

Experimental Evidence for Reduced Mortality of *Agaricia lamarcki* on a Mesophotic Reef

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Abstract:

Mesophotic Coral Ecosystems (MCEs) may act as a refuge for impacted shallow reefs as some of the stressors affecting tropical reefs attenuate with depth. A less impacted population at depth could provide recruits to recolonise shallow reefs. Recently, disturbance has been reported on several mesophotic reefs including storm damage, biological invasions, and coral bleaching; calling into question the extent of deep reef refuges. We report on a reciprocal transplant experiment between shallow and mesophotic reefs in the Caribbean, which occurred during a period of coral bleaching. 102 fragments of *Agaricia lamarcki* were collected down a continuous depth gradient at two sites to a maximum depth of 60m. Fragments were transplanted to either a shallow or mesophotic station at a third site, with controls. This allowed the disaggregation of the effect of the disturbance experienced during the observation period, and any potential acclimation resulting from the historical location of a fragment. Mortality and bleaching were quantitatively assessed. We found the relocation depth of a coral fragment had the strongest effect on both survival and the degree of bleaching recorded. The site a fragment was collected from, and the original collection depth, failed to explain mortality or bleaching with statistical significance. This experiment provides support for the assumption that mesophotic corals may be protected in comparison to shallow reefs, in spite of the potential effects of differing susceptibilities to stress.

Introduction:

Mesophotic coral ecosystems (MCEs) are tropical and sub-tropical reefs containing depth-generalist photosynthetic hard corals, while lacking shallow-specialist taxa [1], [2]. Broadly MCEs are thought to occur between a shallow depth limit of 30 - 40m and end at depths where light levels are too low to support photosynthetic scleractinian holobionts [3]–[6].

1 It has been suggested MCEs may provide refuge for species otherwise impacted on shallow
2 reefs [7]. Specifically in the context of climate change this is formally referred to as the deep reef
3 refugia hypothesis [5], [8]. Such suggestions are underpinned by the assumption that stressors and
4 disturbance on shallow reefs attenuate with depth, leading to lower mortality on MCEs. Instances of
5 corals avoiding disturbance at greater depths have been observed [9]. In 2013 a population of
6 *Seriatopora hystrix* was reported at mesophotic depths, despite extirpation in the shallows after
7 bleaching events in 1998 and 2001 [10]. Similarly, the hydrocoral *Millepora intricata* recovered in
8 Panama from the 1982 and 1997 bleaching events by exploiting a depth refuge [11]. The protection
9 offered by depth has also been detected in other taxa, including fish avoiding over-exploitation rather
10 than climate-related impacts [12]–[14].

11 Despite a number of supportive case studies, MCEs are still under threat from a variety of
12 factors [15]. Storm damage [16], [17], invasive species [18], [19], and seasonal bleaching [20] have
13 been reported on mesophotic reefs. This combined with greater susceptibility to thermal [21] and
14 light-related [22] stress for deeper corals, challenges the suggestion MCEs may provide refuge to
15 organisms present on shallow reefs. What the field lacks in a broad sense, are experimental
16 validations.

17 In 2015 a long-term, factorial, reciprocal transplant experiment was established on the island
18 of Utila, Honduras, to explore potential physiological change over time. Fragments of *Agaricia*
19 *lamarcki* were collected from two mesophotic and two shallow reefs, and transplanted to a third
20 location at different depths. Informal weekly inspections of the transplant stations showed fragments
21 were apparently healthy. After a month had elapsed, colonies of *Agaricia lamarcki* on the reef began
22 to bleach at shallow and mesophotic depths FIGURE 1. This coincided with NOAA’s Coral Watch
23 programme reporting the first Degree Heating Week (DHW) of the year for Utila (Supplementary
24 1b)[23]. These events provided a chance to experimentally assess the potential for depth to provide
25 protection from disturbance. Transplant experiments involving changing the depths of corals have a
26 long history [24]–[28], but this is the first time we are aware of a mesophotic transplant experiment
27 coinciding with a bleaching event.



FIGURE 1 BLEACHING OF AGARICIA LAMARCKI AT MESOPHOTIC DEPTHS

During the 2015 field season, large colonies of A. lamarcki were noticed to be partially bleached at depths of up to 35m. Image credit – Ally McDowell.

Methods:

Research site-

The transplant experiment was conducted at the Coral View research centre (CV) on the island of Utila, Honduras (FIGURE 2). Though the experiment occurred at the research centre, coral material was sourced from The Maze (TMA) on the north shore, and Little Bight (LB) to the south. The research centre reef follows a spur and grove formation in the shallows, with hard substrata declining with depth until a patch reef system is reached on a silt plain at ~ 40m.

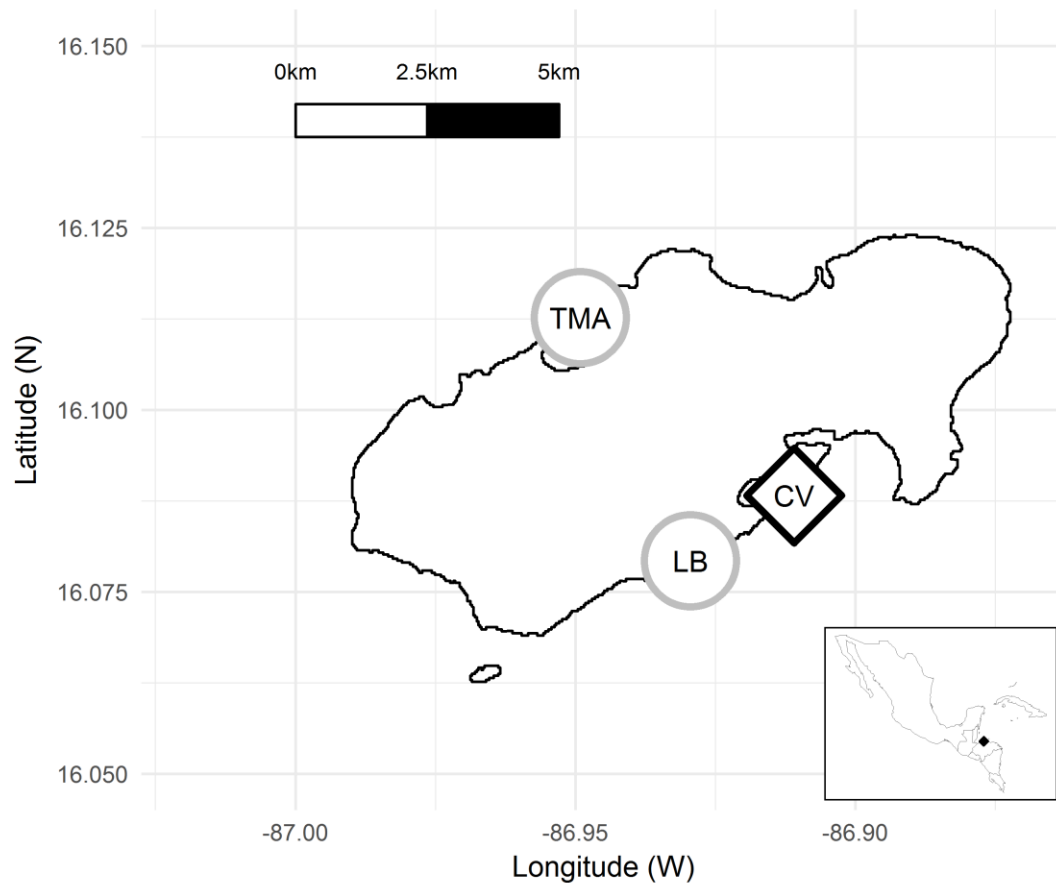


FIGURE 2 STUDY LOCATION, UTILA, HONDURAS

Sites are listed with abbreviations from left to right: The Maze (TMA: N 16.11266214, W -86.94911793), Little Bight (LB: N 16.07926302, W -86.92942222), Coral View (CV: N 16.08823274, W -86.91094506). GPS co-ordinates are in WGS84 format. The hollow diamond denotes the experiment location, grey circles are sites of material collection. Bottom right is an inset map of the Caribbean with a mark for Utila for reference. The base map was sourced from GADM database of Global Administrative Areas under a CC BY licence with permission.

Experimental Setup-

Fragments of *Agaricia lamarcki* were collected by a technical dive team using mixed gas closed circuit rebreathers (Hollis Prism 2, Hollis, San Leandro, California, USA) during July 2015 (Permit number: ICF-261-16). Material was collected evenly across the depth gradient with 48 fragments between 10m and 45m depth at LB and 54 fragments between 16m and 60m at TMA (Figure 3a); the upper and lower bounds of the depth range of *A. lamarcki* at these sites.

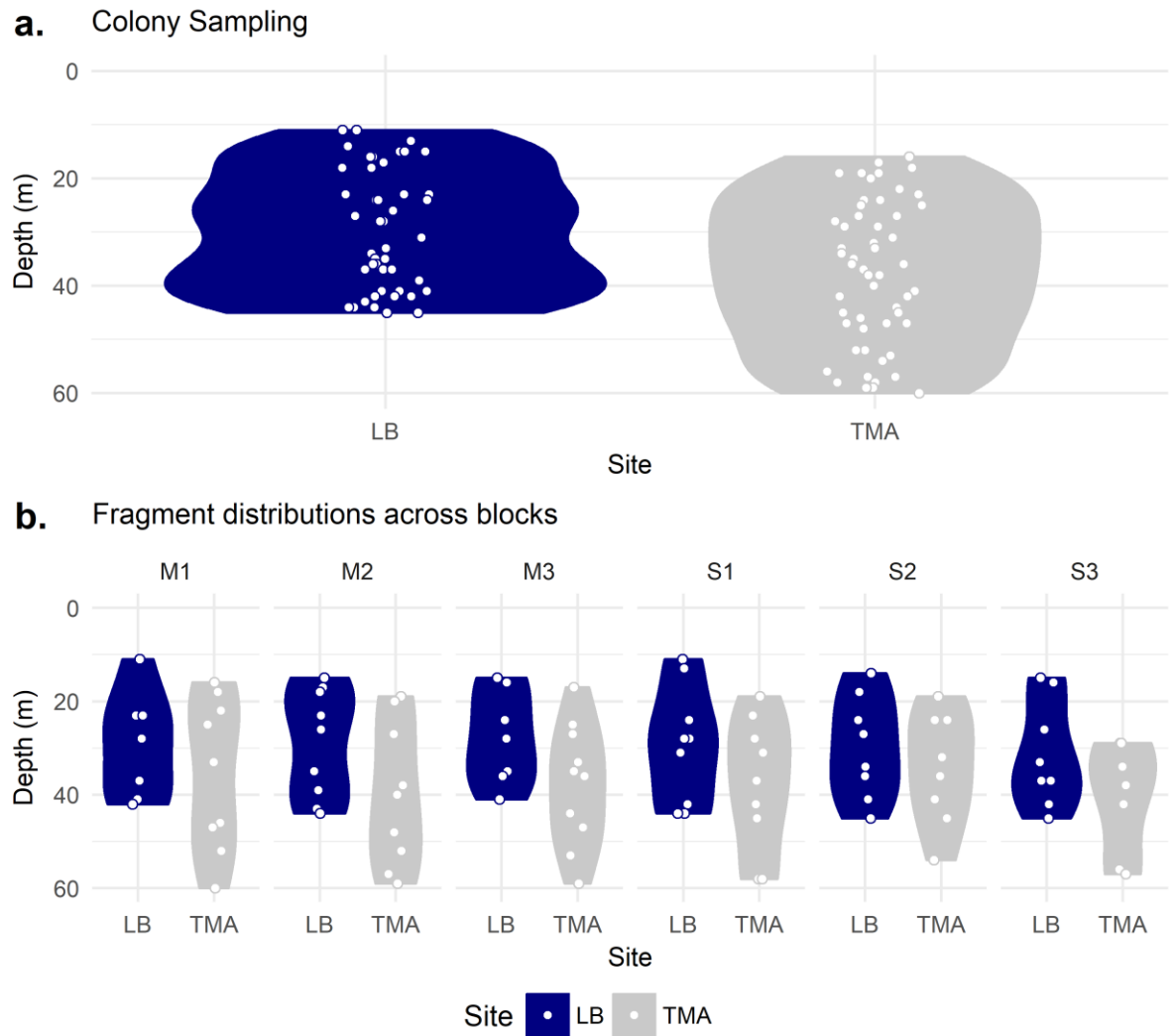


Figure 3 Sampling and transplant distributions of fragments

Violins represent the probability distribution of fragments occurring for a given depth based on sampling. The total coloured area sums to 1. a. Fragments were collected with even intensity from the maximum to the minimum depths of occurrence of *A. lamarcki* at TMA and LB. b. Fragments were then attached to 1 of 3 mesophotic (M) or shallow (S) blocks. 48 fragments were collected and transplanted from LB and 54 from TMA. See *n* in TABLE 2 for the number of fragments used in statistical analyses as attrition occurred over the course of the study.

Transplant racks were made from concrete blocks and sections of PVC tubing glued side-by-side with a hot glue gun (Figure 4). Three racks were placed at a shallow depth (12m) and three at a mesophotic depth (37m). These depths represent the extreme ends of the depth range of *A. lamarcki* at CV [2]. Fragments were attached to transplant racks in the afternoon of their day of collection. This was done in-situ using the same brand of pre-mixed Milliput modelling putty. Two Fragments from unique colonies per 10m depth bin, per site, were placed on each rack to ensure an even spread of material. Depth bins started from the surface and fragments were distributed in this way until the material from a site was completely used, as such a 50-60m depth bin existed for TMA but not at LB,

these bins were not used in statistical analysis as it was possible to include depth as a continuous variable (Figure 3b.). This ensured fragments originally shallow or mesophotic were transplanted back to similar depths, therefore providing control fragments which can disaggregate the effects of acclimation and treatment. NOAA's Coral Reef Watch remote-sensing data [23] were used to contextualise the experiment. Though note there is no guarantee satellite data that are appropriate for shallow reef monitoring will capture the stress experienced by mesophotic reefs. At the point of transplant 0 cumulative DHWs were reported for the preceding three months in the waters of Utila (Supplementary 1a.).



FIGURE 4 EXPERIMENTAL RACK

Two coral fragments from each 10m depth window were placed randomly on one of three blocks, at either mesophotic or shallow depths. Each block had two racks, one for each collection site. Image credit – Ally McDowell.

Fragment assessments-

Formal monitoring of transplanted fragments occurred from six weeks after their placement, when bleaching was observed on the reef, and continued weekly until the end of the 2015 field season in September. All six transplant racks were photographed in-situ with a 20 level #13 Danes-Picta

greyscale card in shot. Fragment mortality was scored from photos for use in survival analyses. A fragment was considered dead when fouled. The reference card was used for quantitative bleaching assessments in Matlab [29] using the colour correction method and script of Winters et al. [30]. The colour intensities of the red, green, and blue channels were recorded for 10 digital quadrats of 25 pixels on each coral fragment at each time point. Digital quadrats were placed evenly across a fragment's surface to within a quadrat width of the fragment boundary, and to avoid the diagnostic white polyp mouths of *A. lamarcki*, which may affect bleaching assessments.

Statistical analyses-

All statistical analyses and data manipulation were conducted in the programming language R [31]. Survival analyses were performed using the package 'survival' [32]. Non-parametric log-rank tests [33] were used to determine the effect of transplant depth and site on fragment survival in two univariate analyses. The effect of collection depth, as a continuous variable, on survival was determined by a Cox Proportional Hazard analysis [34]. The assumption of proportional hazards was assessed by regressing Schoenfeld residuals against time. Statistically significant differences in survival were visualised by Kaplan-Meier survival curves.

Quantitative bleaching assessments were performed with mixed effect linear models, using the maximum likelihood method, with the package nlme [35]. The colour intensities in the red, green, and blue colour channels across time were response variables. Colour intensity was averaged across the 10 quadrats from each fragment at each time point as technical replicates before analysis. The general form of the model equation follows with fixed effects of treatment, site and collection depth grouped by site, then random effects of week (time since transplant) nested within ID shown in brackets permitting varying intercepts and slopes.

$$\text{Colour} \sim \text{Treatment} + \text{Site} / \text{Collection Depth} + (\sim 1 + \text{Week} | \text{ID})$$

Collection depth was nested within Site to account for differing depth ranges of *A. lamarcki* between the two sites. Fragment ID was included as a random effect to respect the chronology between specific points in the analysis, rather than fitting lines through the dataset as a whole. Linearity,

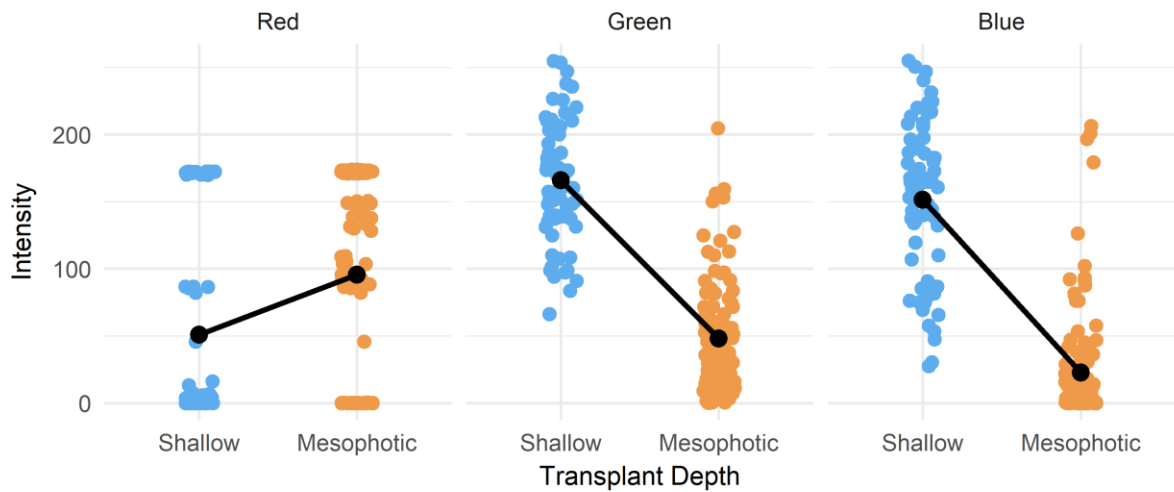
normality and heteroscedasticity were assessed using residual plots. Statistically significant model elements were detected with a likelihood ratio test between a model containing all elements and one omitting the variable of interest. The final data file can be found in Supplementary 3.

Results:

Bleaching analyses-

Transplant to a mesophotic rack appears protective against bleaching. Results of linear mixed effect models (LMEs) explaining variation in coral colour intensity are reported in TABLE 1 and depicted graphically in Figure 5. The residual plots for each model can be found in Supplementary 2. FIGURE 5a shows the effect of transplant depth on mean colour intensity in three channels across the whole observation window. Each fragment at each time point was assessed with 10 digital quadrats, which were averaged for single data points in the analysis. Row b. shows the effect of collection site, and collection depth nested within collection site to account for differing depth ranges, over the observation window. Fragments with greater intensity in the green and blue channels, and weaker in the red channel, are more severely bleached.

a. Bleaching Analysis Fixed Effects



b.

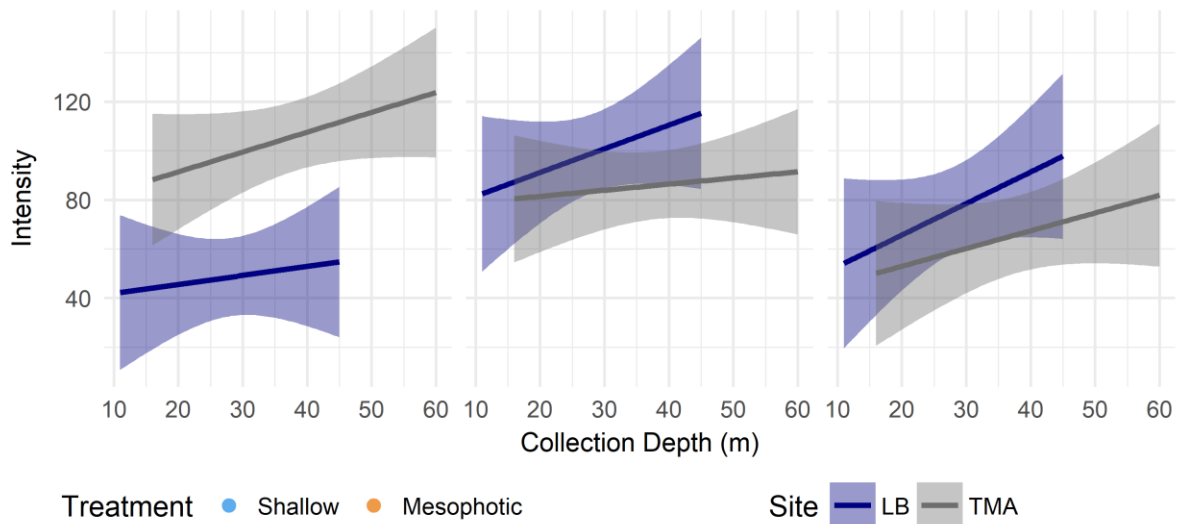


FIGURE 5 QUANTITATIVE BLEACHING ASSESSMENTS OF TRANSPLANTED FRAGMENTS

Row a. shows the effect of transplant depth on mean colour intensity in three channels across the whole observation window. Each fragment at each time point was assessed with 10 digital quadrats, which were averaged for single data points in the analysis. Row b. shows the effect of collection site, and collection depth nested within collection site to account for differing depth ranges, over the observation window. The shaded areas represent the 95% confidence interval of colour intensity. Fragments with greater intensity in the green and blue channels, and weaker in the red channel, are more severely bleached.

TABLE 1 BLEACHING ANALYSIS RESULTS

Likelihood ratio tests of significance for fixed effects in three mixed effects linear models, each fitted to explain variation in one of three colour channels used for quantitative bleaching analysis. All 59 fragments surviving until week 8 were used. Values are reported as they appeared in computer outputs. *P* values < 0.05 are in bold and followed by an *.

Bleaching Analysis	Model element	Effect		Colour
		χ^2	<i>P</i>	
Model 1	Transplant depth	8.579909	0.0034 *	Red
	Site	6.848727	0.0326 *	Red
	Collection depth	1.921921	0.3825	Red
Model 2	Transplant depth	50.43146	<0.0001 *	Green
	Site	0.9742721	0.6144	Green
	Collection depth	2.092902	0.3512	Green
Model 3	Transplant depth	26.13712	<0.0001 *	Blue
	Site	0.687022	0.7093	Blue
	Collection depth	3.721327	0.1556	Blue

Survival analyses-

Only transplant depth had a significant effect on the chance of a coral fragment surviving the observation period. The effect of transplant depth is visualised in Figure 6, while the results of univariate survival analyses are reported in Table 2. A coral fragment transplanted to a shallow rack had a 19 percentage point higher probability of mortality by week 8 in comparison to those on mesophotic racks. Almost one quarter of fragments transplanted to mesophotic racks died during observation, while for shallow fragments this number was closer to a half. Collection depth, and therefore any legacy effects from past acclimation to specific depths, had no significant effect on survival. Multivariate analyses to consider interaction effects were not performed as only a single variable of interest returned statistically significant results.

TABLE 2 SURVIVAL ANALYSIS RESULTS

Values are reported as they appeared in computer outputs. *P* values < 0.05 are in bold and followed by an *. For transplant depth, n1= Shallow, n2= Mesophotic. For Site n1 = Little Bight n2 = The Maze. More fragments were collected at TMA as a constant density of sampling was maintained with depth, and TMA had a larger depth range for *A. lamarcki*. Collection depth was analysed as a continuous variable using a Cox Proportional Hazard model, the assumption of proportional hazards was satisfied with $\chi^2 = 0.435$ and *P* = 0.51.

Survival Analysis	Sample size		Effect	
	n1:	n2:	Z or χ^2	<i>P</i>
Transplant depth	42	48	5.1	0.0235*
Site	39	51	1.2	0.273
Collection Depth	90		1.163	0.245

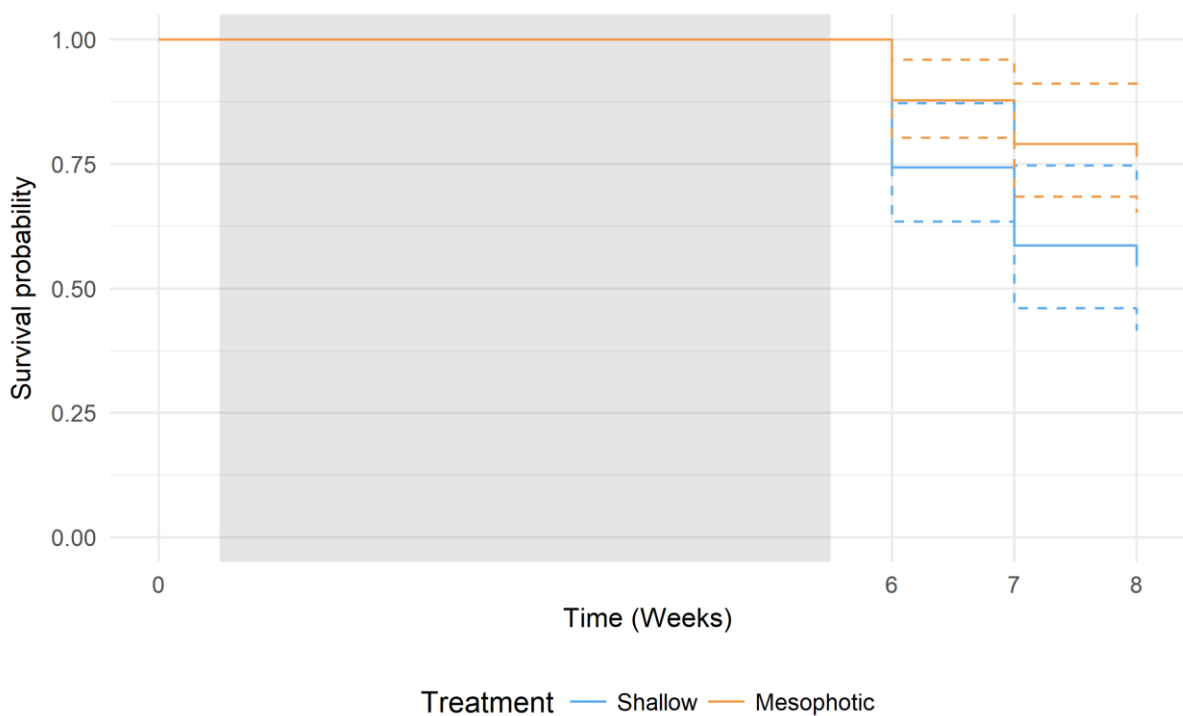


FIGURE 6 SURVIVAL CURVES OF CORAL FRAGMENTS BY TRANSPLANT DEPTH

Survival curves of transplanted fragments from placement date with formal observations at six, seven and eight weeks later. Mortality from time of transplant to week six was not formally assessed, and is represented by the grey shading, but was sufficiently low to go unnoticed. Dashed lines represent the 95% confidence interval.

Discussion:

*Transplanted *Agaricia lamarcki* fragments were more likely to survive, and less likely to be bleached, at mesophotic depths-*

During the three weeks of observation after bleaching commenced, fragments on shallow transplant racks were twice as likely to be completely fouled than those at mesophotic depths Figure 6.

Similarly, quantitative monitoring of bleaching over the three weeks revealed high levels of coral bleaching across shallow transplant racks, with little bleaching observed at mesophotic depths (TABLE 1). The bleaching levels displayed in figure 5 represent completely white fragments in the shallows and pale fragments at depth. Our results corroborate reports of corals surviving at depth during bleaching events in past observational studies [10], [11], in spite of reported greater thermal susceptibilities in mesophotic corals elsewhere [21].

It is important to note that coral bleaching and mortality can be induced by more than thermal disturbances. Coral bleaching has been reported as a response to: high light levels [36], disease [37], ocean acidification [38], and chemical pollution [39], while mortality could also result from direct physical disturbance [40]. Though Coral Reef Watch reported 2-3 DHW for Utila by our last observation (Supplementary 1d), indicating thermal stress in the shallows, we cannot claim to know this as the driver when multiple stresses may interact and in the absence of detailed environmental data. For this study the actual cause of disturbance is not important. A disturbance of some kind did occur and mesophotic reefs were protected for a time.

As well as relating directly to whether natural deep reef refuges can exist, our results have management implications. Current projects involving the rearing of corals outside of an aquarium setting may benefit by moving their operations deeper in times of significant heat, or other, stress. Floating nurseries, designed to accommodate water movement, may be particularly well suited to

1 exploiting the protection of depth. These nurseries may need to be moved shallower once thermal
2 stress abates in the shallows, to avoid delayed thermal stress at mesophotic depths [21].

3 *Where a fragment came from is less important than where a fragment is during stress-*

4 Our results failed to return a statistically significant effect on survival of collection site or
5 depth (TABLE 2). This is despite research showing these two populations of coral have differing
6 physiological profiles (Laverick, under review) and any additional stress caused by transplantation to
7 different depths. Unfortunately, we lack detailed in situ environmental data to help characterise the
8 sites and transplant location. Coral Reef Watch data do show that no thermal stress had accumulated
9 in the shallows until after the transplant experiment had occurred (Supplementary 1a). Further, during
10 the course of fragment collection dive computers reported water temperatures differing by 2°C across
11 the depth range of *A. lamarcki*, leading us to believe that there is likely local acclimation to low light
12 and different temperatures within sites. Even if fragments had experienced similar environments
13 shallow and deep at their site of collection, mortality was still greater once on shallow transplant
14 racks. It appears, in this instance, the stress and disturbance a coral fragment is subject to, is the
15 overriding control on survival, as opposed to any past acclimation.

16 Interestingly our results for bleaching assessments differ slightly. Collection depth again
17 failed to be statistically significant, as did site in green and blue channels, but significant in red. The
18 mean effect of site in the red channel was comparable to the effect of transplant location (40-50,
19 FIGURE 5) . It may be that the base level of pigmentation at TMA was more red than at LB, as TMA is
20 a steep wall while LB a gentle slope. The effect of collection depth in the red channel remained the
21 same for both sites and mortality appeared independent of collection depth.

22 *Limitations-*

23 Unfortunately, the field season ended after three weeks of observation. We are uncertain whether the
24 trends observed will have continued as the bleaching event continued, or whether the mesophotic
25 racks eventually bleached and died after a delay. Coral reef watch reported one additional DHW in the
26 three months after our observation period (Supplementary 1e), however, we cannot know how remote

sensing data will translate to stress on mesophotic reefs as heating at these depths can be delayed [21]. Regardless of this possibility, at a minimum we know that mesophotic corals remained healthier for longer than their shallow counterparts during our observations of a period of shallow water stress.

Though we successfully detected an effect on survival and bleaching of transplant depth, we cannot with certainty claim the bleaching is the causative agent of mortality. Additional pressures are confounded with depth such as: water movement, light levels, proximity to coastal development, and proximity to anthropogenic activity [41]. We have been able to show that depth reduces mortality for *A. lamarcki* on Utila, but because of a lack of environmental data we are unable to explain the mechanisms behind shallow reef mortality with certainty. In addition, reduced mortality at depth is necessary but not sufficient for the realisation of a deep reef refuge [5]. There is a requirement of reproductive connectivity, not yet assessed on Utila, but found elsewhere [42]. We stress the distinction between refuge from general disturbance, and refugium specifically referring to climate related effects [43].

Conclusions-

This experiment reveals that colonies of *Agaricia lamarcki* at deeper depths have a greater chance of survival in the face of shallow water stress on Utila. Further, despite reports of increased thermal sensitivity with increasing depth [21], this particular Caribbean coral was less likely to bleach on mesophotic racks. The assumption for deep reef refuges, that depth affords protection, seems validated. However, meta-population dynamics will only occur if the surviving colonies at depth are reproductively active, and capable of settling in the shallows [22], [44]. Though gaps remain in understanding whether a natural deep reef refuge exists on Utila for *A. lamarcki*, protection at depth could be exploited by nursery and assisted settlement projects.

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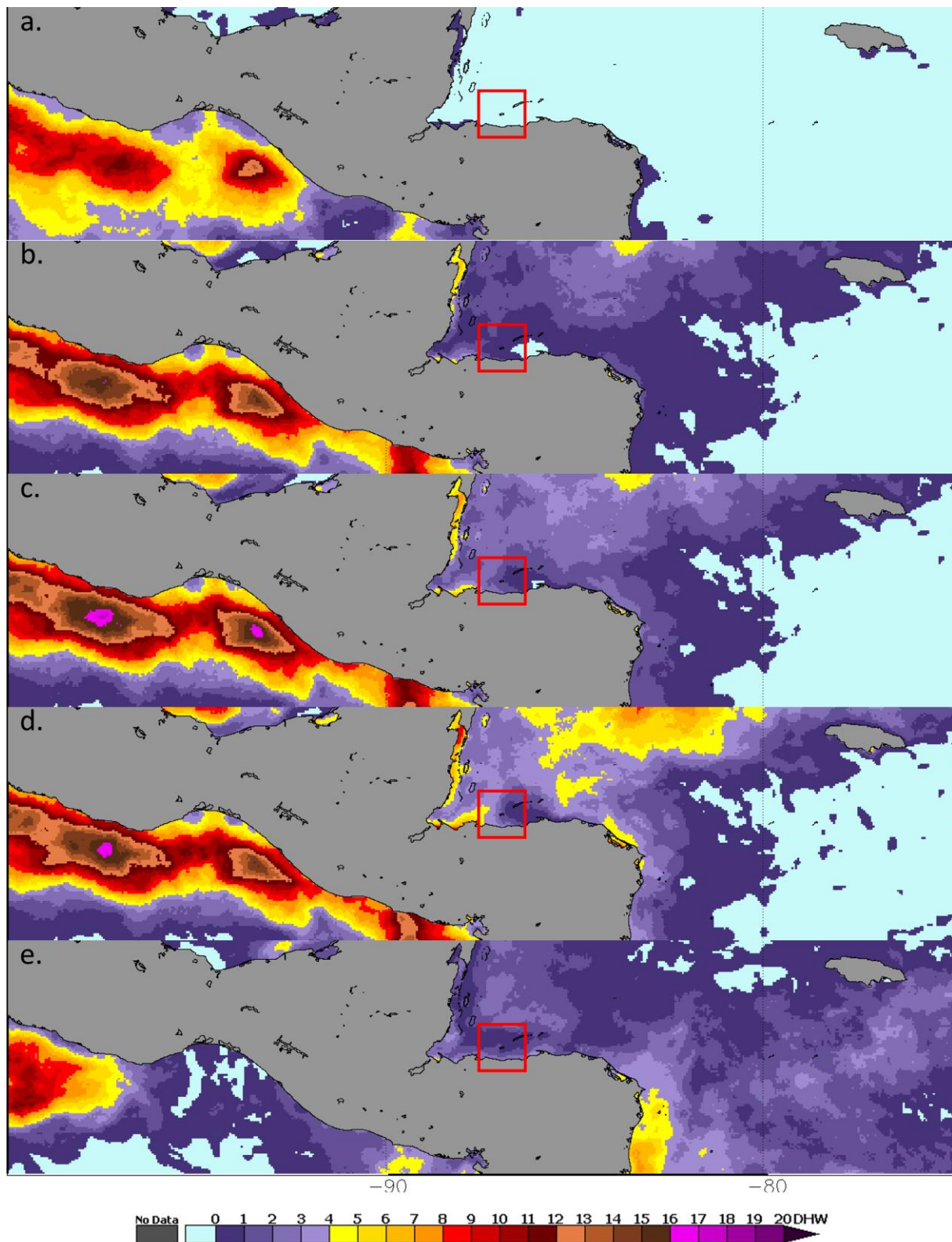
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Supplementary material:



1 **Supplementary 1 Degree Heating Weeks for three months preceding transplant date**

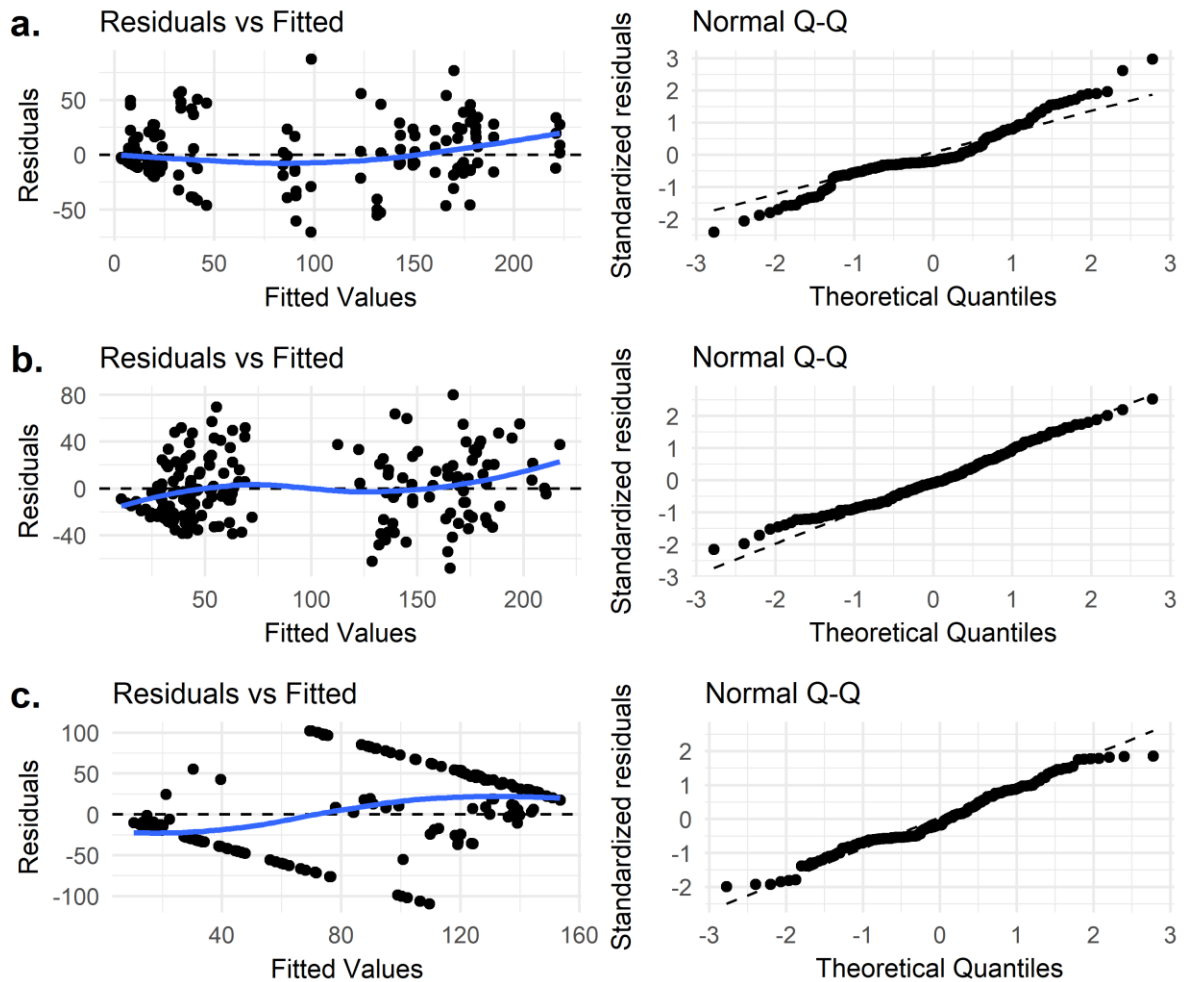
2 *NOAA Coral Reef Watch 5km resolution maps of cumulative degree heating weeks over 3 month windows in the Caribbean.*

3 *Images have been cropped and panelled to centre on Utula (red box). a. At the date of first transplant (July 2015) no heat*

4 *stress had accumulated around Utula. b. One week before observation one (September), 1 DHW. c. At observation one and*

1 *bleaching onset, 2 DHW accumulated. d. By observation three and the end of the study 2-3 DHW. e. Over the 3 months*
2 *directly after the final observation (December 2015), 1 additional DHW accumulated.*

3



4

5 **SUPPLEMENTARY 2 RESIDUAL PLOTS FOR BLEACHING ANALYSIS**

6 *Residual plots for bleaching analyses in three colour channels a. Blue b. Green c. Red. Residual vs fitted plots (left) reveal*
7 *deviations from linearity and heteroscedasticity. Normality is assessed by quantile plots (right).*