UNIVERSITY OF CALIFORNIA SAN DIEGO

Quantifying Life History Demographics of the Scleractinian Coral Genus *Pocillopora* at Palmyra Atoll

A Thesis submitted in partial satisfaction of the
requirements for the degree Master of Science

in

Biology

by

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2018

The Thesis of Sho Michael Kodera is approved, and it is acceptable in quality and form for publication on microfilm and electronically:

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2018

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ACKNOWLEDGEMENTS

I would like to express my gratitude to my advisor Dr. Stuart Sandin, whose vast expertise in all things marine ecology and statistics has considerably added to my growth during my time as a graduate student. Additionally, I would like to thank Dr. Yoan Eynaud, Clinton Edwards, and the rest of the Sandin lab group for all the helpful guidance and support that I have received over the years and for providing me with the motivation to pursue science. On the same note, I would like to acknowledge all the undergraduate volunteers in the Sandin Lab who helped digitize the large-scale imagery necessary for this thesis. I also would like to thank the rest of my thesis committee for supporting my research and providing helpful insights to my work. Thank you to all my friends as well, both at and outside of Scripps, for all the encouragement and great memories. Last but not least, I want to express my gratitude toward my family for all the support to get me where I am now, and for raising me to become the person that I am today.

This thesis uses material currently being prepared for submission for publication as Quantifying Life History Demographics of the Scleractinian Coral Genus *Pocillopora* at Palmyra Atoll. Kodera, Sho: Edwards, Clinton; Eynaud, Yoan; Sandin, Stuart. The thesis author was the primary investigator and author of this paper.

ABSTRACT OF THE THESIS

Quantifying Life History Demographics of the Scleractinian Coral Genus *Pocillopora* at Palmyra Atoll

by

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Master of Science in Biology

University of California San Diego, 2018

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Mechanisms of change in coral colonies are necessary components to accurately predict trajectories of coral reef health. Yet, little in-field data has been quantified regarding the demographic rates of change in colonies and the factors that influence them. In this study, we use a large-area imaging approach to estimate baseline demographic rates of the coral genus *Pocillopora* and test for the influence of colony-specific predictors on growth, shrinkage (i.e. colony survivorship with loss of live tissue), and mortality (i.e. whole colony loss). We found

that a colony's fate was linked to its initial size, with larger colonies experiencing far lower mortality rates but higher shrinkage rates than smaller colonies. In addition, historical effects also significantly affected colony fate, as colonies with recent history of shrinkage experienced further shrinkage and mortality the following year. Finally, we found that significant variability in growth and mortality rates were linked to in inter-island site differences, which we suspect is driven by differences in heterotrophic feeding rates.

Introduction

Coral reef ecosystems, while only covering 1% of the sea floor, are some of the most diverse, most productive, and oldest ecosystems in the world. Known as vital "ecosystem engineers" (Hughes et al. 2003), scleractinian corals and the reefs they create house roughly a quarter of all marine life and provide immense ecological, economic, and cultural value (Moberg and Folke 1999, Plaisance et al. 2011). Yet, coral reefs around the world are experiencing significant levels of change due to threats such as seawater temperature rise and ocean acidification, as well as local anthropogenic pressures such as overfishing and sedimentation (Jackson 1997, Sandin et al. 2008, Hughes 1994, Hoegh-Guldberg et al. 2007). Given these rapid global ecosystem shifts, there is an increasing need for ecological research to become predictive (Pereira et al. 2011, Madin et al. 2014). Here, we quantify how colony-specific characterizations can improve predictions of intra-population variations in coral growth, shrinkage, and mortality rates.

The characterization of key demographic metrics of change in corals can serve as a useful tool in improving predictions of coral community trajectories. Such demographic metrics include rates of increase such as coral colony growth, as well as rates of decrease such as colony shrinkage and mortality. By quantifying rates of physical change in corals, we can develop a greater understanding of their life history and better discern how a community can respond to the presence of external factors. Applications of such knowledge have been useful in the management of several other systems, including forestry, fisheries, and endangered species conservation (He and Mladenoff 1999, Becker at al. 2010, Ochwada-Doyle et al. 2012).

Demographic rates of corals are dictated by the balancing of critical energetic investments towards life history traits such as somatic extension, skeletal excretion, regeneration,

reproduction, and resource storage (Darling et al 2012, Rinkevitch 1996). However, trade-offs occur as corals have finite amounts of energy and resources to allocate to such traits. Certain traits can also be beneficial to an organism in one aspect of fitness while being detrimental in another (Stearns 1989). Due to such trade-offs, significant variation in demographic rates exist as corals retain unique combinations of traits and form their own life history strategies with different ecological strengths and weaknesses.

Taxonomic differences in life history strategies account for a significant level of variation in coral demographic rates. A coral taxon with a competitive life history strategy will tend to experience greater growth rates but higher mortality rates than a coral taxon with a stress-tolerant strategy (Darling et al. 2012, Stearns 1989). However, significant variation in demographic rates also occur across individuals within a coral taxon due to significant amounts of plasticity in traits across individuals within a population (Todd 2008, Darling et al. 2012). Less is known regarding such intra-population variability in growth, shrinkage, and mortality rates, or the mechanisms that drive them. To fully characterize the extent of life history demographics of real world coral communities, we must empirically quantify rates of change at a higher resolution and understand how colony-level traits account for such demographic rates.

Three colony-specific factors believed to affect coral life history demographics are colony size, historical effects, and neighborhood. Colony size is known to play an important role in population dynamics (Hughes 1984, Hughes and Connell 1987). As colonies become larger, demographic rates such as growth, reproduction, and survivorship can change (Vardi et al. 2012, Hughes 1984). It can also be expected that demographic rates are linked to coral colonies' past histories of growth and shrinkage. Historical effects are defined as the influence of past events onto colony fate (Hughes 1984), causing temporal autocorrelations in colony fate through time.

Furthermore, colony life history demographics are likely to be influenced by biophysical gradients. Island-wide variability in oceanographic and biotic forcings such as nutrient availability, upwelling, and wave exposure are believed to largely affect coral health and traits (Gove et al. 2015, Lowe and Falter 2015).

The unique structure of a coral colony must additionally be considered as a biological mechanism of coral demographic rates and their limits. Colonies consist of repeated structures of identical polyps which each contain the necessary components to exist as individuals. As a result, mortality can occur in two forms: full colony-wide mortality and partial colony mortality via polyp death or breakage (Hughes and Jackson 1985, Highsmith 1982). Although colonies are composed of such independent modules, polyps have been shown to integrate within a colony as a cohesive unit. Several studies have demonstrated coral polyps' abilities to pool and internally translocate resources to areas of injury (Oren et al. 2001, Brickner et al. 2006). Demographic rates of change are dependent on such abilities of polyp integration and independence. Maximal growth abilities depend on how polyps translocate energy to the periphery of a colony. Rates of shrinkage and mortality depend on how well healthy polyps can isolate themselves from neighboring polyps that are damaged or diseased. As such, defining the role of polyp independence and integration within its colony is an important step in understanding the mechanisms of life history demographics in a broader context.

The goal of our study was to quantify baseline demographic rates of growth, shrinkage, and mortality for a coral population in the absence of local human impacts, and test the impact of colony size, historical effects, and spatial variability onto these rates. Recent advances in computer science, processing power, and 3-dimensional modeling technology have allowed for new methods in large scale imagery allowing for the efficient collection of data of hundreds of

square meters of reef from a single dive. Captured in the form of orthoprojections, these biological data can then be processed and analyzed quantitatively for several useful colony-specific metrics while removing the perspective bias of traditional imagery. Additionally, these models can be directly compared as time series to generate data of colony-specific planar area change. We incorporate the higher sample size and wider spatial coverage provided to us by large-area orthoprojections to empirically test the impacts of colony-specific life history parameters, as a step to ultimately improving our predictions of coral reef change.

Methods

Sampling design

All work was conducted on Palmyra Atoll located in the Northern Line Islands, Central Pacific (5° 52' N, 162° 06' W). Palmyra is a geographically remote location under protection as part of Pacific Remote Islands National Marine Monument and US Wildlife Refuge. Due to its limited human presence, the coral reefs in Palmyra Atoll serve as an ideal baseline for life historical and demographic studies in the absence of local human impacts (Sandin et. al 2008).

The demographic subjects for this study were colonies of the coral genus *Pocillopora*. As one of the most dominant and widely distributed coral taxa in the Central Pacific, *Pocillopora* is an important reef builder generally characterized as a fast growing, early successional taxon. *Pocillopora* colonies serve as ideal study subjects for life historical studies, as their fast growth, high turnover rates and short life spans allow us to observe significant and apparent physical changes in growth, shrinkage, and death within the course of a year. The corymbose, spherical shape of *Pocillopora* and presence of verrucae allows for quick taxonomic identification using imagery alone, as well as for differentiating individual colonies from one another.

Field Imagery Collection

Field imagery collection was conducted in the same manner as those outlined in Edwards et al. (2018). Four permanent 100m² sites across the fore-reef of Palmyra were surveyed in 2013, 2014, and 2015. Each site was at a depth of 10m and located at the NW, SW, NE, and SE points (Figure 1). Two SLR style cameras (Nikon D7000 16.2 megapixel) mounted to a custom frame were used for the field imagery collection process. The camera used to create large area orthoprojections was set to a 18mm focal length, while a second camera was set to a 55mm focal length to aid in taxonomic identification. The two cameras were attached into a frame to be simultaneously operated by a diver on SCUBA. At each established study site, stainless steel stakes were driven into the reef substrate as a form of permanent site designation, as well as to provide a reference point for subsequent re-survey. Divers then established a 10m by 10m plot using specialized target markers and calibration bars, as well as collecting depths and distances between placed objects. Once a plot has been established the cameras were set to capture images every second and swum by divers in a lawnmower pattern in both along-shore and across-shore directions, approximately 1.5m from the bottom until the entire site was surveyed with significant overlap between images. This entire process was then repeated at the same sites in 2014 and 2015.

Image Processing

Following an approach detailed by Naughton et al. (2015) we used Structure-from-Motion (SfM) algorithms to convert the raw field data into large scale orthoprojections using the commercially available Agisoft Photoscan Professional Edition (Agisoft LLC., St. Petersburg,

Russia). Using the high levels of overlap between the 18mm focal length images, the SfM algorithm estimated locations and depths of recurring pixels across images and projected them as points in 3-dimensional point cloud models. Calibration bars placed inside each plot during image collection provided objects of known distance in the orthoprojections, allowing us to calculate scale. The final 3-dimensional model reflects a spatially accurate visual model of the reef site, with a small and non-biased scale error of within 2.4 mm for a 500 mm distance. Point cloud models were converted into 2-dimensional orthoprojections using the custom developed software *Viscore* (Petrovic et al. 2014). This process removes the effects of parallax, a significant source of error for estimating size of objects from traditional photography. Finally, the orthoprojections were rectified in such a way to be oriented towards the plane of the ocean surface by using depth measurements collected in the field, thus accounting for the reef slope and providing a consistent 2D depiction of the 3D models.

Ecological Processing

The orthoprojections were traced manually via Adobe Photoshop 2016 version CC. First, in-field distance measurements of plot markers as well as calibration bars depicted in orthoprojections created in 2013 were used to create a virtual 10m by 10m plot boundary box. The plot boundary boxes were aligned in orthoprojections from subsequent years, to ensure that the site boundaries remained identical across years. Next, each *Pocillopora* colony present inside the boundaries of the orthoprojections was identified with the aid of the in-field 55mm images with >1mm resolution. Each colony was then traced and digitized using a graphics pen and tablet. For this study, a colony was defined as a continuous patch of polyps sharing a live tissue connection. Once each colony was fully traced, the pixels inside of each tracing were filled to

designate the covered planar area of each specific colony. Only colonies lying entirely within the survey area were included in the analysis. Colonies smaller than 10cm² were not considered in order to minimize detection bias.

Once ecological processing was complete, images were cropped to the 10 meter by 10 meter boundary box and exported as a .PNG onto R Version 3.4.3 language (R Core-Team 2017) via *png* (Urbanek 2013) and *raster* (Hijmans 2016) packages. Each cluster of pixels designated as a *Pocillopora* colony from the original Photoshop layer was then given a unique identification number. Using the known area of the 100m² boundary box, the planar area of each designated colony was also calculated by calculating the proportion between the number of pixels belonging to a colony to the number of pixels present in the total plot. Next, orthoprojection layers were overlapped across time points to match colony identification numbers between the previous time point and subsequent time point (Figure 2). Once colonies were matched, the change in calculated areas between time points were used to define colony changes in growth, shrinkage, and mortality.

An additional categorization was given to each colony in the 2013-2014 orthoprojection data, based on visual evidence of previous colony shrinkage. A colony was visually determined to be "full" if greater than 80 percent of its associated skeleton was covered in tissue, and "partial" if the percentage of live tissue area was less than 80 percent of the colony skeleton, consistent with tissue loss in the past. This classification was later used for statistical analysis.

Statistical Analysis

Size frequency and percent cover were used to describe the demographic characteristics of colonies at each site and time point. Significant changes in size distribution of *Pocillopora*

colonies between the three time-points were tested for using a Kruskal-Wallis test, as all distributions violated assumptions of normality and were highly right-skewed. Additionally, the gain or loss in coral cover due to each process was also calculated at both time-series by combining the changes in area of all coral colonies experiencing growth, shrinkage, or mortality.

Logistic regression models were used in a two-step process to test for the relationship between colony size and its likelihood of growth, shrinkage, and mortality. First, to test for the relationship between colony size and likelihood of mortality, all coral colonies were plotted based on size during the initial time point and survival in the following time point (1 = lived, 0 = died). A slope and intercept were then fitted onto the data to obtain a best fit model of change in the log-odds ratio of mortality/survival as a function of initial colony size. Next, we tested the relationship between colony size and the likelihood of experiencing growth and shrinkage (1 = growth, 0 = shrinkage) using only those colonies that had survived. To account for tracing error and clearly delineate the categorizations of growth and shrinkage, only colonies in which the second time-point colony area was at least 10cm larger than the first time-point colony area was categorized under growth while colonies in which the second time-point colony area was at least 10cm smaller than the first time-point colony area was categorized under shrinkage. The goodness-of-fit of both best-fit models were compared via likelihood ratio test to respective intercept-only models in which likelihood of mortality or growth/shrinkage does not change with colony size.

Separate statistical analyses of historical effects were conducted on two sets of samples: colonies in the 2013-2014 time series classified by previously described “full” and “partial” categorizations, and colonies in the 2014-2015 times series classified by whether a colony grew or shrank in the previous time step. For each set of samples, a χ^2 test of independence was used

to compare differences in growth, shrinkage, and mortality proportions between the two groups. Furthermore, these additional classifications were incorporated into the previous logistic regressions comparing life history and colony size. The resultant multiple logistic regressions tested for differences in fate likelihood between groups while removing the covariate of colony size. We used a likelihood ratio test to for significant departures in goodness-of-fit between the two types of logistic regression models; the previously established models showing the effects of colony size on the incidence of mortality and on incidence of growth/shrinkage ratio, and a multiple logistic regression model in which colonies with previous growth/shrinkage were given separate y-intercepts in log-odds ratio space.

We used χ^2 tests for independence to test for differences in the proportion of total colonies experiencing growth, shrinkage, and mortality at each site for 2013-2014 and 2014-2015. Post-hoc χ^2 tests with Bonferroni corrections were used to individually test for differences in growth, shrinkage, and mortality proportions across sites.

Results

In total, ~2600 *Pocillopora* colonies were identified, measured, and matched across the four 100m² sites in 2013, 2014, and 2015. *Pocillopora* occupied a mean percent cover of 4.3% in 2013, 3.0% in 2014, and 3.4% in 2015 (Table 1). Size distributions of identified *Pocillopora* colonies varied across time points (Kruskal-Wallis $\chi^2 = 10.00$, p-value = 0.007). Yet all distributions displayed strong right skewness as well as a similar range (Table 1). Colony matching across time revealed that between 2013 and 2014, the original colonies experienced 38.1% growth, 34.1% shrinkage and 27.8% mortality. Between 2014 and 2015, colonies experienced 55.0% growth, 17.4% shrinkage, and 27.6% mortality. These proportional

differences led to large variations in the annual impact of growth, shrinkage, and mortality onto the observed coral cover. From 2013 to 2014, corals that grew gained a net total of 1.33m² in area from the 400m² of surveyed plot, while colony shrinkage led to 2.83m² of loss and colony mortality led to 3.19m² of loss. From 2014 to 2015, corals that grew gained a net total of 2.44m² in area from the same 400m² of surveyed plot, while colony shrinkage led to 0.81m² of loss and colony mortality led to 2.45m² of loss.

Effects of colony size:

Logistic regressions comparing the effect of initial colony size on the probability of survival revealed significantly positive slopes at both 2013-2014 and 2014-2015 (2013-2014 log-odds slope = 5.46e-3, p-value << 0.001, Figure 4b, 2014-2015 log-odds slope = 5.89e-3, p-value << 0.001, Figure 4c). Models at both time series were tested via likelihood ratio test to have significantly increased goodness-of-fits compared to an intercept-only model (2013-2014 χ^2 = 77.02, p-value << 0.001, 2014-2015 χ^2 = 67.08, p-value << 0.001). When comparing initial colony size vs. likelihood of experiencing growth/shrinkage with colony survivors, logistic regression slopes were significantly negative at both time series of both time series (2013-2014 log-odds slope = -5.44e-3, p-value << 0.001, Figure 4d, 2014-2015 log-odds slope = -2.72e-3, p-value << 0.001, Figure 4e). Both models were also tested to have significantly increased goodness of fit compared to the intercept-only model via likelihood ratio test (2013-2014 χ^2 = 65.89, p-value << 0.001, 2014-2015 χ^2 = 13.36, p-value << 0.001).

To check the assumption that increasing rates of stasis with colony size does not account for our results, we additionally tested for the influence of colony size on rates of stasis (colony remaining within +/- 10cm² of its original size). Proportions of stasis were non-biased as a

function of size in 2013-2014 (log-odds slope = -1.083e-3, p value = 0.175), and slightly biased towards smaller colonies (log-odds slope = -2.568e-3, p value = 0.013) in the 2014-2015 time series. Such bias is more likely due to our formal definition of stasis (+/- 10cm²). Results of logistic regressions comparing colony size vs. likelihood of experiencing growth/shrinkage remained robust even while accounting for colonies that fell under such definition.

Historical effects:

Significant differences in proportions of growth, shrinkage, and mortality between 2013 to 2014 were found between colonies with "partial" and "full" tissues coverage ($\chi^2 = 58.79$, p-value << 0.001). In a similar manner, significant differences in proportions of growth, shrinkage, and mortality between 2014 and 2015 were found between colonies experiencing growth in the previous time step, and colonies experiencing shrinkage in the previous time step ($\chi^2 = 75.48$, p-value << 0.001). In both instances, colonies with evidence of past shrinkage experienced higher proportions of shrinkage and mortality and a lower proportion of growth compared to colonies with no such evidence.

Multiple logistic regression analysis confirmed partial colonies had significantly higher mortality rates than full colonies in the 2013-2014 data while accounting for colony size as a covariate (Full log-odds intercept = 0.346, Partial log-odds intercept = -0.219, p-value << 0.001, Figure 5a). Similar analysis using 2014-2015 data indicated that colonies with past shrinkage also had significantly higher mortality rates than colonies with past growth (Past growth log-odds intercept = 0.880, Past shrinkage log-odds intercept = 0.0724, p-value << 0.001, Figure 5b). For both analyses, the increased parameterization of separate intercepts between groups provided a significantly greater goodness-of-fit to the model (2013-2014 mortality model LRT against

one-intercept model $\chi^2 = 13.93$, p-value << 0.001, 2014-2015 mortality model LRT against one-intercept model $\chi^2 = 17.64$, p-value << 0.001).

When only using coral colonies that survived from 2013-2014, multiple logistic regression indicated that partial colonies experienced significantly lower growth to shrinkage ratios compared to full colonies, while accounting for colony size as a covariate (Full log-odds intercept = 1.797, Partial log-odds intercept = 0.260, p-value << 0.001, Figure 5c). Similarly, multiple logistic regression of coral colonies that survived from 2014-2014 indicated that colonies with past shrinkage experienced significantly lower growth to shrinkage ratios compared to colonies with past growth (Past growth log-odds intercept = 2.506, Past shrinkage log-odds intercept = 1.102, p-value << 0.001, Figure 5d). Likelihood ratio comparisons indicated that in both instances, the multiple-intercept models had significantly greater goodness-of-fits, (2013-2014 growth/shrinkage model LRT against one-intercept model $\chi^2 = 63.97$, p-value << 0.001, 2014-2015 growth/shrinkage model LRT against one-intercept model $\chi^2 = 36.68$, p-value << 0.001).

Effects of space:

Significant differences in proportions of growth, shrinkage, and mortality across sites were found in the 2013-2014 time-series ($\chi^2 = 37.08$, p-value << 0.001), as well as the 2014-2015 time series ($\chi^2 = 78.15$, p-value << 0.001, Figure 6). Post hoc analyses indicated that growth and mortality proportions significantly varied across sites in the 2013-2014 data (growth $\chi^2 = 16.65$, corrected p-value = 0.098, mortality $\chi^2 = 31.32$, corrected p-value << 0.001), and 2014-2015 data (growth $\chi^2 = 61.47$, corrected p-value << 0.001, mortality $\chi^2 = 64.39$, corrected p-value << 0.001). However, rates of shrinkage were indistinguishable among sites with both the

2013-2014 data ($\chi^2 = 6.309$, p-value = 0.293), as well as the 2014-2015 data ($\chi^2 = 4.74$, corrected p-value = 0.584).

Discussion

In this study, we used large-area imaging techniques in Palmyra Atoll to quantify baseline rates of growth, shrinkage and mortality of *Pocillopora* colonies from 2013 to 2015. In the process we observed that colony fates were linked to several demographic metrics. We found a life history tradeoff between colony size and fate, with larger colonies experiencing lower mortality rates but higher shrinkage rates than smaller colonies. Colonies with a history of previous shrinkage experienced significantly higher rates of re-shrinkage and death the following year, signifying the relevance of historical effects in *Pocillopora*'s life history. Colony growth and mortality rates were highly variable depending on site, yet shrinkage remained relatively consistent around the island. While each coral colony was shown to experience a unique and un-systematic life history timeline of growth, shrinkage, and death, colony fate is also intrinsically linked to biological, ecological, and oceanographic drivers that could largely be generalized by key demographic traits. Our work reinforces the notion that technology-driven large-scale data collection techniques, combined with an improved understanding of colony-specific demographic characteristics, may increasingly allow us to predict how coral communities can and will change in the future.

Size and its role in life history:

A colony's size was shown to be significantly linked to its fate the following year. Logistic regression analysis indicated that colony size was positively associated with the

likelihood of survivorship (Figure 4b, c). Conversely, logistic regressions of colony survivors indicated that colony size was negatively associated with likelihood of growth and positively associated with likelihood of shrinkage (Figure 4d, e). Such opposing results suggest the existence of a life history tradeoff; smaller colonies tend to experience high mortality rates but are almost guaranteed to grow if they survive, while larger colonies experience low mortality rates but are compensated by higher shrinkage rates. Overall, these findings are consistent with results from similar studies. Decreased mortality rates and lower growth rates with size were found in a variety of weedy coral species (Furby et al. 2017, Hughes and Jackson 1985, Bak and Meesters 1998), suggesting that the documented relationship between colony size and fate extend beyond our study population.

The relationship between quantitative areal changes and initial colony size (Figure 3) provide further insights on the nature of the tradeoff between colony size and fate. The data appear as if there is a near constant probability distribution of areal change values along the 1:1 line, regardless of a coral colony's initial size. However, when colonies are small this probability distribution appears to be "veiled" in the negative direction, due to a colony's inability to lose more than its initial area. With increasing colony size and therefore increasing possible area of colony loss, we observe an "unveiling" of this distribution, similarly to concepts discussed by Connolly et al. (2005). As such, the spread of areal change values in *Pocillopora* resemble a wedge-shaped pattern at both 2013 to 2014 and 2014 to 2015.

The trends of "unveiling" in negative area change distributions as a function of colony size suggest that a colony's ability to "survive through shrinkage" appears cumulative with increasing colony size. Instead of damaging all polyps in a colony equally, stressors seem to generally destroy a given area from a colony while leaving the rest intact. We suggest that the

modular nature of corals may account for this pattern of colony loss. While coral polyps all contain the necessary components and energetic reserves to exist as individuals, they can also behave cooperatively via the internal translocation of resources to a colony's areas of highest need (Oren et al. 2001, Brickner et al. 2006). As such, the number of polyps within a colony may be linked to the total amount of energy and resources available towards defense and regeneration (Rinkevitch 1996). Compared to smaller corals which may not have the available resources to withstand a large stressor, larger colonies may have higher survival capacities that can then be strategically allocated towards select polyps to ensure survival through shrinkage. However, it is important to note that the abilities of internal translocation in *Pocillopora* have not been verified at this time.

Interestingly, maximum areal change values remained relatively constant as a function of colony size (Figure 3). Maximum areal changes at all colony sizes hovered near 70cm² from 2013-2014 and near 110cm² from 2014-2015. The existence of a constant ceiling of maximum planar areal growth regardless of colony size is consistent to results by Dornelas et al. (2017), which found constant allometric growth in corals with size. Such phenomena may be due to changes in geometric constraints (Pratchett et al. 2015), energetic partitioning (Rinkevitch 1996) and colony integration (Dornelas 2017) with changes in colony size.

Overall, these results confirm the relevance of a population's size distribution on rates of coral change. A population of smaller colonies is likely to be more dynamic and exploitative because they can grow impressively in proportion to their size but can also suffer drastically from stresses due to high rates of mortality. In comparison, a population of larger colonies will tend to be more stable and consistent throughout time. They tend to not experience radical

changes over a short period of time, but their stability may allow them to have more resiliency in the face of stress.

Historical effects and its role in life history:

Colonies with prior shrinkage histories had significantly greater instances of further shrinkage and mortality the following year compared to colonies without prior shrinkage, as well as reduced instances of growth and recovery. These results remained robust even after accounting for the previously described effect of colony size, confirming the impacts of historical effects on *Pocillopora*'s relatively deterministic life history. Our results are comparable to previous studies which documented higher rates of re-injury and death in previously injured colonies (Hughes 1984).

Historical effects may be facilitated by the fact that factors causing colony injury are often temporally autocorrelated. As corals are sessile organisms, factors leading to colony damage in a previous time point can remain to further cause damage in the next time point. For example, a *Pocillopora* colony competing for space with a neighboring coral may consecutively experience tissue loss over time. Similarly, a diseased colony may experience a slow but eventual process of death. Another likely mechanism of historical effects involves the finite amounts of energy and resources available to contribute towards defense and regeneration. While undamaged colonies have fresh reserves of energy and resources to deal with stressors, colonies that have recently experienced shrinkage are likely to have expended a significant amount of their finite energetic allocations towards defense and regeneration. With limited energetic reserves remaining, colonies may temporarily be in a weakened state and have lowered abilities to defend and recover from more recent injuries (Henry and Hart 2005). Such a mechanism

suggests that coral communities are most vulnerable to further loss shortly after a stressor, and that the intervals between perturbances are as important as the perturbances themselves to predicting coral response and recovery.

The drastic life history differences between previously growing and shrinking colonies were also exacerbated by *Pocillopora's* poor overall regeneration ability, which was apparent regardless of year or site. Very few colonies that previously experienced shrinkage were able to recover and grow in the following year. This is likely due to a heavy life history trade-off between regeneration and reproduction, as hypothesized by Rinkevitch (1996). As the poor yearly survivorship rates and right skewed size distributions of our observed population suggests, the life history strategy *Pocillopora* likely favors recruitment over regeneration and colony longevity. As regeneration of lost tissue and skeleton involves different physiological processes than growth (Rodríguez-Villalobos et al. 2016, Henry and Hart 2005), it may be the case that *Pocillopora* colonies invest little of their energetic allocations towards this process. Comparatively, several coral taxa are known for their ability to quickly repair and regrow after tissue loss (Hall 1997, Furby et al. 2017, Bak 1983, Henry and Hart 2005). Such differences in energetic allocations may serve as an important source of change in community compositions as the frequency and intensity of disturbance regimes change (Hughes et al. 2018).

Space and its role in life history:

We found significant variability in proportions of colony fate across our four sampled sites (Figure 6). Post-hoc analyses revealed that proportions of colony growth and mortality significantly varied from site to site, yet the variability of shrinkage proportions across sites remained statistically indistinguishable. These results remained consistent at both 2013-2014 and

2014-2015; for example, the sites by descending order of growth proportions was FR3, FR9, FR5, and FR7 at both time series.

The differences in the level of variability between mortality and shrinkage rates suggest partial and full mortality primarily occur due to mutually exclusive processes that operate at different spatial scales. While growth and mortality rates were generally inversely related, shrinkage rates and mortality rates were not influenced by one another. This may be because full colony mortality may be significantly influenced by biophysical gradients that vary around an island, while factors that influence shrinkage tend to be more biotic in nature. External factors which cause shrinkage such as disease, competition, and predation may be more consistent factors around Palmyra, due to effects of density dependence and competition. Shrinkage of *Pocillopora* may also be influenced by internally pre-programmed life history traits, as colonies that become excessively large systematically experienced shrinkage regardless of circumstance.

We suspect that a significant biophysical driver of the island-wide spatial variability in colony growth and mortality rates is the availability of particulate organic matter available for coral consumption. Heterotrophic nutrition is a significant component of a coral's trophic ecology, providing essential nutrients linked to growth (Houlbrèque and Ferrier-Pagès 2009). Recent studies have documented increased rates of heterotrophic feeding as a function of food availability (Fox et al. 2018), suggesting that food availability may be linked to life history. Palmyra's lagoon is documented to be rich in particulate organic matter (McCauley et al. 2014) and differences in levels of connectivity between the lagoon and the four sites may provide a key mechanism of the observed spatial variability in growth and mortality. In fact, a hydrodynamic model simulating Palmyra's lagoonal connectivity to the forereef (Rogers et al. 2017, Williams et al. 2018) closely coincide with our observed variability of coral fates, as sites with higher

connectivity to Palmyra's lagoon had higher proportions of growth and lower proportions of mortality. This may also be supplemented by internal waves and upwelling events, which are documented to introducing varying levels of organic matter to a system (Lowe and Falter 2015). Further studies with higher sample sizes and in-situ data is necessary to confirm this hypothesis.

This thesis uses material currently being prepared for submission for publication as Quantifying Life History Demographics of the Scleratinian Coral Genus *Pocillopora* at Palmyra Atoll. Kodera, Sho: Edwards, Clinton; Eynaud, Yoan; Sandin, Stuart. The thesis author was the primary investigator and author of this paper.

Figures and Tables

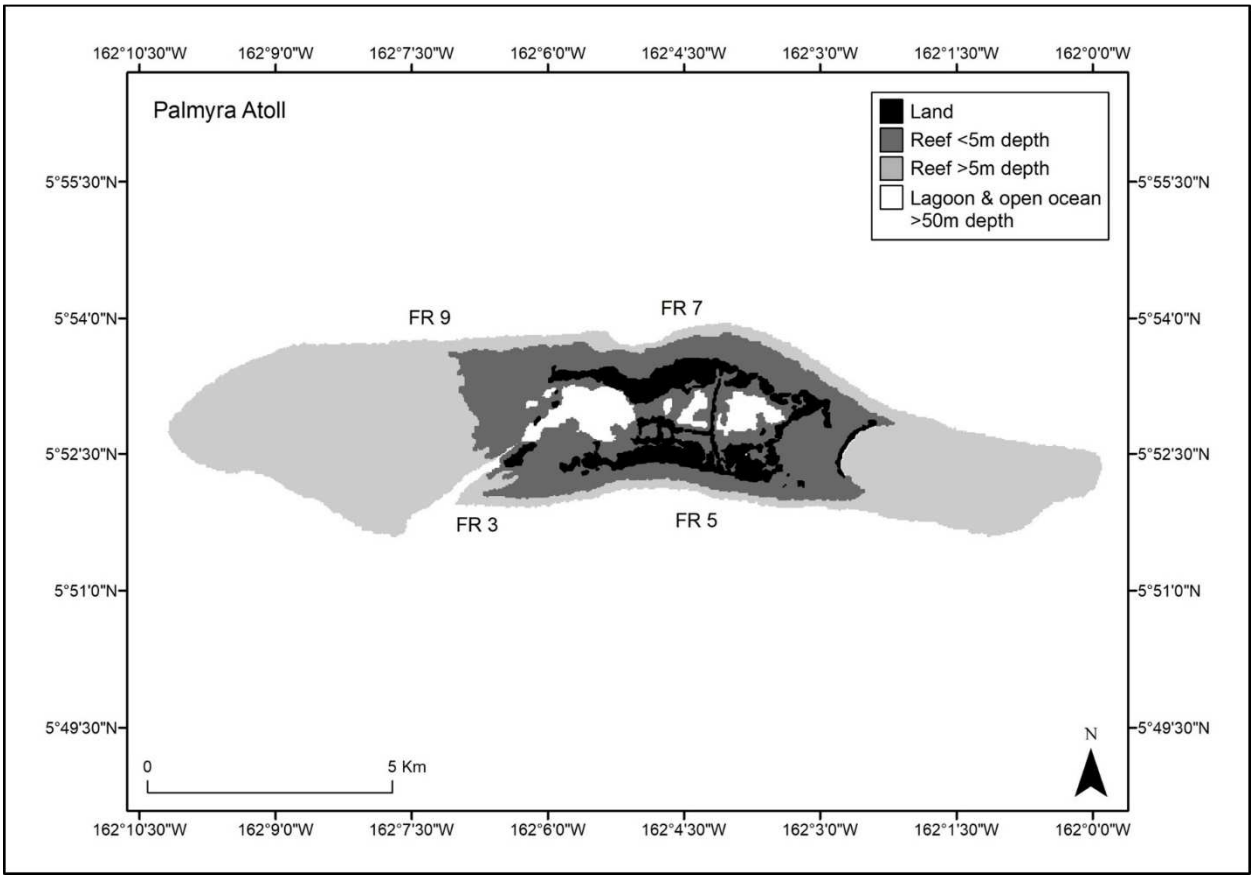

Figure 1: Locations of forereef study sites in Palmyra Atoll.

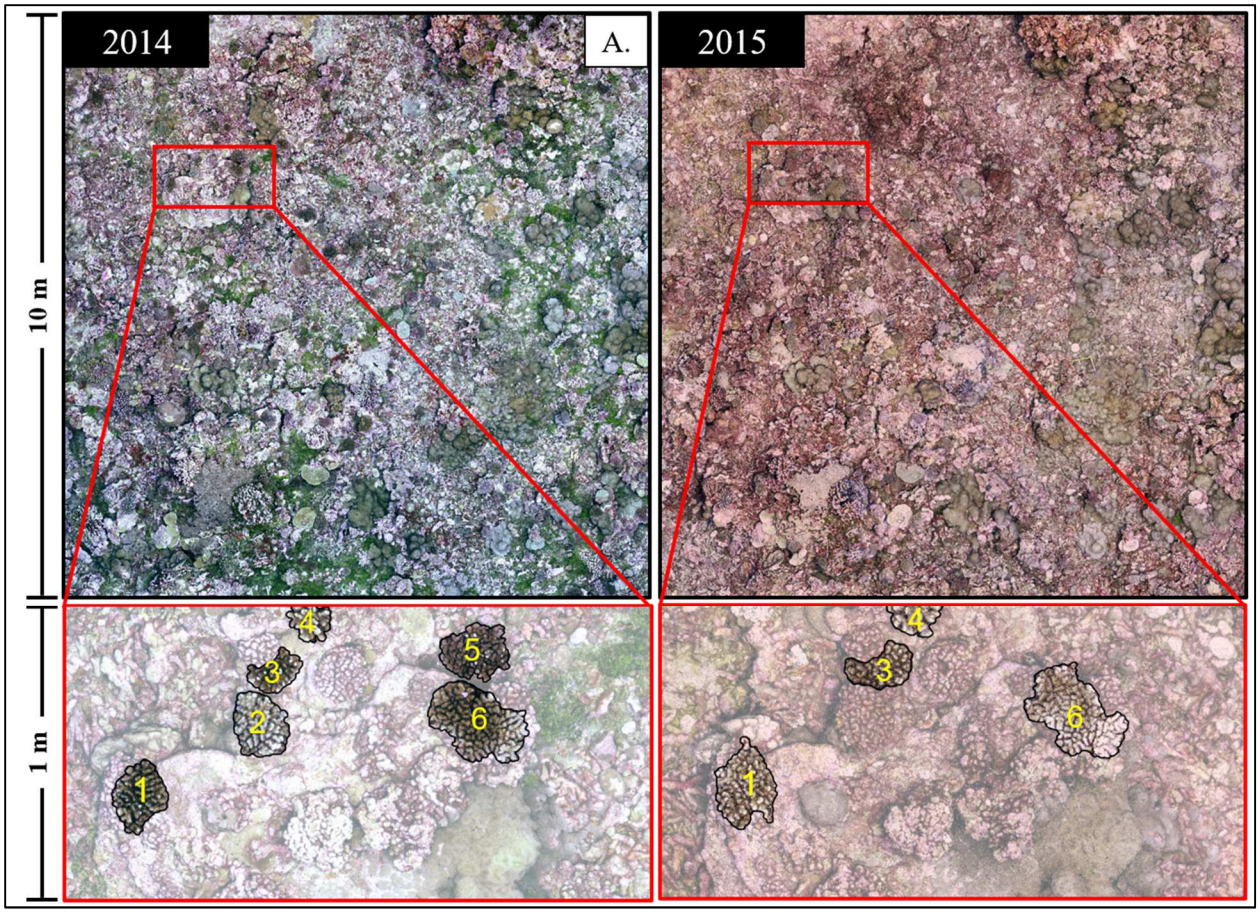

Figure 2: Depiction of 100 m² orthoprojections for site FR5 in 2014 (a) and 2015 (b), as well as close-up examples of the coral colony matching process across years (c, d).

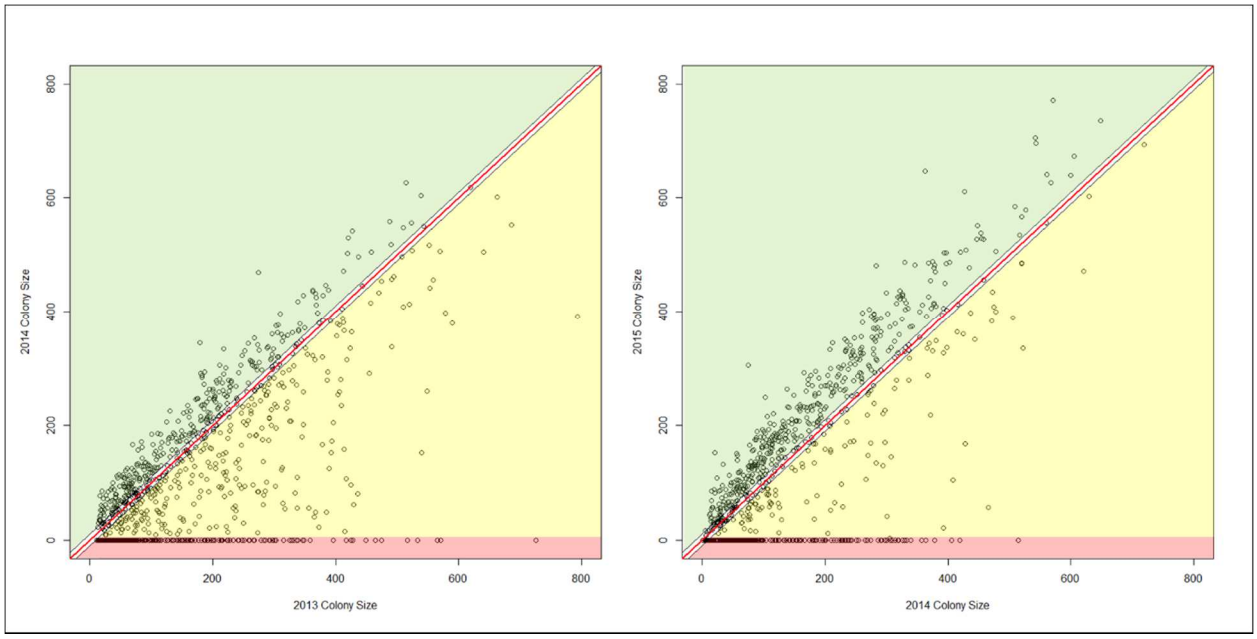

Figure 3: Scatter plot of observed *Pocillopora* colony size at 2013-2014 (*left*) and 2014-2015 (*right*) in cm². The red line indicates the 1:1 slope in which colonies did not change size between years. Points in the green zone indicate growth, points in the yellow zone indicate shrinkage, points in the red zone indicate mortality, and points in the white zone indicate stasis.

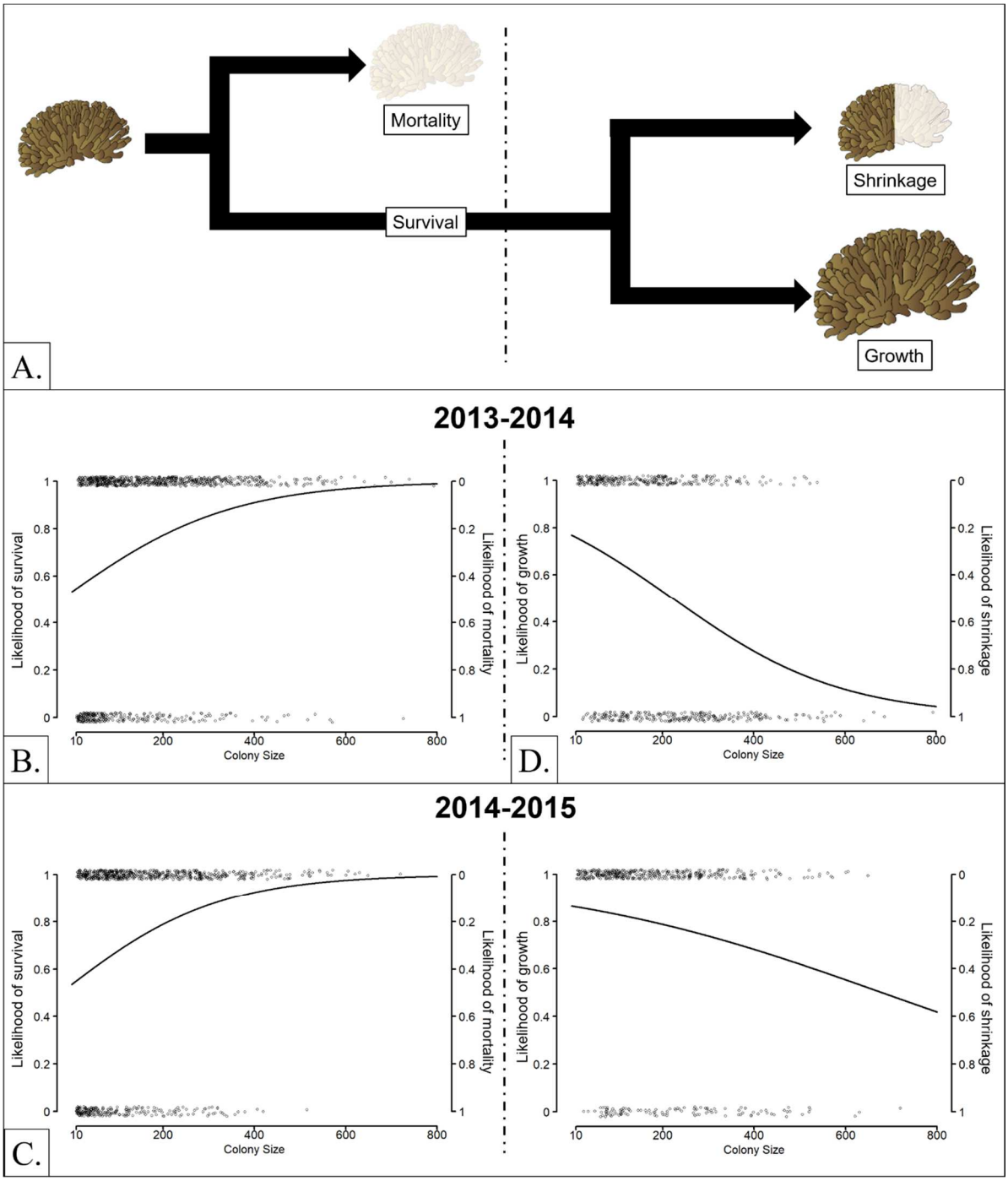

Figure 4: Conceptual decision tree diagram displaying possible outcomes of coral colony fate (a). Best-fit logistic regression probability curves of the likelihood of experiencing life/death as a function of size in 2013-2014 (b) and 2014-2015 (c). Best-fit logistic regression probability curves for the likelihood of growth/shrinkage in coral survivors as a function of size in 2013-2014 (d) and 2014-2015 (e).

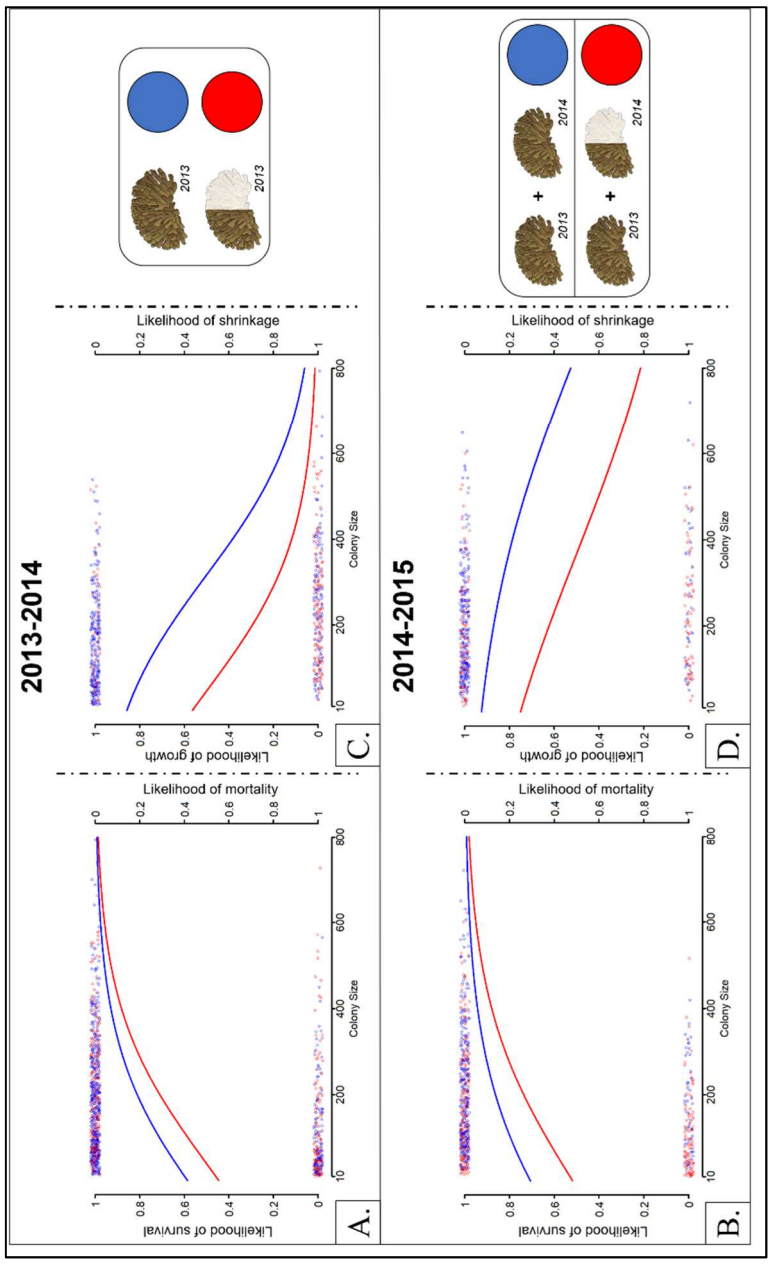

Figure 5: Multiple logistic regression analyses of a colony's likelihood of survivorship (a) and growth/shrinkage (b) as a function of size from 2013-2014, with separate intercepts for "full" colonies (blue) and "partial" colonies (red). Multiple logistic regression analyses of colony's likelihood of survivorship (a) and growth/shrinkage (b) as a function of size from 2014-2015, with separate intercepts for colonies that grew in 2013-2014 (blue) and colonies that shrank in 2013-2014 (red).

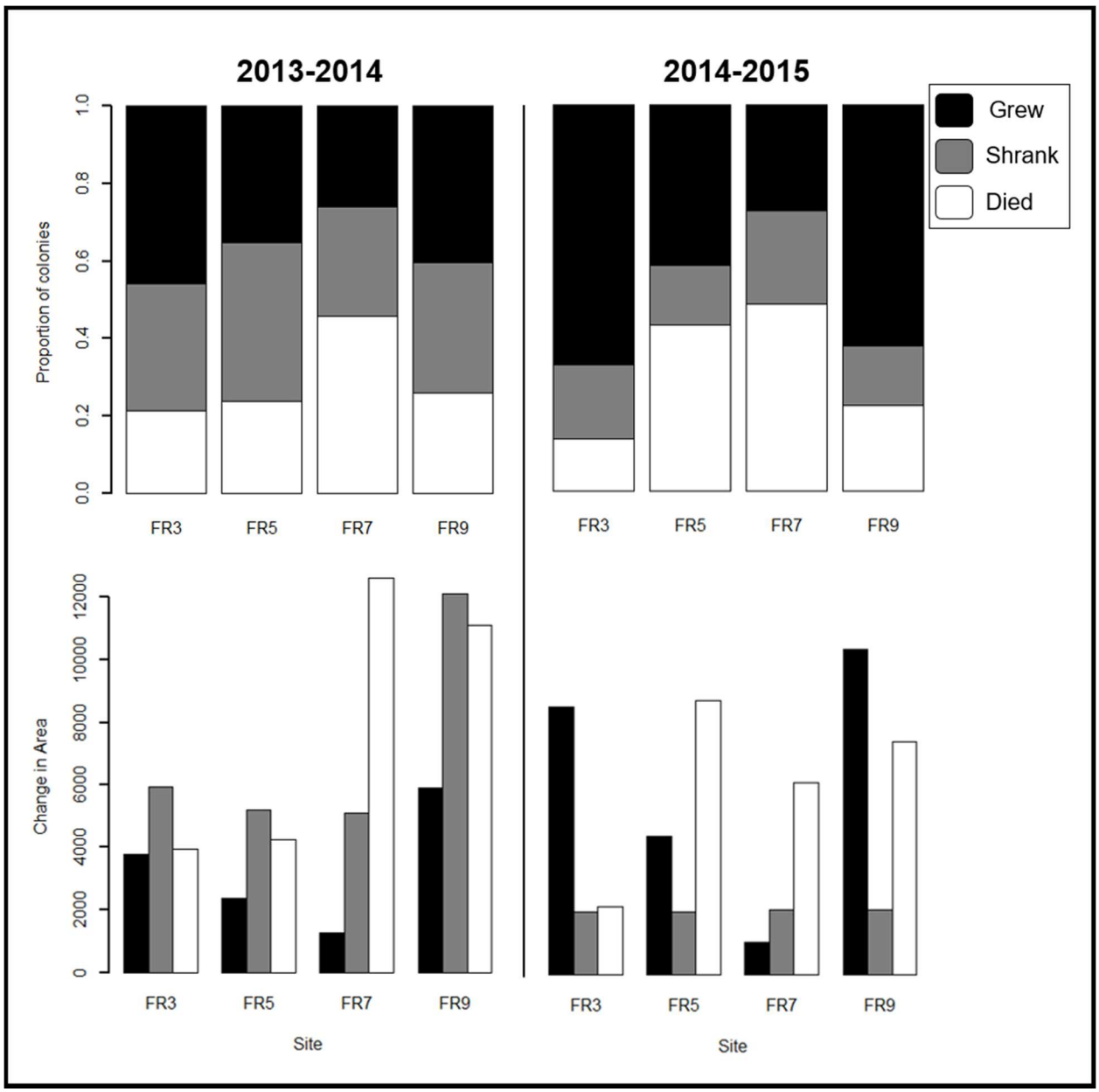

Figure 6: Proportion of colonies experiencing growth, shrinkage, and mortality at each site, between 2013-2014 and 2014-2015 (*above*). Sitewide differences in total areal impact of growth, shrinkage, and mortality between 2013-2014 and 2014-2015 (*below*).

Table 1: Descriptive statistics of colony size distributions and percent cover separated by year and by site.

	Site	*Count*	*Percent Cover*	*Mean (cm²)*	*SD*	*Median*	*Skewness*
2013	FR3	208	4.13%	198.31	168.68	179.79	0.97
	FR5	184	3.40%	184.99	155.79	150.73	1.56
	FR7	159	2.95%	185.41	122.09	168.26	0.41
	FR9	443	6.81%	153.83	128.37	110.98	1.39
2014	FR3	188	3.78%	201.05	156.01	168.96	1.05
	FR5	178	3.03%	170.72	138.42	129.01	0.98
	FR7	95	1.53%	161.06	109.21	129.36	0.84
	FR9	400	5.30%	132.61	116.24	92.94	1.41
2015	FR3	174	4.35%	249.87	175.24	209.14	0.71
	FR5	142	2.67%	187.75	146.85	144.98	0.91
	FR7	71	0.92%	219.13	102.28	105.02	1.18
	FR9	358	5.70%	159.17	134.13	125.01	1.44

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