



Colony size and depth affect wound repair in a branching coral

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Abstract

Coral colonies regularly suffer tissue damage from natural and anthropogenic sources. The resultant wounds can decrease colony fitness and act as sources of infection or algal overgrowth. By systematically breaking branches on 54 *Pocillopora meandrina* colonies and following in situ tissue regeneration (April–August 2017), variation in the wound recovery process was investigated within colonies, among colonies, and across four sites on O‘ahu, Hawai‘i. Ninety-five percent of all wounds healed, with an average healing time of 42 days. Average healing time was not different between initial and subsequent wounds. The relative importance of intrinsic factors, extrinsic factors, and disturbance history for the wound repair process was examined. Previous colony stressors, i.e., percent live coral tissue and bleaching history, were not correlated with wound healing time. These results indicate that wound repair is a priority for *P. meandrina*. Colony size and depth were significantly correlated with wound healing time: larger colonies healed 14 days faster than smaller colonies, and deeper colonies healed 25 days slower than shallower colonies. These findings support the hypothesis that larger colonies have more energy available for tissue regeneration. The observation of longer healing times for deeper colonies is likely driven by extrinsic factors that vary with depth, including temperature, wave energy, and irradiance. Overall, we show that wound healing in *P. meandrina* is physiologically resilient to previous stressors, but is affected by both colony size and depth. Understanding drivers of variation in regenerative processes for corals is critical for predicting coral population recovery after disturbances.

Introduction

Given the myriad of stressors facing hermatypic corals today, including increased frequency and intensity of thermal stress (Hughes et al. 2018b) and high wave energy resulting from storm events (Walsh et al. 2016), characterizing and understanding variation in coral tissue regeneration is critical for predicting coral reef ecosystem resilience. Scleractinian corals are foundational components of the reef

ecosystem, providing most of the habitat’s structural complexity. Branching corals create particularly complex reef habitats. However, they are more susceptible than mounding or encrusting corals to breakage during episodes of high wave energy, or as a result of incidental interactions with boats, snorkelers, divers, and fishing gear (Fong and Lirman 1995; Madin and Connolly 2006; Madin et al. 2014). Tissue damage resulting from these events can negatively affect colony fitness (Rotjan and Lewis 2008; Jayewardene et al. 2009). Further, broken branches present a potential path for pathogens to enter the colony (Ben-Haim et al. 2003; Rodríguez-Villalobos et al. 2015) and for colonization by fouling organisms on the exposed skeleton (Henry and Hart 2005), both of which can affect critical life history processes such as growth rate (Meesters et al. 1994) and reproductive output (Rinkevich and Loya 1989; Rinkevich 1994). While the ability of coral colonies to heal lesions has been found to vary in response to colony parameters and environmental variables (Fong and Lirman 1995; Henry and Hart 2005; Edmunds and Yarid 2017), the relative importance of these drivers and the spatial scale of variation in the wound healing process have not been as well studied.

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Coral tissue regeneration following wounding can be affected by colony parameters including colony size (Hughes and Connell 1987; Henry and Hart 2005; Elahi and Edmunds 2007; Kayal et al. 2015) and morphology (Henry and Hart 2005; Darling et al. 2012; Madin et al. 2016), as well as by the size and shape of the wound (Croquer et al. 2002; Henry and Hart 2005; Fisher et al. 2007; Cameron and Edmunds 2014; Defilippo et al. 2016). Corals typically exhibit allometric growth, such that larger colonies grow more slowly than smaller colonies (Edmunds and Burgess 2016; Dornelas et al. 2017). In contrast, tissue regeneration associated with wound healing occurs at a faster rate in larger colonies (Henry and Hart 2005; Elahi and Edmunds 2007). While colonies with branching and plating morphologies are at a higher risk of damage from extreme wave energy events (Madin et al. 2014), these colonies are able to heal wounds faster than colonies with massive and encrusting morphologies (Hall 1997; Henry and Hart 2005). Furthermore, colonies with greater morphological complexity have more varied wound healing rates within each individual colony, because exterior branches decrease the light, water flow, and particle flux for interior branches (Kaniewska et al. 2011, 2014; Chang et al. 2014; but see Hall 1997).

Environmental factors that impact coral community composition, such as wave energy, sedimentation, irradiance, and temperature (Franklin et al. 2013; Gove et al. 2015), also impact the rate of wound repair in corals (Henry and Hart 2005). In situ, increased growth (Smith et al. 2008) and lesion recovery rates (Sabine et al. 2015) have been recorded at sites with higher flow rates, though these site differences in flow rates co-varied with other environmental factors, including nutrient and turbidity levels. High sedimentation decreases growth and wound recovery rates for photosynthetic corals (Croquer et al. 2002; Piniak and Brown 2008; Bégin et al. 2016), while higher irradiance levels increase energy available for growth (Osinga et al. 2011). Additionally, increased temperatures can increase metabolic rates and coral growth across latitudes (Anderson et al. 2017), seasons (Jokiel and Coles 1977; Tortolero-langarica et al. 2017), and sites (Smith et al. 2008). Thus, wound regeneration rates are expected to be positively correlated with moderate increases in water temperature (Henry and Hart 2005). However, the effects of temperature on wound healing vary across taxa (Lester and Bak 1985; Kramarsky-Winter and Loya 2000; Lenihan and Edmunds 2010), and when temperatures approach bleaching thresholds, coral growth and regeneration rates are reduced (Anderson et al. 2017; Bonesso et al. 2017). These environmental factors often vary with depth, such that deeper sites have lower wave energy (Sebens et al. 2003), decreased sedimentation and irradiance (Nagelkerken et al. 1999; Sebens et al. 2003; Kaniewska et al. 2008), and cooler temperatures (Lester and Bak 1985; Kramarsky-Winter and Loya 2000).

In addition to understanding the effects of colony parameters and environmental variables on the rate of wound recovery, it is critical to understand how a colony's disturbance history impacts the energy available to heal wounds. Previous wounding is expected to limit the resources available for a colony to regenerate tissue for more recent wounds (Henry and Hart 2005). Partial mortality of tissue immediately surrounding wounds can decrease the amount of tissue regenerated at the wound site (Meesters et al. 1994; Fong and Lirman 1995; Defilippo et al. 2016). However, the effect of partial mortality at the colony-scale on tissue regeneration has not been well studied. Coral bleaching decreases energy available for tissue growth (Goreau and Macfarlane 1990; Kenkel et al. 2013), which can impact colony survival (Yamashiro et al. 2005; Grotto et al. 2014; Schoepf et al. 2015) and tissue regeneration (Meesters and Bak 1993; Fine et al. 2002; Rotjan et al. 2006). To date, studies on how bleaching impacts tissue regeneration have focused on wound healing in colonies that were simultaneously bleached. Given predictions for increased frequency and intensity of disturbances, including bleaching events (Hughes et al. 2018a), it is important to understand how a colony's disturbance history, e.g., colony-scale partial mortality and previous bleaching stress, affects wound repair.

To investigate the relative importance of intrinsic and extrinsic factors, as well as disturbance history for wound repair in a common branching coral, we generated wounds on *Pocillopora meandrina* colonies, and then monitored tissue regeneration at the wound site and overall colony health. We focused on *P. meandrina* because this early successional species commonly occurs throughout the Indo-Pacific and hosts one of the most diverse coral-associated cryptofaunal communities (Stella et al. 2010; Counsell et al. 2018). Generated wounds were similar to broken branches observed regularly at sites with periodic high wave energy events, from parrotfish predation, or from direct contact with boat anchors, divers, etc. Each colony was wounded twice to examine differences in the recovery time of an initial wound versus a successive wound, and to consider within-colony variation. We expected low within-colony variation, but we expected that the second wound would take longer to heal than the first due to a reduction in available energy as a result of energy allocated to the initial wound. In addition to studying within and among colony variation, we examined among site variation in wound healing by selecting colonies across four sites around the island of O'ahu, Hawai'i. Sites were chosen based on year-round accessibility that enabled in situ monitoring of colony bleaching history, colony health, and tissue regeneration. To study the relative importance of various drivers affecting the wound healing process, we analyzed correlations between wound healing time and colony parameters (i.e., colony size, inter-branch distance, wound size) and depth (i.e., a proxy for variation

in multiple co-varying environmental factors). We hypothesized that (1) larger colonies would heal wounds faster under the assumption that they have more energy available than smaller colonies, (2) colonies with larger inter-branch distances would heal wounds faster due to increased water flow between branches (Jokiel and Coles 1977; Smith et al. 2008; Anderson et al. 2017), (3) larger wounds would heal more slowly than smaller wounds (Henry and Hart 2005; Defilippo et al. 2016), and (4) wound recovery time would increase with increased depth primarily due to decreased water temperature and irradiance. The health of focal colonies was tracked over 3 years prior to wound generation, allowing us to also evaluate how the disturbance history of each colony affected wound healing. Thus, we further hypothesized that wound recovery time would increase with the severity of previous colony stress (i.e., bleaching history, partial colony mortality) as a result of decreased energy available for tissue growth (Goreau and Macfarlane 1990). Finally, we compared pre- and post-wounding changes in colony-scale partial mortality to investigate the effects of wound generation and subsequent wound healing on overall colony health. Understanding the ability of corals to recover from tissue damage in situ, and drivers of variation in this process, is critical for predicting the recovery of coral populations after disturbances and for forecasting the long-term persistence of corals.

Materials and methods

Systematic wound formation and colony surveys

Using tissue samples ($< 1 \text{ cm}^2$) collected in 2016, 54 *Pocillopora* colonies from four sites on O‘ahu, Hawai‘i were identified as *P. meandrina* via the restriction length polymorphism assay developed by Johnston et al. (2018). On 5th April and 5th May 2017, wounds were generated on each colony using bone cutters (HIMB Special Activity Permit 2018-3), such that the wounds ($13.4 \pm 2.8 \text{ mm}$ diameter, mean \pm SE, $n = 108$) reflected partially broken branches. Following this systematic wound formation, corals were surveyed and photographed (at both the colony and wound scale) weekly for 3 months to track the tissue recovery process and colony-scale responses. Estimates of wound recovery (i.e., exposed stark white skeleton, some tissue regrowth, algae presence, and tissue layer fully covering the wound site) and overall colony percent live tissue were made in situ. The chronological photographs for each colony were used to verify in situ estimates, confirming the date by which each wound healed (i.e., polyps with normal coloration completely covered the wound site), colony percent live tissue on the day each wound was created, and change in colony-scale percent live tissue over 3 months post wound formation. For each

wound in which algal growth was observed, the proportion of wound area covered in algae was measured using ImageJ.

One week after wounds were generated, the surface area of the wound ($L \times W$) was measured with calipers to the nearest mm^2 . Colony size ($L \times W \times H$) to the nearest cm^3 was also measured in situ for each colony. To quantify the interstitial space, the average inter-branch distance for each colony was estimated by measuring the distal distance between two adjacent branches to the nearest mm for five branch pairs haphazardly selected such that one pair was near the top center and the other four pairs were on the sides of the colony. Depth, to the nearest 0.3 m, was measured using a Suunto dive computer at the base of each coral colony.

Survey sites

Three of the four survey sites were shallow (1–4 m: Kewalo Shallow, Lanikai, and Kāne‘ohe Bay), while one site was a deeper reef offshore from one of the shallow sites (7–8 m: Kewalo Deep) (Table 1, Fig. 1). To determine maximum and mean temperatures from April to July 2017, corresponding with the time of wound formation and healing, data loggers (Onset HOBO[®] Pendant Temperature Light Data Logger) were deployed at each site (Table 1). Lanikai and Kāne‘ohe Bay are somewhat sheltered by fringing reefs, while the Kewalo Shallow and Deep sites are exposed to moderate-to-high swell in the summer (Fig. 1). The maximum and mean values for maximum significant wave height (Table 1) were calculated using SWAN model data at hourly intervals from April to July 2017, accessed from the PacIOOS Voyager database for 0.5 km^2 grid cells corresponding to each site. The proximity of the Kewalo Deep and Shallow sites was such that they were associated with the same grid cell. While all sites have exposure to local human impacts, there is variation in their human impact histories (ESM 1).

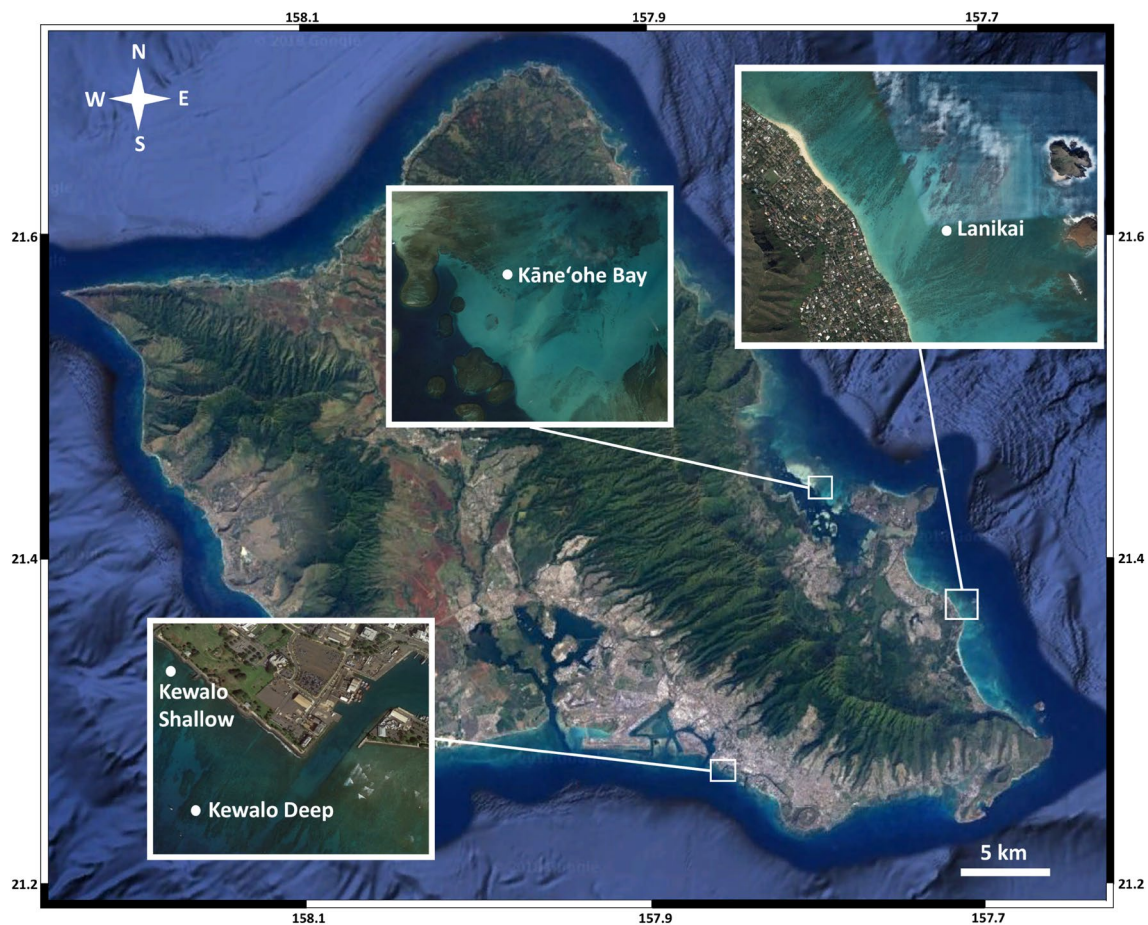
Bleaching history stress

To estimate bleaching history stress (BHS), colonies were surveyed and photographed monthly for 1–3 years prior to wound formation. Using estimates of bleaching made in situ, with verification from chronological photographs, we recorded which years each colony showed any bleaching stress (denoted as shifts in pigmentation from September to December, when seasonal bleaching has been observed in Hawai‘i). We also categorized the severity of bleaching stress on a scale of 1–3, where 1 corresponded to noticeable paling of the colony, 2 to severe paling, and 3 to stark white bleaching (Fig. 2). Using these data, we calculated a BHS index for each colony: (proportion of years bleached) \times (average severity of bleaching). The possible range of this index was from 0 to 3, such that 0 represented a colony with no bleaching history and 3 represented a colony

Table 1 Site names with coordinates, number of *Pocillopora meandrina* colonies sampled, depth, colony bleaching history, average daily temperature, and time to heal wound

Site name	Latitude (deg N)	Longitude (deg W)	Number of <i>P. meandrina</i> colonies	Colony bleaching history (mean \pm SD)	Colony depth (m) (mean \pm SD)	Temperature ($^{\circ}$ C) April–July 2017 (max, mean \pm SD)	Significant wave height (m) April–July 2017 (max, mean \pm SD)	Time (days) to heal wound (min, max, mean \pm SD)
Lanikai	21.3842	-157.7077	12	1.58 \pm 0.26	2.09 \pm 0.40	29.65, 27.25 \pm 0.97	1.03, 0.58 \pm 0.03	21, 56, 35 \pm 8
Kāneʻohe Bay	21.4564	-157.7945	20	0.79 \pm 0.40	3.59 \pm 0.27	29.25, 27.13 \pm 0.92	0.76, 0.56 \pm 0.11	21, 72, 38 \pm 10
Kewalo Shallow	21.2930	-157.8663	6	1.25 \pm 0.42	3.05 \pm 0.17	28.95, 27.03 \pm 0.67	1.50, 0.70 \pm 0.13 ^a	26, 86, 50 \pm 22
Kewalo Deep	21.2898	-157.8628	16	0.42 \pm 0.31	7.83 \pm 0.53	28.26, 26.77 \pm 0.52	1.50, 0.70 \pm 0.13 ^a	34, 86, 52 \pm 13

^aThe proximity of the Kewalo Shallow and Deep sites was such that they were associated with the same 0.5 km² grid cell for the SWAN model data available from the PacIOOS Voyager database

**Fig. 1** Location of study sites around the island of O'ahu, Hawai'i. Images were generated using Google maps. Site details are provided in Table 1 and ESM 1

with a consistent history of severe bleaching. This metric was conservative because 2014 and 2015 had overall higher

bleaching stress than 2016, and we were missing coral health history for some colonies over these years. For a less

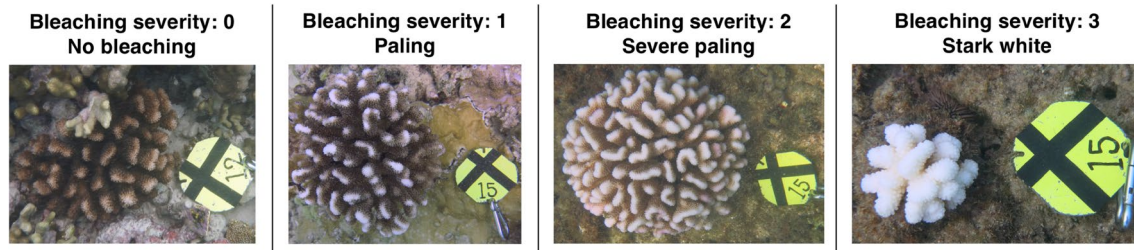


Fig. 2 Examples of 4 levels of bleaching severity rankings for *Pocillopora meandrina* colonies. Each colony was ranked in situ and through a comparison of chronological monthly photographs

conservative estimate, we also calculated an index for each colony that utilized site- and year-specific averages to fill in missing data points (ESM 2). These colony surveys were also used to estimate changes in colony-scale percent live tissue over the 3 months prior to wound formation.

Within-colony wound healing variation

To analyze variation in wound recovery time for the successive wounds imposed on each colony, a linear mixed model (function “lmer” in *R* package *lme4*; Bates et al. 2015) was run with recovery time from the second wound as the response variable and recovery time from the first wound as a fixed effect. Study site was included as a random effect to account for potential non-independence in the data related to site level differences in wound healing. A Type II Wald Chi square test (function “Anova” in *R* package *car*; Fox and Weisberg 2011) was used to evaluate the significance of the correlation between the initial and subsequent healing times. The marginal R^2 , an estimate of the variance explained by fixed factors in a mixed model (function “r.squaredGLMM” in *R* package *MuMIn*; Bartoń 2016), was used to estimate how much of the variation in healing time of the subsequent wound could be explained by the healing time of the initial wound.

Variation in wound healing among colonies

To partition variation in wound recovery times into among sites, among colonies, and between initial and successive wounds, a Poisson Generalized Linear Mixed Model (GLMM; function “glmer” in *R* package *lme4*; Bates et al. 2015) was run with number of days for the wound to heal as the response variable, and with the month of wound formation (April or May) and colony identity nested within site as random effects. The conditional R^2 , a cumulative estimate of the variance explained by both fixed and random factors in a mixed model (function “r.squaredGLMM” in *R* package *MuMIn*; Bartoń 2016), was used to estimate how much variation in healing time was explained among these three factors. Random effect variance estimates were used

to determine the relative amount of variation explained by each factor. To evaluate the relative effects of colony morphology (size and inter-branch distance), the environment (depth), and colony stress (BHS and percent live tissue) on wound healing, a set of additional Poisson GLMMs was run with these factors as fixed effects, the number of days for the wound to heal as the response variable, and, to account for potential non-independence in our data, month of wound generation and colony identity nested within site as random effects. Temperature and wave energy were not included in the models given the site scale resolution of these factors. The cube root of colony size and the square root of wound surface area were used in analyses as linear estimates of colony and wound diameter. The continuous variables included as fixed effects were centered and scaled, and correlation coefficients were evaluated with a threshold of ± 0.75 prior to inclusion in models. Residual plots of all models were visually inspected, and no strong deviations from homoscedasticity or normality were observed.

Effect of broken branches on colony-scale live tissue

To determine whether or not the change in percent live coral tissue was different between the 3-month periods before and after wound generation, a GLMM was run (function “glmer” in *R* package *lme4*; Bates et al. 2015) to compare the change in colony percent live tissue pre- and post-wound generation. This model included the average percent live tissue for each colony over the associated 3-month period as a fixed effect, to account for colonies with lower percent live tissue being more likely to exhibit a continued decline in live tissue, and colony identity nested within site as random effects. The response variable, change in percent live coral tissue for each colony over 3 months, was zero-inflated. As a result, change in percent live coral tissue was reclassified to a binary variable of either negligible change ($\leq 10\%$ over 3 months) or noteworthy change ($> 10\%$ over 3 months), and this response variable was modeled with a binomial distribution. The threshold to distinguish between noteworthy and negligible change, 10%, was selected to reflect the precision of in situ visual estimates of colony-scale percent live tissue.

Results

Systematic wound formation and colony surveys

Of the 108 wounds generated in this study, 103 (95%) healed within 3 months (21–86 days, min–max) to the extent that it was difficult to distinguish which branches had been broken. The remaining five wounds were spread across three different *Pocillopora meandrina* colonies: two at Kewalo Deep (60% live and 40% live on the date of wound generation) and one at Kewalo Shallow (80% live on the date of wound generation). These wounds experienced algal growth that started at the center of the wound, and the coral tissue never out-competed the algae such that these wounds were algal covered at the end of the study. For these colonies, colony-scale decline was recorded pre- and post-sampling (average declines of 28% and 27% live coral tissue, respectively). For the 51 colonies that successfully healed both wounds, colony-scale percent live tissue ranged from 20–100% ($88.5 \pm 17.2\%$, mean \pm SD,

$n = 51$). A similar progression of tissue regeneration was observed for all wounds that healed (Fig. 3; Fig. S1): transition from exposed stark white skeleton, to live polyp coverage with partial pigmentation, to live polyp coverage with full pigmentation. Algal growth, usually in the center of the wound, was a normal part of the healing process exhibited by 96% of all the wounds that healed. The average percent of wound area covered by algae was $13.6 \pm 9.8\%$ (mean \pm SD, $n = 103$).

Within-colony wound healing variation

The linear mixed model comparing within-colony wound healing times did not find a significant correlation between healing times for initial and subsequent wounds (0.29 ± 0.17 , effect size \pm SE; $p = 0.09$; Fig. 4a). Initial recovery time explained 6% (marginal R^2) of the variation in the recovery time for a subsequent wound imposed on the same colony.

Fig. 3 Chronological photographs of wound healing from an initial (April 2017) and subsequent (May 2017) broken branch of a *Pocillopora meandrina* colony

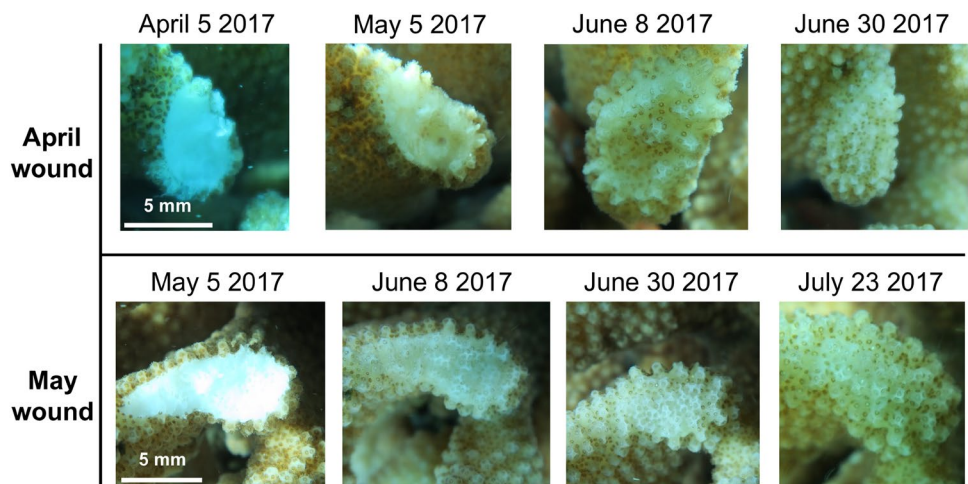
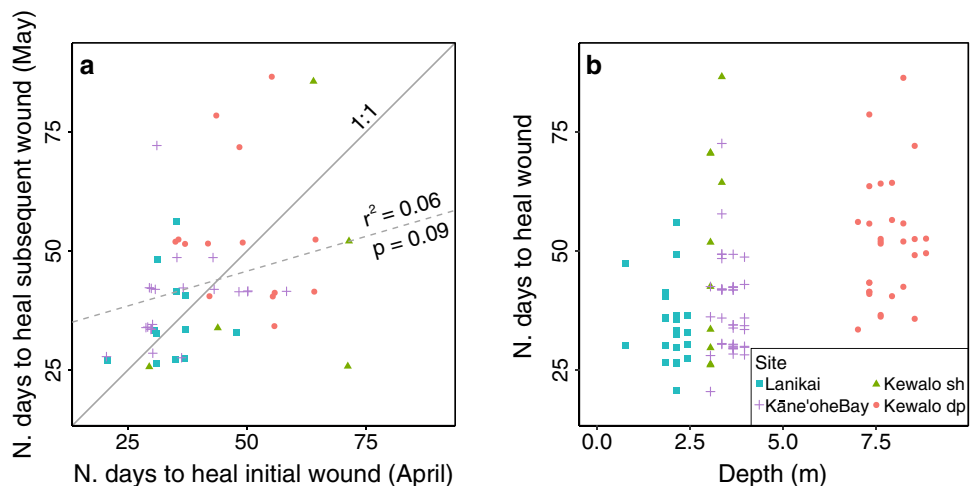


Fig. 4 **a** Scatterplot comparing the number of days to heal an initial wound versus a subsequent wound for each *Pocillopora meandrina* colony. The solid line depicts a 1:1 correlation, and the dashed line shows the relationship predicted by a linear mixed model. **b** Scatterplot comparing colony depth and the number of days to heal wounds. In both plots, the color and shape of each point correspond to the study site



Colony, wound, and site variability

Colony diameters ranged from 13.7 to 44.3 cm (24.3 ± 6.0 , mean \pm SD, $n = 54$), and the average inter-branch distance ranged from 0.9 to 2.1 cm (1.5 ± 0.3 , mean \pm SD, $n = 54$). Wound diameters ranged from 7.9 to 24.2 mm (13.4 ± 2.8 , mean \pm SD, $n = 108$). Lanikai, Kāne‘ohe Bay, and Kewalo Shallow all had a similar depth range (Fig. 4b). Temperature was highest and had the most variation at Lanikai (Table 1). The next highest temperature was at Kāne‘ohe Bay, and then at Kewalo Shallow. Lanikai had a higher maximum and mean significant wave height than Kāne‘ohe Bay (Table 1). Kewalo Deep was approximately twice as deep as the other three sites (Fig. 4b) and had the lowest mean temperature as well as the lowest variation in temperature. Kewalo Deep and Shallow were included in the same grid cell for the SWAN model of maximum significant wave height, with higher maximum and mean wave height estimates than at Kāne‘ohe Bay or Lanikai (Table 1). Across the *P. meandrina* colonies sampled, the BHS index ranged from 0 to 2 (0.90 ± 0.56 , mean \pm SD, $n = 54$). The proportion of bleached colonies was greater in 2014 and 2015 than in 2016 (Fig. S2). Stark white colonies that were ranked as having high bleaching severity were only observed at Lanikai and Kewalo Shallow, while medium- and low-severity bleaching were observed at all four sites (Fig. S2). Percent live coral tissue on the day of wounding ranged from 20 to 100% (86 ± 19 , mean \pm SD, $n = 108$).

Variation in wound healing among colonies

The Poisson GLMM that only included random effects found that colony-scale differences accounted for 39% of the variance, site scale differences accounted for 32% of the variance, and differences between the initial and successive wounds accounted for 0.7% of the variance in the number of days for wounds to heal (Table 2). In the full GLMM, the fixed effects (i.e., colony size, inter-branch distance, wound size, depth, BHS index, and percent live coral tissue) explained 35% of the variation in wound healing time (Table 2), accounting for essentially all of the site scale variation (Fig. S3). Only two fixed effects were significantly correlated with time to heal: depth (0.17 ± 0.04 , effect size \pm SE; $p < 0.001$) and colony size (-0.08 ± 0.03 , effect size \pm SE; $p = 0.01$). Colonies at deeper depths healed an average of 25 days slower than colonies at shallower depths (Fig. 5a). Smaller colonies healed an average of 14 days slower than larger colonies (Fig. 5b). Wound healing was unaffected by inter-branch distance (0.02 ± 0.03 , effect size \pm SE; $p = 0.48$; Fig. 5c), BHS index (0.03 ± 0.04 , effect size \pm SE; $p = 0.47$; Fig. 5d), percent live coral tissue (-0.03 ± 0.03 , effect size \pm SE; $p = 0.32$; Fig. 5e), and wound size (0.02 ± 0.02 ,

Table 2 Marginal R^2 (R^2_m , percent of variance in the response variable that is explained by fixed effects, FE) and conditional R^2 (R^2_c , percent of variance in the response variable that is explained by the full model including FE and random effects, RE) for a set of Generalized Linear Mixed Models run with time for wound to heal as the response variable (Poisson distribution)

AIC	R^2_m (%)	Depth (FE)	Colony size (FE)	Inter-branch (FE)	BHS index (FE)	Percent live coral tissue (FE)	Wound size (FE)	R^2_c (%)	Colony ID (RE, %)	Site (RE, %)	Month (RE, %)
831.3	0	–	–	–	–	–	–	71.2	38.7	31.8	0.7
833.6	1.9	–	–	–	0.011 ± 0.048	-0.037 ± 0.029	–	72.3	35.4	34.4	0.6
829.6	6.0	–	-0.063 ± 0.029	0.047 ± 0.032	–	–	–	71.2	33.2	31.2	0.7
829.7	23.3	0.135 ± 0.046	–	–	–	–	–	70.4	43.3	3.2	0.6
830.8	34.8	0.167 ± 0.042	-0.078 ± 0.030	0.023 ± 0.032	0.030 ± 0.042	-0.029 ± 0.029	0.018 ± 0.022	71.3	36.2	<0.1	0.3
829.4	36.2	0.195 ± 0.046	-0.077 ± 0.030	0.017 ± 0.031	0.064 ± 0.045^a	-0.026 ± 0.029	0.018 ± 0.022	71.2	36.2	<0.1	0.3

For the FE factors, the effect size estimates \pm standard errors are listed; estimates with p values < 0.05 are in bold. For the RE factors, the percent of variance partitioned to each RE [$(R^2_c - R^2_m) / R^2_c$] is listed. Akaike Information Criterion (AIC) scores are provided for each model as a relative measure of model fit

^aThis model included an alternative less conservative BHS index (ESM 2) with year- and site-specific averages used for missing data

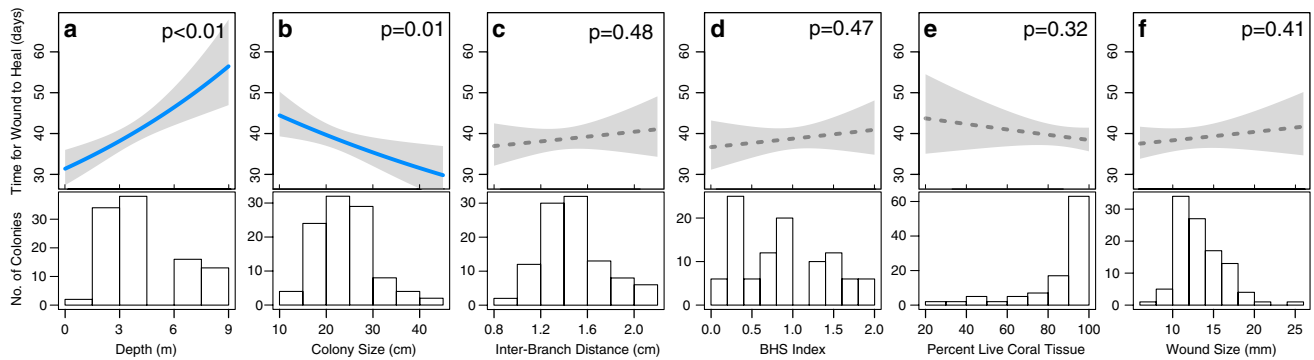


Fig. 5 Plots of the average effect (across colonies, sites, and sampling month) of depth (a), colony size (b), inter-branch distance (c), bleaching history stress (BHS) index, where 0 refers to no bleaching stress across survey years and 3 depicts severe bleaching stress for all survey years (d), percent live coral tissue (e), and wound size (f), on the

time (in days) for wounds to heal in *Pocillopora meandrina*, based on a Generalized Linear Mixed Model. Gray bars show the 95% confidence interval on model estimates. Histograms (below effect plots) illustrate the variation across sample colonies for each variable

effect size \pm SE; $p = 0.41$; Fig. 5f). Results from the model that included an alternative, less conservative BHS index had double the effect size for BHS index, but the effect was still not significant (0.06 ± 0.05 , effect size \pm SE; $p = 0.16$; Table 2).

A model considering only metrics of colony stress as fixed effects, i.e., BHS index and percent live coral tissue, explained $< 2\%$ of the variation in wound healing time. A model that included only metrics of colony morphology as fixed effects, i.e., size and inter-branch distance, explained 6% of the variation in wound healing time. In contrast, the model that considered only a metric of variation in the local environment as a fixed effect, i.e., depth, explained 23% of the variation in wound healing time (Table 2).

Effect of broken branches on colony-scale live coral tissue

When considering changes in colony-scale percent live coral tissue over the 3 months pre- and post-wound generation, only one colony had a shift in percent live coral tissue $> 40\%$. This colony changed from 100% live to 0% live pre-sampling and was subsequently not wounded (Fig. S4a). A binomial GLMM found no difference in the probability of a colony having a noteworthy change ($> 10\%$) in percent live tissue between pre- and post-wound time periods (0.97 ± 1.07 , effect size \pm SE; $p = 0.36$, Fig. S4a). Colonies that had lower average percent live tissue had a higher probability of having a shift in percent live tissue $> 10\%$ (-0.13 ± 0.06 , effect size \pm SE; $p = 0.03$). The average colony-scale percent live tissue was similar between pre- (89 ± 15 , mean \pm SD) and post-wound formation (85 ± 18 , mean \pm SD, Fig. S4b).

Discussion

Our results showed that differences between *Pocillopora meandrina* colonies accounted for slightly more variation in wound healing time than differences in site scale factors (39% compared to 32%, Table 2). Colony size and inter-branch distance explained 6% of this colony-scale variation (Table 2). The effect of inter-branch distance on wound healing time was not significant (Fig. 5c). In contrast, the effect of colony size was significant, with larger colonies healing an average of 14 days faster than smaller colonies (Fig. 5b). While smaller *Pocillopora* colonies have been shown to have faster growth rates than larger colonies (Edmunds and Burgess 2016, 2018), faster lesion healing has been attributed to larger colony size in other coral species (Meesters et al. 1996; Kramarsky-Winter and Loya 2000; Oren et al. 2001). This relationship between colony size and wound healing time may be a result of colony-wide integration of resources during the healing process, enabling larger colonies, which have a larger supply of energetic resources, to heal wounds faster than smaller colonies (Oren et al. 2001). However, this relationship may not be consistent across taxa. Several studies have found no relationship between wound healing time and colony size, finding instead that wound size had a greater effect on healing time (Bak and Steward-Van Es 1980; Meesters et al. 1994, 1997; Oren et al. 1997; van Woessik 1998). We did not find a significant relationship between wound size and healing time despite including a broad range of wound sizes in our study (7.9–24.2 mm diameter; Fig. 5f). Our results suggest that colony size is a better indicator of wound healing time than wound size for broken branches in *P. meandrina*.

Depth was significantly correlated with wound healing time for *P. meandrina*, with healing times an average of 25 days longer for deeper colonies (Fig. 5a). Depth

accounted for 23% of the variation in wound healing time (Table 2) and explained most of the observed site scale variation (Fig. 4b; Fig. S3). Depth was likely a proxy for temperature and irradiance, factors known to influence *Pocillopora* growth rates and distributions (Lenihan and Edmunds 2010; Franklin et al. 2013; Tortolero-Langarica et al. 2017). Across sites with similar depths, increased growth and wound healing rates have been observed for colonies exposed to elevated temperatures (Lester and Bak 1985; Smith et al. 2008; Osinga et al. 2011), which is a pattern that may be attributed to higher metabolic rates in warmer water. While we did not measure irradiance in our study, we did find that the shallower sites had warmer and more variable temperatures than the deeper site (Table 1). The shorter recovery times recorded for shallower colonies may reflect increased tissue recovery potential for colonies exposed to increased temperature, increased irradiance, or a combination of these factors. Decreased wound healing times have also been associated with shallower depths for several other coral species (Nagelkerken et al. 1999; Fisher et al. 2007).

Contrary to our hypothesis, we did not find a significant effect of previous colony bleaching on wound healing time for *P. meandrina* (Fig. 5d, Table 2). This may suggest that allocating resources towards wound healing is a priority for corals, despite possible decreased fitness resultant from previous stressors. Alternatively, 1.5 years may be a reasonable recovery window from bleaching stress. Bleaching was observed in focal colonies at all four sites during the major bleaching events that occurred in Hawai'i in 2014 and 2015, with colonies at Lanikai and Kewalo Shallow experiencing the greatest bleaching severity (Fig. S2). Wounds were generated in April and May of 2017, and no effect of BHS on wound repair was observed. For colonies experiencing bleaching, wound tissue regeneration and coral growth are reduced or completely absent (Goreau and Macfarlane 1990; Henry and Hart 2005; Rotjan et al. 2006; Kenkel et al. 2013). In addition, wound healing in a facultatively symbiotic coral is greater for colonies with symbionts in comparison to colonies without (Defilippo et al. 2016; Burmester et al. 2017), and heterotrophy increases wound recovery rates for both symbiotic and aposymbiotic colonies (Burmester et al. 2018). This suggests that the effect of bleaching on coral growth and tissue regeneration is a direct result of the decreased ability to feed associated with the loss of symbionts. Thus, for colonies that survive bleaching events and successfully regain symbionts, bleaching stress may not have long-term effects on tissue regeneration processes. We still expect that BHS would have a significant effect on wound repair, if the tissue damage occurs soon after a bleaching event.

We did not find significant effects of colony-scale partial mortality (Fig. 5e), nor of previous tissue injury (Fig. 4a), on wound healing time in *P. meandrina*. However, the majority

of our focal colonies had > 75% coral tissue (Fig. 5e), and this skewed distribution may have impacted our ability to detect a significant relationship between percent live coral tissue and wound healing. The difference between wounds formed in April versus May accounted for less than 0.1% of the variation in wound recovery time (Table 2). This suggests that with at least 1 month in between broken branches, *P. meandrina* colonies can recover from successive wounds, such that the healing time of the subsequent wound is not inherently longer than that of the initial wound (Fig. 4a). The healing process we observed for *P. meandrina* was dominated by the migration of cells from the edge of the wound towards the center of the wound (Fig. 3), with algal growth occurring on 96% of wounds (Fig. S1). This process is similar to the healing process described for *P. damicornis* (Rodríguez-Villalobos et al. 2016; Traylor-Knowles 2016). In the current study, *P. meandrina* colonies were able to regenerate tissue and combat fouling organisms for 95% of wounds. For three colonies that were unable to combat fouling organisms and did not heal wounds, colony-scale decline was observed pre- and post-wound generation, indicating some other underlying source of stress. For the remaining 95% of wounds, the tissue recovery process was so thorough that it was challenging to confirm in situ which branches had been broken 3 months after wound generation. Further, the generation and healing of two broken branches did not cause significant changes in the overall health of *P. meandrina* colonies (Fig. S4a). Our results support colony depth and size as stronger drivers for variation in wound healing time than metrics of previous and ongoing colony stress. Nonetheless, we encourage future studies to investigate the effects of bleaching stress after a shorter recovery window, a more balanced range of partial colony mortality, and a greater number of successive wounds on tissue regeneration.

The remaining variation not explained by the fixed effects included in our full model (65%) was divided between colony-scale variation (36%) and wound scale variation (i.e., residual variation; 29%; Table 2). Unexplained colony-scale variation may have been caused by genetic or physiological differences, e.g., efficiency of autotrophy versus heterotrophy (Levy et al. 2016; Burmester et al. 2018), availability of metabolic energy, corallum morphology (Madin et al. 2016; Dornelas et al. 2017), supply of interstitial cells (Meesters et al. 1996; Henry and Hart 2005), or variation in resources as a result of the associated community of mutualistic invertebrates and fishes (Goldshmid et al. 2004; Stewart et al. 2006; Holbrook et al. 2008; Stier et al. 2012). Different predation intensities for specific colonies or sites could also affect wound healing. While our study did not include predator surveys, corallivores, including butterflyfishes, filefishes, and snails, were observed at all four sites. During the 3 months before and after wound generation, bite marks that exposed skeleton were observed only at Lanikai, on 4 of 12

focal colonies. These colonies had average recovery rates for Lanikai, which had the fastest site scale recovery rate. Therefore, our observations do not suggest that predation events impacted wound recovery time. Observed within-colony variation in wound recovery times (Fig. 4a) emphasizes the importance of factors at the wound scale on tissue regeneration. These may include within-colony differences in water flow (Smith et al. 2008; Lenihan and Edmunds 2010; Nakamura 2010; Sabine et al. 2015), energy allocation, or light attenuation (Kaniewska et al. 2008, 2011). We utilized average inter-branch distance as a colony-scale metric of differences in morphology, but this factor was not correlated with healing time (Table 2). Future studies could investigate the effects of colony morphology, wound location, and water flow metrics at both the colony and wound scale on the tissue repair process.

In conclusion, we found that *P. meandrina* colonies exhibited tissue regrowth over 95% of wounds an average of 42 days after wound formation, for wounds that resembled a broken branch, similar to damage that occurs naturally during high wave energy events, from direct interactions with boats and divers, and from parrotfish predation. The rate of wound healing observed in our study is similar to the 30–40 day wound healing timeline recorded for broken branches in *P. damicornis* (Rodríguez-Villalobos et al. 2016). Our results suggest that *P. meandrina* has the capacity to heal sequential wounds without a detrimental effect on overall colony health (Fig. S4a). BHS did not affect wound healing. This suggests that within 1–2 years of a bleaching event, the impact of this stress on a colony's ability to heal wounds is negligible. Over the ranges of partial mortality and wound size investigated, these factors were not correlated with wound recovery time. Instead, our results highlight variation in wound recovery time across depth and colony size, with larger and shallower colonies healing more quickly than smaller and deeper colonies. Given the potential for shifts in the size structure and depth distribution of coral communities amidst a barrage of various stressors, the ability for larger and shallower colonies to heal wounds faster is an important finding for effectively predicting coral population dynamics and reef resilience.

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Data availability All data generated during this study are provided in the electronic supplementary material.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national, and/or institutional guidelines for the sampling, care, and use of animals were followed and all necessary approvals were obtained. Sampling was completed under the HIMB Special Activity Permit 2018-3.

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