***Porites superfusa* mortality and recovery from a bleaching event at Palmyra Atoll**

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Introduction

Understanding mortality and recovery patterns among reef-building corals is foundational to the development of accurate predictions of coral population trajectories (Baird & Marshall 2002). Recruitment has been recognized as important for long-term recovery after major and frequent disturbances, especially for coral populations that have suffered widespread, whole-colony mortality (Dollar & Tribble 1993). However, many disturbance events are less dramatic, leading to a combination of partial and complete mortality. We define partial mortality of colonial corals as the response to a stress event that leads to tissue loss, but with the survival of some colony area.

For colonies suffering from partial mortality, regeneration of tissue following stress is a critical mechanism in assuring individual colony survival (Chadwick & Loya 1990). As such regrowth of corals has been suggested as an important mechanism in coral population recovery (Diaz-Pulido et al., 2009; Gilmour et al., 2013). In this context, analyzing recovery characteristics can help project population resilience.

Given the colonial nature of most reef-building corals, the definition of an 'individual' presents real challenges (Hughes, Ayre & Connell 1992). Coral ecological literature often refers to an individual as a colony. Interactions and population dynamics are sometimes best described at the colony scale, including patterns of size-specific mortality, competition for space on the benthos, and vulnerability to storm damage (e.g., Hughes & Jackson 1980; McCook, Jompa & Diaz-Pulido 2001; Baird & Marshall 2002; Madin et al., 2014). In contrast the physiological definition of an individual is the polyp (Harper 1985). In particular both asexual (fission/ budding) and sexual (spawning/ brooding) modes of reproduction occur at the scale of the polyp. When tracking

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demographic responses to environmental change or disturbance, it is critical to account for dynamics occurring at both the scale of the colony and the scale of the polyp.

Corals are capable of four known mechanisms of loss and recovery: complete-colony mortality, partial colony mortality (tissue loss), recruitment, and partial-colony growth (sometimes referred to as regrowth) (Fig 1). A few recent studies have documented the relative importance of recruitment and regrowth as mechanisms of coral population recovery following a disturbance (Diaz-Pulido et al., 2009; Gilmour et al., 2013; Roff et al., 2014), however, the colonial mechanisms of coral recovery have not been regularly quantified.

Due to its remote location and lack of local anthropogenic impacts, Palmyra Atoll is an ideal location for studying demographic rates of corals in response to global change (Knowlton & Jackson 2008; Sandin et al., 2008; Williams et al., 2011). In 2009, Palmyra Atoll experienced a mild bleaching event associated with an El Nino Southern Oscillation (ENSO) event (Williams et al., 2010). During the 2009 ENSO event, sea surface temperatures reached 1.5°C above the maximum long-term monthly temperatures, and the anomaly continued for four months (Williams et al., 2014). October 2009 through March 2010 had over 4°C-weeks, with November through March over 8°C-weeks (NOAA Coral Reef Watch).

This study examines patterns of change in an encrusting coral, *Porites superfusa*, on Palmyra Atoll during and after the thermal stress event. Specifically, our objectives were to address two complementary questions: (1) Does *P. superfusa* cover change through time from 2009 to 2012 on Palmyra Atoll? (2) What are the relative rates of

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colony survivorship (recruitment/ mortality) versus colony growth (growth/ shrinkage) during and after a bleaching event?

Materials & Methods

Study Species

Porites superfusa is a small coral that is relatively ubiquitous on Palmyra Atoll, reaching almost 400 cm^2 in area with an overall mean colony size of 9.9 cm^2 (median = 4.4 cm^2). Our targeted design involved this species because it is one of the most numerous corals in the area, and its compact morphology allows study of multiple individuals within square meter photoquadrats (see below). In 2009, the coral population showed extensive evidence of bleaching with notable losses from the permanent photoquadrats.

Surveys

Four forereef sites on Palmyra Atoll were selected, two sites on the north and two sites on the south shore, each approximately 2 km apart (Fig 2). Sites were chosen to be representative of Palmyra's forereef habitats. These sites all had high initial densities (C_{2009}) of *Porites superfusa* colonies, and as they are evenly spaced across the island they should capture within-island differences in the forereef habitat. Sites were surveyed four times at approximately annual intervals (September 2009, July 2010, September 2011, and September 2012).

At each site, one 50 m transect was permanently marked, parallel to shore and at a depth of 10 m. In 2009, ten permanent photoquadrats were established at each site,

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positioned every 5 m along the transects. The corners of plots were marked with stainless steel eyebolts held in place with marine epoxy (US Fish and Wildlife Special Use Permit 12533-16006). Each photoquadrat was imaged with a Canon G12 camera attached to a PVC frame (0.54 m^2) by SCUBA divers (Sandin et al., 2008). These marked plots were revisited and re-surveyed at exactly the same location, enabling the tracking of individual colony fates through time. In sum, 40 0.54 m^2 plots were surveyed annually for a total of four time points each.

Image analyses

Within each photograph, colonies of *P. superfusa* ranged in area from 0.2 cm^2 to 440 cm^2. Due to the limitations of the photographic resolution, the tracking of the smallest colonies was not possible and thus we focused our study on colonies exceeding 1 cm^2. Photographs were analyzed using ImageJ to calculate the size (estimated as 2-dimensional area when viewed from the top down) and survivorship of each *P. superfusa* colony within the images (Fig 3, Abramoff, Magalhaes & Ram 2004). Each colony was tagged digitally and tracked through time (similar to methods of Hughes & Jackson 1985). Fates of the colonies were placed into one of five categories – complete mortality, partial mortality, true recruits, growth, and 'resurrected' recruits. Complete mortality was defined as the death of the entire visible coral, with its previous location overgrown by other organisms (Fig 3B-1). Partial mortality (i.e., injury, shrinkage) was recorded when colonies lost tissue (Fig 3B-2). True recruitment (or settlement) indicated a new coral recruit had claimed substrate in an area previously without *P. superfusa* (Fig 3B-3). Growth occurred when a previously present colony created additional tissue (Fig 3B-4).

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‘Resurrected’ recruits were defined as apparent recruits that appear in a location where a colony had been recorded as suffering mortality in previous time points (Fig 3C-5, Fig 1). Because of the limitations of the photographic census, it was impossible to determine whether such recruits were new recruits (new colony settling at the same location) or regrowth from small areas of cryptic remnant tissue. Individual colony cover and total *P. superfusa* cover were calculated per quadrat. Data are reported in two formats: colony-specific fates and total live *P. superfusa* cover summed within quadrats tracked through time.

Data analyses

Analyses assessed patterns of variation in starting live *P. superfusa* cover across sites, thus determining whether changes through time were similar among years. One-way ANOVAs were used to calculate differences of *P. superfusa* cover among sites in 2009 and to determine differences between absolute change and proportional change in coral cover between time points. Absolute change was the difference in coral surface area (cm^2) per quadrat (e.g., cover in 2010 – cover in 2009, or C_{2010}-C_{2009}). Proportional change was the relative difference in coral cover between time points compared to the original coral cover in 2009 (e.g., [C_{2010}-C_{2009}]/C_{2009}). Tukey’s post-hoc tests were used to determine potential differences among sites.

Because the same individual colony can appear in multiple years, analyses assessed the possible effect of independence of colonies through time. ANCOVA was used to determine interaction effects of year and site. Because 109 colonies were repeatedly assessed, data were randomly sampled using each colony only once. A

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binomial logistic regression was used to determine the effect of colony size on survivorship across years. Analyses were performed using R version 3.1.2 (R Development Core Team, www.r-project.org).

Results

The 2009 temperature rise impacted approximately 75% of the *Porites superfusa* population at Palmyra Atoll with bleaching and mortality observed island-wide. The initial size of individual colonies was greater on average than in subsequent years. The number of colonies present in 2009 was also greater than in later time points. True recruit numbers in 2010 (after the bleaching event of 2009) were lower than in 2011 and 2012 (Supplementary Table 1).

All sites surveyed exhibited similar patterns of decline in *P. superfusa* from 2009 to 2010, followed by fluctuations of growth in 2011 and 2012 (Fig 4, 5). From 2009 to 2010, *P. superfusa* mortality was ubiquitous across sites, and the growth for this period was the lowest observed during the study (Fig 4). Mortality was divided into two categories: complete and partial mortality. These mechanisms contributed similarly to the reduction in cover observed (Fig 4, partial mortality: -101.8[56.79] cm^2 per quadrat, mean [SE], complete mortality: -105.7 [39.10] cm^2 per quadrat, mean [SE]). Recruitment and growth were minimal initially, revealing no appreciable difference among growth mechanisms (Fig 4, Recruit: 4.99 [1.31] cm^2, Growth: 4.56 [0.69] cm^2 per quadrat). Across the study duration, the highest rates of growth were observed from 2010 to 2011. Resurrected recruits (i.e., apparent recruits that appear in a location where a colony had

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been recorded as suffering mortality in previous time points) made up a third of total "recruitment" (12.45 [4.45] cm^2). Recruitment contributed less than colonial growth to the overall gain in cover (Fig 4, Recruit: 24.06 [8.77] cm^2, Growth: 39.84[13.19] cm^2). From 2011 to 2012, resurrected recruits played a decreased role (2.702 [0.49] cm^2) in population growth. True recruitment and growth contributed similarly to overall growth (Recruit: 14.29 [18.37] cm^2, Growth: 18.37 [6.45] cm^2).

In 2011, 83 of over 400 colonies (21%) reappeared (after being overgrown by turf and crustose coralline algae in 2010) and began to re-colonize the substrate 10 months later (resurrected recruits, Supplementary Table 1). Out of 1150 colonies tracked, approximately 100 fragmented into apparent daughter clones (due to partial mortality) and 79 fused. Of the 100 colonies that fragmented, 52 fused back with a remnant section of the original colony within 2 years.

This study found that *P. superfusa* colonies gained upwards of 80 cm^2 of new tissue area per year and lost up to 170 cm^2 of tissue area per year, with a mean tissue change of 4.75[0.232] cm^2 per colony. During the time period that included the bleaching event from 2009 to 2010, *P. superfusa* declined an average of 8.3 cm^2 per quadrat (total quadrat size, 540cm^2). From 2010 to 2011, the corals increased an average of 1.7 cm^2 per quadrat (Welch two sample t-test, t = -3.74, p = 0.028) and from 2011 to 2012 corals declined an average of 0.9 cm^2.

Average change in area, when normalized to initial coral size in 2009, was largely negative (Fig 4, 5). When normalized to starting size (in 2009), *P. superfusa* growth was inversely related to size. Smaller corals gained more proportional area relative to larger colonies. The year with the most negative growth was 2009-2010, with the following

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years slightly less negative (Fig 5). The overall change in *P. superfusa* cover from 2009 to 2010 (C_{2010}-C_{2009}) was negative (one sample t-test on C_{2010}-C_{2009}, $p < 0.001$) with no clear differences among sites (Tukey post-hoc). The change in cover from 2010 to 2011 (C_{2011}-C_{2010}) was minimal growth (one sample t-test on C_{2011}-C_{2010}, $p < 0.001$), followed by a slightly negative change from 2011 to 2012 (one sample t-test, $p = 0.09$, Fig 5). There was no statistical artifact associated with including repeatedly measured colonies, i.e., colonies with multiple transition data through time, in the ANCOVA analysis, as the results from bootstrapped subsampled data were comparable to those from the entire dataset (in only one iteration of the random resampling was a significant site effect was noted).

We recorded a significant relationship between initial size of a coral colony in 2009 and survival across time points (Fig 6). Larger corals had the greatest declines in area, but they were more likely to survive across time points. The size of the colony in 2009 predicted survival in 2012, with larger colonies showing a higher probability of survival (binary logistic regression, $p < 0.05$, for all time points). Figure 6 depicts the frequency of colony size classes and their survival from 2009 to 2012. The size frequency between the two groups (survivors and non-survivors) was similar, however the largest size classes all survived to the end of the study, while the smaller size classes….. (Fig 6).

Discussion

The goal of this study was to quantify the population dynamics of a common encrusting coral during and after an ENSO event on a remote reef in the central Pacific. The effects of the ENSO warm-water event on the population of *Porites superfusa* on the

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forereef on Palmyra Atoll were dramatic and widespread. The ENSO event was associated with temperatures up to 30°C at the sites surveyed in 2009 (Maximum degree heating weeks 16, Williams et al., 2010), and in our results *P. superfusa* suffered high mortality rates for over a year after the bleaching event.

The fates of colonies tracked through time revealed that the mechanisms of growth and death changed through time in surprising ways. After the bleaching event in 2009, corals suffered widespread mortality. Although, clonal growth (colony expansion) was recorded in a subset of individuals, complete and partial mortality were sufficiently large so as to overcome the signal of minimal growth (Supplementary Table 1). Regrowth (from colony expansion and resurrected recruits) was an important driver of recovery and contributed to over 50% of the increase in cover of *P. superfusa*. Growth of corals in cryptic habitats, such as crevices in the benthos or areas shaded by other corals, may be responsible for some of this survival and growth. In 2010, after the mortality event, colony growth increased. This is consistent with other documented case studies, which suggest that corals may increase growth rates to heal after injury (e.g., Kramarsky-Winter & Loya 2000). However, the recorded increased growth contradicts the idea that bleaching may decrease regeneration abilities of some corals (Meesters & Bak 1993).

Resurrected recruits played a surprising role in the coral's population growth (over 12% of total growth). The resurrected recruits could be a type of regrowth of cryptic tissue, beyond the observational scope of this study. Some of the regrowth appeared to be emerging out from underneath coral colonies of other species that were shading the underlying benthos, such as *Pocillopora meandrina,* and this survival could indicate that partial mortality was induced from UV stress (Baird & Marshall 2002).

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Reimer James 2017-1-28 9:16 AM
コメント [9]: Deleted "in particular" as you do not mention acquiring data for any other coral species.

Jennifer Smith 2017-1-2 11:14 AM
削除: *show. Porites spp. were among the most affected , in terms of both bleaching severity and genera prevalence (Williams et al., 2010).*

Reimer James 2017-1-28 9:15 AM
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Reimer James 2017-1-28 9:16 AM
削除: in particular

Reimer James 2017-1-28 9:15 AM
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k 2016-11-30 12:32 PM
削除: Just a…ter the bleaching even ... [42]

Stuart 2016-12-21 6:34 PM
削除: so high, it …vercomes ... [43]

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Reimer James 2017-1-28 9:22 AM
コメント [10]: You mean crevices on the substrate?

Stuart 2016-12-21 6:34 PM
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Stuart 2016-12-21 6:35 PM
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Reimer James 2017-1-28 9:23 AM
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However, in many cases, the resurrected recruits appeared on a flat reef surface, emerging from benthic areas apparently covered in turf or crustose coralline algae. Unfortunately, the resolution of the photographs did not allow us to determine without question how the corals may have resurrected, for example, either from a small crevice or a surviving piece of tissue. Alternatively, it is possible that these patterns represent true recruitment of larvae onto the exact same location of the benthos as an adult colony had formerly occupied. Nonetheless, these observations hint at the modularity of coral colonies, and the spatial consistency among 'new' recruits is intriguing and warrants further investigation.

In certain cases the partial mortality of *P. superfusa* resulted in fragmentation (100 colonies) or clone fission (79 colonies). Fragmented coral colonies living in close proximity (groups of daughter clones) have a potentially higher rate of survival, as they are not as easily eliminated from disease or competition (Highsmith 1982). However, fragmentation in this study was relatively low (<10%), and thus it is unclear if the "fused" colonies (<10%) were more likely to survive. While recruitment is important for some coral recovery, within-colony expansion and regrowth were of comparable quantitative importance regarding *P. superfusa* growth at Palmyra Atoll. Some *Porites* spp. have been found to have a limited capacity for recruitment (Potts et al., 1985), which may make regrowth a specifically useful recovery mechanism for this genus. A recent study by Roff and colleagues (2014) found that regrowth was an important contributor to the population-scale recovery of massive *Porites*. The ability of corals to regrow from remnant polyps may prove vital to recovery as climate change continues. If the regrowth of tiny fragments of remnant tissue can bring colonies back from apparent mortality, then

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下へ移動 [3]: This observation hints at the modularity of coral colonies.

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Reimer James 2017-1-28 9:24 AM
コメント [11]: This statement doesn't seem correct to me. All resurrection would come from a surviving piece of tissue, unless I am missing something.

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コメント [12]: Here and there, there is a misuse of this word. "Benthos" are living organisms on the seafloor, and I think you are using this word often instead o ... [51]

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colonies that appear dead in traditional coral surveys may actually have a chance at survival. As a result, traditional coral surveys may overemphasize mortality.

Coral colony size was an important predictor of the coral's ultimate fate (Fig 6). Interestingly, *P. superfusa* seemed to have size-dependent growth and death. Growth decreased with increasing size, suggesting that this species may have determinate growth. This growth pattern could be due to high levels of partial mortality. In addition, as is consistent with the literature, smaller colonies of *P. superfusa* experienced higher rates of overall change, including mortality and recovery (Hughes & Jackson 1985). Large colonies are more likely to suffer partial mortality, which may be part of the declining growth with size phenomenon (ADD REFERENCE). Probabilistically, larger colonies are more likely to suffer injury due to a larger surface area, and this may be a factor in the decline of overall growth. Smaller colonies tend to experience damage in a more binary way: either resisting disturbance entirely or dying completely, suffering less incidence of partial mortality (Connell 1973; Hughes & Jackson 1985).

While this study documents the potential for coral regrowth following anomalous temperature events, it is important to note that recovery did not exceed mortality over the course of this study. The decline in *P. superfusa* cover from 2009 to 2010 occurred more rapidly than the increase in coral cover from 2010 to 2011 and the decline from 2011 to 2012. Full population recovery is a slow process, and the longer-term trajectory of *P. superfusa* on Palmyra remains to be seen.

Understanding the effects of large-scale phenomena on community dynamics in relatively pristine reefs provides critical benchmarks for coral demography (Edmunds 2002). Further studies on this topic will help quantify the importance of fragmented or

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remnant corals for reef recovery processes. Examination of other species at these sites may provide important comparisons among morphologies and between species with different life history strategies, which combined may help infer the likelihood of community level recovery. The causes of bleaching, mortality, resistance, and recovery are clearly complex and species-specific. Thus, additional studies from remote Pacific island coral communities are important for understanding the capacity of these systems for recovery via different mechanisms; such studies will help to directly improve the policies for protection of reefs worldwide.

Conclusions

This study documented a bleaching event and subsequent change in areal cover of a common coral on a remote central Pacific atoll. Coral populations can change via four different dynamic processes: complete mortality, partial mortality, growth, and true larval recruitment. This study suggests a fifth dynamic, 'resurrected' recruits, as a mechanism contributing to coral recovery. Additional study is needed to determine the source of this coral growth (e.g., exploitation of cryptic habitats, regrowth of remnant tissue).

With increasing climate pressures, many coral reefs have experienced rapid decline. In such cases, tissue loss due to mortality is faster and more obvious than tissue gain due to growth. Coral growth is often slow and subtle, making it a difficult research and management target. Despite the challenges associated with quantification, regrowth is a critical process in coral recovery, and it is vital we understand the mechanisms controlling it. The implications from this study of colony-specific patterns of decline and

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recovery should be scaled up to examine the role of regrowth and the future of remote Pacific islands' reef recovery.

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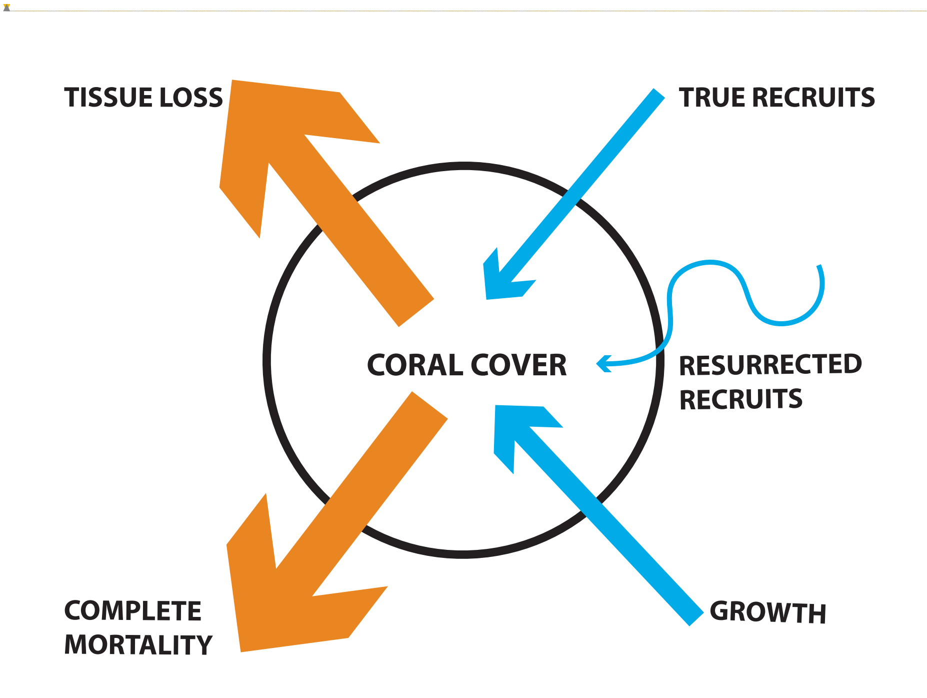

Figure 1. Conceptual diagram of coral demographics contributing to total coral cover for a population. Blue (right side) arrows denote contribution to increasing coral cover (e.g., True recruits, 'Resurrected' recruits, and Growth). Orange (left side) arrows denote contribution to decreasing coral cover (e.g., Partial mortality and Complete mortality). 'Resurrected recruits' is a new term, an operationally defined form of regrowth (see Methods for detailed description). The thickness of arrows indicates the mechanism's relative contribution, as found in this study.

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コメント [16]: Why is the arrow of "resurrected recruits" not straight like the other arrows?

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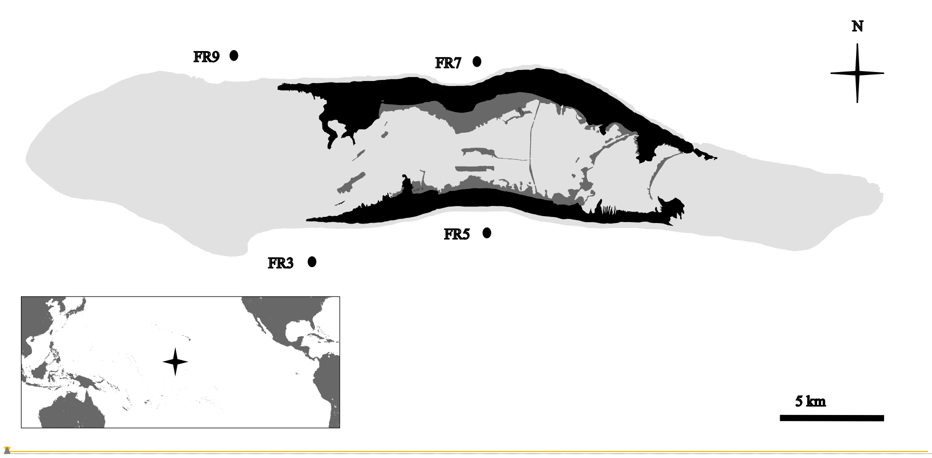

Figure 2. Study sites (yellow dots) around Palmyra Atoll. Map of the Central Pacific (inset) showing the isolation of the island. Data LDEO-Columbia, NSF, NOAA, Image © CNES / Astrium.

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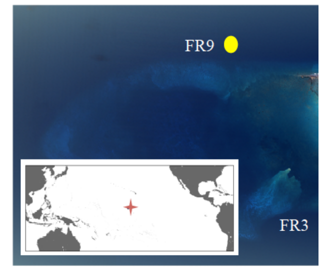

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Reimer James 2017-1-28 9:42 AM

コメント **[17]:** I have a few issues with this map. The Pacific map is so small, and the islands in the Pacific even smaller, so it is hard to show isolation from such an image. You could simply state this is the text, and then use the inset just to show the position of the atoll. The main map of the atoll too is confusing – what do the different colors mean? Sorry to be "old school", but I prefer maps to show a bit more information to be informative to all readers. As well, the dots of sites are black, not yellow.

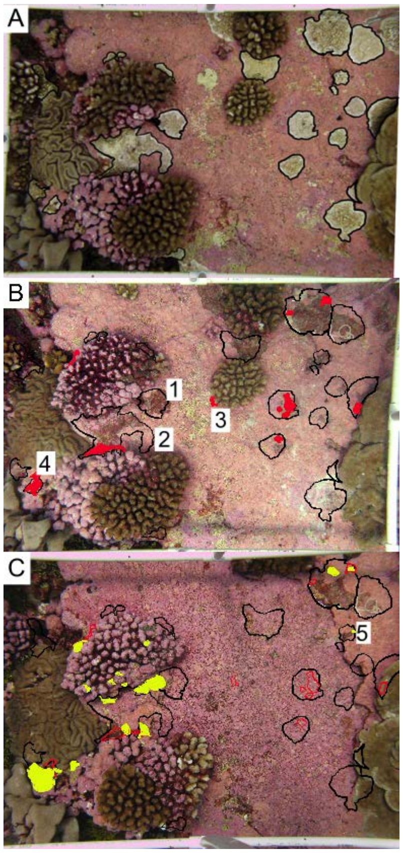

Figure 3. Representative permanent photoquadrat sequence from one site (FR9). (A) September 2009 (C_{2009}) with living *Porites superfusa* outlined in black. (B) July 2010 (C_{2010}) with previous 2009 colony area outlined in black, and living coral highlighted in red. (C) September 2011 (C_{2011}) with previous 2009 colony area outlined in black, 2010 colony area outlined in red, and living coral highlighted in yellow. Colonies that show examples of different fates are labeled with numbers: (1) complete mortality, (2) partial mortality, (3) true recruitment, (4) growth, and (5) resurrected recruits.

Reimer James 2017-1-28 9:43 AM
コメント **[18]:** Scale or mention of size of quadrat possible here?

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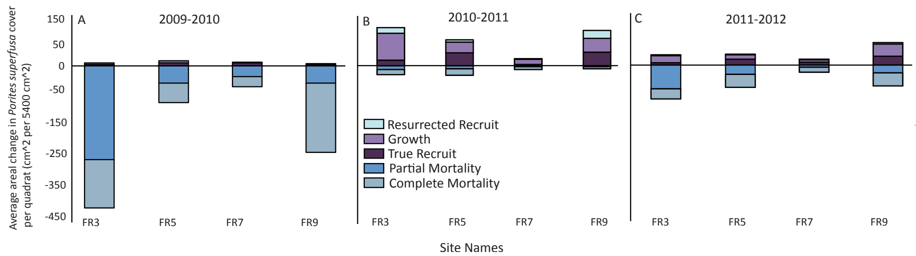

Figure 4. Patterns of gain and loss for *Porites superfusa* during- and post-bleaching event. (A) 2009 to 2010 change in cover, (B) 2010 to 2011 change in cover, (C) 2011 to 2012 change in cover. 'Resurrected' recruits do no exist within the first time transition, as no data exists prior to 2009.

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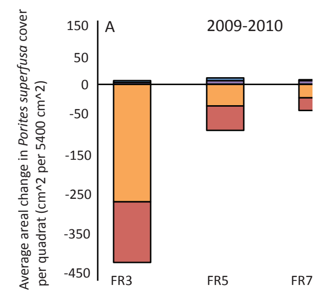

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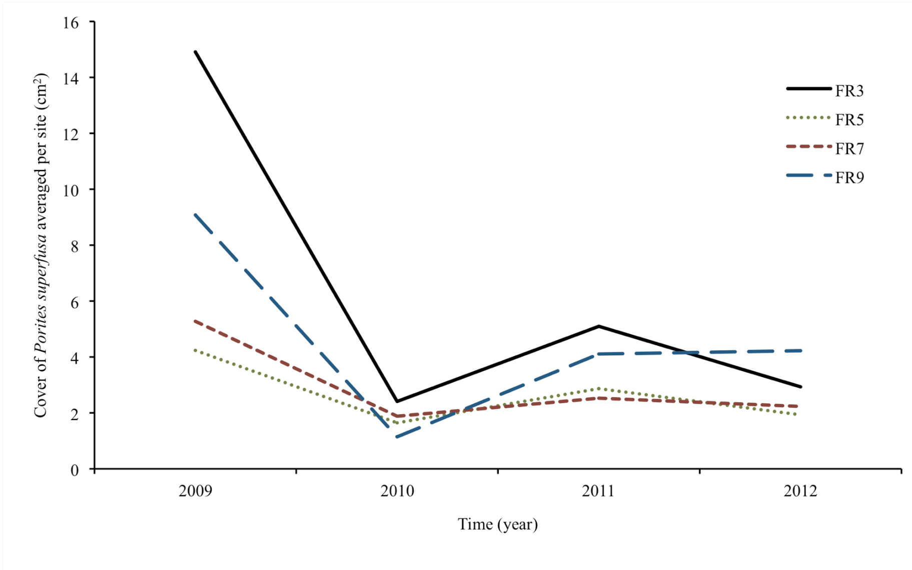

Figure 5. *Porites superfusa* response to 2009 ENSO event averaged by site through time. ENSO event occurs in 2009. Site FR3 is the southeast side of atoll, FR5 is southwest, FR7 is northwest, and FR9 is northeast.

Reimer James 2017-1-28 9:44 AM
コメント **[19]:** Might want to consider rewording this. 2011 and 2012 may not just be response to 2009, but also other events too….

Reimer James 2017-1-28 9:45 AM
コメント **[20]:** Could just refer readers to Figure 1. This figure's legend needs a bit of reconsideration.

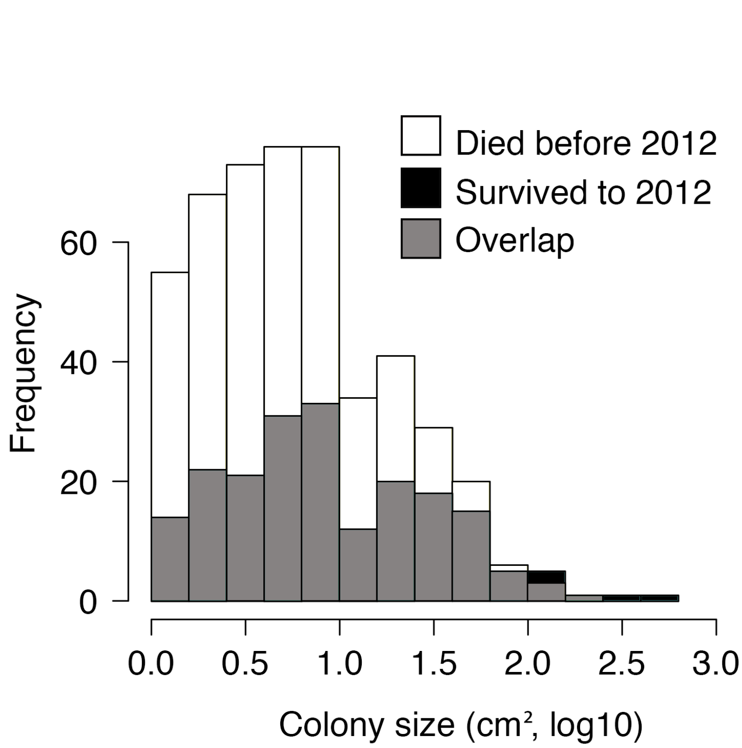

Figure 6. Histogram of initial colony size (in 2009) and survivorship (to 2012). Larger coral colonies were more likely to survive from 2009 to 2012. White denotes coral colonies that died before the 2012 survey. Black denotes coral colonies that survived to 2012. Grey indicates overlap between the white (died) and black (survived).

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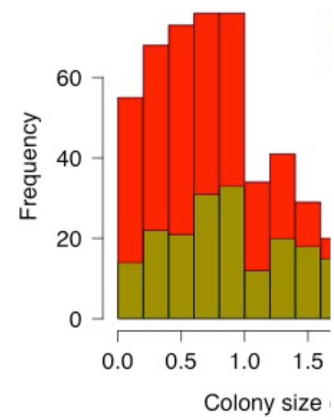

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コメント [21]: Sorry, I am missing something here – what do you mean by overlap? I know you define this here, but do you mean partial mortality? Please keep wording consistent between text and figure legeneds.

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Acknowledgments

Special thanks to Ben Knowles and Genivaldo Gueiros for their comments on the manuscript. Field work completed with the help of Maggie Johnson and Amanda Carter.

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Reimer James 2017-1-28 9:47 AM
コメント **[22]:** No funding sources?

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コメント [24]: No italcis here.

Roff G, Bejarano S, Bozec YM, Nugues M, Steneck RS, Mumby PJ (2014) *Porites* and the Phoenix effect: unprecedented recovery after a mass coral bleaching event at Rangiroa Atoll, French Polynesia. *Mar Biol* 161 (6):1385-1393

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small human population

ページ 3: [2] 削除 Jennifer Smith 2017-01-02 10:19 AM

small human population

ページ 3: [2] 削除　Jennifer Smith　2017-01-02 10:19 AM

small human population

ページ 3: [3] 削除　k　2016-11-30 10:42 AM

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ページ 3: [3] 削除　k　2016-11-30 10:42 AM

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ページ 3: [4] 削除　Jennifer Smith　2017-01-02 10:20 AM

Palmyra atoll is located in the United States Line Islands near the equator (05°N 162°W).

Exacerbating stressors from human populations are particularly low (Sandin et al., 2008).

However i

ページ 3: [5] コメント [1]　Reimer James　2017-01-28 8:02 AM

Do you mean DHW (degree heating weeks)? If so, please state this; as this is now it is a bit hard to understand.

ページ 3: [6] 削除　　k　　2016-09-19 2:39 PM

the demographic

ページ 3: [6] 削除　　k　　2016-09-19 2:39 PM

the demographic

ページ 3: [7] 削除　　Jennifer Smith　　2017-01-02 10:21 AM

While massive *Porites* species can be temperature tolerant (Marshall & Baird 2000), the smaller, encrusting *P. superfusa* is less studied. *Porites superfusa* is a locally common coral genetically similar to *Porites asteroidess,, Porites. rus,* and *Porites. lichen*. (C. Tsang, unpublished data).

ページ 3: [8] 3 ページへ移動 (#1 の移動)　　k　　2016-09-19 6:43 PM

In this study we address two complementary questions: (1) Does *P. superfusa* cover change through time from 2009 to 2012 on Palmyra? (2) What are the relative rates of colony survivorship (recruitment/ mortality) versus colony growth (growth/ shrinkage) during an anomalous event, such as bleaching, and the subsequent years?

ページ 3: [9] 削除	Jennifer Smith	2017-01-02 10:22 AM

The objective of this study was to quantify the relative magnitude of mechanisms that drive demographics for this common central Pacific coral species following disturbance. In this study

ページ 4: [10] 削除	Jennifer Smith	2017-01-02 10:36 AM

. On Palmyra *P. superfusa* appears

ページ 4: [10] 削除	Jennifer Smith	2017-01-02 10:36 AM

. On Palmyra *P. superfusa* appears

ページ 4: [11] 削除	k	2017-01-02 7:01 PM

an average size of 8-10

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an average size of 8-10

ページ 4: [12] 削除 Reimer James 2017-01-28 8:08 AM

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ページ 4: [13] 削除 Jennifer Smith 2017-01-02 10:23 AM

the $0.5m^2$ quadrat frame (see below).

ページ 4: [13] 削除 Jennifer Smith 2017-01-02 10:23 AM

the $0.5m^2$ quadrat frame (see below).

ページ 4: [14] 削除 k 2016-12-02 1:50 PM

because it was an obvious loser in the initial bleaching time point (C_{2009})

ページ 4: [15] 削除 Jennifer Smith 2017-01-02 10:37 AM

P. superfusa is a distinctive coral in this region, and i

ページ 4: [16] コメント [2]　Reimer James　2017-01-28 8:09 AM

Of this species, or the community as a whole?

ページ 4: [17] コメント [3]　Reimer James　2017-01-28 8:12 AM

This wording is a bit vague. Mortality? reduction in cover? I realize this is hard to mention before you present your results, but please consider somethign a bit more concrete here.

ページ 4: [18] 削除　Stuart　2016-12-21 6:07 PM

and disappears

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and disappears

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and disappears

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to track the demographic rates of reef-building corals (

ページ 4: [19] 削除 k 2016-11-30 12:11 PM

to track the demographic rates of reef-building corals (

ページ 4: [20] 削除 k 2016-09-30 2:33 PM

The sites were chosen based on the high initial (C_{2009}) density of *Porites superfusa* colonies.

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ページ 4: [22] 削除 Stuart 2016-12-21 6:09 PM

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ページ 4: [22] 削除 Stuart 2016-12-21 6:09 PM

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ページ 4: [23] 削除 k 2016-11-30 12:11 PM

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ページ 4: [23] 削除 k 2016-11-30 12:11 PM

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ページ 5: [24] 削除 Stuart 2016-12-21 6:12 PM

The sample size of this study includes ten replicate images per surveyed time point per site.

ページ 6: [25] コメント [5] Reimer James 2017-01-28 9:53 AM

This is something you need to check a bit more – particularly as you discuss this in great detail and mention the idea in both figures and your conclusions as something new to come out of this study. Is there any way to investigate this further? being certain (or even more certain) of this is critical.... Otherwise, please tone down your following discussion and conclusion on this matter, at the least by mentioning a caveat in the Discussion and conclusions.

ページ 6: [26] コメント [6] Reimer James 2017-01-28 9:19 AM

I guess in results, but mention if data were normal, or transformed etc. in order to run ANOVA.

ページ 6: [27] 削除	Jennifer Smith	2017-01-02 10:48 AM

customers" and appear multiple times through the study

ページ 7: [28] 削除	k	2016-09-30 2:30 PM

During the 2009 ENSO event, sea surface temperatures reached 1.5°C above the maximum long-term monthly temperatures, and the anomaly continued for four months (Williams et al., 2014). October 2009 through March 2010 had over four degree heating weeks, with November through March over 8°C-weeks (NOAA Coral Reef Watch).

ページ 7: [29] 4 ページへ移動 (#2 の移動)	k	2016-09-30 2:33 PM

The sites were chosen based on the high initial (C_{2009}) density of *Porites superfusa* colonies.

ページ 9: [30] コメント [7]	Reimer James	2017-01-28 9:18 AM

In the M&M you state one-way ANOVA, here one-way t-test. Check this, be consistent with stat terminology used.

ページ 9: [31] 削除	k	2017-01-03 4:33 PM

$F = 3.67, p = 0.041$

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$F = 3.67, p = 0.041$

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$F = 3.67, p = 0.041$

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$F = 3.67, p = 0.041$

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$F = 3.67, p = 0.041$

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$F = 3.67, p = 0.041$

ページ 9: [32] 削除	Jennifer Smith	2017-01-02 11:12 AM

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some

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some

ページ 9: [34] 削除	k	2016-10-10 5:45 PM

(Fig 5)

ページ 9: [34] 削除	k	2016-10-10 5:45 PM

(Fig 5)

ページ 9: [35] 削除	k	2016-10-10 5:51 PM

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ページ 9: [36] 書式変更	k	2016-11-30 10:25 AM

蛍光ペン (なし)

ページ 9: [36] 書式変更	k	2016-11-30 10:25 AM

蛍光ペン (なし)

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(Fig 5,

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(Fig 5,

ページ 9: [38] 削除 Reimer James 2017-01-28 9:15 AM

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ページ 9: [39] コメント [8] Reimer James 2017-01-28 9:20 AM

Just add a bit more information here.

ページ 9: [40] 削除　　k　　2016-12-08 6:38 PM

before,

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before,

ページ 10: [41] 書式変更　　Reimer James　　2017-01-28 9:15 AM

フォント:斜体

ページ 10: [41] 書式変更　　Reimer James　　2017-01-28 9:15 AM

フォント:斜体

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Just a

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ページ 10： [43] 削除　　Stuart　　2016-12-21 6:34 PM

so high, it

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so high, it

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ページ 10: [48] 削除　　Reimer James　　2017-01-28 9:23 AM

heterospecific

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heterospecific

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heterospecific

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ページ 11: [51] コメント [12]	Reimer James	2017-01-28 9:26 AM

Here and there, there is a misuse of this word. "Benthos" are living organisms on the seafloor, and I think you are using this word often instead of "hard substrate" or "seafloor" or "unoccupied coral reef carbonate". Please go through the paper and recheck all the uses of benthos and change where needed.

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Porites

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Porites

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growth/

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has interesting implications for traditional surveys of bleaching and mortality and for reef recovery following disturbances.

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a close to finite or

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a close to finite or

ページ 12: [60] 削除	k	2016-09-19 3:24 PM

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ページ 12: [62] 削除	k	2016-09-19 3:24 PM

, perhaps

ページ 12: [62] 削除	k	2016-09-19 3:24 PM

, perhaps

ページ 12: [62] 削除	k	2016-09-19 3:24 PM

, perhaps

ページ 12: [62] 削除	k	2016-09-19 3:24 PM

, perhaps

ページ 12: [63] 削除　　k　　2016-10-06 10:45 AM

The ultimate fate of these corals remains to be seen

ページ 12: [64] 削除　　Reimer James　　2017-01-28 9:31 AM

so

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and may be more evident when tracked over longer time scales.

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significantly impact

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significantly impact

ページ 13: [67] 削除　Jennifer Smith　2017-01-02 1:00 PM

significantly impact

ページ 13: [68] 削除　k　2016-12-08 6:22 PM

Corals evolved a colonial capacity for regeneration over millions of years, surviving a slow assault of historic storms, bleachings, and changes in climate (Veron 1995). This study documents the bleaching and subsequent decline of a remote central Pacific coral, however, the examination of its modest recovery trajectory illustrates the importance of both recruitment and regrowth mechanisms. As anthropogenic stressors accumulate in our oceans and human impact permeates the globe, remote field sites may be our last glimpse into the natural history and ecology of corals. It is urgent and necessary to carefully document changes through time, in hopes of informing predictions of future coral reefs and the inherent management issues.

ページ 13: [69] 削除	Stuart	2016-12-21 6:44 PM

decline

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decline

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decline

ページ 13: [70] 削除	Jennifer Smith	2017-01-02 1:03 PM

island

ページ 13: [70] 削除	Jennifer Smith	2017-01-02 1:03 PM

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island

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island

ページ 13: [71] コメント [13]　Reimer James　2017-01-28 9:36 AM

Deleted end of this sentence, it is pretty much a rehash of what you have already stated.

ページ 13: [72] コメント [14]　Reimer James　2017-01-28 9:32 AM

See previous comment on this.

ページ 13: [73] 削除　Reimer James　2017-01-28 9:35 AM

although it promises an avenue for recovery that has yet to be explored

ページ 13: [74] 削除　Stuart　2016-12-21 6:46 PM

, including our study sites of *Porites superfusa* at Palmyra Atoll,

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Coral death

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Coral death

ページ 13: [76] コメント [15]　　Reimer James　　2017-01-28 9:37 AM

Deleted “we show that” as this has been shown many times before too; this statement is a bit obvious in fact.

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