# The legacy of stress: Coral bleaching impacts reproduction years later

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## Abstract

1. The extent to which populations persist under environmental stress depends on the reproductive output of individuals that survive the stress. In coral systems, corals bleach in response to stress from elevated water temperature. However, little is known of the extent to which thermal stress impairs the reproductive capacity of the survivors over the following years, limiting the capacity to predict how populations will persist in the Anthropocene.
2. Using histology to quantify the abundance and size of oocytes and spermaries per polyp, we tested how bleaching impairs the reproductive response of the coral *Pocillopora meandrina* over two reproductive seasons following the 2015 mass bleaching event in the Hawaiian Islands.

3. We found that smaller colonies not only had a greater probability of bleaching but also suffered greater reproductive impacts over a longer time. In contrast, larger colonies generated comparable reproductive output regardless of bleaching severity, although bleached colonies generated smaller oocytes the year after bleaching.
4. These results show that reproductive impacts of bleaching are more complex and size-specific than commonly assumed. Therefore, estimates of bleaching mortality may underestimate the true impact of thermal stress on populations, especially as populations lose larger individuals from repeated and co-occurring stressors.

**Keywords:** Coral reproduction, histology, *Pocillopora meandrina*, stress response, symbiotic disruption, scleractinian, temporal effects

## Introduction

When a change in environmental conditions increases organismal stress and reduces reproductive output, it can have a significant impact on the persistence of populations and the rate of evolutionary change (Hoffmann & Hercus, 2000). Increases in global temperature are expected to increase organismal stress (Parmesan, 2006). In coral reef systems, increases in global temperatures are increasing the frequency, severity, and spatial scale of coral bleaching - the disruption of a symbiotic relationship that allows stony corals to thrive in oligotrophic waters (Lough, Anderson, & Hughes, 2018). Many investigations into the effect of bleaching stress on coral populations have focused on mortality (Guest et al., 2016; Loya et al., 2001; Pratchett, Trapon, Berumen, & Chong-Seng, 2010), but the replenishment of colonies that die from bleaching is fundamentally reliant on the reproductive output of those that survive. The cryptic effects of bleaching stress on the subsequent fecundity of surviving colonies are rarely studied, especially over multiple years, and remain unclear (Armoza-Zvuloni, Segal, Kramarsky-Winter, & Loya, 2011; Baird & Marshall, 2002; Hagedorn et al., 2016; Levitan, Boudreau, Jara, & Knowlton, 2014; Mendes & Woodley, 2002). If prior bleaching reduces the fecundity of survivors, then estimates of bleaching mortality may underestimate the true impact of bleaching on populations.

Prior bleaching could reduce the fecundity of survivors by diverting energy away from reproduction and towards colony recovery (Michalek-Wagner & Willis, 2001a). In doing so, bleached colonies may contribute fewer, smaller, or lower quality gametes as a result of severe stress. In marine invertebrates, larger offspring size tends to correlate with higher fertilization success, faster time to development, and higher offspring survivorship (Levitan, 2006; Moran & Emlet, 2001). Oocytes are energetically more costly to make than sperm (Hayward & Gillooly, 2011). For coral colonies that are stressed, reductions in oocyte size have been observed (Cox, 2007; Michalek-Wagner & Willis, 2001a; Piñón-González & Banaszak, 2018), but the effect of bleaching stress on the production and size of the less energetically costly reproductive material, spermaries, has not yet been investigated in corals (but see Hagedorn et al. 2016 for sperm motility reduction following bleaching).

Despite the colonial nature of corals, colony size has the potential to impact both bleaching susceptibility and severity, as well as the generation of reproductive material post-bleaching. Large colonies of branching species have more interstices and branches than smaller colonies, which create more complex flow dynamics (Hearn, Atkinson, & Falter, 2001), and better allow colonies to regulate bleaching susceptibility and post-bleaching survival (Nakamura & van Woesik, 2001). Extended water residence times within larger branching colonies increase feeding capabilities and gas exchange (Chang, Iaccarino, Ham, Elkins, & Monismith, 2014), which in turn increase colony wide energetic reserves (Hughes & Jackson, 1985), resulting in higher fecundity per unit mass (Álvarez-Noriega et al., 2016; Babcock, 1991). Energy available to colonies following stress is anticipated to be limited (Oren, Benayahu, Lubinevsky, & Loya, 2001); therefore, tradeoffs between recovery and reproduction are expected to depend on colony size.

Here, we determined the effect of bleaching stress *in situ* on the subsequent reproductive output of the branching coral *Pocillopora meandrina*, one of the dominant coral species found across Hawaiʻi (Franklin, Jokiel, & Donahue, 2013) and throughout the Indo-Pacific (Gélin, Postaire, Fauvelot, & Magalon, 2017). In 2014 and 2015, Hawaiian reefs experienced their worst bleaching in recorded history, with coral mortality ranging from ~10-50% following the 2015 bleaching event (Bahr, Rodgers, & Jokiel, 2017; Couch et al., 2017; Rodgers, Bahr, Jokiel, & Richards Donà, 2017). The colonies that bleached and survived this mass bleaching event provide a natural experiment to begin to understand how coral bleaching affects the reproduction of survivors post bleaching. We followed 40 individually marked colonies and quantified polyp-scale reproductive output over two post-bleaching reproductive seasons. Marked corals were differentially affected by the bleaching event of 2015 and varied in size across the natural range of size variation. We expected: 1) that reproductive output would decline with increasing bleaching severity, 2) that oocyte production would be more impacted than spermary production because oocytes are more energy intensive, 3) that larger colonies would generate more reproductive material per polyp post-bleaching than smaller colonies, and 4) that reproductive output among severely bleached colonies during the first reproductive season following bleaching would be lower than in the second reproductive season.

## Materials and methods

### *Species identification and site information*

Sixty-one randomly selected coral colonies exhibiting *P. meandrina* morphology, and which encompassed a range of colony sizes and bleaching severities, were tagged at the onset of bleaching (August 2015) at four sites around O‘ahu, Hawai‘i. Fifty-three were confirmed as *P. meandrina* using a restriction fragment length polymorphism gel assay (Johnston, Forsman, & Toonen, 2018). Forty-four of the genetically confirmed *P. meandrina* colonies survived over the course of the two-year study. Forty of these colonies had two years of histological data and were used in analyses (Kewalo Deep, n = 11; Kewalo Shallow, n = 5; Lanikai, n = 10; and Kāne‘ohe Bay, n = 14; Fig. 1a). Focal sites were chosen for their year-round accessibility and the depth of focal colonies (range: 1 – 9 m). HOBO pendant temperature data loggers (Onset Computer Corporation, MA) were deployed at each site from August 7, 2015 to August 7, 2017 following the protocol of Bahr et al. (2016).

### *Reproductive biology and sampling for histology*

Colonies of *P. meandrina* in Hawai‘i have been observed to broadcast spawn 1 – 3 days following the full moon in April and May approximately one hour after sunrise (Kolinski & Cox, 2003). Like other *Pocillopora, P. meandrina* is a simultaneous hermaphrodite and each fertile polyp is expected to contain 6 pairs of male and female gonads (Massé et al. 2013; Fig. 2). Branch fragments approximately 3 cm in length were collected for histology from the colony center five days before the full moon in both April and May of 2016 and 2017 (HIMB Special Activity Permit SAP-2018-3). Due to the prevalence of immature reproductive material observed in April of both sampling years, only data from May were analyzed.

*Bleaching severity and colony size*

Focal colonies were photographed monthly from August 2015 – August 2017. Widespread bleaching occurred from August to December of 2015. Bleaching severity for each colony was estimated *in situ* and confirmed through white-balanced photographs. Following Counsell et al. (2019), each colony was classified into one of four bleaching categories representative of the most severe bleaching that the colony experienced at the height of bleaching (Fig. 3b): 0 = no visible bleaching, 1 = noticeable paling, 2 = severe paling, and 3 = stark white bleaching of the entire colony. The percentage of live tissue for each colony at the time of sampling in 2016 and 2017 was also estimated *in situ* and confirmed with these photographs. The length (L) and perpendicular width (W) of each colony was measured *in situ* to the nearest cm in 2016. Annual colony size was calculated as the elliptical area, based on the colony's length and width in 2016, multiplied by the annual estimate of the percentage of live tissue to account for partial mortality that occurred between 2016 and 2017 as:

$$Colony\ size_{year} = \pi(\frac{L}{2} \times \frac{W}{2}) \times percent\ live\ tissue_{year}$$

*Histology*

Samples were fixed in a solution of 4% Zinc formalin (Z-Fix; Anatech Ltd, MI) and filtered seawater for two days, rinsed with di$H_2O$ and preserved in 70% ethanol, and sent for histological processing to Histo Techniques LTD, OH. Samples were decalcified with Formical 4 (formic acid and formalin mix; StatLab, TX) and the tissue closest to the wounded area was prepared for wax histology to avoid non-reproductive areas near the branch tips. Transverse sections (~6 µm thick) were mounted and stained using Gil's haemotoxylin and eosin. Using one transverse tissue section per colony per time point, the number, gametogenic stage, and size of the reproductive material present was recorded for all complete polyps (i.e., entire polyp wall evident). If no reproductive material was present in a polyp, this was also recorded. For each colony that contained reproductive material, the maximum diameter of the roundest stage IV oocyte (i.e., presence of defined nucleus) and stage IV spermary present were measured in every polyp (approximately 20-30 polyps per colony).

*Statistical analyses*

All statistical analyses were performed in R v.3.6.2 (R Core Team 2019). To determine the probability of bleaching as a function of colony size, we used binomial generalized linear models (base R, function 'glm'). We modelled the probability of no bleaching versus any bleaching (i.e., colonies that paled, paled severely, or bleached stark white) based on colony size. We also modelled the probability of stark white bleaching versus less severe and no bleaching based on colony size. For these analyses, colony size was that measured in 2016, the year following the mass bleaching event.

To determine how the reproductive output of oocytes and spermaries per polyp per colony was impacted by bleaching severity in 2015, we used hurdle Poisson mixed effects models (*glmmTMB* package; Brooks et al. 2017). We used hurdle models to account for zero-inflation in the response variables. This two-part approach allowed us to use the same fixed effects to first model the probability that a zero was observed using a binomial model, and then to model abundance, using only the non-zero data, with a zero-truncated Poisson distribution. Data were analyzed separately by reproductive year (2016 and 2017) because the effect of colony size and bleaching severity was expected to differ by year. Fixed effects were bleaching severity from the 2015 event, colony size, and the interaction between bleaching severity and colony size. To improve model convergence, colony size $x_i$ was mean centered and scaled as $(x_i - \bar{x})/\sigma$, where $\bar{x}$ is the mean and $\sigma$ is the standard deviation of colony size in the population sampled. Therefore, the effects of colony size are reported in units of standard deviation from the mean size. Coral colony identity (coral ID) was included as a random effect to account for repeated measurements within colonies, i.e., from multiple polyps. Including coral colonies as either a random effect or nesting colonies within sites gave essentially the same output from these models. However, given that we were not interested in the site component of variation, we included each unique coral colony as a random effect here to both capture variation among sites and variation among coral colonies within sites. Colony sizes overlapped at each site. Separate models were run with the number of oocytes per polyp and the number of spermaries per polyp as response variables.

To determine if oocyte diameter, an estimate of the quality of reproductive output, and spermary diameter differed as a result of bleaching severity, we modeled oocyte and spermary diameter per polyp with separate GLMMs with gaussian distributions (*glmmTMB* package; Brooks et al. 2017). Data were analyzed separately by reproductive year (2016 and 2017). Fixed effects were bleaching severity and colony size. Coral colony identity was included as a random effect to account for repeated measurements.

## Results

### *Bleaching patterns and colony size across space and time*

The 40 focal *P. meandrina* colonies sampled from four sites around O‘ahu, Hawai‘i (Fig. 1a), experienced bleaching stress ranging from no bleaching (colony retained normal pigmentation) to complete bleaching (colony was stark white) from August to December of 2015 (Fig. 3b). By January 2016, all colonies had visually regained their color and, in 2016 and 2017, no additional bleaching was observed in any of the focal colonies. At all sites maximum temperatures were higher in 2015 than in 2016 and 2017 (Fig. 1b). Among the four study sites, Lanikai experienced the greatest range in temperature (23.0 – 30.0°C) over the two-year period and Kewalo Deep experienced the smallest range (24.2 – 29.4°C; Fig. 1c). Colony size ranged from 198.0 to 888.3 cm$^2$ (546.0 ± 182.1 cm$^2$, mean ± SD) in 2016. Mean percent live coral tissue decreased by 6.3 ± 3.2% (mean ± SD) from 2016 (92.6 ± 15.5%, mean ± SD) to 2017 (86.3 ± 18.7%, mean ± SD).

*Bleaching severity and colony size*

The probability of a colony avoiding bleaching did not vary with colony size (slope = -0.002, -0.005 to 0.0004, 95% CI; Fig. 3c). However, the probability of a colony bleaching stark white (versus severe paling, paling, or no bleaching) decreased significantly with increasing colony size (slope = -0.004, -0.007 to -0.001, 95% CI; Fig. 3d).

*Bleaching severity and reproductive output across colony size*

*Probability of oocytes*

In the first post-bleaching reproductive season (2016), larger colony sizes were associated with increased odds of oocyte presence, increasing the odds by a factor of 9.95 (1.25 to 79.04, 95%CI) in colonies that paled severely and 6.97 (1.09 to 44.70, 95%CI) in colonies that bleached stark white per standard deviation increase in colony size (Fig. 4a). In the second reproductive season (2017), the probability of mature oocyte presence per polyp was most reduced in colonies that had paled (Fig. 4a; Table 1).

*Oocyte abundance*

In the first post-bleaching reproductive season, increasing colony size increased mature oocyte abundance per polyp by a factor of 1.59 (0.88 to 2.86, 95%CI) in colonies that had bleached stark white per standard deviation increase in colony size (Fig. 4b; bold values Table 1). In the second post-bleaching reproductive season, mature oocyte abundance per polyp was reduced in colonies that had bleached stark white in comparison to colonies that had not bleached, paled, or paled severely in 2015 (Fig. 4b; bold values Table 1). In both years, mature oocyte abundance tended to be greatest in average sized colonies that did not bleach (Fig. 4b).

*Probability of spermaries*

The probability of mature spermary presence per polyp was most reduced in colonies that had paled severely, regardless of colony size, in the first post-bleaching reproductive season (Fig. 4d; bold values Table 1). In stark white colonies, larger colony sizes were associated with increased odds of mature spermary presence, increasing the odds by a factor of 12.86 (2.59 to 64.07, 95%CI) per standard deviation increase in colony size in 2016 (Fig. 4d). In 2017, the probability of mature spermary presence per polyp was most reduced in colonies that paled (Fig. 4d; bold values Table 1).

*Spermary abundance*

In colonies that produced spermaries in 2016, larger colony sizes were associated with increased spermary abundance per polyp, increasing the odds by a factor of 1.31 (1 to 1.73, 95%CI) per standard deviation increase in colony size in colonies that had bleached stark white (Fig. 4e). In contrast, in 2017, spermary abundance per polyp declined by a factor of 0.83 (0.76 to 0.90, 95%CI) per standard deviation increase in colony size in colonies that had bleached stark white (Fig. 4e).

### *Oocyte and spermary diameters*

In the reproductive season directly following the bleaching event, oocyte diameter was reduced by 18.70 µm (-31.80 to -4.34, 95%CI) in colonies that had bleached stark white (Fig. 4c). There was no effect of bleaching severity or colony size on oocyte diameter in 2017 (Table 1). There was no effect of bleaching severity or colony size on spermary diameter in 2016 or 2017 (Fig. 4f; Table 1).

## Discussion

Following disturbance events, the replenishment of populations depends on an organism's ability to mitigate stress in order to reproduce (Hoffmann & Hercus, 2000). For severe stress, allocation of resources may be diverted into organismal recovery rather than reproductive effort (Michalek-Wagner & Willis, 2001a), prolonging population recovery. Here, we show that the impacts of severe bleaching stress on a common branching coral depend on colony size. We found that not only were smaller colonies of *P. meandrina* more likely to bleach severely during the 2015 bleaching event (Fig. 3b), they were also more likely to have reduced fitness post-bleaching (Fig. 4). Smaller colonies that bleached severely had a reduced probability of producing reproductive material and, when generated, a reduced abundance of reproductive material following the bleaching event (Fig. 4). In contrast, larger colonies that bleached severely had oocyte abundance comparable to colonies that did not bleach in the first reproductive season post-bleaching (Fig. 4b). In the second reproductive season, more than a year after colonies had visually recovered from bleaching, colonies that had previously severely bleached showed a lasting impact of bleaching on oocyte abundance. Specifically, colonies that did not exhibit stark white bleaching in 2015 showed an increase in oocyte abundance during the second reproductive season (Fig. 4b). We also found that oocyte size was reduced in the first post-bleaching reproductive season for colonies that had severely bleached (Fig. 4c), implying an energetic constraint on simultaneous stress recovery and development of reproductive material.

Thermal bleaching directly impacts populations of coral by first removing individual colonies from the population due to mortality. Then, for colonies that survive, bleaching can have lasting impacts on individual health, reducing colony fitness by decreasing energy reserves and reproductive output (Grottoli et al., 2014; Schoepf et al., 2015). Coral species differ in the rate at which energy reserves are replenished following bleaching, with some Hawaiian species recovering fully within 1.5 months, whereas others required 8 months or more to replenish reserves (Rodrigues & Grottoli, 2007). Here, we found that in the first post-bleaching reproductive season, oocyte production occurred in 78% of *P. meandrina* colonies that paled severely, and 55% of the colonies that bleached stark white (Supplementary Fig. 1). By the second post-bleaching reproductive season, 100% of colonies that had paled severely and 55% of colonies that had bleached stark white (a different subset of colonies than in 2016) produced oocytes.

Colony size impacts thermal susceptibility (Nakamura & van Woesik, 2001), and increases in colony size can increase polyp-level fecundity (Babcock 1991; but see Padilla-Gamiño and Gates 2012). However, the size-specific effects of bleaching on subsequent reproductive output are not well studied (Howells et al., 2016). We found that larger colonies are less likely to bleach severely (Fig. 3d) and less likely to have reduced fitness post-bleaching than smaller colonies (Fig. 4). Following histological sampling in 2017, we also found that larger colonies healed wounds an average of 14 days faster than smaller colonies (Counsell et al., 2019). These wounds healed so thoroughly that within 40-50 days after wounding the wound site was indistinguishable from the rest of the colony and no shift in live coral tissue was documented during the sampling/wound healing process. Because larger colonies have greater energetic reserves than smaller colonies (Oren et al., 2001), we hypothesize that smaller colonies could be prioritizing growth and recovery, following bleaching stress, over reproduction. Larger colonies appear better able to mitigate the effects of thermal stress on reproduction, but we still observed a prolonged impact of severe bleaching on oocyte production for larger colonies during the second post-bleaching reproductive season (Fig. 4b). The interaction we found between colony size and bleaching severity indicates that the extrapolation of colony-level reproductive output, without considering the greater effect of bleaching stress on the subsequent fitness of smaller colonies, will not provide accurate estimates of population-level reproductive potential following bleaching events.

For colonies that experienced a recent severe stress, such as coral bleaching or partial mortality, a decrease in oocyte size is often a consequence of their decreased maternal condition (Mendes & Woodley, 2002; Michalek-Wagner & Willis, 2001a; Paxton, Baria, Weis, & Harii, 2015). In the first reproductive season following the bleaching event of 2015, we found that oocyte diameter was reduced by approximately 15% in *P. meandrina* colonies that had bleached stark white, but by the second reproductive season this impact was no longer evident (Fig. 4c). Smaller oocytes have fewer maternally provisioned energy rich lipids (Michalek-Wagner & Willis, 2001b). Reduced oocyte size contributes to decreased fertilization success and postzygotic survivorship in some marine invertebrates (D. R. Levitan, 1996), but the impact of reduced oocyte size on fertilization success and later life stages in corals is not yet well understood. To the best of our knowledge, only three studies have investigated the effect of oocyte size on fertilization success in corals. Following severe bleaching, a 25% reduction in oocyte size completely halted fertilization in *Lobophytum compactum* (Michalek-Wagner & Willis, 2001a), while a 51% reduction in oocyte size reduced fertilization success by 43% in *Lobactis scutaria* (Hagedorn et al., 2016). Alternatively, a 20% reduction in oocyte size following partial colony mortality increased fertilization success in *Acropora palmata* (Piñón-González & Banaszak, 2018). In these three coral species, photosynthetic symbionts are not vertically transmitted to oocytes, which instead must be acquired from the environment. Photosynthetic symbionts are vertically transmitted to the oocytes of *P. meandrina* (Fig. 2c). Whether a reduction in oocyte size impacts fertilization success in *P. meandrina*, and whether the vertical transmission of photosynthetic symbionts to *P. meandrina* oocytes has the potential to alleviate postzygotic differences in gamete size caused by bleaching stress, remain unknown.

Oocyte resorption in corals has been documented as a response to stress, translocating the energy of unspawned oocytes back into colony tissue to be used for colony repair and growth (Michalek-Wagner & Willis, 2001a; Okubo, Motokawa, & Omori, 2007; St.Gelais, Chaves-Fonnegra, Moulding, Kosmynin, & Gilliam, 2016). This process has been described as the resorption of atrophied or decomposing oocytes in *Stylophora pistillata* (Rinkevich & Loya, 1979), the hollowing and collapse of oocytes in *Acropora formosa* (Okubo et al., 2007), and the cracking and decomposition of oocytes in *Siderastrea siderea* (St.Gelais et al., 2016). Over the course of our study, we did not observe any abnormally shaped or decomposing oocytes or spermaries that would be indicative of resorption. We also did not find evidence for the resorption of reproductive material as a result of histological sampling, i.e., the predominance of immature reproductive material in April that did not mature in May (Supplementary Fig. 2).

Our study confirms that severe bleaching has a greater impact on oocyte development than on spermary development in a common and widespread branching coral, *P. meandrina*, with impacts lasting longer than one reproductive season. The only impact of severe bleaching on spermary output was observed in the first reproductive season in small colonies as a reduction in both the probability of generating spermaries and a reduction in their abundance. In both post-bleaching reproductive seasons, the production of oocytes was either halted or significantly reduced for small colonies that had experienced severe bleaching stress. The continued ability of larger colonies to produce reproductive material following severe bleaching stress may explain why *Pocillopora* spp. are often resilient following disturbances. However, the lasting impact of severe bleaching on oocyte production observed in the second reproductive season indicates that the long-term fitness effects of consecutive bleaching events are likely not independent (Levitan et al., 2014; Michalek-Wagner & Willis, 2001a). The contemporary disappearance of *Pocillopora* spp. has been documented from thermally extreme regions such as the Persian/Arabian Gulf (Riegl et al., 2017) and the heavily urbanized coastlines of Singapore (Poquita-Du et al., 2019). Given that the frequency and severity of bleaching events are expected to increase in the future (Hughes et al., 2018), understanding how demographic change in colony sizes, coupled with the temporal impacts of severe bleaching on reproduction, recruitment, and population persistence, effects the ability of reefs to reassemble following disturbances will be paramount.

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**Authors' contributions:**

ECJ, CWWC, TLS, and RJT conceived the ideas and designed methodology; ECJ, CWWC, and TLS collected the data; ECJ, CWWC, and SCB analysed the data; ECJ, CWWC and SCB led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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**Data sources:** Data are archived online at Dryad and are available at https://doi.org/10.5061/dryad.c866t1g4q

**Table 1**. Probability and abundance of oocyte and spermary production per polyp per colony from mixed effects hurdle models and oocyte and spermary diameter per colony from mixed effects models in *P. meandrina.* The 95% confidence intervals are given in parentheses; values in bold indicate 95% confidence intervals that do not overlap with zero at significance *** = $p < 0$ ; ** = $p < 0.001$; * = $p < 0.01$; . = $p <0.05$

**Figure 1**. Site locations and respective temperature series. (a), Map of O‘ahu, Hawai‘i, showing the locations of the four sites in this study. Inset shows the map of the main Hawaiian Islands (b), Average daily temperature at each site from August 2015 to August 2017. (c), Solid line, mean ± sd; dashed lines, minimum and maximum temperatures. Black arrows indicate when tissue samples were collected for histological analysis, which was five days before the full moon in April and May (spawning was expected several days after the full moon).

**Figure 2**. Oocyte and spermary development in *P. meandrina*. **(a)**, Ovary containing stage I oocytes. **(b)**, Ovary containing stage II oocytes. **(c)**, Stage III oocytes adjacent to stage IV oocytes. **(d)**, Longitudinal section of a polyp showing both stage IV oocytes and spermaries. **(e)**, Stage I spermary. **(f)**, Longitudinal section of a polyp containing stage II spermaries and oocytes. **(g)**, Stage III spermaries. **(h)**, Transverse section of a polyp containing stage IV spermaries. lu, lumen; m, mesentery; mf, mesenterial filament; nu, nucleus; o1, o2, o3, o4, oocyte stages I, II, III, and IV; pw, polyp wall; s1, s2, s3, s4, spermary stages I, II, III, IV; st, mesenterial stalk; v, vitellogenic reserves; z, zooxanthallae. Scale bar is 100um.

**Figure 3**. Colony size distribution by bleaching severity category, representative colonies for each bleaching category, and the probability of colony bleaching severity in 2015 based on colony size. (a), Size distribution of colonies across the four bleaching severity categories of 2015 showing no bleaching (n = 7), paling (n = 13), severe paling (n = 9), and stark white bleaching (n = 11). Elliptical colony area as a function of the percentage of annual estimates of colony live tissue per colony is shown on the left; these same values, centered and scaled, are shown on the right. (b), Representative colonies of each of the four bleaching severity categories at the height of bleaching in 2015. (c), Probability of a colony showing no visual signs of bleaching (0) vs showing evidence of bleaching (1: paling, severe paling, or stark white bleaching) across colony size in 2015. (d), Probability of a colony bleaching stark white (1) vs showing evidence of no bleaching or less severe bleaching (0) across colony size in 2015.

**Figure 4**. Relationship between the probability, abundance, and diameter of oocytes and spermaries in response to colony bleaching severity in 2015 for reproductive years 2016 and 2017 across colony size. (a), Probability that a colony contained polyps with stage IV oocytes. (b), Abundance of stage IV oocytes per polyp per colony in colonies that produced oocytes. (c), Mean stage IV oocyte diameter (um) per colony in colonies that produced oocytes. (d), Probability that a colony contained polyps with stage IV spermaries. (e), Abundance of stage IV spermaries per polyp per colony in colonies that produced spermaries. (f), Mean stage IV spermary diameter (um) per colony in colonies that produced spermaries in response to bleaching severity across colony size. Each symbol represents a single polyp in (a and d), or an individual colony in (b, c, e, and f). Lines represent fitted values from the binomial (a and d) and Poisson components (b and e) of the hurdle models.