Title
Spatial dynamics of crustose coralline algae and turf algae as an indicator of reef recovery

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Publication Date
2018

UNIVERSITY OF CALIFORNIA SAN DIEGO

Spatial dynamics of crustose coralline algae and turf algae as an indicator of reef recovery

A thesis submitted in partial satisfaction of the requirements
of the degree of Master of Science

in

Marine Biology

by

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2018

The Thesis of Christina Rachel Jayne is approved, and it is acceptable in quality and form for publication on microfilm and electronically:

Chair

University of California San Diego

2018

DEDICATION

This thesis is dedicated to my mom, Nancy. Despite caring for triplets on her own and never attending a four-year university herself, she has always encouraged me to pursue my passions and education. She is an excellent example of how hard work pays off, and continues to inspire me to never give up.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

ACKNOWLEDGMENTS

I would like to thank my committee chair, Professor Jennifer Smith for both fostering my love of algae and teaching me how to be a better scientist. I am thankful for all the opportunities she has given me, from when I first started volunteering in the lab, to when we crafted a project which would bloom into my Masters research. Professor Smith is a wealth of knowledge and has shown me there are always more wonderful and surprising things to learn. Her vital guidance and continued encouragement helped me keep my focus and motivation throughout my time at Scripps.

I would also like to thank Dr. Emily Kelly, starting from when she took me under her wing as an undergraduate, her infectious enthusiasm and optimism brightened my days. Her round-the-clock support saved me from feeling lost, and her dedication and passion for sharing knowledge is inspiring. I would also like give my sincere gratitude to my other committee members, Professor Brice Semmens and Professor Stuart Sandin. Both have influenced my undergraduate career and have supported me through my graduate career as well. They taught me to always ask questions and think outside the box. To my Smith-Sandin lab family, thank you for your constructive criticism, encouragement, laughs, and sugary sweets. To my volunteer Jonny Charendoff, who assisted me with both this project and other lab work, keep up the excellent work and thank you for your great efforts, without you this project would not have been completed so soon.

This thesis, in part, is currently being prepared for submission for publication of the material. Jayne, Christina; Kelly, E.L.A.; White, D.; Eynaud, Y.; Sparks, R.; Pedersen, N.; Edwards, C.B.; Zgliczynski, B., Sandin, S.A.; Smith, J.E. The thesis author was the primary investigator and author of this material.

ABSTRACT OF THE THESIS

Spatial dynamics of crustose coralline algae and turf algae as an indicator of reef recovery

by

Christina Rachel Jayne
Master of Science in Marine Biology
University of California San Diego, 2018
Professor Jennifer E. Smith, Chair

In 2015, prolonged warming caused severe bleaching across reefs in the Main Hawaiian Islands resulting in widespread coral mortality. In addition to understanding changes in coral populations, it is also important to study algal dynamics on these reefs, especially with a focus on crustose coralline algae (CCA) and turf algae. CCA can serve as indicator for coral growth and recovery, thus playing a significant role in determining the future of bleached coral reefs. Meanwhile, turf algae quickly occupies available space, competes with corals and prevents coral settlement. To assess the state of these Hawaiian reefs, a large-scale mosaic imaging technique has been in use since 2014 to document the conditions of select sites before and after the bleaching event. These 33 m^2 photomosaics cover three reefs in leeward Maui across a gradient of herbivore biomass and sediment input. Analysis of the mosaics shows marked differences in turf and CCA spatial dynamics and percent cover between sites. Sites more protected from anthropogenic influences had the greatest CCA growth, while the site most impacted by local stressors lost CCA abundance and had the highest increase in turf algae. This suggests local management and stressors around a reef may affect CCA and turf growth, and therefore influence coral recovery. The large-area mosaic imaging method may serve as a useful model for analyses of reef resilience on coral reefs.

INTRODUCTION

Coral reefs are hot spots of productivity and biodiversity in the oligotrophic deserts of the ocean (Connell 1978, Ray 1988). Reefs also provide humans food and other vital ecosystem services and associated economic benefits (Moberg and Folke 1999, Wilkinson 2008, Knowlton et al. 2010, Burke et al. 2011). However, many reefs are under threat in the current regime of ocean warming and escalating anthropogenic pressures such as overfishing, eutrophication, and sedimentation (Rogers 1990, Bellwood et al. 2004, D'Angelo and Wiedenmann 2014, Smith et al. 2016). Rising ocean temperatures due to climate change are triggering coral bleaching events that are increasing in frequency and severity (Hughes et al. 2003, Hoegh-Guldberg et al. 2007). Recently, the National Oceanic and Atmospheric Administration (NOAA) declared the third-ever global bleaching event in 2015 / 2016 (Northern hemisphere in 2015, NOAA; Southern hemisphere in 2016, GBRMPA). Much effort has focused on documenting and characterizing the impacts of warming and subsequent bleaching events on coral reefs around the world (Hughes 1994, Pandolfi et al. 2003, Bellwood et al. 2004, Alvarez-Filip et al. 2009, Stuart-Smith et al. 2018). However, most of these studies have simply focused on documenting how these events affect coral cover over time (Gardner et al. 2003, Bruno and Selig 2007, De'ath et al. 2012, Hughes et al. 2018). This approach is certainly valuable, but in order to truly capture how warming and subsequent bleaching events affect coral reef benthic community structure in a broader sense, the remaining benthos must also be investigated.

Algal-Coral Interactions

Coral and benthic algae are the two most common competitors for space on the reef. As global coral cover declines and algae increase (Hughes 1994, Pandolfi et al. 2005, Jackson et al.

2014), examining benthic algae is becoming increasingly important. After bleaching-induced coral mortality occurs, algae rapidly colonize the newly available space of dead coral skeleton (Wellington and Victor 1985, Gleason 1993, McClanahan et al. 2001, Diaz-Pulido and McCook 2002, Diaz-Pulido et al. 2009). The composition of these algae may be key in influencing reef recovery, as the species of algae present may either hinder or promote coral recovery (Glynn 1993). However, most studies examining algae on disturbed or degraded reefs have focused on ecological phase-shifts where healthy reefs become dominated by fleshy macroalgae (Hughes 1994, McCook 1999, Diaz-Pulido et al. 2009, Dudgeon et al. 2010). Despite fleshy macroalgae not normally being dominant on most reefs (Sandin et al. 2008, Bruno et al. 2009, Vroom and Braun 2010, Smith et al. 2016), not many disturbance or bleaching studies have included other algal groups (McClanahan et al. 2001, Diaz-Pulido and McCook 2002, Diaz-Pulido et al. 2009). Additionally, very few studies have explored the dynamics of individual algal patches quantity (but see, Mumby et al. 2005, Renken et al. 2010). Patch size and number of patches are ecologically important in determining population processes and reveals a more detailed response to disturbance. For example, a survey of percent cover may not show any significant changes in algal assemblages, but an increase in patch size and decrease in number of patches may indicate that conglomerate patches have formed. Depending on the algal taxa involved, this result may be important for future reef recovery or decline.

Here, we examine two algal functional groups that have vastly different impacts on coral growth and recovery: turf algae and crustose coralline algae (CCA). These are often the two most abundant algal groups on a reef (Harris et al. 2015, Smith et al. 2016). Turf algae are a broad group of fast-growing filamentous algae with interwoven cyanobacteria forming a dense mat under 1 cm in height (Connell et al. 2014). Turf algae are often the most abundant coral competitor (Barott et al. 2009, 2012, Haas et al. 2010), and high turf cover is common on degraded reefs (Littler, Littler, and Brooks 2006, Sandin et al., 2008). It is also the first successional algal group to recruit to newly-available substrate, such as coral skeleton (Diaz-Pulido and McCook 2002), and can rapidly outcompete corals, CCA, and other algal groups (Littler and Brooks 2006, Smith et al. 2010). Turf can competitively inhibit coral growth and recruitment (Birrell et al. 2005, Vermeij and Sandin 2008, Vermeij et al. 2009), reduce neighboring coral fitness (Vermeji et al. 2010), and promote harmful pathogens and hypoxic zones along turf-coral borders (Barott et al. 2009, 2011). Turf may even outcompete and kill corals, although this may depend on turf species composition or local nutrient load (McCook et al. 2001, Jompa and McCook 2003, Smith et al. 2006, Vermeij et al. 2010). Large patches of turf algae may have an added negative influence on surrounding corals. These patches may reduce spatial connectivity, or the potential for connectivity, between coral colonies. Regeneration of larger coral colonies may be important for reef resilience, as growth, reproduction, and survivorship is related to colony size (Hughes and Jackson 1980, Szmant-Froelich 1985).

In contrast to turf algae, CCA are a group of red encrusting calcified algae and are accepted as beneficial algae for coral, with high CCA cover used as indicator of reef health (Sandin et al. 2008, Barott et al. 2012, Smith et al. 2016). CCA influences reef health in two principal ways, 1) CCA greatly contributes to reef structure by encrusting over reef rubble, acting as a cement to solidify the reef and prevent erosion (Setchell 1930, Barnes and Chalker 1990). And 2) certain species of CCA promote both the settlement and survival of coral recruits (Morse et al. 1988, Harrington et al. 2004, Price et al. 2010, Tebben et al. 2015). Unlike turf algae, CCA does not increase pathogen load at CCA-coral borders (Barott et al. 2009, 2011). Corals may struggle to outcompete turf unless there is a sufficient herbivore population (Barott et al. 2012) but can easily overgrow CCA, allowing for easier colony expansion or regeneration of lost tissue following mortality.

For coral planula, the size of CCA patches present on the reef may be critically important for settlement and continued survival. Given a larger local beneficial environment in the form of a larger CCA patch, this may allow higher recruitment and lower mortality rates. Compared to a “sprinkling” of many small CCA patches, coral planula may experience increased difficulty in finding a suitable settlement surface and may be in closer proximity to surrounding benthic competitors.

Local impacts on reef communities

Just as herbivore abundance on a reef may be altered by human activity (*via* fishing) and therefore influence benthic community structure, other anthropogenic stressors such as input of terrigenous sedimentation contribute to coral stress (Fabricius and De’ath 2001a, Fabricius 2005), mortality (Richmond 1997, Erftemeijer et al. 2012), and CCA loss (Fabricius and De'ath 2001b). Excess sediment input on a reef may be caused by land erosion and is often intensified in areas of coastal development (Hubbard 1987, Rogers 1990). Sedimentation can inhibit recovery by preventing coral settlement and reducing coral spat survival (Sato 1985, Babcock and Mundy 1996, Richmond 1997, Jones et al. 2015).

Turf algae can exacerbate negative effects from sedimentation as dense turf traps sediment preventing resuspension and further deterring coral settlement (Airoldi 1998, Purcell 2000, Birrell et al. 2005). Sediment-laden turf algae also discourages grazing from some herbivores (Bellwood and Fulton 2008, Goatley and Bellwood 2012, Tebbett et al. 2017), and has even been shown to become an enhanced competitor against CCA (Steneck 1997).

Runoff or sewage injection wells also contribute not only sediment, but bring concentrated nutrients to the reef (Amato et al. 2016). The high levels of nitrogen and phosphorous present in this water can fertilize algae, enhancing growth rates and can contribute to an increase in abundance of turf and macroalgae (Bell 1992, Fabricius et al. 2005).

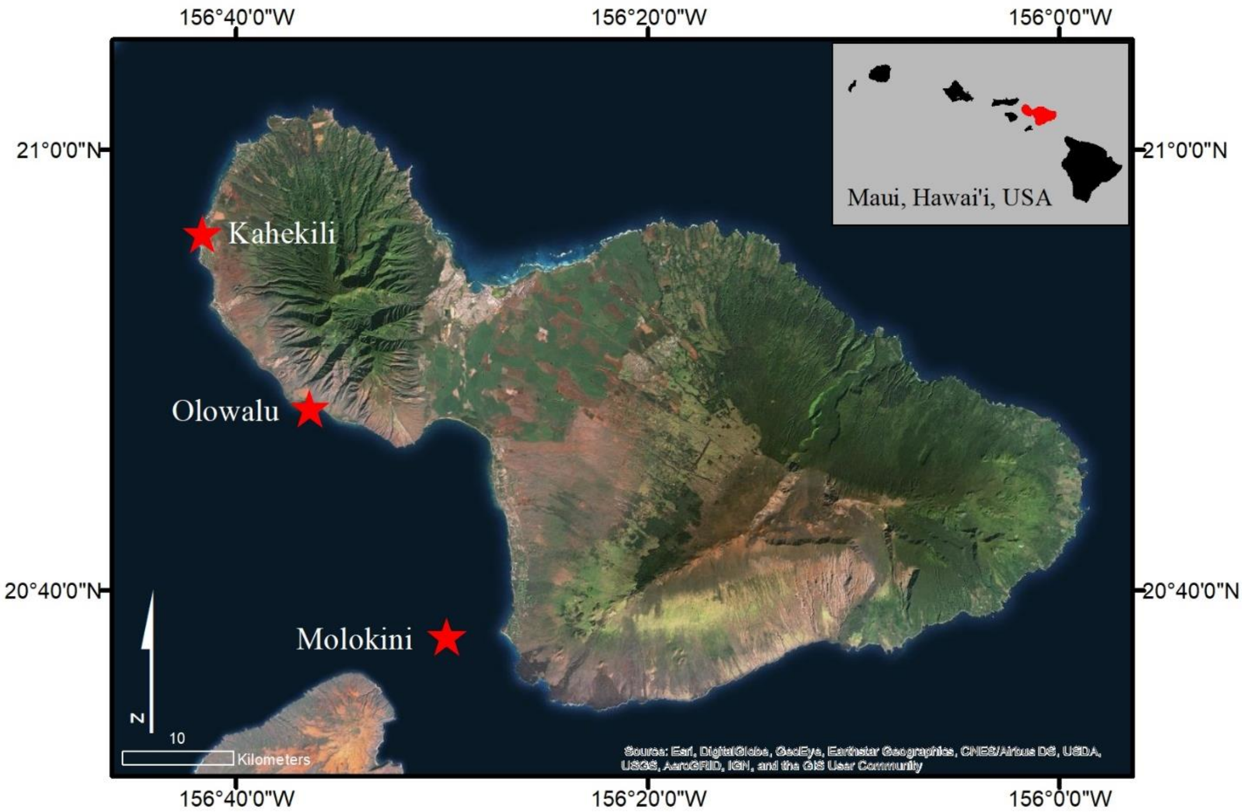
An ideal location to study algal change after bleaching is the reefs of Maui, Hawai'i. These reefs are exposed to a gradient of human impacts and bleached during the 2015 water warm event. We started monitoring several of these reefs in 2014, and were able to collect data before (2014) and after (2016) the bleaching event. While many studies have focused on the impacts of human activity such as fishing, nutrient input, and sedimentation on reef community structure, few have studied algal response to warming in this context (McClanahan et al. 2001, Diaz-Pudilo et al. 2009).

The purpose of this study was to investigate the trajectory of benthic algal communities on coral reefs of Maui, Hawaii following a temperature induced bleaching event. Specifically, I focus on two main questions: 1) How does algal community structure change following a bleaching event? Explicitly, 2) How does the abundance and size distribution of patches of algal functional groups (turf algae and CCA) vary over time? I then discuss how this may relate to the future reef recovery. To address these questions, we analyzed algal community composition, abundance, and patch size dynamics at three sites on leeward Maui with varying degrees of management, before (2014) and after (2016) the 2015 coral bleaching event.

METHODS

Study Sites

This study was conducted on the leeward side of the island of Maui, Hawai'i, USA. The Hawai'i Division of Aquatic Resources (DAR) have maintained multiple long-term monitoring sites across leeward Maui since 1999 to track changes in reef community structure over time. Collaboration between DAR and Scripps Institution of Oceanography led to establishment of large-scale photomosaic plots (see details below) at three of these sites in 2014. These sites, Olowalu (OLO) (20.80465˚, -156.60721˚), Kahekili (KAH) (20.936660˚, -156.693650˚), and Molokini (MOLO) (20.631360˚, -156.496310˚) (Fig. 1) vary in their levels of terrigenous sedimentation and fishing management. During 2015, most of the Hawaiian Islands including Maui experienced extensive warming and severe coral bleaching, resulting in an estimated 20-40% mortality rate of corals for the island (Sparks 2016 unpublished data). All three sites bleached during the global bleaching event in 2015 / 2016. My goals were to explicitly investigate change in algal community structure following this bleaching event from the three sites (described in detail below) between 2014 (pre-bleaching) and 2016 (post-bleaching).



Source: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community

Figure 1 Satellite image of the island of Maui, Hawai'i. Study sites indicated by stars at Kahekili, Olowalu, and Molokini.

Olowalu is located offshore of mile-marker 14 along the Honoapiilani Highway (Route 30) on the central coast of leeward Maui. Olowalu is a popular tourist destination for snorkeling, dominated by encrusting *Montipora,* and is a favorite local site for diving and fishing. Fishing is regulated here according to state-wide regulations. The previous decades of upland sugarcane farming also influence this reef, in which rains can wash sediment from fallow fields onto the reef, producing substantial sediment plumes (Kelly unpublished). Out of the three sites we examined, Olowalu had the highest amount of terrigenous sedimentation (Kelly unpublished) and the fewest fishing regulations. Fish herbivore biomass is lower than the other two sites, Kahekili and Molokini (Kelly 2015).

Kahekili is located on the northwestern shore of Maui and is found within the Kahekili Herbivore Fisheries Management Area (KHFMA). This site is dominated by branching *Porites* *compressa*. Established in 2009, this 2 km^2 management area prohibits take of herbivorous fishes and sea urchins. Since the establishment of the KHFMA, fish herbivore biomass has increased and appears to be continuing to recover from 2008 levels (Williams et al. 2016). The site is also a popular tourist destination for recreational water activities. Of our three study sites, Kahekili has a moderate input of terrigenous sedimentation (Kelly, unpublished) and moderate fishing restrictions (Williams et al. 2016). Kahekili receives agricultural runoff and nutrient input via a sewage injection well (Dailer et al. 2010). Fish herbivore biomass is higher than Olowalu but lower than Molokini (Kelly 2015).

Molokini is located within a partially-sunken crater within the ʻAlalākeiki Channel, approximately 4 km offshore the southwestern coast of Maui. It has the highest coral cover of the three sites, and is dominated by encrusting and plating *Montipora*. Molokini was designated a Marine Life Conservation District area in 1977 and as such, the take of any marine life is prohibited within the islet cove. No-take recreational activities such as swimming, snorkeling and SCUBA diving are allowed. Of the three sites, Molokini has nearly no terrigenous sedimentation due to its remote location, and has the strictest fishing management practices. Molokini has the greatest fish biomass out of the three sites (Kelly 2015).

Traditional benthic sampling methods that use transects of a given length or quadrats of predefined (small; 0.5-1 m^2) areas are used in replicate to estimate percent cover of benthic taxa. However, these techniques are not conductive to measuring population characteristics such as patch sizes and size class frequency distributions of different taxa because the areas are generally not large enough to capture the range of variability that exists in these parameters.

Here we avoided these constraints such as limited area sampled, non-contiguous areas common with quadrat sampling, and restricted dive time to allow for full large-scale analysis of the entire algal community. To do so, we employed a large-area imaging technique to digitally capture a continuous, spatially-accurate large area (~100 m^2) image of the benthos. This allowed for a digital representation of the reef to be thoroughly analyzed in post-processing, revealing community composition, cover, and patch size dynamics.

At each site photomosaic plots of 100 m2 (10 m x 10 m) were created using images collected in the water and processed with custom computer software Viscore. Images were collected in July of 2014 (15 months pre-bleaching) and June 2016 (6 months post-bleaching). Each plot was geo-referenced to steel rods in the reef using GPS coordinated collected from the surface. Olowalu images were captured at approximately 10 m depth, with Kahekili at 8 m, and Molokini at 12 m. Plot size, image collection, and post-processing was determined by procedures established by the Sandin Lab at Scripps Institution of Oceanography (Edwards et al. 2017) based on work by Gracias et al. (2003) and Lirman et al. (2007).

Image Collection

To create large-area photomosaics, a two-member SCUBA dive team photographed the benthos utilizing two DSLR Nikon D7000 16.2 megapixel cameras in Ikelite housings mounted on a custom frame. One camera was equipped with an 18 mm lens and mounted next to a duplicate camera equipped with a 55 mm lens. Images from the 18 mm camera were used to create each photomosaic, while images from the 55 mm served as reference images for algae identification. Each camera’s internal intervalometer was used to automatically capture one photograph every second. Divers swam in a repeated lawnmower configuration (lawnmower, then repeated at 90˚ of original swimming angle) approximately 1.5 m above the benthos at a slow pace (5–7 m min^{-1}) to ensure overlap of images to create a 10 m by 10 m (100 m^2) survey area.

Computer Processing

Raw images collected from each site were processed using Agisoft Photoscan from which 3D models and 2D orthophotographs were made. These products include a 3-dimensional point cloud visualization of the reef. This point cloud model was calibrated with corresponding depth measurements gathered at each site, and flattened into a 2D orthophotograph. This orthorectified composite eliminated edge and perspective distortion and created a spatially accurate orthoprojection image of the reef.

Algae Identification

Each orthoprojection was uploaded to Adobe Photoshop CS6 to annotate the benthic algal community. For data extraction and analysis, one-third (~3.3 m x 10 m, 33m^2) of the full photomosaic was utilized. Using a tablet and pen, every visible algal patch was categorized and traced (Fig. 2). An algal patch was defined as a distinct, continuous area of an algal group. Patches were identified to the finest taxonomic scale possible, with macroalgae identified to genus and other patches identified to functional group. These groups included 10 different functional groups or genera: Crustose coralline algae (CCA), sediment-free turf algae, sediment-laden turf algae, *Amansia glomerata*, *Peyssonellia spp.*, *Halimeda spp*., *Asparagopsis taxiformis*, and cyanobacteria. Each of these groups were traced on separate Photoshop layers using different colors, and the final image with only the algal layers visible was exported as a PNG image file to be processed (Fig. 3) (see Fig. 4-6 for all digitized plots). This same process has been used for coral colonies and produced minimal error (Edwards et al. 2017).

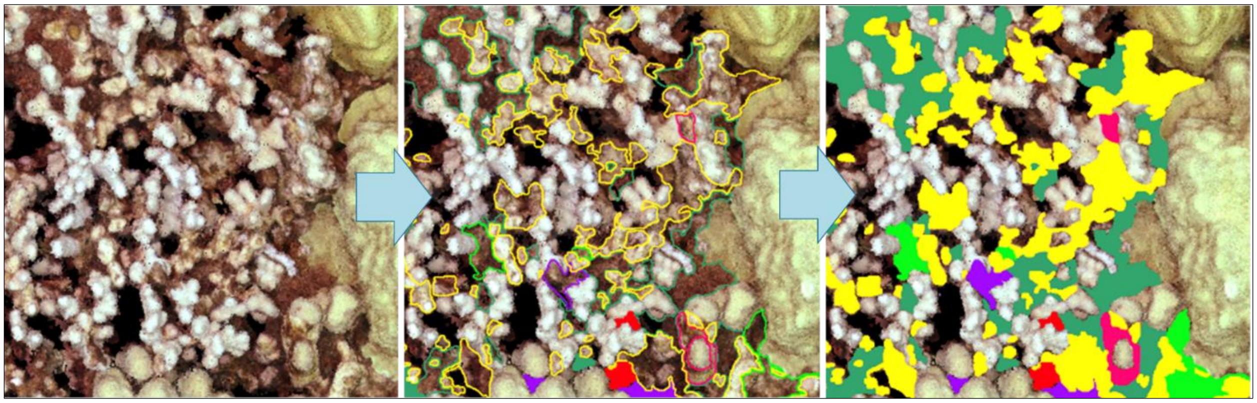


Figure 2 Process of tracing algal patches, from orthoprojection (left) to outlined patches (middle) to completed patch digitization (right).

The PNG image was then analyzed using a custom algorithm package created at SIO (*MosaicAnalysis*) (Edwards et al. 2017) using R 3.4.3 (R Core Team 2017). This algorithm categorized algal patches by identifying RBG pixel values that matched with each designated functional group (colored separately in Photoshop), then enumerated each algal patch and calculated the pixel area using polygon approximation. Each photomosaic was calibrated to *in situ* measurements, creating a pixel-to-cm^2 ratio which permitted the conversion of patch size pixel number to cm^2 area. Algal cover was calculated using the total area from all patches of each algal group, divided by the total area of the plot (33 m^2). For patch size and quantity analysis, only patches with a calculated area of $\geq$ 1cm^2 were considered to eliminate patch count error due to single edge pixels being counted as individual patches.

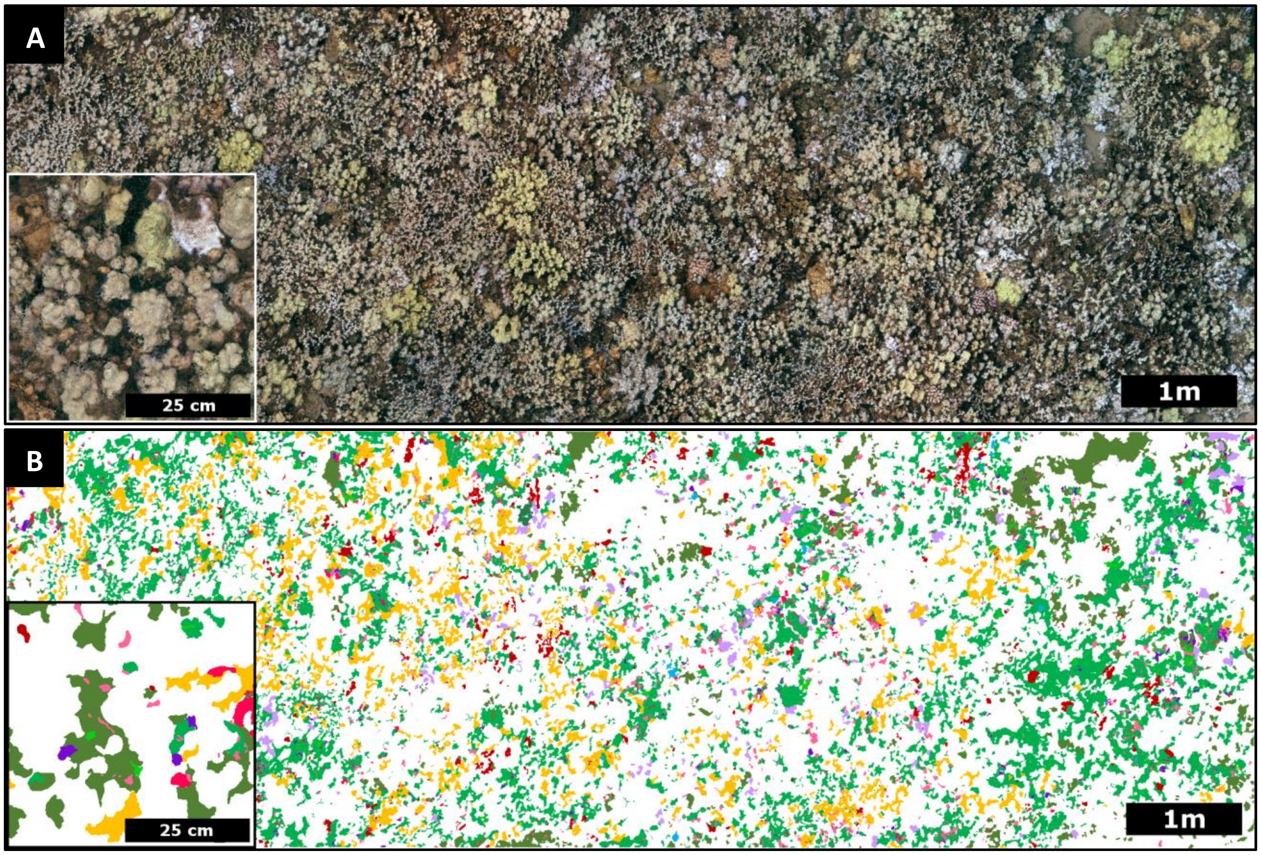


Figure 3 a) 3.3 m x 10 m mosaic orthoprojection of 2014 Kahekili with inset view enlarged to show detail and b) the same plot, showing only the digitally-traced algal groups

Statistical Methods: Patch Dynamics

Change in patch size and number were explored for CCA and turf algae, and as patch size for both groups is heavily skewed towards smaller patch sizes, data were log-transformed. Differences in patch sizes between years were explored using a boostrapping approach. Our null hypothesis was that algal patch size at each site was constant between 2014 and 2016. To do this, patch sizes within a given site from 2014 and 2016 were combined and resampled with replacement 10,000 times. A random sample was then taken for a theoretical group A with n_A=original n from 2014, and a theoretical group B with n_B=original n of 2016. A distribution was then created using distances between these theoretical group values; this represented the null hypothesis. The mean distance between the actual data were compared against the null distribution to calculate the probability of change in patch size between years. An empirical cumulative distribution function was then utilized to determine statistical significance ($\alpha < 0.05$).

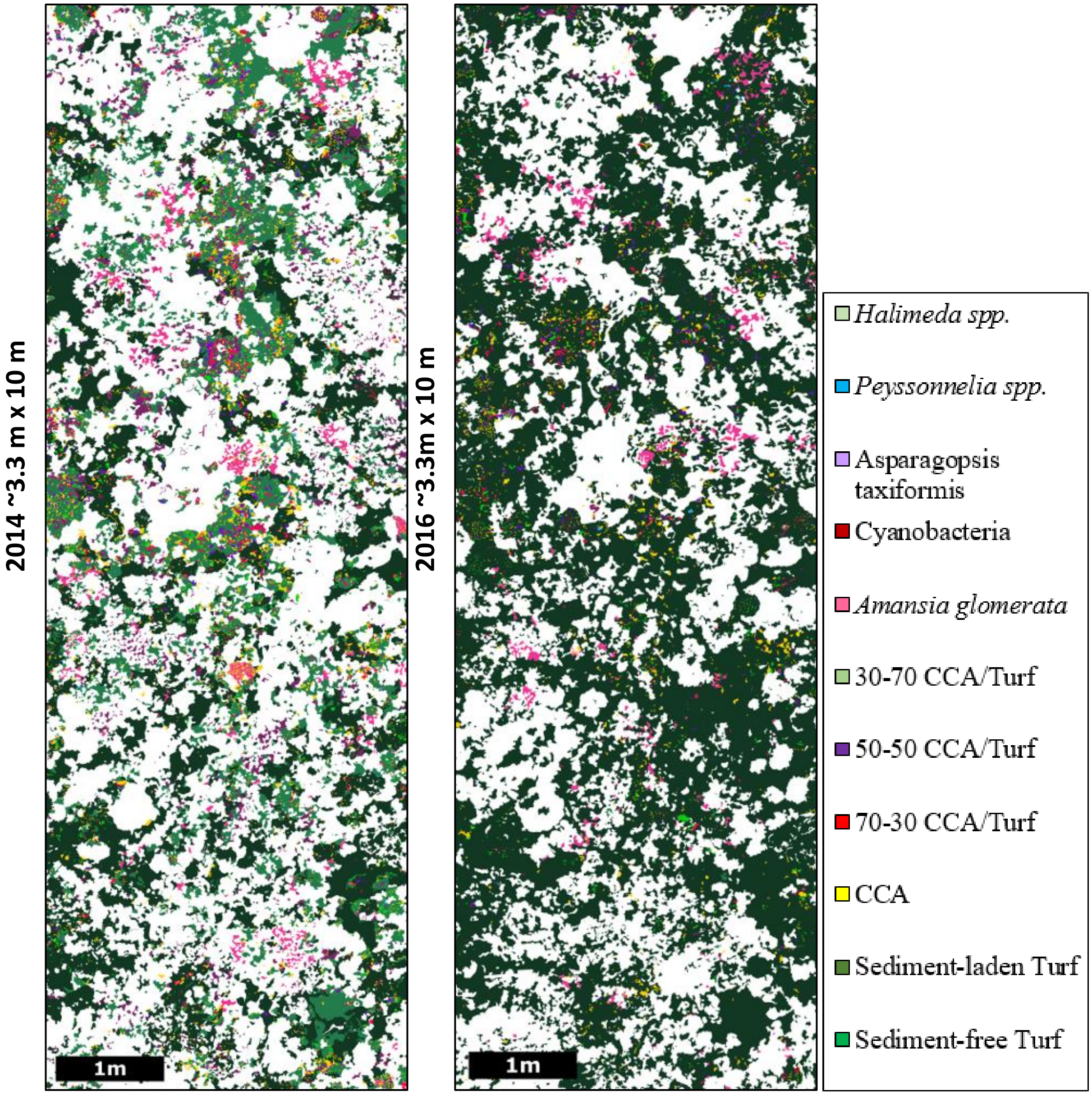


Figure 4 Olowalu digitized algal community plots, 2014 (left) and 2016 (right)

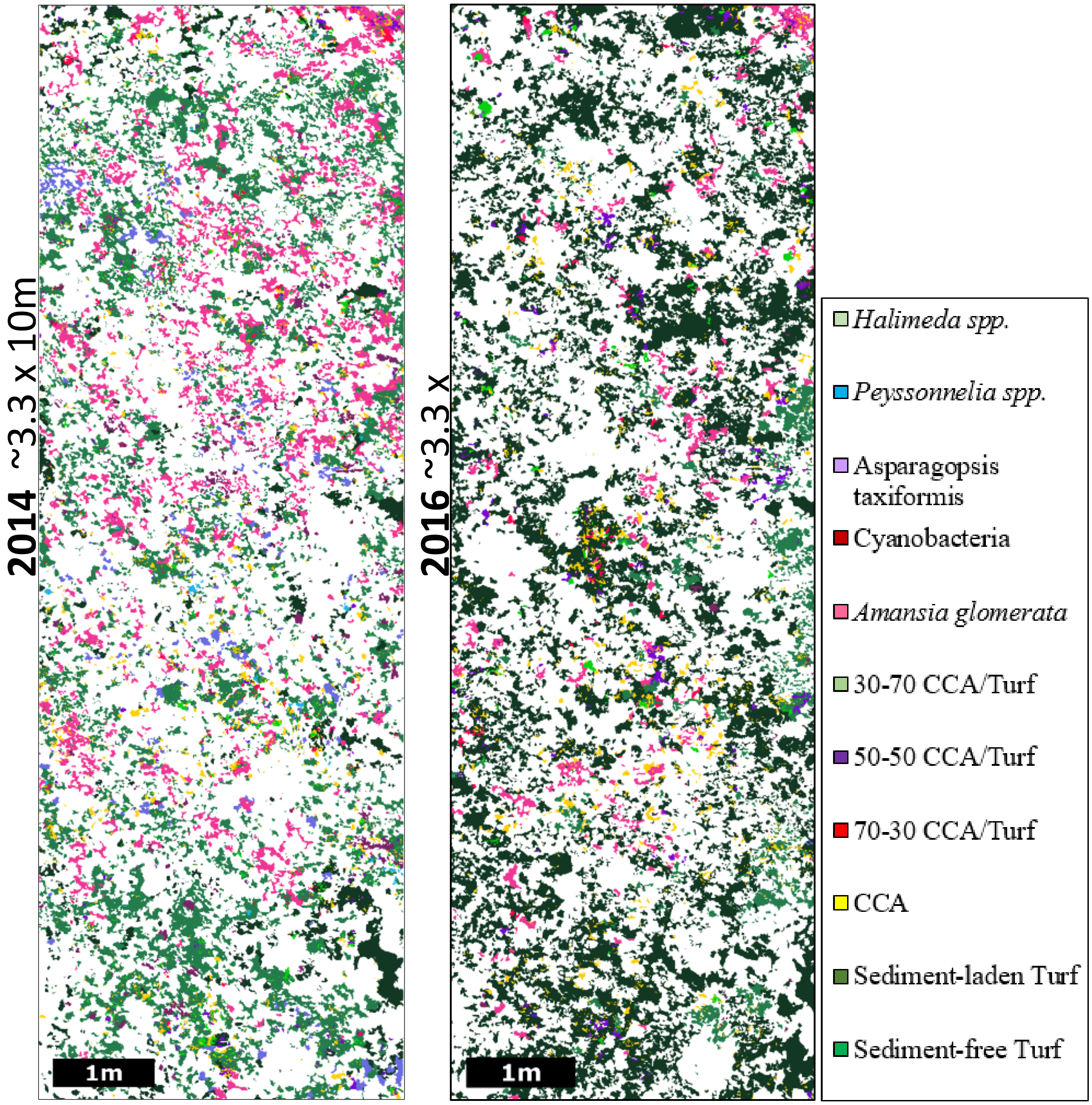


Figure 5 Kahekili digitized algal community plots, 2014 (left) and 2016 (right)

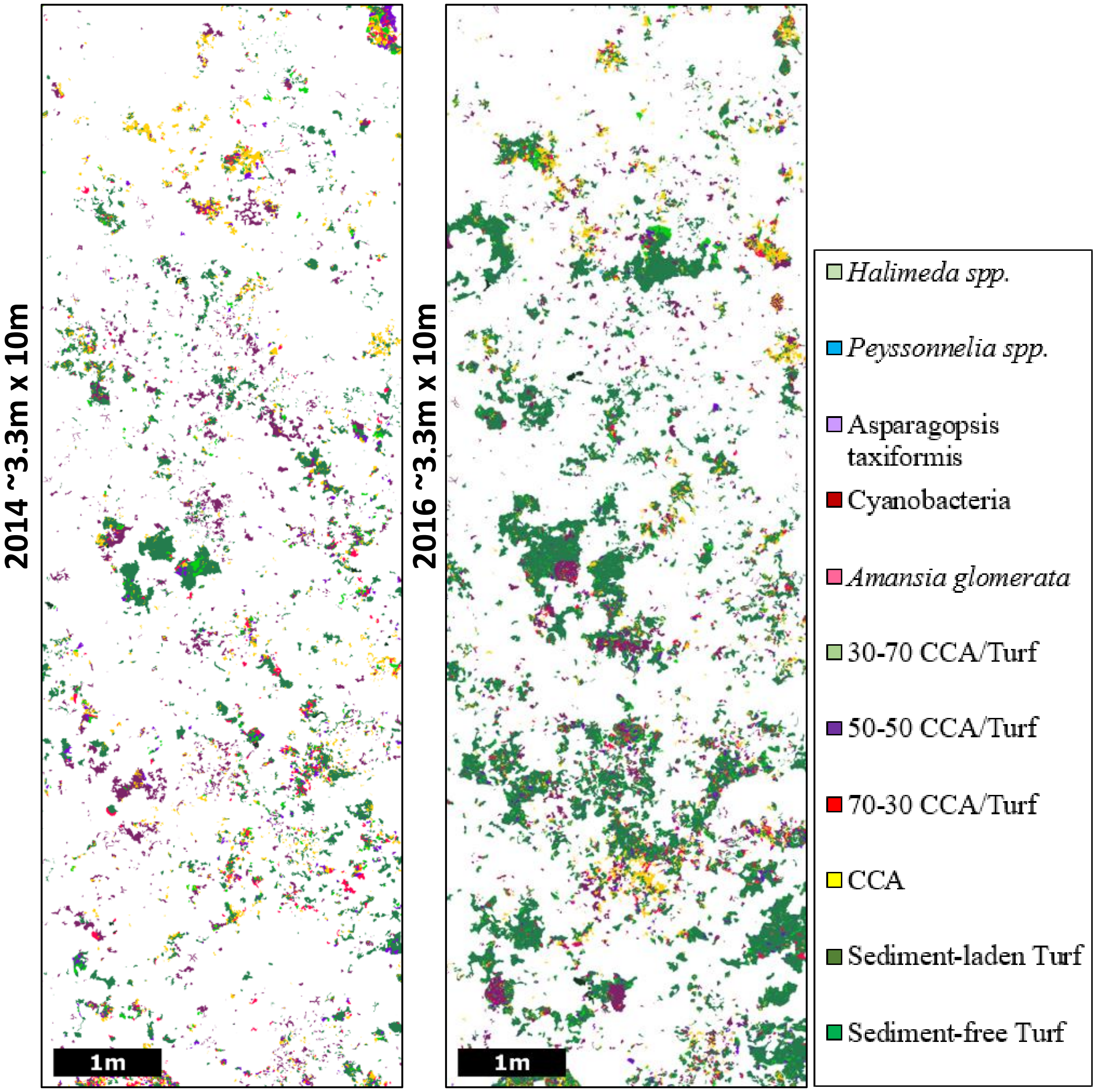


Figure 6 Molokini digitized algal community plots, 2014 (left) and 2016 (right)

RESULTS

Algal Community Composition (Percent Cover)

Algal community composition change was analyzed *via* percent cover. Percentage cover of algal groups was variable between sites, but total algal cover increased at all sites from 2014 to 2016, with total turf algae abundance and proportion increasing the most (Fig. 7 and 8). Turf algae was also the most abundant group at all sites, with CCA, cyanobacteria, and *Amansia glomerata* comprising the top four most abundant groups across sites and years. For our analyses, we use the term “turf algae” to include both sediment-free turf and sediment-laden turf. Although the two nearshore sites (Olowalu and Kahekili) experienced substantial increased turf sedimentation in 2016 (Fig. 7 and 8), it is unknown if this was an ephemeral occurrence. It was also noted that a rain event disturbed Olowalu shortly before images were collected for the 2016 photomosaic.

Olowalu had the highest percent cover of algae of all sites, with an increase from 46.0% to 57.2% (+ 11.2% cover) from 2014 to 2016, with turf algae accounting for the majority of the increase (from 38.4% to 54.3%, + 15.9% turf cover). This accompanied a decrease in other algal groups, with turf algae accounting for 83.5% of the overall algal community in 2014 then increasing to 94% in 2016. Olowalu was the only site with a decrease in CCA cover, which dropped to less than half its previous cover in 2014 (from 3.2% to 1.6%, - 1.6% cover), which is a proportional decrease from 7.1% of the algal community in 2014 to only 2.8% in 2016. *Amansia glomerata* occupied approximately 1% of the plot in both years and did not show a notable change in cover (-0.2% cover). Cyanobacteria covered 3.0% of the plot in 2014 but nearly vanished in 2016, dropping to 0.2% cover.

Kahekili had a moderate abundance of algae compared to the other two sites, with 32.6% total algal cover in 2014 and increasing to 38.9% in 2016 (+ 6.3% cover). Turf algae increased from 21.3% in 2014 to 34.5% in 2016 (+13.2% turf cover) (proportional increase from 65.3% to 88.7% of all algae present), while there was no noteworthy difference in CCA (- 0.03% cover). *Amansia glomerata* composed 20% of the algae in 2014, but decreased to 5.2% in 2016 as cover declined from 6.7% to 2.0% percent cover (-4.7%). The fleshy macroalga *Asparagopsis taxiformis* declined from 1.2% cover in 2014 to 0.004% in 2016.

Molokini had the lowest overall percent cover of algae of all sites, which increased from 10.2% to 22.2% between years (+ 12.0% cover) (Fig. 7). The algal community was dominated by turf algae, CCA, and cyanobacteria. Both *Amansia glomerata* and *Asparagopsis taxiformis* were not found in the imagery. Turf algae cover increased three-fold from 5.3% in 2014 to 15.2% in 2016 (+ 9.9% cover), which proportionally accounted for 52% of the total algae in 2014 and 68% in 2016. CCA cover doubled from 2.4% to 4.9% (+ 2.5% cover), accounting for 23.5% of algae in 2014 and 22.0% in 2016. Molokini had greater cyanobacteria cover compared to the other two sites (2.5% in 2014 and 2.1% in 2016). And although percentage cover remained constant between the two years (- 0.4% cover), the proportion of cyanobacteria dropped from 24.4% in 2014 to 9.4% in 2016 due to the increase of turf and CCA.

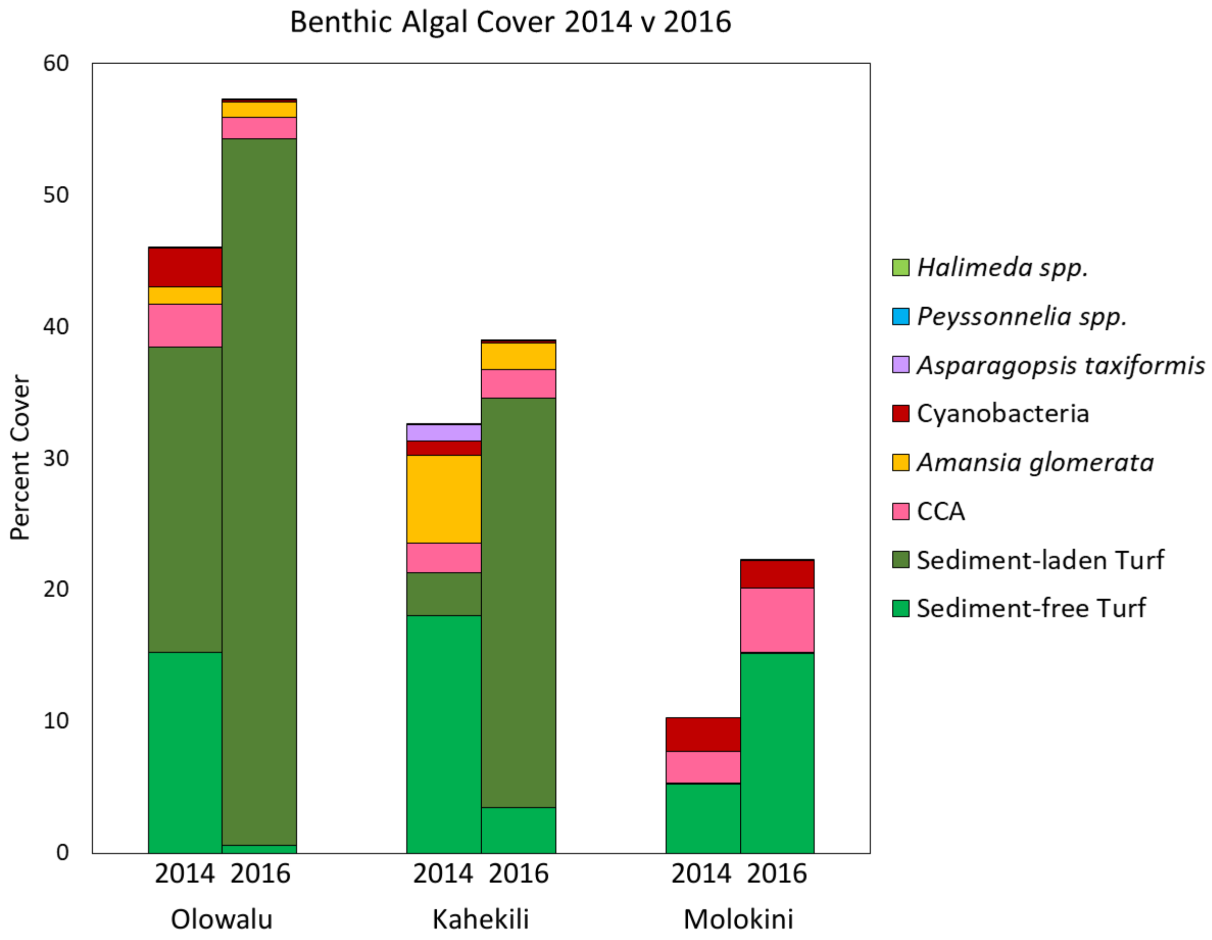


Figure 7 Percent cover of algal groups before (2014) and after (2016) bleaching at each site.

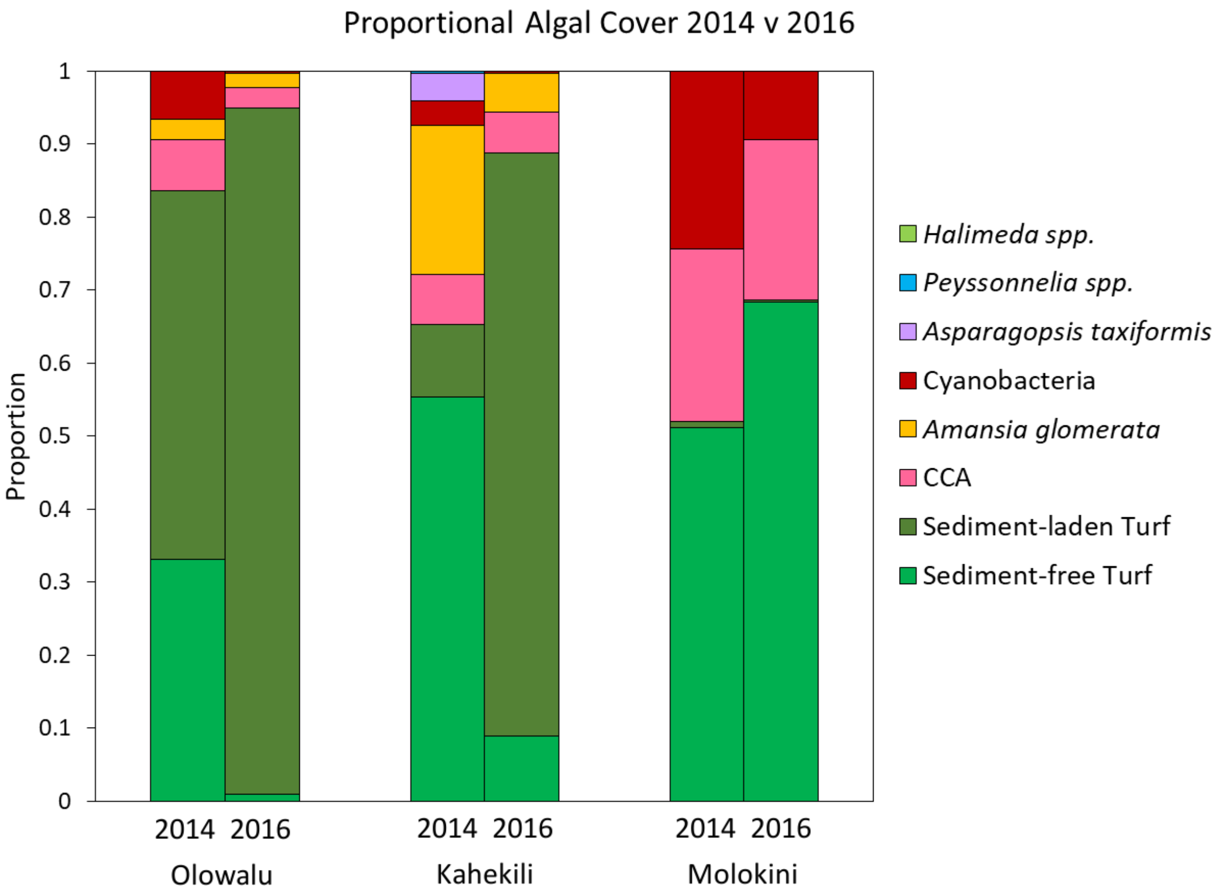


Figure 8 Proportional algal community of each site, before (2014) and after (2016) the 2015 bleaching event.

Sites summary of percent cover change (Fig. 9)

Although turf cover increased at all sites, Olowalu had the greatest increase (+15.9% cover), Kahekili had a moderate increase (+13.2% cover) and Molokini had the lowest increase in percent cover of turf algae (+12.0% cover). Meanwhile, CCA cover decreased at Olowalu (-1.6% cover), did not change at Kahekili (-0.03% cover), and increased at Molokini (+ 2.5% cover).

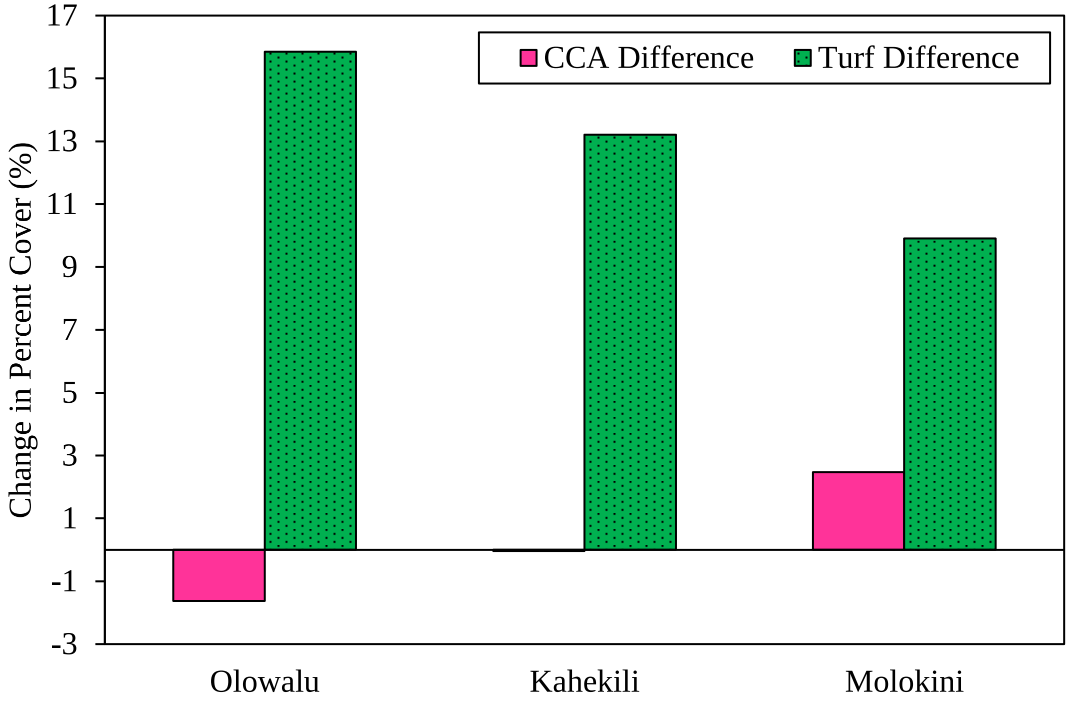


Figure 9 Change in percent cover of turf algae (dotted green) and CCA (pink) at each site.

Algal Patch Size and Number

Shift in algal patch dynamics were examined by analyzing patch sizes and number of patches by site and year. A total of 31,555 algal patches (≥ 1 cm^2) were identified from the photomosaics (3 sites, 2014 and 2016 images, 200m^2 total area). The overall number of algal patches varied by site and by year within a site. However, 2 out of the 3 sites showed a decline in the number of algal patches between 2014 and 2016 (Table 1). Specifically, Olowalu had 7,596 patches in 2014 and 3,139 in 2016, Kahekili had 6,220 patches in 2014 and 3,957 patches in 2016, however, at Molokini, the number of patches increased from 4,589 in 2014 to 6,054 in 2016.

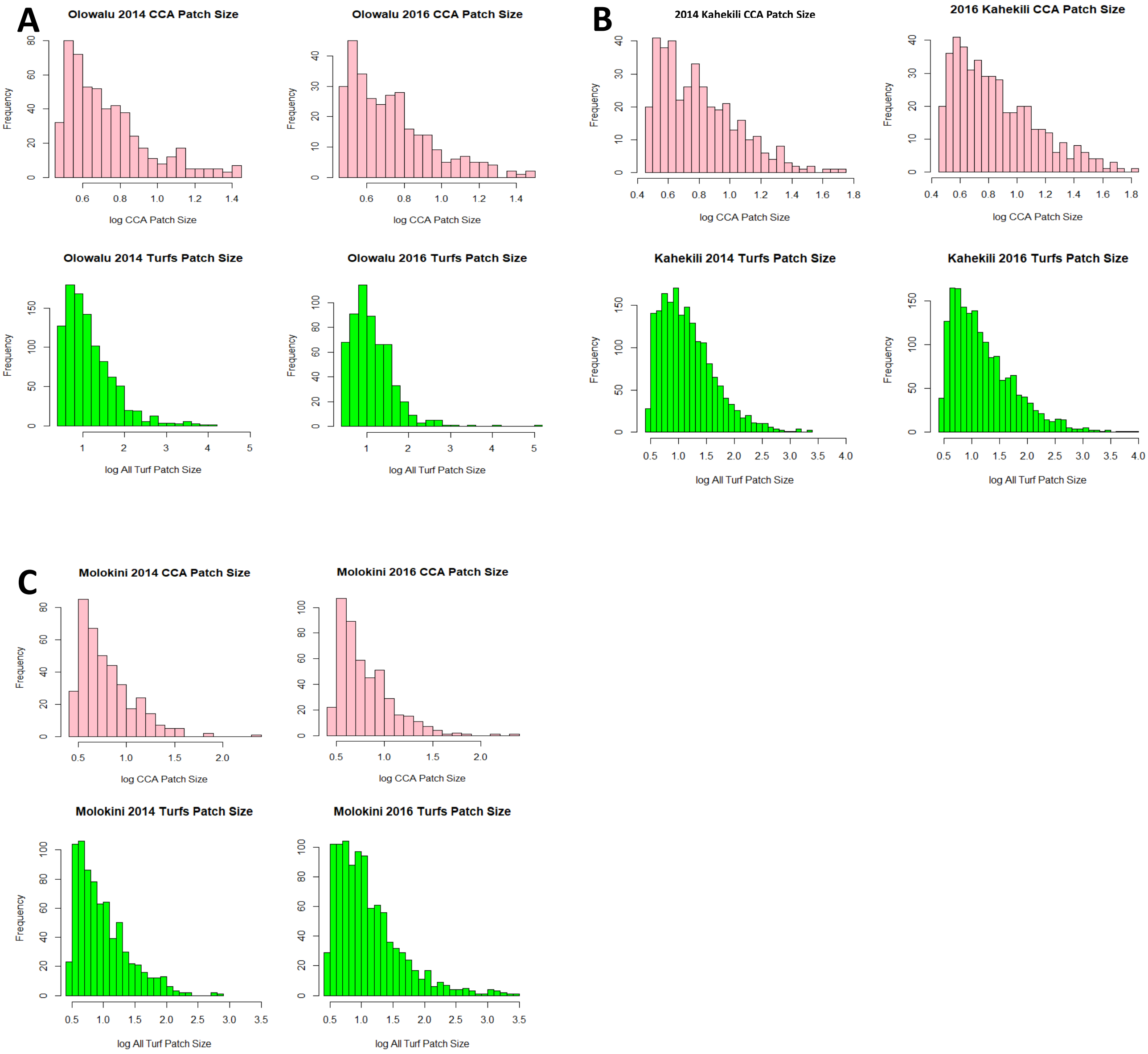


Figure 10 Histograms showing algal patch size data (log-transformed) before (2014) and after (2016) the bleaching event, at each site a) Olowalu, b) Kahekili, and c) Molokini.

At Olowalu, turf patch size changed significantly ($p < 0.0001$) from 2014 to 2016. Although there was a decrease in moderate-size patches (Fig. 10 and 11) mean patch size quadrupled from 54.96 ± 5.92 cm^2 to 224.83 ± 180.72 cm^2 years, driven by a single patch of turf algae that covered $14m^2$ of the $33m^2$ plot area. The total number of turf patches also declined from 2,258 turf patches in 2014 to 792 in 2016. Although CCA percent cover declined at this site, CCA patch size was not found to be significantly different between years ($p = 0.1702$) and mean patch size did not vary (2.85 ± 0.7 cm^2 to 2.99 ± 0.10 cm^2), but the number of patches decreased from 2,065 in 2014 to 1,048 in 2016.

At Kahekili, turf algae patch size significantly increased from 2014 to 2016 ($p = 0.0179$), with the most noticeable difference in larger algal patches (Fig. 10 and 11). The number of turf patches decreased from 2,409 in 2014 to 2,252 in 2016, while mean patch size almost doubled, from 28.32 ± 2.18 cm^2 to 50.29 ± 6.61 cm^2, indicating the coalescing of smaller patches. Despite virtually no change in CCA percent cover between years, patch size significantly increased ($p < 0.0001$) (Fig. 10 and 11). Patch count decreased from 1,203 in 2014 to 1,036 in 2016 with a slight increase in mean patch size (3.61 ± 0.13 cm^2 to 4.94 ± 0.21 cm^2).

At Molokini, turf algae patch size increased significantly ($p < 0.0001$) while CCA patch size was not found to be significantly different ($p = 0.0616$). Mean turf patch size nearly tripled from 11.10 ± 0.96 cm^2 to 31.37 ± 3.99 cm^2. Unlike the other two sites, the number of both turf and CCA patches increased between years. Turf patch number increased from 1,346 to 1,478, while CCA patch number increased from 1,102 to 1,456. Just as any shift in CCA patch size was not significantly different between years, mean patch size also did not change (3.98 ± 0.24 cm^2 to 3.86 ± 0.23 cm^2).

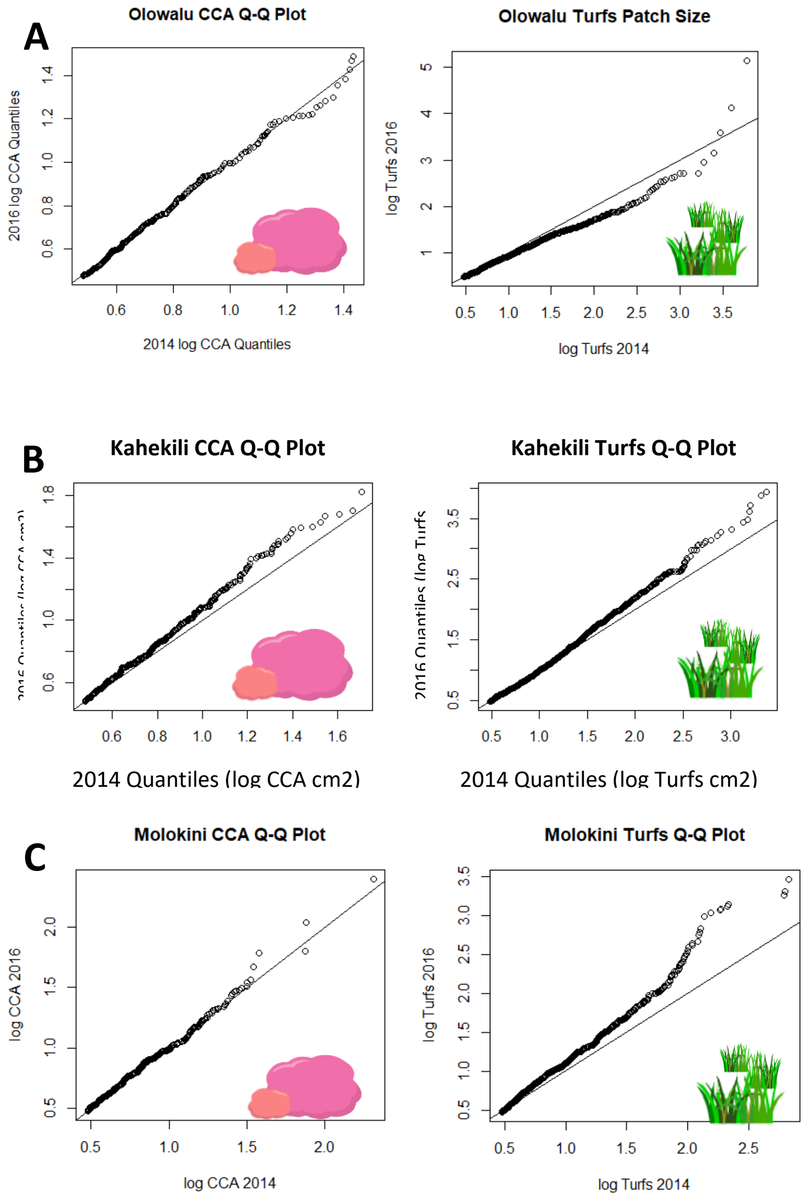


Figure 11 Quantile-quantile plots illustrate algal patch size change between years (2014 and 2016), as each site, a) Olowalu, b) Kahekili, and c) Molokini. Points above the diagonal indicate an increase in patch size between years, while points below the diagonal indicate a decrease.

Sites summary of patch dynamics (Table 1)

From 2014 to 2016, turf patch size increased at Kahekili and Molokini, with a decrease at Olowalu due to the formation of one extremely large conglomerate patch. CCA patch size significantly increased at Kahekili ($p < 0.0001$), but no significant differences were found at Olowalu or Molokini (Fig. 10). To illustrate patch size differences between years, size distributions were compared using Quantile-Quantile (Q-Q) plots (Fig. 11). Points above the 1:1 line, it indicate an increase in patch size from 2014 to 2016 and those below indicate a decrease in patch size between years. Olowalu shows a decrease in turf algae patch size ($p < 0.0001$), with no difference in CCA patch size ($p = 0.1702$). Kahekili shows increase in both turf ($p = 0.0179$) and CCA patch size ($p < 0.0001$), and Molokini shows an increase in turf algae patch size ($p < 0.0001$) with no significant difference in CCA patch size ($p = 0.616$).

Table 1 Summary of algal change between years, at each site. Patches ≥ 1 cm^2 except for percent cover.

Site	Percent Cover (all patches)		Patch Size (patches ≥ 1cm^2)		No. of Patches (patches ≥ 1cm^2)		Mean Patch Size (patches ≥ 1cm^2)	
	CCA	**Turf**	**CCA**	**Turf**	**CCA**	**Turf**	**CCA**	**Turf**
OLO	Decrease	Increase	No diff $p = 0.1702$	Decrease **$p < 0.0001$**	Decrease	Decrease	No diff	Increase
KAH	No diff	Increase	Increase **$p < 0.0001$**	Increase **$p = 0.0179$**	Decrease	Decrease	Increase	Increase
MOLO	Increase	Increase	No diff $p = 0.0616$	Increase **$p < 0.0001$**	Increase	Increase	No diff	Increase

DISCUSSION

Most studies that have documented the impact of disturbances such as warming events and subsequent mass bleaching on coral reefs have focused solely on changes in coral cover. While this approach has been useful in surveying coral loss and recovery (McClanahan 2000, Bruno and Selig 2007, De'ath et al. 2012, Hughes et al 2018), it does not provide a holistic perspective of how the reef community has changed or responded to a particular stress event. Low coral cover does not necessarily equate to a degraded ecosystem, nor does it guarantee reduced potential for coral regrowth and recovery (Diaz-Pulido et al. 2009). Furthermore, many reefs are dominated by benthic algae (Sandin et al. 2008, Bruno et al. 2009, Vroom and Braun 2010, Smith et al. 2016), and the assemblage shifts of these algae are important when considering how a reef system as a whole is functioning (e.g., is it dominated by reef builders or fleshy algae?). Many studies have focused on coral to fleshy macroalgae phase-shifts (Hughes 1994, McCook 1999, Diaz-Pulido et al. 2009, Dudgeon et al. 2010), but most reefs have other dominant algal groups such as turf algae and CCA (Sandin et al. 2008, Bruno et al. 2009, Smith et al. 2016) with few exceptions (Vroom and Braun 2010) yet these groups have received much less attention.

High turf algae cover is often associated with degraded reefs (Littler, Littler and Brooks 2006, Sandin et al. 2008), while high CCA cover is considered the indicator of a healthy, calcifying reef (Sandin et al. 2008, Barott et al. 2012, Smith et al. 2016). Even if relying on solely coral cover for recovery estimations, an increase in coral requires regrowth or the settlement and establishment of new coral recruits, both processes that involve interaction with benthic algae (Hughes 1994, Birrell et al. 2005, Diaz-Pulido et al. 2009). The goals of this study were to explicitly follow benthic algal assemblages through a warming induced coral bleaching event on the island of Maui, Hawaii at a scale never before possible. Specifically, we highlight the following aspects of algal change on bleached reefs: 1) shifts in algal assemblage after bleaching, 2) underlying patch dynamics giving a more nuanced picture of algal change, and 3) since algal dynamics varied by site, a discussion of the possible influence of local environmental conditions on algal assemblage.

Changes in Algal Community Structure Following Bleaching Induced Coral Mortality: Percent Cover

The 2015 bleaching event had severe effects on the reefs of Maui, and the resulting 20-40% coral mortality (Sparks, 2016 unpublished data) created a shift in benthic community structure. Coral mortality opened up space for settlement and growth of benthic algae, as seen in an increase in algal cover at all sites in 2016. However, community composition and abundance shifts varied by location. Turf algae was the dominant group at all sites, and had the greatest abundance and proportional increase out of all algal groups. Our results show increase in turf abundance is consistent with smaller-scale studies (Diaz-Pulido and McCook 2002) that document turf algae as the first and dominant algal group to colonize coral skeletons after a bleaching event. Increase in turf cover varied by site, with the greatest increase at Olowalu, followed by Kahekili, and the lowest at Molokini. Shift in CCA cover also varied by site as CCA either decreased (Olowalu), stayed the same (Kahekili), or increased (Molokini).

The differences in algal community structure and change over time following the bleaching even could be associated with the local context at each study site. Olowalu, the site with minimal fishing restrictions and greatest sediment input (Kelly unpublished) had the highest total algal cover during both years, and the greatest increase in cover. Turf algae was most abundant and had the greatest increase in cover and proportional cover out of all sites. With this amount of turf algae (54.3% in 2016), decreased CCA cover (1.6% in 2016), and 57.2% total 2016 algal cover, Olowalu could be classified as a degraded reef "dominated" (> 50%) by turf. This may lead to slow or reduced coral recovery, if coral planula do not settle on the ungrazed turf or it hinders coral regrowth and reef calcification. Corresponding with this increase in turf algae, there was also a decrease in CCA and cyanobacteria at this site. This may imply turf algae were able to outcompete these groups. However, the decrease in cyanobacteria may also reflect the outcome of a short-lived bloom, which is commonly observed in benthic cyanobacteria (Albert et al. 2005, Paul et al. 2005, O'Neil et al. 2012). Olowalu was the only site that showed a decrease in CCA cover. This may have been due to CCA being outcompeted by turf algae perhaps due to a lack of necessary grazing or smothering by excess sedimentation, or a combination of both factors. Littler, Littler and Brooks (2006) and Smith et al. (2010) have reported that turf algae can rapidly grow over CCA and corals if not consumed by grazers. Fabricius and De'ath (2001b) have recorded CCA sensitivity to heavy sedimentation, which may be the main cause of CCA loss at Olowalu. Further, reductions in CCA may lead to a reduction in coral settlement due to less available preferred settlement substrate. These data collectively suggest that Olowalu may require time and/or intervention for coral recovery.

Kahekili is located within the KHFMA in which take of herbivorous species is prohibited. This site had overall less algal cover than Olowalu. The increase of turf algae in 2016 was accompanied by decrease of two fleshy macroalgal taxa, *Amansia glomerata* and *Asparagopsis taxiformis*. *Asparagopsis* is known to bloom seasonally (Poepoe et al. 2005), but this has not been recorded for *Amansia*. The decrease in these to taxa was unexpected, but these species may also be vulnerable to warming temperatures. Alternatively, turf algae may have truly outcompeted and replaced *Amansia.* Despite this increase in turf algae and loss in other groups, CCA cover remained relatively constant between the two years. This suggests that CCA may have been better able to compete with turf algae at this site perhaps due to more abundant grazers at this site.

Molokini, located within a MLCD with no-take restrictions and very little sedimentation (Kelly unpublished), had the lowest algal cover overall and the lowest increase in algal cover following the bleaching event. Turf algae only modestly increased at this site over the two years since the bleaching event. Unlike the other two sites, Molokini also had an increase in CCA cover between the years. This suggests that with coral mortality and new coral skeleton availability, turf still settled on these surfaces, but CCA was a competent competitor and was able to increase in abundance. With the highest fish biomass out of all sites (Kelly 2015), a sufficient herbivore population may have kept turf cropped allowing for slower-growing CCA to establish patches.

Algal Spatial Patterns: Patch dynamics in algal communities

Only a handful of studies have investigated patch dynamics in algal communities on coral reefs and these primarily focused on macroalgal species (Mumby et al. 2005, Renken et al. 2010). Here we focused on turf algae and CCA due to their abundance, function, and importance on most coral reefs around the world. Mumby et al. (2005) studied extinction and colonization rates of patches of macroalgae to estimate the amount of time corals may in be contact with a macroalgal competitor by monitoring plots every 3 months. We were limited to less frequent imaging, and given the large plot area, processing time was lengthened. However, by using the large-area imaging in established plots, we were able to analyze tens of thousands of algal patches before and after the bleaching event, a feat which could not be done in situ. These patch size data provide a more detailed description of algal change, and may also be important in predicting reef recovery.

Because both turf algae and CCA are "communities" themselves and impossible to differentiate as "individuals" assessing continuous patches of these groups makes the most sense from an ecological perspective. These algal patches may grow through vegetative expansion laterally or via settlement of new propagules onto or next to a patch. Further, smaller patches may undergo fusion which would result in fewer but larger patch sizes. Here we observed variability in patch dynamics that corresponded to particular sites.

At Olowalu, the number of turf patches significantly decreased while patch size quadrupled. A die-off of smaller patches could have accounted for the decrease in number of patches, but not the increase in mean patch size. Instead, we found that thousands of small turf patches had fused to form one large patch, covering almost half of the plot area in 2016 ($14m^2$ patch, out of $33m^2$ plot area). The formation of this extensive patch suggests that as coral tissue began dying turf algae were able to grow over coral skeletons while outcompeting other algae to fuse with adjacent turf patches across the plot. The presence of large turf patches may negatively affect the potential for coral recovery due to an increase in coral surface area in contact with turf algae and/or due to a lack of suitable substrate for coral settlement. Olowalu CCA cover decreased between years, but there was no difference in patch size. However, a halving in the number of patches in 2016 indicates patches may have been lost at the same rate regardless of size. Or, if turf outcompeted small patches of CCA, and overgrew portions of larger patches, this may have given a similar result. Although patch size did not change between years, fewer patches of CCA may limit coral settlement due to reduced availability of preferred substrate.

Like Olowalu, but to a lesser extent, Kahekili turf patch size increased while number of patches decreased. This indicates the fusion of smaller patches to form larger patches. Even though CCA cover stayed constant between years, patch size increased and patch number decreased, also indicating the fusion of algal patches. Because percent cover did not increase, small patches may have died off, while larger patches continued to grow. These larger patches may be the most important for coral settlement, as they provide a larger area for coral spat to settle and grow without directly competing with turf algae. Larger CCA patches are also beneficial for net reef calcification. Because of how CCA encrusts and grows between rubble, larger patches cover more area and provide more stable "cement" for solidifying reef structure.

Molokini was unlike Olowalu or Kahekili, in that although turf patch size increased in 2016, the number of patches also increased, indicating vegetative growth and patch fusion may not have been the only factor driving cover increase. The presence of more new patches may be due to settlement and formation of new turf patches on dead coral skeleton. Since turf algae cover increased, it is most likely that both the growth of old patches and formation of new patches contributed to this result. Although Molokini was the only site with an increase in CCA cover, we did not find a significant increase in CCA patch size. Molokini was the only site in which the number of CCA patches increased, so the settlement and growth of new patches most likely contributed to this increase in cover.

At all of our sites, algal communities shift following the bleaching event tended to shift towards an increased abundance of turf algae, not macroalgae, which has been the focus of related studies. A study by Diaz-Pulido and McCook (2002) found turf dominance with little macroalgal growth on coral skeleton after a bleaching event on the Great Barrier Reef. With our sites, turf and CCA shift varied with location. Olowalu seemed to fare the worst, as the increase of turf was accompanied by a decrease in CCA cover. This site may not have good potential for coral recovery if high turf abundance persists. Kahekili fared better and despite an increase in turf algae, CCA patch size increased, suggesting corals here may have a better chance of successful settlement and growth. Molokini has the greatest potential for reef recovery as the only site with an increase in CCA cover and number of CCA patches. Lack of macroalgae dominance at all sites suggests algal shifts after bleaching may be more subtle than others have proposed. This may be encouraging for reef recovery strategists, as macroalgal dominance seems to be difficult to reverse (Bellwood et al. 2006).

Considerations of local environmental factors

While this study was not explicitly designed to evaluate how different local conditions may affect algal community dynamics (no replication of sites across local impacts), we briefly consider differences between sites that may explain observed variation in algal communities. Both Olowalu and Molokini were dominated by encrusting and plating forms of *Montipora* while Kahekili was dominated by branching *Porites*. Swierts and Vermeij (2016) showed encrusting growth forms were better able to compete with turf algae compared to branching growth forms, regardless of taxa. Since Olowalu and Molokini had the most striking differences in turf abundance following bleaching, this suggests growth form was not a strong factor in determining algal composition after bleaching. Therefore, we must look at other delineating features between sites such as local environmental factors. Each site has known differences in rates of sedimentation and fish biomass. These have all been shown to influence turf, CCA, and coral growth and survival (Sato 1985, Babcock and Mundy 1996, Richmond 1997, Fabricius and

De'ath 2001b, Jones et al. 2015). When compared with our results, these differences suggest algal composition and patch dynamics reflect local conditions.

Olowalu, the site with the most terrigenous sedimentation and moderate fish biomass experienced the greatest increase in turf algae, both in cover and patch size. Olowalu was also the only site where CCA cover decreased, although patch size remained the same. Heavy sedimentation can smother CCA (Fabricius and De'ath 2001b), deter grazing when trapped by turf algae (Bellwood and Fulton 2008, Goatley and Bellwood 2012, Tebbett et al. 2017), and may even give turf a competitive advantage (Steneck 1997), so this may have contributed to the decline in CCA.

Kahekili, the site which experiences moderate sedimentation and wastewater input but has no-take restrictions for herbivorous species, also saw an increase in turf algae, but to a lesser extent than Olowalu. CCA cover remained constant, but patch size increased. Meanwhile, Molokini, a long time no-take conservation district with high fish biomass and minimal sedimentation, had the lowest increase in turf cover, and was the only site with an increase in CCA cover, although CCA patch size did not significantly change. This be due to an adequate number of herbivorous species to graze turf, and very little sediment to smother CCA. This would be consistent with studies that show CCA growth is greater with high turf grazing (Littler, Littler and Brooks 2006, Burkepile and Hay 2009, Sotka and Hay 2009, Smith et al. 2010) and low sedimentation (Fabricius and De'ath 2001b). Further research is needed to disentangle the specific roles of these local factors in driving reef community change and recovery over time.

CONCLUSION

This study has shown the varied response of the often-overlooked turf algae and CCA after a bleaching event, two groups which serve as indicators of reef health. With coral mortality we see clear trends in algal community structure over time and these trends tend to vary by location, likely driven by local conditions. Although no level of fishing regulations will prevent bleaching events due to climate change, abundant herbivore populations will likely help increase the rate of reef recovery by preventing turf algae from dominating. Although further work is needed to determine how drastic shifts in algal assemblage would need to be to influence large-scale reef recovery, study sites such as Molokini gave us hope that despite a devastating bleaching event, coral mortality and increase in turf, CCA was able to compete and grow. If appropriate management strategies can support the growth of beneficial algae, this may assist coral recovery and preserve reef structure.

This study also highlights a new approach for studying large-scale algae patch analysis, which allowed us to identify and enumerate individual algae patches within a landscape over time. We have shown how patch size analysis aids in the evaluation of a reef, providing detail which is otherwise obscured when using percent cover estimates alone. To our knowledge, no other work has been done on algal patch dynamics of non-macroalgae groups such as turf algae and CCA.

With the expected increase in severity and frequency of bleaching events worldwide (Hughes et al. 2003, Hoegh-Guldberg et al. 2007), it is vital to ensure we look at the entirety of the benthos in an effort to not only catalog damages, but to study how algal assemblage shifts might inform us about the future of a reef and its recovery potential. Turf-dominated sites such as Olowalu may indicate a need for improved local conditions, while sites such as Molokini can model an ideal algal shift following bleaching disturbance. We can then investigate the effectiveness of possible local protection efforts such as herbivore protection or sedimentation/eutrophication management in an effort to promote reef recovery following disturbance.

This thesis, in part, is currently being prepared for submission for publication of the material. Jayne, Christina; Kelly, E.L.A.; White, D.; Eynaud, Y.; Sparks, R.; Pedersen, N.; Edwards, C.B.; Zgliczynski, B., Sandin, S.A.; Smith, J.E. The thesis author was the primary investigator and author of this material.

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