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Beyond heat: sediment and wave energy influence bleaching and demography in the coral *Acropora cervicornis*

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The global coral bleaching event of 2023, fueled by record-breaking ocean temperatures, underscores the urgent need to understand the factors shaping coral vulnerability and reef resilience. While elevated temperatures are widely recognized as the primary driver of mass bleaching, local environmental conditions are increasingly acknowledged for their potential to amplify or mitigate thermal stress. In this study, we examined how site-specific environmental variation in light, sedimentation, temperature, and wave energy influenced bleaching susceptibility and the demographic performance of the threatened coral *Acropora cervicornis*. The study was carried out from June 2023 to June 2024 in three restored populations (Maguey, Melones, and Tamarindo) along the western coast of Culebra, Puerto Rico. Bleaching susceptibility was quantified by scoring colonies as bleached or non-bleached based on visible paling or whitening of live tissues and calculating prevalence (proportion of colonies bleached at each time point) and incidence (new bleaching events between surveys). Survival was defined as the presence of live tissue on a colony whereas growth was assessed using change in net total linear length and specific growth rates as metrics. Bleaching onset occurred in mid-September 2023, peaking in November 2023, with 45.5% of colonies affected by the end of the study. Bayesian logistic regression models indicated that sediment ($\beta = 6.16$; 95% CrI: 4.98 to 7.37) and wave energy ($\beta = 2.09$; 95% CrI: 1.61 to 2.59) were the strongest predictors of bleaching probability. At the end of the study, 39% of the colonies survived at Maguey, 63% at Melones, and 67% at Tamarindo. Kaplan-Meier Survival analysis indicated that such spatial difference in survival was statistically different. Surprisingly, chi-squared tests indicated that survival did not differ between colonies that bleached and those that did not. Instead, the results of the Bayesian logistic regression indicated that sediment ($\beta = -0.65$; 95% CrI: -1.16 to -0.15) was the strongest predictor of colony survival. Growth declined sharply during bleaching but mostly recovered three months post-event. Bayesian Gaussian generalized linear mixed-effects model showed that increased sediment ($\beta = -0.340$; CrI: -0.400 to -0.270) and to lesser extent wave ($\beta = -0.006$; CrI: -0.010 to -0.002) led to reduced growth. These results highlight that coral bleaching and its demographic consequences are not solely

dictated by temperature anomalies, but are strongly modulated by site-specific environmental stressors. Incorporating these localized dynamics into restoration and management planning could improve the resilience of restored *A. cervicornis* populations under increasing climate extremes.

KEYWORDS

Caribbean, coral outplants, coral reef restoration, marine heatwave, threatened coral

1 Introduction

Coral reef restoration has emerged as a central strategy to address the widespread degradation of reef ecosystems caused by a combination of anthropogenic (e.g., overfishing), biological (e.g., disease and predation), and physical (e.g., hurricanes, elevated seawater temperatures) stressors. Restoration initiatives aim to recover both the structural complexity and biological diversity of coral reef communities through interventions designed to enhance coral cover and population resilience. One widely adopted technique is human-assisted propagation, which leverages the natural asexual fragmentation ability of many coral species to produce clones for outplanting (Bowden-Kirby, 2001; Hernández-Delgado et al., 2014; Boström-Einarsson et al., 2020). In this approach, small coral fragments are cultivated in *ex situ* or *in situ* nurseries, where they can grow under reduced environmental stress and minimal predation or competition. Once sufficiently developed (i.e., reaching an ecologically relevant size), these fragments are outplanted onto degraded reefs to increase coral cover, promote habitat complexity, and support self-sustaining population growth. While this method has been implemented globally, its long-term ecological benefits and motivations have been critically examined. Some authors argue that, in some contexts, reef restoration efforts may be motivated less by demonstrated ecological outcomes and more by a desire to act-informed by emotional, socio-cultural, or ethical considerations-alongside scientific reasoning (Streit et al., 2024; Suggett et al., 2024).

The effectiveness of coral reef restoration lies in the scientific understanding and intentional, informed design of methods, grounded in knowledge of how corals grow, survive, and reproduce within their environments. In this sense, over the past decade, coral demographic studies have advanced substantially, highlighting the value of population-level data in developing more effective and context-sensitive restoration strategies. However, a major gap remains in our understanding of how coral outplants respond demographically to acute and chronic disturbances, particularly under varying site-specific environmental conditions. Environmental stressors such as light intensity (Torres et al., 2008), sedimentation (Fourney and Figueiredo, 2017), temperature anomalies (Hernández-Delgado et al., 2018), and hydrodynamic forces (Nakamura and van Woeseik, 2001; Lentz et al., 2024) can strongly influence key demographic processes like survival and

growth. Thus, understanding how these factors interact with stressful events is critical to assessing the long-term success of outplanting efforts.

In 2023, tropical and subtropical oceans experienced one of the most intense marine heatwaves on record, with Degree Heating Weeks (DHWs) exceeding 25 °C-weeks across parts of the Caribbean (Miller et al., 2024). DHW, a standard measure of accumulated thermal stress over a 12-week period, reached thresholds known to cause widespread coral bleaching and mortality (Liu et al., 2003). As a result, severe bleaching was reported across the Caribbean basin (Mejias-Rivera and Courtney, 2024; López-Pérez et al., 2024; Hernández-Delgado and Rodríguez-González, 2025), including Puerto Rican reef systems, where active coral reef restoration efforts using the staghorn coral *Acropora cervicornis* were underway. This extreme event provided an opportunity to evaluate the demographic consequences of bleaching in restored populations of this threatened coral. Although the demographic effects of bleaching on *A. cervicornis* have been previously studied (Drury et al., 2017), few investigations have examined how vital rates respond to bleaching across reefs with contrasting environmental conditions, particularly under natural, large-scale disturbance events, like marine heatwaves (Brown et al., 2023; Doropoulos et al., 2025).

Leveraging ongoing restoration activities across three reefs differing in light intensity, sedimentation, hydrodynamics, and temperature in Culebra, Puerto Rico, this study addressed three main questions through a focus on *Acropora cervicornis*, a keystone Caribbean coral whose rapid growth rate, complex morphological properties, demographic sensitivity to even modest variations in environmental conditions, and extensively explored demographic patterns make it particularly suitable for revealing links between performance outcomes and environmental variability. Specifically, we asked: (1) How does bleaching susceptibility vary among environmentally distinct reef sites? (2) How do key demographic responses, specifically survival and growth, differ following bleaching across the studied sites? (3) Which environmental variables best explain observed spatiotemporal patterns of bleaching and demographic performance? By doing so, this study aims to improve our understanding of how local reef conditions influence demographic resilience and to inform the design of more effective, site-adapted restoration strategies in the face of future climate-driven disturbances.

2 Materials and methods

2.1 Study sites

This study was performed in the Island Municipality of Culebra, located approximately 27 km east of Puerto Rico (Figure 1). The three reefs selected for the study are part of an ongoing large-scale coral reef restoration program intended to increase the local abundance of the threatened coral *Acropora cervicornis* across the western coast of the island: Melones, Maguey, and Tamarindo reefs. These are shallow reefs with depth varying between 3 and 8 meters. The reef bottom of the three locations is characterized by low topographic relief, a benthic structure dominated by octocorals, and a percentage of coral cover not exceeding 7% (Santiago-Padua et al., 2023; Velázquez-Alvarado et al., 2025). Water quality is relatively good (i.e., transparent waters, Hernández-Delgado and Ortiz-Flores, 2022), but a recent study by Rodríguez-Casariago et al. (unpublished data) indicates that nutrient concentrations vary across space with levels being highest at Tamarindo, followed by Melones and Maguey, respectively. At these locations we monitored light, temperature, sedimentation, and wave energy for nine months (June 2023 to March 2024; Supplementary Table 1–4) to establish environmentally distinct characteristics. For descriptive purposes, each reef was qualitatively ranked as “highest”, “intermediate”, or “lowest” for each parameter to provide readers with a comparative sense of the reef environments. Maguey was characterized by lowest (in mean values and standard deviation) temperature (posing as the only reef failing to reach bleaching threshold for *A. cervicornis* of 32°C), light intensity, water column sedimentation, nutrients, but highest wave energy. Tamarindo was characterized by intermediate temperature, light intensity, water column sedimentation, wave energy, and highest nutrient levels. Melones reef was characterized by the highest water temperature, light intensity, water column

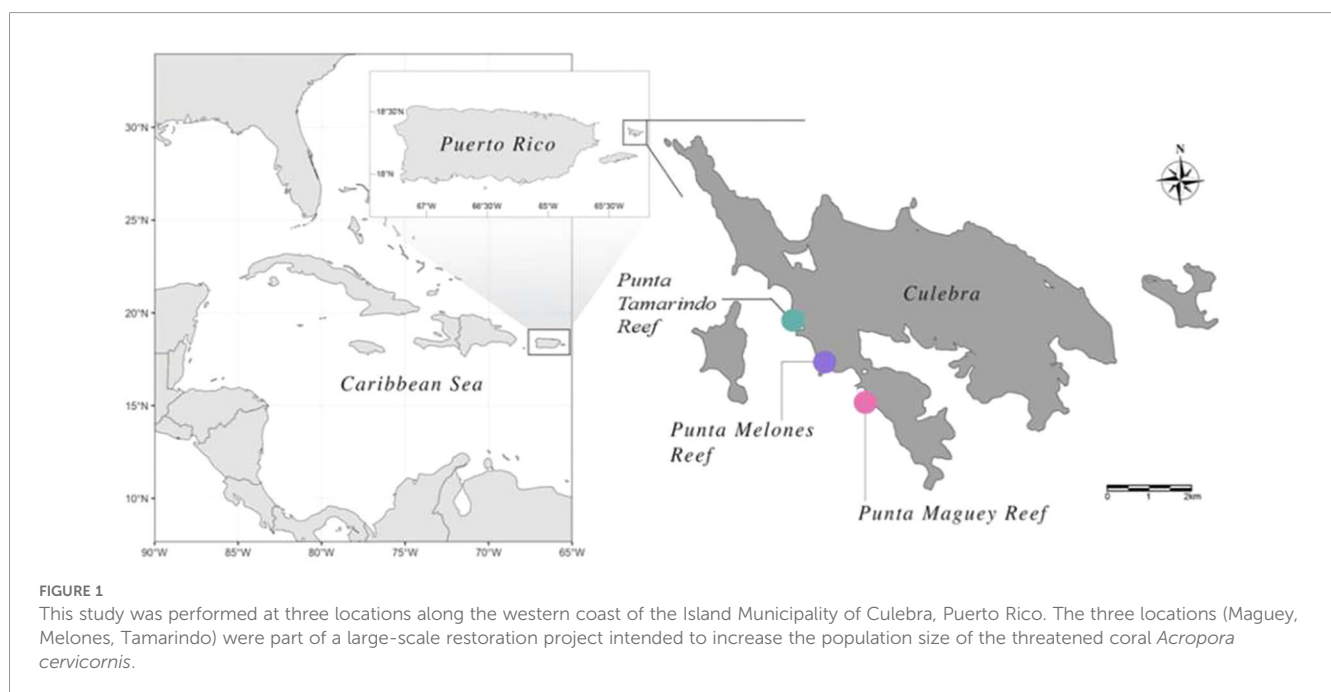
sedimentation, lowest wave energy, and intermediate nutrient levels (Supplementary Table 5).

2.2 Studied populations of *Acropora cervicornis*

Three hundred nursery-reared corals were collected from nurseries run by the local NGO Sociedad Ambiente Marino (SAM) and randomly assigned 100 colonies to each one of three study reef sites. Following Mercado-Molina et al. (2015a), colony fragments measured at least 25 cm in total linear length (mean = 39.9 cm). Coral fragments were fixed to the reef substrate within a 100 m² (10m x 10m) transect, using the zip tie and nail method, referred to interchangeably as “outplants” and/or “colonies” throughout this paper. Each colony was tagged with a 1–100 identifier waterproof tag, allowing their identification throughout the course of the study (June 2023 to June 2024). Although individual colonies were not genotyped in this study, Rodríguez-Casariago et al. (2020) previously documented six distinct genotypes within the SAM nurseries. Therefore, the restored populations likely represent a mixture of these six genotypes, although their exact distribution across sites remains unknown.

2.3 Bleaching incidence and prevalence of *Acropora cervicornis* outplants

During the onset of the massive bleaching event in Puerto Rico (September 2023 to December 2023), colonies were visited monthly to determine their status. After December 2023, once bleaching had subsided, colonies were surveyed every two to three months. Healthy colonies were identified as those with full natural orange



color. Any colony with signs of white tissue or discoloration was considered bleached. Although this approach allowed for consistent comparisons among colonies and sites, it did not capture gradations in bleaching intensity, which may influence subsequent survival or recovery. Future monitoring efforts should integrate quantitative color scales or image-based assessments to characterize intermediate bleaching states. Prevalence was defined as the percentage of colonies showing signs of bleaching during a given time, while incidence was the number of new bleaching events detected in the same period. To quantify temporal dynamics, the dataset was divided into four periods: before bleaching, during bleaching, and three (3 mo) and six months (6 mo) after bleaching was first detected, each representing a three-month interval. We used a Bayesian logistic generalized linear mixed-effects model to evaluate the effects of predictor variables on coral bleaching probability (see section 2.6). Bleaching was treated as a binary response variable (bleached/not bleached) and modeled using a Bernoulli error distribution with a logit link. Fixed effects included Site, Time, and environmental variables, while coral identity was included as a random intercept to account for repeated measures of individual colonies. Models were fitted using Markov chain Monte Carlo (MCMC) sampling implemented in the *brms* package in R, with four chains, 2,000 iterations per chain, and 1,000 warm-up iterations.

2.4 Survival probability of *Acropora cervicornis* outplants

The survival of the coral outplants was quantified every 1–3 months from June 2023 to June 2024. Survival rates at each time point were calculated by dividing the number of live colonies at time t by the number of live colonies at time $t - 1$. Colonies were deemed dead if no live tissue was visible or if the colony was overgrown by algae during the study period. Throughout the study, only three colonies were detached and not found at Maguey. Consequently, when considering this site, analyses were based on a sample size of 97 colonies. Survival dynamics were characterized using Kaplan–Meier curves to visualize temporal patterns, with a log-rank test used to assess whether survival probability varied significantly among locations. In addition, we modeled survival as a function of Site, Time, and environmental variables using the Bayesian logistic generalized linear mixed-effects model (see Section 2.6). Survival was treated as a binary response variable (alive/dead) and modeled using a Bernoulli error distribution with a logit link. Fixed effects included Site, Time, and environmental variables, while coral identity was included as a random intercept to account for repeated measures of individual colonies. Models were fitted using Markov chain Monte Carlo (MCMC) sampling implemented in the *brms* package in R, with four chains, 2,000 iterations per chain, and 1,000 warm-up iterations.

To evaluate the potential influence of bleaching on colony survival, we compared final survival status (alive/dead) between two groups: colonies that exhibited bleaching at any point during the study (Maguey $n = 50$, Melones $n = 45$, Tamarindo $n = 40$) and

those that did not. For each site, a chi-squared test was conducted to determine whether the number of survivors differed significantly between these two groups.

2.5 Growth rate of *Acropora cervicornis* outplants

The growth of the coral outplants was quantified every 3 months from June 2023 to June 2024. Two complementary metrics were used to determine whether coral growth varied over space and time. First, the net growth rate (NGR) was calculated as the absolute daily change in live tissue length for each colony, independent of starting size. NGR was computed as the difference in live tissue length between time t and time $t + 1$, divided by the number of days between surveys. Second, the specific growth rates (Equation 1, Lohr and Patterson, 2017) was calculated as the percentage change relative to the initial size, allowing for size-standardized comparisons across colonies. Colony sizes were calculated by summing the lengths of all live branches (TLL = total linear length; Knowlton et al., 1990). This involved taking a series of photographs *in situ* from various angles with a scale for reference, allowing for accurate measurement of fully extended branches (see Mercado-Molina et al., 2014). All measurements were made using the free software Coral Point Count with Excel version 4.1 (Kohler and Gill, 2006). We analyzed the growth metrics using a Bayesian Gaussian generalized linear mixed-effects model. Growth was modeled as a continuous response with a Gaussian error distribution and identity link. Time, Site (and their interaction), and the environmental variables were included as fixed effects, while coral identity was included as a random intercept to account for repeated measurements of individual colonies. Models were fitted using MCMC sampling implemented in the *brms* package in R, with four chains, 2,000 iterations per chain, and 1,000 warm-up iterations.

$$SpGR = \frac{(\ln(\text{Final Size}) - \ln(\text{Initial Size}))}{t} \times 100 \quad (1)$$

2.6 Model specifications and standardization

To identify the spatial, temporal, and environmental drivers of *Acropora cervicornis* bleaching, survival, and growth, we employed a three-model Bayesian hierarchical framework using the *brms* package in R (Bürkner, 2017). This approach allowed us to disentangle broad spatiotemporal patterns, temporal effects, and direct environmental influences on coral performance while accounting for repeated measurements at the colony level. All models included coral identity as a random intercept. Posterior distributions were summarized using median estimates and 95% credible intervals. Effects were interpreted based on whether credible intervals excluded zero, with inference conducted on the logit scale for bleaching and survival models and on the identity

(Gaussian) scale for growth models. Collinearity among the continuous predictor variables were evaluated before running the models using the `vif()` function in the `car` package. Variance Inflation Factor (VIF) values for the environmental variables (Light = 2.64, Sediment = 1.72, Wave = 2.32, Temperature = 1.73) were all below the commonly used threshold of 3 (Zuur et al., 2009; Smith and Warren, 2019), indicating that multicollinearity is unlikely to bias the results. All models were run with Maguey and “Before” as the reference Site and Time period, respectively.

Model 1: Site and Time as fixed factors

The original goal of this model was to test the interaction between Site (Maguey, Melones, Tamarindo) and Time (Before, During, After 3 mo, After 6 mo) as fixed predictors to capture potential spatiotemporal variation in coral performance. For bleaching and survival, the full interaction model did not converge; in these cases, we ran instead a reduced additive model including Site and Time as separate fixed effects. In contrast, for growth metrics, the Site \times Time interaction could be tested as originally planned. Model 1 was designed to identify broad spatiotemporal patterns across coral responses.

Model 2: Time and environmental variables as fixed factors

This model included Time and all measured environmental predictors (Temperature, Light, Sediment, Wave energy) as fixed effects, while excluding Site to reduce collinearity from spatial structure. Only additive effects were tested, as we aimed to quantify the independent influence of temporal and environmental drivers, and including interactions would have greatly increased model complexity and risked convergence issues. This model allowed evaluation of how environmental factors, together with temporal variation, affected bleaching, survival, and growth.

Model 3: Environmental variables only as fixed factors

This model excluded Site and Time, including only environmental variables as fixed effects to evaluate their direct

influence on coral performance. As with Model 2, only additive effects were tested. By removing temporal terms, this model isolated environmental drivers acting independently of broader temporal trends and stress events.

3 Results

3.1 Bleaching incidence and prevalence of *Acropora cervicornis* outplants

Bleaching of coral outplants was first detected in mid-September 2023 (Figure 2). After the first sighting, the bleaching onset spiked considerably in October 2023, reaching the highest proportion of colonies bleached in November 2023. The delay between the highest rate of new bleaching events in October 2023 and the highest proportion of bleached colonies in November 2023 suggests that coral colonies can remain bleached for longer than a month. This was followed by a stark decline in new bleaching events and proportion of bleached colonies in February 2024, when colonies met their fate as recovered (no signs of discoloration) or dead, suggesting that the affected colonies did not remain bleached for over three months.

In general, colonies outplanted in Maguey were more susceptible to bleaching than colonies outplanted in Melones and Tamarindo, though these findings were not statistically significant (see below). In Maguey, the mean incidence rate per survey time was 11.8% (range: 0 to 34.8%), whereas at Melones and Tamarindo mean incidence was, 8.6% (range: 0 to 31.0%) and 7.5% (range: 0 to 18.9%), respectively (Figure 2). In Maguey, 51.6% of the tagged colonies experienced bleaching at some point over the course of the study period, compared to 45% and 40% in Melones and Tamarindo, respectively. Prevalence followed a similar trend, with Maguey showing the highest prevalence of bleached colonies (Figure 3). At this site, the mean prevalence rate per survey time was 19.8% (range: 0 to 47.8%), whereas, at Melones and

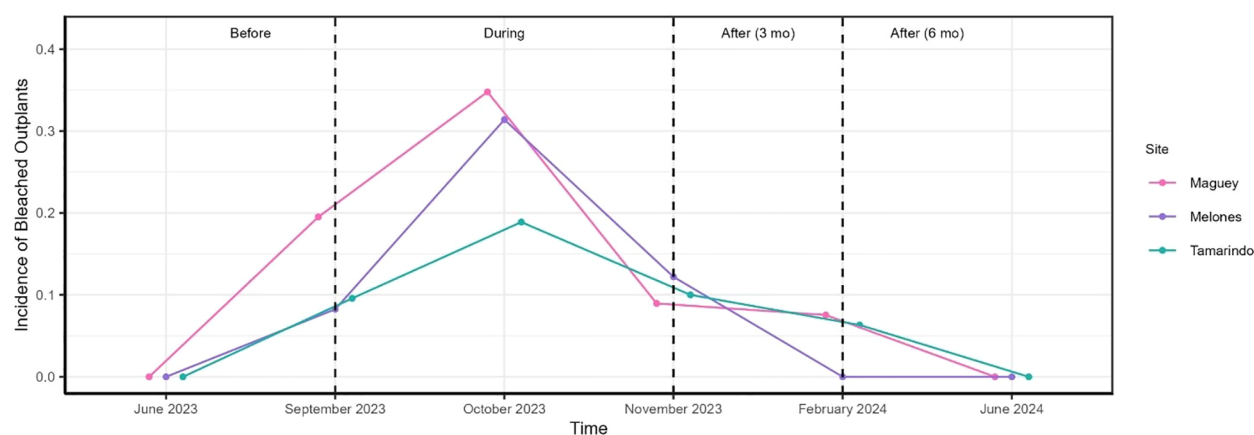


FIGURE 2

Spatiotemporal pattern of bleaching incidence of *Acropora cervicornis* outplants from June 2023 to June 2024 for three distinct reefs (Maguey, Melones, Tamarindo) in Culebra, PR.

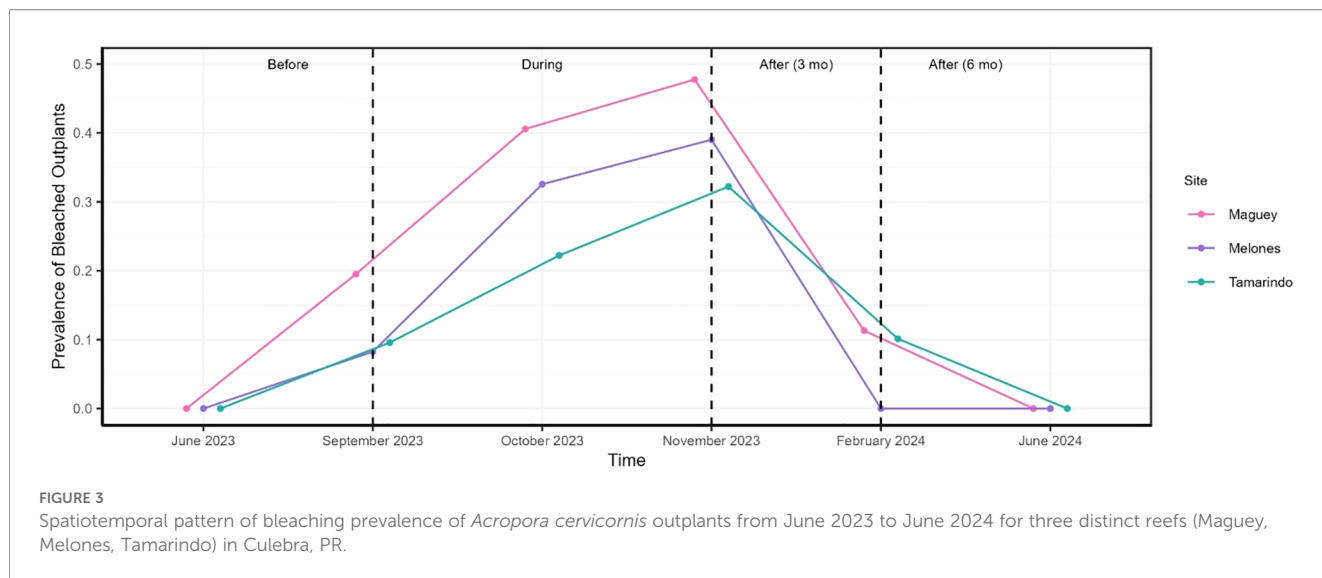


FIGURE 3 Spatiotemporal pattern of bleaching prevalence of *Acropora cervicornis* outplants from June 2023 to June 2024 for three distinct reefs (Maguey, Melones, Tamarindo) in Culebra, PR.

Tamarindo mean prevalence was, 13.2% (range: 0 to 39.0%) and 12.4% (range: 0 to 32.2%), respectively (Figure 3). Approximately 45.5% of all colonies (sites combined) showed signs of bleaching by the end of the study.

The Bayesian logistic model revealed a strong temporal signal in coral bleaching, whereas differences among sites were weak and uncertain (Model 1, Table 1). Bleaching probability was effectively negligible under baseline conditions (June 2023 to August 2023), consistent with field observations showing no bleaching prior to September 2023. From September 2023 to November 2023, bleaching increased considerably (estimate = 13.25, 95% CrI = 5.23

to 37.49), indicating a rapid transition from healthy to bleached colonies during this period. Three months after the bleaching onset, bleaching probability remained elevated relative to baseline (estimate = 10.58, 95% CrI = 2.43 to 34.98), although the effect was reduced compared to the peak bleaching period, suggesting partial recovery across the population. Site-level effects were weak, with credible intervals overlapping zero for both Melones (estimate = -0.49, 95% CrI = -1.01 to 0.04) and Tamarindo (estimate = -0.33, 95% CrI = -0.85 to 0.19), indicating that bleaching severity was broadly similar across sites despite spatial environmental differences.

TABLE 1 Bayesian logistic regression estimates (logit scale; 95% credible intervals) for coral bleaching, showing the effects of Site, Time, and environmental predictors.

Predictor	Model 1	Model 2	Model 3
Melones	-0.49 (-1.01, 0.04) *	—	—
Tamarindo	-0.33 (-0.85, 0.19) *	—	—
During	13.25 (5.23, 37.49) ***	2.35 (1.81, 2.91) ***	—
After 3 mo	10.58 (2.43, 34.98) ***	0.00 (-0.62, 0.63)	—
Light	—	-0.44 (-1.11, 0.11)	0.51 (-0.52, 1.25)
Sediment	—	0.61 (-0.01, 1.25) *	6.16 (4.98, 7.37) ***
Wave	—	0.31 (0.04, 0.59) **	2.09 (1.61, 2.59) ***
Temperature	—	-0.74 (-1.42, -0.11) **	-6.09 (-7.84, -4.74) ***

Asterisks denote effect strength based on the interpretation of odds ratios following Chen et al. (2010). Odds ratios were calculated by exponentiating the posterior logit estimates ($OR = e^{\beta}$). Effect strength annotations: *strong, **moderate, ***very strong. The 6-month survey was excluded from the models because no coral bleaching was recorded at that time.

When environmental predictors were included alongside Time (Model 2), the strong effect of the stressful period remained (During: estimate = 2.35, 95% CrI = 1.81 to 2.91, Table 2), whereas bleaching probability three months after the event showed no consistent effect (estimate = 0.00, 95% CrI = -0.62 to 0.63), suggesting that environmental conditions largely account for the apparent temporal variation in bleaching. Among environmental variables, wave energy (estimate = 0.31, 95% CrI = 0.04 to 0.59) and sediment load (estimate = 0.61, 95% CrI = -0.01 to 1.25) were positively associated with bleaching (i.e., increased bleaching probability), while temperature showed a negative association (estimate = -0.74, 95% CrI = -1.42 to -0.11). Light availability had no consistent effect on bleaching probability (estimate = -0.44, 95% CrI = -1.11 to 0.11).

The environment-only model (Model 3) further highlighted the importance of specific environmental drivers. Sediment load and wave energy emerged as very strong positive predictors of bleaching probability, with large effect sizes and narrow credible intervals (Sediment: estimate = 6.16, 95% CrI = 4.98 to 7.37; Wave: estimate = 2.09, 95% CrI = 1.61 to 2.59, Table 2). In contrast, temperature showed a very strong negative association with bleaching probability (estimate = -6.09, 95% CrI = -7.84 to -4.74), whereas light again exhibited high uncertainty and no consistent effect (estimate = 0.51, 95% CrI = -0.52 to 1.25). These results confirm that sediment and wave energy increased bleaching probability, independent of temporal variation.

TABLE 2 Survival rates of *Acropora cervicornis* outplants over the study year (June 2023 to June 2024), sectioned into before bleaching, during bleaching, 3 months after bleaching, and 6 months after bleaching, for the three distinct reefs (Maguey, Melones, Tamarindo) in Culebra, PR.

Site	Time Period			
	Pre-bleaching Jun–Sept	During bleaching Sept–Dec	After bleaching (3 months) Dec–Mar	After bleaching (6 months) Mar–Jun
Maguey	84.54%	81.71%	80.60%	72.22%
Melones	98.00%	83.67%	90.24%	85.14%
Tamarindo	95.00%	94.74%	86.67%	85.90%

3.2 Survival of *Acropora cervicornis* outplants

The Kaplan-Meier survival analysis revealed significant differences among populations ($X^2 = 21.8$, $df = 2$, $p = 2 \times 10^{-5}$; Figure 4), with Maguey exhibiting the lowest survival (39%) compared to Melones (63%) and Tamarindo (67%) by the end of the study. Pairwise comparisons indicated significant differences between Maguey and both Melones and Tamarindo, whereas survival at Melones and Tamarindo did not differ significantly. Quarterly surveys showed that mortality rates at Maguey remained relatively stable during the first nine months of the study, with the highest levels observed six months after bleaching was first reported (Table 2). At Melones, peak mortality coincided with the rainy season (September–November), likely due to increased sedimentation, although considerable mortality was also observed six months after bleaching began (Table 2). At Tamarindo, peak mortality occurred within the first three months following the bleaching event (Table 2).

The Bayesian logistic model revealed a strong temporal signal in coral survival, whereas differences among sites were moderate (Model 1, Table 3). Survival probability was highest under baseline conditions, consistent with field observations of healthy colonies prior to the bleaching event. During the peak bleaching period, survival probability decreased substantially (estimate = -1.31 , 95%

CrI = -1.90 to -0.75), indicating elevated mortality during this period. Three months after the bleaching onset, survival probability remained low relative to baseline (estimate = -2.05 , 95% CrI = -2.61 to -1.50), and six months after, survival probability was further reduced (estimate = -2.65 , 95% CrI = -3.22 to -2.09), suggesting ongoing mortality and limited recovery. Site-level effects were moderate and positive, with credible intervals excluding zero for both Melones (estimate = 1.25 , 95% CrI = 0.87 to 1.65) and Tamarindo (estimate = 1.45 , 95% CrI = 1.07 to 1.84), indicating somewhat higher survival relative to the reference site Maguey, supporting the findings of the KM survival analysis.

When environmental predictors were included alongside Time (Model 2, Table 3), the temporal decline in survival during the peak bleaching period was partially explained by environmental conditions. Survival probability during the peak period remained reduced (estimate = -0.47 , 95% CrI = -1.18 to 0.24), while three months after the event, survival probability remained very low (estimate = -2.58 , 95% CrI = -4.76 to -0.40), suggesting that environmental factors partly mediate mortality patterns. Among environmental variables, sediment load (estimate = -0.77 , 95% CrI = -1.54 to 0.01) and wave exposure (estimate = -0.04 , 95% CrI = -0.06 to -0.01) showed credible negative effects. Temperature exhibited no clear effect (estimate = -0.30 , 95% CrI = -1.07 to 0.47), and light intensity had no measurable influence.

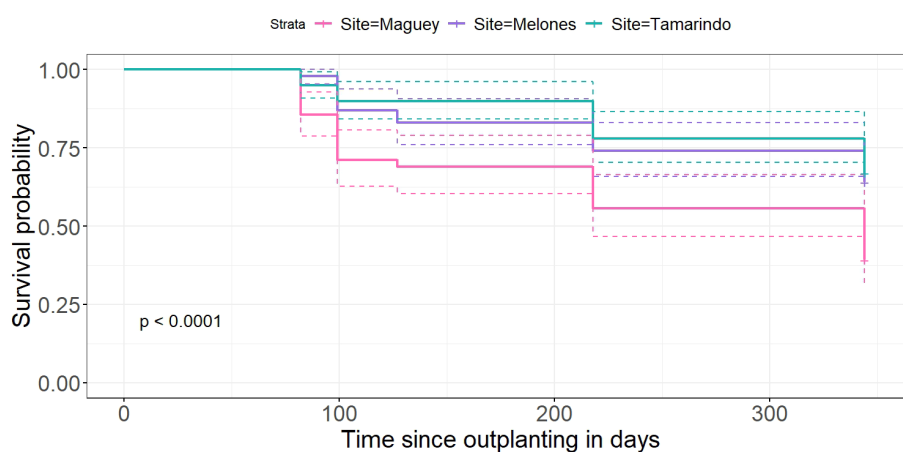


FIGURE 4

Kaplan-Meier survivorship curve demonstrating survival rates of *Acropora cervicornis* outplants from June 2023 to June 2024 for three distinct reefs (Maguey, Melones, Tamarindo) in Culebra, PR. Time since outplanting in days, zero representing day of outplanting, and 344 being the final day of data collection.

TABLE 3 Bayesian logistic regression estimates (logit scale; 95% credible intervals) for coral survival, showing the effects of Site, Time, and environmental predictors.

Predictor	Model 1	Model 2	Model 3
During	-1.31 (-1.90, -0.75) **	-0.47 (-1.18, 0.24) *	—
After 3 mo	-2.05 (-2.61, -1.50) ***	-2.58 (-4.76, -0.40) ***	—
After 6 mo	-2.65 (-3.22, -2.09) ***	—	—
Melones	1.25 (0.87, 1.65) **	—	—
Tamarindo	1.45 (1.07, 1.84) **	—	—
Wave	—	-0.04 (-0.06, -0.01) **	-0.03 (-0.05, -0.01) **
Sediment	—	-0.77 (-1.54, 0.01) *	-0.65 (-1.16, -0.15) **
Light	—	0.00 (-0.00, 0.00)	0.00 (-0.00, 0.00)
Temperature	—	-0.30 (-1.07, 0.47)	0.53 (0.33, 0.74) **

Asterisks denote effect strength based on the interpretation of odds ratios following Chen et al. (2010). Odds ratios were calculated by exponentiating the posterior logit estimates ($OR = e^{\beta}$). Effect strength annotations: *strong, **moderate, ***very strong. The 6-month survey was excluded from the Model 2 and Model 3 because no environmental data was available.

The environment-only model (Model 3, Table 3) further supported the patterns observed in Model 2. Sediment load (estimate = -0.65, 95% CrI = -1.16 to -0.15) and wave energy (estimate = -0.03, 95% CrI = -0.05 to -0.01) remained negatively associated with survival, while temperature now showed a positive effect (estimate = 0.53, 95% CrI = 0.33 to 0.74). Light again showed no measurable effect, with an estimated effect near zero and a 95% credible interval essentially spanning zero. These results suggest that sediment and wave energy could serve as environmental drivers of reduced coral survival, whereas temperature effects appear more context-dependent, with light having minimal influence.

3.3 Effect of bleaching on *Acropora cervicornis* outplant survival probability

Chi-squared tests indicated that survival probability did not differ significantly between bleached and non-bleached outplants at any of the three sites (Maguey: $\chi^2 = 0.03$, $df = 1$, $p = 0.869$; Melones: $\chi^2 = 1.27$, $df = 1$, $p = 0.258$; Tamarindo: $\chi^2 = 0.02$, $df = 1$, $p = 0.896$; Figure 5).

3.4 *Acropora cervicornis* outplant growth

3.4.1 Net growth rates (NGR)

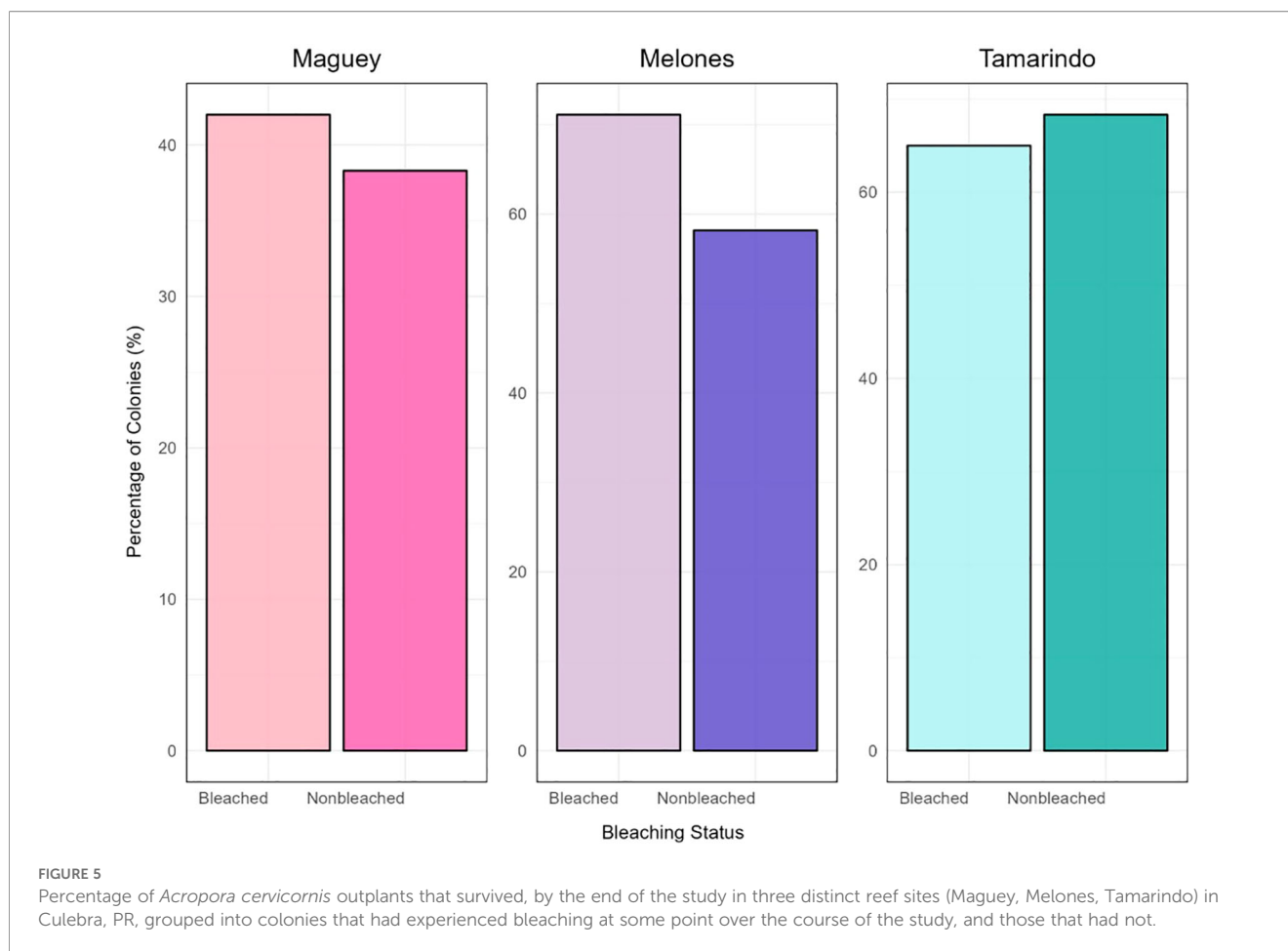
The Bayesian Gaussian mixed-effects model revealed a clear temporal signal in net growth rate (NGR) of *Acropora cervicornis*, whereas site-level differences were weak and uncertain (Model 1, Table 4). NGR declined markedly during the bleaching period (estimate = -0.35, 95% CrI = -0.46 to -0.24), indicating a significant reduction in coral growth during peak stress. Three (estimate = 0.04, 95% CrI = -0.08 to 0.16) and six months (estimate = -0.03, 95% CrI = -0.17 to 0.10) after the bleaching event started, NGR did not differ from baseline, suggesting partial recovery of growth following the bleaching period. Main effects of Site were weak, with credible intervals overlapping zero for both

Melones (estimate = 0.05, 95% CrI = -0.04 to 0.15) and Tamarindo (estimate = -0.06, 95% CrI = -0.16 to 0.04). However, growth responses varied slightly between sites over time. Specifically, NGR at Melones declined more strongly during the bleaching period than at the reference site (During \times Melones: estimate = -0.19, 95% CrI = -0.33 to -0.04), whereas interactions between Time and Tamarindo were weak and uncertain across all periods. These results indicate limited site-specific divergence in growth responses, with the strongest deviation observed at Melones during peak bleaching.

When environmental predictors were included alongside Time (Model 2), the negative effect of the bleaching period on NGR remained strong (estimate = -0.26, 95% CrI = -0.37 to -0.15, Table 4), while post-bleaching growth rates showed no consistent deviation from baseline. Among environmental variables, wave energy and sediment load exhibited negative associations with NGR, with sediment showing a weak effect (estimate = -0.13, 95% CrI = -0.27 to 0.00, Table 4) and wave energy approaching a small negative effect (estimate = -0.004, 95% CrI = -0.01 to 0.00, Table 4). Temperature and light intensity showed no consistent relationships with growth.

The environment-only model (Model 3) further emphasized the role of physical stressors in constraining coral growth. Sediment load emerged as a very strong negative predictor of NGR (estimate = -0.34, 95% CrI = -0.40 to -0.27, Table 4), while wave energy also showed a negative effect (estimate = -0.006, 95% CrI = -0.01 to -0.002, Table 4). In contrast, temperature and light again exhibited high uncertainty and no consistent effects on growth. Together, these results indicate that net growth rate is suppressed during bleaching periods and that sediment and wave stressors further limit growth regardless of overall temporal patterns.

By the end of the study, all three sites exhibited overall tissue loss, as indicated by negative average and median growth rates. Mean net growth rates (pooled across all survey periods) were -0.029 cm/day (± 0.414 SD; median = 0.034) at Melones, -0.055 cm/day (± 0.330 SD; median = 0.017) at Maguey, and -0.095 cm/day (± 0.365 SD; median = -0.011) at Tamarindo.



Across all sites, growth rates declined considerably during the bleaching event, largely because bleached colonies exhibited significantly slower growth than their non-bleached counterparts (Figure 6). For example, bleached colonies had a mean net growth rate of -0.026 cm/day (± 0.114 SD; median = -0.029), while non-bleached colonies showed a net gain of 0.012 cm/day (± 0.105 SD; median = 0.015). Notably, when comparing growth during the bleaching period (September–November 2024), both bleached and non-bleached colonies experienced negative growth (Figure 7). Specifically, bleached colonies declined at a mean rate of -0.39 cm/day (± 0.52 SD; median = -0.23), while non-bleached colonies declined at -0.33 cm/day (± 0.52 SD; median = -0.23). When pooling growth across all sites, net growth rates were 0.037 cm/day (± 0.222 SD; median = -0.008) before bleaching, -0.351 cm/day (0.523 SD; median = -0.233) during bleaching, 0.069 cm/day three months after bleaching (± 0.274 SD; median = -0.069), and 0.031 cm/day (± 0.188 SD; median = 0.037) six months after bleaching. These values indicate a sharp decline during the bleaching event, followed by a partial recovery that peaked at three months post-bleaching, before slightly declining again at six months.

3.4.2 Specific growth rates (SpGR)

The Bayesian Gaussian mixed-effects model revealed a strong temporal signal in specific growth rates (SpGR) of *Acropora cervicornis*, whereas site-level differences were weak and uncertain

(Model 1, Table 5). SpGR declined significantly during the bleaching period (estimate = -1.03 , 95% CrI = -1.31 to -0.75). Three (estimate = 0.12 , 95% CrI = -0.19 to 0.45) and six months (estimate = -0.03 , 95% CrI = -0.39 to 0.31) after the bleaching event, SpGR did not differ considerably from baseline, suggesting some recovery of growth following bleaching.

Main effects of Site were weak, with credible intervals overlapping zero for both Melones (estimate = 0.10 , 95% CrI = -0.16 to 0.35 , Table 5) and Tamarindo (estimate = -0.15 , 95% CrI = -0.41 to 0.11 , Table 5). Although overall site effects were not significant, some evidence of spatial variation in temporal responses was observed. Growth at Melones tended to decline more strongly during the bleaching period than at the reference site Maguey (During \times Melones: estimate = -0.37 , 95% CrI = -0.75 to 0.02 , Table 5), whereas interactions between Time and Tamarindo were weak and uncertain across all periods. These patterns indicate limited site-specific divergence in growth responses during and after bleaching.

When environmental predictors were included alongside Time (Model 2), the negative effect of the bleaching period on SpGR remained strong (estimate = -0.71 , 95% CrI = -1.00 to -0.41 , Table 5), while post-bleaching growth rates again showed no consistent deviation from baseline. Among environmental variables, sediment (estimate = -0.36 , 95% CrI = -0.71 to 0.01 , Table 5) and wave energy (estimate = -0.01 , 95% CrI = -0.02 to 0.00 , Table 5) showed a small but credible negative effect.

TABLE 4 Bayesian Gaussian generalized linear mixed-effects model estimates (95% credible intervals) for coral net growth, showing the effects of site, time, and environmental predictors.

Predictor	Model 1	Model 2	Model 3
During	-0.350 (-0.460, -0.240) ***	-0.260 (-0.370, -0.150) **	—
After 3 mo	0.040 (-0.080, 0.160)	0.100 (-0.320, 0.530)	—
After 6 mo	-0.030 (-0.170, 0.100)	—	—
Melones	0.050 (-0.040, 0.150)	—	—
Tamarindo	-0.060 (-0.160, 0.040)	—	—
During × Melones	-0.190 (-0.330, -0.040) *	—	—
After 3 mo × Melones	0.030 (-0.120, 0.190)	—	—
After 6mo × Melones	0.030 (-0.140, 0.200)	—	—
During × Tamarindo	0.080 (-0.070, 0.220)	—	—
After 3 mo × Tamarindo	-0.070 (-0.230, 0.090)	—	—
After 6 mo × Tamarindo	0.040 (-0.140, 0.210)	—	—
Wave	—	-0.004 (-0.010, 0.000)	-0.006 (-0.010, -0.002) *
Sediment	—	-0.130 (-0.270, 0.000) *	-0.340 (-0.400, -0.270) ***
Temperature	—	0.030 (-0.120, 0.170)	-0.020 (-0.050, 0.010)
Light	—	0.000 (-0.000, 0.000)	-0.000 (-0.000, 0.000)

Asterisks denote effect strength based on standardized regression coefficients from Gaussian models. All continuous predictors were standardized prior to analysis. Effect strength was interpreted following Cohen (1988) as a guideline rather than strict thresholds: *weak ($|\beta| \approx 0.1$), **moderate ($|\beta| \approx 0.3$), ***strong ($|\beta| \geq \sim 0.3-0.5$).

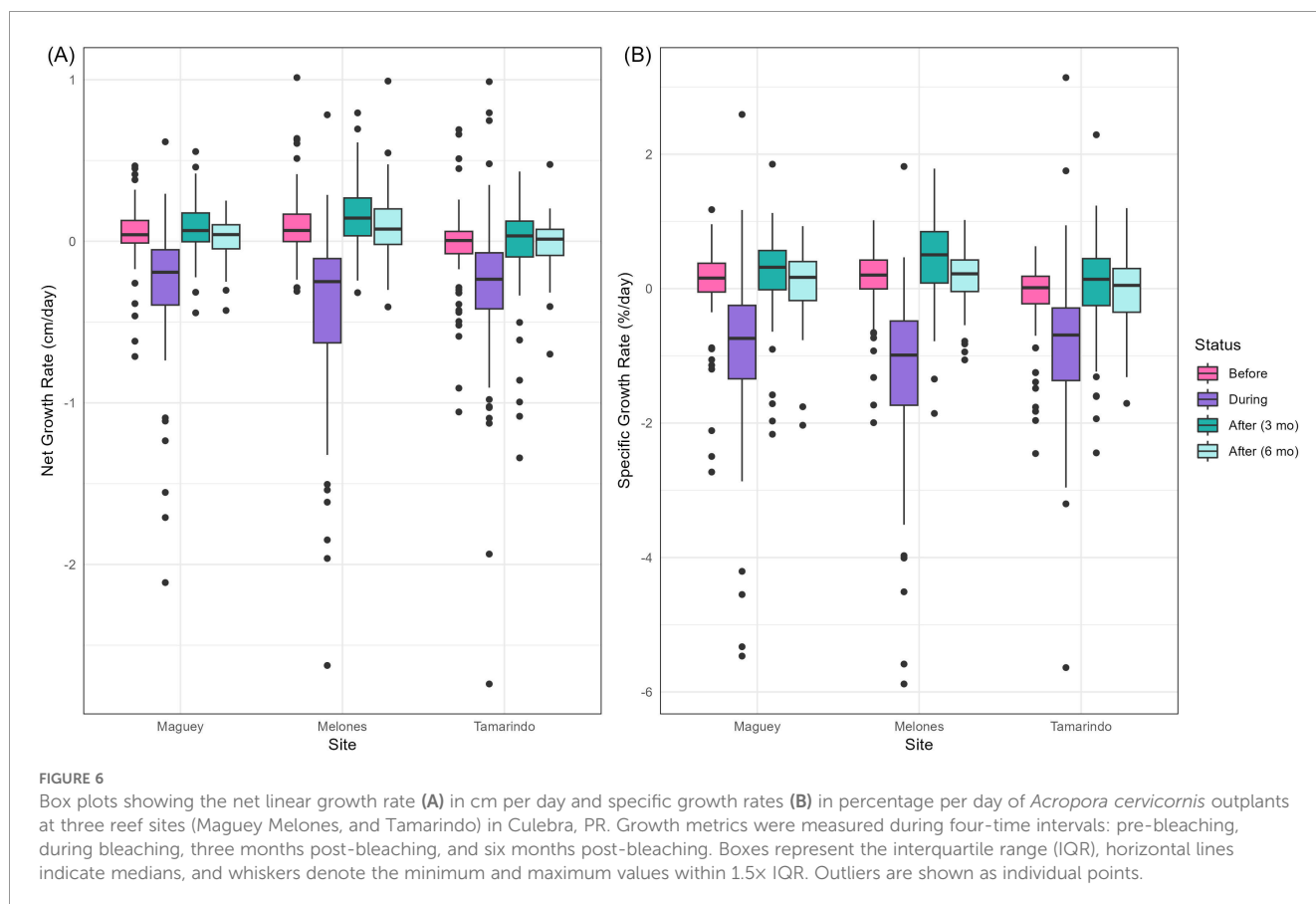


FIGURE 6 Box plots showing the net linear growth rate (A) in cm per day and specific growth rates (B) in percentage per day of *Acropora cervicornis* outplants at three reef sites (Maguey Melones, and Tamarindo) in Culebra, PR. Growth metrics were measured during four-time intervals: pre-bleaching, during bleaching, three months post-bleaching, and six months post-bleaching. Boxes represent the interquartile range (IQR), horizontal lines indicate medians, and whiskers denote the minimum and maximum values within 1.5x IQR. Outliers are shown as individual points.

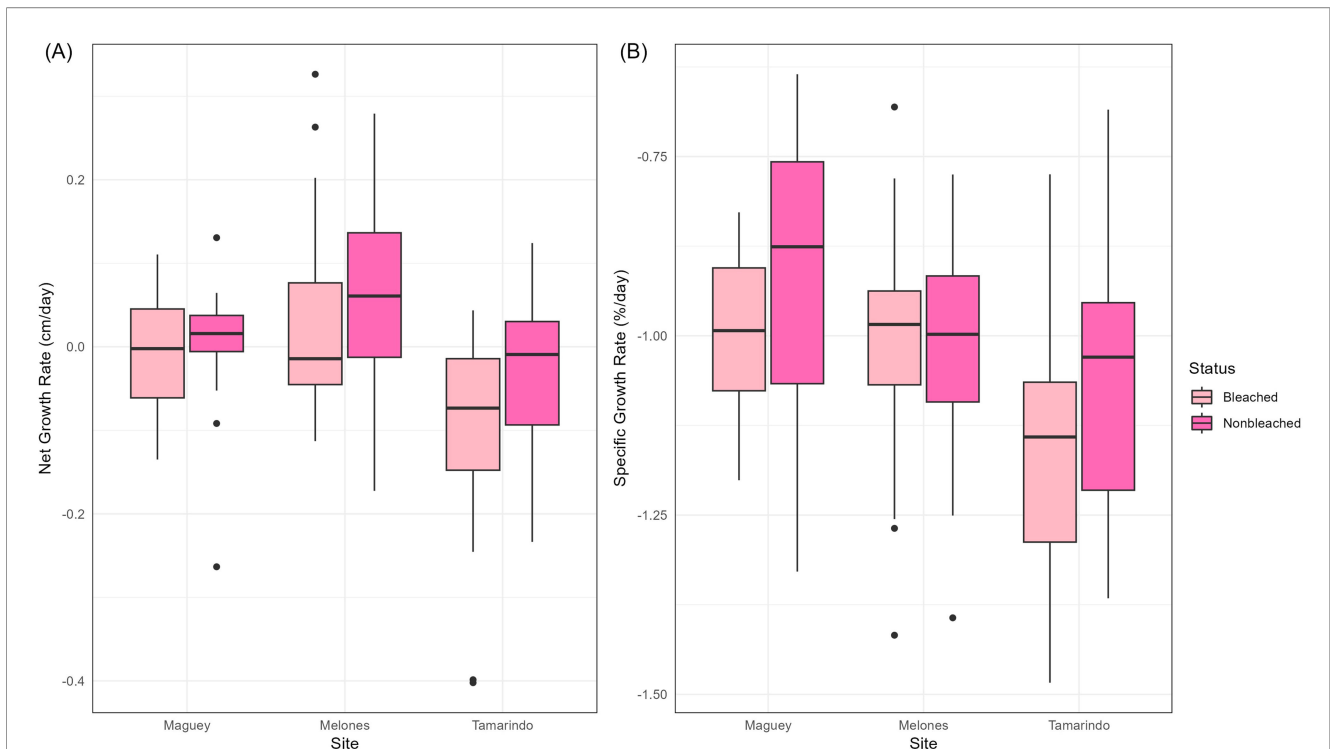


FIGURE 7 Box plots showing the net linear growth rate **(A)** in cm per day and specific growth rates **(B)** in percent per day of *Acropora cervicornis* outplants that experienced bleaching (“Bleached”) and those that did not (“Nonbleached”) over the full study period (June 2023 to June 2024) at three reef sites (Maguey, Melones, and Tamarindo) in Culebra, PR. Boxes represent the interquartile range (IQR), horizontal lines indicate medians, and whiskers denote the minimum and maximum values within 1.5× IQR. Outliers are shown as individual points.

TABLE 5 Bayesian Gaussian generalized linear mixed-effects model estimates (95% credible intervals) for coral specific growth rates, showing the effects of Site, Time, and environmental predictors.

Predictor	Model 1	Model 2	Model 3
During	-1.03 (-1.31, -0.75) ***	-0.71 (-1.00, -0.41) ***	—
After 3 mo	0.12 (-0.19, 0.45)	0.38 (-0.77, 1.51)	—
After 6 mo	-0.03 (-0.39, 0.31)	—	—
Melones	0.10 (-0.16, 0.35)	—	—
Tamarindo	-0.15 (-0.41, 0.11)	—	—
During × Melones	-0.37 (-0.75, 0.02)	—	—
After 3mo × Melones	0.21 (-0.21, 0.62)	—	—
After 6mo × Melones	0.05 (-0.40, 0.50)	—	—
During × Tamarindo	0.36 (-0.04, 0.74)	—	—
After 3mo × Tamarindo	-0.04 (-0.48, 0.39)	—	—
After 6mo × Tamarindo	0.09 (-0.35, 0.53)	—	—
Wave	—	-0.01 (-0.02, 0.00) *	-0.02 (-0.03, -0.01) *
Sediment	—	-0.36 (-0.71, 0.01) ***	-0.94 (-1.11, -0.77) ***
Temperature	—	0.08 (-0.30, 0.46)	-0.07 (-0.15, 0.01)
Light	—	-0.00 (-0.00, 0.00)	-0.00 (-0.00, 0.00)

Asterisks denote effect strength based on standardized regression coefficients from Gaussian models. All continuous predictors were standardized prior to analysis. Effect strength was interpreted following Cohen (1988) as a guideline rather than strict thresholds: *weak ($|\beta| \approx 0.1$), **moderate ($|\beta| \approx 0.3$), ***strong ($|\beta| \geq -0.3-0.5$).

Temperature and light intensity showed no consistent relationships with growth.

The environment-only model (Model 3) reinforced the role of physical stressors in constraining coral growth. Sediment load emerged as a very strong negative predictor of SpGR (estimate = -0.94 , 95% CrI = -1.11 to -0.77 , Table 5), while wave energy also showed a strong negative association (estimate = -0.02 , 95% CrI = -0.03 to -0.01 , Table 5). In contrast, temperature and light again exhibited high uncertainty and no consistent effects. Collectively, these results indicate that specific growth rates are strongly reduced during bleaching periods and are further suppressed by elevated sediment loads and wave exposure, independent of broader temporal variation.

When pooling SpGR across all sites, mean values were 0.015% (± 0.59 SD; median = 0.121) per day before bleaching, -1.03% (± 1.32 SD; median = -0.79) per day during bleaching, 0.21% (± 0.77 SD; median = 0.29) per day three months after bleaching, and 0.03% (± 0.53 SD; median = 0.16) per day six months after bleaching. As was the case for NGR, bleached colonies consistently exhibited lower SpGR than non-bleached colonies across all time points (Figure 6), suggesting a sustained negative impact of bleaching on size-standardized tissue change. Notably, during the peak bleaching period (September–November 2024), both groups showed negative SpGR values, indicating that even non-bleached colonies experienced suppressed growth during the bleaching event (Figure 7).

4 Discussion

To develop effective strategies for managing and conserving natural resources, it is essential to understand how the living world responds to ongoing climate change. In the case of coral reef ecosystems, increased seawater temperature is considered one of the major disturbances shaping overall ecosystem dynamics, primarily due to its role in triggering coral bleaching (Lesser, 2024). While the relationship between elevated temperatures and coral bleaching is well-established, it is important to recognize that temperature does not act in isolation (Anthony et al., 2007). Other environmental factors, such as hydrodynamics (Anthony, 2007; Lentz et al., 2024), light intensity (Anthony et al., 2007; Torres et al., 2008), and sedimentation (Anthony et al., 2007; Zweifler, 2024), may also play significant roles, and their interactions could further complicate our understanding of coral population responses to stress. These factors can vary significantly across small spatial scales, underscoring the need for a more nuanced understanding of how site-specific environmental conditions shape coral health and bleaching susceptibility.

To address this, we monitored restored populations of the coral *Acropora cervicornis* across three reefs in Culebra, Puerto Rico, which differed in temperature, light intensity, sedimentation rates, and hydrodynamics during a widespread Caribbean bleaching event. Across all sites, approximately 45% of colonies bleached, reflecting the high susceptibility of *A. cervicornis*. However, patterns of bleaching and demographic responses were unexpected in several

respects. First, bleaching susceptibility showed spatial variability among closely situated reefs, even though these differences were not statistically significant. Second, statistical analyses suggest that bleaching was not the primary driver of mortality. Third, coral demographics (i.e., survival and growth) were not negatively affected by increased seawater temperatures. Instead, site-specific sedimentation and wave energy conditions appeared to exert stronger effects on coral performance, emphasizing the need to incorporate local environmental drivers into assessments of bleaching dynamics and population resilience.

Not surprisingly, the incidence and prevalence of coral bleaching peaked during the warmest months of the year (September–October), following the pattern observed across the entire Caribbean through 2023. An intriguing finding of this study was the unexpectedly poor performance of outplants at the Maguey reef site. Maguey was characterized by lower temperatures and light intensity but higher wave energy, environmental conditions generally assumed to reduce bleaching risk; thermal stress is typically exacerbated by high irradiance (Brown, 1997; Torres et al., 2008) and mitigated by increased water movement (Nakamura et al., 2003; Finelli et al., 2006; Fifer et al., 2021). Despite these seemingly favorable conditions, colonies at Maguey exhibited the highest bleaching incidence, being approximately 1.15 times more likely to bleach than those at Melones and nearly 1.3 times more likely than those at Tamarindo ($\sim 15\%$ and $\sim 30\%$ higher incidence, respectively), although these differences were not statistically significant. Given the well-documented sensitivity of *Acropora cervicornis* to environmental variation, even modest differences in local conditions may translate into disproportionate population-level effects.

The results of the Bayesian models indicate that sedimentation and wave energy, rather than temperature and light, were the primary predictors of coral bleaching. This finding complements previous work by Drury et al. (2017), who also found no significant relationship between temperature or light intensity and bleaching probability in *A. cervicornis*. Instead, sediment load emerged as a very strong positive predictor of bleaching probability, with a relatively large effect size and narrow credible interval, a result that is not traditionally emphasized in bleaching frameworks dominated by thermal stress. High sediment loads are typically associated with reduced light availability, which has often been assumed to mitigate bleaching risk by lowering photosynthetic stress (Fabricius, 2005; Zweifler, 2024). However, sediment exposure can impose multiple, non-mutually exclusive physiological costs that may instead increase bleaching susceptibility (Wooldridge, 2009; Zweifler, 2024). These include chronic tissue abrasion, increased energetic expenditure for mucus production and sediment rejection, as well as impaired gas exchange at the tissue-water interface, all of which can reduce the energetic capacity of corals to cope with thermal stress (Rogers, 1990; Erftemeijer et al., 2012; Junjie et al., 2014).

Importantly, the strong sediment effect observed in our study occurred in combination with elevated wave energy, suggesting that sediment stress may be amplified under high hydrodynamic conditions. Rather than settling passively, sediments in wave-

exposed environments are frequently resuspended, increasing the frequency and intensity of physical contact with coral tissue (Storlazzi et al., 2004). This repeated disturbance may exacerbate oxidative stress and compromise coral internal physiological balance, thereby lowering the threshold at which bleaching is triggered. Under such conditions, sediment may act not as a light-attenuating buffer, but as a chronic mechanical and metabolic stressor that predisposes colonies to bleaching.

While increased water movement is generally considered beneficial, as it may enhance circulation, dissipate heat, and reduce sediment and nutrient accumulation, our results showed the opposite pattern. When exposed to higher wave energy, colonies exhibited the highest bleaching susceptibility and lowest survival. This counterintuitive result aligns with observations by McClanahan et al. (2005) and Lentz et al. (2024), who also reported that strong hydrodynamic forces can exacerbate physiological stress. We therefore hypothesize that, under stressful conditions, mechanical stress from wave action may directly contribute to both bleaching and mortality, potentially overriding the protective effects of otherwise favorable conditions.

Together, these results indicate that sedimentation should be considered an active contributor to bleaching risk, particularly in dynamic, wave-exposed reef environments. This finding challenges the assumption that reduced irradiance and increased wave motion necessarily confer protection against bleaching and highlights the need to account for interacting physical stressors when predicting coral responses to thermal extremes.

The immediate effect of coral bleaching is the loss of up to 95% of the energy typically provided to corals by photosynthetic microalgae (Muscatine et al., 1981). This energy deprivation generally leads to reduced survival in corals during the bleaching period. For example, in Jamaica, Quinn and Kojis (2008) reported that 90% of bleached *A. cervicornis* colonies died within four months, while Drury et al. (2017) through their work with *A. cervicornis* in the Florida Keys attributed a bleaching event to all subsequent observed mortality. These findings underscore the commonly assumed link between bleaching and mortality. In contrast, in this study it was found that the survival of bleached colonies was 42% at Maguey, 71% at Melones, and 65% at Tamarindo. The relatively high survival (compared to the previous studies) of bleached coral colonies is consistent with recent findings. For example, Page et al. (2023) reported that 94% of the colonies affected by bleaching in the Keppel Islands, Australia, during 2020 survived.

It could be argued that regional differences in survival patterns of bleached colonies may be linked to site-specific genetic pools (Lohr and Patterson, 2017). Nevertheless, the relationship between genotype and thermal tolerance, at least for *A. cervicornis*, remains debated as no clear pattern has been established (Drury et al., 2017; O'donnell et al., 2018). Given such genetic-specific uncertainty, it is plausible that the observed survival patterns in this study could be influenced by factors beyond genetics. Specifically, the colonies used in our study have survived major bleaching events and other environmental disturbances, such as hurricanes, which might

have led to local acclimatization to withstand seawater temperatures (and other stressors) above the normal range (Fox et al., 2021).

Although coral coloration is a widely used indicator of bleaching and physiological stress, our results show that it is not always a reliable predictor of survival. Bleached colonies exhibited survival rates comparable to, and in some cases higher than (Melones and Maguey), those of visually healthy colonies. A similar contradiction between expected stress and demographic outcome was reported by Santiago-Padua et al. (2023) at Melones, where *A. cervicornis* outplants exposed to predation by corallivore fireworms, an interaction traditionally assumed to reduce demographic performance, paradoxically showed higher survival than non-predated colonies. Together, these findings suggest that stressors typically interpreted as detrimental based on appearance or conventional ecological assumptions do not necessarily translate into reduced survival. Instead, such stress signals may reflect prior exposure, selective filtering, or physiological conditioning that enhances resilience under subsequent disturbance.

It is plausible that non-bleached colonies also experience thermal stress but do not expel their symbionts and therefore do not exhibit visible signs of stress (i.e., bleaching), instead managing oxidative stress internally. Under the Oxidative Theory of Coral Bleaching, the expulsion of zooxanthellae can function as a protective mechanism, reducing reactive oxygen species (ROS)-induced cellular damage during periods of stress (Lesser, 2024). In contrast, colonies that retain their symbionts and remain unbleached may still experience comparable oxidative stress, but at levels just below the bleaching threshold, relying primarily on internal antioxidant defenses (Saragosti et al., 2010).

From this perspective, bleaching may represent one of several physiological strategies for coping with oxidative stress, rather than a direct determinant of survival probability. Alternatively, non-bleached *A. cervicornis* colonies may delay the activation of survival mechanisms by prioritizing growth under stressful conditions (see below). By the time severe stress is detected, physiological damage may already be irreversible, resulting in more rapid mortality compared with colonies that activated stress-response pathways earlier. Under this framework, colonies that appear visually healthy may, under certain conditions, be less stress-adapted than bleached colonies that have already reallocated energy toward survival.

The unexpected finding suggests two key possibilities: 1) *A. cervicornis* outplants may be reallocating their physiological energy toward survival strategies during stressful events (e.g., loss of the endosymbiotic algae), and 2) factors at the local scale may be more significant contributors to coral mortality than regional thermal anomalies. Supporting this last argument is the fact that the higher level of mortality recorded at Melones during the study occurred before the bleaching period (i.e. early September), coinciding with significant sedimentation when heavy rainfall caused localized excess sediment runoff from coastal construction. Survival rates increased again to previous levels following this event. In contrast, Maguey and Tamarindo demonstrated a gradual decline in survival rates over the course of the study year, consistent with expected

outplant performance from general outplanting stress (Becker and Mueller, 2001; Schopmeyer et al., 2017; Fogarty, 2012).

Contrary to conventional expectations, higher wave energy was associated with lower survival of *A. cervicornis* colonies in this study. Wave action is often considered beneficial for corals, enhancing circulation, dissipating heat, reducing sediment accumulation, and supporting nutrient exchange (Nakamura et al., 2003; Finelli et al., 2006; Fifer et al., 2021). However, under certain conditions, strong wave action may impose significant mechanical stress, particularly on branching species. Repeated bending, breakage, and abrasion can compromise tissue integrity, reduce feeding efficiency, and divert energy from growth and reproduction toward repair (Okubo et al., 2007).

Additionally, high-hydrodynamic environments can exacerbate the impacts of other stressors. For example, resuspended sediments are more likely to scour coral surfaces under strong water movement, increasing oxidative stress and reducing the energetic capacity to cope with thermal anomalies (see above, Rogers, 1990; Fabricius, 2005; Weber et al., 2012). In this way, wave energy may shift from being a protective factor under moderate conditions to a net stressor when combined with environmental challenges, effectively lowering survival probability. These findings highlight that the ecological effects of hydrodynamics are context-dependent and may interact with local environmental and physiological factors to influence coral performance.

The theory of energy redistribution posits that an organism's energetic budget is finite, and that investment in one demographic function, such as survival, necessarily limits investment in others, such as growth. This energetic trade-off proposal may be supported by the observed reduction in coral growth rates during the bleaching event across all three sites, suggesting a physiological shift from growth toward survival. Notably, the site with the highest survivorship, Tamarindo, exhibited the lowest overall growth rates, further reinforcing the idea of energy reallocation under stress. This aligns with findings by Bay and Palumbi (2017), who documented a fitness trade-off in corals: colonies with higher survivorship following transplantation generally exhibited slower growth, particularly in more environmentally stable locations. Likewise, in this study, unbleached coral colonies grew faster but exhibited lower survival probabilities than their bleached counterparts, which survived better. Although differences were not significant, the finding supports the negative relationship between growth and survival.

By the end of the study, 63% and 67% of corals survived at Melones and Tamarindo, respectively, despite being subject to bleaching. These rates are similar to those observed by Mercado-Molina et al. (2015a) at two reefs also located in Culebra with depth and topographic relief comparable to those of the present study sites. Such rates also fall within the range reported across the region (Becker and Mueller, 2001; Schopmeyer et al., 2017; Van Woesik et al., 2021). However, these broadly comparable survival rates mask spatial differences in demographic performance, as colony survival was significantly lower at Maguey. Spatial differences in the demographic performance of *Acropora cervicornis* (i.e., survival), including within Culebra, have also

been reported by Mercado-Molina et al. (2015a, b). Together, these findings support the need for restoration strategies targeting *A. cervicornis* to be implemented across multiple locations, rather than concentrating all the effort into a single location. Likewise, careful examination of the prevailing environmental conditions across selected locations for restoration is essential.

Although bleaching was observed at all three sites, it did not emerge as the primary driver of mortality. Instead, our results suggest that environmental variability, particularly in sedimentation and hydrodynamics, better accounted for the observed patterns in *A. cervicornis* performance. These site-specific factors likely underlie the spatial variation in bleaching intensity, survival, and growth documented in this study.

Maguey Reef presents a paradox: despite environmental conditions typically associated with stress relief, i.e., cooler temperatures, reduced light, lower sedimentation, and higher water motion, it exhibited the highest bleaching and mortality. This unexpected pattern may reflect a "selective sieve" effect, in which reefs experiencing greater environmental variability filter out sensitive genotypes, thereby enhancing population resilience (Bay and Palumbi, 2017). Conversely, Maguey's relative environmental stability could limit such selection, producing colonies less acclimated to temperature anomalies. This interpretation aligns with observations by Lentz et al. (2024) and McClanahan et al. (2005), who found that high-flow conditions can intensify bleaching despite thermal buffering. Moreover, bleaching under low light may increase reactive nitrogen species (RNS) production (Lesser, 2024), potentially explaining similar mortality between bleached and unbleached colonies. Finally, Maguey's intermediate growth rate may reflect metabolic costs associated with high-flow, lower light conditions, which elevate dark respiration and particle feeding while limiting photosynthesis (Sebens et al., 2003).

Alternatively, Melones Reef was characterized by the highest levels and variability of temperature, light intensity, and sedimentation rate, coupled with the lowest wave energy. This site exhibited intermediate bleaching and survival, alongside rapid growth. According to the "selective sieve" hypothesis, environmental variability may enhance acclimation capacity, resulting in improved survival (Bay and Palumbi, 2017). However, excessive variability may exceed a "beneficial" stress threshold, leading to heightened stress, bleaching, and mortality, which could explain the intermediate bleaching and survival rates observed at this site. As noted above, the decrease in survival at Melones coincided with a specific sedimentation event prior to bleaching, triggered by intense rainfall and terrestrial runoff from adjacent coastal construction. This interpretation is supported by modeling results: the environment-only model (Model 3, Table 3) identified sediment load as a strong negative predictor of survival (estimate = -0.65 , 95% CrI = -1.16 to -0.15), corresponding to an approximately 48% reduction in survival odds per unit increase in sediment load, highlighting sedimentation as a dominant driver of colony mortality.

In contrast, Tamarindo Reef exhibited the lowest bleaching prevalence, highest survival, and slowest growth rates. This site experienced moderate environmental conditions, including lower sediment loads and reduced wave energy compared to Melones,

despite having the highest nutrient concentrations (Casariego-Rodríguez et al., unpublished data). Survival models indicated that both sediment load and wave energy were negatively associated with survival (Model 3, Table 3), suggesting that the absence of extreme physical stressors likely contributed to the favorable survival outcomes at Tamarindo. Although wave energy consistently showed a negative relationship with survival in our models, previous work suggests that intermediate flow regimes can enhance coral performance by balancing mass transfer and mechanical stress, potentially explaining the positive outcomes observed at this site (Lentz et al., 2024).

Considering the theory of energetic trade-offs between growth and survival, the relatively high survival at Tamarindo may reflect an allocation of energy toward maintenance and stress resistance rather than rapid growth. However, this mechanism does not act alone: at Melones, where growth rates were highest, survival was intermediate rather than lowest, illustrating the complex and context-dependent nature of *A. cervicornis* demographic responses. Moreover, the reduced growth at Tamarindo cannot be explained by bleaching alone, as this site also experienced the lowest bleaching prevalence, further decoupling bleaching intensity from patterns of growth and survival.

The slower growth rates at Tamarindo may also be linked to elevated nutrient concentrations, including phosphorus and nitrogen, which have been associated with suppressed calcification and skeletal extension in corals (Hallock and Schlager, 1986; Stambler et al., 1991; Ferrier-Pagès et al., 2000). We hypothesize that runoff from a nearby waste facility contributes to elevated nutrient levels at the reef. Future studies should include direct quantification and identification of nutrients through water column and sediment profiling, stable isotope tracing, and analysis of coral tissue and symbiont composition to further evaluate their influence on outplant performance.

Wave energy emerged as a particularly influential variable, both in isolation and in interaction with other environmental factors (Nakamura, 2010). Previous studies have shown that hydrodynamic regimes can drive fine-scale heterogeneity in bleaching outcomes across reefs separated by only a few kilometers (Nakamura and van Woesik, 2001). Nevertheless, hydrodynamic patterns, including wave energy, remain underreported in coral restoration and conservation research, with over 95% of bleaching studies ignoring water motion entirely (Grottoli et al., 2021; McLachlan et al., 2020). This oversight may reflect the inherently complex and interactive role of water movement in modulating temperature, light, sediment, oxygen, and nutrient dynamics-interactions that are beginning to be explored in this study.

Yamano et al. (2003) described hydrodynamic and other environmental parameters as a consequence of reef orientation on the leeward or windward sides of an island. Similar to their study, Maguey lies on the windward side, exposed to high wave energy and greater stress. Melones is situated on the leeward side, completely protected from prevailing winds by Luis Peña Cay. Leeward reefs, sheltered from open-ocean swells, may be subject to greater sedimentation (Yamano et al., 2003), a pattern consistent with

observations at Melones. Tamarindo occupies a semi-exposed leeward orientation, which has been suggested to be optimal for coral survival. We have begun preliminary collaborations with a geological partner to explore high-resolution bathymetric data, paired with wind and current data, to further map the role of hydrodynamics in conjunction with reef structure in driving the observed reef-specific outcomes.

Conclusions

Overall, our results reveal a complex interplay among environmental variables, coral bleaching, survival, and growth. No single variable or mechanism can fully explain the observed demographic patterns across the three reef sites. These findings highlight the limitations of relying solely on simplified metrics, such as growth rate or bleaching intensity, to assess reef resilience or restoration success. While informative, such metrics do not capture the full complexity of coral physiological responses to increasingly variable environments. Instead, multiple physical and biological processes likely act in concert to determine coral survival and resilience under stress. Furthermore, genotypes that have persisted through prior bleaching events and chronic environmental stress may possess novel adaptive mechanisms, such as enhanced thermal tolerance, shifts in symbiont partnerships, or improved cellular stress responses, beyond those previously described.

Addressing gaps in our understanding of coral outplant demographics within their reef and ecosystem contexts is essential for effective restoration and conservation. By identifying key stressors and relief factors, as well as understanding how corals respond to them, it may be possible to manage systems in ways that promote outplant persistence. This study also underscores the importance of incorporating hydrodynamic patterns into coral restoration and conservation research. The limited understanding of how water movement influences coral demography and restoration outcomes may partly explain discrepancies observed in the existing literature.

Finally, it is worth emphasizing that coral reef field studies are inherently constrained by logistics and cost, with intensive repeated surveys of hundreds of colonies requiring a trade-off between spatial replication and both temporal and individual-level resolution. Our Bayesian mixed-effects models explicitly account for repeated measurements on the same colonies and allow uncertainty to be quantified through posterior distributions. However, inference is still limited by the structure of the data. In particular, the small number of study sites ($n = 3$) limits our ability to fully separate spatial from environmental effects, reduces statistical power for detecting site-level patterns, and constrains the generalizability of spatial and environmental relationships beyond the studied reefs. Although Bayesian models can improve parameter estimation under limited replication through partial pooling, they cannot compensate for the lack of true spatial replication. Consequently, results related to environmental drivers should be interpreted cautiously and within the ecological context of the study system.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Ethics statement

The manuscript presents research on animals that do not require ethical approval for their study.

Author contributions

IC: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. AM-M: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing.

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Conflict of interest

The authors declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2026.1665257/full#supplementary-material>

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