PROJECT SUMMARY

Overview:

Coral reefs have enormous ecological, economic and cultural value, but are threatened by natural disturbances and human activities including those causing global-scale changes. Worldwide, corals increasingly are being replaced by macroalgae or non-coral invertebrates. The reefs of Moorea, French Polynesia, provide an ideal model system to understand factors that mediate ecological resilience and to develop the capacity to forecast the composition and function of reefs in a future ocean of warmer water and a lower pH. The overarching goal of the Moorea Coral Reef (MCR) LTER, established in 2004, is to gain a predictive understanding of the dynamics and functionality of oceanic coral reef ecosystems. MCR science achieves this goal through long-term observations, experiments and modeling. Changes in community structure revealed by the time series are used to generate hypotheses, which are tested using process-oriented studies including long term experiments. Empirical studies are synthesized and modeled to gain novel insight into the responses of coral reefs of Moorea to changing environmental conditions, to search for ecological generality, and to advance ecological theory.

Intellectual Merit :

Ecological resilience provides a unifying principle in MCR III, in which we explore community and ecosystem responses to pulsed disturbances (cyclones, bleaching), human-induced press perturbations (nutrient pollution, fishing), and slowly changing drivers (Global Climate Change, Ocean Acidification). The proposed research will expand our focus on resilience by exploring the causes and consequences of spatially varying patterns of community responses to pulsed perturbations in 2007-10. MCR time series revealed contrasting community dynamics and resilience between the fore reef and the lagoon; the perturbed fore reef is reassembling to a coral community strongly resembling that found prior to the disturbances (albeit with spatial variability in return rates), whereas some lagoon reefs have transitioned from coral to macroalgae. In addition, we will estimate how different community states affect key ecosystem rate processes (GPP, respiration, net calcification). Understanding controls of these processes will provide insight into how they might change in a warmer future ocean with lower pH. To project community composition of future reefs, we will explore traits of corals that may make some taxa winners and others losers under future conditions. The intellectual merits arise from a more predictive understanding of how coral reefs respond to interacting environmental changes at multiple spatial, temporal, and biological scales, together with how these responses alter the provision of critical ecosystem services.

Broader Impacts :

Broader impacts include: (1) K-12 teaching, training, and learning, (2) creative dissemination of results to the broader public, (3) advising of government agencies and NGOs, (4) training the next generation of scientists who are better prepared for interdisciplinary research in a global setting, and (5) provision of a rich data inventory supporting comparative and synthetic research on coral reefs throughout the world. MCR will expand its Schoolyard LTER by developing its professional development program for K-12 teachers, continuing to engage K-12 teachers in research in Moorea, and developing curricula for the MCR children's book (Kupe and the Corals) to serve diverse student audiences. MCR's Schoolyard will strengthen engagement with underserved schools in Southern California, which includes paying for transportation and substitute teacher costs for students and teachers to participate in MCR programs at UC Santa Barbara. We also will continue training diverse undergraduates and serve as a resource for graduate and postdoctoral training. Results from our research will continue to contribute to the scientific community through publications and to the broader public through UCSB and CSUN outreach programs (e.g., UCSB's Research Experience & Education Facility that exposes 10,000 K-12 and public visitors annually to MCR research), interviews with the media, participation in public forums and advising government officials (including the Territorial Government of French Polynesia) and NGOs (including Association Te Pu 'Atiti'a on Moorea composed of local educators). The project will enhance infrastructure for research and education. More broadly, the proposed work will benefit society by increasing understanding of how human activities alter the resilience and functioning of coral reefs on which humans depend.

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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. THE LTER CONTEXT AND MOOREA CORAL REEF LTER RESEARCH PROGRAM

NSF established the Long Term Ecological Research Program in 1980 to address ecological phenomena that occur over multiple decades through site-based research. At the heart of an LTER site is a conceptually motivated time series program that collects data in five core areas[1]. These data are integrated with process studies to inform ecological theory and to advance understanding of the long term dynamics of populations, communities and ecosystems.

The biome of the Moorea Coral Reef (MCR) LTER site, established in 2004, is an oceanic coral reef ecosystem; field operations are conducted from the UC Berkeley Gump Research Station. The MCR LTER site is the coral reef that encircles the ~50-km perimeter of Moorea, French Polynesia, and includes the fringing reef along the shore, the back reef, and the steeply sloping fore reef seaward of the reef crest (Fig. 1). Coral reefs have extraordinary ecological and economic importance, but are at high risk from local and global stressors. ***Within the conceptual framework of ecological resilience, the MCR is addressing the community and ecosystem effects of pulsed (e.g., cyclones, coral bleaching, Crown-of-Thorns Seastar outbreaks) and local press (e.g., fishing, nutrient enrichment) perturbations that occur against a background of slowly changing environmental drivers associated with Global Climate Change (GCC) and Ocean Acidification (OA)***.

In MCR I (2004-2010), we developed an island-scale understanding of community structure in relation to variation in physical forcing, and advanced understanding of key aspects of scleractinian coral biology to better project how coral reefs will respond to local and regional-scale drivers of community change. At the end of MCR I, the fore reef was impacted by a natural outbreak of the corallivorous Crown-of-Thorns Seastar (COTS), followed in early 2010 by a strong cyclone. These natural events killed almost all corals on the fore reef but had little immediate effect in the lagoon (Fig. 2). *While coral reefs are often disturbed, we have had the opportunity to study intensively the re-assembly of a complex ecological system contextualized by extensive research and time series measurements made before, during, and after the perturbations. This is unique for a coral reef ecosystem and is what LTER sites are specifically intended to accomplish*.

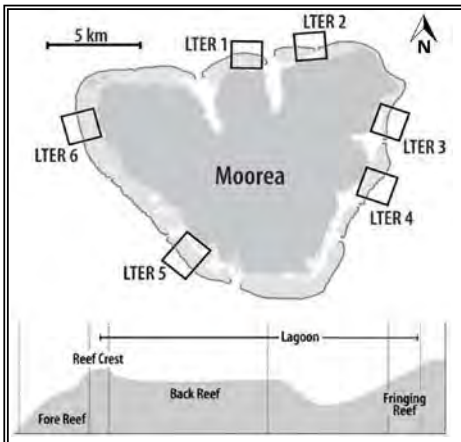


Figure 1. *(Top)* Map of Moorea with locations of MCR time series sampling sites around the ~50 km perimeter of the island. *(Bottom)* Schematic cross-section of the ecosystem, stretching from the 20 m depth on the offshore fore reef (left) to the shore (right), which illustrates the 3 habitat types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

The perturbations are enabling us to address issues related to **ecological resilience**, a fundamental concept in ecology that is of particular relevance to coral reefs. The first part of MCR II (2010-2012) focused on processes that prevented the fore reef from undergoing a transition to a community dominated by macroalgae following large-scale disturbances. During the last 4 years of MCR II (2012-2016) we extended that perspective by exploring processes that influence return of the coral-dominated community.

During MCR II, our time series revealed that the fore reef is returning to its pre-disturbed (coral-dominated) community, but lagoon communities are displaying qualitatively different dynamics (Fig. 3). In the lagoon, coral cover has remained high at some sites, but has declined at others and been replaced by macroalgae. Thus lagoon communities appear less resilient than the fore reef to shifts in community state. These dynamical patterns form the basis of our proposed research in MCR III (2016-2022), which is focused on *the causes and consequences of spatial heterogeneity in resilience*.

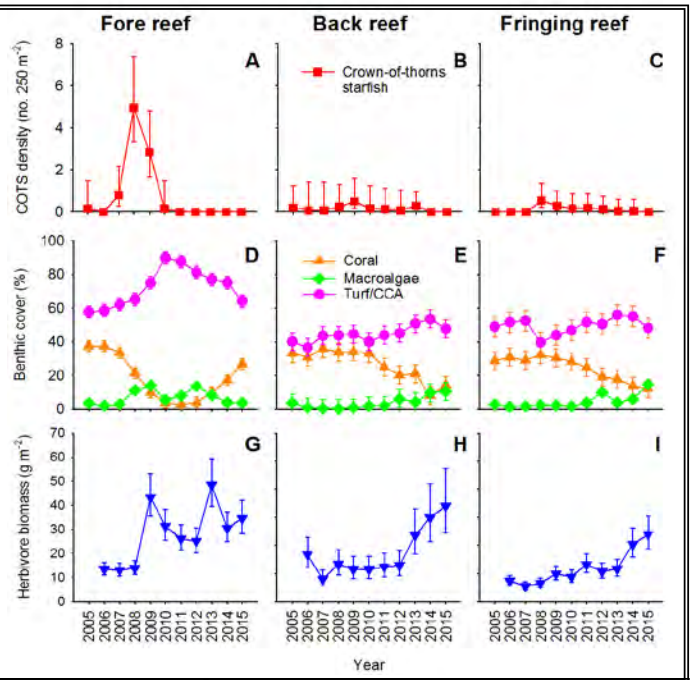
[1] The five core LTER areas are: (1) primary production, (2) population dynamics and trophic structure, (3) organic matter accumulation, (4) inorganic inputs and movements of nutrients through the ecosystem, and (5) patterns and frequency of disturbances.

Figure 2. Island-wide patterns of community dynamics in the habitats sampled in the MCR time series program (data are the mean density or cover ± 95% CI).

Dynamics of (**A–C**) corallivorous Crown-of-Thorns Seastar (COTS), (**D–F**) coral, macroalgae, turf algae and crustose coralline algae (CCA), and (**G–I**) herbivore biomass on the fore reef (*left panels*), back reef (*center*), and fringing reef (*right*) habitats.

The COTS event and cyclone (Feb. 2010) had an immediate effect on the benthos of the fore reef (*left panels*), which is beginning to return to a coral community without a transition to macroalgae.

By contrast, composition of the benthic community on lagoon reefs (c*enter and right panels*) has been changing more slowly with macroalgae increasing as coral cover gradually declines.



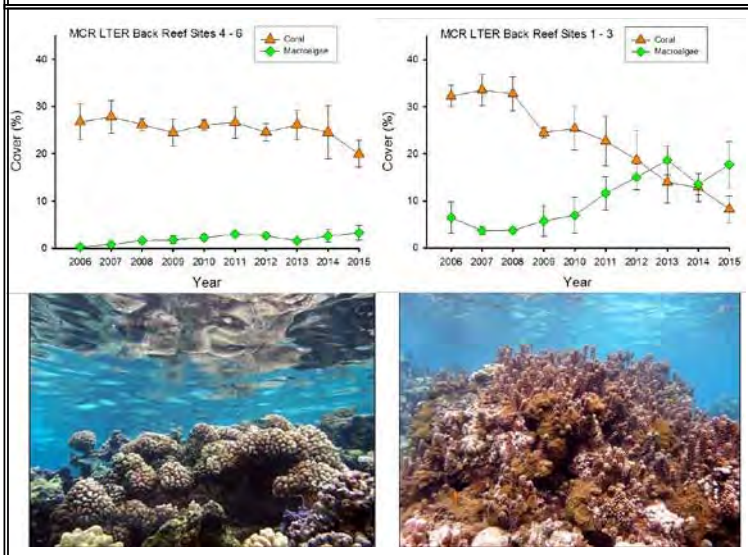


Figure 3. Contrasting coral – macroalgae dynamics on lagoon habitats as illustrated by back reef sites sampled as part of the MCR time series program (data are the mean cover ± 1 SE). The macroalga in the picture on the right is *Turbinaria ornata*.

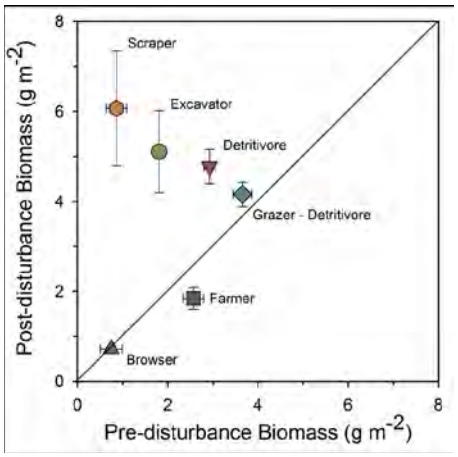


Figure 4. Mean (± SE) biomass of herbivore functional groups for the pre- (n = 2) and post-disturbance (n = 5) time periods on an island-wide scale. The diagonal line indicates no change in biomass over time.

SECTION 2 - RESULTS FROM PRIOR SUPPORT

MCR LTER II: Long Term Dynamics of a Coral Reef Ecosystem (2010-2012) OCE 1026851; Funding: $1,880,000 (excluding supplements); MCR LTER IIB: Long Term Dynamics of a Coral Reef Ecosystem (2012-2016) OCE 1236905; Funding: $3,760,000 (excluding supplements).

2.1 RESEARCH

Major Findings MCR II has produced 236 publications to date. Much of MCR II focused on the dynamics of the fore reef community (Figs. 1, 2) to leverage the scientific opportunities provided by the perturbations that occurred from 2007-10. Additionally, we began to address how major reef calcifiers (corals, crustose coralline algae), community structure, and reef production and calcification are

responding to Global Climate Change (GCC) and Ocean Acidification (OA). Citations in this section are all MCR publications; 10 significant publications that motivate MCR III research are in **bold**.

Given that high cover of macroalgae can prevent re-colonization of corals, our initial questions in MCR II following the perturbation events (Fig. 2) addressed processes that can prevent macroalgae from becoming a dominant space holder following the sudden liberation of space. Our time series revealed that the biomass of herbivorous fishes increased rapidly island-wide shortly after the disturbances (Fig. 2) (**Adam et al. 2014**, **Han et al. 2016**), while field experiments indicated their grazing prevented a state shift to macroalgae on the fore reef (**Adam et al. 2011**). The herbivores that increased in biomass were primarily fast growing parrotfishes (scrapers, excavators) that prevent macroalgae from becoming established (Fig. 4) (Tootell & Steele 2015, Han et al. 2016). These fishes initially recruit to inshore nursery habitat before moving to the fore reef. Thus our work reveals critical connectivity between inshore and offshore reefs, and indicates that protecting nursery habitat of key herbivores is essential to reef resilience. Our field experiments also allowed us to estimate, for the first time in any coral reef system, the functional shape of the herbivory–macroalgae relationship (Holbrook et al. in review). This novel experiment revealed a strongly non-linear relationship with a clear threshold level of herbivory where macroalgae escaped control (Fig. 5). However, the tipping point on the fore reef was far below ambient levels of herbivory (Holbrook et al. in review).

While herbivory was sufficient on the fore reef to keep macroalgae suppressed, return to a coral-dominated state requires coral recruitment, which has been robust but spatially heterogeneous (Fig. 6A) and potentially based on recruits of local origin (Edmunds et al. 2016a, Bramanti & Edmunds 2016; for fish self-recruitment, see Beldade et al. 2012). Sites with higher recruitment are recovering faster than those with lower recruitment, suggesting that spatial variation in coral input is a major driver of recovery rates, at least among shores of the island (Fig. 6B). Our coral demographic studies have revealed more subtle variation in post-settlement growth and survival of corals among shores that also contribute to spatial heterogeneity in return rates (Bramanti & Edmunds 2016). Thus while the fore reef appears resilient (Fig. 2), there is marked heterogeneity in the rate of return to coral dominance (Fig. 6).

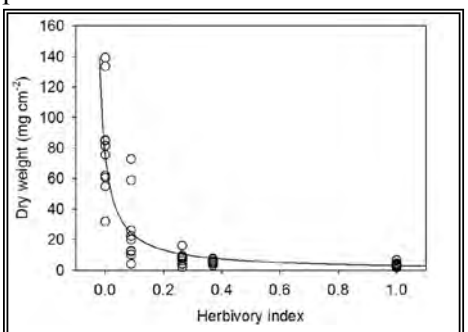


Figure 5. Non-linear relationship between herbivory and biomass of macroalgae. Dry weight of macroalgae that developed over 3 years plotted against relative levels of herbivory (ambient = 1) across the herbivory treatments. Curve is the best fit hyperbolic function. Biomass of algae increases dramatically once herbivory is reduced to ~ 10% of ambient.

Coral cover is a centrally important yet incomplete indicator of community resilience. Also critical is whether the perturbed communities are re-assembling to their pre-disturbed composition. Our time series data reveal that sites are re-assembling to their pre-disturbed (2005) structures in terms of representation of coral and algal taxa and functional groups of benthic space holders (Fig. 7). As with coral cover, there is considerable spatial heterogeneity in re-assembly rates, with communities on north and northwest shores (LTER 1, LTER 2, LTER 6) re-assembling faster than those at south and east sites (LTER 3, LTER 4, LTER 5). Temporal patterns in the structure of the fish assemblage mirror changes in the benthic community (Fig. 8), reflecting in part changes in habitat provisioning and food availability.

Lagoon habitats show strikingly different dynamics compared to the fore reef (Fig. 2). The perturbations of 2007-2010 had no immediate effect on benthic communities on back reef or fringing reef sites, but communities on different lagoon reefs now are displaying different dynamics, with some sites becoming dominated by macroalgae, particularly the large brown alga *Turbinaria ornata* (Fig. 3). As many coral communities in the lagoon appear to be transitioning into a potentially persistent macroalgae state, they may be much less resilient than on the fore reef. To address the mechanisms driving the differences in resilience between the lagoon and fore reef, we developed a novel experimental approach. Multi-year experiments spanning many generations of *Turbinaria* estimated the intensity of herbivory needed to prevent the establishment of macroalgae as well as the intensity needed to remove it. The experiment was done on a fore reef and a lagoon site. Results (Fig. 9) show, for the first time in any coral

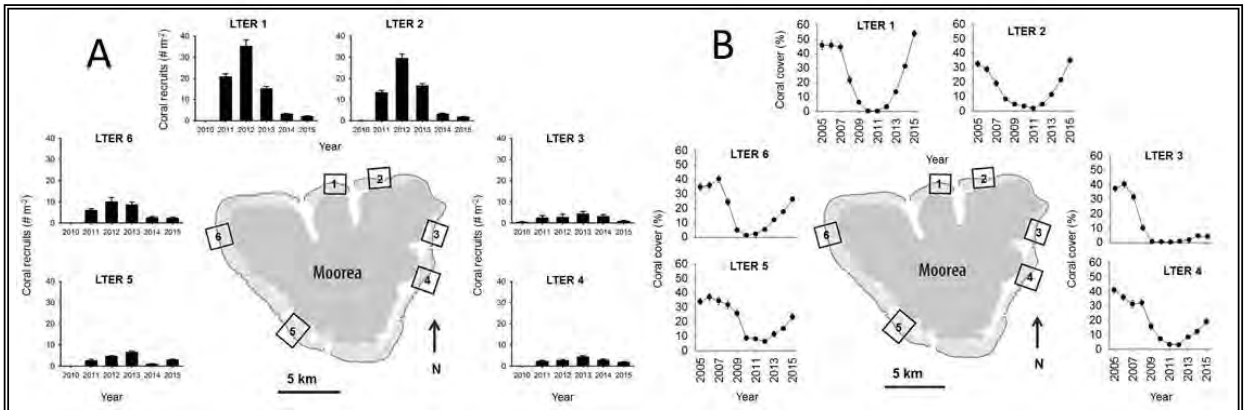


Figure 6. A. Density (no. $m^2 \pm 1$ SE) of juvenile coral (< 3 cm dia) at 10 m depth isocline on the fore reef at each MCR sampling location each year after the perturbations of 2007-2010. **B.** Trends in cover of coral at 10 m depth at the same sites. Note the rapid reduction in coral cover between 2007-09 due to consumption by Crown-of-Thorns Seastars (COTS) followed by among site / shore variation in the rate of return of coral cover. **Below**: Community on the fore reef (L-R) had high coral cover when MCR started in 2005, was eaten by COTS and then damaged by a cyclone; little live coral was left by early 2010. Recovery was well underway in 2014 and coral is approaching its pre-disturbance cover on the north shore.

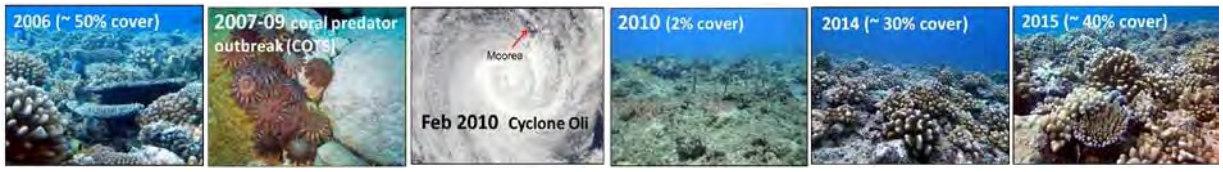


Figure 7. Trajectories in metrics of community structure at each of the 6 fore reef time series sites between 2005 and 2014. Green symbols represent the value in 2005 and the red in 2014.

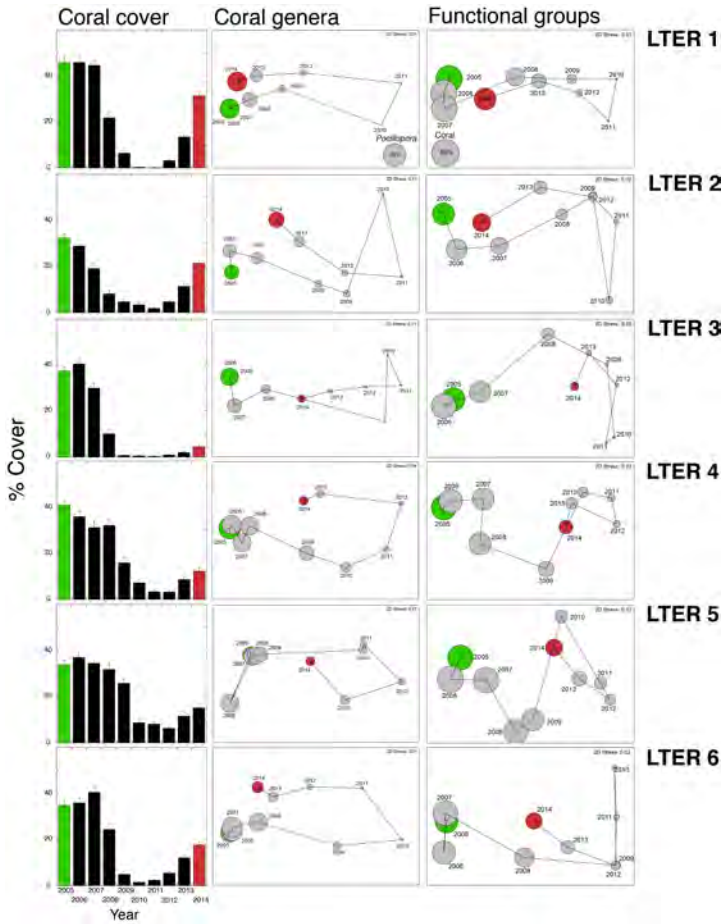
The *left* column shows coral cover through time.

The *middle* and *right* columns are MDS plots of Bray Curtis Similarity values of each year with 2005 for that site; lines connect adjacent years and the circle size is scaled to percent coral cover.

The *middle* column represents the re-assembly trajectory with respect to coral genera.

The *right* column represents the re-assembly trajectory for functional groups of benthic space holders. The functional groups are coral, macroalgae, turf algae, crustose coralline algae / bare space and sand.

See Fig. 8 for spatial and temporal changes in the fish assemblage at these sites.



reef ecosystem, the existence of hysteresis in the herbivore-macroalgae relationship. This experiment indicated that more herbivory was needed to remove than prevent establishment of macroalgae, and as a consequence there is a level of herbivory where either macroalgae or substrate suitable for coral colonization can dominate. However, the region of state space over which the two communities can both occur appears to be much larger, and ambient levels of herbivory much closer to the macroalgae 'tipping point' in the lagoon compared to the fore reef. This raises the possibility that corals and macroalgae could represent alternative, self-reinforcing community states in at least some areas of the lagoon. Understanding the drivers of these dynamical patterns and causes of spatial heterogeneity in resilience are a major focus of research proposed in MCR III.

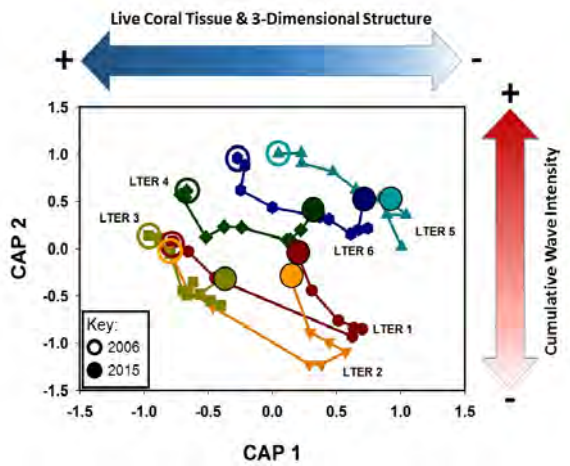


Figure 8. Spatio-temporal changes in the fish assemblage on the fore reef as revealed by ordination analysis using species specific abundances. For each site, a line connects successive years from 2006 to 2015. Separation along the y-axis reflects differences in species composition related to spatial variation in cumulative wave intensities. The x-axis reflects temporal shifts associated with the 2007-10 disturbances that killed coral (and reduced reef rugosity at LTER 1 and LTER 2), followed by subsequent increases in coral cover and architectural complexity as the benthic community re-assembles (see Fig. 7).

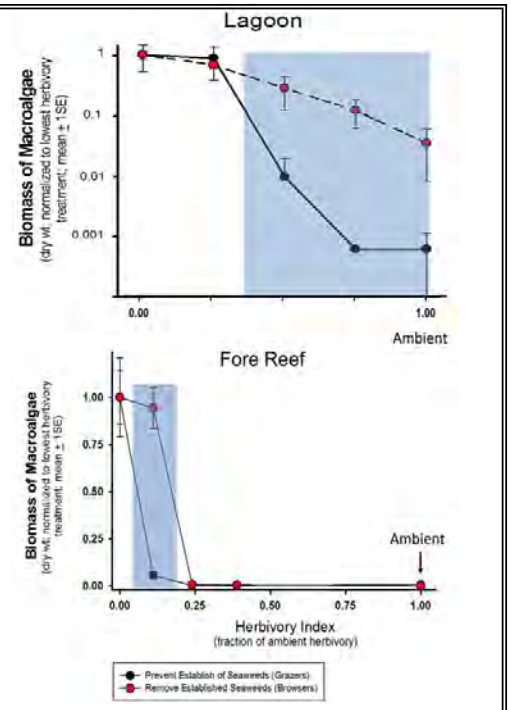


Figure 9. Results of multi-year experiments that spanned several generations of the macroalga *Turbinaria ornata* showing hysteresis in the macroalgae – herbivory relationship. More herbivory was needed to remove *Turbinaria* than to prevent it from becoming established. The region of hysteresis (*blue shading*) was narrower and much further away from ambient herbivory on the fore reef (*bottom*) compared to the lagoon (*top*), where even ambient herbivory was not sufficient to completely remove adult macroalgae.

Overfishing and pollution are important local press drivers that affect the resilience of coral reefs. During MCR II, MCR investigators teamed with an environmental anthropologist and a fisheries ecologist to address the former issue through an NSF Coastal SEES award, which explored dynamic feedbacks between Moorea's fishers and the reef fishes (especially herbivores) they harvest (Leenhardt et al. 2016). This year MCR investigators began to explore effects of nutrients using NSF RAPID funding to take advantage of a bleaching event that is forecast for 2016. This work will continue into MCR III to explore community (including microbes) and ecosystem responses to multiple stressors, particularly nutrient enrichment, rising seawater temperature and declining pH.

In MCR II we began to build our understanding of the microbial ecology of the reefs in the context of the surrounding ocean and the global trend of shifts to macroalgae. This area of coral reef science previously was poorly understood, but it is central to understanding how microbial recycling may facilitate productive reefs in oligotrophic waters and modulate the resilience of coral reefs to anthropogenic disturbances. We established for the first time how reef microbial communities and organic matter composition are distinct from the surrounding ocean (**Nelson et al. 2011**, McCliment et al.

2012). Subsequent process studies linked coral and algal community structure to rates of organic matter and microbial production (Haas et al. 2011), microbial autotrophic and heterotrophic metabolic balance (Haas et al. 2013) and the potential for shifts in bacterial phylogenetic and community composition induced by algal phase shifts (Nelson et al. 2013). This set the stage for collaborative, synthetic papers describing how microbial metagenomic and phylogenetic structure is related to environmental factors and anthropogenic impacts on multiple Pacific reefs (Kelly et al. 2014), as well as identifying global microbialization of coral reefs in concert with macroalgal phase shifts (Haas et al. 2016).

MCR investigators also explored longer-term effects of slowly changing global drivers on structural and functional aspects of coral reefs. We asked which corals are likely to become ecologically dominant in the future and what features allow them to function in this role. Our efforts focused on rising sea water temperature due to Global Climate Change (GCC) and declining oceanic pH due to Ocean Acidification (OA), which have distinct but synergistic modes of action on coral reefs. We have evaluated the factors favoring coral species functioning as 'winners' versus 'losers' (Edmunds et al. 2014a), codified benchmarks against which their performance can be evaluated (Edmunds et al. 2011), and developed dynamic energy budget (DEB) (Edmunds et al. 2011) and integral projection models (IPM) (Edmunds et al. 2014a) to help elucidate the mechanistic basis and demographic criteria of winning corals.

Using the MCR time series of coral community structure to identify winning and losing corals, we conducted experiments to evaluate the factors promoting coral success under contemporary conditions. One aspect of this work has been evaluating the role of acclimatization to thermal stress, which highlights the role of pre-exposure to high temperatures in ameliorating response to high temperatures (Edmunds 2014). This work is continuing through common garden experiments to evaluate the roles of phenotypic plasticity versus genetic adaptation in determining the response of corals and coralline algae to climate change effects. Research with the massive coral *Porites* spp. revealed that biomass plasticity can confer resistance to the effects of OA on calcification (**Edmunds 2011**). Factors determining susceptibility to OA are complex, however, for we have also found that the coral *Porites rus* and the alga *Porolithon onkodes* can buffer their response to OA through use of HCO^{3-} in addition to CO_3^{2-} (**Comeau et al. 2013a**), and high flow speeds attenuate the susceptibility of reef communities to OA (Comeau et al. 2014a). By contrast, rapid growth predisposes corals and algae to greater sensitivity to OA (Comeau et al. 2014b). The lack of a tipping point in the response of eight reef calcifiers to rising pCO_2 (**Comeau et al. 2013b**) suggests that future changes in coral reef community structure due to OA will be gradual.

Figure 10. Research on the response of corals and coral reefs to OA has progressed from experiments on individual organisms to intact communities assembled in replicate flumes (A) operated outdoors in Moorea. Flumes have a 5.0 x 0.3 m working section in which coral communities are assembled (B) to replicate those quantified by MCR time series. Here a back reef community has been assembled and exposed to high pCO2 (1300 µatm, *black bars;* ambient, *grey bars*) with the result that calcification was greatly impaired over 8 weeks (C), largely through sediment dissolution (Comeau et al. 2015).

With additional funding from the NSF OA initiative, we constructed outdoor flumes to conduct OA experiments with corals and algae assembled to mimic the community structure described by the MCR time series. These experiments revealed the importance of sediment dissolution in driving a net reduction in community calcification for back reef communities exposed to OA (Fig. 10), and also showed that the net accretion of outer reef communities will decline at high pCO_2, with dissolution threatening the carbonate foundation of the reef (Comeau et al. 2015a, b). A major challenge identified by these experiments is the capacity to scale results from organisms to ecosystems (and the reverse). To address

this, we have led workshops to extend appropriate theory (Edmunds et al. 2016b), and are exploring the use of the Metabolic Theory of Ecology (MTE) as well as Dynamic Energy Budget (DEB) models.

- ***Cross-cutting Projects and Model Integration*** During MCR II we continued to characterize and model ecologically important physical phenomena. A major effort centered on a 20-day cruise in 2014 by the R/V Kilo Moana to understand linkages between 'blue water' processes and the coral reef ecosystem. The cruise involved 37 scientists (including 11 graduate students) and three K-12 teachers and included measurements of a wide variety of processes including: multi-beam bathymetry, physical oceanography, and the flux of POC and DOC. Efforts to map both shallow and deeper regions of the bathymetry of Moorea on the cruise were further enhanced by an aerial LiDAR survey of the lagoons in 2015. The latter provided data critically needed for our 3-D circulation models, specifically bathymetry of shallow areas (< 5 m) that could not be measured using multi-beam sonar deployed by ship. Bathymetry data are being incorporated into our 3-D circulation modeling efforts.

In addition to time series data (Fig. 11) and models (Fig. 12) that describe physical processes (Hench et al. 2008, Rosman & Hench 2011, Leichter et al. 2012, 2013, Hench & Rosman 2013, Monismith et al. 2013, **Herdman et al. 2015**, Carpenter et al. in review), we are continuing to explore coupling between physical and biological processes, including modulation of interactions between corals and macroalgae (Gowan et al. 2014, Brown & Carpenter 2015) and between corals and corallivores (Lenihan et al. 2011,

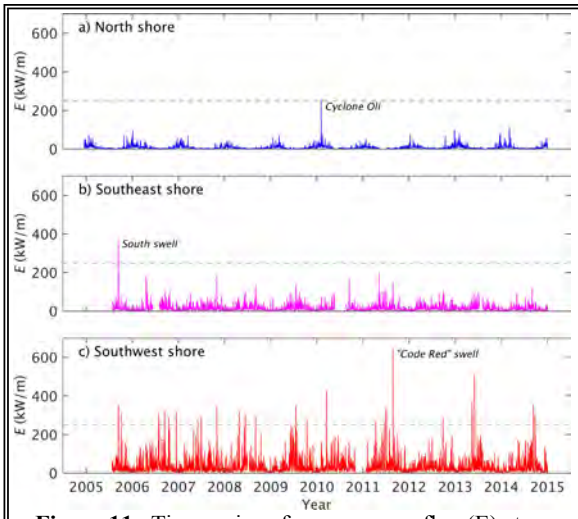


Figure 11. Time series of wave energy flux (E) at LTER sites 1, 4, and 5 for the past 10 years. The dashed horizontal lines indicate the 250 kW/m level for reference. Annotated with the single largest wave disturbance event at each site.

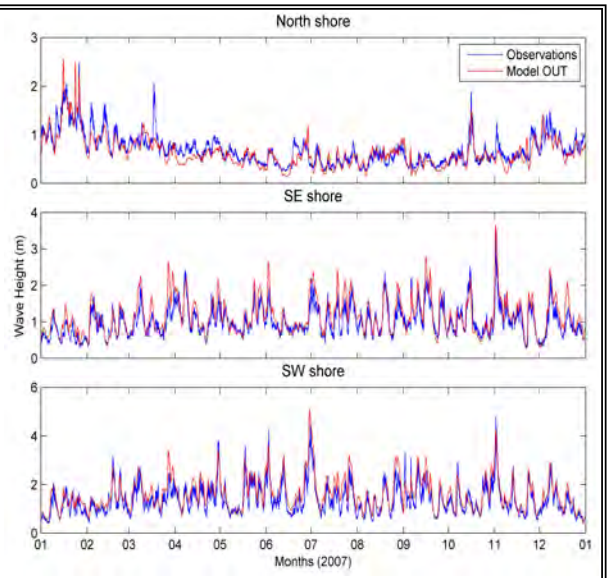


Figure 12. Comparison of our regional wave model output and the MCR wave time series for the fore reef in 2007.

2015). Our spatially nested ROMs-based circulation models, which will be further developed in MCR III, will be linked with biogeochemical and community metabolism models, including some we are developing with colleagues at ETH Zurich (N. Gruber). For example, we have developed statistical models that use our 11+ years of reef metabolism data to explore relationships between the components of reef metabolism (gross primary production PP, respiration R, net calcification G) and the primary environmental drivers of light and water flow. Flow across the reefs is driven primarily by offshore waves, and volume flux of water across the back reef is highly correlated with wave energy flux on the fore reef (Hench et al. 2008, Monismith et al. 2013). For a given community composition, PAR (photosynthetically active radiation) explains ~80% of temporal variation in primary productivity with water flow explaining the other 20%. Further, we now can define the relationship between primary production and calcification for a given community structure and use this to estimate G from PP. A key finding, which we will pursue in MCR III, is that following transition from coral to macroalgae, rates of primary production remain high, but rates of net calcification can become negative (i.e., dissolution).

We are developing biological models that help scale across levels of biological organization,

including cellular to organismic (Ananthasubramaniam et al. 2011, Muller et al. 2009, Muller & Nisbet 2014, Jacobson et al. 2016), organism to population (Edmunds et al. 2011, Eynaud et al. 2011) and population to community (Baskett et al. 2010, Buenau et al. 2007, 2011, 2012). As part of our focus on state transitions and dynamics of coral populations, we developed a structured landscape competition model to describe the conditions under which abrupt community shifts can occur (Buenau et al. 2007) and explored the effect of algal stage-structure in facilitating hysteresis in the relationship between herbivores and macroalgae (Briggs et al. in review). Regarding our focus on future reefs, we have expanded Dynamic Energy Budget (DEB) theory to a syntrophic (cross-feeding) symbiotic relationship that involves calcification (Muller et al. 2009, Muller & Nisbet 2014) to describe the response of a coral to varying light intensities and differing concentrations of nutrients (Eynaud et al. 2011). We used this model to explore the effects of resource limitation on the ability of massive corals to survive times of stress (Jacobson et al. 2016). We expanded the basic DEB model to achieve synthetic capacity in a compilation of coral trait values (Edmunds et al. 2011) and are currently using it to explore effects of OA and temperature on stability of the host-symbiont relationship. Our size structured models of dynamics of coral hosts and their algal symbionts on ecological and evolutionary scales help us evaluate conditions promoting high coral cover in an increasingly disturbed world (Baskett et al. 2009, 2010).

- ***Syntheses and Cross-Site Projects*** During MCR II we reviewed the effects of OA on calcification at scales ranging from the organism to the ecosystem (**Hofmann et al. 2010**). Additionally, an NCEAS working group led by MCR scientists addressed the concept of 'winning' corals and their role on future reefs. Winning and losing was quantified in a demographic landscape using an Integral Projection Model (IPM) approach (Edmunds et al. 2014a); winning genera may occur on both Indo-Pacific and Caribbean reefs while other taxa are likely to become extinct (Edmunds et al. 2014b). Additional synthetic papers include efforts to identify critical gaps in our understanding of how assemblages of coral reef fishes will be affected by GCC and OA (Wilson et al. 2010) and exploration of the negative interaction between human population density and reef fish biodiversity on ecosystem functioning (Mora et al. 2011). A cross-LTER site synthesis effort used time series data to detect abrupt state transitions and hysteresis in the underlying driver–response relationship (Bestelmeyer et al. 2011). Another synthesis involved a global-to-local comparison of coral recruitment and post-recruitment performance, which suggested that differences in post-settlement success may drive variation in the structure of the coral assemblage between Pacific and Caribbean reefs (Edmunds et al. 2015). MCR researchers will be involved in a March 2016 workshop at the Okinawa Institute of Science and Technology focused on coral reef connectivity using Moorea, Okinawa, and Hawaii as model systems, and have secured support from the USGS Powell Center for a synthesis of the ecological implications of coral reef 'oases' (reefs that remain in good condition while those around them decline).

MCR investigators engaged in a substantial number of cross-site projects during MCR II. Among them were multi-ecosystem comparisons of high frequency dynamics of ocean pH (Hofmann et al. 2011, Hofmann et al. 2013), and participation in the MIRADA (Microbial Inventory Research Across Diverse Aquatic) LTERs biodiversity inventory project (McCliment et al. 2012). A collaboration with colleagues from Australia's ARC Centre of Excellence for Coral Reef Studies involved conducting the same field experiment at locations across the Indo-Pacific diversity gradient (from Moorea to Papua New Guinea) to explore how habitat diversity structures local assemblages of reef fishes (Messmer et al. 2011); notably this study revealed that the proportional reduction (sensitivity) in fish biodiversity to the same loss of coral diversity was greater for regions of higher species richness (**Holbrook et al. 2015**), which is counter to the notion that diversity promotes stability. We collaborated with researchers at Scripps Institution of Oceanography to develop an automated system to analyze benthic imagery (Beijbom et al. 2012, 2014, 2015). In addition, Investigators Gates and Putnam developed GeoSymbio, a web application to facilitate discovery, visualization, and sharing of *Symbiodinium* data (Franklin et al. 2011), which has been expanded into the web site coraltraits.org.

Perhaps the most ambitious effort that the MCR has been central in developing with partner institutions is the Moorea IDEA (Island Digital Ecosystem Avatar) project, which seeks to integrate

disparate data into digital 'avatar' models to enable prediction of landscape-scale dynamics on Moorea as the basis for scenario modeling. The project, which was featured as a news article in *Nature* (Cressey 2015), involves more than 80 scientists from the U.S., Europe and French Polynesia (Davies et al. 2016).

2.2 Broader Impacts

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 24 postdoctoral researchers, 66 graduate and 151 undergraduate (19 REU, 2 ROA) students, 1 ROA faculty researcher and 17 K-12 teachers (6 RET). They are involved in MCR research and outreach activities and participate in the annual MCR All-Investigator Meeting; graduate students co-organize a bi-annual MCR-SBC-CCE LTER (an alliance of 3 southern California based LTER projects) Graduate Student Symposium. A focus of MCR Schoolyard is the development of resources on our website, including: (1) a Marine Life in Moorea Encyclopedia, (2) research pages for MCR graduate students, with photos and descriptions of their projects and (3) a teacher resource section developed largely by our RET participants. We have partner schools that have large enrollments of under-represented and/or economically disadvantaged groups and whose teachers use curricula based on MCR research, attend our professional development activities, and travel to Moorea for research experiences. Another of our Schoolyard efforts is an annual visit by > 100 fourth graders from Washington Accelerated School in Pasadena to learn about marine biology. MCR graduate students lead K-12 activities at our coral reef booth at the annual Earth Day celebration in Santa Barbara, and 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.

Outreach in Moorea is made through the Tahitian association *Te Pu 'Atiti'a*, which partners with the UC Berkeley Gump Research Station. During MCR II our LTER Children's book, *Kupe and the Corals* (authored by MCR postdoc J. Padilla-Gamino) was published in various combinations of English, French, Spanish, Hawaiian, Tahitian and Paumotu. The *Te Pu 'Atiti'a* association worked closely with us on the Polynesian language translations and to insure cultural context.

MCR research has great relevance to resource managers, policy makers and stakeholders in French Polynesia and beyond, and we illustrate this with a few examples. MCR PIs annually brief the Ministry of the Environment of French Polynesia on MCR findings. Recently this has included information central to the sustainable management of a threatened local fishery (Yau 2011, Yau et al. 2014), results from our lagoon circulation studies (Hench et al. 2008, Leichter et al. 2013, Herdman et al. 2015) that have implications for land use practices, and our work on resilience (Adam et al. 2011, 2014) that revealed the critical importance of protecting nearshore nursery habitats that are vulnerable to human activities. MCR Investigators Gates and Putnam and CNRS CRIOBE researcher Hedouin are conducting workshops and training exchanges, funded by the French American Cultural Exchange Partner University Fund.

The MCR cooperates with the NSF-funded LTREB coral reef site on St. John (USVI) in the Caribbean, including management and hosting on our web site of its 29-year time series data.

MCR recent research findings have been highlighted often in the popular press and television. For example, the TV series Voice of the Sea produced by the Sea Grant Program at the University of Hawaii and shown on OCEANIC channels in multiple Pacific Rim audiences produced 12 episodes featuring MCR research and graduate students. Our work regarding how parrotfish prevent phase shifts (Adam et al. 2011) was disseminated broadly on the internet, both in the United States and internationally. Our research on ocean acidification and symbiosis (Edmunds 2011, Putnam et al. 2012, Comeau et al. 2015a, b) has been featured by NSF as Top Discoveries from NSF Research.

2.3 Results of Supplemental Support

Education and Outreach Activities funded by our Schoolyard, REU and RET supplements are described above. An ROA supplement (2010) enabled Professor J. Idjadi and two students from Eastern Connecticut State University to conduct research in Moorea.

Information Management With IM supplemental funds, MCR participated with Georgia Coastal (GCE), Santa Barbara Coastal (SBC) and Coweeta (CWT) to implement GCE's relational metadata model. This model supports metadata-mediated data access.

Equipment/Infrastructure The MCR received 4 supplemental awards to repair, replace or upgrade field instruments/sensors (including pH sensors), infrastructure for marine operations (e.g., outboard engines, trailers, mooring repair), and laboratory equipment. Funds also were used to purchase expendables (e.g., lithium batteries), for shipping and to acquire an OA mesocosm facility at the Gump Research Station.

UNOLS Cruise A 20-day MCR UNOLS cruise in the waters around Moorea occurred in July-August 2014 to obtain vital bathymetry measurements and to better link offshore and onshore oceanographic and biogeochemical processes. Two supplement awards supported the participation of graduate students and the purchase of supplies for biological and physical sampling, and for sample analysis.

Airborne LiDAR Bathymetry The UNOLS cruise provided detailed bathymetry of the ocean floor >10 m depth using multi-beam sonar. In 2015, the Tahitian Territorial Government commissioned a LiDAR survey of the lagoon system of Tahiti. An NSF supplement for extra flight days, together with cooperation with the French *Service Hydrographique et Océanographique de la Marine* (SHOM) and the Territorial Government, enabled the MCR to obtain LiDAR bathymetry of the shallow waters of Moorea.

International MCR received a supplement to partner with scientists from Walailak University, Thailand to foster development of a coral reef study site as a potential ILTER site on Racha Island. It enabled MCR investigators and graduate students to visit Racha Island twice for training of Thai students and scientists in techniques for gathering biological time series data on coral reefs.

2.4 Responses to Mid-term Review Recommendations

The 2013 Mid Term Review identified five weaknesses, which we have addressed as described below.

1. *The microbial component of the program needs to be more strongly justified and integrated if it is continued into MCR III.* We have better integrated and justified the proposed microbial work in MCR III, and also have added two additional marine microbial ecologists to the project: R. Vega Thurber (Oregon State Univ.) and C. Nelson (Univ. Hawaii). M. Hay (Georgia Tech), who is an expert in coral–macroalgae interactions, has also joined the MCR [as have D. Burkepile (UCSB), T. Adam (UCSB) and H. Putnam (Univ. Hawaii)]. Together with current investigators R. Gates and C. Carlson, they will address the role of microbes in key ecological processes. As noted in the Related Research section below, they have already attracted funding for some of these projects.

2. There appear to be some methodological issues that should be addressed in order for MCR to provide transformative data in the context of OA. Following this input, we undertook a broad scale survey of pH at a regional offshore scale and compared those data with simultaneous measurements at the reef scale in Moorea. The larger scale measurements were made during the 2014 UNOLS cruise. Reef scale measurements were made on the north shore of Moorea using a Sunburst Sensors SAMI-pH instrument moored in the water column on the fore reef 10 m above the bottom and 10 m below the surface. Synoptic pH measurements were virtually identical and bracket those obtained from oceanic water samples taken 5 kms north of Moorea over the past 10 years. Based on these data, we will continuously deploy a SAMI in the water column on the north shore fore reef. These measurements will be compared to pH measurements of water samples taken at our 5 km offshore station every three years as a check. We also will continuously deploy a bottom-mounted SAMI on the back reef, to quantify variation in pH resulting from reef metabolic processes. Additional measurements of spatial variation in pH will be obtained by shorter-term deployments of SeaFET sensors.

3. Better integration between experimental results (as they are produced) and the DEB modeling efforts is encouraged. This is our goal and we have made progress. For example, a recent MCR paper by Jacobson et al. (2016) used results from experiments in a DEB framework to explore implications

regarding the ability of corals to modulate metabolic rates to enhance survivorship under stress. An ongoing project is using results of empirical studies to develop a DEB model of the coral-*Symbiodinium* symbiosis to better understand the mechanisms that regulate its stability under environmental stress. Data collected during MCR III will directly inform ongoing DEB modeling efforts.

4. Data on nutrient concentrations and hydrodynamics could be better integrated into the experiments and models on the algal-coral phase shift and possible hysteresis. We have proposed research to explore the effects of these (and other) drivers (see Theme 1, Campaigns 2 and 3, and Modeling and Integration). Empirical findings also will continue to be incorporated into our next generation of biogeochemical and ecological state change models.

5. Productivity measurements used to predict this aspect of reef function should be done at sites on the east and west shorelines, in addition to the north shore. In response to these comments, we expanded the spatial extent of our measurements of reef scale metabolism, including rates of primary production, respiration, and calcification. In early 2015, we established five additional back reef sites around Moorea that varied in community structure and in abundances of calcifiers. These differences, coupled with variation in the main environmental drivers of metabolism (light, water flow) resulted in rates of primary production varying by a factor of 3, respiration by a factor of 4, and daytime rates of calcification by a factor of 20 (see Fig. 21). Rates of nighttime calcification were negative indicating net dissolution of the reef at night. These data will form the foundation for evaluating the relative importance of variation in community structure and environmental drivers. Measurements will continue on the north shore biannually (summer/winter) and the expanded measurements will be repeated regularly during MCR III. The data also will facilitate the development of algorithms to model rates of metabolism over larger reef scales (see Modeling, Integration and Synthesis).

SECTION 3 - PROPOSED RESEARCH

3.1 GENERAL CONCEPTUAL FRAMEWORK

The overarching goal of the MCR LTER is to gain a predictive understanding of the dynamics and functioning of oceanic coral reef ecosystems through long term observations, experiments and modeling. Building on our prior research and patterns emerging from our time series, MCR III will advance understanding of resilience properties of coral reef ecosystems, and how key community and ecosystem functions are likely to be altered by long term drivers associated with Global Climate Change and Ocean Acidification and local stressors such as nutrient enrichment. This forms the basis for the two core questions of the MCR III research program.

Core Question 1: ***What processes and attributes underlie the ability of coral reef ecosystems to buffer environmental perturbations to maintain or restore community structure and function?***

Core Question 2: ***How will changing environmental drivers alter resilience, community composition, and ecosystem functioning*****?**

Ecological resilience has its origin in dynamical systems theory and has two components: the capacity of an ecosystem to remain qualitatively unchanged in the face of pulse and press drivers, and the propensity for - and the rate at which - a community re-assembles to its pre-disturbed state following a disturbance. A measure of the latter component, sometimes referred to as Engineering Resilience (Holling 1996), is the speed at which a perturbed system returns to its initial state. Our focus is on the ability of a coral reef to absorb perturbations and to continue to re-assemble to the coral state without switching to a persistent alternate state (Hughes et al. 2010).

Coral reefs are among the most biologically diverse of ecosystems, but also are among the most threatened (Mumby & Steneck 2008). Recent trends in the dynamical behavior of coral reef communities emphasize the vital *need to understand more fully why some coral reefs degrade to a non-coral community while others do not* (Hughes et al. 2003, 2005, 2010). Until recently, coral communities demonstrated the capacity to re-assemble to their prior state following a pulse perturbation such as a

cyclone (Jackson 1992, Aronson & Precht 1997, Pandolfi & Jackson 2006). Observations in the past few decades, however, show that many perturbed reefs either undergo a phase shift to macroalgae or otherwise fail to return to coral dominance (Hughes 1994, Shulman & Robertson 1996, Aronson & Precht 1997, Rogers & Miller 2006, Bruno et al. 2009). Nonetheless, time series data from some reefs, including Moorea, indicate that in the absence of chronic stress, it is possible for coral reefs to recover from large disturbances within a decade or two (Connell 1997, Connell et al. 1997, Sheppard et al. 2008, Smith et al. 2008, Adjeroud et al. 2009, Trapon et al. 2011, Gilmour et al. 2013). The modern paradigm is that coral reefs are an increasingly stressed ecosystem that is structured by strong positive and negative feedbacks (Mumby & Steneck 2008) and where alternative domains of attraction (e.g., a persistent, self-reinforcing non-coral community state) are possible (Knowlton 1992, Mumby et al. 2013). The latter issue - the existence of non-coral states that persist via a different set of stabilizing feedbacks (Mumby & Steneck 2008) - has been a subject of considerable debate (e.g., Bruno et al. 2009, Dudgeon et al. 2010, Mumby et al. 2013). There is broad agreement that a general lack of definitive field tests has hampered progress and consensus (Mumby et al. 2013).

Many of the recent state changes away from corals on tropical reefs, particularly those involving macroalgae, are regarded as regime shifts that may be difficult to reverse (Hughes et al. 2005, 2010, Mumby & Steneck 2008). The underlying cause of these shifts has been attributed to a combination of human-induced drivers that lower ecological resilience (Jackson et al. 2001, Bellwood et al. 2004, 2011, Mumby & Steneck 2008, Hughes et al. 2010). Two important local press drivers are fishing and pollution (particularly nutrient loading), and both can foster growth of macroalgae (Bellwood et al. 2004, Fabricius 2005, Bruno et al. 2009). Overfishing of herbivorous fishes has been identified as one major driver of state shifts from corals to macroalgae (Hughes 1994, McManus et al. 2000, Hixon 2015). In addition to lower fish abundance, intense fishing pressure can result in a reduction in body size of fishes due to size-selective harvesting (Garcia et al. 2012, Edwards et al. 2014).

Human-driven reduction of top down control of macroalgae via fishing of herbivores often is accompanied by intensification of bottom up forcing via nutrient loading on coral reefs. Nutrient enrichment is a major anthropogenic force altering coastal ecosystems worldwide, particularly in oligotrophic systems such as oceanic coral reefs. By increasing algal productivity, nutrient enrichment can alter competitive interactions between corals and algae, making reefs more susceptible to undergoing a state shift to a macroalgae-dominated state (Jompa & McCook 2002). Increasing nutrient availability also can directly impact coral reproduction, growth, and survivorship negatively (Koop et al. 2001), intensify coral diseases (Bruno et al. 2003, Voss & Richardson 2006), and increase the susceptibility of corals to bleaching (Vega-Thurber et al. 2014). However, the effects of nitrogen (N) on corals may depend on the form in which it is delivered (Meyer & Schultz 1985, Holbrook et al. 2008, 2011, Shantz & Burkepile 2014, Ezzat et al. 2015). Different forms of N (NO_3^- versus NH^{4+}) and therefore different sources (anthropogenic versus fish-derived) can have contrasting effects on coral biology (Ezzat et al. 2015), with anthropogenic-derived nutrients potentially being more harmful than fish-derived nutrients (Shantz & Burkepile 2014).

While overfishing and pollution are present-day threats to coral reefs, they occur against a background of intensifying global stresses created by increasing temperature and declining pH of ocean waters (Pandolfi et al. 2011). GCC-related rises in sea surface temperature (SST) increase the severity of coral bleaching (Hoegh-Guldberg 1999), foster outbreaks of coral disease (Bruno et al. 2007), and possibly alter the frequency and/or intensity of large storms (Knutson et al. 2010, Ruggiero et al. 2010, Young et al. 2011). Rising temperatures also result in rising sea level (Stammer et al. 2013). This may negatively impact reef communities and increase the frequency with which sudden thermal anomalies exceed bleaching thresholds (Oliver et al. 2009) or of coral breakage events (Madin 2005). Thus it is critical not only to understand the interactive effects of multiple stressors (e.g., nutrient loading and elevated temperatures on coral bleaching), but also to understand the capacity of corals to acclimatize or adapt (genotypic response) to thermal stress (Edmunds & Gates 2008, Brown & Cossins 2011).

While the worldwide coral bleaching events of 1997 and 2010 raised alarm regarding the future of coral reefs, some scientists believe that ocean acidification (OA) ultimately may be a greater long term

threat to coral reefs because it may result in a fundamental decline in calcification rates (Kleypas & Langdon 2006, Hofmann et al. 2010). Rising concentrations of atmospheric CO_2 are slowly lowering both the pH and the calcium carbonate saturation state (Ω) of the ocean. As Ω declines, the precipitation of calcium carbonate becomes increasingly difficult (Cohen & Holcomb 2009, Erez et al. 2011). The ecological consequences of reduced Ω are largely unknown, but pessimistic projections suggest net dissolution of coral reefs (over 24 h) may occur within a century (Silverman et al. 2009). Although little is known regarding mechanisms corals and other calcifiers may use to resist low pH (Hofmann et al. 2010, Tambutté et al. 2011, Comeau et al. 2013a), we have found that some massive corals and other calcified macroalgae can ameliorate the effects of OA (Edmunds 2011, Comeau et al. 2013a) and that slower-growing taxa are less susceptible (Comeau et al. 2014b).

The above considerations coupled with our observed, spatially-explicit dynamical patterns and prior research findings for Moorea form the basis of the research proposed here. MCR III will focus on *the causes and consequences of spatial heterogeneity in resilience*, together with *how future changes in environmental conditions will alter community structure and key ecosystem functions*. Figure 13 illustrates our general conceptual framework for MCR III; Figures 14 and 20 illustrate frameworks specific to our two main research themes.

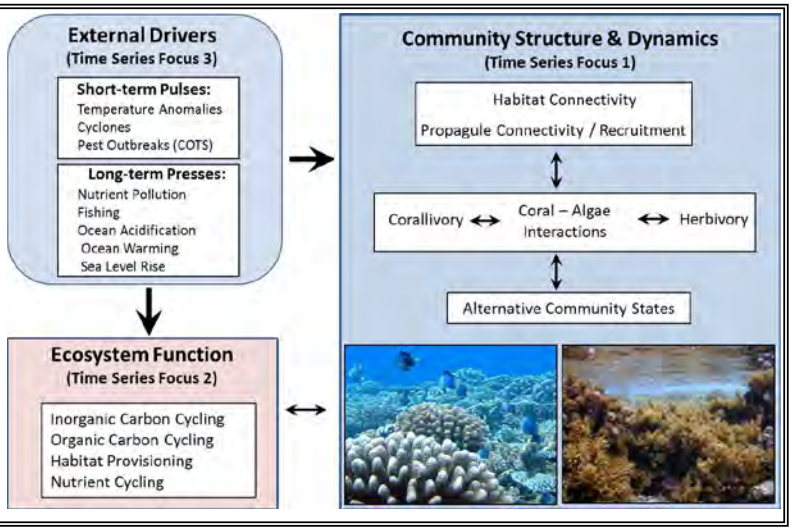


Figure 13. The MCR III framework that highlights major drivers, processes and interactions that shape the structure and function of coral reefs. The three foci of the MCR time series program are indicated. This framework underlies our two major research themes, which focus on reef resilience under contemporary conditions (Theme 1) and how the structure and function of reefs in the future are likely to be altered by slowly changing drivers associated with Global Climate Change and Ocean Acidification (Theme 2). Specific frameworks for each theme are presented in Figs. 14 and 20. Data from our time series and process studies are incorporated in MCR models and syntheses.

3.2. MCR III Research Themes

While the perturbations of 2007-2010 provide an unparalleled opportunity to address fundamental questions regarding the response of coral reefs to acute disturbances and multiple stressors, we recognize that such disturbances are embedded in slowly changing environmental conditions. The latter arise from GCC and OA, and will alter multiple aspects of coral reef ecosystems in the future. Accordingly, two themes focus our research program.

- ***Theme 1 - Resilience of Contemporary Reefs*** focuses on factors that promote the return of a perturbed reef community to a coral-dominated state (including associated microbes, fish, algae, etc.) under current levels of GCC- and OA-related stress, and explores time scales of ~ 1 to 2 decades. *The focus is on the processes and attributes that affect the capacity of a coral reef to absorb perturbations and re-assemble to a coral community without degrading to an alternative state (e.g., macroalgae).*

- ***Theme 2 - Structure and Function of Reefs in the Future*** addresses a longer time horizon (~ 3 to 5 decades) and seeks insight into how forecasted changes in GCC and OA may alter community structure and how those changes affect ecosystem processes and resilience. *The two foci within this theme are: (1) the attributes and adaptive capacities of key ecological species (e.g., corals, crustose coralline algae) that will shape their responses to changing temperature and seawater pH, and (2) how GCC and OA conditions and the altered community composition in the future will affect ecosystem function.*

3.3 RESEARCH PROGRAM

Our research program is shaped by patterns emerging from our time series program and results from MCR I and II. Here we describe the MCR III research program: (**A**) time series program, (**B)** Theme 1 research, (**C)** Theme 2 research, and **(D)** modeling and integration activities. Data arising from our time series (**A**) and process studies (**B** and **C**) feed directly into our modeling and synthesis efforts (**D**). Our time series, research campaigns and modeling address all 5 core LTER research areas (see Summary Data Sets Table). The role of each Associate Investigator is given in the Project Management Plan.

A. Time Series Our time series provides critical information on three key aspects (Fig. 13): (1) community dynamics of major functional groups, (2) rates of key ecosystem processes, and (3) patterns of key physical environmental processes.

Time Series Focus 1 *Community dynamics and long term trends of key functional groups within each major coral habitat*

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). Estimates are made visually along permanent band transects or from permanent quadrats that are surveyed *in situ* (e.g., sea urchins, macroalgae, fishes) or using photo-quadrats (e.g., corals). Abundances of corals and fishes are estimated at 2 to 3 additional fore reef sites on each shore every 4 to 6 years to evaluate the extent to which our core sites are representative of broad patterns around the island. The additional sampling will be repeated at least once for each group during MCR III. Organisms (~ 400 taxa) are identified to the lowest taxon possible (typically species or genus). These data reveal different responses and rates of recovery of the reefs to disturbance and attributes that influence resilience (Adam et al. 2014, Han et al. 2016).

In addition to measuring coral abundance in photo-quadrats at the 18 core MCR sites (6 sites in 3 habitats), we will continue sampling coral recruits (on settlement tiles) and juvenile corals (colonies ≤ 40 mm diameter) *in situ*. Sampling will include genetic analysis of *Pocillopora* recruits to inform our knowledge of connectivity among islands. After sampling the back reef from 2005-2006 for coral recruits, in 2007 sampling was re-focused on the north shore and has continued in the back reef (3 sites), and outer reef (2 sites, 10 m and 17 m depth). Surveys of densities of juvenile corals will continue using visual estimates on the outer and fringing reef around the island. Analyses of overall coral community structure are based on digital images, and these will be continued, aided by next-generation image analysis tools [CoralNet, developed by our collaborators at SIO (Beijbom et al. 2012, 2015)].

Time Series Focus 2 *Temporal patterns in rates of key ecosystem processes*

Rates of reef metabolism (primary production and respiration) are estimated twice annually along with PAR using a Lagrangian approach at two locations on the north shore and every 3 years on the other shores. In addition to the benthos, we estimate water column primary production in vertical profiles using standard ^{14}C tracer/bottle techniques in three habitats (fringing reef, mid-lagoon and fore reef) on the north shore. 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 DIC and nutrients. Concentrations of nutrients (NO_2^-, NO_3^-, PO_4^{3-}, SiO_4^{2-}) are measured concurrently with water column primary productivity (along with bacterioplankton biomass, DOC and POC concentrations, phaeo-pigments, Chl a, and turbidity). We also estimate nutrient concentrations (NO_2^-, NO_3^-, PO_4^{3-}, SiO_4^{2-}) at these locations approximately biweekly. Concentrations of nutrients in Moorea are low and near detection limits (see Fig. 18) and 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 CHN in two macroalgae (*Sargassum*, *Turbinaria*) collected in all three habitats from each of our six permanent sampling sites as an integrated estimate of nutrient flux over longer periods. In MCR III, we

will test nutrient 'osmo-samplers' that are under development as another means to obtain a time-integrated measure of nutrient flux. Regional scale variables related to ocean color (e.g., sub-surface concentrations of Chl a, light absorption and particulate backscattering), are derived from measures of spectral radiometry using satellite imagery (MODIS, VIIRS, Sentinel 3-OLCI).

Time Series Focus 3 *Patterns of temporal and spatial variation in major physical factors that influence coral reefs*

We have instrumented the reefs around Moorea with a suite (~105) of sensors to measure abiotic conditions [water temperature, salinity, current speed and direction, offshore wave statistics (height, direction, period), water levels]. Simultaneous measurements of wave heights and currents 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). Time series information on regional scale properties such as currents, water mass variability and meso-scale eddies comes from satellite remote sensing of sea surface topography (TOPEX Poseidon, ERS) and temperature (AVHRR, MODIS, VIIRS). Data obtained from *in situ* sensors and derived from satellite imagery along with our recently acquired high resolution bathymetric data provide critical input parameters and boundary conditions for our models of reef, island and regional circulation patterns. These data will be critical in the future in assessing rates of local climate changes and their relation to global climate patterns. Oceanographic measurements are complemented by surface environmental data from our met station at the Gump Station, and by data obtained from meteorological stations operated by Météo France. Data on long term changes in sea level are obtained through the Permanent Service for Mean Sea Level for the Papeete, Tahiti station, 20 kms east of Moorea.

In addition to quantifying other metrics associated with GCC, we measure variables associated with OA. To date this has been accomplished by collecting seawater samples from a site 5 km offshore to establish ambient background values of DIC and pH as well as deploying SeaFET and SAMI pH sensors across the north shore. In MCR III we will deploy a SAMI pH sensor in the water column on the north shore fore reef at 10 m depth, and obtain pH measurements of water samples taken at the 5 km offshore station every 3 years to test whether the fore reef sensor and offshore pH measurements remain indistinguishable. Additionally, we will deploy a second, bottom-mounted SAMI on the back reef to quantify spatial variation in pH resulting from reef metabolic processes. Additional measurements of spatial variation in pH will be obtained by shorter-term deployments of SeaFET sensors.

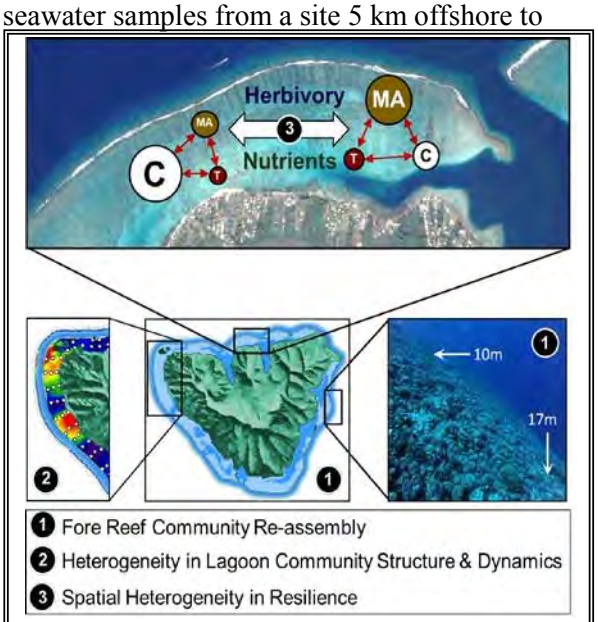


Figure 14. Conceptual diagram for Theme 1 (Resilience of Contemporary Reefs).
Campaign 1 seeks to understand the causes of spatial variation in the rate of re-assembly of the perturbed community on the fore reef, both around the island (*bottom middle*) and among depths (*bottom right*).
Campaign 2 (*bottom left*) explores landscape-scale heterogeneity in the structure and dynamics of communities in lagoon habitats.
Campaign 3 (*top*) addresses the causes and nature of spatial heterogeneity in ecological resilience. C = coral, T = turf algae, MA = macroalgae.

B. Research Theme 1: Resilience of Contemporary Reefs

Figure 14 depicts the conceptual framework that guides Theme 1 research. Numbers in black circles on the figure refer to the 3 proposed campaigns. We envision the project as a set of integrated campaigns that also bridge to Theme 2 research campaigns, with data from all campaigns feeding directly into our modeling and synthesis efforts. Table 1 lists the research activities and sources of data that will be collected to answer the specific questions (Q) posed in each campaign.

Table 1. Theme 1 Research Tasks & Data Sources	Campaign Questions							
	Q 1.1	Q 1.2	Q 2.1	Q 2.2	Q 2.3	Q 2.4	Q 3.1	Q 3.2
Time Series Focus 1 – Community Dynamics	✓	✓	✓	✓	✓	✓	✓	✓
Time Series Focus 2 – Ecosystem Processes				✓	✓	✓	✓	
Time Series Focus 3 – Abiotic Drivers	✓	✓		✓	✓			
Coral Recruitment Plots & Settlement Tiles	✓							
Coral Demographic Study	✓	✓						
Among-Depth Juvenile Coral Performance	✓							
Coral Population Genetic Studies	✓	✓						
Coral Recruitment Priority Effects Assay		✓						
Lagoon Habitat Spatial Mapping (WV-3)			✓		✓		✓	
Island-wide Nutrient & Herbivory Spatial Mapping				✓	✓		✓	
Island-wide Coral Bleaching Surveys					✓			
Coral Microbiome & Symbiodinium Surveys						✓		
Coral – Macroalgae Interaction Assays						✓		
Nutrient Enrichment Experiments						✓		
Macroalgae Colonization Arrays							✓	
Macroalgae Tipping Point & Hysteresis Experiments							✓	
Alternative Community State Experiments								✓
Reef Resilience & State Transition Modeling	✓	✓	✓	✓	✓	✓	✓	✓
Circulation Modeling	✓	✓		✓	✓	✓		
DEB & IBM Modeling						✓	✓	
Population Trajectory Modeling (IPMs)	✓	✓						

Campaign 1 – Spatial Variation in Fore Reef Community Trajectory and Re-assembly Rates ❶

Question 1.1 *What causes spatial variation in rate of return to the pre-disturbed coral community on the fore reef? Are different processes responsible for variation among sites compared with among depths?*

Rationale Campaign 1 addresses two issues regarding the response of coral reefs to pulse perturbations: (1) does the community re-assemble to its pre-disturbed structure (ecological resilience), and if so, (2) what factors cause variability in the rate at which different reefs return? Our time series data indicate coral communities (including associated fish) on the fore reef have high resilience, but also that there is spatial variation in this property, both among sites (Figs. 6, 7) and between depths (Fig. 15). This spatial heterogeneity is not related to differences in substrates suitable for coral settlement, rather it is shaped by variable colonization rates and post-settlement success. Structural heterogeneity provided by coral skeletons has long been thought to be a major determinant of reef resilience (Colgan 1987, Connell et al. 1997), in part because it can enhance recruitment and early survival of benthic organisms. During MCR II, we found evidence this was not the case. The recovery rate has been greatest at sites where structure was completely removed by the disturbances (north shore sites; Fig. 6B). Indeed, our studies have revealed that structure provided by dead coral skeletons is a sink for recruiting coral due to rapid erosion. At the among-site scale, community return rates roughly scale with variation in recruitment of juvenile corals (Fig. 6A). However, depth shows a different pattern with deeper sites exhibiting a much slower return rate despite similar recruitment levels (Figs. 15, 16). ***Here we test the hypothesis that different processes drive spatial variation in the rate of return to the pre-disturbed community across sites and among depths. Specifically, we hypothesize that variation in community return rates among sites is driven primarily by differences in input rates, but that variation among depths is driven by differences in post-settlement processes.***

Approach We are using three approaches to test this hypothesis. *First*, data from our time series will provide measures of community re-assembly on the fore reef. *Second*, data on coral input, growth, and survivorship from ongoing studies will be used to test demographic mechanisms driving variation in coral recovery rates around the island. Data come from 5 x 5 m Coral Recruitment Plots established in 2010 at 10 m depth at each of our six sites to estimate recruitment of very small corals, and serve as locations for our Coral Demographic Study. So far these data have shown that corals on the fore reef grow and survive better on the north shore than elsewhere, reinforcing the patterns observed for coral recruitment.

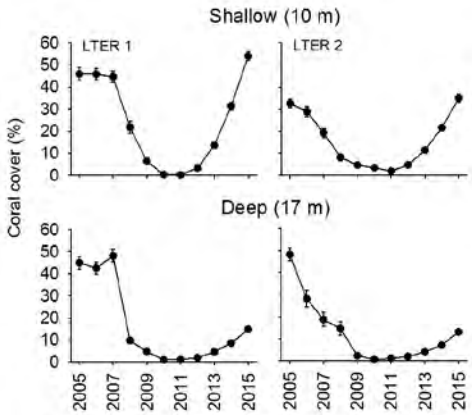


Figure 15. Coral cover (mean ± SE) at LTER 1 (*left*), LTER 2 (*right*), and at 10 m (*top*) and 17 m (*bottom*) depth. Both sites and both depths were severely impacted by COTS and Cyclone Oli (2010), and recovery has since been strong, but it differs between depths.

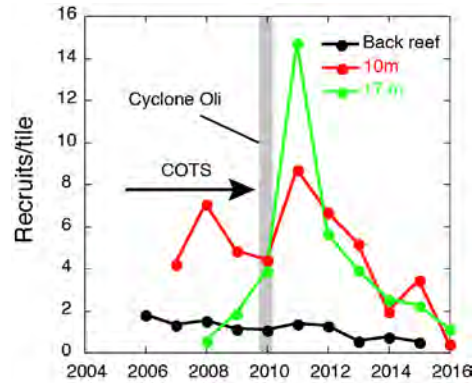


Figure 16. Annual coral recruitment to settlement tiles (15 x 15 cm) on the fore reef (10 m and 17 m) and back reef (~2 m depth). Values were obtained by summing mean recruitment rates at LTER 1 and LTER 2 within each year.

We currently are developing multi-scale statistical models to estimate and compare return rates among sites and depths, which we will use to explore the contribution of potential explanatory variables (e.g., input rates, coral growth and survivorship). *Third*, we will initiate field studies and experiments to explore reasons for the slower recovery of the community at 17 m compared with 10 m depth, and will contextualize the work by the constructs of depth-dependent zonation of coral reefs (Goreau 1959, Done 1983, Loya 1972). Our activities will include: (1) use of photoquadrats and individually marked corals to evaluate annual growth and survivorship of naturally-settled small corals at both depths, (2) out-planting of recruits on settlement tiles to measure post-settlement success, (3) reciprocal transplantation of small corals between 10 and 17 m to quantify depth-dependent growth rates, and (4) manipulations of coral density to estimate effects on subsequent coral recruitment, growth, and survival. We will continue to estimate recruitment of corals using settlement tiles at 10 and 17 m on the north shore. In addition to our statistical model approach mentioned above, these data will be used to parameterize Integral Projection Models (IPMs) (Easterling et al. 2000, Ellner & Rees 2006, Yau et al. 2014) to explore the demographic properties and possible density dependence driving site- and depth-dependent variation in coral community structure. We have now completed initial IPM models for three major coral taxa (*Pocillopora, Acropora, Porites*).

Question 1.2 *To what extent does the sequence of arrival of coral recruits to vacant space determine the tempo and direction of community dynamics?*

Rationale Another potential cause of spatial variation in benthic community structure is the type and number of species that colonize vacant substrates (Connell & Slatyer 1977), a concept that has shaped ecological theory as 'priority effects' (Shulman et al. 1983, Chase 2010). In this model, early colonizers of vacant space determine community trajectories until successional events are interrupted by disturbances (Connell & Slatyer 1977). This hypothesis has potential to reconcile previous results of analyses of coral connectivity among islands (i.e., Magalon et al. 2005 versus Edmunds et al. 2016a), which sometimes have demonstrated strong genetic connection of coral populations between islands (Magalon et al. 2005), and at others times strong separation (Edmunds et al. 2016a). These contrasting results suggest the capacity for the transport of coral larvae between islands and their subsequent establishment is not simply a function of seawater flow, but also the availability of larvae, and the likelihood they can settle and survive when they reach a destination. ***We hypothesize that if the order of arrival of different species is a primary driver of benthic community structure, then space opened during the peak recruitment times of different taxa will become dominated by those taxa and will not be displaced by later colonizers***.

Approach The role of priority effects in modulating coral recruitment and mediating trajectories of change in the coral community will be evaluated through an experiment in which areas of hard surfaces are made available at different times of the year over 2 years. These experiments will be conducted adjacent to the MCR time series plots, and will guide a mechanistic interpretation of the pattern-oriented analyses emerging from our benthic time series. We will use rugose patio pavers deployed at 10 m depth on the fore reef in four intervals separated by 3 to 4 months, and subsequently assayed for community development (using photography) until at least the end of MCR III. The pavers will be the same size as photoquadrats (0.5 x 0.5 m) used in the time series analyses. Community structure will be quantified using CoralNet, and MDS and PERMANOVA will be used to test for differential community development as a function of time of patch creation.

Campaign 2 – Landscape-scale Heterogeneity in Community Structure and Dynamics of Lagoon Habitats ❷

Question 2.1 *What are the spatial patterns of distribution of benthic communities on lagoon reefs and how are they changing through time?*

Rationale Campaign 2 builds on our time series to extend our view of the structure and dynamics of benthic communities in the lagoon. Research during MCR II suggested transitions to macroalgae such as *Turbinaria ornata* in the lagoon may be difficult to reverse, since small-scale experiments indicate more herbivory was required to remove established macroalgae than to prevent them from becoming established (Fig. 9). These observations are consistent with dynamics of many coral reefs, where persistent, often abrupt transitions from coral-dominated to macroalgae-dominated communities have been observed (Hatcher 1984, Done et al. 1991, Ledlie et al. 2007, Cheal et al. 2010). A critical question is how state transitions at small spatial scales (meters to 100s m) interact to influence community organization at larger scales (km) (van Nes & Scheffer 2005, Nyström et al. 2008). The patchy shifts in community structure in the lagoon provide an opportunity to address fundamental questions about the spatial extent and tempo of abrupt transitions between contrasting community states. We will analyze time series of high resolution habitat classifications of benthic communities at the island scale to better understand the timing, spatial extent, and spatial dynamics of coral to macroalgae state transitions within the lagoon. Specifically, ***we will determine how state transitions from coral to macroalgae propagate in space, and at what scales different community states coexist within the landscape***.

Approach To quantify habitat patch structure, in 2010 we began to acquire a time series of satellite imagery. Our French collaborators provided us with ground-truthed habitat classifications for the entire lagoon from WorldView-2 imagery (50 cm resolution) for 2010 (Fig. 17), when macroalgae began to increase in cover in some areas (Fig. 3). We have access to 2013 imagery from the Pleiades Satellite (50 cm resolution). We have commissioned WorldView-3 imagery (30 cm resolution) for early 2016 and will continue to obtain imagery every other year. Imagery will be used to identify 22 different benthic space holders (e.g., coral taxa, macroalgae genera, dead coral, sand, pavement) and quantify their spatial distribution within lagoons. This will leverage a benthic community classification system that has already been developed specifically for Moorea by our French colleagues (Collin et al. 2013, 2014), and provides an extraordinary opportunity to explore the spatial dynamics of coral to macroalgae state transitions. We will use spatial statistics to quantify the spatial and temporal dynamics of patch types (Sherman 2011).

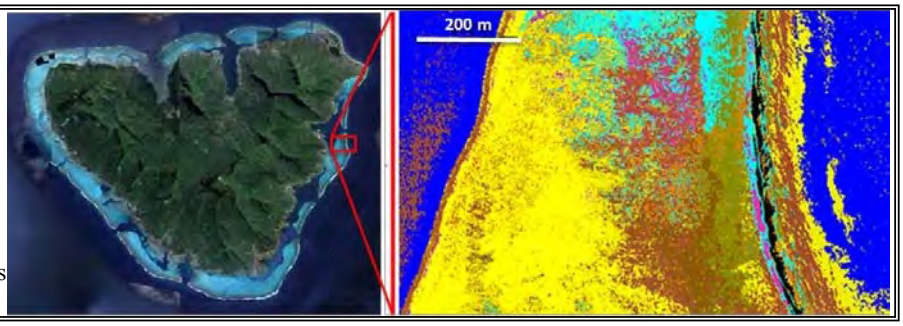


Figure 17. Image of Moorea (*left*) and section of reef showing habitat classifications derived from World View satellite imagery (*right*). Areas of reef are classified as 1 of 22 types of coral taxa, algal taxa, and substrates. Pink represents the macroalga *Turbinaria ornata*, shades of brown are different taxa of coral, yellow is sand, dark blue is deep water, and reef crest is black.

Question 2.2 *How do spatial patterns of dynamics of lagoon communities reflect landscape-scale heterogeneity in nutrient regimes and herbivory?*

Rationale The patchy shifts from coral- to macroalgae-dominated communities we are observing in lagoons were also observed following major disturbances in the 1980s (Done et al. 1991). At that time, nutrient enrichment was viewed as an unlikely cause of the proliferation of macroalgae in lagoon habitats because of low concentrations of N and P (Galzin & Pointier 1985, Done et al. 1991). While our time series data also reveal low concentrations of water column nutrients (Fig. 18), our time-integrated estimates (i.e., %N in macroalgae) reveal spatially-varying patterns of nutrient enrichment (Fig. 19). Two of the three back reef sites that have experienced large declines in coral cover and increases in macroalgae show evidence of N enrichment. In addition to being enriched in N, these two sites are near dense human populations and may be more heavily fished (spatial distribution of fishing effort around Moorea is the subject of an NSF proposal in review). Coral to macroalgae state transitions have been associated with the loss of key herbivores due to overfishing and/or nutrient enrichment (e.g., Maragos et al. 1985, Hughes 1994, Shulman & Robertson 1996), and it is possible that both factors play a role in Moorea. To better understand whether spatial heterogeneity in the dynamics of benthic communities within the lagoon is related to variation in nutrient availability and/or attributes of the herbivore community, we will create high resolution maps of both factors. ***Patterns of spatial covariation derived from these maps will enable us to test whether observed transitions to macroalgae are correlated with spatial variation in top-down (herbivory) and/or bottom-up (nutrients) forcing.***

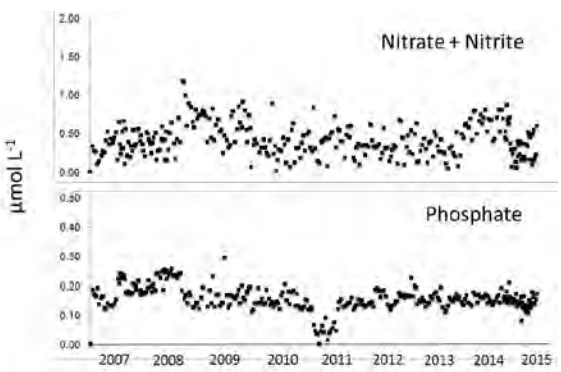


Figure 18. Water column nitrate + nitrite (*top*) and phosphate (*bottom*) concentrations over time in fringing and back reef habitats on the north shore of Moorea. Concentrations are consistently low and are an order of magnitude less than those in other coastal marine environments.

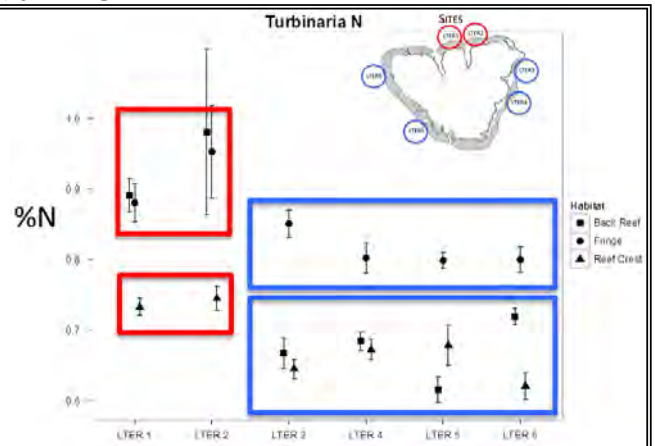


Figure 19. Mean (±SE) %N in tissues of the alga, *Turbinaria ornata*, collected at each MCR sampling site around Moorea in 3 reef habitats (fringing reef, back reef, reef crest). N content is lowest in reef crest habitats and increases toward shore. On the SW and SE shores, N content of back reef thalli is similar to thalli from the reef crest (low %N) while on the north shore, %N of back reef thalli is similar to the enriched values of thalli from the fringing reef, suggesting that land-derived N is reaching back reef habitats on the north shore.

Approach To create a high resolution landscape-scale map of nutrient enrichment we will use algal nutrient content data (C:N percentages) for the brown alga *Turbinaria ornata* as a time-integrated proxy for N availability. MCR Investigator Burkepile is developing a passive 'osmo-sampler' to provide an additional means to obtain time-integrated measurements of key water column nutrients (see Related Research). In addition to the sites where we have collected long term data on nutrient content in algae, we will re-sample our grid of 188 sites near the reef crest, mid lagoon, and fringing reef on reef crest-to-shore transects spaced every ~ 1 km around the island. This work will leverage a recent RAPID award (see Related Research), which supported the first such high spatial resolution sampling of nutrients around Moorea in January 2016 (Austral summer). We will resample this grid in the Austral winter of 2016, and again in the Austral summer and winter of 2018. We also will create maps of the biomass

density of different functional groups of herbivores by conducting surveys of herbivorous fish and sea urchins along the same reef crest-to-shore transects used for algal nutrient sampling. We will use these data in spatially explicit statistical models (Sherman 2011) to explore whether state transitions to macroalgae observed in our time series of habitat maps are positively associated with nutrient enrichment and/or negatively associated with the biomass density of different herbivore functional groups.

Question 2.3 *What is the spatial covariation in patterns of nutrient enrichment, coral bleaching and transition to macroalgal dominance?*

Rationale Warm water anomalies that cause corals to bleach have accounted for a substantial amount of coral loss worldwide, especially during 1997-98 and in 2010. The last decade of work in Moorea suggests that a bleaching event is likely in the next 6 years, particularly in 2016 as a result of the current El Niño. Warm water associated with the ongoing El Niño is forecast to bleach corals through much of their geographic distribution including Moorea. A goal of the RAPID grant is to explore the effect of nutrient enrichment in altering the susceptibility of corals to bleaching when further stressed by warm water anomalies. The RAPID award is supporting field surveys and sample collections ***to test the hypothesis that on a landscape scale, corals in more nutrient enriched sites will incur greater bleaching and bleaching-associated mortality compared to corals at nutrient poor sites***. Pre-bleaching data were collected in Jan. 2016 at 188 sites throughout the lagoon [C:N percentages and ^{15}N levels in *Turbinaria ornata*, the prevalence of coral bleaching using the visual reference color card technique (Siebeck et al. 2006), water temperature, PAR]. In MCR III, we intend to explore the hypothesis that ***bleached reefs subjected to higher nutrient enrichment are more likely to transition to a macroalgae state than to return to a coral-dominated community.*** This hypothesis follows from evidence that nutrient enrichment from anthropogenic sources can fuel blooms of macroalgae (Lapointe 1997, Loya 2004, Hughes et al. 1999, McCook 1999, Fabricius 2005).

Approach Following a bleaching event that we anticipate will occur in 2016 (and almost certainly in the next 6 years), we will re-survey all reefs sampled in Jan. 2016 to quantify spatial patterns of bleaching. Patterns of bleaching will be mapped onto patterns of nutrient enrichment, microbial load (see Question 2.4) and water flow speeds estimated from our lagoon circulation models. We will use these data in spatially explicit statistical models to explore covariance patterns. We also will commission WorldView-3 imagery of the lagoon shortly after bleaching, and every two years thereafter to quantify post-bleaching trajectories of reef communities at the landscape scale. Satellite imagery will be ground-truthed using our geo-referenced lagoon time series sampling plots, and habitat classification will follow the classification scheme developed for Moorea.

Question 2.4 *How do anthropogenic stressors impact the coral microbiome and coral-algae interactions and thereby influence the spatially heterogeneous decline in coral cover across lagoon communities?*

Rationale Symbiotic microbes, including dinoflagellates, bacteria and viruses, are critical to the success of corals as they serve functions ranging from photosynthesis to nitrogen fixation to pathogen inhibition (Knowlton & Rohwer 2003, Lesser et al. 2004, Ritchie et al. 2006, Ainsworth et al. 2010, Thompson et al. 2014). However, coral microbiomes are sensitive to multiple stressors such as elevated temperatures, nutrient pollution, disease, and competition. Competition from macroalgae may be especially harmful as they release DOC, which increases growth and O_2 consumption of bacteria, potentially harming corals through hypoxia (Kuntz et al. 2005, Kline et al. 2006, Smith et al. 2006, Nelson et al. 2013). Recent research in the Caribbean by Vega Thurber and Burkepile has shown that nutrients and macroalgal competition destabilized coral microbiomes resulting in stochastic blooms of putative pathogens and a >2-fold increase in coral disease, ultimately resulting in an >8-fold increase in coral mortality (Zaneveld et al. in revision). Elevated temperatures exacerbated the impact of local overfishing and nutrient pollution, further destabilizing microbiomes of unhealthy corals and concentrating 80% of coral mortality in warm months. ***We hypothesize that one mechanism driving heterogeneity in declining coral cover in the lagoon is spatial variability in the disruption of the coral microbiome via nutrient pollution,***

thermal stress, and algal competition. This work will take advantage of new MCR investigators (Vega Thurber, Nelson, Putnam, Burkepile) who have expertise in the area, as well as by Hay who brings expertise in the mechanisms underlying coral-macroalgae interactions (see Related Research).

Approach To assess these hypotheses, *first* we will compile time series data on the coral microbiome for massive *Porites* and *Pocillopora* sp., two common corals in the lagoon. We will collect these data at both coral-dominated and macroalgae-dominated sites as identified in Q2.1. At each sampling, we will collect coral biopsies of each species at each site for DNA extraction. Microbial, viral, and *Symbiodinium* amplicon data will be used to evaluate shifts in microbiome community composition. *Second*, we will photograph each coral to correlate changes in the coral microbiome with coral tissue loss/gain, disease, bleaching, corallivory, and algal competition. We also will assess how differences in nutrient availability and water quality across sites influence the coral microbiome via data collected in Q2.2. *Third*, at these same sites, we will quantify the frequency and extent of coral-macroalgae contacts, the visible effects of these interactions (e.g., bleaching), and the dynamics of these interactions (e.g., Bonaldo & Hay 2014). This will yield estimates of how the most frequent interactions and their outcomes vary spatially and through time, and how the patterns co-vary with nutrients and the coral microbiome. *Fourth*, patterns that emerge from the correlative approaches will be tested through short-term experiments and other process studies. For example, a nutrient enrichment field experiment being done as part of a recent RAPID award (see Related Research) will be leveraged to yield information on how nitrogen loading and the form of N (nitrate versus ammonium) alter coral-algae interactions and the coral microbiome community.

Campaign 3 – Experimental Investigations of Spatial Heterogeneity in Ecological Resilience 3

Question 3.1 *What causes spatial heterogeneity in the coral to macroalgae community transition?*

Rationale In addition to the lower ecological resilience of lagoon communities compared to the fore reef, there is fine-scale spatial heterogeneity within the lagoon with respect to reefs that are shifting to macroalgal dominance. Here we propose long term experiments, informed by findings of Campaign 2, to explore causes underlying observed patterns of spatial heterogeneity in the coral to macroalgae transition. ***We hypothesize that compared to the fore reef, rates of herbivory in the lagoon are often closer to the tipping point where control of macroalgae by herbivores is lost***. ***We further hypothesize that where the local system lies in relation to the coral to macroalgae tipping point will vary among lagoon reefs, reflecting spatial variation in the herbivore community and the potential for population growth by macroalgae***. In addition to the cause(s) of the transition of some lagoon reefs to macroalgae, we also are interested in the reversibility of these shifts. Some have hypothesized that transitions from coral to macroalgae represent alternative community states, each governed by their own sets of processes and feedbacks (Mumby et al. 2013). When self-reinforcing feedbacks are sufficiently strong, systems can exhibit hysteresis, whereby a larger change in a parameter is required to restore a system to its original state than was needed to initiate the shift to the alternate state (i.e., the relationship between state variables and environmental drivers is not the same before and after the shift) (e.g., Bestelmeyer et al. 2011). Field experiments can provide compelling evidence for hysteresis and self-reinforcing alternative community states. This requires testing whether the threshold parameter value for a shift in one direction differs from the threshold value for the shift back (Petraitis & Dudgeon 2004, Petraitis et al. 2009, Dudgeon et al. 2010, Mumby et al. 2013). The region of hysteresis in our MCR II experiments was narrow and far below ambient herbivory on the fore reef, whereas it was broader and closer to ambient herbivory for a lagoon reef (Fig. 9). We will identify processes that create variation in the existence, size and relative position of hysteresis in the herbivory-macroalgae relationship. ***We will test the hypothesis that the nature of the nutrient regime and herbivore assemblage greatly influence the reversibility of the macroalgae state.***

Approach We will take two experimental approaches. *First*, we will use our herbivore exclusion technique to estimate spatial variation in the time for macroalgae to colonize suitable substrate in the

(near) absence of herbivory. We will employ the same design that we used previously on the fore reef (Holbrook et al. in review): tiles cut from coral skeletons will be affixed to the bottom in a plastic-coated wire cage (2.5 cm mesh), which excludes virtually all herbivores (Adam et al. 2011). Communities developing in exclosures will be quantified monthly for a year. Response variables are the time interval between deployment and first appearance of juvenile macroalgae and the accumulation rate of macroalgae. There will be two comparisons. To compare macroalgal colonization between the fore reef and lagoon, Macroalgae Colonization Arrays (MCA) will be deployed at each of the 6 MCR sites (Fig. 1). To examine within-lagoon variation in macroalgae colonization rates, we will deploy arrays at 10 to 12 lagoon sites chosen based on our spatial mapping (Campaign 2). Arrays will be distributed across the range of nutrient enrichment and herbivory levels measured in Campaign 2.

Second, at each of the lagoon locations where Macroalgae Colonization Arrays will be deployed, we will conduct a two-year-long Macroalgae Tipping Point Experiment to explore patterns of spatial variation in how close ambient herbivory is in relation to the threshold where macroalgae escape herbivore control. We will use the same design as we used previously (Fig. 9) to create a gradient in herbivory. In addition, to explore whether the existence and magnitude of hysteresis in the herbivore-macroalgae relationship vary spatially as a function of the local nutrient regime and herbivore assemblage we will include two sets of treatments. The first set of treatments will consist of seasoned tiles representative of the benthic community following a major disturbance (i.e., turf algae), while the second set will consist of the same tiles with an initial community of mature stages of *Turbinaria ornata*, as this is the most prominent macroalga in the lagoon. To estimate herbivory across the herbivore reduction treatments, we will video each treatment. This experiment will yield site-specific estimates of the tipping point in the herbivory-macroalgae relationship as well as the existence and magnitude of hysteresis (Fig. 9). To the extent that these aspects vary among the reefs examined, we will explore how that variation maps onto our estimates of local variation in nutrient availability, macroalgae colonization and growth rates, and characteristics of the herbivore assemblage.

Question 3.2 *Is the* Turbinaria*-dominated state self-reinforcing?*

Rationale While our proposed multi-year but small-scale Macroalgae Tipping Point Experiments can yield insight into the existence and magnitude of hysteresis, additional evidence is needed to evaluate whether alternative community states arise and are maintained by new sets of stabilizing feedbacks. Four general conditions need to be met in experiments that evaluate the existence of persistent alternative states (Petraitis & Dudgeon 2004, Petraits 2013; also see Peterson 1984, Schröder et al. 2005). First, the spatial scale of the experimental treatment must match the patch scale of a community state. Second, the event that triggers a switch in state cannot be a chronic change in the value of an underlying driver that also maintains the community in its new configuration. Third, the time scale of the experiment must be long enough to evaluate whether the alternative community is self-sustaining. Finally, repeated experiments at the very same locations can distinguish between highly localized (and difficult to detect) site-specific effects and alternative states. ***We will test the hypothesis that lagoon reefs of Moorea dominated by the macroalga*** *Turbinaria ornata* ***reflect a self-sustaining alternative community state.***

Approach Our long term patch-scale experiment will follow the criteria for testing for the existence of alternative communities that are self-sustaining (Petraitis & Dugeon 2004, Petraitis 2013). We will conduct Alternative Community State Experiments in 3 lagoon locations that have a large number of co-occurring bommies (dead massive *Porites*) interspersed on sand, where adjacent bommies either support a dense stand of *Turbinaria* or a community consisting of a mixture of cropped turf algae and some coral. We developed the necessary protocols and methods and initiated this experiment at one location in August 2015. At each of the 3 locations, 60 bommies will be selected to design 15 replicate blocks of 4 treatments: (1) bommies that support the turf-coral (no-macroalgae) community that will remain unmanipulated, (2) bommies dominated by *Turbinaria* that also will remain unmanipulated, (3) *Turbinaria* dominated bommies where all macroalgae are removed as a 'pulse' event, and (4) the same as (3) but with an herbivore exclusion cage over a portion of the bommie. Treatment (4) will help guide

interpretation of results (e.g., if macroalgae failed to return to that bommie, was that due to lack of colonizing embryos or because young life stages were subsequently removed by herbivores?). If both macroalgae and turf-coral (no-macroalgae) communities can persist at a given location, the expectation is that some of the bommies where *Turbinaria* is removed will return to a macroalgae state but that other replicates will transition to and remain in a non-macroalgae state (initially dominated by turf algae with subsequent colonization by corals). Once experiments are set up, they will run through MCR III.

C. Research Theme 2: Structure and Function of Reefs in the Future

MCR III Research Theme 2 addresses a multi-decadal time scale, and seeks insight into how forecasted changes in GCC- and OA-related conditions will affect the ***structure and function*** of benthic communities. We will evaluate changes in reef communities that will occur during MCR III (2016-2022), and towards the 100-year horizon of IPCC projections (IPCC 2014). Figure 20 represents the conceptual framework for Research Theme 2 and interrelationships of the campaigns, and Table 2 summarizes the research activities and sources of data for the Theme 2 campaign questions.

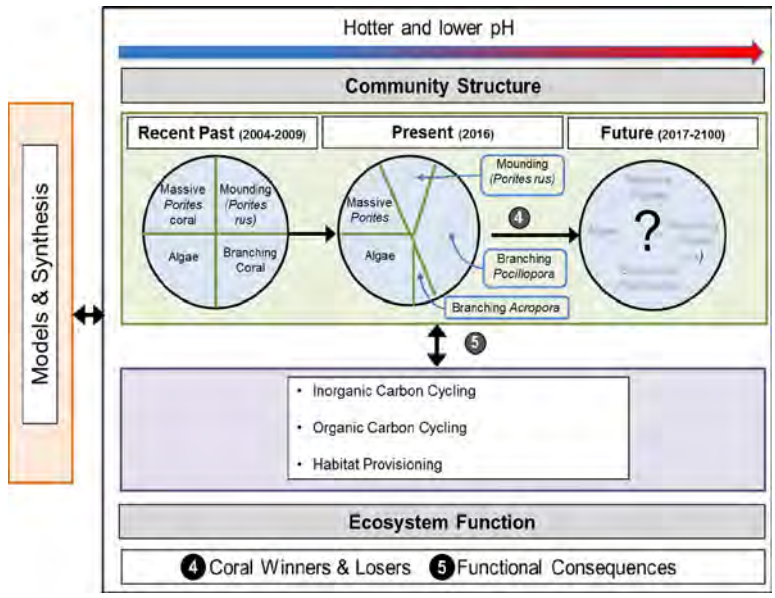


Figure 20. Conceptual diagram describing research under Theme 2 (Reefs of the Future). Among the most severe perturbations to coral reefs in the future are likely to be those caused by increasing seawater temperatures (GCC) and ocean acidification (OA). Understanding of the recent past and present community structure through the MCR time series will be a key part of projecting structure (Campaign 4) and function (Campaign 5).

Campaign 4 – Evaluating which Corals will be Ecological Dominants on Future Reefs ❹

Question 4.1 *What determines the ecological success of select coral taxa under contemporary and future conditions?*

Rationale With 12 years of time series data, we are poised to deepen our understanding of which coral taxa function as ecological winners and losers, and under what conditions this ranking will change. Recent discoveries in Moorea (Bramanti & Edmunds 2016) have shown that winning is contextualized by time and conditions under which it is defined, and today's winner can become tomorrow's loser (van Woesik et al. 2011). Winners and losers based on changes in abundance do not necessarily reveal the particular traits (e.g., organismic growth rates versus sensitivity to bleaching) that confer success, nor enhance the ability

Table 2. Theme 2 Research Tasks & Data Sources	Campaign Questions				
	Q 4.1	Q 4.2	Q 4.3	Q 5.1	Q 5.2
Time Series Focus 1 – Community Dynamics	✓		✓	✓	✓
Time Series Focus 2 – Ecosystem Functioning				✓	✓
Time Series Focus 3 – Abiotic Drivers	✓	✓		✓	✓
Coral Recruitment Plots	✓		✓		
Coral Demographic Study	✓	✓	✓	✓	
Reef Metabolism & Calcification Studies				✓	✓
Mesocosm Experiments			✓		✓
Dynamic Energy Budget Modeling				✓	✓
Population Trajectory Modeling (Matrix & IPMs)		✓	✓	✓	
Reef Metabolism Modeling				✓	✓
Reef Biogeochemistry Modeling				✓	✓

to project coral performance under future conditions. These outcomes can better be achieved through demographic approaches in which coral performance (the key trait of interest) is captured using intrinsic rates of population growth (λ), as measured through demographic models (Edmunds et al. 2014a). Our research has identified Integral Projection Models (IPMs; Easterling et al. 2000, Ellner & Rees 2006) as a powerful tool, and in MCR III this tool will be exploited in hypothesis driven frameworks to better understand the causes of change in coral communities. Our evaluation of which corals are winning or losing will be enabled using data from our time series. We will describe the trajectories of changing abundance over time by taxon and explore the role of physical environmental conditions (from the MCR time series) in driving changes in coral cover. We will address two questions: (1) ***what is the relative role of pulse (e.g., bleaching, COTS, and cyclones) versus press (e.g., nutrient loading, altered wave forcing, gradually rising seawater temperature and declining pH) disturbances in driving coral community dynamics on a decadal scale***, and (2) ***what combinations of environmental conditions promote changes in the ranking of taxa by performance (i.e., winners versus losers), as determined from trajectories of changing abundance***? We will address these questions using tests of association based on MCR time series data, and while we are cognizant of the limitations of establishing cause-and-effect relationships from associations, the results of the analyses will increase the capacity to predict how changing environmental conditions will affect benthic community structure. Critically, they will also improve the capacity for early identification of taxa with the capacity to function as winners (or losers), and to better understand the conditions under which such categorization is justified.

Approach Analyses will be conducted using: (1) benthic community structure determined from annual MCR photoquadrats, and (2) a combination of physical conditions (temperature, pH, light intensity, flow speed, wave height, etc.) and biological features focused on fish communities that are recorded in our time series and which we have shown to have strong effects on coral communities (Burkepile & Hay 2008, Holbrook et al. 2008, 2011, Adam et al. 2014). The photoquadrats are analyzed to provide percentage cover by genus, year, and site; the physical conditions and fish community structure will be summarized using descriptive statistics by year. To answer Question 1, biological and physical data will be converted to resemblance matrices based on Bray-Curtis dissimilarities or Euclidian distances (respectively for biological and physical data), and associations between the two tested with Mantel-style tests in a permutation framework using the BEST routine in Primer E software. To answer Question 2, biological data (% cover of coral taxa) will be expressed as the change between consecutive years, with increases identifying short-term winners, and decreases identifying short-term losers. Resemblance matrices and Mantel-style tests (as described above) will be used to test for associations between these changes and physical/fish conditions. Together, the results of these analyses will sharpen our ability to project how reefs will change in the future (over decades) based on the best available projections for changing environmental conditions (IPCC 2014).

Question 4.2 *What is the temporal stability of winners and losers among coral fauna, and how are these categories affected by physical environmental conditions?*

Rationale A central issue in coral reef ecology is the extent to which corals can endure the current environmental challenges (Hoegh-Guldberg et al. 2007), which is a notion polarized as 'winners versus losers' (Loya et al. 2001); such categorization is time sensitive (van Woesik et al. 2011). Therefore, evaluating the coral community structure of the reefs of the future will require understanding of the temporal stability of a winning functional categorization, as well as the environmental conditions favoring this status and its transition to a losing categorization. Critically, winning (and losing) must be defined rigorously, and for this purpose, these concepts are best defined by demographic principles (Hughes & Tanner 2000, Edmunds et al. 2014a). Here we will define coral performance by the intrinsic rate of population growth (λ) (e.g., Edmunds et al. 2014a) and answer three questions: ***(1) does λ differ among taxa, (2) does λ vary over time (to explore time-sensitive reversals of success rankings), and (3) which physical conditions are most strongly associated with λ?***

Approach We will focus on the corals *Pocillopora verrucosa*, *Acropora hyacinthus,* and massive *Porites*, that are common on the fore reef and tractable to demographic analyses. We will evaluate the growth and survivorship of individual colonies over time using a tagging procedure that has been used in MCR II. The fates of individual colonies will be used to prepare IPM models, with fitness kernels prepared using fecundity values from the literature. These models will be used to calculate the rate of population growth (λ), with a permutational framework used to prepare confidence intervals for and to compare λ among taxa and over time (i.e., the 6 y duration of MCRIII) (Questions 1 and 2). Mantel procedures in PRIMER software (BEST routine) will be used to explore the role of physical conditions in driving changes in λ.

Question 4.3 *Under what conditions are coral populations more strongly structured by adult performance versus recruitment and post-settlement success?*

Rationale The MCR time series has identified spatial structuring of coral communities in all sampled habitats, and elucidating the mechanisms driving this variation is a key objective of MCR III. Here we will address these effects by evaluating the roles of recruitment (a product of connectivity within Moorea and among islands) versus the performance of adult colonies (e.g., through the potential for thermally-mediated variation in growth rates, bleaching, and fecundity among years) in determining population growth. Our research already has demonstrated the strong role of coral recruitment in determining early trajectories of change (Bramanti & Edmunds 2016, see also Question 1.2), but following recruitment, community structure is determined by post-settlement success and the performance of adult colonies. We will bring these two themes together through IPMs for two model species that will allow explicit consideration of the role of recruitment versus the 'physiological' response to environmental conditions in determining community structure on an ecological time scale (i.e., decadal). During MCR II we tested the effects of temperature and pH on the physiology of *P. verrucosa* (e.g., Comeau et al. 2014b; see Related Research) and currently are preparing an IPM using data from the MCR time series. In MCR III, these approaches will be extended to *A. hyacinthus*. These two species are common in Moorea, and represent genera with critical functional roles throughout the Indo-Pacific.

Approach Using *P. verrucosa* and *A. hyacinthus* we will: (1) use mesocosm experiments to parameterize IPM kernels under factorial combinations of temperature and pCO_2 in which growth is used as a dependent variable, and (2) use population surveys on the reefs (using both tagging of individual colonies and tracking of colonies in MCR photoquadrats) to develop the demographic component of IPMs. We are developing techniques (with S. Burgess, FSU) to exploit the Metabolic Theory of Ecology (Brown et al. 2004) into IPM kernels that capture the effects of temperature and pCO_2 on coral growth. These two components will be combined into IPM models for each species that will be used to test for the relative importance for population growth of recruitment versus physiological response to environmental conditions using a permutational framework.

Campaign 5 – Forecasting Ecosystem Functions of Future Reefs 5

Two key aspects of reef ecosystem function that will be addressed during MCR III include community metabolic rates on the fore reef and how this relates to community state following disturbance, and the response of fore reef and back reef communities to changes in major environmental conditions (climate change, OA, sea level rise).

Question 5.1 *How does altered community composition affect key ecosystem function?*

Rationale Our time series of reef metabolism at sites LTER 1 and LTER 2 on the north shore illustrates the temporal dynamics of primary production, respiration, and calcification. Over months to a few years the majority of the variation in metabolism is the result of variation in environmental drivers (light, water flow). However, over longer periods, community structure changes as a function of disturbance and recovery, which adds to the variation in community metabolism. To disentangle the effects of variation in

environmental drivers from the effects of changing community, we need to establish quantitative relationships between environmental forcing and rates of primary production, respiration, and calcification for a range of community types.

Approach We will continue our time series measurements of reef metabolism and calcification as a function of environmental drivers (light, water flow) on the same transects over time (LTER 1 and LTER 2 back reefs). Additionally, we will measure reef metabolism at additional transects around the island that have varying benthic community structure. We initiated these added measurements in MCR II (Fig. 21) and will continue them every 3 years (2018, 2021 in MCR III) as checks on our statistical models.

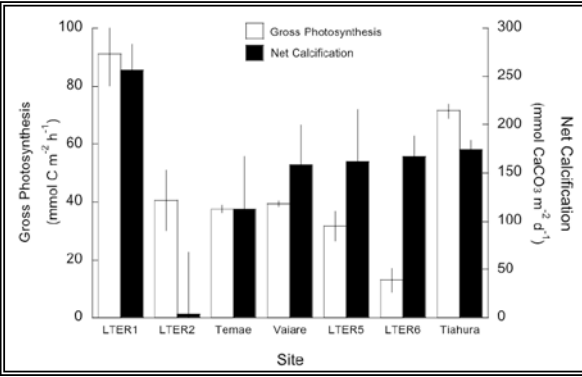


Figure 21. Mean (±SE, n=3-6) rates of gross photosynthesis (*white bars*) and net calcification (*black bars*) across 500 m back reef transects on the north shore (LTER1, LTER2, Tiahura), SE shore (Temae, Vaiare), and SW shore (LTER5, LTER6) during Jan.-Feb. 2015. Spatial variability in metabolism was associated with variation in environmental drivers (light, water flow) and varying benthic community structure.

Question 5.2 *What are current rates of reef metabolism and calcification on the fore reef and how might they change in the future?*

Rationale Fore reefs are responsible for the majority of reef vertical accretion and tend to be dominated by calcifying taxa with the highest rates of calcification. At the same time, fore reef communities are the most vulnerable to disturbances by cyclones and COTS outbreaks. While much is known about the dynamics of fore reef benthic community structure, there are few data on rates of metabolism for fore reef communities. Variation in the main environmental drivers of light and water flow over depth gradients undoubtedly plays a large role in determining rates of metabolism. Furthermore, the function of fore reefs will be related to benthic community structure, which is influenced by both depth and the intensity and frequency of disturbance. It is predicted that fore reef habitats in the future will have altered relative abundances of taxa as well as decreased overall cover due to climate change, ocean acidification, and other press and pulse disturbances and it is likely that this will alter rates of fore reef metabolism. The current state of fore reefs in Moorea provides the opportunity to: (1) quantify rates of metabolism as a function of depth, and (2) to measure rates of metabolism as a function of community structure, as the fore reef recovers from recent disturbance. This will provide insight into the function of future fore reef communities.

Approach We will conduct a research campaign to quantify metabolism of the fore reef at different depths using the gradient flux (GF) technique (McGillis et al. 2011). This non-enclosure method quantifies the vertical concentration gradient (in O_2) above the benthos resulting from reef metabolism and together with measurements of turbulent diffusivity this gives an integrated estimate of upstream metabolism with a foot print between 3 and 40 m^2 (for common fore reef flow conditions). This method (already tested successfully by us in Hawaii in 2015) allows measurements of metabolism on spatial scales that are useful for quantifying gradients (e.g., depth) and for communities of known composition. *First*, we will make GF measurements of metabolism over depth gradients on the fore reef at our north shore sites (LTER 1 and LTER 2). These will be the first measurements (to our knowledge) of fore reef metabolism for any Pacific coral reef. *Second*, we will make similar measurements at fore reef locations around Moorea to quantify variation in reef function as it relates to hydrodynamic exposure and variation in benthic community structure. *Third*, we will conduct flume experiments (Comeau et al. 2014a, 2015a, b) to establish relationships between primary production (PP) and calcification (G) for fore reef communities that vary in species composition. These relationships will allow us to estimate G for fore

reef communities from direct measurements of PP. As instrument development advances, we will be able to measure G directly using total alkalinity sensors that are in development but close to being released on the market (Sunburst Sensors). These measurements will quantify how fore reefs function currently and will allow predictions, based on space for time substitution, about how fore reefs in the future may function. While these predictions will be based on changes in calcifier relative abundance and total cover, incorporating data on how climate change and OA affect rates of metabolism (both separately and synergistically) into models of future performance (Edmunds et al. 2016b) could give robust estimates of functional attributes of coral reefs in the future.

D. Modeling, Integration and Synthesis

Our time series and process studies are synthesized and modeled to gain novel insight into the responses of coral reefs of Moorea to changing environmental conditions, to search for ecological generality, and to advance ecological theory. An additional goal is to federate our physical and ecological models to enable scenario modeling to forecast changes in the ecosystem under different assumptions of environmental change and human activities.

A major effort in MCR III will be to further develop our high resolution regional 3-D ***ocean circulation/wave models*** needed to address long term ecological questions. Our model uses ROMS for circulation (Warner et al. 2008, Haidvogel et al. 2008), which is coupled to the wave model SWAN (Booij et al. 1999). Using high resolution bathymetry from our 2014 UNOLS multi-beam measurements and 2015 airborne LiDAR survey we have constructed a nested model that spans Tahiti, Moorea, and Tetiaroa. Model resolution is 500 m in the outer grid, 50 m around Moorea, and 20 m at the reef scale. The wave model uses boundary conditions from the global model WaveWatch III to capture remote forcing that drives much of the circulation on Moorea (Fig. 22). Local wind forcing is from a non-hydrostatic WRF meteorological model (from our Tahitian collaborator M. Hopuare, Univ. French Polynesia) that accounts for orographic effects around the steep mountain topography of the islands. We use MCR time series data (Focus 3) to calibrate and verify model predictions around Moorea and across the full range of forcing conditions (Figs. 11, 12, 22). The high resolution circulation/wave modeling framework will permit us to resolve spatial and temporal patterns in physical forcing and their role in driving ecological variability on the reefs.

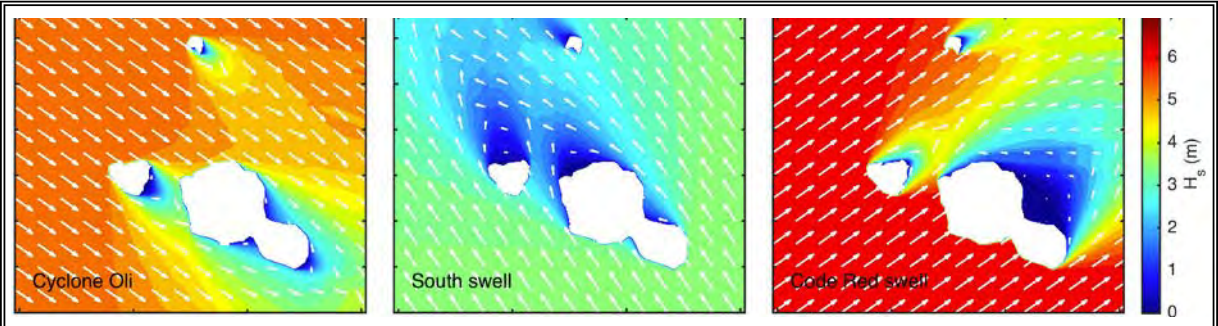


Figure 22. Computed wave fields for extreme events from our Society Island wave model (see Fig. 11). Colors are significant wave heights (Hs) in meters and arrows indicate direct of the swell.

We also will extend our statistical models of ***extreme event return times*** (Fig. 23). Physical forcing events that are rare but large in magnitude or duration (e.g., cyclones, extreme waves, thermal extremes) can have large ecological effects (Woodley et al. 1981, Connell et al. 1997, Madin 2005, Adam et al. 2011). Understanding extreme events therefore is critical to interpreting ecosystem resilience, recovery, and possible shifts to alternate community states. There is evidence for more frequent storm events under GCC (Ruggiero et al. 2010, Young et al. 2011) although some studies indicate decreases in some regions (e.g., Dowdy et al. 2014). Statistical and dynamical climate models suggest that under projected GCC scenarios, there will be a globally averaged decrease in the frequency of tropical cyclones, but a shift toward stronger storms with variability between ocean basins (Knutson et al. 2010). Using long term 3-D

circulation/wave model simulations and MCR time series data we are extending our application of statistical models of extreme events to predict recurrence intervals for large disturbance events.

We also plan to use the models above to explore effects of ***sea level rise***. We expect increased mean water level to permit increased wave energy to propagate across the back reef, with multiple ecological consequences including increasing larval and biogeochemical fluxes, reduced residence times (Monsen et al. 2002, Lowe et al. 2009, Safak et al. 2015), altered heat fluxes (Herdman et al. 2015), and increased dispersion, drag forces, and inertial forces on reef organisms (Rosman & Hench 2011, Hench & Rosman 2013). Model runs will be used to understand the magnitude and spatial distribution of these altered conditions, and how they may translate to long term changes in ecosystem structure and function.

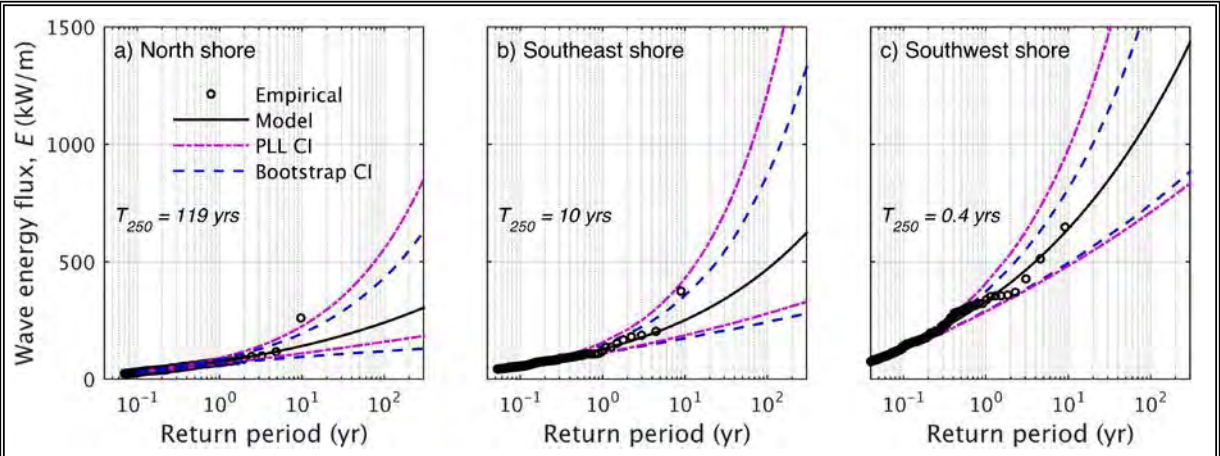


Figure 23. Output of return periods from extreme value statistical models for the extreme wave events measured to date in MCR time series on each of the three shores of Moorea (see Figs. 11, 22). Wave energy flux as great as that generated by Cyclone Oli (Fig. 11) is calculated to impinge once every 119 years on the north shore (*left*), every 10 years on the southeast shore (*middle*), and every *5 months* on the southwest shore (*right*). The 'Code Red' Swell of August 2011 (Fig. 11) was calculated to have a return time to the southwest shore of ~10 years. These models will be extended in MCR III to forecast the frequency and periodicity of physical disturbance events on each shore.

Topographical complexity on coral reefs varies at a wide range of spatial scales and affects many reef processes. Quantifying the structure of coral reefs (see Related Research) is therefore important for understanding a wide range of physical, chemical, and biological processes. Using our newly acquired high resolution airborne LiDAR bathymetry we will compute multiple roughness metrics (Wilson et al. 2007) and relate those to patterns in our time series and process-based studies (e.g., Kuffner et al. 2007).

We will continue to use existing data and ongoing data collection to construct and refine statistical ***models of reef metabolism*** by relating reef primary production, respiration, and calcification to the primary physical drivers (light and water flow). We have 11 years of measurements at two back reef locations (LTER 1 and LTER 2) made during summer and winter (44 datasets). Using a subset of those data, we have constructed a multiple regression model that can explain ~90% of the variation in primary production as a function of light and flow. We will continue to evaluate and refine that model with additional data to achieve the highest explanatory capacity. To date, we have modeled *temporal variability* in metabolism across reef sections that have not changed dramatically in community structure. Our goal is to model *spatial variation* across reef sections that vary in community structure to generate PP-G relationships for different community types; these relationships will serve as inputs into larger scale models of biogeochemistry (see below). We will drive this statistical model with data on offshore wave height and period (to estimate water flux across the back reef) and PAR (measured on the back reef), both collected continuously, to calculate estimated hourly primary production continuously on the back reef. These estimates will be ground-truthed by additional reef metabolism measurements.

On a larger scale, we propose to build a spatially-explicit ***dynamic model of coral reef biogeochemistry*** (BGC) starting with a ~6 km stretch of lagoon on the north shore of Moorea (between

Cook's and Opunohu Bays). The approach will couple our emerging 3-D lagoon circulation models (see above), spatially-explicit habitat classifications, and statistical models of reef metabolism to forecast reef function at kilometer scales. We will use this to explore reef metabolic responses to future scenarios of seawater temperature, lower pH, and higher sea level (i.e., altered circulation). Initial inputs to the model will be benthic community structure (<1 m scale from satellite imagery), *in situ* PAR (measured), wave energy flux (from our circulation models), and rates of metabolism (PP, R, and G) for given community types. A second, complementary effort will be to compare predictions of our statistical modeling approach with models being developed in collaboration with the Moorea IDEA project (including N. Gruber at ETH Zurich). One Moorea IDEA approach involves coupling physiologically-based photosynthesis-calcification-respiration models of coral reef organisms (e.g., Nakamura et al. 2013) with our 3-D ocean circulation models following Carbonate System Dynamics (CSD) models using existing (e.g., Watanabe et al. 2013) and developing constructs (e.g., N. Gruber) for coral reefs. The goal is to calculate (and test) spatio-temporal dynamics in key parameters (DIC, DO, Total Alkalinity, pH, aragonite saturation state, calcification rate). Our partnership with ETH Zurich (M. Troyer) also will extend to high resolution visualization of our simulations of future reef BGC to gain a better fundamental understanding of how functionality of Moorea reefs will respond to future conditions.

To date, MCR's ***ecological modeling*** efforts have proceeded along two complementary tracks relating to effects of environmental change on *individual* organisms (primarily corals), and on coral reef *communities*. In MCR II we used *Dynamic Energy Budget (DEB) models of corals* (Muller et al. 2009, Edmunds et al. 2011) to predict the effects of multiple stressors (e.g., OA, nutrient loading) on growth, calcification rate, and survival of individuals (Eynaud et al. 2011, Jacobson et al. 2016) (see Related Research), and we are incorporating increasing levels of realism into relatively simple *community state shift models* of the interactions between corals and macroalgae to explore the factors leading to coral/macroalgae phase shifts and other community changes (Fig. 24) (Briggs et al. in review). In MCR III, work on both tracks will continue. The DEB modeling of corals will emphasize effects of anthropogenic stressors on the coral symbiont community and on the coral microbiome. At the community level, the two modeling approaches will come together, as we will use DEB-based models to guide the development of spatially-explicit community models.

The next phase of DEB modeling aims to provide testable, mechanistic, representations of the effects of environmental drivers on reef-building coral species. First, a core of generic DEB models will be extended with modules that allow prediction of changes in flows of energy, carbon, and nitrogen in response to changes in the symbiont community. Further modules will include effects on the microbiome (Question 2.4). DEB theory is the ideal framework for modeling DOC production, its effects on growth and reproduction of bacteria, and the interaction of these processes with nutrient dynamics.

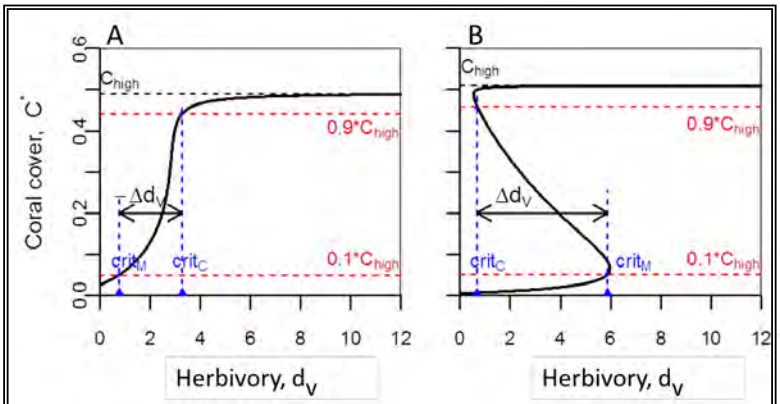


Figure 24. Our models of herbivory – macroalgae – coral interactions reveal that stage structure in the vulnerability of macroalgae to herbivores can promote hysteresis. Panel A is a bifurcation diagram showing an abrupt transition in the relationship between herbivory (d_V) and community state (as measured by coral cover at equilibrium C*) in a model where macroalgae remain vulnerable to herbivores throughout their life; adding an invulnerable life stage can create hysteresis (Panel B). Δd_V is a metric of the existence and magnitude of hysteresis that is of use in exploring processes that promote self-replacing coral or macroalgae states. Δd_V is ($crit_M - crit_C$) where d_V is the level of herbivory, $crit_C$ the lowest value of d_V for which the equilibrium coral cover is ≥ 90% of the maximum possible (C_{high}), and $crit_M$ is the highest value d_V for which the equilibrium coral cover is < 10% of its maximum. Alternative states only exist when $\Delta d_V > 0$ (as in B).

In the community level models that we have developed to date, the effects of OA or other stressors can be investigated only by making assumptions about how specific parameters (e.g., coral growth) might be altered. DEB theory provides an opportunity to build these models in a more mechanistic way, based on the impacts of the various stressors on the physiology of the organism, and seamlessly incorporating the constraints and feedbacks in the system. We will model community interactions at two spatial scales. *First*, on the relatively small scales used in many of our field experiments (sub-meter scale), we will use DEB models representing coral symbioses and macroalgae to specify the bioenergetics and viability of 'individuals' in an *individual-based model (IBM) of interacting species* (the DEB-IBM approach of Martin et al. 2012). *Second*, we will use these small-scale spatial models to guide the development of *large-scale, spatially-explicit population- and community-level models*. Our large-scale spatial model will be well suited for asking questions about how the scale of dispersal and recruitment of corals, algae, and herbivores influences the potential for multiple attractors in coral-macroalgae phase shifts. By explicitly incorporating a spatial component into our detailed model of Moorea, we will be able to ask questions about how perturbations that operate over different spatial scales or differentially impact different parts of the system (e.g., contrasting the shallow fore reef versus the lagoon) affect the system as a whole.

Together our MCR III empirical and modeling efforts will advance predictive understanding of spatial heterogeneity in community dynamics, ecosystem processes and ecological resilience. Further synthesis will be achieved by our involvement in the Moorea IDEA (Island Digital Ecosystem Avatar) project, which the MCR has been central in developing with partner institutions (UC Berkeley, ETH Zurich, Oxford University, CRIOBE/University of Perpignan) to enable visualization and scenario modeling (Cressey 2015, Davies et al. 2016). The goal of the Moorea IDEA project is to develop a federated set of coupled physical, biological and social models as a digital representation ('avatar') of Moorea's ecosystems to facilitate sophisticated scenario modeling. Thus the physical and ecological data and models we are developing in MCR III to capture and predict dynamics of the reef community and key ecosystem rate processes at multiple spatial and temporal scales will be coupled with computational infrastructure for visualization. MCR's acquisition of high resolution shoreline to deep ocean bathymetry already has been merged with terrestrial satellite imagery of Moorea to produce a 3-D digital representation of Moorea and surrounding waters, and the (scalable and transferable) computational machinery needed for visualization and scenario modeling is being developed by our collaborators at ETH Zurich. The MCR is leading the domain science application regarding the ecosystem and community effects of disturbances and GCC/OA-related drivers (e.g., altered storm regimes, sea level rise, declining pH, warming waters) on the coral reef system. Thus, MCR III science will contribute more broadly to understanding and forecasting dynamics of coupled social-ecological systems.

SECTION 4 – RELATED RESEARCH PROJECTS

MCR investigators have leveraged the MCR to obtain additional funding to conduct mechanistic studies and modeling efforts relevant to MCR III science. Edmunds (OCE 1619893) is addressing the effects of the 2015-16 El-Niño on coral recruitment (Theme 1, Campaign 1). With respect to nutrient sampling, dynamics and effects (Theme 1, Campaign 2), Burkepile has obtained NSF (OCE 1547952) and University of California funds to develop osmo-samplers to acquire better time-averaged temporal and spatial resolution on nutrient dynamics. These sources also are supporting development of nutrient excretion models and, using MCR time series data, assessment of trends in storage and excretion of nutrients by fish and mechanistic studies of how different types of nutrients (fish-derived versus anthropogenic) affect growth and physiology of algae and corals. Project IRON (a collaboration with Univ. Perpignan, CRIOBE, Max Plank Institute for Microbiology, funded by LabEx CORAIL, Burkepile is the main MCR participant) will examine whether iron limitation affects benthic primary production and community composition. An NSF RAPID (OCE 1619697, Holbrook, Burkepile and Schmitt) is enabling baseline mapping of benthic community composition and nutrient availability in the lagoons prior to the

forecasted 2016 coral bleaching event as well as initiation of longer term experiments to explore the effect of the form of nitrogen on susceptibility of coral to bleaching, which will be followed up during MCR III.

Regarding the functional roles of microbes (Theme 1, Campaign 2), Burkepile has received funding from UCSB and in collaboration with Vega Thurber is investigating how nutrient pollution combines with corallivory to change the coral microbiome and lead to coral mortality and explain some of the recent losses of corals from the back reef and fringing reefs. Carlson and Nelson are investigating the organics produced by macroalgae, the microbes that metabolize the organics, and the impacts of these processes on coral health and growth (OCE 1538393, OCE 1538428). They will test mechanisms by which microbially-mediated feedbacks may facilitate the spread of macroalgae and explore how the composition of corals and macroalgae interacts with microbial communities to influence reef ecosystem resilience to macroalgal phase shifts. This will result in a clearer understanding of coral-associated microbiomes as a factor in reef resilience to anthropogenic impacts and global change.

Edmunds and Carpenter (OCE 1415268) explore the effects of Ocean Acidification on calcifying organisms using outdoor flumes, CO_2 treatments administered to fully intact reef ecosystems *in situ*, and replicated common garden cultivation techniques. Key experiments in these thematic areas will be designed to exploit integral projection models (IPMs) to couple organism with community responses, and to support the use of the metabolic theory of ecology (MTE) to address scale-dependence of OA effects on coral reef organisms and the function of the communities they build (Theme 2, Campaign 4).

MCR modeling efforts have been supported by NSF (OCE 1435133) and Duke University grants to Hench to examine how flow interacts with topography in shallow lagoon environments and to develop models of circulation useful for understanding connectivity. Nisbet and Gates work with postdoc Ross Cunning (DBI 1400787) to integrate genomics, bioinformatics, and dynamic energy budget (DEB) theory and modeling techniques to examine the coral-*Symbiodinium* symbiosis.

SECTION 5 - EDUCATION AND OUTREACH

Education MCR education activities include the training of undergraduates, graduate students and postdoctoral fellows. At all levels, students are integrated in MCR research, participate in the annual MCR All-Investigator meeting, the bi-annual MCR-SBC-CCE Graduate Student Symposium, joint SBC-MCR seminar courses at UCSB and activities associated with the MCR Schoolyard program. We also exploit the intellectual and pedagogical merits of partnering our lead institutions (UCSB and CSUN) to create a pipeline for students, expertise, and intellectual engagement between a 4 year, teaching oriented institution, and an R1 research institution. Undergraduates are involved in MCR as REU participants, research assistants on investigator projects and as recipients of mentoring by graduate students, postdocs and investigators. MCR senior scientists present their research findings to undergraduate and graduate students during evening 'Pizza and Science' seminars. Our site fosters international partnerships and collaborations with coral reef research groups and institutions including those in Japan, Taiwan, Thailand, Australia, China, France, the United Kingdom, Switzerland and French Polynesia.

Outreach We have an active program involving local outreach in California, outreach in French Polynesia, and web-based projects to reach the broadest possible audiences. MCR senior personnel, graduate and undergraduate students have been featured in several television and web related videos that highlight MCR site science. MCR students participate in many of our outreach activities.

<u>*Local outreach in California*</u> The REEF (Research Experience & Education Facility) is an interactive marine educational facility at UCSB that provides educational tours for K-12 and community groups and serves over 10,000 visitors annually. REEF programs support California State Science Content Standards and are developed in partnership with the Channel Islands National Marine Sanctuary, Center for Ocean Sciences Education Excellence (COSEE) and Marine Activities, Resources and Education (MARE) at the Lawrence Hall of Science. The REEF provides visitors with a hands-on, inquiry-based experience into marine science and research conducted at UCSB, including the MCR LTER. MCR science is showcased to visitors by MSI staff and UCSB undergraduate interns as well as by MCR senior scientists, graduate

and undergraduate students. In addition to continuing to work with The REEF staff, we will maintain our partnership with Washington Accelerated School (Pasadena Unified School District) to bring all 4th graders (~115 students; 90% economically disadvantaged; 40% English language learners) on a trip to UCSB. Students visit the REEF and participate in interactive presentations and demonstrations led by MCR senior scientists and graduate students.

We work with teachers from our partner schools, including Washington Accelerated, Kellogg Elementary School (Goleta Union School District; 47% Hispanic, 28% classified as English language learners), the Dunn School (a private school in Los Olivos, CA), Calabasas High School (Las Virgenes Unified School District) and Viewpoint School (a private school in Calabasas, CA) to develop science curricula based on MCR research themes. The NSF RET program has been instrumental in developing our partnerships and we will continue to pursue additional RET opportunities. During MCR II, 6 teachers were awarded RETs to work with us in Moorea, including 3 who participated as onboard scientists during our 2014 20-day UNOLS cruise in Moorea. We will expand our collection of inquiry-based curricula. The units are written in collaboration with K-12 teachers (particularly our RET recipients), are aligned with Next Generation Science Standards and then refined using feedback from local teachers. At the high school level, we will continue our Marine Biology Clubs in which students are exposed to LTER research.

A major effort during MCR III will be to work with K-6 teachers in California and Hawaii to develop curricula associated with the recently published MCR children's book *Kupe and the Corals*. In addition, we are working with the LTER Schoolyard Children's Book Series editor and Apple Education Group to upgrade *Kupe and the Corals* to the ePub3 format, which allows for the inclusion of video and audio files, links to data sets, and other features that enrich the interactive experience.

The MCR will continue its community outreach activities at the annual Earth Day education event in Santa Barbara. We continue to develop outreach materials regarding the status of and threats to coral reefs to showcase at our Earth Day booth. The MCR and SBC sites partner to provide activities that demonstrate synthetic concepts related to MCR and SBC site science. Participants walk through simulated examples of coral and temperate reefs and explore these ecosystems with MCR and SBC graduate students acting as guides to convey important concepts drawn from site research. The event draws ~ 30,000 visitors, and > 500 K-12 students participate in our activities each year.

Community Outreach in Moorea We will continue to work with the Atitia Center, the public outreach unit of the Gump Station, and the Association Te Pu 'Atiti'a, to make MCR LTER personnel and education resources available to K-12 students and the public on Moorea. The Marine Biology Research Camp brings classrooms of Tahitian students (ages 10-15) to the Gump Station for three days for hands-on exercises that expose them to research findings that are relevant to local citizens. This provides us with a forum for outreach in Moorea since local regulations preclude our direct involvement in K-12 classrooms. One recent example of this effort has been a field opportunity in coral culturing using in-water 'gardens' that local children are able to tend. This vehicle provides exposure to important techniques utilized in the MCR, and also provides a means to provide instruction in coral restoration and conservation.

Web Presence We will add to our online collection of inquiry-based curricula and to our Online Encyclopedia of Marine Life website. The Encyclopedia now highlights over 125 common reef organisms. Information is displayed as taxonomically organized species identification cards that are linked to websites containing additional biological information. Our online content describing MCR graduate student research continues to grow as new students provide additional photos and 'plain language' descriptions of their research. We propose to add additional videos featuring MCR Investigators.

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FACILITIES, EQUIPMENT AND OTHER RESOURCES

Laboratory
All MCR LTER investigators have laboratory space (typically ~1,000 sq. ft. each), modern instrumentation for a broad range of chemical and biological analyses, computing facilities and a variety of other support services at their home institutions. The UCSB Marine Science Institute (MSI) Analytical Laboratory is a professionally managed, shared-use instrumentation and chemical analysis facility that is well equipped to perform all of the chemical analyses anticipated for this project. Major capabilities of the Analytical Lab include elemental analysis of inorganic and organic substances, stable isotope ratio determination of biological materials, and automated determination of nutrients in natural waters. Major equipment in the MSI Analytical Lab include: two atomic absorption spectrophotometers (AAS) with auto samplers, one instrument equipped for flame atomization, and the other a dedicated furnace system with Zeeman background correction; a microprocessor-controlled gas chromatograph (GC) with various detectors, including flame ionization and photo-ionization; and two automated organic elemental analyzers for CHN analyses, an isotope ratio mass spectrometer interfaced with a CHN sample introduction system, and an automated 5-channel wet-chemical analyzer (FIA) for nutrients. Water samples from the MCR Offshore Station are analyzed by the Oceanic Carbon Dioxide Quality Control Analytical Laboratory operated by A. Dickson at Scripps Institution of Oceanography.

Clinical
Not required for this project.

Animal
Not required for this project.

Computer
Internet connectivity (up to 20 Gb/s) between Moorea and the mainland US occurs over a dedicated fiber optic cable via Hawaii. Internet service is provided to all users of the Gump Station on its wireless network. In addition, the MCR LTER operates two additional secure, internet connections through Mana, the local internet service provider; one connection is dedicated to data transmission and a second is for general internet use by MCR LTER personnel. The MCR LTER maintains 2 desktop and 2 laptop PCs for the exclusive use of MCR LTER personnel while in Moorea. All investigators in this project maintain computing capabilities at their respective institutions commensurate with their specific research activities and most travel to the field with wireless equipped laptop PCs.

Data management for the MCR LTER uses the computing capabilities of the Marine Science Institute (MSI). MSI has a 1000Mb/s connection to the UCSB campus backbone, which provides shared access to a 622Mb/s CALREN-2 connection, which in turn provides access to the Internet. MSI supports the principal research servers. The main data server providing network file sharing (Samba and NFS) and an Apache web server both run on CentOS Linux 5 (64-bit). The primary database server for research use is running CentOS 6 (64-bit) and provides PostgreSQL 9.2, and MySQL 5.1. There is a departmental server available for subversion and git revision control systems as well as a computational server running CentOS Linux 6 (64-bit) with Matlab, R, GSLIB and PERL along with other scientific applications. MSI runs an Enterprise-grade SAN for storage. Currently, MCR is allocated 12 TB (expandable) of storage on that system. The Server room is connected to E-Power, and redundant power is provided by an APC 6000 UPS battery backup. Distributed server backups (via Amanda and BackupPC) are coordinated with MSI. The UCSB Earth Research Institute (ERI) provides computational support for the processing of satellite imagery. It consists of a network of more than 50 UNIX servers, workstations, and clusters. A Linux cluster is used for high performance MATLAB post-processing and analysis of satellite imagery. It has 16 Quad-Core 2 GHz AMD 8350 CPU's, with 16 GB of RAM and 5.5 TB of disk. We also have

access to a 1008 CPU MPI cluster that was funded on a NSF Major Research Infrastructure grant (http://csc.cnsi.ucsb.edu/clusters/knot).

Office

In addition to office space and equipment provided to visiting researchers at the Gump Station, we have a dedicated office that has a telephone/fax machine, photocopier, dry work space, internet connectivity, and a printer. An additional 240 sq. ft. of dedicated office space is available to long term MCR researchers and technical support staff. This space includes a printer, flatbed scanner, two general use computers and internet connectivity. All investigators have adequate office space provided at their home institutions to meet their needs and those of the postdocs and graduate students associated with this project. All offices are equipped with phone line and internet services.

Other

All field work will be conducted at the Richard Gump South Pacific Biological Station (http://moorea.berkeley.edu/) on the island of Moorea in French Polynesia. The Station, which is administered by the University of California Berkeley, has all of the equipment and facilities needed to support extensive marine research including those needed to support SCUBA operations (dive lockers, Bauer 10 MiniVerticus air compressor, scuba tanks). Diving operations, under the auspices of the UC Berkeley Diving Safety Office (AAUS member), are conducted out of small boats within the lagoons and larger vessels for work on the outer reef slope. An NSF Field Station Improvement Grant supported the purchase of a 7.6 m, twin engine (150 HP) boat that has been modified to support offshore research, as well as a 6 m single engine vessel that also is capable of working the outer reef. Boats may be launched from the on-site launch ramp and moored at the Station dock immediately adjacent to the SCUBA facility at the lab. The Station has a running seawater system with sufficient water tables and large outdoor tanks to support our proposed work. With funds from MCR, this facility was previously upgraded to support (1) a tank farm of 15 large (750 liter) outdoor tanks suitable for holding fish and large invertebrates, and (2) an indoor wet lab designed to meet the needs of our seawater flumes, mesocosm, and indoor seawater table needs. Additional research space includes a wet laboratory supplied with flowing seawater, a dry laboratory and air conditioned office space. A multi-use laboratory containing a large teaching lab (~25 students), smaller research labs, a molecular lab, library, meeting room, collection and visualization lab, IT center, chemical and storage rooms, and office space was completed in 2008 with support from the Gordon and Betty Moore Foundation. A small fleet of vehicles is available for general transportation. Station housing options include a dormitory building, and seven hillside bungalows that can each accommodate 4 visitors. In addition to facilities, the Station has a permanent on-site staff of 7, which consists of a director, facilities manager, book-keeper/administrative assistant, an outreach coordinator/liaison with the Territorial Government, two maintenance persons, and a housekeeper.

Major Equipment

The MCR LTER owns and operates a fleet of research boats (10 total), including eight skiffs (five 3.9 m with 30 HP engines, three 5.1 m with 40 HP engines), an offshore-capable vessel (6.1 m with 150 HP engine), and a larger vessel capable of deploying oceanographic instruments (8 m Safeboat with 225 HP engine). Additionally, we have a Land Rover 130 pickup truck (extended crew cab) to trailer boats around the island, and have trailers for all boats to facilitate servicing and shore-based deployment. With the opening of the new lab building in 2008, we acquired ≈ 1000 sq. ft. (2 rooms) of dedicated space that has been allocated equally to organismic/ecology research and molecular/physiology research. DSL/wireless internet is available throughout the laboratory building. Our laboratory spaces are equipped with a wide range of microscopes (graduate-grade compound and dissecting microscopes, through to a state-of-the art compound microscope), scintillation counter, water purifier, gel doc system, balances, fluorometer, spectrophotometer, refrigerator, freezer, drying ovens, muffle furnace, stabilized power supplies, tissue disruptor, centrifuge, PCR machine, and autoclave. Also, we have additional dedicated air-conditioned space for the storage of sensitive equipment and to provide clean work space for the

maintenance and programming of oceanographic instrumentation.

MCR LTER oceanographic instruments include 1 profiling CTD (SBE 19+), 1 DO sensor (SBE 43), 75 thermisters (SBE 39), 10 temperature/pressure instruments (SBE 39P), 4 wave-tide gauges (SBE 26+), 12 CTDs (SBE 37), 1 CTD (SBE 16+), 5 ADCPs (RDI Workhorse), 5 ADPs (Nortek), 2 ADVs (Nortek), 1 diving PAM (Waltz), 4 DO sensors, 2 Li-Cor 1400 light meters in UW housings with sensors, 4 SAMI pH instruments (Sunburst Sensors), 4 SeaFET and 1 SeapHOx sensors (Martz lab SIO), and a variety of underwater still and HD video cameras.

With NSF supplemental funding, we constructed an Ocean Acidification mesocosm facility at the Gump Station. The facility currently consists of 12 tanks in which light, temperature and pCO_2 can be controlled precisely. The system uses gas mixing technology (Qubit Systems, Ontario, Canada) to manipulate pCO_2 and create step-less adjustment within a range simulating atmospheric conditions expected under contemporary climate projections. The system is scalable, can support experimental volumes ranging from 2–200 liters and can be used in combination with both tanks and flumes. In 2011, we augmented this system in two significant ways. First, we replaced the metal-halide lamps with state-of-the-art, high intensity LED systems. These provide similar light intensities (to ~1,200 µmol quanta m^{-2} s^{-1}) to the metal halides, but they operate at a fraction of the power and have almost no heating effect. Additionally, they are fully scalable and programmable, offering the potential to simulate sunlight in a sine curve. Second, through separate NSF funding for OA research, we added a 300 liter acclimation tank to stage corals between field collection and experimental treatments. The acclimation tank has independent heating and lighting, and is fitted with a rotating table (4 revolutions d^{-1}) to remove position effects as the corals adjust from field to laboratory conditions. The mesocosm and acclimation systems are matched with a seawater analysis facility (equipped in a manner consistent with the SOP for DIV analysis of Dr. Andrew Dickson, SIO) in which we can evaluate the DIC treatment conditions we create.

The MCR LTER maintains a research-grade weather station (Campbell Scientific) incorporating wind speed and direction, rainfall, solar irradiance, barometric pressure, relative humidity and temperature sensors.

Other Resources

Major equipment available to this project owned by the Gump Station in addition to that described above includes two 5.1 m skiffs with 40 HP engines and two smaller 3.5 m skiffs with 25 HP engines. The lab building provides air conditioned space for group meetings/classes (equipped with AV/computer technology), additional lab space for spill-over projects, and office space for visitors (each hillside bungalow also has air conditioned space for office work). The Station also has a -80°C freezer for storage of samples.

The Gump Station has a facility and personnel for the repair of small boats and outboard engines. More extensive repairs can be made in Papeete on the island of Tahiti (30 minutes away by ferry). The Station has a small machine shop and UCSB maintains a 500 sq. ft. machine shop, containing a table saw, radial arm saw, band saw, drill press and a full complement of small hand and power tools. More extensive fabrication requirements can be handled by commercial operations on Moorea or Tahiti. The Integrative Oceanography Division at SIO maintains an instrument calibration center at the Hydraulics Laboratory with facilities to calibrate temperature sensors and instrument compasses. Equipment necessary to fabricate and maintain buoys and drifters is provided at the Hydraulics Laboratory.

SUPPLEMENT - MCR III DATA MANAGEMENT PLAN

The MCR LTER Information Management System (IMS) serves both site needs and LTER Network goals. Information Management facilitates the archival cataloging of data for long term preservation, and also enables the discovery of data and enhances its suitability for synthesis. The LTER Network's capabilities continue to grow, maintaining the lead in ecological data archiving and synthesis. MCR contributes to these advances and benefits from the broader community's increasing interest in data sharing and citation.

The MCR Information Management System The MCR has chosen cross platform internet standards designed for the LTER Network exchange specification in order to simplify our data presentation and delivery and to increase awareness of LTER data-sharing practices. The MCR IMS meets or exceeds all LTER Network requirements as defined in the most recent (2009) guidelines. We anticipate the IM standards of the LTER Network will continue to evolve in response to emerging technologies and information needs. We have been very active in the planning and development of the LTER Network Information System and we will maintain our leadership role in this area to ensure that the MCR IMS is well positioned to understand and meet the future expectations for LTER IM. To prepare for this we will continue to streamline the MCR IMS and converge on standard practices during MCR III. This will enable us to facilitate and improve data integration with other sites in the LTER Network.

IT Resources and System Features The Marine Science Institute (MSI) provides infrastructure and IT resources (see Facilities, Equipment and Other Resources) including a web server, database server, and file system server with a Storage Area Network (SAN) supporting snapshots. Purposeful redundancy in backup systems provides for disaster recovery with off-site copies stored in a separate building on the UCSB campus, and for file restores from more frequent on-site backups. Features and specifications of the MCR IM system are summarized in Table 1 below. The MCR IMS is co-located with the IM system of the Santa Barbara Coastal LTER project. Their information manager, Margaret O'Brien, has collaborated closely and jointly planned projects since 2004. O'Brien is well acquainted with the MCR IMS. Many IM tools have been developed jointly and are shared by the two sites, which provides planned redundancy to cover absences and affords increased return on investment in training assistants. During 2011, NSF supplemental funds to the two sites were combined to support a shared assistant during the porting and adoption phase of GCE Metabase. In 2013 combined supplement funds supported sharing of a software developer who produced our current system to export EML from Metabase.

Database Design MCR uses the metadata relational database model Metabase, in common with other LTER sites including GCE, CWT, SBC and HBR (in order of adoption). Investment in converting all dataset metadata into relational database storage to generate EML has facilitated more smooth adaptation to new network expectations such as the move toward anonymous data access.

Public Website The website is the most publicly visible part of the IM system. The MCR website (http://mcr.lternet.edu/) meets or exceeds the Guidelines for LTER Web Site Design and Content (version 1.1 2009). We use hierarchical navigation to provide single-click access to the data catalog, publications and research foci. All recommended links and features are implemented. The data catalog is searchable by the five LTER Network Core Research Area, MCR research theme or activity, measurement or derived variable, category and topic or investigator. Core ('Signature') datasets are highlighted. We continually update the website to present fresh content and up-to-date indexes. The website seamlessly integrates both static content and dynamic content from a database. Both scientific and outreach areas of the website continue to receive significant traffic (Fig. 1 below).

Table 1. Key features of the MCR LTER Information Management System.

Type	Feature	Specification
Website, searchable catalogs and directories	http://mcr.lternet.edu Bibliography Personnel directory Data catalog Sampling sites	XHTML, CSS2, PHP, Perl, XSLT, Javascript EndNote & PostgreSQL LDAP EML KML & EML
Datasets in LTER Network Catalog	79 data packages containing 236 data tables & non-tabular data files	EML 2.1.1
Database	MCR_Metabase	GCE Metabase2, PostgreSQL
Servers and user accounts	Web, database, file systems with backup 84 user accounts	LINUX Apache, SAN, EXT4, rsync LDAP
Code Repository	Versioning of code including hydrographic and biological models, database models, website revision control and system documentation	SVN, mediaWiki, GitHub

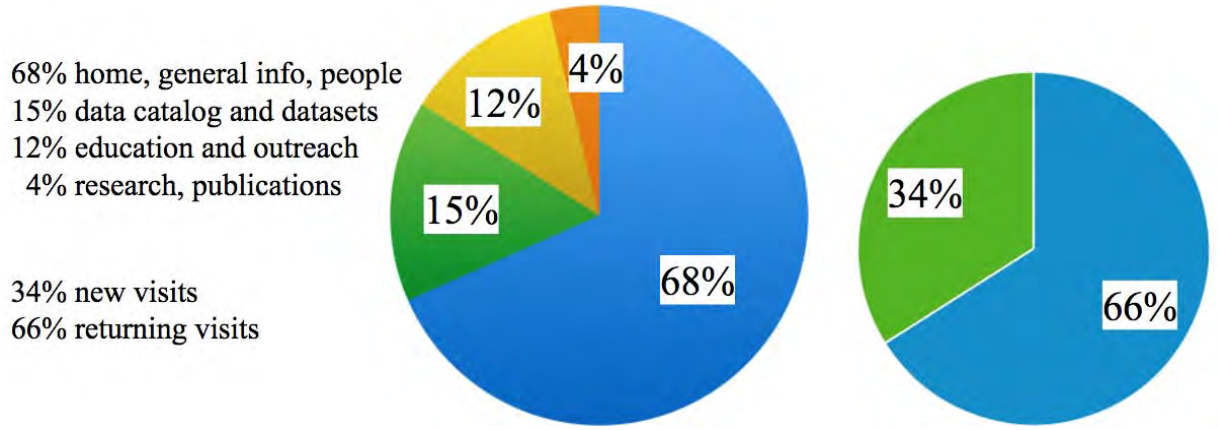

Figure 1. MCR website traffic for the 2015 calendar year.

<u>Data Access Policy and Data Distribution</u> MCR strives to make site data maximally accessible and useful within and beyond the LTER Network for synthesis, education, and other purposes. MCR data use policy and data release policy are consistent with the LTER Network policies and use 'Type I versus Type II' terminology. With few exceptions that conform to LTER data policies, all MCR data are Type I, i.e., publicly available. There is no delay in releasing MCR data to the public once Quality Assurance has been verified. In accordance with LTER policy, graduate student thesis data are archived and cataloged

as Type II, and are not released until thesis publication. MCR collects data use information upon acknowledgement of the data access policy. Data downloads from the local site catalog offer voluntary self-identification while downloads of recent revisions of data from the network catalog are anonymous.

To be fully accessible, data must be discoverable. To this end, our data packages are thoroughly described with appropriate keywords, geo-location, taxonomy and authorship. These metadata fields improve results from faceted searches such as from the DataONE catalog where LTER data are aggregated with other contributors. MCR is aware of the need to contextualize our data in ways that are appropriate for the wider data use community.

Data downloads from the network catalog ceased to be tracked with the switch from the Metacat catalog to the Data Portal commonly known as 'PASTA' (Provenance-Aware Synthesis Tracking Architecture) in spring 2015. Despite this under-reporting, MCR experienced the same surge in data downloads (Table 2) as did the closely aligned SBC LTER site in 2015.

Table 2. Public dataset downloads from the MCR website only.

	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	Total
Academic Research	60	105	331	171	163	268	355	375	568	68	**2464**
Education (College)	0	9	32	47	86	213	227	167	222	16	**1019**
Education (K12)	11	1	4	8	8	17	0	2	14	0	**65**
Government Agency	2	1	0	4	4	1	0	1	2	0	**15**
Non-Profit Organization	0	0	0	0	4	0	0	7	0	0	**11**
other	3	36	9	17	4	22	24	28	40	10	**193**
Total	**76**	**152**	**376**	**247**	**269**	**521**	**606**	**580**	**846**	**94**	**3767**

Metadata All MCR data packages are described in the most recent (August 2011) version of Best Practices for LTER dataset EML. Metadata features include embedded or online links to methods and protocols, full temporal, spatial, and taxonomic coverage, keywords from the MCR vocabulary, the NBII thesaurus, and/or the LTER Controlled Vocabulary, and units registered in the LTER Unit Dictionary. All EML is version 2.1.1. All data tables are 100% free of errors or warnings from the EML Congruency Checker in its current production version in the LTER Network Data Portal. Currently the MCR is the only LTER site free of data congruency warnings. Beyond the required elements, some MCR datasets provide explicit indexing keys and table-joining keys to facilitate cross-dataset synthesis.

Dataset Management (Data Life Cycle) Coral reef data are both expensive to collect and much sought after, which warrants considerable effort to preserve their value through data curation for maximal discoverability, accessibility and fitness for synthesis. Assuring current and long term usefulness of these data require metadata of the highest quality. MCR datasets vary in update frequency, e.g., monthly for weather station data, semi-annually for physical oceanography, and annually for the biotic surveys. Data reach the IM office in different stages of maturity depending on their type. Physical oceanographic data and water column profile data are fully processed including Quality Control (QC) in Matlab before submission to the IMS. A subset of our core time series datasets are further controlled by maintaining these data in a relational database where taxonomy, location and observation metadata are constrained to controlled vocabularies and value bounds. Biotic surveys require reformatting within the IMS prior to uploading to the database. QC is done first automatically within the database, flagging further QC for

human inspection. We continue to refine this process by scripting more of the quality assurance metrics and incorporating feedback from data users. Scripting takes substantial investment of time because each dataset requires knowledge of the expected characteristics and custom definition of the quality control criteria and quality assurance metrics, but the return on investment is high and immediate.

Each new proposed research project at MCR requires a data management plan. Investigators provide an outline of expected data products and the relationships to ongoing projects. The information manager provides advice on naming conventions for sites and taxonomy, guidance for file organization and format, and designates space on the server to back up raw files from the field. The MCR Deputy Program Director, A. Brooks, ensures the information manager is aware of new projects and coordinates with investigators before projects are initiated. Continued participation in core activities is contingent upon timely contribution of collected data to the MCR catalog. The Deputy Program Director is responsible for ensuring all data are added to the catalog in a timely fashion.

IM Staff M. Gastil-Buhl is the Information Manager for MCR. M. O'Brien, Information Manager for SBC LTER, works in close collaboration and is familiar enough with the MCR system to provide reinforcement during absences. C. Gotschalk performs data analysis and quality control for the physical oceanographic and meteorological data. High-level system administration is provided by J. Woods, Computing Resources Manager for MSI. A. Brooks provides oversight and logistical support to the IMS. M. Gastil-Buhl provides graduate and undergraduate training in a variety of areas related to the MCR IMS.

LTER Network Activities Gastil-Buhl contributes regularly to LTER Information Managers Committee (IMC) activities. She has served as co-chair of the LTER Network Information System Advisory Committee (NISAC), and currently serves on the LTER IM Executive Committee. MCR has contributed MCR site content to the LTER Network databases PersonnelDB, BiblioDB, SiteDB and ClimDB and plans to continue submissions once these systems are implemented at the new LTER Network Communication Office (LTER NCO). MCR submits datasets to the LTER Network Data Catalog (PASTA) regularly. Gastil-Buhl has contributed articles and served a term as editor of DataBits, the twice-annual newsletter for advances in LTER information management. She convened a working group at the 2012 All Scientists Meeting on managing seawater carbonate chemistry data.

Other Activities outside of LTER MCR collaborates with other coral reef research groups in informatics as well as cross-site science activities. Gastil-Buhl served as IM for Co-PI P. Edmunds' LTREB project at the Virgin Islands National Park and trained an assistant IM to assume these responsibilities once the LTREB IMS was fully implemented. The MCR website hosts the data from the Virgin Islands LTREB project.

In consultation with the Biological and Chemical Oceanography Data Management Office (BCO-DMO), we cross-link the MCR project within the BCO-DMO data catalog. Non-MCR LTER data collected from Moorea as part of non-LTER projects funded by the Division of Ocean Science (OCE) within NSF will appear alongside MCR LTER data in search results once BCO-DMO successfully federates with DataONE.

Recent Accomplishments Below we list a few key recent accomplishments in MCR II.

2011 GCE_Metabase ported from Microsoft SQL-Server to open source PostgreSQL. **Deliverable**: open source version of an already-proven metadata database.

2012 Previously manual processes for EML document creation were replaced by generation of EML from Metabase. **Deliverable**: EML generation tool has increased efficiency, especially for time series updates.

2012 Once the LTER NIS prototype became available in 2012, MCR submitted all MCR datasets to the PASTA prototype. **Deliverable**: feedback to NIS developers.

2012 Explored incorporation of GCE Data Toolbox as a quality control and data reformatting tool into the MCR IM system. Data Toolbox semi-automates metadata collection for Metabase. However, direct entry of metadata into Metabase required less specialized knowledge and worked for a wider variety of datasets, so this option was not implemented.

2013 All metadata content was migrated to MCR-Metabase. We began building datasets with Metabase in 2011 as part of system development. In 2013 this went into full production using software created with supplement funding. Added benefits included a newer version of EML, 2.1.1, more standardized measurement descriptions, and ability to more rapidly respond to new requirements or policy.

2014 PASTA development, initially due for completion in 2014, was accelerated and went into production in January 2013 at which time all MCR Type I datasets were submitted. Type II data continue to only be available through the local site catalog. **Deliverable**: PASTA-ready datasets.

2015 Current manual synchronization of local site databases for publications and personnel was to be replaced by web service enabled synchronization with the LTER Network databases BiblioDB and PersonnelDB. However, the network side of that system was not implemented. These may become available at the newly formed LTER National Communication Office (LTER NCO). We continue to maintain our local directory and bibliography.

2016 Inclusion of DOI in local data catalog metadata display to facilitate data citation.

Future Directions and Challenges: Proposed Products and Milestones We continue toward our goal of a more cohesive, efficient and user-friendly system, taking advantage of LTER Network resources as they become available. MCR plans to interact closely with the LTER Network Information Management Office (LTER NIMO) should that grant be awarded. In addition, we seek to continually lower technical barriers to enable the broader MCR community to participate in IM tasks. This includes efforts to continue training of IM assistants to increase availability of competent data managers to research groups.

Ongoing An anticipated future LTER requirement to register site measurements with a network-wide standardized dictionary will facilitate data synthesis. The first step, to standardize measurements at the site level with complete descriptions, has already begun at MCR (in conjunction with SBC LTER) within the Metabase metadata database. Completion ultimately depends on contributions from all LTER sites. **Deliverable**: standardized attributes (measurement column definitions).

2016 Migration of website static pages into Drupal, a content management system, to allow less technically-oriented staff to update content. **Deliverable**: mobile device compatibility.

2018 MCR LTER will adopt the Best Practices for quality control and archiving of streaming sensor data as it is developed by the LTER working group SensorNIS. **Deliverable**: improved quality assurance (http://wiki.esipfed.org/index.php/Sensor_Data_Quality). This milestone depends on an improved internet connection with Moorea.

SUPPLEMENT - MCR POSTDOCTORAL MENTORING PLAN

The collaborative and interactive nature of the MCR LTER program will help to hone the specific research skills of the postdoctoral researchers as well as prepare them for professional interactions and job interviews. The training of postdocs will focus on both research and teaching. Regarding research, their training and mentorship will include guidance in designing and executing collaborative and interdisciplinary field and laboratory research programs. Individuals will receive training in field and laboratory techniques as well as data reduction and analysis, web and journal publication and professional presentations. They will also gain experience in supervising and working with technicians, graduate students, and REU students, to set up, maintain, and collect data from experiments in the lab and field. Each postdoc will work in a specific laboratory of an MCR LTER investigator, and will participate fully in all MCR LTER programmatic activities such as the annual MCR All Investigator Meeting, regular working group meetings, and seminars. There will be ample opportunity to present research findings and receive feedback. In addition, postdocs will be encouraged to participate in LTER Network-wide activities, such as the All Scientists Meeting, workshops and working groups, and training programs, as appropriate. Guidance will be provided in preparation of new research proposals. Additional aspects of postdoctoral mentoring include advising about long term employment options and opportunities, facilitation of professional networking, and providing research opportunities such as visiting other labs, trips to scientific meetings and to research sites. Regarding teaching, the postdocs also will be provided opportunities to improve their mentoring skills as they work with graduate and undergraduate students. The MCR LTER has developed a vibrant outreach program with local schools, and we will entrain postdocs into these activities to give exposure to this important aspect of their science career.

Professional development of postdoctoral researchers will be enhanced through a number of structured mentoring activities, and interactions with diverse groups of scholars at UCSB and at the other universities associated with the MCR LTER (California State University Northridge, UC San Diego, UC Santa Cruz, University of Hawaii, Duke University, Georgia Tech, Oregon State University). UCSB provides a rich atmosphere for mentoring postdoctoral scholars. UCSB's Center for Science and Engineering Partnerships (CSEP) and the Society for Postdoctoral Scholars (SoPS) offer an intensive Professional Development for Postdoctoral Scholars (PDPS) program that helps provide the skills, knowledge, and practical experience necessary for postdoctoral researchers to be successful in their chosen career paths. We will encourage postdoctoral researchers on our project to participate in this program, which focuses on (1) teaching and mentoring, (2) communicating science, and (3) networking and interviewing. Each academic quarter PDPS presents a series of 2-hour workshops and intensive sessions on topics such as teaching with technology, interviewing for academic positions, grant writing, scientific collaboration, and work-life balance.

To accommodate the career goals of recruited postdoctoral scholars, an adaptive mentoring strategy will be implemented. Our overall goals will be to strengthen each individual's skills in their respective discipline, the preparation of manuscripts and grants, teaching and outreach. The specific goal of most (but not all) postdoctoral researchers is to work towards a permanent academic position (e.g., a tenure-track faculty position). If this is the case, we will place special emphasis on mentoring each scholar in the skills that will make him/her successful in the academic job market, including the preparation of an effective CV and research/teaching statements, job talks, and interviewing skills. If a scholar is interested in enhancing his/her teaching skills and experience, (s)he will be given the opportunity to present guest lectures, develop and teach modules for classes in ecology or mathematical modeling, and/or help mentor undergraduate and graduate students.

Mentors and scholars will meet weekly to discuss research progress. We will specifically aim for scholars to take the lead role and spearhead specific papers and projects within the grant activities. Postdoctoral researchers also will disseminate results to colleagues at regional, national, and international meetings. This will provide an opportunity to showcase their research, communicate with researchers in the field, and establish future collaborations.

Table 1. MCR LTER data sets currently deposited into the LTER Network Information System (NIS) and their associated LTER Core Research Area(s). *see footnote below for the 5 core areas* Twelve additional, restricted (Type II) data sets, e.g. those associated with graduate student theses, are not listed here. Type II data sets will be added to the NIS upon graduate student publication, or when the NIS fully supports the cataloging of Type II data sets.

Non-Temporal		
Data Set Title	**Package ID**	**Core Area***
Bathymetry Grid for North Shore	knb-lter-mcr.1036	N/A
Fish Taxonomy, Trophic Groups and Morphometry	knb-lter-mcr.6001	2

Ongoing Time Series		
Data Set Title	**Area**	**Core Area***
Benthic Community Dynamics: Island Scale Coral Cover Analysis	knb-lter-mcr.4003	2
Benthic Photosynthetically Active Radiation (PAR)	knb-lter-mcr.4005	1
Benthic Water Temperature	knb-lter-mcr.1035	5
Estimates of Component Primary Production and Respiration	knb-lter-mcr.19	1
Gump Station Meteorological Data	knb-lter-mcr.9	5
Long-term Community Dynamics: Backreef (Lagoon) Corals Annual Survey	knb-lter-mcr.1038	1,2,3,5
Long-Term Coral Population and Community Dynamics: Annual Island Wide Coral Demography Survey 2011 to present	knb-lter-mcr.4009	1,2,3,5
Long-term Population and Community Dynamics: Benthic Algae and Other Community Components	knb-lter-mcr.8	1,2,3,5
Long-term Population and Community Dynamics: Corals	knb-lter-mcr.4	1,2,3,5
Long-term Population and Community Dynamics: Fishes	knb-lter-mcr.6	2,3,5
Long-term Population and Community Dynamics: Other Benthic Invertebrates	knb-lter-mcr.7	2,3,5
Long-term Population Dynamics of *Acanthaster planci*	knb-lter-mcr.1039	2,5
Macroalgal CHN	knb-lter-mcr.20	1,3,4,5
Ocean Currents and Biogeochemistry: Salinity, Temperature and Current at CTD and ADCP Mooring, North Shore	knb-lter-mcr.30	5
Ocean Currents and Biogeochemistry: Salinity, Temperature and Current at CTD and ADCP Mooring, Southeast Shore	knb-lter-mcr.31	5
Ocean Currents and Biogeochemistry: Salinity, Temperature and Current at CTD and ADCP Mooring, Southwest Shore	knb-lter-mcr.32	5
Optical Parameters and SST from SeaWiFS and MODIS, Ongoing since 1997 and AVHRR-derived SST from 1985 to 2009	knb-lter-mcr.5	1,3,5
Population Dynamics: Adult Threespot Dascyllus and their Host Anemones	knb-lter-mcr.2	2,4,5
Population Dynamics: Time-series of *Symbiodinium* Populations in Corals of Moorea	knb-lter-mcr.15	1,2,5
Rates of Benthic Coral Reef Community Metabolism from 2007 Ongoing	knb-lter-mcr.18	1,5
Sensor Network: Bottom-mounted CTD Data - GUMPR	knb-lter-mcr.4004	5
Temperature and Salinity Subset of Three Mooring Sites	knb-lter-mcr.1040	5
Water Column: Nearshore Water Profiles, Conductivity, Temperature, Depth, Primary Production and Chemistry	knb-lter-mcr.10	1,3,4,5

Ongoing Time Series - continued Data Set Title	Area	Core Area*
Water Column: Nutrients	knb-lter-mcr.1034	4,5
Water Column: Offshore Ocean Acidification: Water Profiles, Conductivity, Temperature, Depth and Chemistry	knb-lter-mcr.1037	4,5

Suspended Time Series Data Set Title	Package ID	Core Area*
Community Dynamics: Abundance and Species Richness of Fishes Associated with the Coral *Porites rus*	knb-lter-mcr.1	2,3,5
Population Dynamics: Mean Daily Recruitment of Three-spot Dascyllus to Gump Reef	knb-lter-mcr.3	2
MCR LTER: Genetics: Settlement Dynamics in the Three-spot Damselfish, *Dascyllus trimaculatus*	knb-lter-mcr.16	2
MCR LTER: Genetics: Settlement Dynamics in the Clownfish, *Amphiprion chrysopterus*	knb-lter-mcr.17	2
Ocean Currents and Biogeochemistry: Moored Thermistor String Data – Cooks Bay	knb-lter-mcr.33	5
Water Column: Particle Sedimentation on the Forereef, Back Reef and Fringing Reef	knb-lter-mcr.12	4,5
Water Column: Zooplankton Composition and Abundance	knb-lter-mcr.13	2,3,5
Demersal Zooplankton Composition and Abundance	knb-lter-mcr.21	2,3,5

Short Term Studies Data Set Title	Package ID	Core Area*
Changes in the Abundance of Fish Functional Groups: Adam et al. 2014 Oecologia	knb-lter-mcr.1041	2,3,5
Computer Vision: Moorea Labeled Corals	knb-lter-mcr.5006	1,2,5
Computer Vision: Pacific Labeled Corals	knb-lter-mcr.5013	1,2,5
Coral Growth in Temperature and Alkalinity Treatments: Edmunds 2011 Limnology & Oceanography	knb-lter-mcr.5005	2,5
Coral Larval Metabolism in pH and Temperature Treatments	knb-lter-mcr.2008	2,5
Coral Reef Resilience: Juvenile Parrotfish Habitat Associations at North Shore Fringe and Backreef in March 2011	knb-lter-mcr.7003	2,3,5
Data in Support of Edmunds 2012 Global Change Biology, v18 2173-2183	knb-lter-mcr.5009	1,2,5
Data in Support of Wall and Edmunds 2013 Biological Bulletin, v225 no. 2. 92-101	knb-lter-mcr.5011	1,2,5
Diadema Predation and Recruitment in Moorea, French Polynesia	knb-lter-mcr.2003	2,5
Effects of Flow and Temperature on Growth and Photophysiology of Scleractinian Corals in Moorea, French Polynesia	knb-lter-mcr.2006	2,3,5
Fish Counts versus Coral Diversity for Holbrook et al. PLoS One 2015	knb-lter-mcr.5016	2,5
Growth and Scaling of Photosynthetic Energy Intake in *Fungia concinna*: Elahi & Edmunds 2007 JEMBE	knb-lter-mcr.2002	1,2,3,5
Growth and Survivorship of *Dascyllus trimaculatus*	knb-lter-mcr.2009	2,3,5

Short Term Studies - continued Data Set Title	Package ID	Core Area*
Habitat Utilization and Pairing Patterns of Mutualistic Shrimps and Gobies from 7 Indo-Pacific Regions	knb-lter-mcr.5008	2,5
pH Time Series from Bottom-mounted SeaFET on the Fringing Reef, January-February 2011	knb-lter-mcr.2004	3,5
Porites Growth, Respiration, and Photophysiology Data in Support of Edmunds 2012 Marine Biology, v159, 2149-2160	knb-lter-mcr.5010	1,2,3,5
Sand Flat Sampling: Sand Infaunal Surveys	knb-lter-mcr.5001	2,5
Water Column: Offshore Water Profiles: Conductivity, Temperature and Depth Transects	knb-lter-mcr.5003	3,4,5
Water Column: Bay Water Profiles: Conductivity, Temperature and Depth Transects	knb-lter-mcr.5004	3,4,5
Seawater pH, Temperature and Depth Time Series from Bottom-mounted Sensors on the Fringing Reef, January-March 2012	knb-lter-mcr.5014	3,5
Taiwan Coral Reef: Seawater pH, Temperature and Depth Time Series from Bottom-mounted Sensors on the Fringing Reef in Nanwan Bay, May-July 2012	knb-lter-mcr.5015	3,5
Satellite Remote Sensing: Landsat ETM from 2001 to 2010	knb-lter-mcr.6002	N/A
Satellite Remote Sensing: Landsat 7 in 1999 and 2000	knb-lter-mcr.6003	N/A
Satellite Remote Sensing: Landsat MSS in 1979	knb-lter-mcr.6004	N/A

*LTER Core Research Areas are defined as: Core Area 1 - Primary Production; Core Area 2 - Population Studies; Core Area 3 - Movement of Organic Matter; Core Area 4 - Movement of Inorganic Matter; Core Area 5 - Disturbance Patterns

SUPPLEMENT - MCR III PROJECT MANAGEMENT PLAN

Site Governance

The MCR LTER is a partnership between the University of California Santa Barbara and California State University Northridge, and is governed by an Executive Committee that consists of the Lead PI (Schmitt), the three Co-PIs (Holbrook, Carpenter, Edmunds) and six Associate Investigators (Alldredge, Briggs, Burkepile, Hench, Putnam, Vega Thurber). Associate Investigator members of the committee serve staggered, three year rotating terms. The Deputy Program Director (Brooks) and Information Manager (Gastil-Buhl) serve on an Ex-Officio basis. As such, members of the Executive Committee represent the major science and programmatic elements of the site. The Committee addresses science and budgetary priorities, advises on program policy issues, reviews progress on major program elements, identifies potential new science initiatives, sets priorities on supplement requests, and helps with communication to the broader MCR community. The Executive Committee will continue to develop and implement policies regarding: (1) data access and sharing, (2) use of MCR vehicles, boats, instrumentation and mesocosm facilities, and (3) collaborative activities with groups outside the MCR LTER. These policies are posted on the internal MCR website. The Executive Committee also plays a central role regarding the composition of the MCR research team, including the identification of potential new Associate Investigators and Collaborators. With respect to selecting new Associate Investigators, the Executive Committee considers the need to broaden diversity as well as attract younger investigators. Decisions typically are made by consensus; in the rare event that consensus is not reached the Lead PI makes the final decision.

Project Management

The MCR LTER is administered by UC Santa Barbara and field operations are based at the Gump Research Station on Moorea, which is administered by UC Berkeley. Lead PI Schmitt and Co-PI Holbrook serve on the Gump Research Station Advisory Committee, which reports to the Vice Chancellor for Research at UC Berkeley. The University of California and the Territorial Government of French Polynesia have a formal cooperative agreement that enables the MCR to operate from the Gump Station. Scientists must hold a research permit issued by the Territorial Government, and the Gump Station handles the paperwork and facilitates the process.

The Lead PI (Schmitt) serves as the Project Director and is responsible for the overall quality and direction of the research. He is the point of contact with the NSF Program Officers, serves as a member of the LTER Science Council, and is the liaison between the MCR and the UC administration. In close cooperation with the three Co-Principal Investigators, Schmitt oversees day-to-day operations of the project and implementation of all of its components. The four PIs (Schmitt, Holbrook, Carpenter, Edmunds) meet several times monthly, either in person or via video conference. Deputy Program Director (Brooks) is in daily contact with the PIs and assists with all aspects of project management. He is an important liaison between the project's investigators and (1) the Information Management team, (2) various University committees (e.g., Diving Safety, Small Boat Safety), and (3) the Gump Research Station. Together, this 5 person management team coordinates the activities of MCR research teams, plans MCR meetings and events, prepares project reports, and prepares responses to inquiries from the LTER Network Office, NSF and many other entities.

Information transfer among researchers of the MCR LTER site is crucial because individuals are located at eight universities, and considerable effort goes into maintaining open channels of communication and maximizing the input of all participants. Each year we hold a 2-day MCR All Investigator Meeting at UC Santa Barbara, which is attended by > 50 investigators, postdocs, graduate students, undergraduates (including REU students), ROA and RET participants, MCR staff and national and international collaborators. Activities at these meetings include presentations and posters, working group meetings for research synthesis and planning, and training sessions. The MCR All Investigator Meeting is one means we use to introduce potential collaborators or new Associate Investigators to the project, and it has proven to be an effective recruitment tool (6 new Associate Investigators joined MCR III). These individuals participate in all meeting activities and their meeting costs are paid by the MCR.

The annual All Investigator Meeting also is a platform for initiating actions to address upcoming events, such as mid-term reviews, renewal proposals, and potential new research and synthesis opportunities. Follow-up typically is done by our standing working groups that carry out the site research. These meet regularly (weekly to monthly) during the academic year. Currently there are three working groups: physical – biological coupling (led by Carpenter), reef resilience (led by Holbrook), and reefs of the future (led by Edmunds). Modeling (led by Briggs) and physical oceanography (co-led by Hench & Leichter) are integrated into each group. Lead PI (Schmitt) meets regularly with leaders of the working groups and ensures communication and coordination among the groups. The participation of MCR researchers in the time series and MCR III research campaigns is given in Table 1 below.

The MCR LTER website is another tool for communication with both MCR personnel and other entities via sharing project-related information, data and documents. Sharing of data, documents, model results and other project related products is made easy through our central data server to which all participants have access (see Data Management Plan). MCR LTER research occurs at a distant research station in Moorea, French Polynesia, and our internal website provides researchers with information regarding travel and research station logistics and scheduling, visas, permits, requirements for SCUBA and boating certifications.

Interactions & Integration with Non-LTER Scientists

The MCR does not have formal agreements with any Federal agency or other entity that supports the research and outreach missions of our program. For site-based research, the MCR relies heavily on fostering interactions with scientists who do – or could – conduct research on Moorea. In addition to scientists from US institutions (see below), one avenue for this has been to build collaborations with scientists in French Polynesia (e.g., Le Centre de Recherches Insulaires et Observatoire de l'Environnement de Polynésie Française (CRIOBE), Institut de Recherche pour le Développement (IRD), Université de la Polynésie Française). This has resulted in a number of collaborative projects. These activities are further fostered by the participation of MCR investigators in the Moorea IDEA Project, the Moorea Marine Protected Area Advisory Committee, and an annual CRIOBE-Gump-MCR Roundtable Meeting. MCR provides resources for the participation of MCR scientists in these collaborative activities. The Office of the President of the University of California signed an MOU with all French agencies that conduct coral reef research in the Pacific ('*International Research Network (GDRI) Agreement for Biodiversity of Coral Reefs*'). The four named UC participants in the agreement are the Lead PI Schmitt, Co-PI Holbrook, Associate Investigator Bernardi and the Director of the Gump Station (Davies). We anticipate that this agreement will further facilitate collaborative activities.

As a second avenue, the MCR has reached out to US scientists to offer our assistance in their efforts to provide research collaboration opportunities with our personnel and site, as well as to secure extramural funding. This has led to several collaborative proposals that have been funded by NSF and the Gordon and Betty Moore Foundation. MCR provides infrastructure support to these projects and the collaborating scientists participate in MCR activities (e.g., the All Investigator Meetings). Finally, the MCR has provided seed funding to targeted US scientists to engage them in collaborative projects with MCR personnel; some of these individuals subsequently have become Associate Investigators on the MCR project (e.g., Vega Thurber, Nelson, Putnam) while others remain as collaborators that enable them to use MCR infrastructure on joint projects.

Because coral reef science is an interdisciplinary and international endeavor, from the beginning the MCR Executive Committee has been pro-active in developing interactions and collaborations with international partners at other coral reef sites. Our strategy for achieving this has been to secure funding from NSF for planning trips (e.g., Taiwan, France, Monaco, Thailand), international workshops (Japan, Taiwan, People's Republic of China, Thailand), and collaborative research (Japan, Taiwan, Australia).

We actively have sought collaborations with scientists and engineers interested in using the MCR site as a test bed for technology development that is relevant to the MCR in particular and the coral reef scientific community in general. Projects our site has facilitated include efforts to develop real time environmental sensor networks, cyber-enabled image analysis, true-color subtidal imaging technology,

autonomous robotic vehicles, underwater data transmission technology and underwater navigation. The MCR is beginning to incorporate some of these developments into its research (e.g., CoralNet http://coralnet.ucsd.edu), and will continue to be receptive to similar opportunities to serve as a test bed for emerging environment-related technologies.

With respect to efforts to increase participation of under-represented groups, the Executive Committee seeks new Associate Investigators and collaborators from these groups to the fullest extent possible. Our efforts to recruit under-represented students include our participation in formal outreach efforts at our campuses as well as individual efforts by MCR investigators. We have been successful at attracting undergraduate and graduate students from under-represented groups at Hispanic-serving MCR campuses (CSUN, UCSB) who go on to graduate or postdoctoral positions at other MCR campuses.

Planning for the Future

We propose no change in the leadership for the coming cycle but have continued to engage young and mid-career scientists as Associate Investigators. We added 6 new investigators (5 early career) through active recruitment to fill specific research needs or by invitation to already collaborating scientists who have expressed interest in a more formal association with the project (we also added 5 early career scientists in MCR II). Short term continuity of leadership will be achieved by a Co-PI filling the role of Lead PI should Schmitt become unable to continue. We have formalized the process for change in the Lead PI in MCR IV, and will mentor leadership by including key Associate Investigators on the Executive Committee with the goal of adding one or two as Co-PIs at the next renewal. We plan for transition of the Lead PI mid-cycle in MCR IV, with the successor Lead PI functioning as a Co-Lead in preparing and directing the program for the initial three years of the transition cycle.

Table 1. Participation of MCR Investigators in the time series and research campaigns of MCR III. The 6 investigators new to MCR III are in **bold**.

MCR Investigator	Times Series Focus (TS) & Campaign Number (C)								
	TS 1	TS 2	TS 3	C 1	C 2	C 3	C 4	C 5	Modeling
Thomas Adam	✓			✓	✓	✓			
Alice Alldredge		✓	✓					✓	
Giacomo Bernardi	✓				✓				
Cherie Briggs				✓		✓			✓
Andrew Brooks	✓			✓	✓	✓			
Deron Burkepile		✓			✓	✓			
Craig Carlson		✓	✓		✓			✓	
Robert Carpenter	✓	✓						✓	✓
Peter Edmunds	✓			✓	✓		✓		
Ruth Gates					✓		✓		
Mark Hay					✓	✓			
James Hench			✓				✓	✓	✓
Sally Holbrook				✓	✓	✓			
James Leichter		✓						✓	
Hunter Lenihan				✓			✓		✓
Hollie Putnan					✓		✓		
Stephane Maritorena			✓		✓				
Craig Nelson		✓			✓			✓	
Roger Nisbet					✓		✓		✓
Russell Schmitt				✓	✓	✓			
Rob Toonen	✓			✓					
Rebecca Vega Thurber		✓			✓				
Libe Washburn			✓				✓	✓	