the Federated States of Micronesia, Marshall Islands and French Polynesia.

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*Proposers may select any numbering mechanism for the proposal. The entire proposal however, must be paginated. Complete both columns only if the proposal is numbered consecutively.

PROJECT DESCRIPTION

SECTION 1 – MOOREA CORAL REEF LTER RESEARCH AND THE LTER CONTEXT

The Moorea Coral Reef (MCR) Long Term Ecological Research (LTER) site, like all sites in the network, addresses ecological phenomena that occur over multiple decades. The MCR site is an oceanic coral reef ecosystem, which encircles the ~50 km perimeter of Moorea, French Polynesia, and includes the fringing reef along the shore, the back reef in the lagoon, and the steeply sloping fore reef seaward of the reef crest (Fig. 1). MCR research activity is based at the University of California Gump Research Station and is motivated by patterns in our time series that collect data in the five LTER core areas: (1) primary production, (2) population studies, (3) movement of organic matter, (4) movement of inorganic matter, and (5) disturbance dynamics. These data are integrated with experiments and other process-oriented studies to inform ecological theory and to advance understanding of the long-term dynamics of populations, communities, and ecosystems. Like many coral reefs, Moorea's reefs are impacted by acute disturbance events (e.g., cyclones, marine heat waves, outbreaks of coral predators) superimposed on a heterogeneous template of chronic local stressors (e.g., fishing, nutrient enrichment) and directionally changing climate drivers (e.g., ocean temperature, ocean acidification). A goal of the MCR is to gain predictive understanding of how these factors affect community dynamics, ecosystem function, and resilience. Of particular interest is understanding causes and consequences of state shifts from coral (the foundation species) to macroalgae (or other taxa), a phenomenon occurring on many tropical reefs.

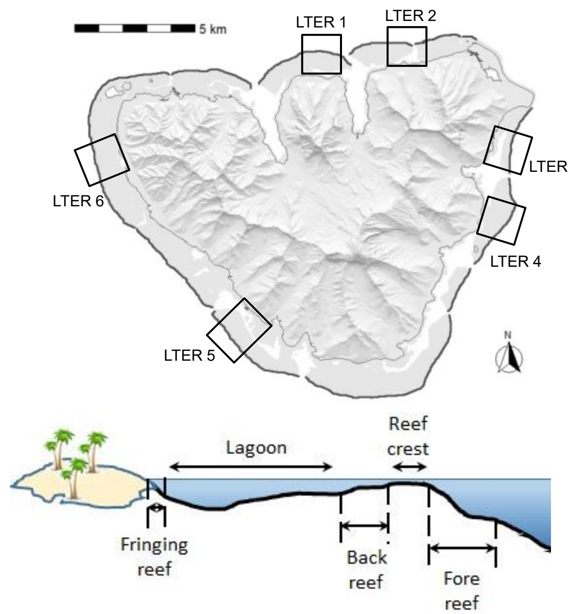


Figure 1. (Top) Map of Moorea with locations of MCR time series sampling sites around the ~50 km perimeter of the island. **(Bottom)** Schematic cross-section of the ecosystem, stretching from the shore (left) to 20 m depth on the offshore fore reef (right), illustrating the 3 habitat types (fore reef, back reef, fringing reef) sampled at each site around the island (top).

In MCR I (2004-2010), we developed an island-scale understanding of community structure and ecosystem function and how these vary with physical forcing. We advanced understanding of coral biology to better project how reefs will respond to local and regional drivers of change. Beginning in MCR I, an outbreak of the corallivorous Crown-of-Thorns Seastar (COTS), *Acanthaster planci*, killed the majority of coral colonies on the fore reef and was followed by a cyclone in 2010 that removed the dead coral skeletons. These back-to-back perturbations focused MCR II research on ecological resilience of the fore reef community. The focus of MCR II (2010-2016) was on processes preventing the fore reef from undergoing a transition to macroalgal dominance, as well as those influencing the return of corals. We further explored the physiological and ecological mechanisms determining which corals are 'winners' or 'losers' under current and future ocean conditions. Our time series revealed that the fore reef was returning to the pre-disturbed, coral-dominated community, but at different rates across sites and depths. By contrast, lagoon communities displayed different dynamics where coral cover remained high at some sites, but at others, coral declined while macroalgae increased. Thus, the lagoon was less resilient than the fore reef and had more fine-scale spatial heterogeneity in community structure and dynamics.

Community dynamics revealed by our core time series motivated the focus of MCR III (2016-2022) on the causes and consequences of spatial heterogeneity in reef resilience. We also began to explore how future ocean conditions might impact resilience, community structure, and ecosystem function. On the

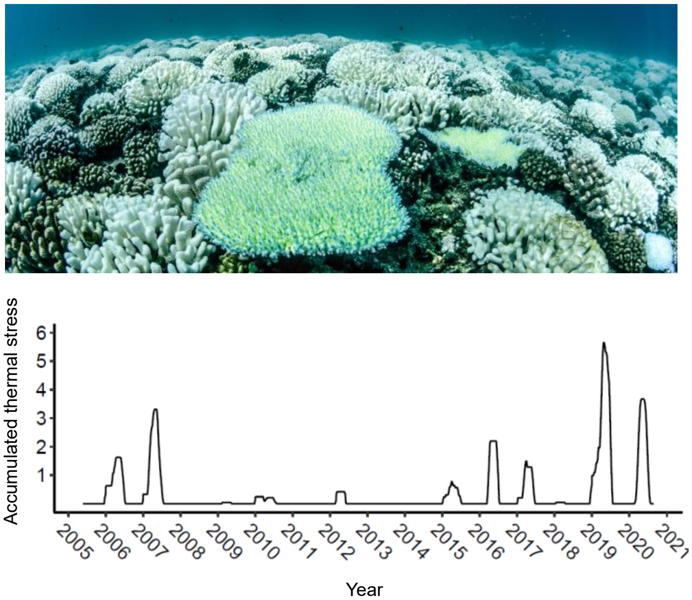


Figure 2. (Top) Coral bleaching on the fore reef during the 2019 marine heat wave. **(Bottom)** History of accumulated thermal stress in the MCR time series. Accumulated thermal stress is calculated as the weeks above 29°C, the temperature threshold that predicts thermal stress for corals in Moorea. Note the recent increase in frequency/intensity of heat waves.

fore reef where herbivory by fishes is high, variation in the recruitment of sexually produced coral propagules was the primary factor creating heterogeneity in the rate of coral recovery. In the lagoon where herbivory by fishes is much lower, some communities exhibited bistability, existing as either coral- or macroalgae-dominated habitats under identical conditions that are determined by their starting community state. Importantly, nutrient enrichment was a strong driver of heterogeneity in the lagoon that exacerbated coral bleaching and facilitated declines in coral and increases in macroalgae.

In 2019, Moorea experienced an intense marine heat wave (MHW, an episode of unusually warm water), resulting in widespread coral bleaching and mortality on the fore reef and at some locations in the lagoon (Fig. 2). This event left large numbers of dead coral skeletons in place and may result in fundamentally different post-disturbance dynamics than did the COTS/cyclone disturbance in MCR I, which killed and then removed dead corals. Our time series also indicate that marine heat waves are becoming more frequent (Fig. 2), a pattern being observed worldwide. **Thus, MCR IV (2022-2028) will explore ecological consequences of the changing disturbance regime, particularly how two different types of disturbances (heat waves vs. cyclones) affect ecological resilience.**

SECTION 2 - RESULTS FROM PRIOR SUPPORT

MCR LTER III: Long Term Dynamics of a Coral Reef Ecosystem (2016-2022) OCE 1637396; Funding: $7,070,118 (including supplements). The major goals of MCR III were to advance understanding of two general questions that remain poorly resolved for coral reef ecosystems:

(1) What processes and attributes underlie the ability of coral reef ecosystems to buffer environmental perturbations to maintain or restore community structure and function?

(2) How will changing environmental drivers alter resilience, community composition, and ecosystem functioning?

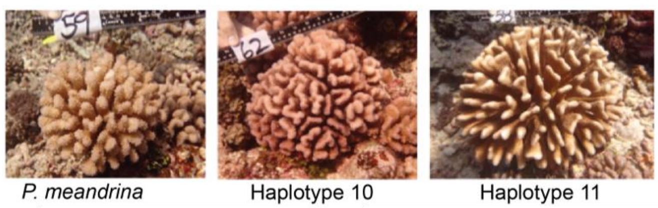
RESEARCH - PRIOR

Major Findings. Here we summarize major MCR III findings. To date (2016-present), this research has resulted in 180 publications, 25 MS theses, and 13 PhD dissertations. Citations in **bold** represent contributions from our **10 most significant papers** (Table 1).

Unprecedented resilience of coral communities: Our time series revealed that following the disturbances over 2007-2010 (a COTS outbreak followed by a cyclone), the denuded fore reef did not transition to macroalgae, but returned to a coral-dominated community because high rates of herbivory prevented macroalgae from proliferating (Adam et al. 2011, Holbrook et al. 2016). However, the rate of return of coral cover varied around Moorea and across depths, with the fastest coral recovery on the north shore and in shallow water (10 m) (**Holbrook et al. 2018**). Recovery was more strongly influenced by the

Table 1. 10 Most Significant Publications from MCR III

1. Adam, T.C. et al. (2021) Landscape-scale patterns of nutrient enrichment in a coral reef ecosystem: implications for coral to algae phase shifts. *Ecological Applications* 31:e2227	6. Holbrook, S. J. et al. (2018) Recruitment drives spatial variation in recovery rates of resilient coral reefs. *Scientific Reports* 8:7338
2. Burgess, S.C. et al. (2021) Response diversity in corals: hidden differences in bleaching mortality among cryptic *Pocillopora* species. *Ecology* 102:e03324	7. Maher R.L. et al. (2020) Coral microbiomes demonstrate flexibility and resilience through a reduction in community diversity following a thermal stress event. *Frontiers in Ecology and Evolution* 8:555698
3. Clements, C.S. and M.E. Hay. (2021) Biodiversity has a positive but saturating effect on imperiled reefs. *Science Advances* 7:eabi8592	8. Munsterman, K.S. et al. (2021) A view from both ends: shifts in herbivore assemblages impact top-down and bottom-up processes on coral reefs. *Ecosystems* 24:1702-1715
4. Donovan, M.K. et al. (2020) Nitrogen pollution interacts with heat stress to increase coral bleaching across the seascape. *PNAS* 117:5351-5357	9. Schmitt, R. J. et al. (2019) Experimental support for alternative attractors on coral reefs. *PNAS* 116:4372-4381
5. Edmunds, P.J. et al. 2018. Density-dependence mediates coral assemblage structure. *Ecology* 99:2605-2613	10. Wegley Kelly, L. et al. (2022) Distinguishing the molecular diversity, nutrient content and energetic potential of exometabolomes produced by macroalgae and reef building corals. *PNAS* 119:e2110283119



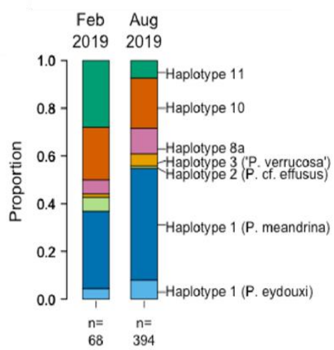


Figure 3. (Top) Three haplotypes (cryptic species) of *Pocillopora* in Moorea. **(Bottom)** Relative abundance of haplotypes in February 2019 (before coral bleaching) and August 2019 (after coral bleaching). Note the large decrease in thermally-sensitive Haplotype 11.

supply of sexually produced coral recruits than by other factors such as coral growth, herbivory, or corallivory (**Holbrook et al. 2018**, **Edmunds et al. 2018a**). This 'supply-side' interpretation of recovery is supported by Integral Projection Modeling (IPM) that shows that fore reef sites re-assembled to pre-disturbance coral cover with a similar community structure (Kayal et al. 2018). Field experiments revealed that coral diversity may accelerate recovery (**Clements and Hay 2021**).

In 2019, Moorea experienced a marine heat wave (MHW) that was one of the most intense of the past several decades. This resulted in extensive bleaching of coral on the fore reef as their photosynthetic algal endosymbionts (Symbiodiniaceae) were lost (**Burgess et al. 2021**, Speare et al. 2022). Bleaching mortality was most extensive for the largest corals and smallest recruits of the dominant genera of branching corals, *Acropora* and *Pocillopora* (Speare et al. 2022). Cryptic species of *Pocillopora* showed widely different patterns of bleaching and mortality, thus revealing a mechanism driving the positive association of colony size and bleaching (Fig. 3; **Burgess et al. 2021**). Resilience to bleaching might have been modulated by corallivorous fishes that consume, digest and egest coral tissues, thereby dispersing live Symbiodiniaceae symbionts across the reef and aiding in coral recovery (Grupstra et al. 2021). The 2019 bleaching left stands of dead coral skeletons intact on the fore reef, which contrasts with the effects of the previous COTS/cyclone disturbances that removed skeletons. A goal of MCR IV is testing the effects of disturbances that retain dead coral skeletons vs. those that do not on ecological resilience.

<u>*Coral reefs are vulnerable to disturbance-induced regime shifts*</u>: We tested a theoretical prediction that multiple basins of attraction could exist in an ecosystem where a large enough disturbance can induce a state shift without any change in an underlying driver. On coral reefs, the rise of coral-to-macroalgae 'phase shifts' (Fig. 4) suggests that a hysteretic dynamic could trap these systems in a macroalgae-dominated state. We tested for hysteresis in driver-response relationships that create the potential for bistability, and demonstrated that hysteresis existed under ambient conditions in the lagoon but not on the

Figure 4. Examples of lagoon reefs either in **(Top)** coral-dominated state or **(Bottom)** macroalgae-dominated state.

fore reef (**Schmitt et al. 2019**). These experiments showed that when a large disturbance removes the dominant macroalga (*Turbinaria*) from patch reefs, they remained macroalgae-free and were re-colonized by corals (Fig. 5; **Schmitt et al. 2019**, 2021). Thus, depending on their starting conditions, reefs could respectively either remain macroalgae-dominated or return to a coral-dominated state, thus suggesting that macroalgae and coral can behave as alternative basins of attraction. Modeling revealed that reduced vulnerability of macroalgae to herbivory as macroalgae grow and mature could contribute to bistability (Briggs et al. 2018). The model shows that when macroalgae are palatable to herbivores as juveniles, but resistant as adults (e.g., for *Turbinaria*, Davis 2018), coral- and macroalgae-dominated states are bistable. Bistability may contribute to the patterns in our time series where some back reef sites transitioned from coral to macroalgae (**Adam et al. 2021**). Regions of bistability also exist on the fore reef, but below ambient levels of herbivory (Holbrook et al. 2016, **Schmitt et al. 2019**), which helps explain the return to coral after the 2010 cyclone (**Holbrook et al. 2018**, Kayal et al. 2018).

<u>*Nutrient pollution, algal phase shifts, and coral bleaching*</u>: Our time series across 18 sites has shown heterogeneity in nutrient (nitrogen, N) availability, with higher N concentrations on the north shore, and closer to land vs. offshore (**Adam et al. 2021**). In 2016, we increased the spatial resolution of our nutrient data by sampling 188 lagoon sites to quantify seascape-scale N enrichment. Nitrogen availability was associated with several factors, including rainfall, wave-driven circulation, and proximity to nutrient sources (**Adam et al. 2021**). Our time series shows that corals have decreased in abundance while macroalgae have increased at N-enriched sites compared to sites with lower nutrient enrichment. Transitions to macroalgal dominance were not associated with reduced fish herbivory (**Adam et al. 2021**). In fact, the degree of nutrient enrichment and intensity of fishing on herbivorous fishes are spatially decoupled due to the contrasting long- vs. cross- shore relationships between them (Holbrook et al. 2022). However, sites dominated by coral vs. macroalgae have different fish communities, resulting in altered ecosystem processes such as herbivory, detritivory, and nutrient cycling (**Munsterman et al. 2021**). Shifts from coral to macroalgae likely change reef biogeochemistry, as coral and algae exude significantly different types of dissolved organic matter (**Wegley Kelley et al. 2022**). Thus, nutrient-driven phase shifts result in cascading impacts on key ecosystem processes.

One mechanism driving decline of corals in the lagoon may be the impact of N on thermal tolerance of corals. By quantifying coral bleaching during modest thermal stress in 2016, we showed that increased temperature and N availability were positively associated with bleaching prevalence in *Acropora* and *Pocillopora* (**Donovan et al. 2020**). Temperature and high N availability also affected bleaching severity, suggesting that increased N can cause more intense bleaching at a lower temperature. The type of N matters, with more human-derived forms of N (e.g., NO_3^-) exacerbating bleaching mortality (Burkepile et al. 2020). A key theme in MCR IV is to understand how nutrients, temperature, and other drivers influence spatial heterogeneity in abundance of coral and macroalgae across the lagoons.

<u>*Winners and losers in coral communities on current and future reefs*</u>: During MCR I, our time series indicated that virtually all corals were ‘losers’ (i.e., they declined in abundance) as a result of COTS and the cyclone in 2010 (**Holbrook et al. 2018**, Edmunds 2018). Yet, recovery from these events has revealed winners, with *Pocillopora* fueling recovery on the fore reef (**Holbrook et al. 2018**, Edmunds 2018). Its

rate of recruitment, while consistently high on the fore reef (Edmunds 2021), is influenced by biological and physical factors (Edmunds 2017, 2021, **Edmunds et al. 2018a**). *Pocillopora* species in Moorea are a complex of cryptic species that are differentially distributed across depth (Johnston et al. 2021) and respond differently to thermal stress (**Burgess et al. 2021**). Thus, while the last decade reveals *Pocillopora* as a winner on the fore reef (**Holbrook et al. 2018**, Edmunds 2018), a goal of MCR IV is to understand which cryptic species of *Pocillopora* are responsible for this effect and why.

Demographic analyses of coral genera have revealed mechanistic drivers of 'winning' on present-day reefs of Moorea, in particular the roles played by sexual recruitment for *Pocillopora* and tissue relics for *Porites* (Kayal et al. 2018). These analyses reveal the limitations of identifying coral winners only by instantaneous growth (Edmunds and Putnam 2020) rather than seeking the demographic or functional causes of elevated fitness (e.g., Edmunds and Putnam 2020, Leinbach et al. 2021). Advances in understanding the coral holobiont (i.e., the association of the coral animal with a host of symbiotic microorganisms) (Sogin et al. 2017) are revealing the wide diversity of mechanisms through which corals can modify their performance (Putnam 2021). These mechanisms include changes in the taxa of algae and bacteria with which they associate (Thompson et al. 2015, **Maher et al. 2020**), and means by which information legacies can be transferred between generations (Eirin-Lopez and Putnam 2019). Importantly, restructuring their microbiomes to favor beneficial symbionts may be a key strategy for corals to cope with environmental stresses such as marine heat waves (**Maher et al. 2020**).

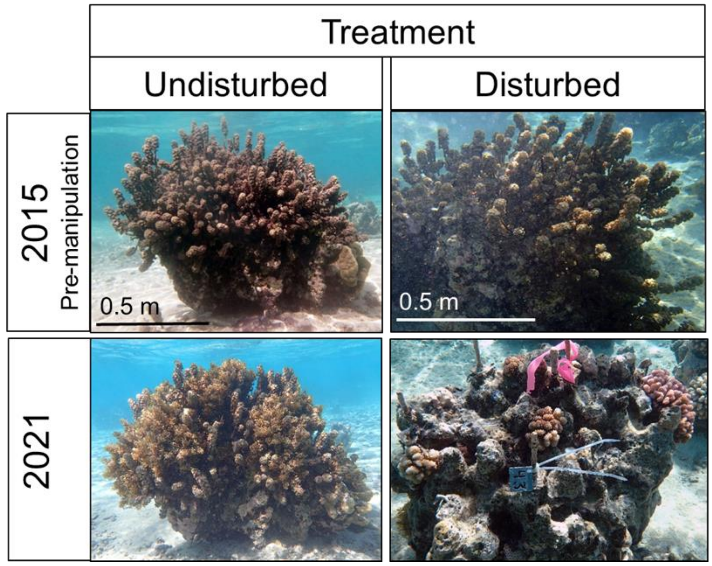


Figure 5. Representative patch reefs (bommies) from two treatments of an experiment that tested whether a disturbance that removed macroalgae would trigger a regime shift back to a coral state without a change in herbivory. The bommie on the left was undisturbed, while the bommie on the right was cleared of macroalgae once to mimic a cyclone. **(Top)** Bommies just before macroalgae were removed. **(Bottom)** The same bommies 6 years later. Undisturbed bommies remained dominated by macroalgae but disturbed bommies stayed free of macroalgae and were transitioning back to a coral state (**Schmitt et al. 2019**, 2021).

Synthesis, Integration, and Cross-site Products. The MCR has led numerous synthetic efforts to understand the ecology of coral reefs as well as to develop new approaches and techniques for data analysis. An MCR-led workshop at the Okinawa Institute of Science and Technology (OIST) focused on global patterns of temporal variation in coral recruitment (Price et al. 2019), and a second workshop (co-funded by NSF), addressed larval connectivity among reefs (Edmunds et al. 2018b) and latitudinal variation in coral growth (Nozawa et al. 2021). We led a 2016 workshop at the USGS Powell Center on coral reef oases (Guest et al. 2018, Courtney et al. 2021). A 2017 working group at USC's Boone Center explored cross-site contrasts in long-term coral reef community dynamics (Edmunds et al. 2019), followed in 2018 by an exploration of the role of coral demography in a changing world (Edmunds and Riegl 2020), and in 2019, by an international workshop on coral demography (Pisapia et al. 2020). MCR investigators also participated in synthesis and cross-site activities organized by others (e.g., Cinner et al. 2018, Gaiser et al. 2022, Safaie et al. 2018, Grottoli et al. 2021, Cowles et al. 2021, Reed et al. 2022). An ongoing cross-site collaboration involves a group of scientists from ETH Zurich (Switzerland), University of Modena (Italy), Florida State University, and Microsoft (Quantum Computing) to develop underwater photogrammetric techniques and machine learning for habitat quantification. Five workshops were held during MCR III; test beds include the MCR site, and locations in the Caribbean and Mediterranean (Capra et al. 2017, Neyer et al. 2018, Nocerino et al. 2019, 2020, Rossi et al. 2020).

BROADER IMPACTS - PRIOR

MCR has made significant contributions to postdoctoral, graduate, and undergraduate training, to multi-national public outreach, and to data dissemination. In the past 6 years, MCR has engaged 30 postdoctoral researchers, 101 graduate and 131 undergraduate (11 REU, 4 ROA) students, 2 ROA faculty researchers and 7 K-12 teachers (5 RET). They are involved in MCR research and outreach and participate in the annual MCR All-Investigator Meeting. MCR fosters a welcoming, supportive and inclusive community that embraces the diversity of our society. Thus, diversity, equity and inclusion are central pillars of our training and outreach efforts, and we have built a diverse, inclusive and empowered community.

The MCR Schoolyard program emphasizes connecting underrepresented groups in K-12 with the ocean. Our web resources include: (1) a Marine Life in Moorea Encyclopedia, (2) research pages for MCR graduate students, and (3) teaching resources developed by our RET participants. Our partner schools have large enrollments of underrepresented and/or economically disadvantaged groups. Teachers use curricula based on MCR research, participate in our professional development activities, and some travel to Moorea for summer research experiences (4 during MCR III, despite pandemic limitations). An important Schoolyard effort is an annual visit to UCSB by >100 fifth graders from Washington STEM Magnet School in Pasadena (98% minority enrollment, 90% disadvantaged, 40% English language learners) to learn about marine biology and participate in interactive lessons that are the basis for subsequent classroom activities. MCR graduate students and investigators lead K-12 activities at our coral reef booth at the annual Earth Day in Santa Barbara. Our undergraduates serve as docents at the REEF (Research Experience & Education Facility), which is an interactive marine educational facility at UCSB that serves over 10,000 K-12 and public visitors annually.

MCR has partnered with the UCLA Diversity Project, funded by NSF and the UC-HBCU Initiative (PI Barber, UCLA) that strives to increase participation of underrepresented students in marine biology. Diversity Project students visit UC Santa Barbara to meet MCR researchers, tour facilities, learn about LTERs, and get introduced to MCR research. MCR investigators and Diversity Project students overlap during the summer at the UC Gump Station in Moorea, which facilitates in-person interactions and mentoring, and results in a pipeline into graduate programs of MCR faculty investigators (5 Diversity Project alumni are currently graduate students in MCR investigator labs).

Outreach to Polynesians and Pacific Islanders is made through the Tahitian association *Te Pu 'Atiti'a*, which partners with the Gump Station, and through the University of Hawaii's Sea Grant Program TV series *Voice of the Sea* that airs in Hawaii and US territories in the Pacific. Examples of our outreach in French Polynesia include research presentations to the public and educators, working with the Teavaro School on Moorea to develop student-based monitoring for rivers and lagoons, and collaborations with the fisher community to exchange information about the status of reef resources.

MCR research has great relevance to resource managers, policy makers, and stakeholders in French Polynesia and beyond. MCR PIs annually brief the Ministry of the Environment of French Polynesia on MCR findings. This briefing has included information central to the sustainable management of nearshore reefs, including the importance of land-derived nutrient inputs to state shifts from coral to macroalgae (**Adam et al. 2021**) as well as the role nutrients play in bleaching and hindering reef recovery during heat waves (Burkepile et al. 2020, **Donovan et al. 2020**).

SECTION 3 – RESULTS FROM SUPPLEMENTAL SUPPORT

Equipment/Infrastructure. The MCR received supplemental funds to repair, replace or upgrade oceanographic instrumentation (thermistor strings, PAR sensors, wave/tide recorders), for critical infrastructure for marine research operations (outboard engines, boat trailers), for MET station components and for associated expendables (e.g., lithium batteries). Funds also were used to ship the items to Moorea.

RET – Research Experiences for Teachers. Three RET awards supported the activities of 5 K-12 teachers from our partner schools; 4 traveled to Moorea for field research experiences.

ROA – Research Opportunity Awards. Two ROA awards enabled faculty from Cabrillo College and Santa Monica College, along with 4 undergraduate students, to conduct field research in Moorea alongside MCR researchers. An REU student also was funded from Cabrillo College.

SECTION 4 – RESPONSE TO MID-TERM REVIEW

The NSF summary of the 2019 Mid-term Report concurred with the Review Team's overall assessment that "*the Moorea Coral Reef (MCR) Long Term Ecological Research (LTER) remains a stellar LTER* …" The three directives aimed at the MCR in the NSF summary are (verbatim):

Because of the positive nature of the review, the NSF comments will be brief and few.

1. *Arguably, the major concern was extensive modeling efforts that were not well integrated to explain their role in furthering the specific research objectives. This was not viewed as a weakness in the modeling, but the panel recommendation for a clearer development in the renewal proposal is sound advice.*
2. *Similarly, while presentations made it clear that the outreach efforts were extensive and probably influencing under-represented students at several levels, this was not strongly developed in the proposal. While acknowledging that tracking and documenting the efficacy of education and diversity building activities requires some effort, this review criterion continues to grow in importance. As with modeling, the weakness was not in the activities but the documentation.*
3. *There were modest suggestions where sharing some of the data products might be improved.*

1. The sole recommendation regarding MCR science was the need to better describe and integrate our modeling efforts with our time series and process studies. The Review Team and NSF noted that this <u>was not a concern about the science</u> but about the structure and integration of our MCR III proposal. We have taken this recommendation seriously and have integrated our modeling and synthesis efforts into each appropriate research theme in the MCR IV proposal. We agree that this improves clarity and understanding of the roles modeling efforts will play in advancing our specific research objectives.

2. The other major recommendation from the Review Team was to more effectively detail our efforts, successes, and challenges in broadening participation of groups underrepresented in science. We appreciated that the Review Team and NSF concurred that <u>the weakness was in our documentation and not our efforts,</u> as the MCR strives to create opportunities and promote diversity, inclusion, and equity in the marine sciences. Following the mid-term review recommendation, the MCR charged a standing DEI committee to evaluate current MCR efforts, recommend and implement enhancements, and identify needs and opportunities. Several new initiatives are planned for MCR IV (detailed below). We are currently working with the LTER Network Office to obtain the demographic information needed (via LTER Hub) to evaluate the efficacy of efforts to enhance diversity at all career stages within the MCR community.

3. With respect to suggestions regarding sharing of identified non-standard data products, after the review the MCR III Information Manager (Gastil-Buhl) engaged the LTER Network Information Managers Committee to develop best practices guidelines to increase consistency of these products across sites. Our new IM, Hillary Krumbholz, continues to work with the LTER Network towards these goals.

SECTION 5 - PROPOSED RESEARCH

CONCEPTUAL FRAMEWORK

Anthropogenic climate change is altering the structure and function of ecosystems worldwide. The impact of climate change is from both directionally-changing drivers (e.g., increasing mean ocean temperature) as well as periodic weather anomalies that disturb ecosystems (e.g., marine heat waves, or episodes of unusually warm water) (McPhillips et al. 2018). Severe weather events are now a major threat as they increase in intensity and frequency (White and Jentsch 2001, Turner 2010, Hughes et al. 2017a, McPhillips et al. 2018). Thus, we need to better understand how these severe events contribute to

changing disturbance regimes (Trumbore et al. 2015, Turner et al. 2020). These climate-driven disturbances are occurring while a growing human footprint also intensifies local stresses to ecosystems. Consequently, the impact of a severe event can depend on ***interactions among multiple drivers*** that can amplify or attenuate an ecosystem's response (Rocha et al. 2018, Wong et al. 2021). For example, in Moorea, nutrient pollution can reduce the thermal threshold for coral bleaching during marine heat waves (Burkepile et al. 2020, Donovan et al. 2020). Due to their site-based, long-term perspective, LTER sites are ideal for exploring changing disturbance regimes, interacting drivers, and ecosystem dynamics.

An ecosystem's response to a severe event not only depends on the nature of the shock, but also on its history of disturbance and species attributes (Martin et al. 2015, Hughes et al. 2018, Ratajczak et al. 2017, 2018, Castorani and Baskett 2020, Turner et al. 2020). Past disturbances can generate persistent legacies that influence the trajectory of an ecosystem (Moorhead et al. 1999, Franklin et al. 2000, Monger et al. 2015, Johnstone et al. 2016, Hughes et al. 2019). Such legacies collectively are termed ***ecological memory*** and consist of two components. First, ***material legacies*** (sensu Jõgiste et al. 2017) are biotic or abiotic constituents left after a pulse event that influence post-disturbance dynamics. Material legacies such as standing dead trees in a forest after a drought or skeletons of dead branching corals on a tropical reef after a heat wave can either strengthen or weaken the capacity of the disturbed system to return to its initial state (Graham and Nash 2013, Johnstone et al. 2016). The second component of ecological memory, ***information legacies***, arises from conditioning of the biological community as a longer-term outcome of a disturbance regime (Franklin et al. 2000, Johnstone et al. 2016, Safaie et al. 2018, Eirin-Lopez and Putnam 2019, Johnson et al. 2021). For example, on coral reefs repeated mortality from heat waves can select for coral taxa that may make coral communities less susceptible to future bleaching, or a heat wave may alter the physiology of surviving corals to make them less likely to bleach in the future (Wall et al. 2021, Sully et al. 2022).

Both components of ecological memory can influence the ***resilience*** of an ecosystem (Johnstone et al. 2016, Jõgiste et al. 2017). In this context, resilience refers broadly to the capacity of a current ecosystem state to maintain or regain its structure and function in the face of perturbations without switching to a persistent alternative state with different structure and functions (Gunderson 2000, Standish et al. 2014, Lam et al. 2020, Van Meerbeek et al. 2021). Loss of resilience often leads to ***abrupt change in ecological systems***, where shifts in state are rapid relative to the rate of change in underlying drivers (Turner et al. 2020). For example, combined disturbances of drought and fire can shift forested ecosystems to a persistent non-forest state as trees fail to regenerate (Stevens-Rumann et al. 2017, Davis et al. 2019). Indeed, ecosystems across the LTER network have experienced abrupt state shifts (e.g., McGlathery et al. 2013, Rocha et al. 2015, Cowles et al. 2021, Zinnert et al. 2021). These state shifts are difficult to anticipate (Scheffer and Carpenter 2003), can have profound effects on ecosystem services (Suding and Hobbs 2009), and can be difficult to reverse (Bestelmeyer et al. 2011, Graham et al. 2013), making them major concerns to scientists, resource managers, and other stakeholders.

Coral reef ecosystems are known for being at risk from changing disturbance regimes and interacting stressors such as fishing and nutrient pollution, often driving state shifts from the foundation species of coral to macroalgae or other space holders (Nystrom and Folke 2001, Bellwood et al. 2004, Graham et al. 2015, Lam et al. 2020, Mumby et al. 2021). Throughout their geological history, the primary disturbance to tropical reefs has been cyclonic storms that kill and remove large swaths of coral and other benthic organisms via strong hydrodynamic forces (Woodley et al. 1981, Scoffin 1993). Climate change may be increasing the strength of these storms, although substantial uncertainty remains in future projections (Trenberth 2005, Vecchi et al. 2021). By contrast, there is compelling evidence that climate change is increasing the frequency and severity of marine heat waves (MHWs), causing major episodes of mass coral bleaching and mortality since the 1980's (Glynn 1984, Baker et al. 2008, Lough et al. 2018, Sully et al. 2019). MHWs break down the critical mutualism between the coral host and its photosynthetic endosymbionts (dinoflagellates in the family Symbiodiniaceae). The coral and its associated microorganisms (i.e., the coral holobiont; Rohwer et al. 2002, Sogin et al. 2017) live near their upper thermal tolerance limit. Thus, a relatively small MHW can break down the coral-algae symbiosis, with corals turning pale (bleaching) as their photosynthetic algal endosymbionts are lost. If the MWH is

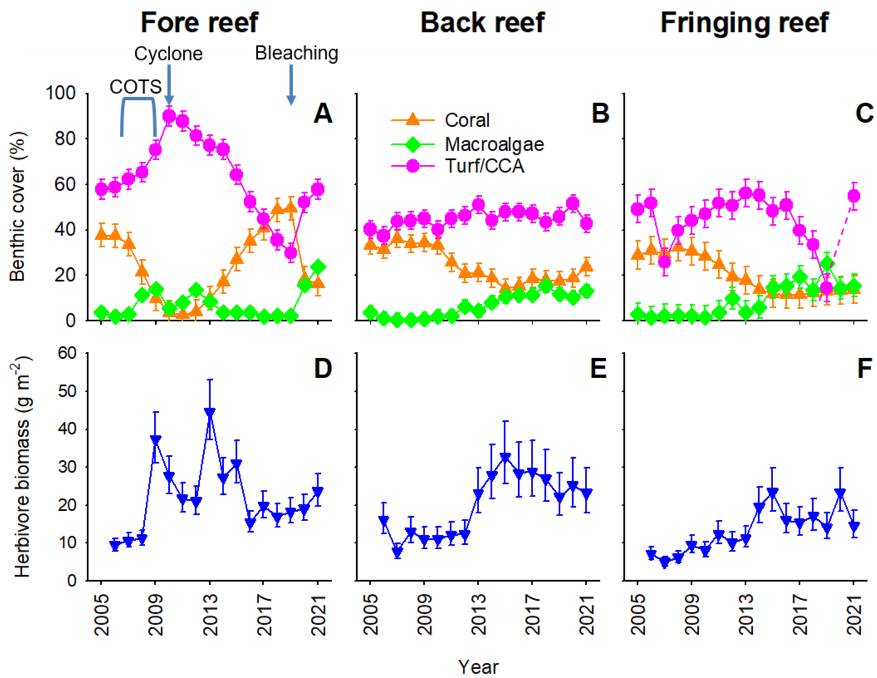


Figure 6. Island-wide community dynamics across habitats in the MCR time series (data are the means +/- 1 SE). Dynamics of **(A-C)** coral, macroalgae, and turf algae/ crustose coralline algae (CCA) as well as **(D-F)** herbivorous fish biomass on the fore reef (*left panels*), back reef (*center*), and fringing reef (*right*) habitats. Note coral cover on the fore reef has declined in response to periodic disturbance from COTS/cyclone (2007-2010), from which it showed dramatic recovery, and coral bleaching (2019). In contrast, benthic communities on lagoon reefs have exhibited gradual declines in coral and increases in macroalgae.

intense and prolonged, corals will not recover their endosymbionts and may starve to death (Baird and Marshall 2002, Baker et al. 2008, Lough et al. 2018). The recent increase in bleaching-induced mass mortality of corals represents a profound shift in the disturbance regime to now include recurrent MHWs in addition to storms and other local pulse events. There is urgency to identify how this altered disturbance regime can lead to legacies that affect resilience (Graham et al. 2015, Hughes et al. 2017a,b, 2018, Leggat et al. 2019).

On Moorea, the history of disturbance and the responses of reefs have differed significantly between the fore reef and lagoon. On the fore reef (Fig. 1), major historical coral mortality events have come from outbreaks of the corallivorous Crown-of-Thorns Seastar (COTS), first in 1979-1983 and again in 2007-2010, and from a MHW and coral bleaching event in 1991 (Adam et al. 2011, 2014, Pratchett et al. 2011, Trapon et al. 2011). COTS outbreaks and bleaching both lead to similar mortality patterns in that corals are killed in place and their dead skeletons remain. However, in all three of these specific disturbance events on Moorea, cyclones followed shortly after the initial coral mortality, pulverizing and removing the dead coral skeletons and reducing the fore reef to a relatively planar structure. After these disturbances where dead skeletons were removed, coral recovered to its pre-disturbance cover without macroalgae becoming dominant (Trapon et al. 2011, Holbrook et al. 2016, 2018).

MCR III research showed that two key processes accounted for the observed high resilience of the coral state following the 2010 cyclone (Fig. 6). First, herbivorous fishes increased in biomass in response to increased food availability and, as a result, were able to prevent macroalgae from proliferating, thereby keeping the vast, newly-disturbed area of the fore reef surface suitable for re-colonization by corals (Adam et al. 2011, Holbrook et al. 2016). Second, there was a high rate of recruitment of sexually produced coral propagules, especially of the branching coral *Pocillopora*, likely coming from other locations, to these suitable surfaces (Edmunds 2018, Holbrook et al. 2018, Kayal et al. 2018).

In contrast to the fore reef, our time series data reveal that lagoon reefs suffered lower coral mortality than did the fore reef during the 2007-10 disturbances (Fig. 6). Yet, there has been much more spatial heterogeneity in community dynamics in the lagoon, with some lagoon reefs remaining dominated by coral while others have transitioned to high cover of macroalgae (Adam et al. 2021). Importantly, compared to the fore reef, reefs in the lagoon exist across a far more heterogeneous template of local stressors such as nutrient pollution and fishing. Our work in MCR III suggested that these local stressors may interact with climate drivers to impact spatial heterogeneity of dynamical responses in the lagoon.

For example, corals in lagoon areas with high nutrient enrichment had a higher probability of bleaching compared to corals in areas with low nutrients (Donovan et al. 2020), and higher nutrient availability was correlated with a rise in macroalgae and decline in corals (Adam et al. 2021). Lagoon reefs also tend to be more vulnerable than the fore reef to shifts to macroalgae because herbivores are less capable of keeping macroalgae under control (Schmitt et al. 2019), possibly due to nutrient enrichment that increases the probability that macroalgae will escape control (Adam et al. 2021). Further, less herbivory is needed to prevent the establishment of macroalgae than to remove mature plants, resulting in hysteresis in the herbivore-macroalgae relationship that enables coral and macroalgae to be alternative basins of attraction under some range of environmental conditions (Schmitt et al. 2019, 2021). Thus, if disturbances and/or local stressors drive shifts to macroalgae states in the lagoon, they may be difficult to reverse. The dynamics of the lagoon ecosystem appear strongly influenced by the disturbance regime and how it interacts with the template of local stressors to influence resilience.

Now, we appear to be undergoing a significant change in the disturbance regime in Moorea. The austral summers of 2019 and 2020 resulted in the two largest MWHs in the history of the MCR, and 3 of the 4 hottest MHWs have occurred since 2016 (Fig. 2). The MWH in 2019, the mid-point of MCR III, resulted in a substantial amount of coral bleaching and mortality on the fore reef and in parts of the lagoon (Fig. 6; Burgess et al. 2021, Speare et al. 2022). This disturbance followed a decade of MCR research focused on understanding the dynamical response of these same coral communities to disturbance from a powerful cyclone. The fundamentally different disturbance generated by the 2019 MHW provides the MCR with an extraordinary opportunity to address unresolved questions regarding dynamics of coral reefs from severe events that have substantially different material legacies by removing dead coral skeletons (e.g., cyclones) or leaving them intact (e.g., MHWs; Fig. 7). Further, the changing disturbance regime will allow us to study how local stressors shape the information legacies created by MHWs and how they impact corals at individual, population, and community levels. Our research is motivated by key patterns in our time series data and is organized around the following core question:

How is a changing disturbance regime altering the resilience of coral reefs and what are the ecological consequences of altered resilience?

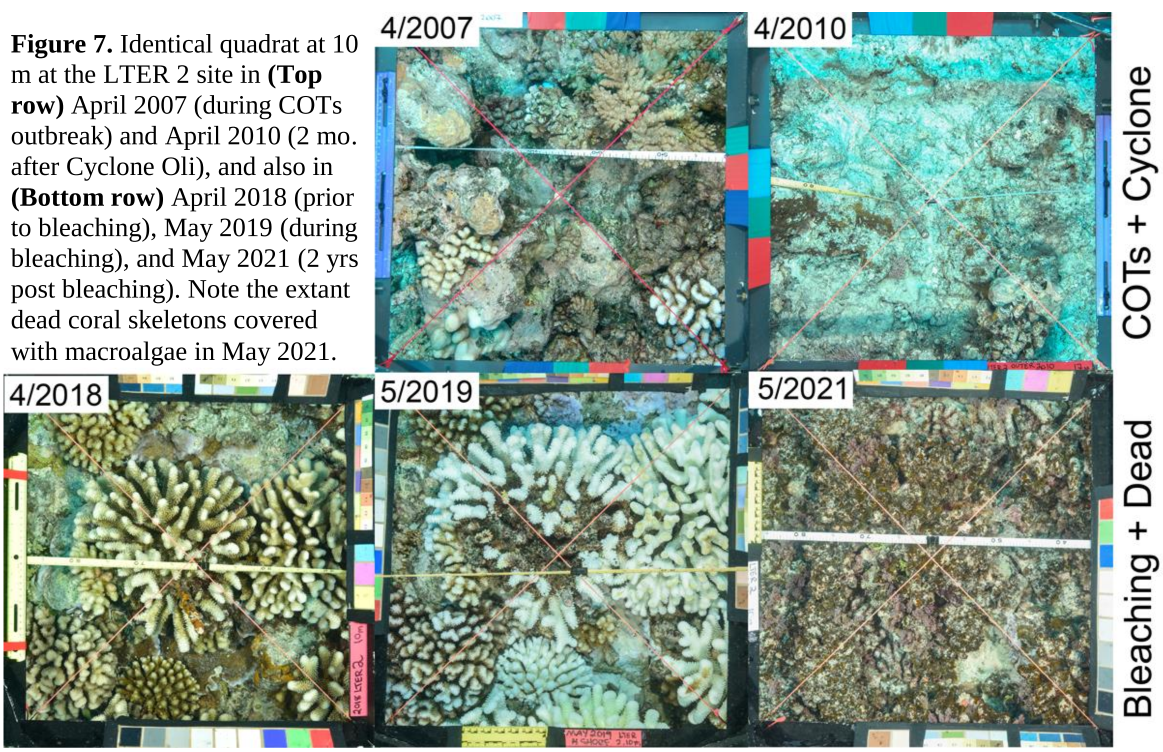


Figure 7. Identical quadrat at 10 m at the LTER 2 site in **(Top row)** April 2007 (during COTs outbreak) and April 2010 (2 mo. after Cyclone Oli), and also in **(Bottom row)** April 2018 (prior to bleaching), May 2019 (during bleaching), and May 2021 (2 yrs post bleaching). Note the extant dead coral skeletons covered with macroalgae in May 2021.

The MCR IV Research Program

Our proposed research is organized around three themes that have emerged from our time series, described next.

The MCR Time Series Component

Our time series provides critical temporal and spatial information on three key aspects: (1) population and community dynamics of major functional groups, (2) rates of key ecosystem processes, and (3) patterns of environmental drivers of community structure and ecosystem function. This provides a framework for quantifying trends in ecosystem dynamics, including responses to and recovery from disturbance and consequences to ecosystem function, as well as the key abiotic factors that influence the ecosystem.

Time Series Focus 1: *Community dynamics and long-term trends of key functional groups*
Abundances of corals, other macro-invertebrates, algae and fishes are estimated yearly on the fore reef, back reef, and fringing reef at six sites, two on each side of Moorea (Fig. 1). These data reveal different responses and rates of recovery of the reefs to disturbance as well as attributes that influence resilience (Adam et al. 2014, Edmunds 2018, Holbrook et al. 2018). Organisms (~500 taxa) are identified to the lowest taxon possible (typically species or genus). Estimates are made visually along permanent band transects or from permanent quadrats that are surveyed *in situ* by SCUBA divers (e.g., sea urchins, fishes) or using photo-quadrats (e.g., corals, macroalgae). Analyses of community structure based on digital images (i.e., photo-quadrats) are aided by image analysis tools (CoralNet, developed via a collaboration with MCR, Beijbom et al. 2012, 2015, Miller et al. In review). To better link coral abundances with the demographic causes of changing population size, early coral recruits are enumerated using tiles immersed for 6-month periods at locations on the north shore of the island (fore reef at 10 m and 17 m depth, and the back reef; Edmunds 2018, 2021). In addition, juvenile corals (colonies ≤ 40 mm diameter) on natural substrates are quantified *in situ* to augment the information obtained from the photo-quadrats.

Time Series Focus 2: *Spatio-temporal patterns in rates of key ecosystem processes*
Rates of reef metabolism (primary production and respiration) are estimated twice annually using a Lagrangian approach at two locations in the lagoon on the north shore and every 3 years on the other shores. Coral reefs typically have low production in the water column and high rates of gross benthic primary production (GPP). Because reef heterotrophs normally consume almost all of that production each day, the net primary production (NPP) of the community typically approaches zero (Atkinson 2011); our data fit this paradigm. Variation in gross production is driven largely by differences in light and water flow that determine the fluxes of dissolved inorganic carbon and nutrients (Comeau et al. 2017, Carpenter et al. 2018, Doo et al. 2019). Concentrations of nutrients in Moorea are low and near detection limits, making spot sampling of water column nutrients a poor proxy for long-term patterns in nutrient availability. Further, current velocity, rather than concentration alone, is typically the dominant component of nutrient flux (Atkinson 2011). Accordingly, we measure current velocities on appropriate spatial and temporal scales, and use estimates of % nitrogen in the tissues of a long-lived macroalga (*Turbinaria*) collected in all three habitats from our six permanent sampling sites as an integrated estimate of nutrient flux over longer periods (Adam et al. 2021). Variables related to ocean color (e.g., sub-surface Chl a concentration, light absorption by dissolved and detrital matter, particulate backscattering) are derived from satellite spectral radiometry (MODIS-Aqua, VIIRS on Suomi-NPP and JPSS1), and regional satellite sea-surface temperature data from the MODIS sensors are also assembled.

The ability of coral reefs to maintain net positive calcification is essential to their biological and physical functions, yet these foundational roles are challenged by changes in the benthic community structure (e.g., declining abundances of massive corals) and reduced seawater pH. Reef accretion (i.e., growth) is the net outcome of $CaCO_3$ deposition and dissolution. We will initiate a new time series in MCR IV to address these processes. Rates of net reef bioerosion will be evaluated through annual deployment of accretion-erosion blocks (Silbiger et al. 2016, 2017) left for a 2-year 'soak' time in four habitats near one of our north shore sites (LTER 1). These deployments will leverage the biological and physical environmental data we collect there, and allow $CaCO_3$ loss to be placed in an accretion context estimated through coral cover and the ReefBudget module within CoralNet (Courtney et al. 2021). Replicate blocks (N = 5) will be placed in each habitat, and following their 'soak' time, they will be recovered and processed to quantify voids within the rock using µCT scanning (Silbiger et al. 2016).

Time Series Focus 3: *Patterns of temporal and spatial variation in major physical factors*
Reefs of Moorea are affected by several types of physical forcing (Leichter et al. 2013). Cyclones physically damage coral and other reef organisms, marine heat waves trigger coral bleaching and mortality, and currents transport nutrients and propagules such as coral larvae. We have instrumented the reefs encircling Moorea with a range of physical oceanographic sensors to measure factors known to influence coral reefs including abiotic conditions [PAR, ocean temperature, current speed and direction, offshore wave statistics (height, direction, period), salinity, water levels]. Simultaneous measurements of wave heights and currents on the offshore fore reef are critical given that water flow in lagoons and local circulation patterns are driven primarily by the offshore wave climate (Hench et al. 2008, Monismith et al. 2013). We have one heavily-instrumented fore reef site on each side of the island, with additional deployments at the other three fore reef sites and throughout the lagoons (Fig. 8). We have used these data on physical factors to help explain patterns in community dynamics and ecosystem processes (e.g., Adam et al. 2014, 2021, Donovan et al. 2020, Wyatt et al. 2020). In 2021, we greatly intensified our spatial coverage of seawater temperature by deploying a grid of 48 additional high-resolution thermistors throughout the lagoons for a multi-year study. These will reveal fine scale spatial patterns in seawater temperature that will be critical for our ongoing studies of coral bleaching as well as for incorporation into our lagoon circulation models (see Question 2.1 for details). Data obtained from *in situ* oceanographic sensors and derived from satellite imagery (e.g., regional sea surface temperature) along with our high-resolution bathymetric data from LIDAR surveys (Collin et al. 2018) provide critical input parameters and boundary conditions for our circulation models, as well as metrics of major disturbance events (e.g., cyclones, coral bleaching) and ongoing climate change. Oceanographic measurements are complemented by surface environmental data from our MET station at the Gump Station. Data on long-term changes in sea level are obtained through the Permanent Service for Mean Sea Level for the Papeete, Tahiti station, 20 km east of Moorea.

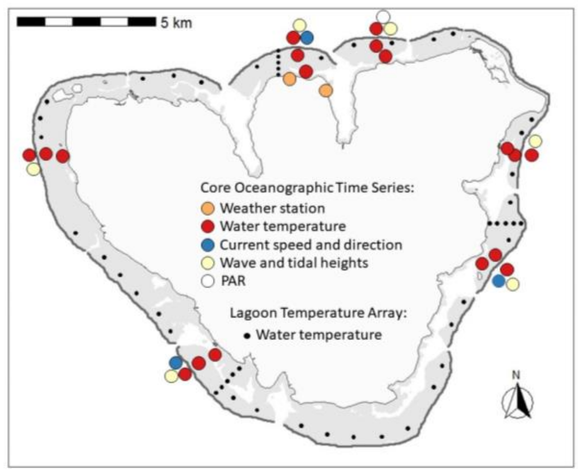


Figure 8. Map of Moorea showing the locations of the physical oceanographic sensors deployed on the fore reef and in the lagoons around the island.

Proposed Research

Our three research themes (Fig. 9) are motivated by patterns in our time series and new questions sparked by our prior findings. We first provide a general motivation for each theme, and then state our specific research questions and give a description of the research approaches we will take to answer them.

Theme 1: How do material legacies from different disturbance types affect community dynamics, changes in state, and resilience?

Coral bleaching events from marine heat waves (MHWs) are becoming the most frequent disturbance on coral reefs. Bleaching events leave dead coral skeletons in place, providing a very different material legacy from storm-driven disturbances that typically remove coral skeletons. Following the 2019 bleaching event, herbivores on the fore reef appear less capable of keeping macroalgae suppressed on the coral skeletons and disturbed surfaces compared to the 2010 cyclone (Figs. 6, 7). The macroalgae may slow or prevent a return to a coral state if the dead coral legacy remains for extended periods. In Theme 1, we will examine how the ecological legacies of different types of disturbances (MHWs vs. storms) shape community structure, alter the probability of state shifts, and change ecosystem function (Figs. 9, 10). We will focus largely on the fore reef where coral mortality from storms and bleaching is the most severe.

Theme 2: How do local stressors interact with new disturbance regimes to drive spatial heterogeneity in community dynamics, ecosystem processes, and spatial resilience?

Theme 2 will largely focus on the lagoon where there is high spatial heterogeneity in stress levels from multiple sources. In MCR III, we showed that spatial patterns in top-down (herbivory) and bottom-up (nutrient flux) forcing shape spatial heterogeneity in community dynamics on lagoon reefs. The MHWs that are increasing in frequency (Fig. 2) are also having variable spatial impact across the lagoon in triggering coral bleaching and mortality. In Theme 2, we will focus on understanding how MHWs interact with local anthropogenic stressors (e.g., nutrient enrichment, fishing) to drive shifts in community state that have profound implications for ecosystem processes such as primary production, nutrient cycling, and organic matter accumulation (Figs. 9, 16). Additionally, we will explore how feedbacks between coral- and macroalgae-dominated regions of connected landscapes may generate complex spatial patterns at intermediate scales and lead to more gradual shifts between states at the whole-reef scale.

Theme 3: How do disturbances generate information legacies in corals and coral reef communities that influence their resilience under current and future environmental conditions?

The information legacies that disturbances and local stressors create by altering traits of species as well as species composition of communities can determine the future resilience of ecosystems. Understanding the responses of scleractinian corals, the foundation group of the coral reef ecosystem, to changing environmental conditions is of critical importance in determining whether the coral community can remain resilient. In Theme 3, we will explore the organismal responses of branching corals, mainly *Pocillopora* spp., to changing conditions, and how these effects scale up to modulate the structure and function of the reef community (Figs. 9, 21). Evaluating whether these responses ultimately can ensure their survival under changing disturbance regimes is central to the debate of whether (or not) coral reefs will persist.

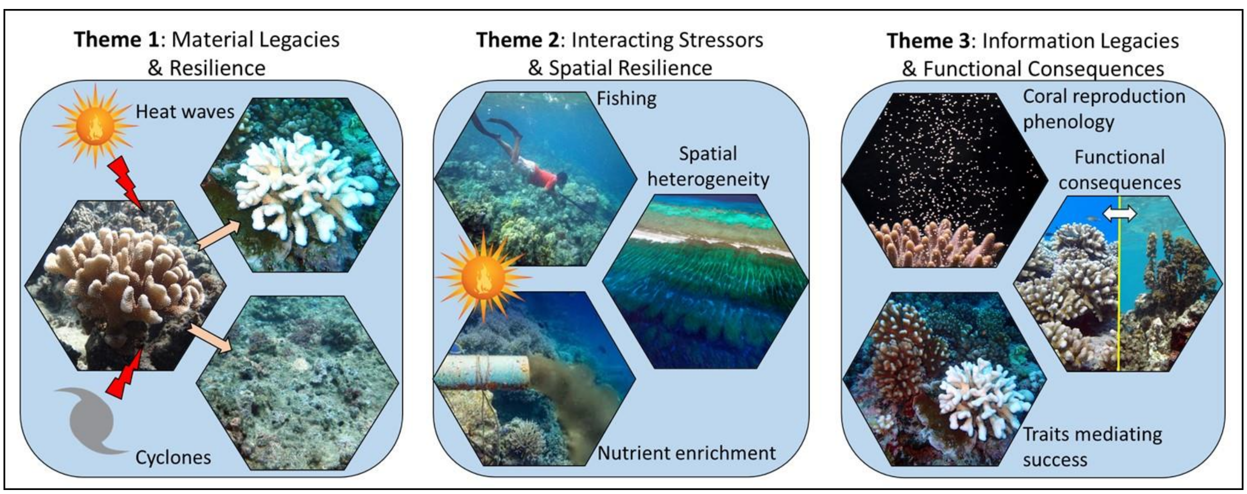


Figure 9. Integrative diagram of the three themes of MCR IV research, integrating time series with process-based studies to address patterns, processes, and future projections. **Theme 1** explores how material legacies left by different types of disturbances (cyclones vs. heat waves) impact community dynamics and ecosystem processes. **Theme 2** examines how heat waves interact with spatially varying local stressors (fishing, nutrient loading) to drive state shifts in communities and alter ecosystem function. **Theme 3** tests how information legacies from changing disturbance regimes impact individual to ecosystem-level functional consequences.

Research Themes

Theme 1: How do material legacies from different disturbance types affect community dynamics, changes in state, and resilience?

<u>Question 1.1:</u> *What factors drive heterogeneity in coral recovery across the landscape (among sites and depths) following coral bleaching? How does the presence of the dead coral skeleton material legacy alter community dynamics and influence the ability of coral to recover?*

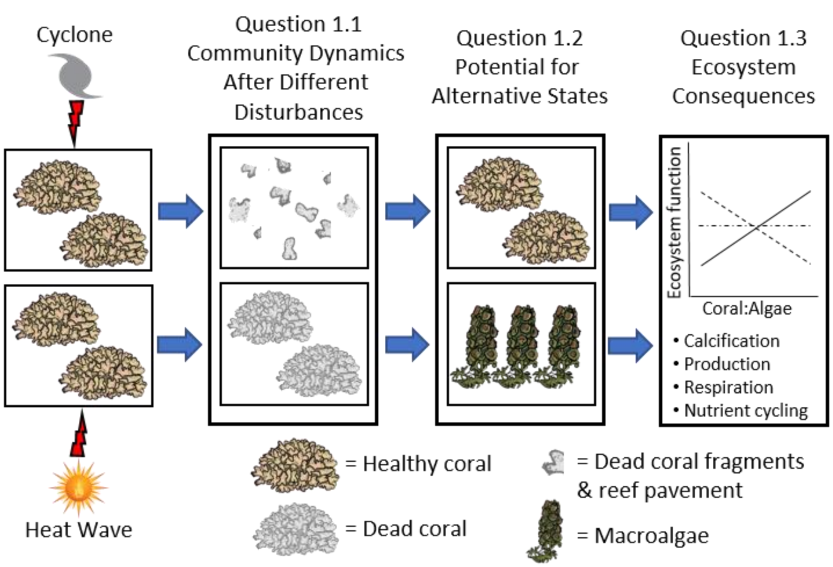


Figure 10. Conceptual diagram outlining the major questions in **Theme 1**. Inspired by the recent disturbances affecting the reefs of Moorea, we will quantify how the material legacies of different disturbances influence post-disturbance dynamics **(Q1.1)**, potentially mediating switches to alternative states **(Q1.2)**, and altering ecosystem functions **(Q1.3)**.

<u>Rationale:</u> Our time series showed that the 2019 MHW caused significant coral bleaching and mortality that varied around the island and across depths with highest mortality at shallower depths (Fig. 11) and on the north shore (Fig. 12). In MCR III, our time series and process studies showed that following the 2010 cyclone, the rates of coral recruitment strongly influenced the rate of coral recovery around the island and across depths. Importantly, the cyclone removed dead coral structure resulting in open substrates suitable for coral recruitment (Holbrook et al. 2018). By contrast, the 2019 MHW left dead coral colonies in place, thus providing rugose surfaces that rapidly were colonized by the macroalga *Lobophora* that deters coral settlement (Adam et al. In review). The material legacy of dead coral colonies potentially promotes a different community dynamic compared to the previous cyclone disturbance: now, the recovery of corals will be influenced by coral recruitment as well as the rate of erosion of dead coral colonies and the creation of suitable substrates for coral settlement. Our research will explore whether coral recruitment rates interact with erosion rates of dead coral colonies to control the pace and trajectory of recovery of the coral community.

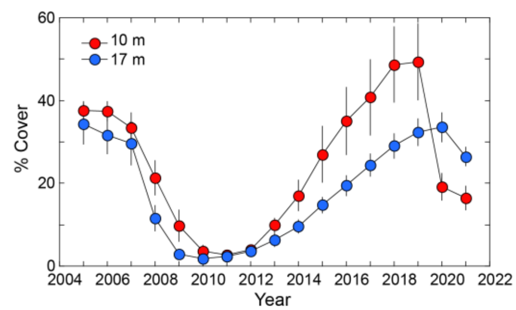


Figure 11. Island-wide mean (± SE, N = 6 sites) coral cover around Moorea at 10 m and 17 m depth.

<u>Approach:</u> We are using three approaches to understand the factors driving heterogeneity in coral recovery following bleaching. *First*, we will use our core time series to quantify the trajectories of changing coral cover around the island. In 2020, we established additional benthic transects at 4 sites along the north shore at 5 m, 10 m, and 17 m depths (N = 4 transects per depth per site) to supplement our core times series transects and provide a platform for process studies. These new transects allow us to quantify coral recovery at shallow depths (5 m) where bleaching mortality was highest and where physical forcing is strongest compared to deeper depths. *Second*, data on coral recruitment, growth, and survivorship from our time series will be used to link demographic processes in corals to recovery rate across sites and

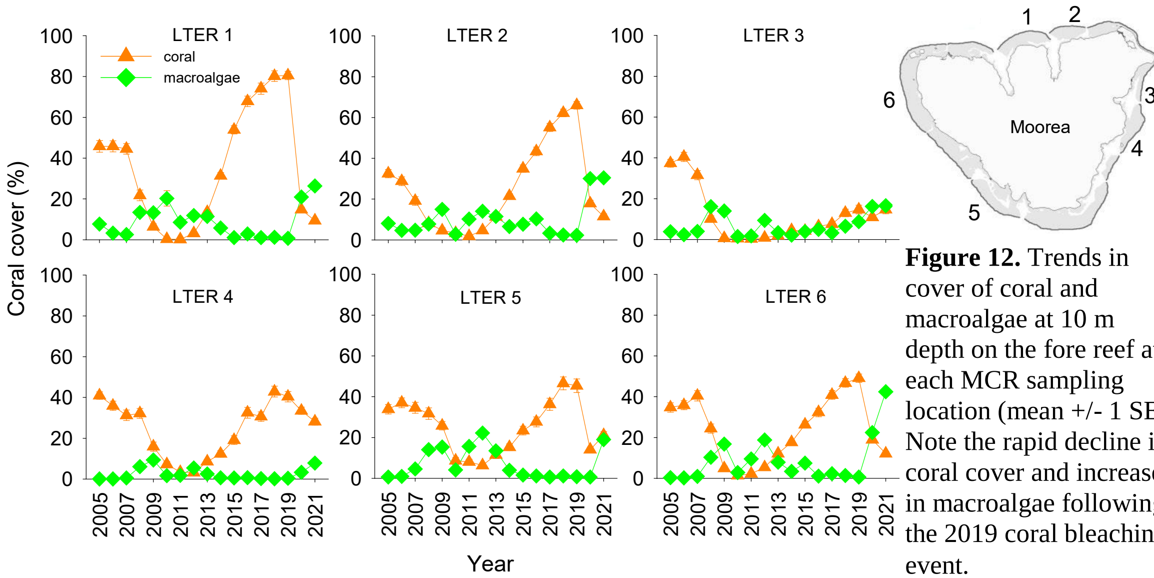


Figure 12. Trends in cover of coral and macroalgae at 10 m depth on the fore reef at each MCR sampling location (mean +/- 1 SE). Note the rapid decline in coral cover and increase in macroalgae following the 2019 coral bleaching event.

depths. We will examine how coral recovery is mediated by erosion of dead coral colonies by quantifying rates of colony erosion using a time series of photographs (Adam et al. 2014). Further, erosion rates will be related to wave climate using data from our core physical oceanographic time series. Process studies will explore how biotic processes such as herbivory and corallivory influence coral demographic rates and the trajectory of community dynamics across depths (e.g., Ladd et al. 2021). Given that coral diversity is an important determinant of coral growth and production (Clements and Hay 2021), we will use our time series data and *in situ* experiments to examine how different levels of coral diversity (including cryptic diversity of *Pocillopora* species; Burgess et al. 2021) affect recovery.

Third, we initiated a ***Dead Coral Removal Experiment*** to test how the presence of dead coral skeletons influences community dynamics. In this experiment, following the 2019 bleaching event dead coral skeletons were removed in 4 m^2 plots (N = 10 per removal and control treatments) at one 10 m site to address mechanisms underlying the influence of coral skeletons on community trajectories. We are using high-resolution 3D photogrammetry methods, which the MCR helped develop (Nocerino et al. 2019, 2020), to track the growth of surviving corals (at mm scales) and quantify how the presence of dead coral skeletons in the local neighborhood influences coral growth and mortality. The photomosaics also are being used to quantify coral recruitment, coral-coral competition, and coral-algal competition. Additional short-term process studies and assays will assess how rates of herbivory and corallivory in these plots influence community dynamics in the presence and absence of dead coral skeletons.

Question 1.2: *Do structure-retaining disturbances increase the basin of attraction (region of bistability) of macroalgae-dominated states? Are the macroalgae states that arise from structure-retaining disturbances self-reinforcing?*

Rationale: MCR III research revealed that macroalgae and coral states can behave as alternative basins of attraction when herbivores can prevent initial colonization of macroalgae but cannot extirpate established plants (Davis 2018, Schmitt et al. 2019, 2021). Further, life-stage-related decline in vulnerability of macroalgae to herbivory promotes alternative stable states in theoretical models of herbivore – macroalgae – coral interactions (Briggs et al. 2018, Rassweiler et al. 2021). These findings underlie our hypothesis that compared to a structure-removing disturbance, dead coral skeletons remaining after a structure-retaining disturbance increase the probability of a state shift from coral to macroalgae by shielding vulnerable young stages from herbivory. This mechanism facilitates survival and growth of macroalgae to herbivore-resistant stages and the establishment of positive feedbacks that promote self-replenishment (e.g., associational defenses; Bittick et al. 2010, Davis 2018). Our conceptual model (Fig. 13) is depicted as a response surface (left panel) showing how the equilibrium abundance of macroalgae hypothetically varies as a function of herbivore biomass and the amount of spatial refugia for young macroalgae; the right panels illustrate how herbivore-macroalgae relationships at two locations on the resilience landscape can produce qualitatively different dynamical responses to a disturbance. Under conditions with few algal refugia (Fig. 13, purple line), only one equilibrium abundance of macroalgae exists for any given biomass of herbivores in the environment, and a system located anywhere along the purple line is highly resilient to a large disturbance (Fig. 13, top right). Hysteresis in the herbivore-macroalgae relationship when algal refugia are abundant (Fig. 13, red line) creates the potential for coral and macroalgal states to be bistable over some range of herbivore biomass (see Schmitt et al. 2019, 2021). A large disturbance to a system in the bistability portion can flip the community from one basin of attraction to the other (Fig. 13, lower right). We hypothesize that a skeleton-retaining disturbance moves the system along the 'Algal Refugia' dimension of the resilience landscape toward - and potentially into - the region of state space where hysteresis exists in the herbivore-macroalgae relationship, without a change in herbivore biomass (Fig. 13). As such, a structure-retaining disturbance could weaken resilience of the coral state and foster a regime shift to macroalgae.

Approach: The above questions will be addressed using long-term experiments, field process studies and modeling, together with data from core time series and relevant findings from Question 1.1. *First*, we will establish a ***Hysteresis Experiment*** on the fore reef to quantify the relationship between variation in herbivory and the resultant biomass of macroalgae as a function of two factors: the starting community (macroalgae vs. invasible turf algae) and disturbance type (presence vs. absence of dead coral skeletons). The starting community treatment will reveal whether the herbivore-macroalgae relationship for either disturbance type changed from before to after a shift to macroalgae, which is diagnostic of hysteresis (Bestelmeyer et al. 2011, Schmitt et al. 2019). Comparison of the relationships for the two disturbance types (skeletons present vs. absent) will reveal whether the location of hysteresis differs between skeleton-retaining and skeleton-removing events under otherwise identical environmental conditions. The experiment will use the same techniques and design that we have employed in several previous multi-year probes for tipping points, hysteresis and effects of herbivory (Holbrook et al. 2016, Schmitt et al. 2019, 2021, Adam et al. In review). Briefly, a gradient in the biomass of herbivores that have access to focal benthic plots will be created using semi-permeable cages bolted to the reef framework; a series of exclosures that have different size holes sequentially will reduce the maximum body size of an herbivorous fish that can enter (Holbrook et al. 2016). We plan 5 herbivore (determined by hole size in cages) treatments (N = 5 per treatment), plus a cage control, which will create graded variation in herbivory ranging from ambient to almost none on a 0.25 m^2 plot. *In situ* videos of each hole size treatment will quantify the herbivory gradient (Holbrook et al. 2016, Schmitt et al. 2021). The experiment will run for 3 years, after which the composition and biomass of macroalgae will be quantified. Our hypothesis will be supported if the region of hysteresis in the herbivore - macroalgae relationship is (statistically) further away from ambient in the 'skeleton absent' treatment relative to the 'skeleton present' treatment.

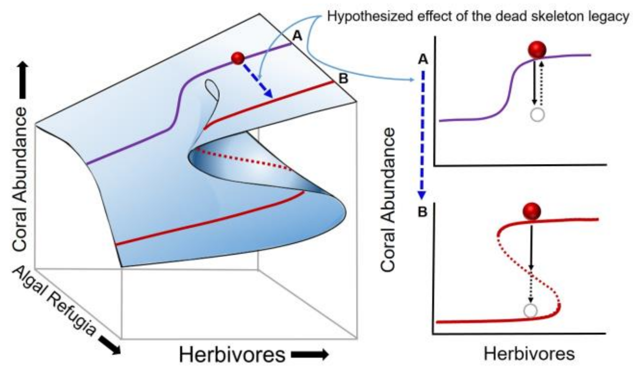


Figure 13. (Left) A hypothetical response surface showing how the equilibrium abundance of coral might vary as a function of herbivore biomass and amount of physical refugia that facilitate the proliferation of macroalgae. Skeletons of coral can provide vulnerable stages of algae protection from herbivores, thereby shifting the system into a region of state space where coral and macroalgae can be bistable, profoundly affecting resilience of the coral state **(Right)**. See text for more detail.

Second, we will explore hysteretic dynamics via differential equation modeling. MCR researchers have developed an initial model that involves dead coral skeletons based on an established set of state variables and interactions. Specifically, the model assesses the relative impacts of structure-removing and structure-retaining disturbances on the potential for coral to recover by comparing post-disturbance trajectories following varying intensities of each disturbance type. Preliminary analyses indicate that gradually eroding skeletons support bistability and increase the likelihood of transitions to macroalgae-dominated states. The amount of refuge space for macroalgae and the dissolution rate of dead skeletons determine transition likelihood and speed, and these will be quantified from the experiment and our time series transects (Question 1.1) and will be used to parameterize subsequent iterations of the model.

Third, a ***Regime Shift Experiment*** was initiated in August 2021. The experiment consists of 45 similar-sized patch reefs (bommies) all initially covered with the macroalga *Turbinaria* assigned haphazardly to one of 3 disturbance treatments (N = 15 per treatment). The first treatment represents a powerful structure-removing event (cyclone), the second mimics a bleaching event that left coral skeletons intact, and the third consists of unmanipulated controls. For the bleaching treatment, 10 intact dead *Pocillopora* skeletons were affixed to each bommie (after removal of macroalgae), spaced to replicate the dead coral cover following previous major bleaching events in 2019 (Fig. 11) and 1991 (Edmunds et al. 2015). The 15 bommies in the cyclone treatment were cleared of macroalgae to simulate storm scouring (Schmitt et al. 2019). Community trajectories on all 45 bommies and the erosion rate of bleached coral will be quantified 2 to 3 times per year using high resolution photogrammetry developed for this application (Nocerino et al. 2020). We anticipate it will take at least several years for the dead skeletons to erode (Swanson 2016); the experiment will be terminated a year after that point in order to assess whether macroalgae (if established) remains self-replenishing. At termination, benthic communities will be quantified and data analyzed using the same criteria and methods as in previous MCR state change experiments (Schmitt et al. 2019, 2021) to facilitate direct comparison. The hypothesis will be supported if a greater proportion of bommies in the bleaching disturbance treatment transitioned to a self-replenishing macroalgae community compared to the structure-removing disturbance treatment.

Question 1.3: *How does post-disturbance coral recovery influence key ecosystem processes? How do different disturbance types differentially impact ecosystem processes?*

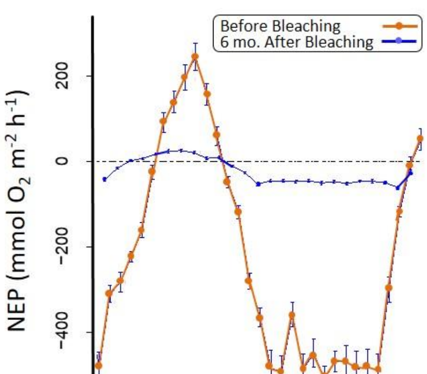


Figure 14. Rates (mean ± SE) of hourly net ecosystem production (NEP) at LTER 1 fore reef at 10 m depth before and 6 months after the coral bleaching event in 2019. Rates of NEP were measured using a gradient flux method that estimates NEP over a footprint of 10-50 m^2 of reef.

Rationale: The composition of the benthic communities on coral reefs influences ecosystem processes. For example, the abundance of live coral is strongly linked to calcification rates, while the ratio of corals to algae influences benthic production and respiration (Carlot et al. 2021). These differences in community composition and ecosystem metabolism drive biophysical feedback loops that further alter local biogeochemical conditions (Silbiger et al. 2018, Silbiger and Sorte 2018, Fields and Silbiger 2022). Fishes represent the largest pool of organic biomass and nutrients on coral reefs (Newman et al. 2006, Allgeier et al. 2017), and our time series shows that the amount of habitat structure provided by corals influences the abundance and diversity of fishes (Adam et al. 2014), which then affects a host of ecosystem processes such as herbivory and nutrient cycling (Burkepile et al. 2013, Munsterman et al. 2021). Thus, the two different disturbances in our system (cyclone vs. bleaching event) are likely to result in fundamentally different impacts on ecosystem processes.

Approach: We will use three approaches to address the dynamics of ecosystem processes in response to coral-killing disturbances. *First*, to address benthic-associated ecosystem processes, we will continue our time series, begun during MCR III, using the gradient flux technique to measure reef metabolism (primary production and calcification) on the fore reef (Fig. 14). This work was expanded after the 2019 bleaching event via a RAPID award (PI Carpenter). The gradient flux measurements are combined with photomosaics of the benthos to link changes in the benthic community with changes in reef metabolism. These data will allow us to quantify how the material legacy of dead coral skeletons influences reef metabolism, how these impacts change as dead corals erode, and how reef metabolism changes with future trajectories of the benthic community.

Second, to characterize the effect of coral-killing disturbances on biophysical feedback loops, we will pair the data described above with measurements of pH, dissolved oxygen (DO), temperature, and light taken just above the reef and at the ocean surface to characterize not only how changes in the environment affect reefs, but how altered reefs change the local biogeochemical conditions. Prior research found that loss of foundation species and/or a disturbance that changes their physiology led to immediate changes in local pH, DO, and light, in turn impacting organismal and community processes (Silbiger et al. 2018, Fields and Silbiger 2022). By pairing environmental data with community composition and community metabolism we can understand mechanisms that lead to altered biogeochemical conditions and thereby better predict the effect of disturbances on ecosystem function.

Third, to examine how disturbances impact fish-associated ecosystem processes, we will combine data from our fish time series (Fig. 15) with models estimating ecosystem process rates of fishes. Existing relationships between individual fish biomass and rates of ecosystem processes (N and P excretion/egestion, C/N/P storage, herbivory, piscivory) will be used to generate community-wide estimates of these processes from our time series data on fish communities (e.g., Allgeier et al. 2021, Munsterman et al. 2021, Schiettekatte In press). These data will allow us to examine how changes to the fish communities driven by different types of disturbances (coral skeleton removing vs. coral skeleton retaining) affect ecosystem processes.

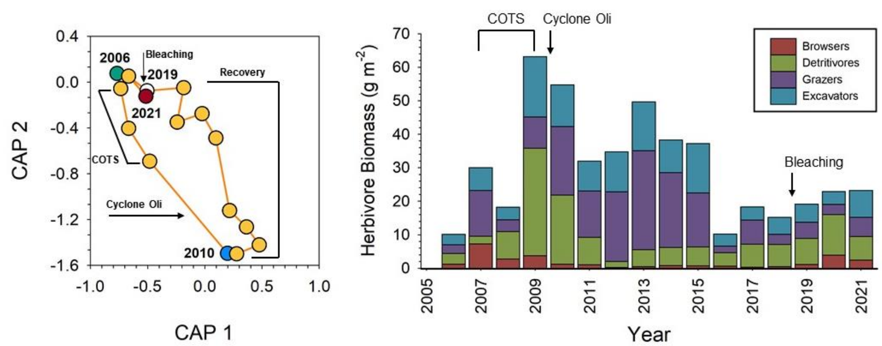


Figure 15. (Left) Ordination showing changes in the fish community observed at fore reef site LTER 2. The first two axes of the ordination, CAP1 and CAP2, accounted for 31% and 17%, respectively, of the variation in the community. Indicated on the graph are the first year, 2006, in the time series (green circle), the first year of Crown-of-Thorns Seastar (COTS) outbreak, the impacts of Cyclone Oli (blue circle), the coral bleaching event in 2019 (white circle), and the most recent year in the time series, 2021 (red circle). **(Right)** Trends in herbivore biomass by feeding guild at fore reef site LTER 2.

Theme 1 Modeling and Integration: *How disturbance, herbivory, and nutrients affect coral resilience*

Ongoing modeling work has allowed us to: (1) use photogrammetric measurements to project the growth of coral communities using Integral Projection Models (IPMs; e.g., Kayal et al. 2018) and (2) integrate data on macroalgal herbivory into differential equation models for state shifts on Moorea's reefs (e.g., Briggs et al. 2018). During MCR IV, we propose to unite these successful (but, thus far, separate) modeling efforts using data collected as part of Theme 1 and MCR-associated work on how disturbance and nutrient availability interact to affect growth and competition between corals and macroalgae. This effort will occur via an ongoing **Resilience Working Group** that will be established in Year 1. Along with the other working groups proposed for Themes 2 and 3, it will meet in Santa Barbara after our annual All Investigator Meeting, and at other times (in person or virtually) through the year.

We will begin by expanding our existing community-level coral IPMs to include data on coral-skeleton and coral-macroalgae interactions, and by creating IPMs for macroalgae. We will use data from the ***Dead Coral Removal Experiment*** (Question 1.1) to estimate demographic rates (e.g., recruitment, growth rate, and mortality) of macroalgae and coral in the presence and absence of dead coral skeletons. To obtain similar data as a function of nutrients and herbivory, we will use data from another ongoing experiment where corals were removed to mimic a cyclone or corals remained intact. A gradient of herbivory was created with exclosures, and slow-release fertilizer (Osmocote) enriches half of the exclosures with N and P (sensu Schmitt et al. 2019, Burkepile et al. 2020). Fortuitously, this experiment experienced high loss of corals in the 2019 bleaching event, thus allowing us to assess how altering herbivory and nutrients impacts benthic dynamics in response to different disturbances.

To synthesize our IPMs with models of benthic cover, we will use two approaches. *First*, we will use empirical data on macroalgal biomass and coral colony size to build statistical scalars that translate IPM outputs to areal footprint. This allows use of the mechanistic IPMs to drive the growth and mortality rates that are typically loosely defined as changes in areal extent in coral-macroalgae hysteresis models (e.g., Mumby et al. 2007, Baskett et al. 2014). *Second*, we will develop new, cellular automata models (e.g., Eynaud et al. 2016) that explicitly represent benthic space as an occupancy grid (where grid locations can be occupied by species of coral, macroalgae, or turf). We will use empirical data on how coral and macroalgal growth is affected by context (e.g., nutrient availability, neighboring coral skeletons or live individuals) to derive updating rules for this model, and contrast its predictions for individual expansion (e.g., the rate at which a *Pocillopora* colony extends to neighboring cells) with the IPMs and its predictions for benthic cover with state-shift models. These approaches complement modeling efforts described in Theme 2 that will explore the effects of spatial heterogeneity on resilience.

Theme 2: How do local stressors interact with new disturbance regimes to drive spatial heterogeneity in community dynamics, ecosystem processes, and spatial resilience?

Question 2.1: *How do key external drivers of benthic communities vary spatially within the lagoons?*

Rationale: Reefs in the lagoons of Moorea are influenced by a combination of natural physical forces (e.g., water flow, temperature) as well as exposure to chronic anthropogenic stressors such as fishing and nutrient pollution, all of which can be spatially heterogeneous. At the same time, these reefs are experiencing the effects of a warming climate, including an increase in the frequency and severity of marine heat waves (MHWs) that cause coral bleaching and mortality (Fig. 2). Spatial heterogeneity in temperature dynamics can result in divergent patterns of coral bleaching and mortality across small spatial scales (e.g., < 1 km; Safaie et al. 2018, Donovan et al. 2020). Temperature can also interact with other spatially heterogeneous physical factors and anthropogenic stressors to drive patterns of coral bleaching and mortality during a MHW. For example, during a MHW in Moorea in 2016, sites impacted by nitrogen enrichment from sewage and agriculture experienced increased coral bleaching, with excess nitrogen exacerbating the negative impacts of that moderate thermal stress event on corals (Donovan et al. 2020). Over longer time scales, our core time series data have

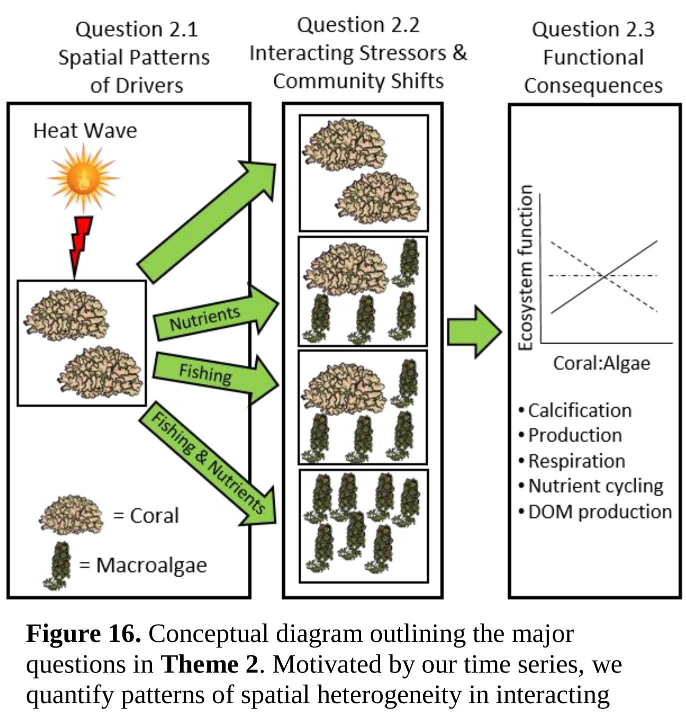


Figure 16. Conceptual diagram outlining the major questions in **Theme 2**. Motivated by our time series, we quantify patterns of spatial heterogeneity in interacting stressors **(Q2.1)** that create heterogeneous community responses to marine heat waves **(Q2.2)** with resulting effects on ecosystem processes **(Q2.3)**.

revealed that nitrogen enrichment is associated with coral-to-macroalgae phase shifts in the lagoons (Adam et al. 2021). Spatial patterns of nitrogen enrichment are shaped by oceanographic processes that influence the delivery of nutrients from local anthropogenic sources by driving patterns of water flow (Adam et al. 2021). Water flow in the lagoons affects a range of additional processes, including primary production, the dispersal of propagules, accessibility of feeding locations to herbivorous and corallivorous fishes, temperature dynamics, and coral bleaching (Lenihan et al. 2008, 2015). Lastly, we have found significant heterogeneity in the structure, stability, and resilience of coral and water microbiomes across the lagoon, which suggests that variation in environmental factors influences coral holobiont features that, in turn, may affect their ability to resist or recover from disturbance. Here, we will quantify spatial patterns of key drivers of lagoon spatial heterogeneity, including physical processes (e.g., temperature) and local anthropogenic stressors (e.g., nutrient pollution, fishing) that interactively drive benthic community dynamics.

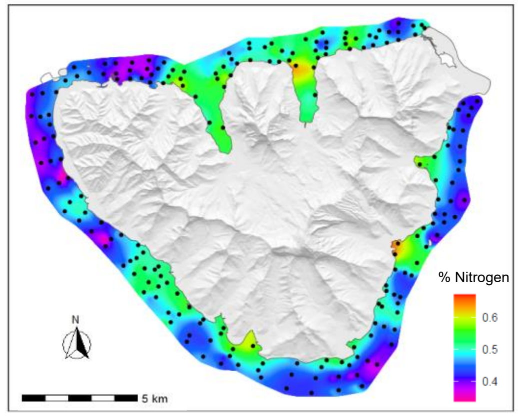


Figure 17. Location of sampling sites around Moorea (black dots) with spatial patterns of nitrogen enrichment (percent nitrogen in tissue from the macroalga *Turbinaria ornata*). Nitrogen is represented as a continuous surface where warmer colors represent higher nitrogen and cooler colors represent lower nitrogen.

Approach: To better understand spatial heterogeneity in physical factors and anthropogenic stressors that can influence benthic community dynamics, we will build on our existing core time series and current research campaigns to document, at high spatial resolution, how temperature dynamics, nutrient enrichment, and fishing pressure vary across the lagoons. During 2021, we installed an array of thermistors (SBE-56, resolution ±0.002°C) at 48 new sites in the lagoon, to expand on water temperature data from our core time series (collected on the fore reef, fringing reef and back reef at the six core MCR sites, Fig. 8). The new array consists of a ring of 36 sensors encircling the island (at ~1 km spacing), deployed 200 m shoreward of the reef crest plus 3 cross-shore transects (each consisting of 4 sensors) spanning from the reef crest to the shoreward edge of the lagoon (Fig. 8). This array will characterize how temperature dynamics within the lagoons vary both across-shore and along-shore around the island. With respect to nutrient enrichment, we will quantify inorganic nutrients in the water column and nitrogen tissue content in the brown macroalga *Turbinaria ornata* across our grid of 200 lagoon sites around the island annually at the end of the warm rainy season in April/May (Fig. 17). Water column nutrients provide a snapshot of nutrient conditions while nitrogen tissue content in *Turbinaria* yields a time-integrated proxy of nitrogen availability during a time when nutrient enrichment from anthropogenic sources is likely to be high due to increased rates of surface water runoff and submarine groundwater discharge (Adam et al. 2021). In addition, given that ocean temperatures are at their peak during the rainy season, corals are most likely to be experiencing thermal stress and associated bleaching at this time, allowing us to link spatial patterns of nutrient enrichment with patterns of coral bleaching and associated mortality. The local-scale fishery in Moorea heavily targets the lagoons (Rassweiler et al. 2020). We will quantify spatial patterns of fishing intensity using data from our detailed surveys of fishing and fish consumption conducted around Moorea in 2018-2022, including focal fisher observations, market surveys, household surveys and socioeconomic data from the territorial census (Rassweiler et al. 2020, 2021, Nassiri et al. 2021, Holbrook et al. 2022).

Question 2.2: *How do patterns of acute temperature stress during a marine heat wave interact with anthropogenic stressors to determine the overall vulnerability landscape to climate-driven disturbances?*

Rationale: Chronic anthropogenic stressors such as nutrient pollution and fishing can exacerbate the impacts of climate-driven disturbances by impacting both the short-term responses of corals and longer-

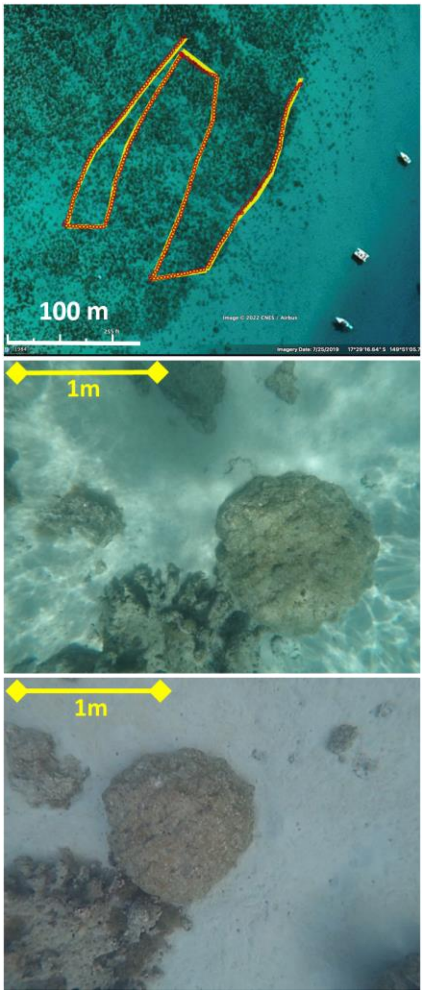


Figure 18. Our autonomous surface vehicle (ASV) can conduct photographic surveys of lagoon habitats at 1,800 m per hour. We have programmed it to repeat prior surveys **(Top)**; black dots indicate locations surveyed by a diver in 2020, the yellow line traces the ASV repeating the same 700 m path. Bottom photos show images of the same coral bommie in 2020 **(Middle)** and 2021 **(Bottom)**.

term responses of the benthic community. While the importance of these stressors has been demonstrated by our small-scale studies (e.g., Holbrook et al. 2016, Zaneveld et al. 2016, Schmitt et al. 2019, Burkepile et al. 2020), there is considerable controversy about their relative importance at the reef scale (Bruno et al. 2019) and even less clarity about their combined effects. Moorea's lagoons offer an opportunity to disentangle these effects, as stressors are differentially correlated across space (Holbrook et al. 2022), resulting in a variety of stressor combinations. By following outcomes of individual corals and benthic communities at sites with different stressor combinations, we can assess their relative importance.

Approach: Using the data collected for Question 2.1, we will create a 'vulnerability map' identifying locations exposed to high levels of nutrient pollution, fishing, and thermal stress both individually and in combination. We will assess the effect of these stress combinations on outcomes for individual corals (bleaching and death) and on the occurrence of transitions between benthic community states (particularly transitions in and out of macroalgae dominance). We will measure these responses in two ways. *First*, our autonomous surface vehicles (ASVs) will conduct annual surveys of benthic communities at 30 locations chosen to span a range of combinations of vulnerability. At each site, an ASV will survey a 200 m x 100 m area, driving exactly the same grid pattern each year, and taking photographs of the reef below it (Fig. 18). Recently developed computer vision approaches will enable us to quantify organisms and substrates from these large numbers of images (Miller et al. In review), revealing community state transitions as well as changes in the prevalence of bleached and dead corals. By covering exactly the same grid each year, the surveys will allow us to follow the individual fates (bleached and/or dead) of a large number of corals that can be identified in the images and test how the probability of each outcome depends on the combinations of stressors present. *Second,* surveys of corals, benthic communities, and water column microbiomes will be done at our 200 lagoon sites (Fig. 17) that we currently sample for nitrogen enrichment and coral bleaching annually at the end of the warm rainy season. These surveys are spatially extensive and involve rapid assessment of ecological state and rates of bleaching over a broad range of contexts. Using data from these sites that exist across a range of nutrient enrichment, temperature stress, fishing intensities, reef microbiome structure/function, as well as benthic community state, we will test predictions about how specific chronic anthropogenic stressors interact with variation in temperature during a MHW to shape coral bleaching responses and any subsequent change in the benthic community.

Question 2.3: *What are the relationships between benthic community states and ecosystem processes?*

Rationale: In Question 2.2, we will identify areas of the lagoon that exist in different community states functionally dominated by coral vs. macroalgae (Fig. 4). Here, we will examine the consequences of these states on key ecosystem processes as mediated by benthic communities, microbes, fishes, and environmental context. Primary production and calcification rates are influenced by whether reefs have abundant corals or algae. Corals and algae are both significant sources of dissolved organic matter (DOM) but each produces different types and concentrations of dissolved organic matter (Fig. 19; Wegley Kelly et al. 2022). This differential DOM production has different effects on pelagic microbial communities and microbially-driven ecosystem processes (Haas et al. 2013, Nelson et al. 2013). Further, fishes process organic matter and recycle inorganic nutrients in different ways on coral- vs. macroalgae-dominated reefs (higher herbivory and ratio of N:P recycling but lower detritivory on coral-dominated reefs) due to fundamental shifts in the fish community with transition to macroalgal dominance (Fig. 19; Munsterman et al. 2021). We will assess how organisms from microbes to corals to fishes impact the dynamics of DOM, recycling of inorganic nutrients, and rates of primary production and calcification.

Approach: We will address how state shifts influence ecosystem processes using three approaches. *First*, we will focus on patterns in benthic metabolism as influenced by benthic state (coral or macroalgae). The goal is to obtain estimates from a much larger number of sites than we do currently, potentially allowing us to examine time series of ecosystem processes before, during, and after benthic state shifts as some of these locations transition between states. We have a time series of net ecosystem production (NEP), respiration (R), and net ecosystem calcification (NEC) at two sites (LTER 1, LTER 2) on the north shore. Additional data include *in situ* measurements of light (PAR) and water flow, the two primary physical drivers of coral reef metabolism, as well as benthic community structure, allowing changes in benthic metabolism to be related to changes in community structure. We will continue to build these relationships along several cross-reef transects at the 3 instrumented locations in the lagoon around Moorea (LTER 1, LTER 4, LTER 5). Three transects will be chosen at each location that vary in community structure and spatial complexity (coral, sand, pavement, macroalgae), and reef metabolism will be measured using established MCR methods. Community structure will be quantified from benthic photographs taken along the transects using our ASVs (described above). The main product from this campaign will be a set of algorithms that relate physical drivers to reef metabolism (NEP and NEC) for communities that vary in relative abundance of benthic components. These algorithms will allow

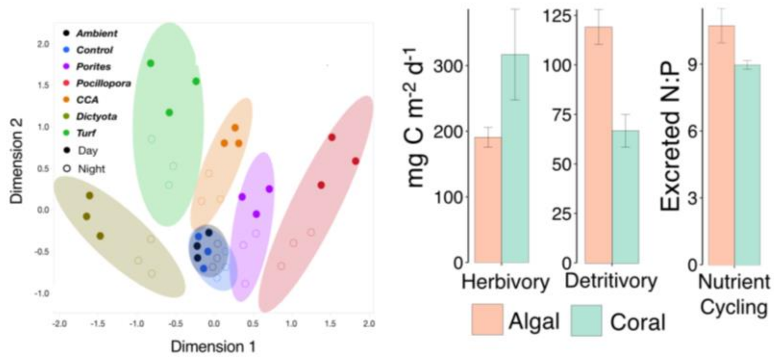


Figure 19. (Left) Ordination of dissolved organic matter (DOM) molecules released from different benthic primary producers. Notice separation among taxa in the suite of DOM released as well as differences between corals (*Porites*, *Pocillopora*) and algae (*Dictyota*, turf, CCA) (From **Wegley Kelly et al. 2022**). **(Right)** Rates of herbivory, detritivory, and ratio of N:P in fish excretion on reefs in either coral or algae-dominated state (From **Munsterman et al. 2021**).

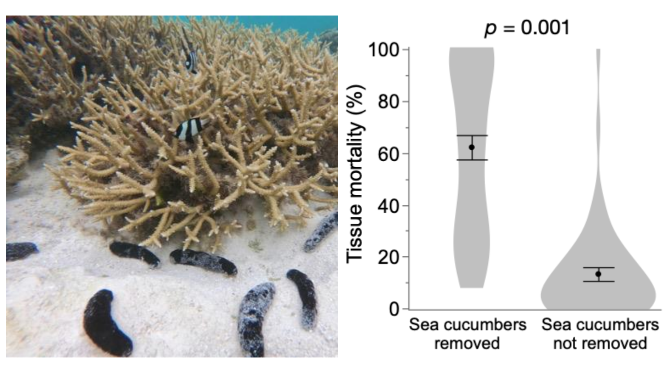


Figure 20. (Left) Sea cucumbers aggregated around a stand of the staghorn coral (*Acropora pulchra*). **(Right)** Violin plot of data on coral tissue mortality showing increased mortality in areas where sea cucumbers have been removed vs. those where sea cucumbers were left in place.

for estimates of reef metabolism across our 30 ASV sites on the north shore from combining data of benthic community structure from the ASV surveys with data on physical variables (light from *in situ* measurements and flow from our circulation model of the north shore lagoon). To augment the NEP and NEC data across a broader spatial scale and to test the efficacy of these models, we will sample total alkalinity (TA) and dissolved inorganic carbon (DIC) at all 30 ASV sites in concert with the water column sampling described next. This will allow rapid replication of ecosystem metabolism measurement and can be used as a proxy for NEP and NEC rates (Cyronak et al. 2018, Silbiger et al. 2020).

Second, we will explore the relationships between benthic state, dissolved organic matter (DOM) production, and microbially-driven ecosystem processes. At each of our 30 ASV sites, we will measure multiple components of DOM (DOC, DON, DOP, fDOM; e.g., Wegley Kelly et al. 2022) and inorganic nutrients (nitrate, ammonium, phosphate) from the water (1 m above the bottom) as well as examine water-column bacterial communities to assess how organic and inorganic nutrients are cycled differently across benthic state. To link organic matter and nutrient cycling to bacterial communities, we will assess both community structure (using 16S amplicons) and physiological function (using metagenomics) of the bacterial communities in the water column to examine how benthic state shifts relate to the functions of pelagic microbial communities. *Third*, the impact of mobile animals on ecosystem processes (herbivory, detritivory, nutrient cycling) will be quantified by combining data on fish community structure with models estimating ecosystem process rates of fishes (as described in Question 1.3). In addition, we have shown that sea cucumbers are important detritivores that help maintain healthy corals in the lagoon by altering microbial communities in reef-associated sediments (Fig. 20; Grayson et al. 2022). We will test how benthic state correlates with the abundance of sea cucumbers and use experiments to assess how sea cucumbers alter the dynamics of particulate organic matter and sediment microbial communities (using 16S sequencing).

Theme 2 Modeling and Integration: *Predicting ecological change and resilience across the lagoon*

Theme 2 explores the spatial distribution of multiple stressors within Moorea's lagoons and the consequences for the benthic community and associated ecosystem function. A particular concern is that these stressors are eroding reef resilience, and enabling large-scale shifts from coral- to macroalgae-dominated states. Both theory and small-scale field experiments have demonstrated that strong positive feedbacks can reinforce and stabilize either ecological state in Moorea's lagoons (Buenau et al. 2007, Davis 2018, Briggs et al. 2018, Schmitt et al. 2019, 2021), raising the fear that shifts to macroalgae might be difficult to reverse. However, feedbacks that generate alternative ecosystem states at small scales often result in more complex self-organizing patterns on spatially extended landscapes (Gandhi et al. 1998, Rietkerk et al. 2021). Thus, ecological responses to stress and disturbance at the landscape scale may differ from those suggested by prior theory and experiments. Outcomes at the landscape scale depend on the strength of spatial feedbacks and the scales over which they occur (Rassweiler et al. 2021).

In Year 1, we will form a **Lagoon Resilience Working Group** that will meet in Santa Barbara after our annual All Investigator meeting and regularly throughout the year. It will develop a suite of spatially explicit models focused on understanding how the mechanistic feedbacks documented in small scale experiments will operate over spatial scales of 10^3-10^6 m^2. The models will explore several key questions: (1) As stressors alter the competitive balance between coral and macroalgae, how do the abruptness and reversibility of a transition from coral to macroalgal dominance differ at small vs. large spatial scales? (2) What is the role of processes such as feeding behavior of herbivorous fish in synchronizing benthic dynamics within the lagoons, and what are the consequences for spatial pattern and resilience? (3) How well do models reproduce empirical patterns of patch size and stability?

We will represent benthic and fish dynamics using complementary partial differential equation models and spatially explicit simulation models. At the local scale, these models will parallel non-spatial models developed in Theme 1; they will use similar parameters for coral and algae interactions and demographics, and will incorporate similar effects of herbivory and nutrient enrichment on the benthic community (e.g., Detmer et al. In press). At larger scales, these models will incorporate empirically-grounded spatial patterns of habitat availability, nutrients, temperature, and fishing. Habitat patterns, such as the distribution of sand and hard substrates, will be parameterized based on georeferenced ASV surveys (Question 2.2). Spatial variation in nutrient and temperature stress will be based on data collected in Question 2.1. Spatial variation in fishing stress will be based on maps of fishing developed in a recent related project (Holbrook et al. 2022). Key spatial dynamics will be included, such as fishing behavior that redistributes effort across the lagoon (Rassweiler et al. 2021) and herbivore movement and behavior (based on the literature, e.g., Davis et al. 2017). These models will reveal how local dynamics scale up to spatially extended landscapes, and will predict how the spatial configuration of habitat and stressors will translate into spatial patterns of ecological state. They will extend the value of data collected in Theme 2 and complement the modeling proposed in Theme 1.

Theme 3: How do disturbances generate information legacies in corals and coral reef communities that influence their resilience under current and future environmental conditions?

Question 3.1: *How will rising ocean temperature and MHWs affect the phenology of coral reproduction and the thermal tolerance of coral recruitment to modulate coral community dynamics?*

Rationale: One important information legacy of climate change and its impact on disturbance regimes is the alteration of temporal patterns of reproduction and recruitment in foundation species (Smith et al. 2012, Ernakovich et al. 2014, Giuliani et al. 2014, Ward et al. 2018, Piao et al. 2019). Pocilloporid corals are foundation species on the reefs of Moorea, where their populations have rapidly recovered after recent disturbances (Holbrook et al. 2018). Our work in MCR III has shown that high rates of *Pocillopora* recruitment from sexually produced larvae are vital to this recovery (Edmunds 2018, Holbrook et al. 2018, Kayal et al. 2018). Detecting this trend was possible because of our 16-year time series of coral recruitment. Yet, we know surprisingly little about the dynamics of reproduction, dispersal, or recruitment in *Pocillopora*, or how rising ocean temperature and periodic MHWs could change the timing and success of coral reproduction, recruitment, and, ultimately, coral resilience. Our data suggest that environmental conditions could operate through multiple pathways to influence reproductive resilience (e.g., effects of

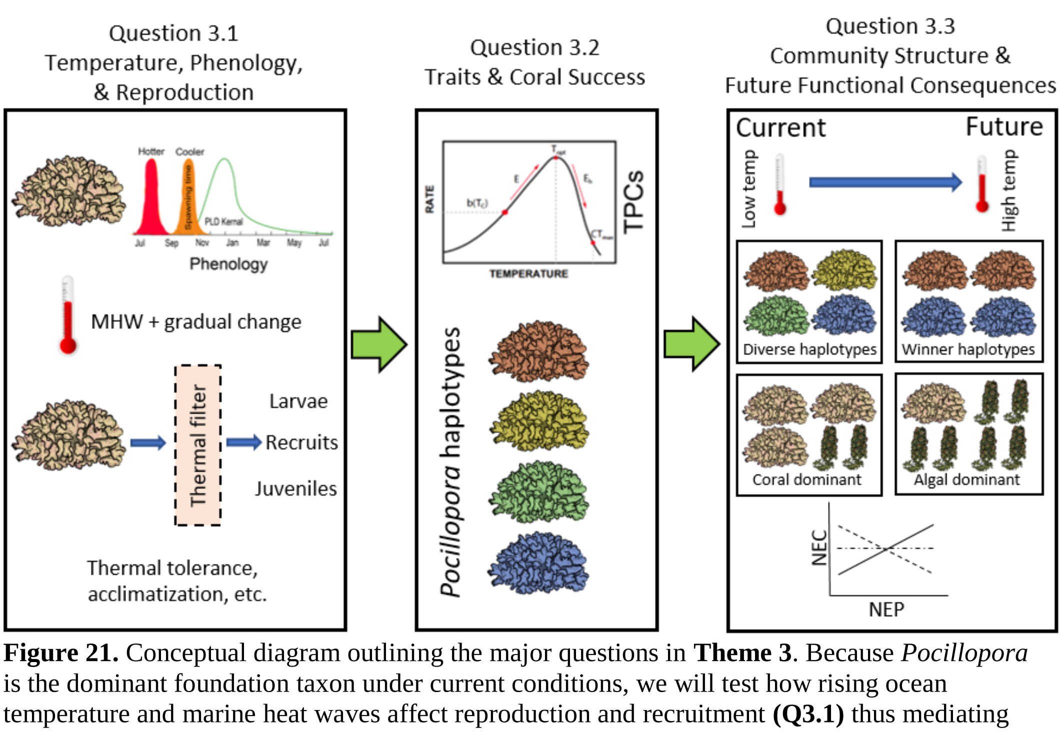
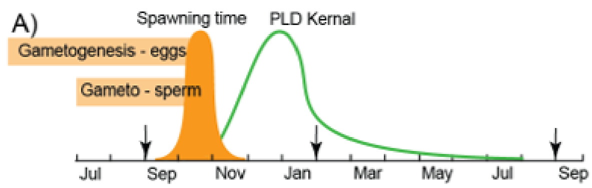


Figure 21. Conceptual diagram outlining the major questions in **Theme 3**. Because *Pocillopora* is the dominant foundation taxon under current conditions, we will test how rising ocean temperature and marine heat waves affect reproduction and recruitment **(Q3.1)** thus mediating the abundances of *Pocillopora* haplotypes that likely have functional differences **(Q3.2)** and then explore the ecosystem consequences of changing community composition under current and future conditions **(Q3.3)**.

temperature on gametogenesis, larval dispersal, and post-settlement success) (Fig. 22; Edmunds 2021). Climate change (i.e., rising ocean temperature) will likely affect reproduction and recruitment of *Pocillopora* by modifying the chronology of key reproductive events (Shlesinger and Loya 2019) as well as lowering fecundity (Johnston et al. 2020, Leinbach et al. 2021). These effects constitute an information legacy that could significantly impact the replenishment of coral populations following disturbances.



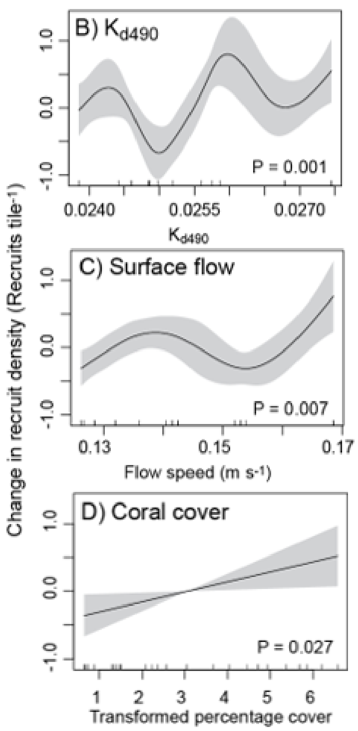


Figure 22. (A) Schematic describes the likely timing of key pocilloporid reproductive events, dictating the environmental conditions to which larvae are exposed. Vertical arrows show timing of recruitment tile deployments in MCR time series. **(B-D)** Line graphs describe the significant relationships between pocilloporid recruitment and environmental conditions on the fore reef at 10 m from 2008-2021 (after Edmunds 2021).

<u>Approach:</u> To better understand how rising seawater temperature mediates pocilloporid recruitment, and hence coral community resilience on the fore reef of Moorea, we will *first* begin a sampling program to describe the chronology of reproduction and recruitment in *Pocillopora*. Rising temperatures and MHWs alter the timing and extent of gametogenesis in many marine animals (Poloczanska et al. 2013) including corals (Shlesinger and Loya 2019, Leinbach et al. 2021). Given that spawning in *Pocillopora* corals in Moorea occurs around Oct/Nov (Edmunds 2021), monthly sampling of *Pocillopora* branches surrounding this time every year will be used to detect developing gametes through histological analyses (as in Johnston et al. 2020). Sampling for this purpose was recently initiated for *Pocillopora*, and has been expanded to select *Acropora* that appear to be increasing in abundance. In MCR IV, our use of settlement tiles (as in Edmunds 2021) will be expanded to enhance our understanding of where and when coral larvae settle. One key effort will be to build upon our time series to understand how gradually rising temperature and MHWs impact the timing and extent of coral recruitment. To develop more accurate estimates (i.e., with monthly resolution) of the timing of recruitment, which is information necessary to test for the response of this vital rate to seasonally varying conditions, tiles will be deployed at monthly intervals at multiple sites between November and March, the period of peak coral recruitment (Edmunds 2021). Further, to evaluate spatial variation in recruitment in the back reef with respect to the water circulation cells that cross the reef (Hench et al. 2008, Leichter et al. 2013), settlement tiles will be deployed in a 24-month sampling program both along the margins of the circulation cells (perpendicular to the reef crest) and parallel to the crest, and they will be sampled every 6 months. These data will be critical for understanding how future changes in ocean conditions (e.g., rising sea levels, changing lagoon circulation) may impact the spatial and temporal dynamics of coral recruitment.

Second, we will use replicate outdoor flumes (5.0 m × 0.5 m) (Edmunds et al. 2020) to test the effects of high temperature on the information legacies created through the reproduction of broadcast spawning *Pocillopora* and *Acropora.* During months-long experiments we will measure the timing of reproduction (gametogenesis and spawning) as a function of seawater temperature (ambient vs. ambient +1°C vs. ambient +2°C), to test the hypothesis that high temperature temporally advances gametogenesis and spawning (Shlesinger and Loya 2019). Specifically, we predict that high temperature will advance the lunar day of spawning (using circular statistics sensu Fan et al. 2017) and reduce fecundity (Johnston et al. 2020). Changes in timing of spawning are important because they can create mismatches between larval availability and the environmental conditions such as seasonal variation in waves and currents that are required for their dispersal and settlement. These effects can help explain why *Pocillopora* recruitment varies among years (Edmunds 2021), and provide an empirical context for modeling the interactive effects of seawater flow on coral recruitment (see Theme 3 Modeling and Integration).

Question 3.2: *What are the traits mediating the success of coral species and their genetic variants?*

Rationale: One of the important information legacies of disturbances arises through the differential performance of species that ultimately influence community structure and ecosystem function (Poloczanska et al. 2013). For example, our time series has revealed 'winners' and 'losers' in response to the recent MHW that caused bleaching in Moorea, with some cryptic *Pocillopora* species surviving better than others (Fig. 3; Burgess et al. 2021). Our time series suggests several *Acropora* species may also be increasing in abundance after this event. Here, we will explore the mechanisms that create these information legacies by testing for the traits (e.g., growth, respiration, microbiomes) characterizing winners and losers in response to changing seawater temperature. Further, given that our work has shown that the thermal biology of corals can vary depending on the nutrient regime to which they are exposed (Burkepile et al. 2020, Becker et al. 2021), we will examine how nutrients impact the information legacies that MHWs create. These experiments will help reveal mechanisms behind the island-wide relationships between nutrients, coral bleaching, and state shifts that we are addressing in Theme 2. Finally, a key question regarding the information legacies created by MHWs is how these effects may 'prime' corals to respond in beneficial ways to further climate change effects including ocean acidification (OA). To explore these effects, we will take advantage of our experience addressing the effects of OA on coral performance (e.g., Comeau et al. 2014) to test if the current impact of climate change (e.g., MHWs) creates information legacies with negative implications for responding to future conditions.

In Question 3.2, we will address the information legacies that occur at the organismal scale (i.e., changes to individual performance) in response to elevated temperatures. However, some of the information legacies are expressed at the genetic level, which MCR researchers are addressing using other sources of funding (see Related Research). Using *Pocillopora* as a model system, we have started to characterize the sensitivity of different life stages to environmental conditions and to describe the mechanisms by which cross-generational (genetic and non-genetic) effects can be mediated. Combined, the research on the information legacies that occur across levels of biological organization will present a powerful picture of how rising ocean temperature and MHWs are altering coral dynamics.

Approach: We will use our mesocosms consisting of twelve 150 L tanks to control environmental conditions (e.g., light, temperature, pH, nutrients) for weeks to months. This system will be used in factorial experimental designs to test for main and interactive effects of environmental conditions on coral performance, particularly as they might differ between species, host genetic variations, and corals differing in informational legacies (i.e., dissimilar histories of exposure to environmental conditions). We will address thermal effects administered both as: (1) a gradient of exposure using supporting tests of variation in thermal performance as captured through thermal performance curves (TPCs) (Silbiger et al. 2019) and described using the Arrhenius function (Brown et al. 2004), and (2) as a pulse disturbance (i.e., a MHW). TPCs will be prepared both through acute sequential thermal trials (e.g., 1–2 h at each temperature) to generate robust relative metrics of thermal performance (Silbiger et al. 2019), and through acclimated responses (e.g., ~2 weeks at each temperature) to test for absolute responses to thermal treatments. The experiments will compare cryptic species within the *Pocillopora* complex and several common *Acropora* (e.g., *A. retusa*, *A. hyacinthus*, *A. cerealis*), which showed variable responses to the 2019 MHW, and expose them to temperatures representing the decadal empirical range (including during the recent MHW). To test for variation in thermal performance among taxa, we will statistically extract key parameters from TPCs based on performance metrics characterizing the host (respiration, calcification), the algal symbionts (photosynthesis, symbiont densities), and the holobiont (growth) (Silbiger et al. 2019, Becker et al. 2021). Another key metric of coral response to thermal effects is in the microbiome, which our work shows often changes dramatically after thermal stress such as MHWs

(Maher et al. 2020), and can play a key role in determining the response to thermal stress (Torda et al. 2017). Thus, we will use 16S sequencing to examine how the microbiomes of different coral species respond to MHWs and test for associations with coral performance (e.g., growth). We will expand the mesocosm analysis of thermal effects to test for interactive effects with nutrient regimes for *Pocillopora* and *Acropora* as occurs during exposure to nutrient pollution that we will document in Question 2.2.

In MCR III, we showed that future OA conditions have significant, but variable, impacts on the physiological performance of different coral species (Comeau et al. 2014). In MCR IV, we will assess how cryptic species of *Pocillopora* respond to OA conditions and contrast this performance under OA conditions to their performance under MWHs as described above. This scenario of experiments will allow us to determine which taxa may be winners and losers under current and future impacts of climate change.

Question 3.3: *How do information legacies of disturbances on benthic community structure impact ecosystem function and their capability to withstand additional MHWs?*

Rationale: Here, we will address how information legacies that MHWs generate on communities translate into functional consequences for ecosystem processes. We will focus on two information legacies of MHWs that are a focus of both Theme 2 and Theme 3 and test how they affect ecosystem metabolism before, during, and after a controlled MHW. The first legacy we will examine is when a MHW causes mass coral bleaching and mortality and acts as the trigger for a state shift from coral- to macroalgae-dominated communities. We will experimentally examine the impact of this state shift on ecosystem function as a complement to our descriptive approach in Theme 2 (Question 2.3). The second information legacy we will examine is when a MHW differentially impacts the cryptic species of *Pocillopora* and shifts coral community structure by selecting for a subset of cryptic species as 'winners' (e.g., Burgess et al. 2021). For both of these, we will examine impacts on net ecosystem calcification (NEC) and production (NEP), which are community metabolic rates assessing ecosystem functioning. Because NEC and NEP can be measured instantaneously, they can be used as early warning signs for how quickly reefs may respond to and recover from a disturbance. By following benthic communities composed of different taxa through a simulated MHW, we will advance our understanding of how reef ecosystem metabolism has changed in the past and will change in the future as a result of thermal stress.

Approach: Using replicate outdoor flumes (5.0 × 0.5 m), we will create ecologically relevant flow and temperature conditions that mimic those from our physical oceanographic time series (Carpenter et al. 2018). For Experiment 1, testing coral- vs. algae-dominated communities, we will create benthic communities that are representative of coral- or algae-dominated reefs that we identify in Question 2.2. The flumes will have benthic communities composed of amounts of coral, macroalgae, turf algae, bare substrate, and sand to create coral- or algae-dominated treatments. For Experiment 2, testing for the effects of different cryptic *Pocillopora* species, we will create benthic communities representing *Pocillopora*-dominated communities with contrasting relative abundances of different cryptic species identified as either 'winners' or 'losers' from the experiments in Question 3.2. These experiments will each run for 3 months during the Austral summer - the time in which MHWs typically occur in Moorea. We will measure NEP and NEC (e.g., Doo et al. 2019, Silbiger et al. 2018) multiple times including before, during, and after the simulated MHW. Additionally, we will assess how the different treatments in the two experiments impact the cycling of organic matter by sampling the different components of DOM (e.g., Wegley Kelly et al. 2022), as we did in Question 2.3, multiple times throughout the experiment.

Theme 3 Modeling and Integration: *Effect of information legacies on dispersal, retention and connectivity*

Theme 3 explores how information legacies from MHWs influence population dynamics, community structure, and ecosystem processes. An important concern is how these patterns may change as climate change continues to alter ocean temperatures and, eventually, physical processes such as lagoon circulation that will affect larval transport and coral community dynamics. Marine organisms take advantage of persistent oceanographic features to maximize larval retention close to natal habitat (Black et al. 1991, Sponaugle et al. 2002), through timed spawning during seasonal doldrums (Paris et al. 2005, van Woesik 2009) or through vertical larval movements that exploit stratified flow (Paris et al. 2007, North et al. 2008, Tay et al. 2011). It is unknown how rising sea surface temperatures and sea levels could influence the dispersion or retention of coral propagules in nearshore oceanographic features, and thus affect the spatial dynamics of coral reef replenishment. We will form a **Connectivity Modeling Working Group** to examine how information legacies and a changing physical environment due to climate change will affect the potential for connectivity among habitats. Biophysical models of coral larval dispersal (e.g., Limer et al. 2020) will be used to evaluate how information legacies of MHWs (e.g., altered spawning times or fecundities from Question 3.1) interact with physical oceanographic conditions (alongshore currents, waves, fore reef to back reef circulation cells, coastal jets, nearshore eddies, etc.) to modulate connectivity among habitats (Fig. 23). Hydrodynamic models with spatial extents useful for population studies (> several square km) and with grid sizes on the order of meters have only recently become more widely available and validated, and recent studies have shown that coastal areas are highly dynamic for dispersing larvae (e.g., Fujimura et al. 2014, 2017, Shanks et al. 2015).

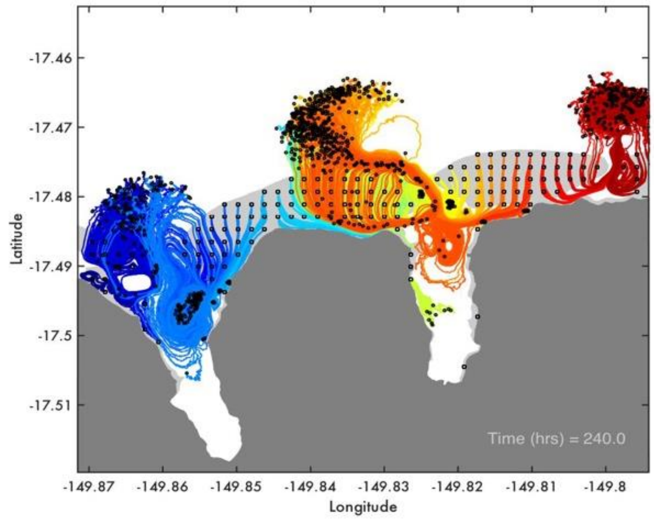


Figure 23. Simulated Lagrangian dispersal trajectories of larval propagules on the north shore of Moorea, demonstrating the potential for retentive circulation features that could reduce dispersion away from natal habitats, and/or entrain immigrating propagules. Colors indicate spawning location, and points are propagules.

Additionally, in Moorea sea level and wave climate determine hydrodynamic connectivity between the fore reef and the lagoon by determining the extent of reef crest overtopping (Hench et al. 2008) and, therefore the extent to which fore reef and back reef habitats remain ecologically distinct (Moritz et al. 2021). This biological and physical context provides a platform to explore how sea level rise will affect reefs in future decades, specifically by modulating cross-reef transport, boundary layers, and erosion of reef crest features that currently restrict cross reef transport. The Connectivity Modeling Working Group will convene a workshop in Year 3 to address the consequences of information legacies from MHWs and rising sea level for coral community dynamics.

Integration and Synthesis

Our three research themes address different but related aspects of how the changing disturbance regime (increasing frequency of MHWs) coupled with rising ocean temperature will influence the dynamics, function, and resilience of coral reef communities. Our plan to consider our specific findings in a larger context and seek generality involves both within-site synthesis activities and cross-site comparisons.

Within-Site Synthesis Activities. *First*, the ongoing working groups associated with each of our three research themes will use appropriate modeling constructions, parameterized by data from our time series and process studies, to gain predictive understanding of the effects of multiple stressors and spatial heterogeneity on system dynamics and resilience. Additionally, several of the quantitative approaches will provide the capacity for scenario modeling of responses to future environmental change, targeting increasing mean ocean temperature, sea level rise, and changing ocean carbonate chemistry (ocean acidification). *Second*, as mentioned above, we will conduct a small number of workshops focused on themes emerging from MCR IV research. Participants from outside of the MCR community will be included, specifically to cover areas of expertise not represented by MCR investigators. *Third*, we will convene an additional workshop to use MCR data and findings to address a broad, understudied issue: how to anticipate abrupt regime shifts triggered by a large stochastic (disturbance) event. Much of the early warning literature focuses on regime shifts that are triggered when a critical threshold (tipping point) in an underlying parameter is crossed (Scheffer et al. 2012). However, these types of early warning indicators have less utility for ecosystems subjected to large, punctuated disturbances such as heat waves, droughts, cyclones, or fires, suggesting different metrics may be needed to predict the likelihood of state shifts in disturbance-driven ecosystems. A more useful 'warning' metric for ecosystems with multiple attractors that are subjected to extreme disturbance events may be whether the system is approaching (or in) a region of state space that has more than a single basin of attraction.

***Cross-Site Synthesis Activities*.** In the past, we have used funding by the MCR, LTER Network, national agencies (e.g., NSF and USGS), and international partners (e.g., Okinawa Institute of Science and Technology (OIST), ETH Zurich) to expand the temporal and spatial scale of our synthesis work. We will continue with this model in MCR IV and propose three types of efforts. *First*, we will network with other LTER sites to identify common interests in disturbance legacies, spatial resilience, and indicators of multiple attractors for possible topics for workshops at annual Science Council meetings, LNO-sponsored working groups, and symposia at LTER All Scientist Meetings. *Second*, we will pursue opportunities outside of the LTER community through the USGS Powell Center (that supported our synthesis focused on Coral Reef Oases in 2016) to address the ecosystem effects of structure-forming foundational taxa (e.g., trees, giant kelp, branching corals) in marine and terrestrial systems exposed to shifting disturbance regimes. This effort will integrate NSF and USGS researchers and address emergent properties with common functional origins in terrestrial and marine LTER sites (e.g., HFR, MCR, SBC). *Third*, we are developing plans for a joint US-Japan-Asia workshop focused on hydrodynamic larval connectivity among Pacific Rim islands. Planned workshop products include: (1) peer-reviewed publications addressing range expansion and connectivity of pocilloporid corals (the corals key to ecological resilience of the reefs of Moorea), (2) planning of field experiments to explore resilience of coral communities that can be conducted using the same methodological approaches at multiple locations throughout the Pacific Rim, and (3) catalyzing the submission of NSF AccelNET or RCN proposals to integrate regional-scale networks addressing coral reef science in human-coupled ecosystems.

Collaborative Research

MCR investigators and collaborators are leveraging the site to obtain additional funding to conduct mechanistic studies and some of the modeling efforts relevant to MCR IV science. For example, Burkepile, Vega Thurber, and Adam (OCE-2023701/2023424) are addressing how reductions in herbivory and increases in nutrients impact coral and algal dynamics on the fore reef. The project is generating data to parameterize our models of community dynamics of the fore reef under different scenarios of anthropogenic stress and disturbance in Theme 1. Nelson and Silbiger, with Co-PI Donahue (U. Hawaii), are examining the spatiotemporal biogeochemistry of submarine groundwater discharge across Moorea and its influence on coral reef ecology, from organismal physiology to ecosystem processes (OCE-1923877/1924281). This work will be a key component in describing spatial heterogeneity in the lagoon (Theme 2) as well as understanding how abiotic forcing impacts coral physiology and performance (Theme 3). Additionally, Nelson, with co-PI Wegley Kelly (Scripps), is quantifying the diel dynamics of bacterioplankton and dissolved organic matter in the lagoons (OCE-1949033) and, with additional Co-PIs Aluwihare and Dorrestein (Scripps/UCSD) is resolving the composition and microbial transformation of coral reef DOM (OCE-2023298), dovetailing with central foci of both Themes 2 and 3. Burkepile, Adam, and Co-PI Donovan (Arizona State U.) are examining how land use change on Moorea has impacted near-shore nutrient dynamics and the subsequent impacts on coral reef communities (Zegar Family Foundation). This will complement Theme 2 by helping explain the spatial heterogeneity in coral and algal communities across the lagoon and how this heterogeneity is influenced by changes in land use. In addition, Hay and Co-PI Stewart (Montana State) are exploring the role of coral biodiversity (e.g., species, genotypes, etc.) in ecosystem function, informing Themes 1 and 3

(OCE-1947522). Hay is also funded (Teasley Foundation) to study the functional role of sea cucumbers as detritivores and their impacts on coral dynamics and ecosystem processes (Theme 2).

Several other collaborative efforts will work synergistically on the Theme 3 goal of understanding how changing patterns of anthropogenic stressors create information legacies in coral communities. Edmunds and Burgess are exploring the role of cryptic species diversity within the *Pocillopora* lineage to understand the contribution of genetic and phenotypic variation to resilience (OCE-1829898/1829867). Putnam and Moeller, funded by NSF Rules of Life Epigenetics Emerging Frontiers (EF-1921465/1921356), are examining how energetic shifts in the coral symbiosis under local (e.g., nutrients) and global stressors (e.g., temperature) influence epigenetics, ecology, and evolution. Their energetic and epigenetic findings are contextualized by MCR LTER ecological and oceanographic time series. This work supports Theme 3 by including a molecular mechanistic understanding of epigenetic triggers and their role in organismal acclimatization and adaptation, which is critical to understanding ecosystem function in a changing climate. Putnam (with Laetitia Hédouin, a French collaborator at CRIOBE) has received French funding to address effects of climate change on coral reproduction, working at the interface of developmental biology, epigenetic approaches, ecology, and inheritance to enhance predictive capacity for coral reef futures. MCR modeling efforts are being supported by NSF (OCE-2123708) and Duke University grants to Hench to examine how flow interacts with topography in shallow lagoon environments that will be key in Theme 2 as well as to develop models of circulation useful for understanding connectivity, which is an important element of Themes 2 and 3. Moeller is integrating genomics, bioinformatics, and dynamic energy budget (DEB) models to create a generalizable, predictive eco-evolutionary model that links nutritional interactions, metabolic states, and subsequent epigenetic effects to eco-evolutionary outcomes in the coral-algal symbiosis, key for understanding the information legacies that impact the success of corals (EF-1921356).

BROADER IMPACTS

Broadening Participation. The MCR remains committed to maintaining an accessible and safe environment where each participant's unique identity is valued and celebrated regardless of their race, gender identity, religion, sexual orientation, socio-economic status, nationality or career stage (see our Project Management Plan for the outline of our vision for inclusion). MCR's education, training, and outreach efforts emphasize broadening participation in STEM fields and strengthening STEM literacy, particularly from marginalized groups in marine science. We will continue to promote a more inclusive and equitable experience for all individuals engaged in MCR research, outreach, and science education. We strive to bring about enduring changes that accelerate and solidify the inclusion and advancement of marginalized scientists in our program, and marine science more broadly, by engaging diverse community members both locally and internationally.

Investigators, Leadership and Staff. With respect to site leadership and staffing, progress toward our demographic representation goal is reflected in the composition of the MCR IV Executive Committee (54% female, 23% URM) and 5 MCR staff (4 females, 1 URM); DEI is a major consideration when turnover of PIs and Senior Personnel occurs. A mechanism we use to enhance diversity and maintain a stable career-stage distribution of our team, is to recruit early career scientists, particularly from URM groups, to collaborate; we bring in individuals who become engaged formally on the project as Investigators at the next renewal (see Project Management Plan). The cohort of 7 new Investigators thus recruited to MCR IV (4 females; 2 URM) represents a 30% turnover of the MCR III investigator team.

Graduate Students. To enhance diversity of our graduate community, our MCR investigators have partnered with programs designed to increase participation of URM groups. We have partnered with the UCLA Diversity Project (DP) (PI Paul Barber), which increases participation of URM students in marine biology through an integrated undergraduate research experience at the Gump Station. Prior to traveling to Moorea, DP students participate in a research seminar series given by MCR investigators and graduate students, and visit UC Santa Barbara to meet MCR scientists. In addition, MCR investigators and graduate students overlap with DP students at the Gump Station, facilitating interactions and mentoring of

DP students. As a result, several DP alumni have entered graduate programs with MCR faculty, including four PhD and one MS so far in the MCR IV cohort of students. Further, eleven institutions are involved in MCR IV, with researchers converging at the Gump Station, which provides a mechanism for recruitment as it enables students to move to another MCR institution for training. For example, CSUN is a Hispanic Serving Institution that has a MS but not a PhD program, and CSUN MS students have moved to other MCR institutions for their PhD. MCR uses a tiered mentoring structure where graduate students are mentored by post-docs and faculty and, in turn, mentor undergraduates.

Undergraduate Students. MCR will continue to actively recruit a diverse and inclusive group of REU students, building on our success in MCR III in mentoring an REU group that included URM, veterans, and self-identified members of the LGBTQ+ community. UCSB, which administers the MCR and SBC LTERs, is a Hispanic Serving Institution, and this year we initiated a new partnership with SBC and the UCSB Marine Science Institute (MSI) to address the chronic underrepresentation of UCSB Latinx students in the AAUS scientific diving community. Our past assessment of our summer REU applicants revealed that the low number of Latinx students who apply for these field research internships was due almost entirely to the financial burden of becoming an AAUS Scientific Diver (required for conducting SCUBA diving-based research at US Institutions). As a consequence, we secured private funding to support training and equipment for up to 4 financially-disadvantaged URM undergraduates annually; the first cohort of the *DIVErsity in Diving Program* begins AAUS dive training this year. Our mission is to engage more diverse and underserved community members who are just beginning to explore field ecology as a career option but may not have the necessary resources to do so.

MCR continues to actively participate in NSF Research Opportunity Awards (ROAs) and associated REUs to engage faculty and undergraduates from Primarily Undergraduate Institutions that have a majority of URM students. In addition to continuing our partnership with Cabrillo College (student body 52% UMR), in MCR IV we will explore ROA/REU opportunities with Santa Barbara City College (61% URM), a local 2-year institution that has an agreement with UCSB for junior-level transfer students who seek a Bachelor's degree, and Santa Monica College (54% URM) that has close ties with CSUN.

Public Outreach and Schoolyard. The MCR website is a primary source of public information and resources. We will augment our online collection of inquiry-based curricula (see below) and our Online Encyclopedia of Marine Life website, which highlights >125 reef organisms. Our online content describing MCR graduate research continues to grow as students provide media (videos, pictures) and 'plain language' descriptions of their research, which is a grass-roots effort led by the students.

Local K-12 Outreach & Education. The MCR Schoolyard Program includes a long-running partnership with the K-6 Washington STEM Magnet School in Pasadena, California (student body 93% URM, 90% low income). Each year, 120 5th grade students are brought to UCSB, situated directly on the ocean, and engage in a day of educational talks by MCR graduate students, exploring marine life in touch tanks and coral reef displays, and conducting active learning exercises with MCR scientists. The field trip is preceded and followed by classroom lesson plans on coral reef science developed jointly by MCR Education staff, STEM teachers from Washington STEM Magnet School and Research Experience for Teachers (RET) participants; the initial lessons were tested and refined based on internal assessments by STEM teachers, and Washington Magnet School considers the field trip and lesson plan module to be highly effective. A former RET recipient continues to collaborate with the MCR Education and Outreach staff to translate MCR research and RET experiences to the classroom. This has resulted in a series of science lesson plans for six different K-12 grades that are compliant with Next Generation Science Standards and California Common Core State Standards. In 2022, the MCR will submit to the LTER Educational Digital Library a 10-lesson plan module targeted at students in Grade 3 that features three MCR female PhD researchers to highlight marine ecology research by diverse women scientists. MCR targets diverse representation among the K-12 teachers who participate in MCR field research and who teach at schools with low income, high minority student populations [Pasadena Unified School District (77% URM), Los Angeles Unified School District (88%) and Goleta Union School District (64%)].

MCR continues to partner with UCSB's Research Experience & Education Facility (REEF) to expose

> 10,000 K-12 students/y (pre-Covid19) to MCR science and the living fishes and invertebrates found on reefs of Moorea. The REEF draws K-12 class visits mainly from the Goleta, Santa Barbara and Carpinteria school districts, whose student bodies are primarily from URM groups. MCR graduate students run a booth at the annual Santa Barbara Earth Day and World Ocean Day with bilingual (English - Spanish) educational materials to raise awareness about MCR research and the ocean.

Tahitian K-12 Outreach & Education. In Moorea, we work with local partners to enhance science literacy of Tahitian school children through experiential learning. The MCR partners with the Tahitian educational NGO *Te Pu 'Atiti'a* to incorporate MCR science into local classrooms, and MCR graduate students run a Marine Biology Research Camp at the Gump Station each summer, which engages Tahitian grade school students in hands-on science exercises using MCR research findings relevant to daily lives of local citizens. During MCR III, a graduate student-led effort with teachers at a middle school led to the establishment of a program where students monitor the health of the stream and coral reef adjacent to their school. During MCR IV, MCR scientists will be involved in expanding these existing school-led watershed monitoring programs in collaboration with *Ati Vai*, a citizen science organization based at *Te Pu 'Atiti'a*, and the Teavaro primary school. MCR graduate students and local educators will take K-12 students into local watersheds to collect water samples, make site observations, and discuss ridge-to-reef connections from both scientific and traditional knowledge perspectives. Expansion of this program during MCR IV will involve new schools, and MCR personnel will help develop standardized curricula, and provide materials and assistance with data analysis. The MCR also aims to incorporate the water chemistry data and student-collected metadata and analysis as an MCR database.

Media–based Outreach to Pacific Islanders. In MCR II and III, we partnered with the TV series *Voice of the Sea*, which is associated with the University of Hawaii, to produce 13 episodes that highlight MCR research and researchers. *Voice of the Sea* is in its 9th season, and the 30-min episodes they produce air in Hawaii, American Samoa, Guam, Palau, the Federated States of Micronesia, and the Marshall Islands. In MCR IV, narration of existing MCR episodes will be translated into French and Tahitian for local dissemination, and we plan to develop new episodes (with Hawaiian, French and Tahitian translations) that highlight recent MCR findings and early career scientists. Additionally, in collaboration with *Te Pu 'Atiti'a*, the Teavaro Primary School, and a group of US-based filmmakers and animators, MCR graduate students have begun developing a series of 2-3 minute videos explaining cornerstone coral reef ecosystem processes. The first two videos are currently in production and focus on (1) the water cycle and ridge to reef connectivity and (2) the life cycle of corals. Further videos will utilize a combination of footage shot on location in Moorea and animation to illuminate more complex processes related to each subject. Audio and subtitles will be recorded in English, French, and Tahitian, and videos will be hosted on the MCR website and broadly available to both US and Polynesian partner schools.

Application of Findings to Policy & Management. The MCR annually reports its scientific findings to the Head of Research of the Territorial Government of French Polynesia, who in turn briefs relevant ministers of the Territorial Government (e.g., Minister of the Environment) and the High Commission of France. MCR findings were included in a recent process that resulted in a major revision of the Maritime Space Management Plan (PGEM) for Moorea, which was ratified in 2021. One modification was to expand shared governance via a PGEM committee composed of all relevant stakeholders. We plan to report MCR IV findings regularly to the PGEM Committee to assist in developing policy and management decisions intended to sustain the health and multiple uses of Moorea's reefs. In addition, we will continue our relationship with local fisher associations to engage citizen scientists on development of potential means to control macroalgae and quantify ecological effects of rotational closures of protected reef areas they plan to implement. We also are developing information exchanges with scientists associated with the Moorea Coral Gardeners, an NGO that seeks to restore degraded reefs.

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