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Legacy effects of a mild mass bleaching event on coral survival and growth

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Abstract

Coral bleaching can cause substantial mortality, with well-documented consequences for reef structure and function. However, comparatively little is known about the sublethal demographic impacts of bleaching, despite their potential to influence population persistence and recovery. It remains unclear whether phenotypic responses of corals to heat stress (e.g., remaining unbleached, partially bleached or fully bleached) scale predictably with lethal and sublethal outcomes, or whether even mildly affected corals experience lasting demographic consequences of thermal stress. This study examined changes in coral growth and survival dependent on phenotypic bleaching response, following a mild but spatially extensive bleaching event in the central Great Barrier Reef, in 2022. By using large-area orthomosaics, we tracked >5000 colonies before, during, and after bleaching to quantify coral growth, bleaching response and mortality. We assessed how bleaching severity influenced vital rates of common coral taxa, accounting for taxonomic identity, colony size, water clarity, temperature and velocity. Initial colony size, heat stress and bleaching severity significantly influenced survival and growth in the year following bleaching. Importantly, even the survival and growth of colonies that did not bleach declined during the year with heat stress compared with the year prior. These results suggest that the ecological consequences of mild bleaching events may be substantially underestimated when assessments focus only on visibly bleached colonies. We also demonstrate that partially and fully bleached colonies differ significantly in demographic responses, emphasising the importance of accounting for bleaching severity in ecological assessments and forecasting efforts.

Keywords: photogrammetry, large-area-images, climate change, demography, coral bleaching,

sublethal impacts

Statements and Declarations

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Funding Declaration

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Declaration of competing interest

The authors declare no conflict of interest.

Authors contribution

Marine Lechene: conceptualisation, data curation, formal analysis, methodology, visualisation, writing – original draft, writing – review and editing. **Deborah Burn:** methodology, writing – original draft, writing – review and editing. **Mariana Álvarez-Noriega:** conceptualisation, data curation, formal analysis, methodology, writing – review and editing. **Madison Becker:** data curation, methodology, writing – review and editing. **Maren Toor:** data curation, methodology, writing – review and editing. **Sophie Gordon:** data curation, methodology, writing – review and editing. **Eoghan Aston:** formal analysis, methodology, writing – review and editing. **Mia Hoogenboom:** methodology, writing – review and editing. **Renata Ferrari:** funding acquisition, methodology, project administration, resources supervision, writing – review and editing.

Data availability statement

Datasets and R code are available at https://github.com/maalechene/Bleaching-legacy-effects.git

Introduction

Rising sea surface temperatures pose a major threat to coral populations, leading to widespread coral bleaching events (Eakin et al., 2026; Hoegh-Guldberg, 1999). Since 1998, the Great Barrier Reef (GBR) has suffered six mass coral bleaching events (2002, 2006, 2016, 2017, 2020, 2022) leaving limited time for recovery of coral cover between disturbances (Emslie et al., 2024). As stress events accumulate, the trajectory of ecosystem recovery is influenced not only by present-day environmental conditions but also by the legacy of past disturbances retained through surviving organisms (Franklin et al., 2000; Johnstone et al., 2016; Monger et al., 2015; Seidl et al., 2014; Walker et al., 2024).

In coral reef ecosystems, this memory is evident in the legacy effects of repeated heat stress, which have contributed to long-term declines in coral cover (Gardner et al., 2003; De'ath et al., 2012), recruitment (Hughes et al., 2019), and habitat structural complexity (Madin et al., 2018), along with shifts in species composition and size structure (Carlot et al., 2020; Tebbett et al., 2025). At the colony level, legacy effects also include sublethal responses such as reduced growth, impaired fecundity and partial mortality (Cantin & Lough, 2014; Johnston et al., 2020; Marshall & Baird, 2000; Ward et al., 2002). These biological legacies constrain demographic performance and can limit a colony's contribution to population recovery and future stress resistance.

Despite broad recognition of the ecological consequences of mass bleaching, there remains a critical gap in our understanding of how mild (i.e., with sublethal effects) bleaching events influence individual-level demographic responses – specifically, coral growth and survival – across taxa and environmental gradients. Most studies have focused on severe bleaching events and mortality outcomes (Guest et al., 2016; Loya et al., 2001; M. S. Pratchett et al., 2021), with limited attention to sublethal impacts that can accumulate over time and affect population

trajectories (Leinbach et al., 2021; Levitan et al., 2014). Moreover, demographic responses to heat-stress are known to vary with colony size, species identity, and local environmental conditions (Álvarez-Noriega et al., 2025), yet few studies have tracked thousands of coral colonies through bleaching events *in situ,* across environmental gradients (Dunn et al., 2025; Johnston et al., 2020; Morais et al., 2021; Stratford et al., 2025).

Bleaching responses – and how they vary across life-history stages – are not consistent but instead depend on the interaction between taxonomic or morphological identity and environmental conditions over time (Álvarez-Noriega et al., 2025). For instance, branching species are often more susceptible than massive forms (Loya et al., 2001; Marshall & Baird, 2000; Swain et al., 2016; van Woesik et al., 2011), yet this pattern can shift depending on local factors such as depth (Baird et al., 2018; Grimsditch et al., 2010; Smith et al., 2014; but see Diaz et al., 2023), turbidity (Sully & van Woesik, 2020) or water flow (Fabricius, 2006; Finelli et al., 2006; Nakamura & van Woesik, 2001), through effects of such factors on light and heat. Similarly, size-dependent responses within species are mixed. Juveniles (<5 cm in diameter) may be more resistant than adults in some cases (Mumby, 1999; Shenkar et al., 2005), though this pattern is not universal , and other studies report greater susceptibility in smaller colonies (Pratchett et al., 2013) or no clear size effect at all (Wagner et al., 2010). Among adult colonies, bleaching susceptibility has been found to increase with size in some cases (Brandt, 2009; Shenkar et al., 2005; Winslow et al., 2024), decrease in others (Álvarez-Noriega et al., 2025; Johnston et al., 2020), or show no clear relationship (Hoogenboom et al., 2017; Ortiz et al., 2009).

While much attention has focused on bleaching susceptibility and severity, what happens after bleaching - whether a colony fully recovers, partially recovers, or dies – is more important for understanding population trajectories. Recovery capacity is influenced by biological traits,

environmental conditions and legacy effects. As colonial organisms, corals exhibit size-dependent demographic rates (Hughes, 1984). Larger corals typically have higher survival probability and growth (Meesters et al., 1997) , both in times of acute and chronic disturbances (Álvarez-Noriega et al., 2025). Colonies with top-heavy morphologies are more prone to dislodgement in storms (Madin et al., 2014; Madin & Connolly, 2006), but are better able to survive partial tissue loss and continue contributing to population processes through growth (Lachs et al., 2025). However, net growth in large colonies often slows or ceases due to increasing partial mortality with size (Hughes & Jackson, 1980; Meesters et al., 1997; Dornelas et al., 2017). Bleaching can reduce growth (Cantin et al., 2010) and increase mortality either directly through physiological damage or indirectly via heightened predation (Glynn, 1985; Stimson et al., 2002) and susceptibility to disease (Miller et al., 2009). These effects can be especially pronounced in colonies already weakened by prior stress, reinforcing ecological memory through demographic feedback (Hoffmann & Hercus, 2000; Johnston et al., 2020; Ward et al., 2002). Despite its importance, the interaction between bleaching severity, colony size and environmental variation on coral demography remains understudied – particularly in the context of mild, sublethal bleaching events, which may still generate lasting, legacy effects, and are increasingly frequent under climate change. Moreover, most studies have only surveyed a subset of colony sizes, often missing colonies larger than 50 cm in diameter, or surveyed small sample sizes (less than 1000 colonies). During the last decade, novel technologies such as underwater photogrammetry, have created a unique opportunity to investigate the role of colony size in bleaching response (Ferrari et al., 2017; Kopecky et al., 2023).

We quantified growth and survival rates of > 5,000 coral colonies across five common coral morphotaxa using high-resolution large-area orthomosaics spanning three consecutive years (2021-2022-2023): one with no recorded major disturbance (2021-2022) and one including and following a mild mass bleaching event (2022-2023). Our objectives were to (1) compare

growth and survival probability of visually healthy colonies (i.e., not bleached) between years without and with heat-stress (0 vs. 5 DHW), and to (2) examine the effect of bleaching severity, colony size and key environmental variables on coral survival and growth at least eight months after bleaching.

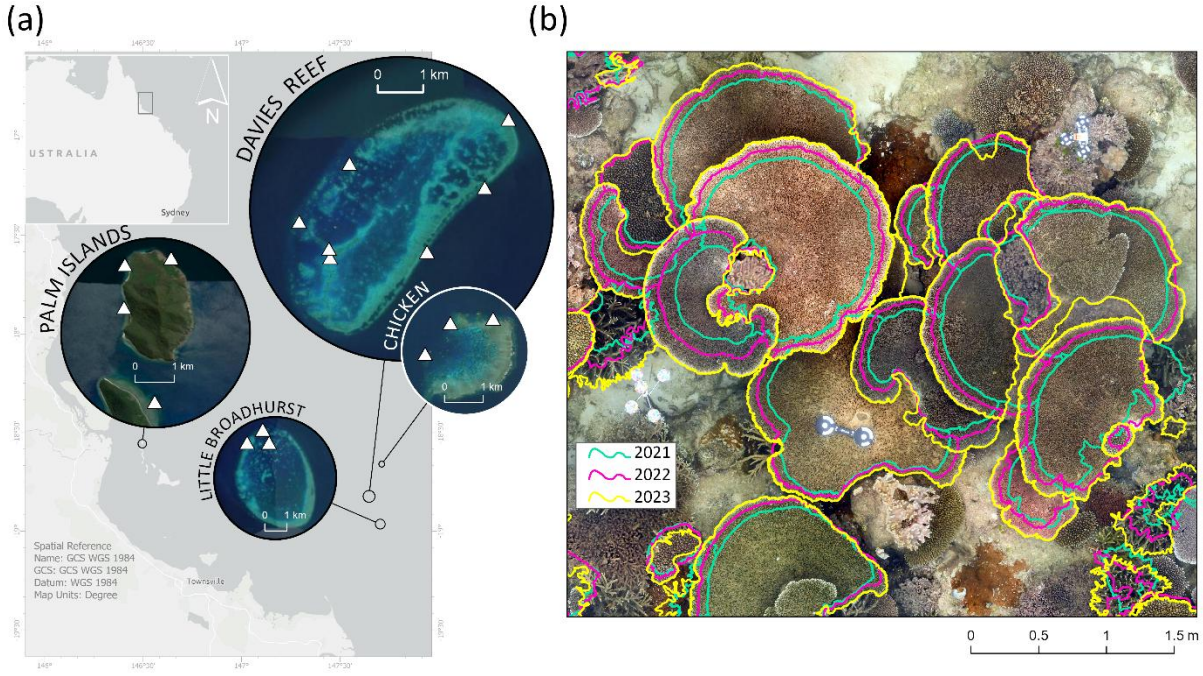
Materials and methods

In situ sampling

One inshore reef (Palm Islands) and three offshore reefs (Davies, Little Broadhurst and Chicken) were surveyed in the central GBR between January 2021 and 2023. The Palm Islands and Davies reefs were initially surveyed in January 2021, while Little Broadhurst and Chicken reefs were initially surveyed in May 2021. All subsequent surveys across all four reefs took place in January 2022 (no bleaching observed), April 2022 (at peak of bleaching) and in January 2023. Surveyed sites were distributed along the reef slope and around the perimeter of the reef across a wave exposure gradient at a depth range between 3-8 m ('shallow'). Additionally, sites were also established at a depth range between 9-15 m ('deep') at Palm Islands and Davies. Each site had four replicate plots ~12 x 6 m (72 m^2) spaced approximately 10 m apart and laid parallel to the depth gradient. A total of 26 sites and 98 plots were surveyed (Fig.1).

Photogrammetric surveys of the permanent plots were conducted on SCUBA. Two divers used a custom-designed camera rig consisting of two Nikon D850 DSLR cameras with 20 mm Nikkor lenses housed in Nauticam housings with 8" dome ports and mounted 57 cm apart (Gordon et al., 2023). The divers swam at 1 – 1.5 m altitude in a 'lawn mower' pattern consisting of five passes in each of the long and short-directions of the plot while taking photos every 0.5s (~ 3000 photos per plot). At each site, the cameras were white-balanced at the

97 targeted depth before taking photos. Each plot had 13 ground control points (five pairs and one
98 with bubble levels) to capture depth, scale and orientation of the 3D models (Gordon et al.,
99 2023). Each plot had also two permanent reference points used to align 3D models through
100 time (Lechene et al., 2024).



101

102 **Fig. 1** (a) Map of the four reefs with site locations marked by white triangles. (b) Detail of an
103 orthomosaic from 2023 with colony outlines from 2021 (teal), 2022 (pink) and 2023 (yellow)

104 **Image processing**

105 The photos were processed in Agisoft Metashape Professional v. 1.7.6 (Agisoft LLC, 2023) to
106 generate a 3D model and a 2D orthomosaic per plot. Orthomosaics had an approximate
107 resolution of 0.3 mm.pixel^{-1} and were used to estimate colony size (planar area) and assign
108 bleaching severity categories by a single observer (categories described below). To accurately
109 quantify changes in planar area, 3D models from different years (January 2021 and 2023) were
110 co-registered using the January 2022 survey as the reference (Fig. 1). This method achieved a
111 mean precision of 1.3 mm (s.d. 16.5 mm) in 3D space (Lechene et al., 2024) and ensured

consistent model orientation for generating orthomosaics, enabling precise size measurements by maintaining identical viewing angles for the same coral across years.

Colonies of five coral morphotaxa (staghorn *Acropora* spp., corymbose *Acropora* spp., *Pocillopora aff. damicornis*, *Pocillopora aff. verrucosa* and *Seriatopora hystrix*) were digitised on each orthomosaic (n = 98) using the high-accuracy '4-clicks' tracing AI-tool in TagLab (Pavoni et al., 2022). We followed the workflow described in Toor et al. (2025) to extract colony size estimates and in Becker et al. (2026) to quantify bleaching severity. Colonies were digitised if they met these requirements: (i) taxonomically identified with at least 80% certainty (threshold based on inter- and intra-observer error, González-Rivero et al., 2020; Williams et al., 2019, for full description of colony identification see section 5.2 in Toor et al.), (ii) clearly reconstructed (i.e., not blurry or distorted), (iii) 75% of the colony was visible (not cryptic or hidden), colonies that were obscured were noted as such and (iv) entirely within the boundaries of the orthomosaic. Only live tissue was digitised and colonies with partial mortality were noted as such.

Instead of digitising colonies every year, colony segments from 2021 were transferred onto the 2022 orthomosaic, and 2022 onto 2023. After transferring, each segment was reviewed to refine edges to align with the colony shape and to note the fate of the colony, for example whether the colony was now unusable (poor quality imagery), dead, missing or with partial mortality. Colonies were noted as dead when 100% of the tissue was dead and the skeleton structure was still visible. Missing colonies were also noted as dead if they could not be found within a 2 m search radius from the original location.

A single observer used the April 2022 orthomosaics to assign a bleaching category to each colony. The bleaching categories were 1) no bleaching, 2) minor bleaching (with less than 50% of the colony bleached), 3) major bleaching (with 51-95% of the colony bleached), 4) fully

bleached (more than 95% of the colony bleached) and 5) fully bleached with signs of recent partial mortality (hereafter referred to as the recent partial mortality category) (Becker et al., 2026). These categories differed from common practice (i.e., three categories: fully bleached, partially bleached and recently dead) to better reflect differences in bleaching susceptibility, especially the "recent partial mortality" category, which includes fully bleached colonies with signs of partial mortality. This category allows us to capture taxonomic differences in injury incidence and bleaching susceptibility. Colonies were scored as having partial colony mortality whenever they presented mortality during the bleaching survey but did not show any signs of mortality during the January 2022 survey. Partially dead colonies were considered survivors when they still had living tissue. Colonies that could not be assigned a bleaching category confidently were removed. Colonies that were digitised in January 2022 but not found in April 2022 were excluded from the analyses, not classified as recently dead, as we did not want to include mortality that happened prior to the bleaching event. Colony segments and associated data were extracted from TagLab as shapefiles, with one shapefile per orthomosaic (i.e., one shapefile per plot and year). Shapefiles were standardised in ArcGIS Pro v.3.0 (ESRI, 2023) using custom scripts to calculate planar area of each colony in square meters, and to add metadata (e.g., plot ID and year). Colonies were matched across time using the Spatial Join tool between year pairs (2021 was joined with 2022, then this 2021-2022 join was joined with 2023). Colonies were matched based on largest overlap with a search radius of 15 cm if no overlapping colony was found. The final shapefile contained three columns for colony size (one per year) and one row per colony. Colony matches were checked and incorrect matches and duplicates were deleted (when one polygon overlapped multiple ones, see full QA/QC steps in Toor et al. (2025)).

Growth was estimated as the difference in planar area between sampling years via the traced outlines of colonies in the orthomosaics, thus growth can be positive (increase in planar area)

or negative (decrease in planar area). The shapefiles from April 2022 (at peak of bleaching) only contained bleaching scores as size was not estimated in April. We assumed all colonies experienced similar levels of heat stress as demonstrated by the very narrow range (4.1-5.2) of Degree Heating Weeks (DHWs) across all sites (Álvarez-Noriega et al., 2025).

Environmental variables

We examined the effect of three environmental variables – water velocity, water clarity and water temperature – on the relationship between survival and growth and bleaching severity. These environmental variables were chosen based on existing knowledge about their effects on light intensity, temperature, and spatial variation of bleaching severity (Penin et al., 2007; Wooldridge & Done, 2004). For instance, because high light levels and warm temperatures exacerbate bleaching, deeper habitats can provide a refuge from bleaching (e.g., Baird et al., 2018; Grimsditch et al., 2010; Smith et al., 2014). Light intensity also decreases with turbidity; thus, it is expected that moderately turbid reefs should experience less bleaching during thermal stress events (Sully & van Woesik, 2020). Strong water flow can mitigate thermal stress by transporting cooler water (Fabricius, 2006) and clearing away harmful photosynthetic byproducts (Finelli et al., 2006; Nakamura & van Woesik, 2001). Consequently, it is expected that bleaching severity decreases with increasing flow.

Horizontal water velocity near the seabed ($m.s^{-1}$), referred to as "water velocity" hereafter, was derived from maps of wave metrics generated using fetch-based and process-based models, which incorporated long-term wind data and fine-scale bathymetry (Callaghan, 2023; Callaghan et al., 2015, accessible at https://espace.library.uq.edu.au/view/UQ:8246441). Since water velocity data was available only as time series summaries, the mean was used to represent routine water velocity. These estimates were extracted at a 15 x 15 m horizontal resolution at the seabed, so each site and depth had a unique value. Water clarity and temperature were

extracted from *eReefs*, an information platform using data and models to estimate a series of environmental variables across the Great Barrier Reef (Steven et al., 2019). Daily estimates of Secchi depth (vertical integral of light attenuation at 488 nm) were extracted from the eReefs biogeochemical model (GBR4), which as a ~ 4km pixel resolution, using the R package *ereefs* (Robson, 2023). Similarly, daily estimates of water temperature were extracted from the eReefs hydrodynamic model (GBR1) at ~1km pixel resolution. The mean values for the extracted time period (1 January 2022 to 1 January 2023) were calculated for both Secchi depth and temperature, hereafter referred to as 'mean clarity' and 'mean temperature', respectively. We acknowledge the difference in spatial resolution at which these environmental variables were extracted. While this spatial mismatch introduces some uncertainty, particularly in fine-scale spatial interpretation (which we discuss later), our analyses focus on broader patterns in how environmental gradients mediate the effects of bleaching severity on coral growth and survival. To help reduce potential bias associated with resolution mismatches and spatial autocorrelation, we included a random intercept for site to account for the unmeasured site-level variation and the hierarchical structure of the data (see statistical models' description below).

Data analyses

Effect of heat stress on survival and growth of healthy colonies

To examine the effect of heat stress on survival and growth on healthy colonies (with no signs of bleaching) we fitted two generalised linear mixed-effect models (GLMMs), one survival model and one growth model. To account for variation in the number of days between surveys, we included survey interval duration as a fixed-effect covariate in both growth and survival models. During the 2021–2022 transition, colonies were surveyed either in January 2021 or May 2021, whereas all subsequent surveys were conducted in January. Survey intervals were therefore coded as either 365 or 240 days. This variable was centred on a 365-day reference

interval to produce the covariate Days_2022c, such that annual intervals had a value of 0 and shorter intervals had a negative value of -125 days.

The survival model had Survival as a binomial response and included the interaction between Taxa, Year and Days_2022c as fixed effects. A random intercept for Plot nested within Reef was included to account for the hierarchical sampling design. Site was initially included as a random effect, but as most variation was attributed to Plot and Reef, Site was excluded from the final model.

We modelled growth as the relationship between the log-transformed planar area at time t_1 and the log-transformed planar area at time t_0 (Dornelas et al., 2017; Ferrari et al., 2012; Madin et al., 2014). In a log-log scale the stasis line - defined by a slope of 1 and an intercept of 0 - represents no change in size. Colonies above this line have increased in size, while those below have decreased in size between time points. A slope less than 1 indicates slowing growth and when the growth curve intersects the stasis line, colonies begin to shrink on average. The point of intersection highlights how different predictors influence the average colony size at which growth is cancelled out by partial mortality (Madin et al., 2020) in a given environment, as well as how this threshold shifts with changes in environmental conditions. For instance, increased bleaching severity would be expected to flatten the slope, leading to an intersection point at a smaller colony size, indicating that the average size at which growth ceases decreases as bleaching severity intensifies.

The growth model had Size at t_1 (log-transformed) as a response and included the interaction between size at t_0 (log-transformed), Taxa and Year as fixed effects along with the covariate Days_2022c. A random intercept for Colony nested within Plot was included to account for the hierarchical sampling design and non-independence between colony size measurements.

Effect of bleaching severity, colony size and environmental variables on survival and growth

To estimate the effect of bleaching severity on survival, accounting for initial size, and to test the influence of the environment, we built GLMMs for each of the five taxa. We first defined a base model structure for each taxon based on prior exploratory model comparisons using Akaike's Information Criterion (AIC). Specifically, we tested whether including an interaction between initial size and bleaching severity (categorical variable) improved model performance over an additive structure. The selected base structure was retained in all subsequent models for that taxon. In addition, random intercepts were included to account for spatial structure, with Site used for all taxa except *S. hystrix* for which Plot nested within Site was found to better capture the nested sampling design. We then tested the influence of environmental variables on survival by comparing a set of candidate models. These models extended the base structure to include standardised estimates of mean temperature, water clarity and water velocity, both as additive effects and as interactions with bleaching severity. Specifically, we fitted a full model including all three interactions, a null model with no environmental variables and a suite of intermediate models with one or more environmental variables removed. In total, this resulted in a consistent set of models across taxa that allowed evaluation of the relative importance of environmental variables in modulating survival under varying bleaching severity and initial size. The best-fit survival model for each taxon is presented in table 1.

Table 1 Survival model formula of the best-fit model for each taxon. Models were ranked using AIC, preference was given to simpler models when $\Delta AIC < 2$

Taxa	Model formula
A. staghorn	Survival ~ initial size : bleaching severity + (1 | Site)
A. corymbose	Survival ~ initial size + bleaching severity + (1 | Site)
P. damicornis	Survival ~ initial size + bleaching severity + (1 | Site)
P. verrucosa	Survival ~ initial size + bleaching severity + (1 | Site)

S. hystrix	Survival ~ initial size : bleaching severity + temperature * bleaching severity + (1 | Site/Plot)

To examine the effect of bleaching severity and the environment (water clarity, temperature and water velocity) on growth, we fitted a suite of GLMMs for each taxon. All models included log-transformed size at t_0 and its interaction with bleaching severity, with colony size at time t_1 as the response variable. A full model included interactions between size at t_0 and all standardised environmental variables, as well as their interactions with bleaching severity. A null model included only size at t_0 * bleaching severity, and intermediate models systematically excluded one or more environmental predictors or interactions. All models included site as a random intercept. The best-fit growth model for each taxon is presented in table 2.

Table 2 Growth model formula of the best-fit model for each taxon. Models were ranked using AIC, with preference given to simpler models when $\Delta AIC < 2$

Taxa	Model formula
A. staghorn	size at t_1 ~ size at t_0 + size at t_0 : bleaching severity + size at t_0 : temperature + size at t_0 : temperature : bleaching severity + (1 | Site)
A. corymbose	size at t_1 ~ size at t_0 + size at t_0 : bleaching severity + size at t_0 : water clarity + size at t_0 : water velocity + size at t_0 : temperature + (1 | Site)
P. damicornis	size at t_1 ~ size at t_0 + size at t_0 : bleaching severity + (1 | Site)
P. verrucosa	size at t_1 ~ size at t_0 + size at t_0 : bleaching severity + size at t_0 : temperature + size at t_0 : temperature : bleaching severity + (1 | Site)
S. hystrix	size at t_1 ~ size at t_0 + size at t_0 : bleaching severity + size at t_0 : temperature + size at t_0 : temperature : bleaching severity + (1 | Site)

All statistical analyses were performed using R version 4.3.1 (R Core Team, 2023). For all analyses we fitted GLMMs in a frequentist framework using the *glmmTMB* package (Brooks et al., 2017). We plotted the models' predictions using the *ggeffects* (Lüdecke, 2018) and *ggplot2* (Wickham et al., 2016) packages. Environmental predictors were standardised (z-transformed) prior to model fitting to facilitate comparison of effect sizes and reduce

multicollinearity. Model diagnostics were conducted using the *DHARMa* package (Hartig, 2022). Simulated residuals were used to assess residual distribution, dispersion, and zero-inflation, and to identify potential deviations from model assumptions. Model comparisons were based on AIC. The model with the lowest AIC was selected as the best-fit model for each taxon (Table 1), if AIC were similar (i.e., less than two units difference), the most parsimonious model was chosen. Models that failed to converge were excluded. Collinearity among predictors was assessed using variance inflation factors (VIFs) via the *performance* package (Lüdecke et al., 2021). In general, collinearity was low to moderate, however, VIFs were inflated in models with higher-order interactions involving rare bleaching categories, particularly for *P. verrucosa* and *S. hystrix*. These models were retained for completeness but interpreted cautiously.

Results

Effect of heat stress on survival and growth of visually healthy colonies

Survival probability was consistently lower in the year with heat stress (2022-2023) compared to the year before (2021-2022) for all taxa except *P. verrucosa* but was only significantly lower for *S. hystrix* (99% pre-bleaching versus 77 % in the bleaching year) (Fig. 2). Survival probability was high for all taxa in the pre-bleaching period (> 92%) with *Acropora* staghorn showing no colony mortality in 2021-2022.

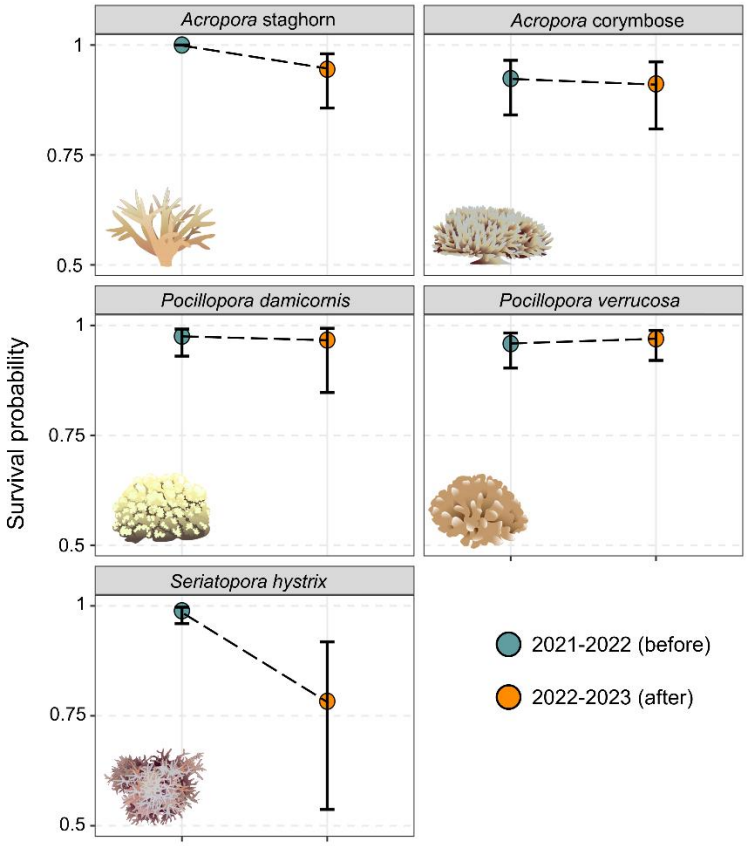


Fig. 2 Survival probability between years and taxa. Points represent the fitted model predictions, and the error bars represent the 95% confidence intervals

For all models of growth of healthy colonies, the slopes were positive but less than one, with positive intercepts (Fig. 3). This indicates that growth rate decreases with increasing size, eventually intersecting the stasis line at a certain size, where partial mortality is higher than growth. A consistent pattern was observed across most taxa, except for *A.* staghorn, where growth curves intercepted the stasis line at a smaller size during the bleaching year (2022-2023) compared to pre-bleaching (2021-2022) (Fig. 3), indicating a decrease in growth during bleaching. Slopes differed significantly between years for all taxa except *P. damicornis* (Table S1).

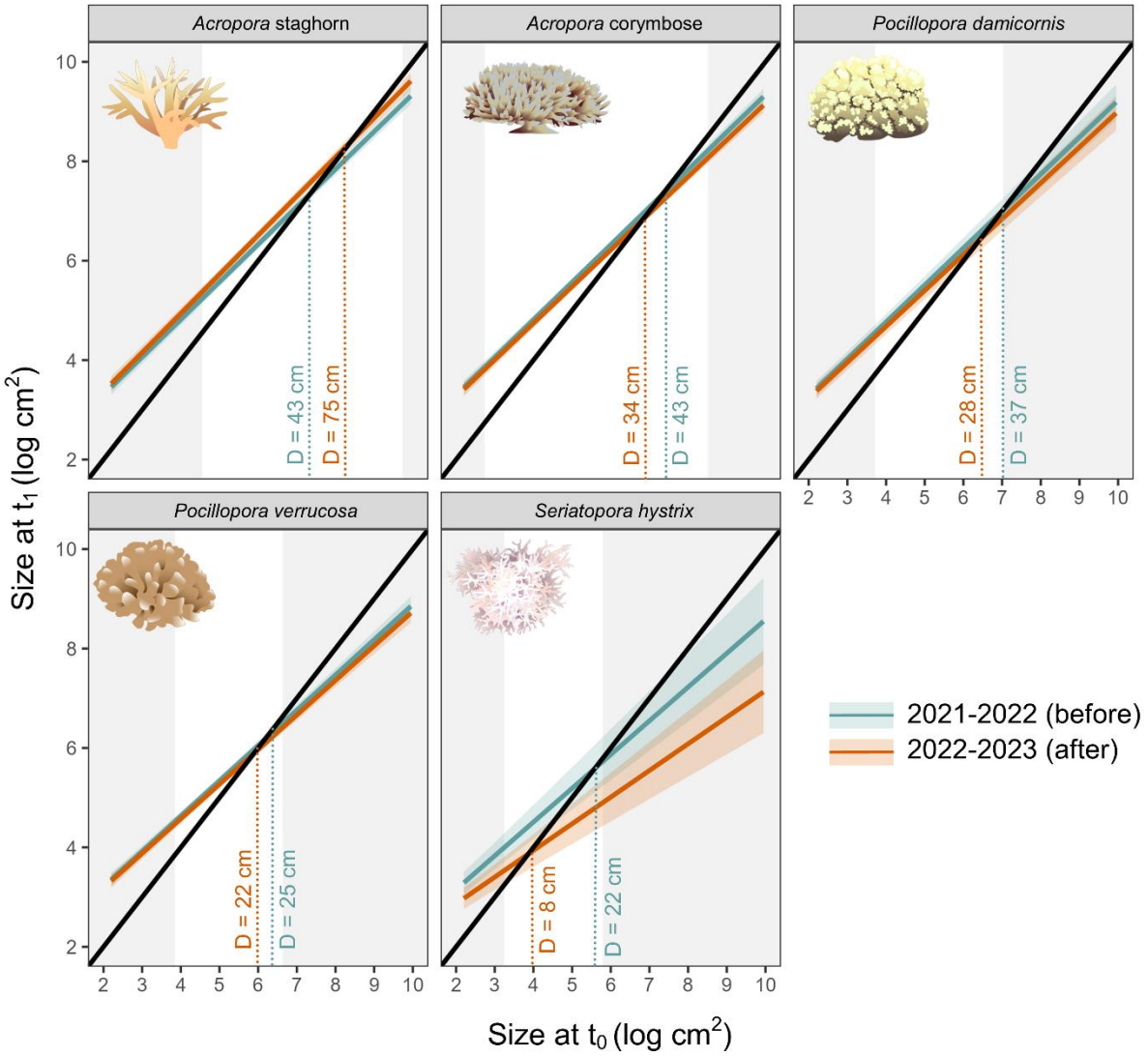


Fig. 3 Size at t_1 as a function of size at t_0, year and taxa. Ribbons represent the 95% confidence intervals. Diagonal black lines indicate the stasis line where size at t_1 = size at t_0. Grey-shaded regions represent areas where predictions are outside of the observed size range. The size at t_0 at which the curves cross the stasis line are indicated by the dotted vertical lines. An approximation of size in diameter (cm) is also given for ease of interpretation

Effect of bleaching severity, colony size and environmental variables on survival and growth of coral colonies during a mild mass bleaching event

General trends

Across all taxa, survival probability and growth significantly increased with colony size and decreased with bleaching severity (Table 3). Bleaching severity had a particularly negative

impact when colonies were fully bleached and/or with signs of recent partial mortality. The effect of environmental variables tested was taxon-dependent and predominantly influenced coral growth rather than survival during bleaching. The exception was *S. hystrix,* for which survival probability was also significantly influenced by mean temperature (Fig. 8b-c).

The environmental variables tested were rarely retained in the best-fit models of growth, with the exception of mean temperature (Table 3). Mean water clarity had no effect on growth following bleaching. Mean water velocity had a significant negative effect on growth for *A.* corymbose, but no effect for other taxa (Fig. 5d). The direction of the effect of mean temperature on growth changed depending on the bleaching category (Figs 4c, 8c).

Survival and growth did not differ significantly among colonies with no signs of bleaching, minor bleaching, or major bleaching. Significant decreases in survival were observed only for colonies bleached severely (fully bleached or fully bleached with signs of partial mortality).

Taxon-specific trends

Acropora staghorn

Survival probability increased with initial size and decreased with bleaching severity (Fig. 4a). Growth was negatively impacted by bleaching severity, particularly in the fully bleached and recent partial mortality categories (Fig. 4b). Mean temperature was positively related to growth

and interacted with bleaching severity to modulate its impact. The effect of temperature was only negative for the colonies that fully bleached with signs of partial mortality (Fig. 4c).

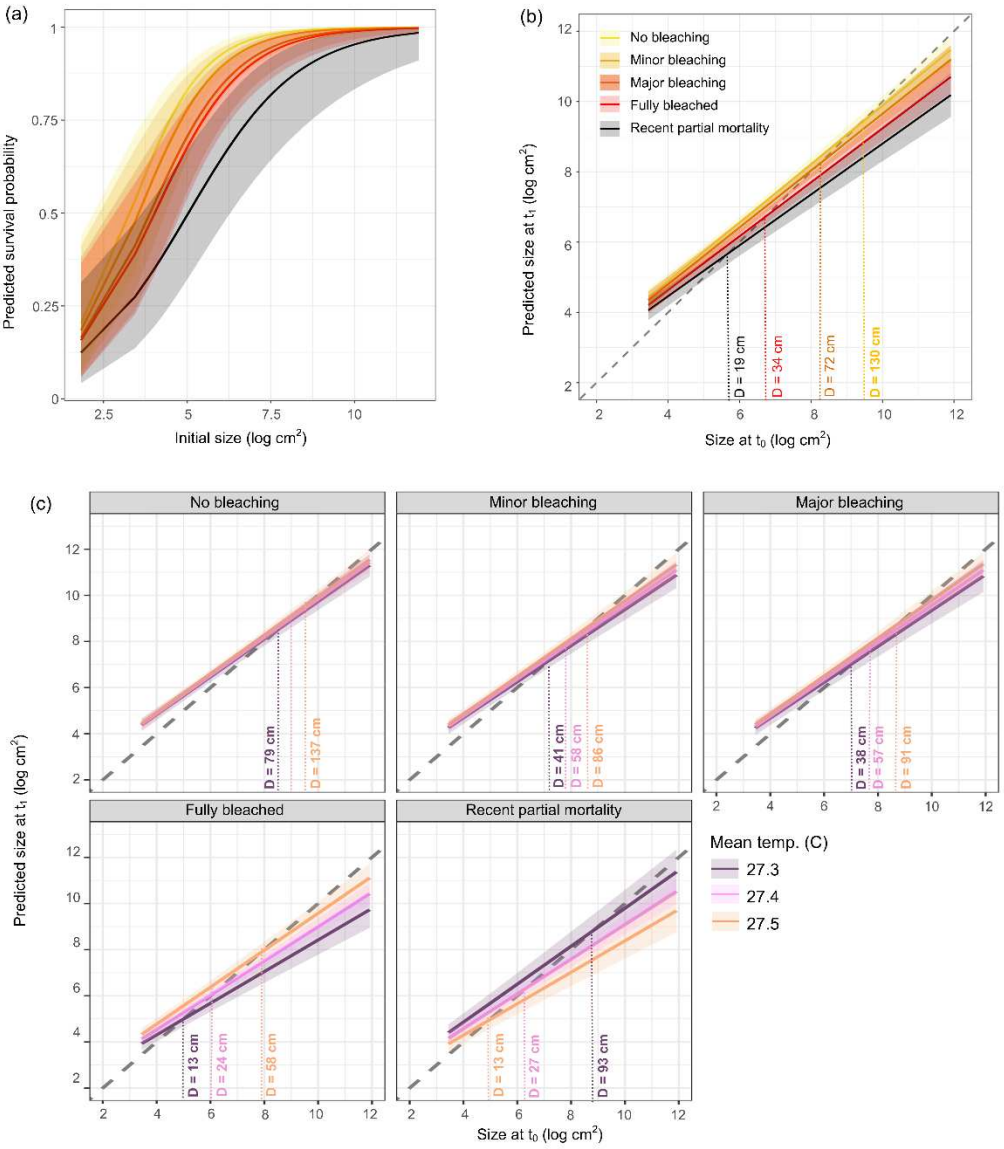


Fig. 4 Survival and growth model outputs for *A.* staghorn. (a) Predicted survival probability as a response of the interaction between initial size and bleaching severity, error bars represent 95% confidence intervals. Predicted size in 2023 as a function of size in 2022 and (b) bleaching severity and (c) mean temperature across levels of bleaching severity (facet labels). Shaded ribbons represent 95% confidence intervals. The dashed line represents the stasis line (slope = 1). Vertical dotted lines denote the approximate diameter where growth curves intersect the stasis line, indicating the size threshold beyond which colonies are expected to shrink under the given conditions

Acropora corymbose

Survival probability increased with initial size and decreased with bleaching severity, with significantly lower survival for colonies showing signs of recent partial mortality compared to non-bleached and partially bleached colonies (Fig. 5a-b). Growth was negatively related to bleaching severity, specifically in the major bleaching category, which was significantly different from the non-bleaching category (Fig. 5c). Additionally, water velocity had a significant negative effect on growth (Fig. 5d).

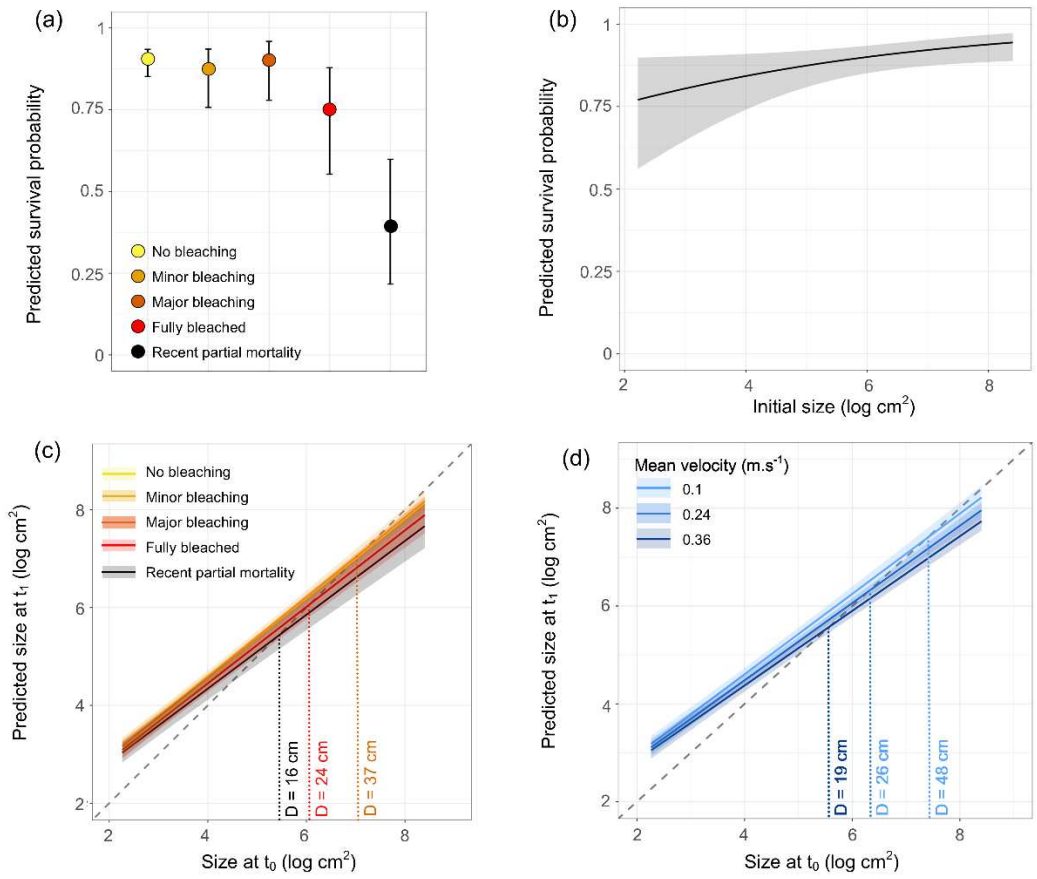


Fig. 5 Survival and growth model outputs for *A.* corymbose. (a) Predicted survival probability as a response of bleaching severity, error bars represent 95% confidence intervals. (b) Predicted survival probability as a response of initial size, shaded ribbon corresponds to 95% confidence intervals. Predicted size in 2023 as a function of size in 2022 and (c) bleaching severity, and (d) mean water velocity. Shaded ribbons correspond to 95% confidence intervals. The dashed line represents the stasis line (slope = 1). Vertical dotted lines denote the approximate diameter where growth curves cross the

stasis line, indicating the size threshold beyond which colonies are expected to shrink under the given conditions

Pocillopora damicornis

Survival probability increased with initial size and decreased with bleaching severity, with colonies showing signs of recent partial mortality exhibiting significantly lower survival probabilities than other categories (Fig. 6a, b). Growth was negatively related to bleaching severity, particularly for colonies in the recent partial mortality category compared to the 'no bleaching' category (Fig. 6c). Due to the limited sample size (n = 4, recent partial mortality), these results should be interpreted with caution.

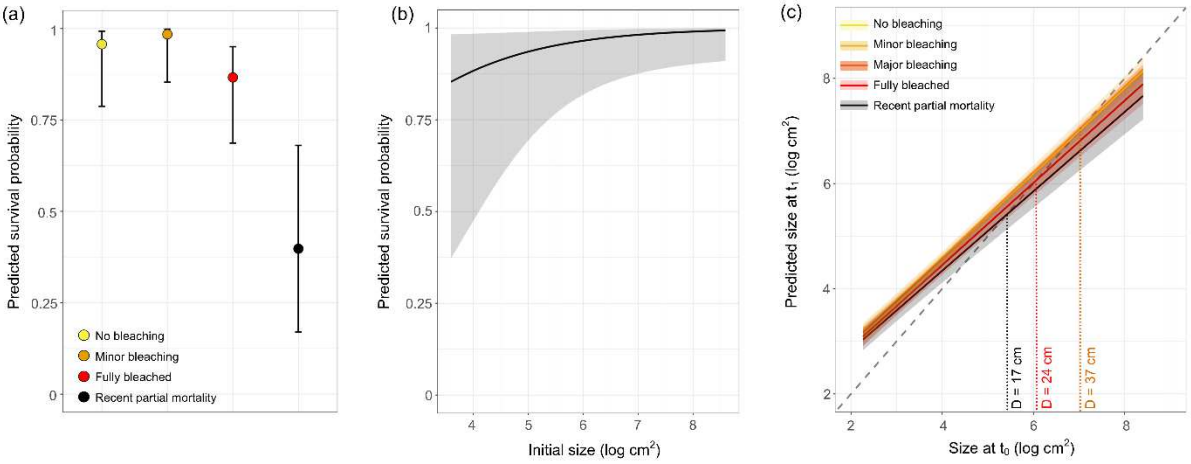


Fig. 6 Survival and growth model outputs for *P. damicornis*. (a) Predicted survival probability as a response of bleaching severity. Error bars represent 95% confidence intervals, note the absence of confidence intervals for the major bleaching category was caused by the fact that no colonies died in this category. (b) Predicted survival probability as a response of initial size, shaded ribbons represent 95% confidence intervals. (c) Predicted size at in 2023 as a function of size in 2022 and bleaching severity. Shaded ribbons correspond to 95% confidence intervals. The dashed line represents the stasis line (slope = 1). Vertical dotted lines represent the approximate diameter at which growth curves cross the stasis line, indicating the size threshold beyond which colonies are expected to shrink under the given conditions

Pocillopora verrucosa

Survival probability increased with initial size and decreased with bleaching severity, especially colonies with signs of recent partial mortality (Fig. 7a, b). Growth was negatively related to bleaching severity, but this was significant only for the recent partial mortality category which had a very low sample size (two colonies out of 207) (Fig. 7c). Although mean temperature was retained in the best-fit model, its effect was small and statistically inconsistent across bleaching categories (a significant negative effect was detected only for the recent partial mortality category), likely reflecting the narrow temperature range in the study (mean = 27.4 °C, sd = 0.09). As a result, we visualised the more interpretable relationship between colony size and bleaching severity, with predictions shown at mean temperature (Fig. 7c).

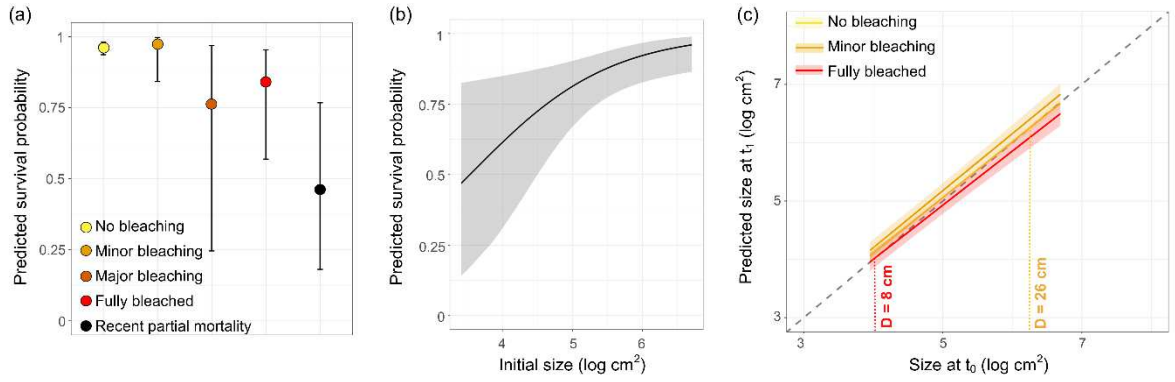


Fig. 7 Survival and growth model outputs for *P. verrucosa*. (a) Predicted survival probability as a response of bleaching severity, error bars correspond to 95% confidence intervals. (b) Predicted survival probability as a response of initial size, ribbon represents 95% confidence intervals. (c) Predicted size in 2023 as a function of size in 2022 and bleaching severity. Shaded ribbons correspond to 95% confidence intervals. The dashed line represents the stasis line (slope = 1). Vertical dotted lines represent the approximate diameter at which growth curves cross the stasis line, indicating the size threshold beyond which colonies are expected to shrink under the given conditions

Seriatopora hystrix

Survival probability increased with initial size and mean temperature and decreased with bleaching severity (Fig. 8a, b). While bleaching severity did not independently modify the size at t_1 – size at t_0 relationship, colony growth was more sensitive to small temperature differences among fully bleached colonies, with higher temperatures associated with steeper growth declines (Fig. 8c).

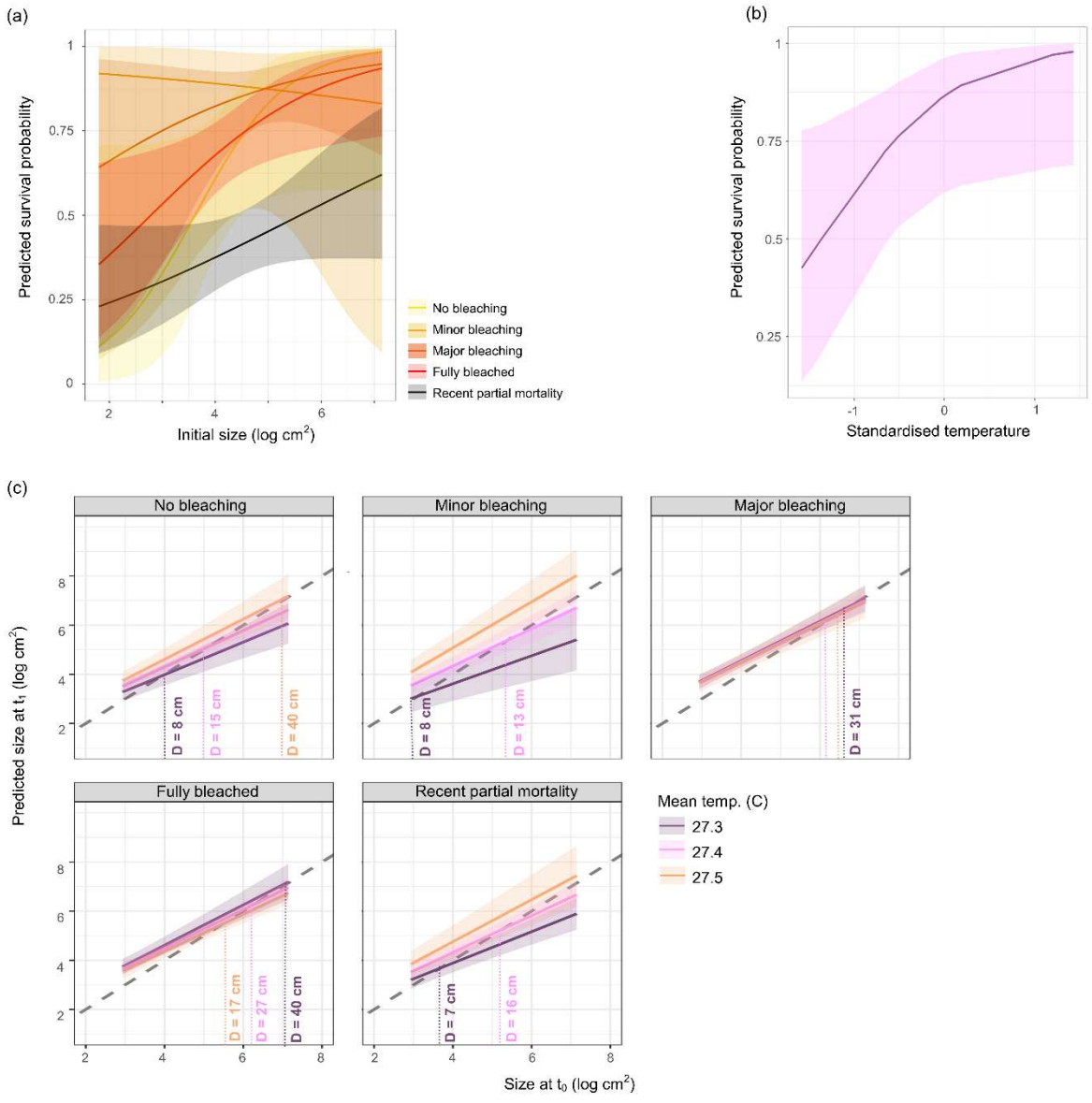


Fig. 8 Survival and growth model outputs for *S. hystrix*. (a) Predicted survival probability as a response of bleaching severity and initial size. (b) Predicted survival probability as a response of mean annual temperature (standardised). (c) Predicted size in 2023 as a function of size in 2022 and mean water temperature across levels of bleaching severity (facet labels). Shaded ribbons represent 95% confidence

intervals. The dashed line represents the stasis line (slope = 1). Vertical dotted lines denote the approximate diameter where growth curves intersect the stasis line, indicating the size threshold beyond which colonies are expected to shrink under the given conditions

Table 3 Summary table of the significant effects (and directionality) of tested predictors on survival probability and growth of five morphotaxa. Predictors with significant but varied effects are shown as "+-"

		***Acropora* staghorn**	***Acropora* corymbose**	***Pocillopora damicornis***	***Pocillopora verrucosa***	***Seriatopora hystrix***
Survival	Initial size	+	+	+	+	+
	Bleaching severity	-	-	-	-	-
	Velocity					
	Clarity					
	Temperature	-				+
Growth	Bleaching severity	-	-	-	-	
	Velocity		-			
	Clarity					
	Temperature	+-			+-	+-

Discussion

This study showed that bleaching severity was strongly associated with both lethal and sublethal demographic impacts. However, demographic declines were not restricted to visibly bleached colonies, even colonies classified as visually healthy experienced declines in survival and growth following heat stress. These findings indicate that the consequences of thermal stress extend beyond colonies exhibiting obvious phenotypic bleaching responses and suggest that assessments based solely on changes in coral cover or bleaching related mortality may underestimate the ecological impacts of heat stress, particularly during mild bleaching events that do not result in substantial coral loss (Page et al., 2023).

Hidden impacts of heat stress

Even when no signs of visible bleaching were recorded, colonies from most taxa experienced declines in survival and growth during the year with heat stress (2022-2023) relative to the previous year (2021-2022) and survival probability declined significantly for *Seriatopora*

hystrix, reflecting the high sensitivity of this taxon to heat stress (Hoegh-Guldberg & Smith, 1989; Moriarty et al., 2023). These patterns suggest that heat stress can impair colony performance without producing obvious visual symptoms, potentially through physiological damage or shifts in energy allocation towards maintenance and recovery rather than growth or reproduction, ultimately delaying population recovery and increasing susceptibility to future stress (Johnston et al., 2020; Leinbach et al., 2021; Ward et al., 2002). Bleaching incidence and severity are commonly quantified at the peak of heat stress to assess disturbance impacts (e.g., Hughes et al., 2017, 2018), yet our findings suggest that bleaching status alone may not reliably predict colony fate. Colonies that appear visually healthy may nevertheless experience demographic costs that become apparent only after the heat stress event has passed (Johnston et al., 2020). Consequently, surveys conducted solely during peak heat stress may underestimate the full demographic consequences of heat stress events, especially as these events lengthen (A. Baird & Marshall, 2002; Claar & Baum, 2019).

Effects of bleaching severity on growth and implications for recovery

Coral colonies that did show signs of bleaching experienced decreasing growth with increasing bleaching severity across all taxa examined. Colony-level bleaching severity influenced the average size at which colonies ceased growing (i.e., began to shrink), with more severely bleached colonies reaching lower maximum sizes than less severely affected colonies. Notably, even in fast-growing taxa such as *Acropora* staghorn, partial mortality following bleaching was sufficiently extensive to result in net colony shrinkage despite approximately nine months of subsequent regrowth. Together these results indicate that bleaching can alter not only colony survival but also the size structure of survivors (Dietzel et al., 2020; Lachs et al., 2021).

Changes in growth rates and colony size have important implications for population recovery because coral demographic performance is strongly size dependent (Babcock, 1991; Hughes

& Connell, 1987; Hughes & Jackson, 1980). Reduced growth and colony shrinkage slows the progression of colonies into larger size classes. Because large colonies contribute disproportionately to reproductive output of the population (Hall & Hughes, 1996), population fecundity is decreased and recovery prolonged (Gilmour et al., 2013; Johnston et al., 2020). Reduction in the abundance of medium and large colonies could also affect reef carbonate budgets, resulting in net deficit in carbonate production and calcification, reducing reef accretion over time (Lange & Perry, 2019; Pisapia et al., 2020). Coral growth, especially fast-growing branching colonies, can also be tied to habitat complexity and thus decrease in growth may result in decrease in complexity (but see Ferrari et al., 2016) with cascading effects on reef associated organisms (Pratchett et al., 2004; Graham et al., 2007). Consequently, bleaching events that cause relatively little immediate mortality may nevertheless generate substantial demographic and ecological consequences through persistent reductions in colony growth.

Effects of bleaching severity on survival and importance of bleaching severity levels

Survival probability also declined with increasing bleaching severity, with fully bleached colonies and colonies exhibiting signs of recent partial mortality experiencing the lowest survival probabilities. These results reinforce the value of distinguishing among levels of bleaching severity rather than treating bleaching as a simple presence-absence response. Intermediate bleaching categories captured substantial variation in mortality risk and therefore provide a more informative proxy for colony fate than binary classifications alone (Khen et al., 2023; Rivera-Sosa et al., 2025). More broadly, our results support previous work demonstrating that visual assessments of bleaching severity can predict subsequent colony mortality (Baird et al., 2002).

Colony size further modified the relationships between survival and bleaching severity. Survival generally increased with colony size across all bleaching severity levels, consistent

with previous studies demonstrating higher survival of larger colonies in years with no or low heat stress (Madin et al., 2014; Speare et al., 2022). However, severely bleached colonies often had to be larger than less severely bleached colonies to achieve comparable survival probabilities, suggesting that bleaching severity alters the demographic advantages normally associated with larger colony size. These findings highlight the interactions between bleaching severity and colony size in shaping post-disturbance trajectories.

Environmental variables

In contrast to bleaching severity and colony size, the environmental variables tested here – water velocity, water clarity and temperature - were only weakly associated with growth and survival across bleaching categories and taxa. This suggests that post-bleaching demographic outcomes may be more strongly influenced by colony-level responses to thermal stress than by broad-scale environmental variation – at least within the environmental range encompassed by this study. However, caution is warranted when interpreting these results. Environmental conditions were represented using modelled annual estimates rather than high-resolution in situ measurements and may therefore not reflect the fine-scale conditions experienced by coral colonies during periods of peak thermal stress, particularly during short-term extremes. In addition, the narrow temperature range among sites (mean = 27.4C, sd = 0.09) may have limited our ability to detect temperature-related effects. Future work incorporating broader environmental gradients and temporally explicit environmental measurements may provide greater insight into how local conditions influence post-bleaching demographic performance. Another possible limitation is error in the visual classification of bleaching severity. While care was taken to apply consistent criteria when scoring colonies, some level of subjectivity is inherent in such assessments, especially when distinguishing among intermediate bleaching categories (Burn et al., In Press; Khen et al., 2023; Rivera-Sosa et al., 2025). Nonetheless, the

strong and consistent influence of colony size and bleaching severity across models suggests that these factors are robust predictors of colony fate in the immediate aftermath of bleaching.

Methodological strengths and future work

By using photogrammetry, we were able to capture a consistent snapshot of the thermal stress event across multiple reefs and track the fate of individual coral colonies through time. By recording the state and size of colonies several months before the bleaching event, we were able to confidently attribute signs of mortality to the thermal stress event. This approach is particularly valuable for fast-growing branching taxa, which typically have fast regenerative abilities (Pratchett et al., 2015), making recent partial mortality difficult to quantify accurately (Burn et al., 2022). Our method allowed us to quantify actual bleaching response rather than observed capacity of regeneration. Although manual tracing of corals remains time intensive, advances in automated segmentation and imaged-based bleaching classification offer opportunities to increase efficiency and reduce observer bias in future studies (Kopecky et al., 2023). Continued monitoring of these colonies will also be important for determining whether growth and survival return to pre-bleaching trajectories and whether recovery dynamics differ among bleaching severity levels.

Our results demonstrate that bleaching severity is a strong predictor of post-disturbance demographic performance, but they also reveal that demographic consequences of thermal stress extend beyond colonies that visibly bleach. Even relatively mild heat stress events can reduce growth and survival, alter colony size structure and potentially slow population recovery despite causing limited immediate mortality. As marine heatwaves become increasingly frequent and lasting, understanding these often-overlooked demographic costs will be critical for predicting coral population trajectories and the persistence of reef ecosystems in a warming world.

529

Supporting information

Supplementary Table S1. Pairwise comparisons of log size at t1 – log size at t0 slopes between years for each taxon, significant p-values are in bold.

Taxa	Estimate	p-value
Acropora staghorn	-0.16909	**0.00021**
Acropora corymbose	0.12593	**0.00001**
Pocillopora damicornis	0.15304	0.19614
Pocillopora verrucosa	0.10454	**0.01148**
Seriatopora hystrix	0.89431	**0.00260**

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