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Author

Martinelli, Maurizio

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What happened to Big Mama?

Changes in size class distribution of mounding *Porites* on Maui reefs following the 2015 thermal bleaching event

Maurizio M. Martinelli
MAS MBC Capstone Report

Committee Chair: Dr. Emily Kelly – Scripps Institution of Oceanography, UCSD
Committee Members: Dr. Jennifer Smith – Scripps Institution of Oceanography, UCSD; Darla J. White – Special Projects Coordinator, Department of Land and Natural Resources, Division of Aquatic Resources, Maui

Abstract

Coral reefs worldwide are threatened by thermally induced bleaching. In 2015, the National Oceanic and Atmospheric Administration declared the third recorded global thermal bleaching event during which Hawaiian coral reefs were severely impacted. In order to understand how Hawaiian reefs responded to this event, data were examined from benthic imagery from three sites on leeward Maui that represent a gradient of management. Data were extracted from composite 100 m^2 photomosaic images of reef benthos, which were constructed for July 2014 (prior to bleaching) and June 2016 (following bleaching). In each photomosaic, colonies of mounding *Porites* (*P. lobata*, *P. evermanni*, and *P. lutea*) were individually outlined and numbered in order to compare colony size class distribution before and after the 2015 bleaching event. Overall, the mounding *Porites* communities of leeward Maui reefs experienced a shift towards smaller size classes from 2014 to 2016. Changes in size, quantified in both absolute and percent changes, were not correlated with management regimes. These data suggest that management of local stressors may not be sufficient to mitigate the immediate effects of thermal bleaching events on coral reefs.

Introduction

Coral reef ecosystems worldwide are threatened by a litany of global and local stressors. Of major concern is the impact of the steady rise in global sea surface temperature on reef-building coral (Hughes et al., 2003; Hoegh-Guldberg et al., 2008; Hughes et al., 2017). When seawater temperature is elevated above ambient conditions by just a few degrees for days or weeks, the symbiosis between coral and the photosynthetic algae living in coral tissue breaks down. As a result, 'coral bleaching' occurs in which the coral expels its symbiotic community, thus exposing the white coral skeleton beneath (Brown, 1997). While a bleached coral is not dead, it is left without its primary source of energy and experiences lowered fitness and growth (Muscatine, 1990; Baird & Marshall, 2002). If a coral remains bleached for a prolonged period, it may experience tissue necrosis and eventual mortality (Brown, 1997). Such bleaching events can be local or regional in scale, or can impact tropical oceans globally. The most recent global thermal bleaching event occurred in 2015 in the northern hemisphere (NOAA, 2015) and 2016 in the southern hemisphere (GBRMPA, 2016). Extensive bleaching and mortality on the Great Barrier Reef during 2015-2016 (Hughes et al., 2017) garnered widespread media coverage and renewed a focus on the impacts of global climate change on marine environments.

Coral reefs are also impacted by local stressors (Pandolfi et al., 2005; Carilli et al, 2009; Smith et al., 2016). Local stressors include overfishing and destructive fishing practices (Jackson et al., 2001), extensive coastal or upland development and associated sedimentation (Rogers, 1990), nutrient loading from freshwater runoff (Fabricius, 2011), and even tourism and recreational activities (Lamb et al., 2014). All these stressors can lead directly to reduced live coral cover on a reef, and may also decrease coral resilience in the face of additional stressors such as global climate change (Pandolfi et al., 2005; Carilli et al, 2009; Smith et al., 2016).

Hawaiian coral reefs are subject to many of these local and global stressors, and are a conservation priority to this author. The Hawaiian archipelago accounts for approximately 85% of all coral reefs in the United States (van Beukering & Cesar, 2004). These reefs support subsistence and industry on Hawaii (van Beukering & Cesar, 2004), and are of great cultural importance to the Hawaiian people. Further, there is low coral diversity as compared to the South Pacific, but high endemism of the marine species found on Hawaiian reefs (Wilkinson, 2008). During the most recent global thermal bleaching event, the National Oceanic and Atmospheric Administration (NOAA)

estimated that 95% of US coral reefs experienced conditions sufficient for coral bleaching, and the Hawaiian Islands were severely impacted (NOAA, 2015; Rodgers et al., 2017).

As colonial organisms, corals may experience partial mortality as a consequence of bleaching: a colony may lose some portion of its living surface area but still have continuous tissue or it may fragment into multiple non-contiguous patches of tissue. Such changes have important biological consequences as the processes of growth, survivorship, and fecundity are a function of colony size rather than other parameters such as age or location (Hughes & Jackson, 1985; Szmant, 1991; Soong, 1993; Meesters et al., 1996). At the ecosystem level, changes in demography may impact population-wide reproductive success and local recruitment (Richmond, 1997). From an anthropocentric perspective, smaller colonies provide fewer ecosystem services such as coastal protection and habitat formation (Moberg & Folke, 1999).

Porites is a genus of reef-building coral commonly found on Hawaiian reefs (Wilkinson, 2008). Massive and submassive (collectively, 'mounding') *Porites* species are generally long-lived, slow growing, and exhibit low recruitment (Grigg, 1981; 1997). These species are considered to be relatively resilient to many environmental stressors (e.g. Adjeroud et al., 2005; Levas et al., 2013), and thus may prove important to future reef accretion in Hawaii in a rapidly changing ocean. Understanding how Hawaiian *Porites* are responding to bleaching events can be useful in guiding coral conservation efforts in Hawaii.

The purpose of this project is to characterize any changes in the size-class distribution of mounding *Porites* following the 2015 thermal bleaching event on the reefs off leeward Maui, and to explore whether local management strategies can be correlated with any such community shifts. This project tests two hypotheses: 1) that the size class distribution of live mounding *Porites* across leeward Maui shifted towards smaller colony sizes following the 2015 thermal bleaching event, and 2) that sites with broader management experienced less severe demographic shifts.

Methods

Study Sites

Three reefs off leeward Maui were selected as study sites. All sites are highly used by locals and tourists alike, but are characterized by varying levels of local stressors and different management strategies. The first site, Olowalu, is impacted by terrestrial pollution in the form of terrigenous sedimentation and other consequences of long-term upland agricultural activities, and lacks any significant spatial or fishing management. The second site, Kahekili Beach Park, hereafter referred to as Kahekili, is impacted by point source wastewater that introduces both excess nutrients and a variety of toxicants to the reef. The site is within the Kahekili Herbivore Fisheries Management Area (KHFMA), a protected area established in 2009 that prohibits the removal of any herbivorous fish or urchins but allows fishing for other organisms. The final site, Molokini, has the most robust spatial and fishing management regime. The site sits within the protective waters of a semicircular islet roughly 4 km (2.5 miles) from the main island and is within a Marine Life Conservation District in which all fishing is prohibited and there are limits to the number of recreationalists who can access the site each day. All three sites are part of an ongoing long-term monitoring project jointly run by the Hawaii Division of Aquatic Resources (DAR) and the Scripps Institution of Oceanography, UCSD.

Data collection

As part of the ongoing monitoring of these sites, researchers on SCUBA collected sequential photos of the reef benthos during July 2014 and again during June 2016. High-resolution, 3D point clouds were constructed from these images using Adobe Agisoft Photoscan modeling software. The point clouds were exported in the custom visualization software "Vidware," in which the 3D models were converted into a 2D orthoprojections (or, 'photomosaics'). While some resolution is lost, the orthoprojections are advantageous as they eliminate the perspective distortion of traditional 2D photography, thus maintaining the spatial accuracy of the 3D models in a format that can be annotated and analyzed. The orthoprojections were then exported into Adobe Photoshop for annotation.
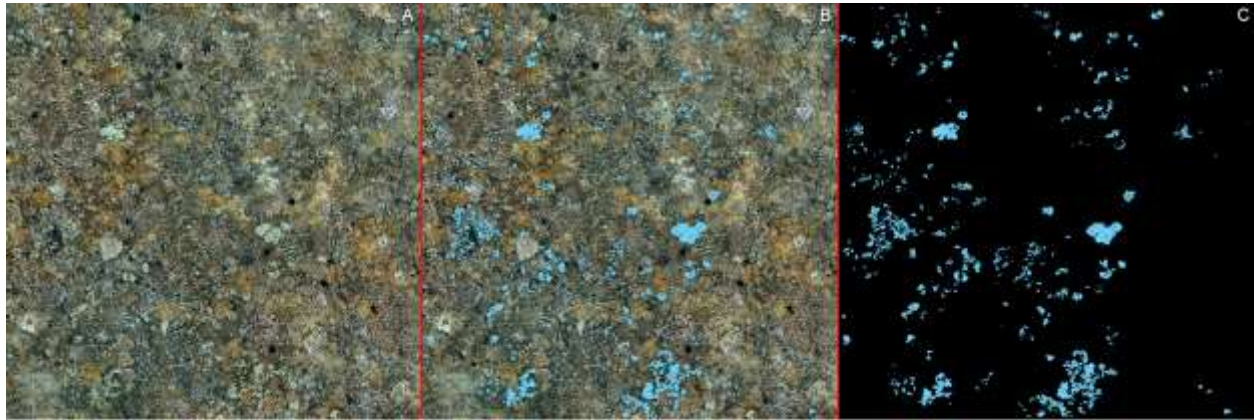

Figure 1: Example annotation of a study site, Olowalu 2014. A: Unannotated study site photomosaic; B: Study site photomosaic with mounding Porites colonies identified in light blue; C: Spatial data extracted from the study site photomosaic.

Annotation began with the designation of the 10 m x 10 m study area for each site, standardized across time points using permanent steel stakes and other persistent reef features. The raw images used to create the 3D models were associated with the photomosaic area they represent to establish a higher resolution visual reference. On the basis of their mounding growth form and visual taxonomic cues, individual colonies of mounding *Porites* were identified, outlined, and numbered (Fig. 1). A colony was defined as any area of discrete, continuous tissue. As mounding *Porites* species on Maui reefs cannot be confidently differentiated from the photographs without genetic verification, all relevant species were considered together as a single taxonomic group. This group likely comprises colonies of *P. lobata*, *P. evermanni*, and *P. lutea*.

Colony size data were collected by extracting the number of pixels representing a given colony and converting to cm^2 based on pixel-to-cm measurements taken within each orthoprojection. These data should not be considered true colony size or surface area measurements, as there is some loss in information from the vertical surfaces of colonies during the conversion from 3D model to 2D orthoprojection. These data are useful, however, for comparison of datasets generated with these same methods.

For two study sites, Olowalu and Molokini, all mounding *Porites* colonies within the study area were sampled at both time points. For the final site, Kahekili, where mounding *Porites* were particularly prevalent, random stratified subsamples were collected for each time point. Results of a power-analysis of ~2,600 haphazardly sampled colonies from the 2016 orthoprojection suggested that a sample of 400 colonies was sufficient for statistical significance and an acceptable standard deviation (± 2 cm^2) from the median. As a precaution, 484 samples were drawn from each Kahekili orthoprojection. Each time point was sampled using a unique stratified random sample. For each orthoprojection, colonies were assigned a single center point and the colony with the

closest center point to a stratified random sample point was included in the study. Colony centers were assigned while the stratified random sample points were not visible to avoid sampler bias.

<u>Statistical Analysis</u>

For all sites at all time points, sampled colonies < 3 cm^2 were excluded from analysis to avoid the potential misidentification that can occur at such small scales. This resulted in the following reductions in sample size at each site: Olowalu 2014: -63; Olowalu 2016: -172; Kahekili 2014: -33; Kahekili 2016: -36; Molokini 2014: -13; Molokini 2016: -33. It should be noted that the excluded samples would have skewed the results towards smaller size classes, and that all samples from 2016 had more exclusions than their 2014 counterparts.

Size class distributions were tested for significance using a bootstrapping approach. The two colony size datasets from each site were combined and resampled with replacement 10,000 times, and the distance between randomly selected data points was calculated and used to create a distribution representing the null expectation that colony size distribution remained constant between 2014 and 2016. The mean distance between the actual 2014 and 2016 data was plotted against the null distribution to calculate the likelihood of the mean distance (i.e., observed size class shift) occurring. An empirical cumulative distribution function was employed to measure type I error, and is our measure of statistical significance (*alpha* < 0.05).

For each site and the combined datasets (i.e., data from all three sites combined according to year collected), the mean, median, and maximum colony size were compared between time points. In addition, as coral communities already skew towards smaller colonies, and following previous studies on coral size class distribution (Bak & Meesters, 1998; Vermejj & Bak, 2002; Adjeroud et al., 2007), the data were log$_{10}$ transformed for graphical representation and comparison. Transforming the data somewhat normalizes the distribution and offers greater resolution among smaller size class bins. Common metrics for the normality of such distributions are skewness and kurtosis. Skewness refers to the deviation from the symmetricity of a normal distribution (where skewness = 0); a positive skew indicates that the data are drawn out on the right, while a negative skew indicates that the data are drawn out on the left. Kurtosis is a measure of the 'weight' of the data tails. A normal distribution has a kurtosis = 3. A kurtosis < 3 implies that there are fewer and less extreme outliers, producing 'heavy' tails on the data, while kurtosis > 3 suggests that outliers are more common and extreme, producing 'lighter' tails on the data.

Results

<u>Mean, median, and maximum colony size</u>

Olowalu, Kahekili, Molokini and the combined datasets had significantly different (*p* < 0.05) size class distributions between time points, with the following significance: Olowalu *p* < 0.0001; Kahekili *p* = 0.0114; Molokini *p* = 0.0267; Combined p < 0.0001.

In 2014, Molokini had the greatest mean (104.60 cm^2) and maximum (2663.25 cm^2) colony sizes, while Kahekili had the largest median (29.97 cm^2) colony size. Olowalu in 2014 had the smallest mean (60.81 cm^2) and median (22.59cm^2) colony sizes, while Kahekili had the smallest maximum (1374.51 cm^2) colony size.

Mean and median colony sizes decreased at all sites between 2014 and 2016 (Table 1). Olowalu had the most dramatic percent decreases in both metrics, as mean colony size decreased by 47.7%

(28.99 cm^2) and median size decreased by 63.1% (8.74 cm^2) from 2014 to 2016. Molokini, however, experienced the greatest absolute decreases in these metrics over the same period, as mean size decreased by 30.34 cm^2 (29.0%) and median size decreased by 12.50 cm^2 (47.4%). Kahekili experienced the least loss in both metrics, in terms of both absolute and percent decreases: mean size decreased by 11.97 cm^2 or 14.8%, while median size decreased by 7.16 cm^2 or 23.9%. When combined, the data showed an overall decrease in the mean size of 23.72 cm^2 (32.8%) and a decrease in the median size by 7.36 cm^2 (29.4%) from 2014 to 2016.

Table 1: Metrics of mounding Porites at Olowalu, Kahekili, Molokini, and all sites combined in 2014 and 2016.

Site	Year	n	Mean (cm²)	Median (cm²)	Maximum (cm²)
Olowalu	2014	629	60.81	22.59	2271.65
Olowalu	2016	662	31.82	13.85	866.63
Kahekili	2014	451	81.16	29.97	1374.51
Kahekili	2016	437	69.19	22.81	1799.53
Molokini	2014	101	104.60	26.35	2663.25
Molokini	2016	95	74.26	13.85	2264.04
Combined	2014	1180	72.35	24.96	2663.25
Combined	2016	1193	48.63	17.60	2264.04

Maximum colony sizes decreased at both Olowalu and Molokini. Olowalu exhibited the greater loss in both absolute and percent declines (1404.93 cm^2 and 61.9% respectively). The Kahekili samples produced a maximum colony size increase of 425.02 cm^2 between time points, which represents a 30.9% increase in maximum colony size. This increase, however, appears to be an artifact of the subsampling methodology utilized at Kahekili rather than colonial growth. When followed back through time, the coral that produced the maximum colony value in 2016 had actually decreased in size since 2014 (from 1902.13 cm^2 in 2014 to 1799.53 cm^2 in 2016, a loss of 102.60 cm^2 or 5.4%). Overall, when the data from each time point are combined, sites on leeward Maui saw a reduction in maximum size of 399.21 cm^2, which was a 15.0% decline. These last figures represent the same values reported for Molokini, as the site had the largest colonies sampled in both 2014 and 2016.

Size distribution of colonies

All sites at both time points exhibited positive skewness of log-transformed colony size, indicating a preponderance of smaller colonies. Skewness increased from 2014 to 2016 at all sites (Table 2). In the combined data, skewness increased from 0.50 to 0.70. Demography from all three sites produced kurtosis values < 3 in 2014 and > 3 in 2016, meaning that outliers became more extreme and the tails of the data thinned. This was particularly apparent at Molokini, which had the greatest increase and the highest value for kurtosis in 2016. Combined, sites on leeward Maui in 2014 produced kurtosis = 2.84, while 2016 data produced kurtosis = 3.4.

Table 2: Metrics of normality and distribution of log$_{10}$(cm^2) transformed data for Olowalu, Kahekili, Molokini, and all sites combined.

Site	Year	Skewness	Kurtosis
Olowalu	2014	0.48	2.97
Olowalu	2016	0.56	3.04
Kahekili	2014	0.43	2.57
Kahekili	2016	0.61	3.09
Molokini	2014	0.66	2.90
Molokini	2016	0.91	3.69
Combined	2014	0.50	2.84
Combined	2016	0.70	3.42

Figure 2: _Size distribution (log_$_{10}$_(cm_^{2}_)) data of mounding Porites at Olowalu, Kahekili, Molokini, and all sites combined in 2014 and 2016._
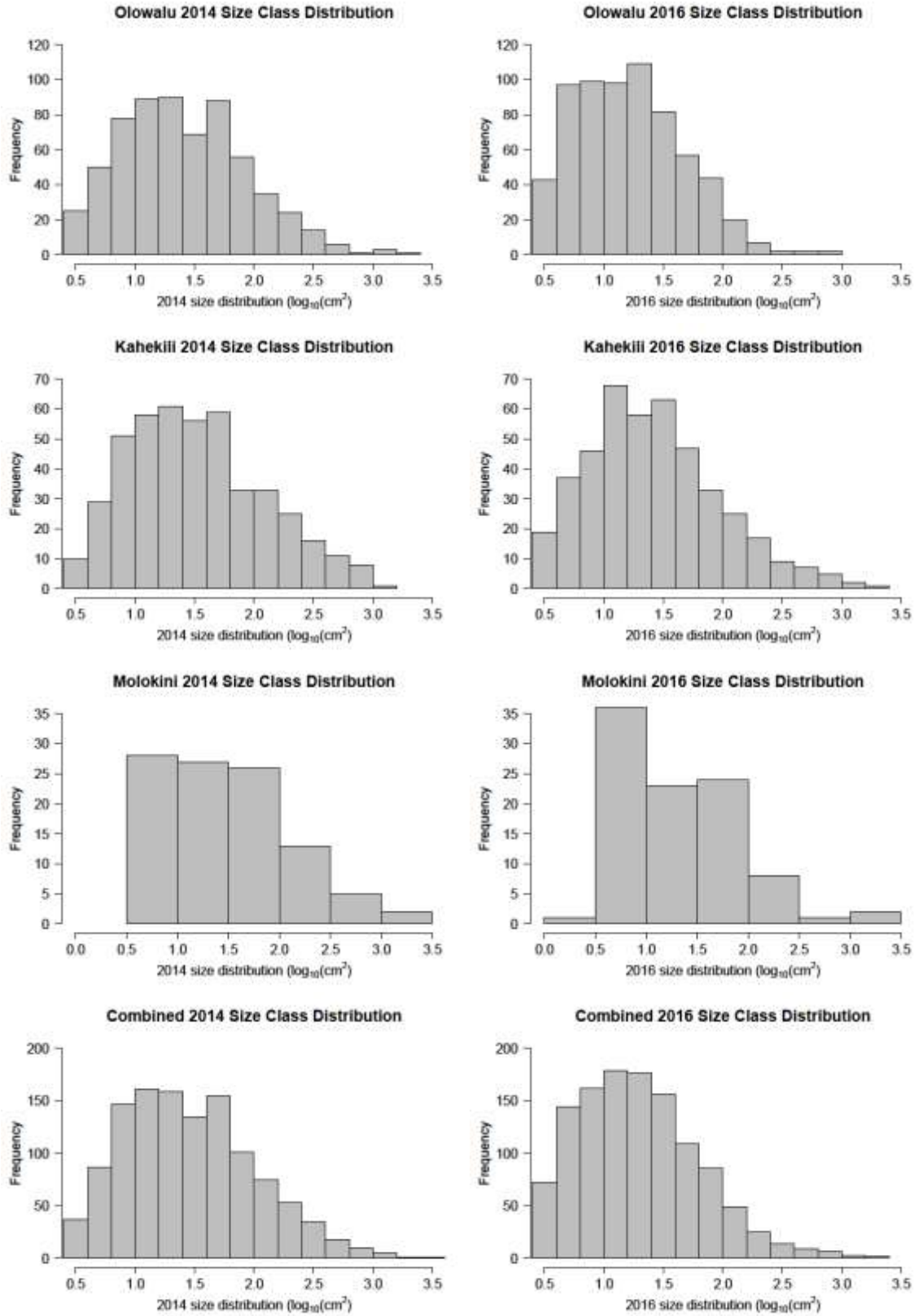
Figure 3: Quantile-quantile plots of size distribution ($\log_{10}(cm^2)$) data of mounding Porites at Olowalu, Kahekili, Molokini, and all sites combined in 2014 and 2016.
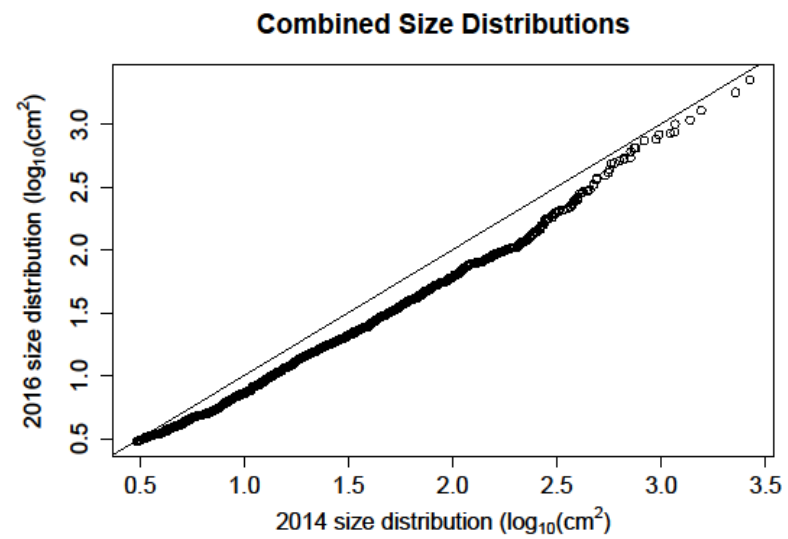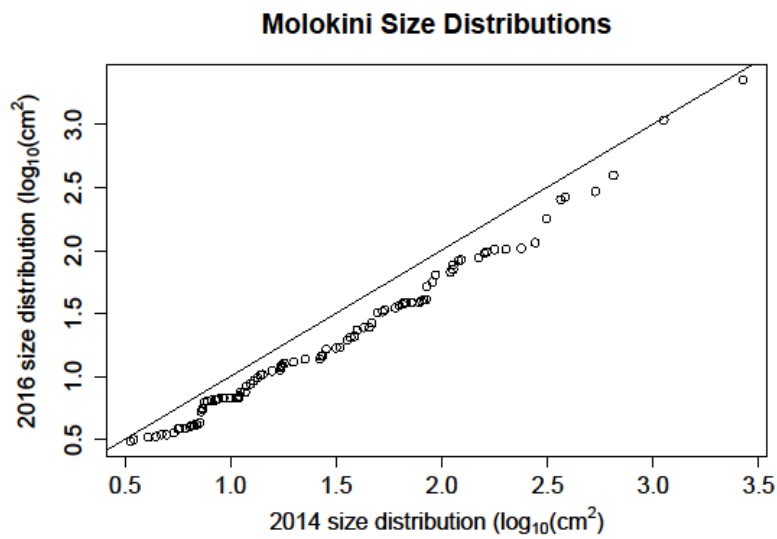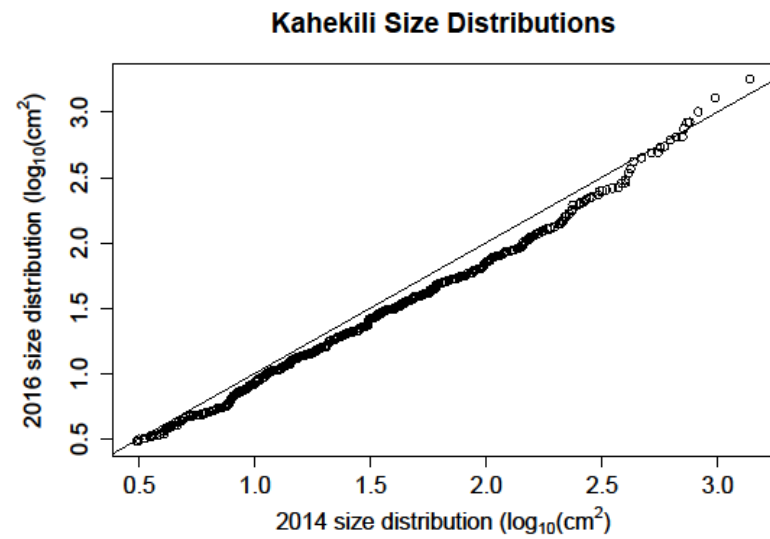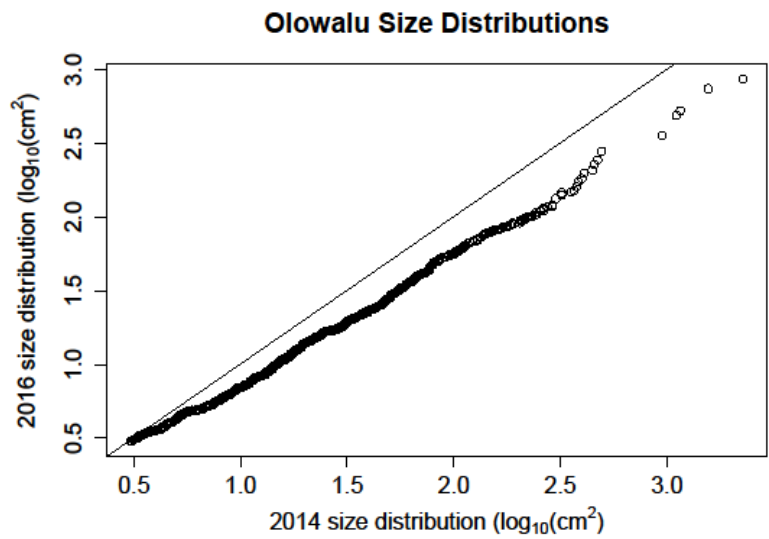
Discussion

The data presented here support the hypothesis that there was a shift in the size class distribution of the mounding *Porites* community towards smaller colonies following the 2015 thermal bleaching event on leeward Maui (Figs. 2, 3). Qualitative analysis of the orthoprojections and the raw images suggests that the majority of this shift is due to partial mortality or fragmentation of colonies rather than recruitment. Further, the exclusion of colonies < 3 cm^2 in our analysis avoids the influence that recruitment might have had at these sites, as slow-growing mounding *Porites* recruits would not have had sufficient time to grow large enough to be included in the sample (Grigg, 1981; 1997).

Of the three study sites, the reef with the least spatial and fishing management, Olowalu, experienced the greatest percent declines in all metrics of size class distribution shifts and the greatest absolute decline in maximum colony size. These data alone might support the hypothesis that more limited management would lead to more severe consequences from thermal bleaching events. However, the greatest absolute declines in mean and median colony sizes were experienced at the most protected site, Molokini. Log transformed data of the mounding *Porites* community at Molokini skewed positively the furthest from a normal distribution, meaning that larger colonies became more extreme outliers of the dataset. The site with herbivore fishing management and moderate spatial management, Kahekili, experienced some of the lowest declines of the sites sampled. Together this suggests that, while there were generally declines in colony size island-wide, management strength and type as categorized in this study were not determiners of coral success following the 2015 thermal bleaching event on leeward Maui.

This study therefore suggests that regardless of other local conditions, if a coral colony experiences elevated water temperatures for a sufficient period of time, it will bleach. This trend has been described on others reefs as well. In 2016, as coral reefs in the southern hemisphere bleached, the northern Great Barrier Reef, though least influenced by local anthropogenic stressors, suffered more extensive bleaching and mortality than the central and southern portions (Hughes et al., 2017). The question we are faced with now is, how will the reefs recover? Further, does limiting local stressors better allow coral to rebound following thermal bleaching events? Monitoring recovery and maintaining long term datasets can be instrumental in answering these questions.

One major factor that this study does not address, and is an area ripe for future research, is the extent and severity of bleaching experienced at each site. There are numerous factors at each site that can determine bleaching. For example, subtle differences in temperature, currents, or shading from suspended sediments could create a varied landscape of bleaching on local scales. However, these small-scale influences are beyond the scope of this project. Anecdotally, however, the sites likely experienced different levels of bleaching (pers. comm., White).

Regardless of drivers of change, a shift towards smaller sized colonies of one of the major reef builders on Maui can have significant impacts on ecological and evolutionary processes. For one, as fecundity and mortality rates are determined most directly by a coral's size, a population of smaller colonies may be less likely to successfully reproduce than a population of larger individuals (Hughes & Jackson, 1980; Szmant-Froelich, 1985; Hughes & Connell, 1987). This can have effects on the ability of this species to persist through time, especially as thermal bleaching

events are predicted to become more frequent and severe in the future (IPCC, 2014). Reduced reproductive capacity may also have impacts on larval export and exchange over large spatial scales, and thus further research into population dynamics and larval dispersal in this area should be conducted.

For Hawaiian reefs in particular, significant loss of this foundation species can have profound impacts on the natural history, ecosystem services, fishing access, and culture related to these reefs. *Porites* build some of the largest, most charismatic colonies found on Hawaiian reefs. Loss off these 'Big Mamas' represents a loss of hundreds of years of natural history and heritage to the people of Hawaii, for whom coral reefs are culturally very important. Loss of these habitat engineers may reduce shoreline protection and threaten local populations of reef organisms, many of which are found nowhere else on earth (Wilkinson, 2008). Loss of coral-dependent species may manifest more tangibly in losses of fishing and economic activities that rely on a healthy reef ecosystem.

Conclusion

The data presented in this study suggest that, while local stressors may often drive reef health, they may not be the sole determinants of long-term success in the face of rising sea water temperatures. While coral loss to bleaching may be substantial, they need not be total. Effective management of local stressors may allow some recovery of coral reefs following bleaching events. However, in order to secure a future for coral reefs, we need to address the atmospheric carbon pollution that is driving global temperature increases. We can partially achieve this through personal changes in lifestyle – limiting our use of personal vehicles, reducing our meat consumption, reducing home energy use, buying local goods and foods, and supporting renewable energy to name a few (Dietz et al., 2009; Jones & Kammen, 2011). However, it will also require changes at higher levels. Supporting politicians and policies, both domestically and internationally, that move the world towards reduced carbon emissions will be critical to saving not only coral reefs but many ecosystems worldwide.

Acknowledgements

References

Adjeroud, M., Chancerelle, Y., Schrimm, M., Perez, T., Lecchini, D., Galzin, R. & Salvat, B. (2005). Detecting the effects of natural disturbances on coral assemblages in French Polynesia: A decade survey at multiple scales. *Aquatic Living Resources*, *18*(2): 111-123. http://doi.org/10.1051/alr:20050144

Adjeroud, M., Pratchett, M.S., Kospartov, M.C., Lejeusne, C. & Penin, L. (2007). Small-scale variability in the size structure of scleractinian corals around Moorea, French Polynesia: patterns across depths and locations. *Hydrobiologia*, *589*: 117-126. http://doi/org/10.1007/s10750-007-0726-2

Baird, A.H., & Marshall, P. A. (2002). Mortality, growth and reproduction in scleractinian corals following bleaching on the Great Barrier Reef. *Marine Ecology Progress Series*, *237*: 133–141. http://doi.org/10.3354/meps237133

Bak, R.P.M. & Meesters, E. H. (1998). Coral population structure: the hidden information of colony size-frequency distributions. *Marine Ecology Progress Series*, *162*: 301–306. https://doi.org/10.3354/meps162301

Brown, B.E. (1997). Coral bleaching: causes and consequences. *Coral Reefs*, *16*(Suppl 1): S129–S138. http://doi.org/10.1007/s003380050249

Carilli, J.E., Norris, R.D., Black, B.A., Walsh, S.M., & McField, M. (2009). Local stressors reduce coral resilience to bleaching. *PLoS ONE*, *4*(7), e6324. http://doi.org/10.1371/journal.pone.0006324

Dietz, T., Gardner, G.T., Gilligan, J., Stern, P.C. & Vandenbergh, M.P. (2009). Household actions can provide a behavioral wedge to rapidly reduce US carbon emissions. Proceedings of the National Academy of Sciences of the United States of America, 106(44): 18452-18456. http://doi.org/10.1073/pnas.0908738106

Fabricius, K.E. (2011). Coral reefs: An ecosystem in transition. In Z. Dubinsky & N. Stambler (Eds.), *Coral Reefs: An Ecosystem in Transition* (pp. 493–505). http://doi.org/10.1007/978-94-007-0114-4

Great Barrier Reef Marine Park Authority (GBRMPA). (2016). Interim report: 2016 coral bleaching event on the Great Barrier Reef. http://hdl.handle.net/11017/3044

Grigg, R.W. (1981). Coral reef development at high latitudes in Hawaii. *Proceedings of the Fourth International Coral Reef Symposium, Manila*, *1*: 687-693.

Grigg, R.W. (1997). Paleoceanography of coral reefs in the Hawaiian-Emperor Chain – revisited. *Coral Reefs*, *16*: S33-S38. https://doi.org/10.1007/s003380050239

Hoegh-Guldberg, O., Mumby, P. J., Hooten, A. J., Steneck, P., Greenfield, P., Gomez, E., … Hatziolos, M. E. (2008). Coral Reefs Under Rapid Climate Change and Ocean Acidification. *Science*, *318*(5857): 1737–1742. http://doi.org/10.1126/science.1152509

Hughes, T.P. & Jackson, J.B.C. (1980). Do corals lie about their age? Some demographic consequences of partial mortality, fission, and fusion. *Science*, *209*(4457): 713-715. http://doi.org/10.1126/science.209.4457.713

Hughes, T.P. & Jackson, J.B.C. (1985). Population dynamics and life histories of foliaceous corals. *Ecological Monographs*, *55*(2): 141-166. http://doi.org/10.2307/1942555

Hughes, T.P. & Connell, J.H. (1987). Population dynamics based on size or age? A reef-coral analysis. *American Naturalist*, *129*(6): 818-829. http://doi.org/10.1086/284677

Hughes, T.P., Baird, A.H., Bellwood, D.R., Card, M., Connolly, S.R., Folke, C., … Roughgarden, J. (2003). Climate change, human impacts, and the resilience of coral reefs. *Science (New York, N.Y.), 301*(5635): 929–933. http://doi.org/10.1126/science.1085046

Hughes, T.P., Kerry, J.T., Álvarez-Noriega, M., Álvarez-Romero, J.G., Anderson, K.D., Baird, A.H., … Wilson, S.K. (2017) Global warming and recurrent mass bleaching of corals. *Nature*, *543*: 373-377. https://doi.org/10.1038/nature21707

Intergovernmental Panel on Climate Change (IPCC). (2014). Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, R.K. Pachauri and L.A. Meyer (eds.)]. IPCC, Geneva, Switzerland, 151 pp.

Jackson, J.B.C., Kirby, M.K., Berger, W.H., Bjorndal, K.A., Botsford, L.W., Bourque, B.J., … Warner, R.R. (2001). Historical Overfishing and the Recent Collapse of Coastal Ecosystems. *Science*, *293*(5530): 629–637. http://doi.org/10.1126/science.1059199

Jones, C.M. & Kammen, D.M. (2011). Quantifying carbon footprint reduction opportunities for U.S. households and communities. Environmental Science & Technology, 45(9): 4088-4095. http://doi.org/10.1021/es102221h

Lamb, J.B., True, J.D., Piromvaragorn, S., & Willis, B.L. (2014). Scuba diving damage and intensity of tourist activities increases coral disease prevalence. *Biological Conservation*, *178*: 88–96. http://doi.org/10.1016/j.biocon.2014.06.027

Levas, S.J., Grottoli, A.G., Hughes, A., Osburn, C.L. & Matsui, Y. (2013). Physiological and biogeochemical traits of bleaching and recovery in the mounding species of coral *Porites Lobata*: implications for resilience in mounding corals. PLoS ONE 8(5): e63267. http://doi.org/10.1371/journal.pone.0063267

Meesters, E.H., Wesseling, I. & Bak, R.P.M. (1996). Partial mortality in three species of reef-building corals and the relation with colony morphology. *Bulletin of Marine Science*, *58*(3), 838-852.

Moberg, F., & Folke, C. (1999). Ecological goods and services of coral reef ecosystems. *Ecological Economics*, *29*(2): 215–233. http://doi.org/10.1016/S0921-8009(99)00009-9

Muscatine, L. (1990). The role of symbiotic algae in carbon and energy flux in reef corals. In: Dubinsky, Z. (Ed.), *Ecosystems of the World. Coral Reefs*: 75–87.

National Oceanic and Atmospheric Administration (NOAA). (2015, October 8.) NOAA declares third ever global coral bleaching event [web page]. Retrieved through the National Oceanic and Atmospheric Administration on January 31, 2017 from http://www.noaanews.noaa.gov/stories2015/100815-noaa-declares-third-ever-global-coral-bleaching-event.html

Richmond, R.H. (1997). Reproduction and recruitment in corals: critical links in the persistence of reefs. In: Birkeland, C. (Ed.), *Life and Death of Coral Reefs*: 175-197.

Rogers, C.S. (1990). Responses of coral reefs and reef organisms to sedimentation. *Marine Ecology Progress Series*, *62*: 185–202. http://doi.org/10.3354/meps062185

Rodgers, K.S., Bahr, K.D., Jokiel, P.L & Donà (2017). Patterns of bleaching and mortality following widespread warming events in 2014 and 2015 at the Hanauma Bay Nature Preserve, Hawaiʻi. PeerJ, 5:e3355. http://doi.org/10.7717/peerj.3355

Pandolfi, J. M., Jackson, J. B. C., Baron, N., Bradbury, R. H., Guzman, H. M., Hughes, T. P., … Sala, E. (2005). Are U.S. Coral Reefs on the Slippery Slope to Slime? *Science*, *310*(5716), 1725–1726. http://doi.org/10.1126/science.1104258

Smith, J.E., Brainard, R., Carter, A., Dugas, S., Edwards, C., Harris, J., … Sandin, S. (2016). Re-evaluating the health of coral reef communities : baselines and evidence for human impacts across the central Pacific. *Proceedings of the Royal Society B: Biological Sciences, 283*(August): 20151985. https://doi.org/10.1098/rspb.2015.1985

Soong, K. (1993). Colony size as a species character in massive reef corals. *Coral Reefs*, *12*(2): 77-83. http://doi.org/10.1007/BF00302106

Szmant-Froelich, A. (1985). The effect of colony size on the reproductive ability of the Caribbean coral *Montastrea annularis* (Ellis and Solander). *Proceedings of the Fifth International Coral Reef Congress, Tahiti*, *4*: 295-300.

Szmant, A.M. (1991). Sexual reproduction by the Caribbean reef corals *Montastrea annularis* and *M. cavernosa*. *Marine Ecology Progress Series*, *74*: 13-25. https://doi.org/10.3354/meps074013

Van Beukering, P., & Cesar, H.S.J. (2004). Economic valuation of the coral reefs of Hawaii. *Pacific Science*, *58*(2): 231–242. https://doi.org/10.1353/psc.2004.0014

Vermeij, M.J.A. & Bak, R.P.M. (2002). Inferring demographic processes from population size structure in corals. *Proceedings of the 9th International Coral Reef Symposium*, *1*: 598–593.

Wilkinson, C. (2008). *Status of coral reefs of the world: 2008*. Global Coral Reef Monitoring Network and Reef and Rainforest Research Center, Townsville, Australia, 296 p.