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Dominique McCowan *

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Resolving Bootstrap Paradoxes in Coral Bleaching Dynamics Through Nonlinear System States and Recursive Frameworks

Dominique McCowan

Indiana University Southeast; dmccowan@iu.edu or dmmccowa@gmail.com

Abstract

Ecological vulnerability of coral reefs contrasts sharply with their persistence through geologic time, creating a paradox from mis-scaled assumptions of time, mortality and organismal dimensionality, namely bleaching susceptibility, mortality, and recovery are treated as linear or sequential outcomes. Recursive definitions built on such mis-scaled assumptions generate straw-man inferences by conflating vulnerability with fragility and obscuring cryptic recovery dynamics. Using *post hoc* meta-analyses integrating datasets on coral bleaching, life history, reproductive strategy, morphology, and taxonomy, I evaluate system behavior across matrixed categories of thermal exposure and observation timing. Susceptibility emerges as a graded physiological response with weak coupling between predictor importance and variance, whereas mortality exhibits thresholded dynamics consistent with collapse behavior. Partial overlap in predictor structure indicates that bleaching does not represent a direct trajectory toward death, but rather a regulated buffering phase preceding potential tissue-level failure. Skeletal architecture consistently appears as a strong predictor across susceptibility and mortality, while taxonomic identity shows weak and variable effects. Recovery dynamics further indicate host–symbiont restructuring consistent with recursive evolutionary filtering rather than deterministic trait replacement. Together, these findings reframe coral bleaching as a regulated physiological state decoupled from mortality and demonstrate how recursive logic frameworks resolve paradoxes of timing, scale, and resilience in coral bleaching dynamics.

Keywords: coral bleaching; susceptibility; mortality; recovery; cryptic evolution; organismal dimensionality; intermediate disturbance; ecogeological timeframes; non-linear systems science

1. Introduction

Reefs are among the earliest fossils in the geological record and have nearly continuously persisted through deep time, with shifts occurring primarily in the identity of the dominant ecosystem engineer [1–5]. Stromatolites, the oldest form of reefs (>3.5 billion years), host chemosynthetic symbionts at depth near hydrothermal vents and photosynthetic symbionts in the shallow continental shelves [1–3]. The proliferation of stromatolitic reefs in shallow water produced oxygen as a metabolic byproduct of photosynthesis, gradually transforming Earth's early reducing environment into an oxidized state in which life has since flourished [1,4].

Photosymbiosis enables reef-building organisms to accrete biomass through both growth and mortality, forming a structural matrix that ultimately biomineralizes into limestone through time [1,4]. However, the conditions required for mineralization and reef accretion are largely restricted to shallow, oligotrophic tropical environments [4–7]. This constraint renders the identity of the dominant reef-building ecosystem engineer variable through geological time [1] and leaves the niche itself highly vulnerable to perturbations from global environmental change, disturbance, and competition [8–13].

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Rugosa and Tabulata corals originated during the Ordovician (480–440 million years ago) and were present within shallow-water reef systems that were largely structured by calcifying stromatoporid sponges, which functioned as the dominant ecosystem engineers during this interval [6]. These reef systems persisted until the Permian–Triassic mass extinction approximately 242 million years ago [1,3,14]. The extinction of Rugosa and Tabulata in shallow environments, together with the collapse of sponge-dominated reef frameworks, created an ecological vacancy within the reef-building niche [1]. As environmental conditions stabilized, Scleractinian corals ascended as the dominant reef builders [15], consistent with a Lazarus-type recovery dynamic [Lazarus Effect; 3].

During the Triassic (~200 Ma), approximately half of extant Scleractinian corals evolved symbiotic relationships with photosynthetic dinoflagellates of the genus Symbiodinium [7,16]. Through this symbiosis, zooxanthellae allocate a substantial proportion of photosynthetically derived energy to their host coral [6], while the hosts provide protection and inorganic nutrients [1; but see 17]. This energetic reorganization allowed both partners to redirect energy previously invested in independent survival strategies (e.g., armored free-roaming dinoflagellates), facilitating the expansion of reef accretion in shallow, oligotrophic environments. Consequently, the Scleractinian–Symbiodinium symbiosis has been implicated in the mass radiation of corals as dominant ecosystem engineers and is widely considered energetically fundamental to the formation of coral reefs and their associated biodiversity [1,7].

As reef accretion became established through this symbiotic framework, fossilization of Scleractinian corals increased [1]. However, gaps in the fossil record and molecular records indicate that Scleractinians persisted cryptically at depth [15], leading to their classification as Lazarus taxa and to the concept of “naked corals” lacking skeletal accretion during unfavorable conditions [3]. This interpretation is supported by experimental and field observations demonstrating the persistence of coral tissues independent of their skeletons. In particular, [18] showed that decalcified coral tissues survived, were returned to natural conditions, and re-precipitated calcium carbonate from seawater to reconstruct their skeletons, providing direct evidence for tissue-level resilience and skeletal regeneration. Rugosa and Tabulata corals originated during the Ordovician (480–440 million years ago) and were present within shallow-water reef systems that were largely structured by calcifying stromatoporid sponges, which functioned as the dominant ecosystem engineers during this interval [13]. These reef systems persisted until the Permian–Triassic mass extinction approximately 242 million years ago [1,3]. The extinction of Rugosa and Tabulata in shallow environments, together with the collapse of sponge-dominated reef frameworks, created an ecological vacancy [1]. As environmental conditions stabilized, scleractinian corals ascended as the dominant reef builders, consistent with a Lazarus-type recovery dynamic [Lazarus Effect; 3].

The geologic, ecologic and functional resilience shown through the animal tissues is in stark contrast to our ecological perception of the coral-algal symbiosis and related disturbance vulnerability, often defined by the dissociation of corals and zooxanthellae, termed bleaching. Bleaching has gone from rare, localized occurrences to repeated global events (termed mass bleaching events) due to global thermal anomalies [10,11]. Over large spatial scales, thermal data and aerial observations provide resolution of the effects of mass bleaching [19–21]. It has been somewhat apparent that biological mechanisms hold underlying variability in bleaching responses [22], whereby the proportion of colonies that are affected and those that experience mortality vary among species, genera and families [22,23]. Furthermore, there has been further considerable evidence that different corals have intrinsic characteristics that influence bleaching susceptibility [11], including the predominant clade of zooxanthellae supported within each coral [24], growth form/morphology, tissue thickness [23], size [25], fluorescent pigments [26,27], mycosporine-like amino acids and reef morphology [28].

Bleaching is the general dissociation of the symbiosis and was coined due to the white skeleton becoming visible though the translucent tissues of the coral animal due to a decline in the density of zooxanthellae and/ or declines in the concentration of photosynthetic pigments within the zooxanthellae [9,10,29]. Therefore, bleaching is often reported based on the conspicuous “paling” of

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individual coral colonies, species, or assemblages [30], utilizing coral colour charts [31] as a rapid and assumed reliable method to diagnose the status of individual colonies [32]. However, visual techniques poorly resolve the extent of algae loss (since algae can also lose their pigment while remaining in the host) and therefore underscore the potential for recovery or exploration of phenotypic or genotypic variation [33]. Quantification of changes in zooxanthellae densities and/or pigment concentrations through time provides a reliable metric for determining if bleaching has occurred [29], however, the methods require protracted laboratory processing and sampling may become impractical for lengthy experiments. One alternative measure of bleaching incidence is non-invasive Pulse-Amplitude Modulated (PAM) fluorometry [34–36], which measures the photosynthetic capacity of the endosymbiont population in real time [34–39].

Current measurement techniques—visual assessment, pigment and algal density analysis, and PAM fluorometry—suffer from further limitations in that visual techniques are subjective, laboratory analyses are protracted, and experimental studies often rely on arbitrary algebraic means determined after a set timeframe, failing to capture the full range of variation in responses. This subjectivity has undermined our capacity to determine the precise functions and true extent of the bleaching response. In experimental studies, bleaching has been established as an average of different physiological parameters (e.g. zooxanthellae density, pigment concentration and/or fluorometry values) at different physiological levels (e.g. branches, fragments, colonies) and stopping time when the colonies were in variable phases of health and comparing the algebraic means of control and experimental corals [40,41]. These studies almost invariably show that there are some corals that do not bleach, reflective of marked intra-specific variation in bleaching susceptibility, but these studies do not effectively capture the full range of variation in bleaching susceptibility due to the subjective nature of the current definition of coral bleaching. However, I tried a different approach in one of my PhD experiments (herein referred to as the Orpheus Island Simulated Experimental Observation, OISEO, [42]), where I simulated the timing and thermal stress accumulation of a mass bleaching event (Orpheus Island, Great Barrier Reef;) and observed and measured the variability in the timings of the bleaching response, inclusive of recovery for two commonly susceptible species with contrasting life history and reproductive traits, *Acropora nasuta* and *Pocillopora damicornis*.

Bradbury [42], measured colony dysfunction through time with PAM Fluorometry, coral colour cards, and *post hoc* zooxanthellae densities to confirm. I redefined bleaching as a rapid colony-wide dysfunction noted by severe photoinhibition at the level of the colony (e.g. 3-day decrease in photosynthetic yield), chronic photoinhibition leading to rapid expulsion of zooxanthellae [42]. The results of year 1 (5 total years of observations) of the OISEO [42] revealed distinct cohorts of bleaching responses in time and demonstrated cryptic survival mechanisms, such as tissue sloughing followed by recovery patches (The Phoenix Effect, [43]) linking survival directly to the cryptic evolutionary trait of porous or complex skeletal architecture; moreover, recovery from the first year was limited to partial mortality under monitored conditions. Lastly, bleaching cohorts in time were associated with cryptic evolutionary methods, such as hybridization, ecomorphs and species complexes [42]; these observations suggest that survival pathways are encoded in co-evolved life history and reproductive traits—mechanisms that embody non-Mendelian inheritance and challenge our anthropomorphized notions of organismal dimensionality and death.

The intensity of research on coral bleaching (see database literature reviews within [19,32,42,44,45]) stresses the critical need to understand the basic nature of the dissociation oi the symbiosis, and the rules of bleaching responses inclusive of susceptibility, mortality, resistance and resilience, as these will provide an indication of what coral populations, hence coral reef ecosystems, will be like in the future. However, this effort has suffered from insufficient recognition of the paleoecology and evolutionary biology of these organisms. Life history traits have not been as frequently used to determine coral bleaching susceptibility, but see [46–48] in comparison to say, taxonomy [44,45], although life history characteristics have shown to accurately determine the susceptibility of plants and other animals to climate change, as they represent co-evolved traits from mass extinctions [50]. The aim then blossomed into defining the bleaching response and testing

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whether these life history and reproductive traits would better suit discussion of the disturbances as a form of sentinel trophic/disturbance guild. For this report, I intend to thoroughly analyze and merge qualitative observations (*a posteriori*) with and transform them into quantitative measurements (*a priori*) so that we include our bias, present it transparently, and ponder alternative perceptions of the notions that we may have gotten wrong. I propose that a simple change in our pillar assumptions about the relativity of time, physical dimensionality of organisms, and death—is the unifying field theorem needed to move forward. By quantifying our existing data from this freshly scaled perspective, we can employ the relativity of time, aging, and adaptability for conservation.

Reef managers have historically been cautious in their interpretation of disturbance data, shaped in part by earlier experiences with the so-called Cassandra Syndrome [51], most notably during predictions of widespread reef collapse associated with outbreaks of the crown-of-thorns seastar (Acanthaster spp.). Although many reefs were severely impacted, large-scale extinction and irreversible loss did not occur, and subsequent recovery was observed across multiple systems. This history underscored the risks of projecting system-wide collapse from short-term disturbance data and contributed to increased skepticism among both managers and the public when predicted outcomes were not realized.

Importantly, subsequent research [52] demonstrated that crown-of-thorns outbreaks are strongly mediated by life-history traits and environmental context, particularly nutrient enrichment that enhances larval survival during critical windows. In response, management strategies shifted toward mitigating land-based nutrient inputs, exemplified by collaborative efforts between the Great Barrier Reef Marine Park Authority and adjacent agricultural stakeholders to reduce runoff into reef systems. More recently, the Cassandra Syndrome has been revisited in the context of climate change, emphasizing the need to sustain urgency while avoiding credibility erosion arising from projections grounded in insufficiently resolved assumptions [53]. Accordingly, the aim of this work is not to minimize the severity of ongoing climatic change, but to strengthen inference by refining how disturbance responses are measured, interpreted, and scaled across time.

In this document, the objective is not to diminish the severity of contemporary climate change, nor to downplay the ecological consequences of mass bleaching events, but to refine how disturbance responses are defined, measured, and interpreted across biologically relevant scales of time and organization. By integrating long-term observational data with quantitative analyses that resolve variation in susceptibility, mortality, and recovery, this work seeks to move beyond endpoint-based interpretations of bleaching as failure. Instead, bleaching responses are examined as dynamic trajectories shaped by co-evolved life history traits, tissue-level resilience, and skeletal architecture. By re-scaling existing datasets through this framework, it becomes possible to distinguish vulnerability from persistence and collapse from transformation. Such a shift in perspective is essential for producing defensible predictions of reef futures and for developing conservation strategies grounded not in fear or oversimplification, but in the full dimensionality of coral biology and evolutionary history.

2. Materials and Methods

2.1. Zooxanthellae Density Meta-Database

To account for apparent variation in published estimates of zooxanthellae densities from within samples of host tissues, I first explored differences in the methods used [54] and compared waterpiking the tissue off the coral skeletons with decalcifying the skeleton and measuring a known surface area. The waterpik method requires *post hoc* calibration of the area of tissue sampled by comparing the surface area of the skeleton to determine the surface area of the tissue slurry, (e.g. use aluminum foil to cover the skeleton after the tissue is piked off and compare that with a calibration curve of various surface areas and the weights of the foil). In contrast, the decalcification method utilizes coral's well-adaptedness and dissolves the skeleton in 100% hydrochloric acid while the tissues and the algae inside them are kept safe, and areas are measured to be tested directly. The

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decalcification method provides higher average densities, which is likely because the tissue within skeletons (of Complex clade corals) are included in this method.

Since methods to determine results were a known source of variation in average estimates of zooxanthellae densities [54], I added it to the composition of the Zooxanthellae Density Database [42] and when I assessed variability, I found the top 3 F factors were methods. The process of determining the density of algal symbionts in coral tissues involves three recorded steps:

i) Select a Sample Size (method SS): branch, colony, core, fragment, nubbin, and sample

ii) Method for Tissue Removal (method TR): studies either decalcified the skeleton (decalcification) or stripped tissue from the skeleton (airbrushing and waterpiking). Data were first examined without pooled categories.

iii) Method to determine the Surface Area (method SA); e.g. measured or inferred, were various: aluminum foil, calculated, vernier callipers, graph paper, imaging analyses, measured, paraffin wax, modification of paraffin wax, photography, spectrophotometry, submerged weight, normalized to weight, colony volume, normalized to polyps.

For this study, a recursive logic framework is proposed from *post hoc* results of mass bleaching susceptibility, mortality, and recovery [Tables 3, 4, and 7], which afforded a new perspective of coral-algal co-evolutionary adaptations. Therefore, databases on taxonomy [55,56], morphology [55], and life history and reproductive traits [57] were amalgamated to create the Zooxanthellae Density Meta-database (ZDM). Taxonomy was recorded from original studies (at whatever taxonomic level they observed) and if at species, placed into genera and/or families based upon [55] and then reorganised via molecular analyses following [56]. Where possible, data were arranged by morphology (at species level) based upon major categories of growth morphologies: (1) branching, (2) tabular, (3) columnar, (4) sub-massive, (5) massive, (6) encrusting, and (7) free-living [55]. These categories were later pooled into 'low' (encrusting, free-living), 'medium' (massive or submassive) or 'high' (branching, tabular and columnar) levels of colony integration based upon *post hoc* analyses of the Bleaching Response Meta-database [Table 8]. Furthermore, life history characteristics were added at the level of species from [57] including, generalist or specialist, reproductive mode (brooder, spawner or both), sex (gonochoric or hermaphroditic), transmission of algae (zooxanthellae) to offspring (yes, no, or both), and complexity of skeleton (robust or complex).

As methods were a known cause of significant variation [42,55], every possible variable was recorded, including: i) the size of the experimental unit in which zooxanthellae densities are quantified, be it a polyp, branch (or nubbin), fragment, core sample, sampling across a coral colony, or any of these spatial factors through time (and for how long) ii) the specific method used to separate coral tissues from the underlying skeleton were separated (due to Tukey's *post-hoc* test results, [42]) by decalcification of the skeleton or stripping tissue from the skeleton, iii) different methods used to estimate the surface area of host coral tissue from which zooxanthellae were extracted were pooled into callipers, foil, image analysis (spectrophotometry and photography), calculated (calculated and graph paper), and paraffin wax (both original and modified), iv) number of replicate counts, <6, 6-8. >8 counts. The length of observations were also recorded, as many authors [58,59] looked at only one point in time, whereas other others studied the reef numerous years,e.g. [60–63], and the data were separated thusly: one day, < one week, < 2 weeks, < 3 weeks, < 1 month, < 3 months, < 6 months, < 9 months, < 1 year, < 3 years, > 3 years. Another factor was the author of the methods, and results suggest that the same author follows his/her own way of determining mean zooxanthellae density. Variation was recorded due to changes in depth (transplant depth, intraspecific variation as recorded through depth gradients, aerial exposure), as well as inter-colonial variation, (such as lengthy observations or branch gradients). All categories are present that were used previously [42].

The proportional variation is a mathematical option is to compare the trends as completed in [55], which shows that as long as the same methods are used to quantify the zooxanthellae densities in healthy versus bleached colonies, the resulting estimates of proportional loss of zooxanthellae will not be biased by the methods used; while the absolute values may not be comparable, the

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proportionate trends remain consistent. By this logic, the results of [42] showed that a monitored decline of >55% of their algal population are bleached, but likely to recover, while corals that experience a loss of >78% of their zooxanthellae density are likely to at least experience partial mortality and that is tested against the Zooxanthellae Density Metadatabase, by re-examining records for their noted recovery, lethality, or unknown effect. For corals that were bleached, changes in zooxanthellae densities were expressed as the percent loss compared to the mean (highs and lows recorded) and wherever possible, were separated into those that ultimately recovered ("sublethal paling") versus those that died ("lethal bleaching"). Two studies which reported >100% change in zooxanthellae densities were removed from these analyses as they represented special circumstances: [64] represented an experimental observation in which corals were transplanted from the intertidal zone into a cave environment, where they lost all zooxanthellae and acquired a type of cave zooxanthellae, which differed in average healthy population densities and therefore caused a >100% change in zooxanthellae density. Additionally, [61] showed variability over a decade likely due to nutrient supply, with fluctuations of >300%. Furthermore, where "natural variation" was occurring seasonally, it was entered as sublethal paling as well as healthy variation.

Natural variation data were explored previously [42] and collected from both field observations and experiments (categorized as such). Experiments that showed variations in the controls over time or expressed error as standard deviation (large counts) were used in natural variations but categorized by experimental. Furthermore, seasonal observational studies noted that they may have shown bleaching [60], and this was accounted for by data entry into both the natural variation and the percent loss associated with sublethal bleaching of colonies (for percentage data). The cause of variation was recorded; however, the data only provide a rough estimate of variation due to differences between causes, rather than looking at differences within them (e.g. variation caused by light compared to temperature, rather than specifying differences between light levels or levels of any of the variables, aside from depth).

Multiple causes of bleaching were identified among the published studies considered [42], but these were pooled into four categories, (1) changes in temperature (including experimental tests of temperature exposure, as well as transplants between depths or latitudes), (2) changes in light (darkness, irradiance, light, light transplants, UVB and UVR), (3) changes in salinity (4) pollutants (antifoulant, copper, cyanide, herbicide, insecticide, lubricants, metal pollution). Nutrient enrichment and seasonal fluctuations are shown to increase mean zooxanthellae population densities outside of the realm of natural variations [42], so they are only discussed, not included in analyses. Moreover, nutrient enrichment has the potential to help replenish the zooxanthellae population, in quite contrast to the effects of pollutants (antifoulant, copper, cyanide, herbicide, insecticide, lubricants, metal pollution) and declining water quality, so they were distinguished thusly.

2.2. Defining Phases of Health by Fluorometric Analyses

In OISEO [42], I compared two common corals representative of variable life histories and reproductive traits, *Acropora nasuta* (a complex, spawning hermaphroditic coral that does not transmit algae to its offspring) and *Pocillopora damicornis* (a robust, brooding hermaphroditic coral that does transmit algae to its offspring). I completed preliminary *in situ* heath definitions with PAM Fluorometry (alongside visual observations and *post hoc* confirmation with zooxanthellae densities) to enable the distinguishment of bleaching as a rapid decrease in colony health over 6 sampling times. One fluorometer measurement provides information on 6 variables; minimal fluorescence (F – how many receptors are being used) and maximal fluorescence (Fm – how many receptors are present) values of Photosystem II (PSII), of which the ratio is the quantum yield, which summarises the efficiency of PSII. In other words, you're looking at the ratio between how many there are and how many are being used to compare the efficiency of the system. When PSII is under stress, two opposing processes are displayed, photoprotection and photoinhibition (34). Reversible damage, or photoprotection, is displayed as a sudden increase in minimal fluorescence (F) and a decrease in maximal fluorescence (Fm), which regulates the quantum yield, while a decrease in minimal

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fluorescence (F) implies photodamage [Walz 1998]. Photoinhibitors, which inhibit or quench the quantum yield, play a major role in the repair and damage of PSII [65]. Two photoinhibitory pathways are in direct competition for de-excitation processes 1) photochemical energy conversion at the PSII reaction centres (photochemical quenching qP) and 2) non-photochemical loss of energy through heat dissipation at antennae (antennae are chlorophyll or xanthophyll) (NPQ) and reaction centres (qN) [35,65].

In an aim to better define phases of health for the coral-algal symbiosis, the qualitative, subjective definitions for the phases of health [65] were translated into preliminary objective quantitative data phases of health [Table 1] and are used herein to test the definitions of the phases of health upon the OISEO fluorometric data [42]. The OISEO fluorometric data were rearranged to reflect these categories and to consider the relative proportional frequency of the branch site health phases at each level of changed experimental thermal conditions. Importantly, the first step to using a fluorometer is to calibrate your instrument measurements to a range of F values from 0-300, so hypothetically, with these new ranges, if you standardize quenching analyses to a dark control coral, it represents a relative comparison of quenching efforts that is much quicker than direct measurement, although direct measurements are needed to finetune the predicted quantitative definitions and more thoroughly grasp the intricacies of the mechanisms that are used.

Table 1. A unified interpretive framework resolving the dimensionality of zooxanthellae population flux. Recalibrating the x-axis to mean density removes misinterpreted temporal noise in natural fluctuations, revealing underlying system architecture. This exposes the contrast between healthy variation (NV high/low) and the perpendicular transition into sublethal and lethal states, clarifying how scale misinterpretation has obscured coral survival dynamics. The Architecture of Density Flux: Comparison of the Dimensionality of Zooxanthellae Population Densities, resolved the Misinterpreted Scale between homeostatic Natural Variation and the Phase Transition into sublethal and lethal states (expressed as percentage deviation from the system mean).

Healthy	**±SE**	***n***	**Pale**	**±SE**	***n***	**Bleached**	**±SE**	***n***
21.37	1.86	349	56.26	1.23	195	8.15	1.01	163

A) Architecture of density flux. Comparisons of zooxanthellae population dimensionality across healthy, pale, and bleached states, expressed as percent deviation from the system mean. This analysis resolves misinterpreted scale between natural homeostatic variation and phase transitions into sublethal and lethal states.

	Healthy			**Sublethal bleaching**			**Bleached**		
Source	Average	*n*	±SE	Average	*n*	±SE	Average	*n*	±SE
Within-colony	16.42	37	6.43	63.45	11	2.45			
Temperature	25.34	195	2.70	56.16	141	1.49	82.76	129	1.13
Habitat	8.99	75	3.43	66.13	18	3.10	83	3	0
Pollutant	28.54	39	2.07	43.18	22	2.62	74.17	27	2.32

B) Environmental forcing and systemic response. Analysis of functional drivers shaping system architecture, illustrating how within-colony integration and external stressors (temperature, habitat, pollutants) influence the direction and magnitude of symbiotic variation across bleaching states.

Source	**SS Type III**	**df**	**n**	**MS**	**F**	**p**
Natural Variation	76.548	3	345	0.216	3.863	<0.05*
Sublethal bleaching	9.248	3	191	0.044	6.876	<0.001***
Sublethal, pollution removed	8.200	2	169	0.047	2.858	>0.05
Lethal bleaching	9.312	1	155	0.056	11.292	<0.01**

*Significant, **strongly significant, ***highly significant.

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2.3. Mass Bleaching Response Meta-Database

The Mass Bleaching Response Database [42,44,66,67] hosts records (>3200 susceptibility, >2700 mortality, <150 recovery) of over 300 studies, which span greater than 80 years of research and all geographical regions of extensive coral reef formation, that have specifically quantified variations in temperature-related bleaching susceptibility within and among Scleractinian corals. It is important to note that this database extends to 2015, so new information may show more intricacies than presented here. The first publishing of the Mass Bleaching Response Database [66] reported results on an interaction between taxonomic families and morphologies with regards to the bleaching response, and noted that for durational studies, there was no significant difference between susceptibility of differing growth forms; however, mortality was less for massive growth forms. The second publishing of the Mass Bleaching Response Database was a full breadth analysis of taxonomy and location on the bleaching responses of corals [44], while [67] focussed on the impacts of size, the inter-connectedness of growth forms and hinted towards reproductive phase (e.g. juvenile non-reproductive vs. adult reproductive coral and their energy investments) being an important attribute to the bleaching response. Moreover, [67] was part of a long-term monitoring effort in French Polynesia that showed lessoned impact through repeated bleaching incidence with similar disturbance regimes; a mechanism of selective removal from within populations that bolstered the community assemblage resilience.

The Bleaching Response Database was initially a compilation of observations of mass bleaching events [42,44], and as I analysed it, I became aware that other databases could help fill in the gaps of knowledge, such as the global thermal data from the National Oceanographic and Atmospheric Administration (NOAA) and the Australian Institute of Marine Sciences (AIMS) to help calculate the timing of observations witnessed in comparison to the length of thermal stress accumulation for each record (unless given, which was not often). The data collected were based on the Degree Heating Week (DHW, wherein the first mass bleaching episodes in the 1980s occurred when sea temperatures exceeded normal local limits by > 1.0^{o}C for more than 1 week (e. g. >1 Degree Heating Week, DHW, [68]). The DHW Indices of the locations are examined through *post hoc* data entry of NOAA and AIMS temperature datasets for time made relative by recalibrating the data to the onset of thermal stress and related to when researchers took observations in comparison to when thermal stress began accumulating. Thermal stress accumulation was recorded from temperature data given in studies, where mean temperature, the years that determined the mean temperature, and the source of information (e.g. data loggers at sites or satellite information) were recorded. The number of weeks above the mean (e.g. +1oC, +2oC, +3oC, etc.) were multiplied by the increase above the mean (e.g. 4 weeks at 2oC = 8 weeks) and, for each site, the DHW were added to show the thermal stress accumulation (e.g. (4 weeks x +2oC) + (6 weeks x +1oC) = 14 weeks)). However, in 2007, NOAA updated the metric to 4DHW to initiate widespread distress on coral reefs. This is reflected in the category of bleaching occurrence, where the history of reported thermal stress was determined for each location and recorded based on previous published work. For instance, many study areas had experienced 5 repeated bleaching events (e.g. Eastern and Southern Pacific), while at least one bleaching was very notably the first recorded in the Central Pacific [69]. Additionally, the Bleaching Response Meta-database (BRM) is combined with databases on taxonomy [55,56], morphology [55], and life history and reproductive traits [57], as well as the thermal data from NOAA and AIMS and the calculated timing of observations based on dates provided and retrospective viewing of the thermal history and timing of anomalous waters. Lastly, while the decade of observations was recorded, there appeared to be some fluctuations due to the advent of new technologies.

2.4. Aims and Statistics

The following analyses are structured to evaluate competing definitions of bleaching by examining their internal consistency, biological interpretability, and predictive alignment with observed outcomes. The overarching aims are to define bleaching and explain bleaching responses. Bleaching is first explored by attempting to define healthy fluctuations in zooxanthellae densities

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[Section 2.4.1], then comparing healthy and bleached zooxanthellae densities for absolute densities to distinguish them [Section 2.4.2], which leads to the creation of dynamic equations [Section 2.4.3]. Zooxanthellae density data are then interpreted through proportional loss [Section 2.4.4], fully explored [Section 2.4.4.1], analyzed [Section 2.4.4.2], and then related to the causal agents [Section 2.4.4.3]. The bleaching definition [Section 2.1] is then linked to bleaching responses [Section 2.2] which forms the basis for the perceptual shift in our biased assumptions of the relativity of time to organismal dimensionality and cryptic evolutionary resilience [section 2.3].

The OISEO [42] Pam Fluorometry data are grouped into subjective categories for the phases of health and expressed in multiple perspectives on graphics [Section 2.4.5]. Overall bleaching responses of paired durational susceptibility and mortality records are explored [Section 2.4.6]. The aims then move to fully exploring bleaching responses [Section 2.4.6]. Bleaching susceptibility and mortality are overviewed [2.4.6.1] along with recovery [2.4.6.2]. Data are then grouped based on *post hoc* test results [2.4.6.3] and mapped through a descriptive statistical matrix of thermal stress accumulation and the relativity of the timing of the observations to the onset of thermal stress [2.4.6.4].

The zooxanthellae density data are then revisited to compare and contrast healthy and bleached zooxanthellae densities with mass bleaching susceptibility and mortality by *post hoc* categories of the level of colony integration and *post hoc* categories of locations, subregions within ocean basins [Section 2.4.6.5]. The final section is the preliminary exploratory analyses of zooxanthellae genomic diversity with coral life history strategies [Section 2.4.7].

2.4.1. Examine Healthy Fluctuations in Zooxanthellae Densities to Define a Bleached State

The full records of the Zooxanthellae Density Database were used to explore variations in seemingly healthy corals. Descriptive statistics and ANOVAs were completed. As counts had been too low to search for an absolutely healthy or bleached zooxanthellae density from the zooxanthellae density database, a series of independent 1-way ANOVAs were run for each variable (with Tukey's *post-hoc*, where appropriate), including all appropriately categorized estimates of zooxanthellae density (where $n > 5$). For each analysis of variance, the F factor was recorded and used to compare the relative importance of the contribution of each factor to the 'noise' present in the database [following 42]. This data is reported at a base level, as analyses were recompleted with the Zooxanthellae Density Meta-Database when comparing healthy and bleached zooxanthellae densities and likely mortality; trends within factors remained the same, but new factors were added, and *post hoc* groupings (recorded in results text and Table 7) were used that slightly changed the overall results.

Examine a Bleaching Definition Through Absolute Zooxanthellae Densities

The primary aim of the zooxanthellae density database was to attempt to define bleaching via an absolute density of zooxanthellae, but due to the wide range of variability, this aim had to be modified to two subaims, 1) create dynamic equations that weigh the relative importances of factors and provide standards to be used for averages to fill in the blanks of the dynamic equations or compare, 2) calculate the relative proportional loss in zooxanthellae densities through time and compare the proportional variability amongst causes.

Dynamic Equations for Absolute Healthy and Bleached Zooxanthellae Densities

First, data were updated to be the Zooxanthellae Density Meta-database, and then data were restricted to pairwise entries for healthy and bleached (and if mortal or recovered), Regression analysis and a Student's T-test were utilised to compare all healthy and all bleached zooxanthellae population densities. Then, due to differences in the methods used to assess variation (reported in the results text herein), attributable to the Sample Size used (method SS: branch, colony, core, fragment, nubbin, and sample), the Method for Tissue Removal (method TR; airbrushing, decalcification, and waterpiking), the method for the determination of tissue Surface Area (method

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SA; calculated, callipers, foil, image analyser, modified paraffin wax, paraffin wax), species (*Acropora millepora, Acropora nasuta, Goniastrea aspera, Montastrea annularis, Montastrea faveolata, Pocillopora damicornis, Porites cylindrica, Porites lobata, Porites lutea, Seriatopora hystrix, and Stylophora pistillata*), genus (*Acropora, Favia, Goniastrea, Montastrea, Montipora, Pavona, Pocillopora, Porites, Seriatopora, Goniastrea*) family (Acroporidae, Agariciidae, Faviidae, Oculinidae, Pocilloporidae and Poritidae), morphology (branching, encrusting, foliose and massive), and depth (<3m, 4-6m, 7-10m, 11-19m, >20m), it was not possible to do a single comprehensive analysis and partition variance accordingly. Instead, a series of independent 1-way ANOVAs were run for each variable (with Tukey's *post-hoc*, where appropriate), including all appropriately categorized estimates of zooxanthellae density (where n > 5). For each analysis of variance, the F factor was recorded and used to compare the relative importance of the contribution of each factor to the 'noise' present in the database [Bradbury 2013], assuming most variability is captured. Variability was partitioned to groups of similar characteristics (methods, location, taxonomy, and biology/ecology) to further enable a relative importance of factors to overall variability (F factor/Total F factor x 100). The grouped relative importance of factors (Table 2) can then be used in a dynamic equation, such that one can look up the standards for average values (Table 1) and place them in the weighted categories to estimate and compare zooxanthellae densities (ANOVAs and correlations in Table 2 for estimating accuracy). Additionally, Pearson's correlation tests were completed for significant variables.

Table 2. Operational definitions for distinguishing healthy, sublethally stressed, and bleached coral states using PAM fluorometry.

A) Comparison of healthy and bleached colonies using fluorometric parameters (F′, Fm′, effective quantum yield, qP, qN, NPQ) and quenching dynamics. Thresholds are based on short-term temporal patterns (3-day means) to distinguish sustained dysfunction from transient fluctuation.

Variable	F′	Fm′	Yield	qP	qN	NPQ
Control	130-300; mean 185	400 – 700, mean 600	0.61-0.7, mean 0.66	1	0	0
Bleached	Significant increase followed by a rapid decline, for 3 days	3-day mean of 200 (within SE)	3 consecutive decreasing days: 3-day mean <0.45 (within SE)	3-day mean of 0 or >2 (within SE)	3-day mean of 0 or >2 (within SE)	3-day mean of 0 or >2 (within SE)

B) **Objective phase classifications of photosynthetic health derived from PAM metrics, defining functional states including photoprotection, photorepair, photodamage, photoinhibition, and recovery. Together, these criteria translate continuous photophysiological measures into discrete, repeatable health states, providing a standardized framework for identifying phase transitions in coral bleaching dynamics.**

Phase of Health	F′	Fm′	Quantum yield	qP	qN	NPQ
Healthy	200-325	600-800	0.6-0.8	1	0	0
Photoprotection	250+	800+	0.6+	1	0	0
Photorepair	150-250	500-600	0.5-0.6	>1	<1	1
Photodamaged	100-200	<500	<0.5	0	>1	>1
Photoinhibited	<100	<300	<0.5	0	>1	>5
Recovering	50-150	>400	0.6+	>0	<1	<1

Proportional Loss in Zooxanthellae Densities as a Metric to Define Bleaching

The results for absolute densities of zooxanthellae were a dead end, so proportional loss in zooxanthellae population density for nominally bleached corals (anemones were included for proportional variation) was used to test for differences in the severity of bleaching associated with different causes.

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Exploratory Analysis of Proportional Variation in Zooxanthellae Densities

Natural variations (above and below the mean) are compared to sublethal (bleached, recover), and lethal bleaching (noted mortality).

Proportional Loss as a Metric to Define Bleaching Lethality

Proportional loss related to lethality (recovery, death, unknown) are displayed as a function of frequency.

Statistical Exploration of Proportional Loss

ANOVA was used to explore differences between healthy variation and sublethal and lethal bleaching for each of the grouped factors of causes. Descriptive statistics are also shown.

Variability in the Proportional Loss Associated with Bleaching Due to Causes

ANOVAs were used to explore differences between healthy variation and sublethal and lethal bleaching for each of the grouped factors of causes based on the proportional variation (percentage data were arcsine transformed to meet the assumptions), and descriptive statistics are shown.

2.4.2. Quantitative Fluorometric Definitions for the Phases of Health

Fluorometric analyses from OISEO [42] were regrouped based on subjective definitions turned quantitative [Table 1], coded and graphically explored.

2.4.3. Exploration of Bleaching Responses with Regards to New Perspective of Bleaching

An overall scatterplot of the Mass Bleaching Response Metadatabase is presented as paired records of susceptibility and mortality, with the quadratic formula and correlation coefficient shown on the graph.

Exploratory Statistics for Bleaching Responses

This subsection evaluates bleaching definitions by catabolizing zooxanthellae density into absolute, proportional, and dynamic components, and by examining their statistical and biological consequences. Since new categories were added to the meta-database on bleaching responses, exploratory descriptive statistics were completed first, followed by partitioned ANOVA results, then data were regrouped based on Tukey's *post hoc* tests so that some of the variability in the responses could be lessoned, and enable a better picture of what is actually happening during mass bleaching events. Descriptive statistics and overall comparisons were completed. As bleaching susceptibility and mortality were limited to pair-wise values, analyses began with a scatterplot regression and a Student's T test. Then, the data were explored though a series of independent 1-way ANOVAs for each variable (with Tukey's *post-hoc*, where appropriate) and F factors were compared, as done with zooxanthellae density data. This exploratory analysis included all appropriately categorized estimates of bleaching susceptibility and mortality for which there were >10 records. ANOVA was used to establish the level (and significance) of variation in bleaching susceptibility due to taxa (family, genus and species), biology/ecology (morphology, habitat, depth, life history characteristics) location (ocean, subregion, country and location) and timing (how far into the event that observations were made and rather they were complete observations, as well as decade and bleaching occurrence - which is how many times that geographic region has experienced mass bleaching. *Post hoc* test results are shown, where applicable. Additionally, Pearson's correlation tests were completed for significant variables. All data were arcsine square root transformed for normality to meet the assumptions of ANOVA.

Another *post hoc* category was added to susceptibility and mortality averages (throughout where applicable) – the bleaching efficiency, mirrored from the photosynthetic efficiency through quantum yield, in this case (Susceptibility – Mortality)/Susceptibility; where 0 would relate to a net loss and

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susceptibility equals mortality, while 1 represents no mortality from the response. An interesting 'non-defined' operation, dividing by zero is very defined here, bleaching responses can be 0 Susceptibility and 0 Mortality; these were marked with asterisks, however, this begs the question of why this is considered undefinable as I define it – it is important to note when there is no susceptibility to events, we need that information.

Exploratory Statistics on Recovery

The time to recover (in months) was analysed using independent ANOVA s for the various factors, and correlation tests were completed for factors that affect recovery. F ratios from the ANOVAs were compared to create relative importance of the factors. Due to the low number of records (n = 152), cases were included where $n \geq 3$.

Post Hoc Groupings

Due to the large number of factors that cause variation in bleaching susceptibility and mortality (n = 34) Tukey's *post hoc* results were used to regroup factors for simplicity [Table 8]. Data were combined when the Sum of Squares showed similar results as did the F ratio. For instance, degree heating weeks, and other thermal data (e.g. annual temperature, peak temperature) were replaced with thermal stress accumulation (low – 0-19 degree heating weeks, medium (20-39 degree heating weeks, high >40 degree heating weeks). Months of observations after anomalous thermal stress led to three different categories (beginning – 0-3 months; middle 3-6; end 7+ weeks). Location was simplified from to subregions within ocean basins. Growth form was exchanged for the level of colony integration (high- branching, columnar and tabular; medium – massive and submassive corals; low – encrusting and free-living. Anthropogenic input (yes/no, as well as y/n for protection, which replaced marine protected area and anthropogenic stress. Lastly, weather categories combined to express either relief or exacerbation of effects. For instance, there may be upwelling but also doldrums, so there were four groups: No relief, no relief + doldrums, yes relief, and yes relief with doldrums.

Map Bleaching Through a Matrix of Temperature and Time

Timing of observations (months) relative to the onset of thermal stress and thermal stress accumulation were the two greatest causes of significant variations in bleaching responses (Tables 4 and 5), so I used Tukey's *post hoc* tests (Table 7) to regroup and matrix the data. The timing of observations relative to the onset of thermal stress were grouped into 'Beginning' (0-2 months), 'Middle' (3-6 months), and 'End' (7+months), while the categories of thermal stress accumulation were 'Low' (0-20 Degree Heating Weeks), 'Medium' (21-39 Degree Heating Weeks) and 'High' (40+ Degree Heating Weeks). ANOVAs were completed before and after the *post hoc* groupings to show any impacts on significance within the data categories (Table 7). ANOVA's were completed for as many factors as possible within these nine categories (Table 9) and average values are shown (Table 10). Dynamic equations can be created using the weighted average importance with the standard values, per previous dynamic equations (Tables 9 and 10). Additionally. Data were restricted to recovery, susceptibility, and mortality triplet values to compare bleaching responses with recovery capabilities; scatterplots are presented.

Compare and Contrast Bleaching Definitions with Bleaching Responses

Dynamic equations for healthy and bleached zooxanthellae densities and proportional loss in the zooxanthellae population compared to the mean of the means through time are assessed as bleaching definitions in relation to their explanatory power towards bleaching responses. The locations of observations/ experiments were added; and, separated into ocean, subregions of oceans, country, location and then after *post-hoc* results (Tables 7), subregions within oceans, which will be used as the platform to study the relationship between healthy variation in zooxanthellae densities and susceptibility and mortality to bleaching through correlation analyses, ANOVA, and descriptive

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statistics. Location (ocean basin and subregion) and the level of colony integration appear were tested and data were compared to bleaching susceptibility and mortality at the same level. MANOVA was used on ocean basin to compare pair-wise healthy and bleached zooxanthellae densities.

Survival of Genetic Material and Disturbance Guilds

Genetic variation of the zooxanthellae population was determined by combining the life history data [55] with a database on zooxanthellae population diversity [72]. I tested the hypothesis that the genetics of the zooxanthellae populations will be markedly different with regards to fight and flight responses, as the functions of certain types of zooxanthellae have been shown to vary (e.g. 71, 72). Genetic diversity due to life history traits were tested by observing the number and diversity of symbionts among the different life history characteristics (entered at species level, except for complexity ok skeleton which was entered at Family level).

3. Results

3.1. The Architecture of Resilience

The results presented herein delineate the foundational components of recovery mechanisms and quantitatively reframe the narrative of coral bleaching from a passive state of failure to an active, architectural strategy for survival. This work synthesizes greater than 350 records for symbiont density, 2,200 records for bleaching susceptibility and mortality, almost 150 records for recovery, and over 250 records of symbiont cladal diversity to explore the 'static' or 'noise' of methodological variation and traditional taxonomic assumptions to reveal a structured decision matrix. This analysis begins with the Architecture of Resilience identifying the physiological limits of the symbiosis between coral and algae and culminates in a systems-level exploration of BEQ – a metric that identifies bleaching not as a terminal event, but as a well-adapted survival protocol forged through 200 million years of evolutionary history.

Limits of a Stable Symbiosis

Reported zooxanthellae densities for healthy (unbleached) and bleached corals have enormous ranges of reported values [Figures 1, A1, 3A, Table 1A]. Healthy values reflected up to 369 records, while bleached values for 103 records are reported here for comparison [Figure 2, Table 1A]. Healthy zooxanthellae densities ranged from 0.1 x 10^6 cells/cm^2 to 18.0 x 10^6 cells/cm^2; [Table A1] and are largely attributable to methods used to estimate densities [Figure 2A and Table 1A]. In comparison, the mean densities of zooxanthellae recorded for bleached corals were 1.26x10^6 (SE±8.78x10^5) and ranged from 0.001 x 10^6 cells/cm^2 in a massive *Porites* exposed to high temperature and high UVR [62] to 6.5 x 10^6 cells/cm^2 in *Plesiastrea versipora* following cyanide exposure [63, Table 1A]. Moreover, when comparing bleached densities by methods, the data range from 5.00x10^5 for *Acropora nasuta* (branch that was "peeled and squashed") up to 6.5x10^6 for *Plesiastrea versipora* (massive fragment that was waterpiked and used image analysis). Additionally, the highest bleached zooxanthellae density (1.16x10^7 ±2.28x10^6 SE) was recorded for *Coelastrea aspera*, a massive coral, while the lowest mean healthy zooxanthellae density was from *Stylophora pistillata*, a common branching coral (1.87x10^6 ±5.92x10^5 SE) [Table 1A].

The full breadth of variability in healthy and bleached densities by frequency of occurrence [Figure 3A] shows that there are notable fluctuations that need to be quantified. Methods are known to cause a significant amount of variation in healthy measurements of zooxanthellae densities [42], and further analyses [Table A1, Figure 2A] further support that notion. Furthermore, methods limit the records that could be used alongside taxonomy to find an absolute universal zooxanthellae density for healthy or bleached corals [Figure 2A, Tables 2A and 3A]. Given the diverse combinations of methods possible in quantifying zooxanthellae densities there were very low numbers of records remaining that provided the resolution for directly comparable estimates of healthy or bleached zooxanthellae densities [e.g. Figure 2A, Table A1], although it is apparent that the "normal" density

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for some is well below that which characterises bleaching in others [Figure 3A, Tables 1A-3A]. Due to this high variability in absolute measures, and the known capacity for the trends in results to stay similar when comparing methods [54], I began exploring the proportional variation [Figure 2] (loss of zooxanthellae density from the mean healthy values) in [42] alongside indirect absolute values that can be created using the dynamic equations [Tables 1 and 2], which provide standard substitutes and their relative importances.

Zooxanthellae densities vary and fluctuate naturally; however, there were few cases where variations within healthy organisms exceeded the loss associated with the bleaching threshold [Figure 1] Nutrient enrichment (e.g. ammonia) was the only causal agent that dramatically increased mean zooxanthellae density [Figure 1]. Depth was the greatest source of natural variation as it caused the greatest percent difference from the mean zooxanthellae density, 136%, in *Montastrea annularis* colonies; this was also the greatest source of natural variation for above (95%) and below (41%) the mean zooxanthellae density [Figure 1]. The sublethal bleaching category presented in [Figure 1] are the data from the OISEO, where time was variable and health status was controlled, and the total number are representative of the algebraic means of colonies averaged on their individual bleaching days.

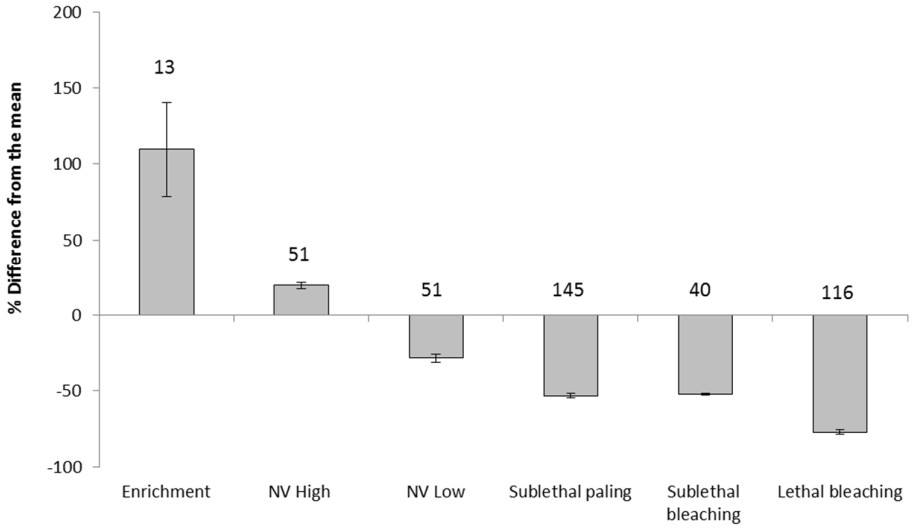

Figure 1. Architecture of Resilience Across Zooxanthellae Population States. Mean percent difference in symbiont density relative to the overall mean is shown across enrichment, natural variability (NV high, NV low), sublethal paling, sublethal bleaching, and lethal bleaching conditions. Values are centered on the mean to standardize comparisons across studies and sampling contexts. Positive deviations characterize enrichment and NV-high states, while progressively negative deviations correspond to sublethal and lethal stress states. Error bars represent variability within each category; numbers above bars indicate sample size. This normalization reveals discrete population states rather than continuous temporal decline, distinguishing natural fluctuation from transitions associated with bleaching severity.

Generally, the trends for healthy and bleached both form normal distributions, if slightly skewed [Figure 2], where recovery is highest when only between 61-70% of zooxanthellae is lost], and mortality is highest where >71% of zooxanthellae were lost. Corals that bleached and did not recover [lethal bleaching, Figure 2] were reported to have an average of $<1.3x10^6$ zooxanthellae per cm^2, which is higher than earlier estimates of "normal" zooxanthellae densities [Figure 3A]. One million cells/cm^2 has commonly been cited as an average healthy zooxanthellae density [68,69], but this is dependent upon the methods and scales of samples [Figures 1A-3A, Tables 1A and 2A]. Moreover, when I separated out the causes of bleaching in comparison to natural fluctuations [Figure 4A], and analyzed them further [Table 1], pollutants caused the highest proportion of variability to healthy

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zooxanthellae densities and produce sublethal and lethal bleaching lower than other causes. Additionally, when pollution data were removed from the sublethal bleaching category [Table 3c], the data were not significantly different within the category.

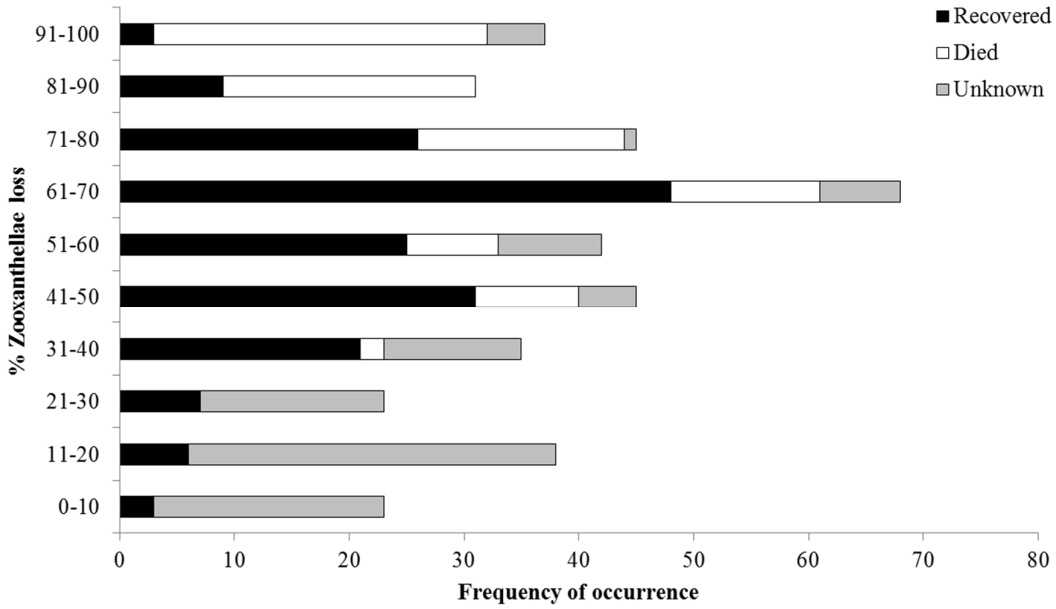

Figure 2. Frequency Distribution of Symbiotic Loss States and Associated Outcomes. Observed frequencies of recovery, mortality, and unknown outcomes are shown across binned percentages of zooxanthellae density loss. Recovery persists across a wide range of loss states, including levels commonly classified as severe bleaching. Mortality increases nonlinearly with increasing loss but does not follow a single deterministic threshold. This distribution reflects the underlying architecture of bleaching, where outcome states emerge from system structure rather than proportional loss alone.

In an attempt to further describe and define bleaching [Table 3], I compared the mean deviation in average densities between healthy, paled and bleached corals, to find that bleached corals should be readily distinguishable [8.15% colony deviation in variability, Table 1a] as more of the variability is captured in fewer attempts, the true mean is less variable than healthy or natural fluctuations [Table 1a]. Variability in the percent loss associated with both sublethal and lethal bleaching of corals [Figure 2] was affected by the methods SS, causal agent, and timeframes of observations. Methods SS caused significant variability (sublethal, $F_{(6,165)} = 2.423$, $p<0.05$): samples (n=10) and fragments (n=20) were lower (separated by Tukey's *post hoc*) than other sizes (49% and 52%, respectively), while core samples (n=13) were higher than other sizes (72%). The range of sublethal bleaching from other categories of methods SS (anemone (n=14), branch (n=33), colony (n=65) and subsamples (n=11)) was 55-60%. Lethal bleaching percentage loss was also affected by methods SS ($F_{(5, 92)} = 9.553$, $p<0.05$). Samples (n= 28) were separated by Tukey's *post hoc* as lower (64%), while colonies (n=18) were separated as higher (89%): the range of other categories (anemone (n=9), branch (n=12), fragment (n=20), subsample (n=6)) was 68-83%.

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Table 3. Multidimensional drivers of recovery time following bleaching events. Factors associated with variation in recovery duration (months), where n ≥ 3; all values square-root transformed to meet ANOVA assumptions. The table synthesizes biological, environmental, and spatial variables to resolve recovery as a structured, non-linear process rather than a uniform temporal outcome. Recovery times vary systematically across colony position, thermal stress accumulation, anthropogenic input, habitat, geography, and genus, indicating that recovery reflects interaction between system architecture and historical exposure rather than bleaching intensity alone.

A) Mean recovery times (± SE) across categorical drivers, illustrating differential recovery trajectories associated with internal colony structure, external forcing, and biogeographic context.

Factor	Source	Recovery (months)	±SE	*n*
Shelf Position	Inner	8.00	0.00	3
	Middle	2.29	0.33	11
	Outer	1.94	0.30	16
Relief from Weather	No	7.00	0.53	43
	Yes	3.59	0.31	80
Thermal Stress Accumulation	Low	3.98	0.49	82
	Medium	8.20	0.75	54
	High	10.33	1.69	6
Anthropogenic Input	Low	6.72	0.44	32
	Medium	6.67	1.33	4
	High	12.00	0	5
Locations	Caribbean	5.00	1.00	8
	Centre of Biodiversity	10.33	1.71	20
	Eastern Pacific	6.72	0.44	32
	French Polynesia	3.29	0.27	66
	Great Barrier Reef	8.05	1.66	23
Habitat	Bay	5.62	0.21	13
	Reef Flat	3.00	1.73	4
	Reef Crest	1.50	0.00	14
	Reef Slope	4.15	1.04	20
Sex	Gonochoric	4.99	0.67	30
	Hermaphroditic	3.44	0.35	46
Genus	Acropora	3.18	0.49	20
	Astrea	4.20	1.10	5
	Montipora	13.00	4.02	7
	Pavona	6.43	1.15	7
	Platygyra	2.85	1.10	3
	Pocillopora	3.72	0.56	16
	Porites	3.46	0.57	11
	Psammocora	7.58	1.85	6
Bleaching Occurrence	First	7.15	1.25	33
	Second	4.71	0.86	55
	Third	6.00	0.00	26
	Fourth	5.60	1.60	5
	Fifth	5.85	0.10	27
Species	*Acropora gemmifera*	4.50	1.50	3
	Acropora hyacinthus	3.08	0.78	7
	Acropora millepora	2.19	0.48	3

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	Astrea curta	4.20	1.10	5
	Pavona cactus	7.25	1.97	4
	Platygyra daedalea	2.85	1.10	3
	Pocillopora damicornis	6.00	0.00	3
	Pocillopora elegans	6.00	0.00	3
	Pocillopora meandrina	3.00	1.50	3
	Porites lobata	2.51	0.85	4
Transmission of Algae to Offspring	No	4.58	0.53	44
	Yes	3.42	0.43	23
Level of Colony Integration	Low	3.60	1.16	10
	Medium	4.28	0.44	31
	High	5.96	0.81	51
Generalization	Generalist	3.78	0.38	49
	Specialist	4.49	0.65	29
Reproductive Mode	Brooder	4.44	0.55	8
	Spawner	4.04	0.39	67
Family	Acroporidae	6.14	1.24	37
	Agariciidae	6.08	0.68	12
	Fungiidae	4.45	1.18	10
	Merulinidae	5.58	1.17	20
	Mussidae	4.00	0.00	3
	Pocilloporidae	4.94	0.95	24
	Poritidae	4.21	0.53	17
	Psammocoridae	7.58	1.85	6
Dominant Topography	Acropora and Montipora	8.25	1.33	16
	Acropora hyacinthus	6.00	0.00	16
	Montastrea	4.00	0.00	4
	Pavonids and Pocilloporids	5.77	0.13	22
	Pocilloporidae, Fungiidae, Acroporidae, and Poritidae	6.00	0.00	5
	Porites lobata, *Pocillopora damicornis*, and *Pocillopora elegans*	6.00	0.00	6
Complexity of Skeleton	Complex	5.67	0.72	66
	Robust	5.48	0.58	65

B) Analysis of variance identifying dominant structural drivers of recovery duration following mass bleaching. Recovery time varies significantly with shelf position, relief from weather, thermal stress accumulation, anthropogenic input, location, habitat, sex, and genus, while species identity, reproductive mode, transmission mode, and structural complexity show no independent effect.

Source	**SS (Type III)**	**df**	***n***	**MS**	**F**	**p**
Shelf Position	8.501	2	29	0.108	25.908	<0.001***
Relief from Weather	86.023	1	122	0.593	23.972	<0.001***

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Thermal Stress Accumulation	144.314	2	141	0.828	17.655	<0.001***
Anthropogenic Input	10.106	2	40	0.171	10.623	<0.001***
Location	147.165	4	148	0.817	9.042	<0.001***
Habitat	57.530	3	92	0.495	5.826	<0.001***
Sex	36.405	1	75	0.463	4.648	<0.05*
Genus	57.856	7	74	0.592	4.392	<0.001***
Bleaching Occurrence	145.510	4	145	0.966	2.418	>0.05
Species	14.550	9	37	0.309	2.127	>0.05
Transmission of Algae to Offspring	33.485	1	66	0.502	1.735	>0.05
Level of Colony Integration	73.084	2	91	0.795	1.490	>0.05
Generalization	37.160	1	77	0.484	0.803	>0.05
Reproductive Mode	35.957	1	74	0.489	0.550	>0.05
Family	119.113	7	128	0.955	0.536	>0.05
Dominant Topography	35.463	6	73	0.518	0.252	>0.05
Complexity	121.788	1	130	0.944	0.026	>0.05

C) Pearson correlations between key environmental and biological variables and average recovery time following mass bleaching events. Recovery duration is strongly structured by exposure-related gradients and cumulative thermal stress, while intrinsic biological traits show weaker or inconsistent associations.

Source	***n***	**Pearson's Correlation Coefficient**	**p**
Shelf Position	30	-0.654	<0.001***
Anthropogenic Pressure	41	0.533	<0.001***
Degree Heating Index	142	0.446	<0.001***
Relief from Weather	123	-0.407	<0.001***
Sex	76	-0.243	<0.05*
Location	149	-0.173	<0.05*

*Significant, **strongly significant, ***highly significant.

D) Relative contribution of major driver classes to variation in recovery time, derived from F-ratio importance values. Environmental forcing (weather exposure and cumulative heat stress) accounts for the majority of explained variance, with secondary contributions from habitat, location, and limited biological traits, reinforcing recovery as an emergent property of system context rather than species identity.

Factor	**Importance**	**Source**	**F**	**Relative Importance**
Weather	63.5%	Relief from Weather	23.972	36.58%
		Degree Heating Index	17.655	26.94%
Biology and Ecology	16.0%	Habitat	5.826	8.89%
		Sex	4.648	7.09%
Location	13.8%	Location	9.042	13.80%
Taxonomy	6.7%	Genus	4.392	6.70%

3.2. Defining Bleaching

Methods have caused considerable variability in the measurement of healthy fluctuations for zooxanthellae densities [Figures 1A, 2A; Tables 1A, 2A], and have made distinguishing healthy and bleached corals difficult by an instantaneous, absolute density [Figure 2]. However, one can use the dynamic equations [Tables 1A and 2A] or look for overall decreased variability in the measurement [Table 1], as bleached corals have low intra-colony variability in comparison to paled and healthy corals. If one has the opportunity of measuring zooxanthellae densities through time, then one can

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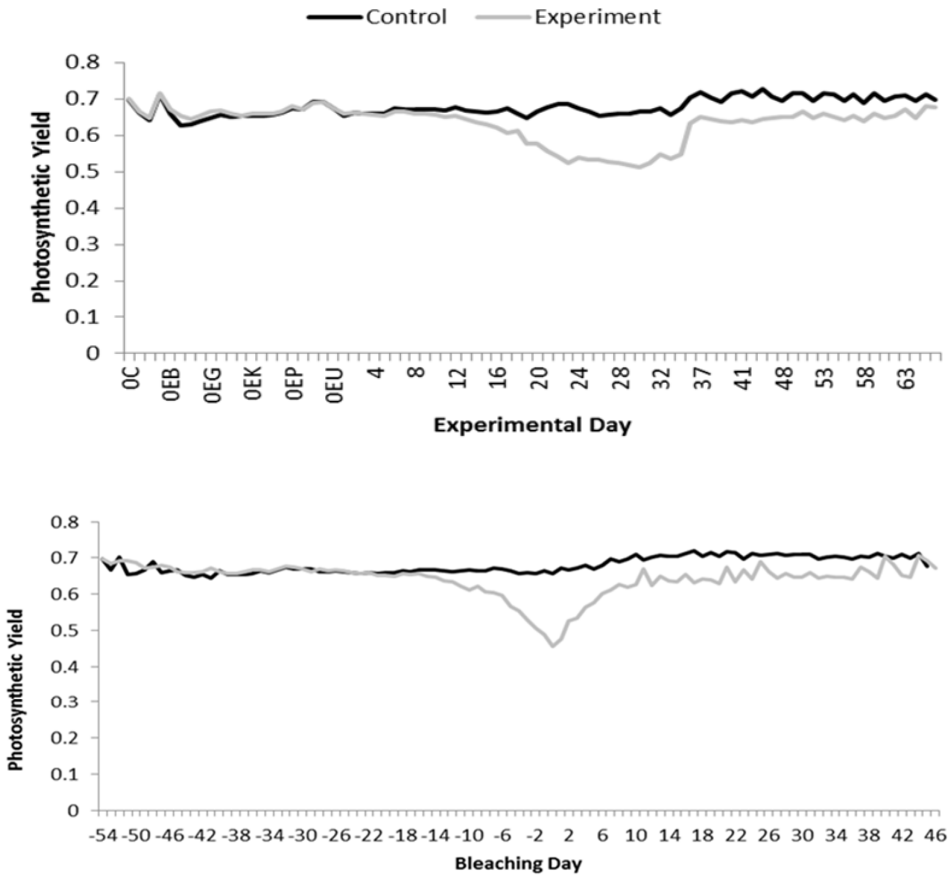
use proportional loss to categorize natural variations from bleaching [Figure 4] and estimate likely lethality [Figure 5], particularly if the cause of bleaching is known [Figure 6].

As I, [42], took a different approach with OISEO and experimental analysis and measured the variability of time and controlled the health status, the end date of experimental conditions was variable amongst experimental days for colonies [Figure 3a]. Time was recalibrated as it was variable [Figure 3b], and because samples were collected on experimental day regimes (zooxanthellae densities and zooxanthellae genetics) they turned into an uneven distributions with the new time calibration, but therefore allowed a more detailed overall vantage point and confirmed the rapidity of the process [42].To showcase the change in interpretation of data, the average quantum yield is presented with variable assumptions of time [Figure 3, 42]. [Figure 3 (a, top)] is by experimental day and would be the perception of business as usual culminating in moving time onto the y axis after I was alerted [pers. comm. Prof. Peter Ridd] that I was not placing time on the dependent axis, which provides a much more fruitful exploration of the data [Figure 3c] and supports present assertions of the bleaching definition.



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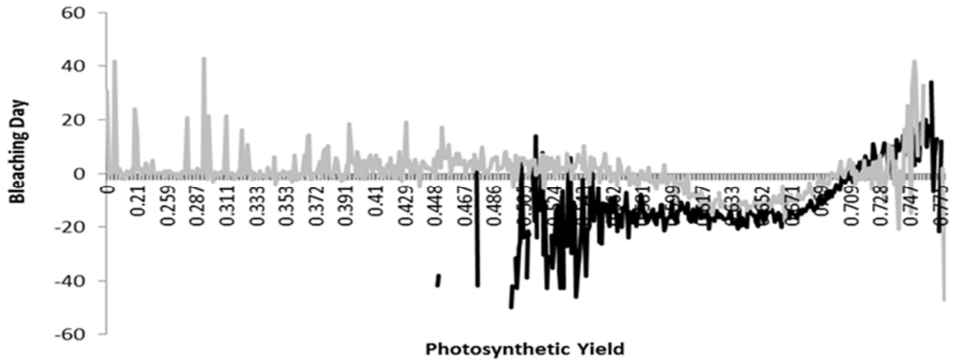

Figure 3. Comparison of photosynthetic quantum yield trajectories under alternative temporal frameworks. Data are shown for colonies of *A. nasuta* and *P. damicornis* pooled across species (no significant differences based on yield alone). (a) Time series arranged by experimental day illustrates apparent stability punctuated by transient declines. (b) Recalibration by bleaching day reveals a coherent depression in yield aligned with the bleaching event, followed by recovery, resolving temporal ambiguity. (c) Yield plotted against bleaching intensity identifies the inflection region where sublethal stress transitions toward structural instability. Together, these views demonstrate that yield dynamics are more interpretable when time is treated as a state-dependent variable rather than a linear experimental axis.

To transform subjective observations [Table 2a], the PAM Fluorometry data [42, Figure 3] were synthesized into phases of health that takes the F, Fm, Yield, qN, qP, and NPQ into simultaneous consideration [Table 2, Figure 4]. Background phases of health; healthy, photoprotection, photorepair, and recovery were normal for controls [Figure 8, top], and there was some noted photodamage and photoinhibition once moved to recovery conditions. In contrast, experimental corals [Figure 4, bottom], began experiencing less photorepair and more photodamage at the last thermal increase [experimental day 16, Figure 3] and contained few branch sampling sites in healthy or photoprotected phases nearing bleaching, the bulk proportionality moving towards photodamage and photoinhibition. Notably, the green category of recovery [Figure 4] is parsed throughout controls and experiments, and further quenching analyses is needed to explore this category, although it is interesting that experimental corals in recovery had the lowest percentage of 'recovery' phased branch sites at the end of monitored recovery.

The proportional shift in perspective of time [Figure 3] into proportional variation [Figure 4] validates the multi-metric definition of bleaching [42]. Corals show a rapid loss of colony-wide photophysiological function and a move towards a colony that is proportionally covered with branch sites in the bulk of photodamaged or photoinhibition [definitions, Table 2; Figure 4] when the colony expels dysfunctional zooxanthellae [Figure 1, where the sublethal n=40 category are the results from OISEO, e.g. Figures 3 and 4; data shown dispersed through time in B42]. Notably, deviations from the true mean healthy values are less than when chronically photoinhibited [Table 2]; therefore, as the proportional variability of colonies is less in bleaching [Figure 4, Table 2], bleaching should be readily distinguishable in one sampling time across a colony. This definition of bleaching is essentially what the photoinhibition model of coral bleaching predicts occurs at the molecular level [36]; however, [42] witnessed this reflected across the holobiont [Figures 3 and 4]. Furthermore, this is in contrast to short term, high stress conditions, which elicit a flight response, where the colony expels photosynthetically healthy zooxanthellae in an effort to prevent further damage [39]. So, I hypothesized and herein test that bleaching can be observed as a spectrum of fight and flight responses based upon the strength and timing of the stressors and the co-evolutionary adaptations that the coral holobiont has acquired through deep co-evolutionary time with intermediate mass extinctions [42]. If bleaching were not a mechanism of survival, we would expect a 1:1 ratio with susceptibility and mortality; however, [Figure 5] shows the relationship between susceptibility and mortality is not a straightforward one, with susceptibility having a 40% predictive power of mortality.

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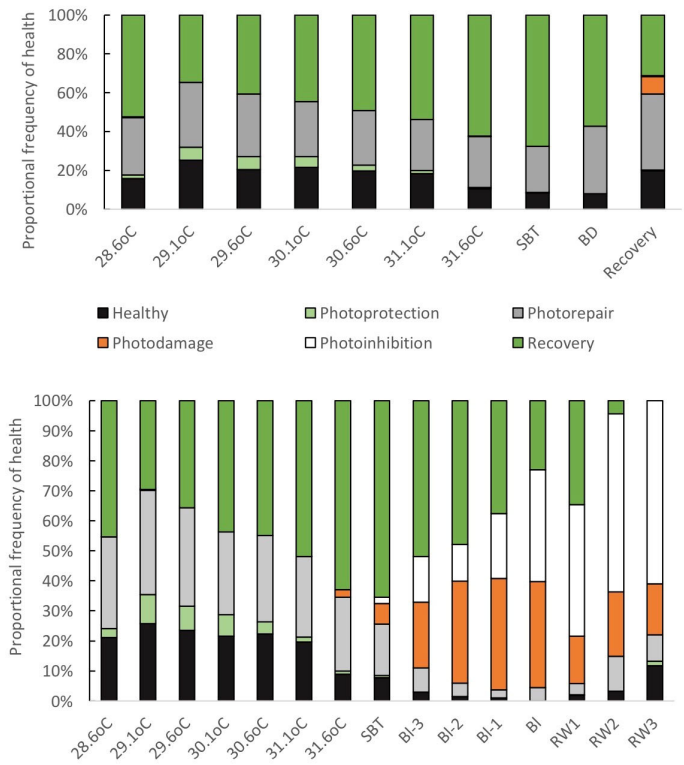

Figure 4. Shifts in photosynthetic health states across temperature exposure and recovery. Stacked bar plots show the proportional frequency of health phases (healthy, photoprotection, photorepair, photodamage, photoinhibition, recovery) across control (top) and experimental (bottom) coral samples. Experimental corals were exposed to incremental temperature increases (0.5 °C every 3 days) leading to the Standard Bleaching Temperature (SBT; 31.6 °C), followed by recovery. Health phase distributions illustrate progressive reorganization of photosynthetic function with increasing thermal stress, highlighting non-linear transitions among protective, damaged, and inhibited states rather than a simple monotonic decline. Recovery bars represent post-stress reassembly of functional states.

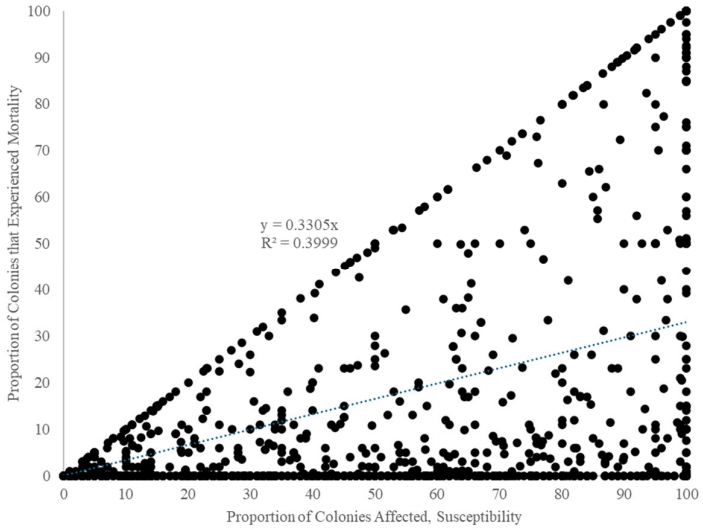

Figure 5. Scatterplot of paired bleaching susceptibility and mortality data (n = 1363), illustrating the non-linear relationship between susceptibility and lethal outcome. While a positive upper-bound trend is present,

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susceptibility alone explains limited variance in mortality, revealing substantial dispersion across the response space. This triangular distribution demonstrates that high susceptibility does not deterministically predict mortality, and that lethal bleaching represents a perpendicular transition rather than a linear extension of susceptibility. The structure highlights the limits of susceptibility as a predictive metric and underscores the role of system architecture and state-dependent thresholds in coral survival outcomes.

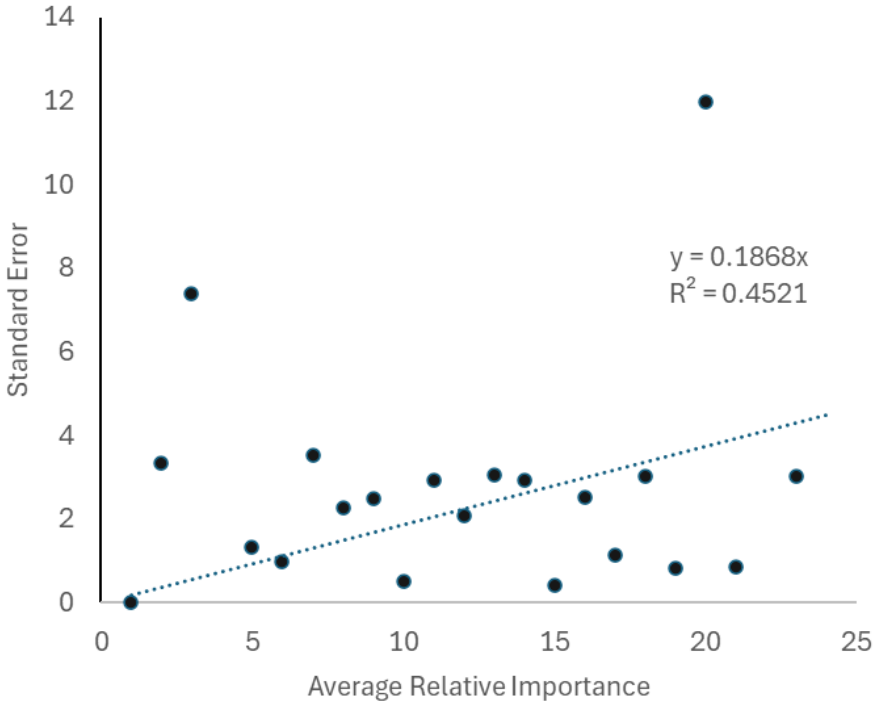

Figure 6. Summary of the relationship between average relative importance (ARI) of predictor variables and their standardized effect sizes on bleaching susceptibility. While a positive trend is observed (R^2 = 0.45), substantial dispersion indicates that high explanatory importance does not uniformly translate into strong effect magnitude. This decoupling highlights the presence of multiple susceptibility architectures, where some drivers exert consistent but modest influence, while others produce disproportionate impacts despite lower relative importance. The pattern reinforces a non-linear, multi-dimensional susceptibility landscape rather than a single dominant causal hierarchy.

3.3. The System Architecture of Mass Bleaching Responses

Mass Bleaching Events represent coordinated responses within a complex biological system rather than isolated failures of individual colonies. Across datasets, bleaching susceptibility and bleaching mortality do not scale linearly, indicating that loss of symbionts and colony death represent related by distinct outcomes within the holobionts response space. To characterize this system-level structure, the Bleaching Response Metadatabase was explored to identify how environmental, biological, and temporal inputs partition variation in bleaching susceptibility and mortality across contexts.

To move beyond binary observations of bleaching presence or absence, a standardized metric was developed to quantify the relationship between susceptibility and mortality, The Bleaching Efficiency Quotient (BEQ), is defined as [(Susceptibility – Mortality) / Susceptibility]. The BEQ provides a normalized scale to compare bleaching outcomes across studies, enabling evaluation of how susceptibility and mortality co-vary through time and across environmental and biological drivers.

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3.3.1. Factored Components of Mass Bleaching Susceptibility and Mortality

Bleaching responses are undeniably confounded by a lot of variables [Table 4A], and taxonomy represents less than 2% of the overall variation in bleaching susceptibility [Table 4Aa] or mortality [Table 4Ad]. 35 variables (some made redundant and denoted on the tables with asterisks) were tested [Table 4Aa, susceptibility; 4Ab, mortality] and ANOVA found 22 variables highly significant for susceptibility and 27 variables highly significant for mortality. Less significance was also recorded ($p<0.01$ and $p<0.5$) and reflected 4-6 variables while only 7 variables (of the 35 tested) were not significant for susceptibility, and only 4 (of 35) variables were not significant for mortality. Pearson's correlation coefficients for susceptibility [Table 4Ae] help further define, but still include 12 highly significant variables, while mortality coefficients [Table 4Af] had 20 variables that showed significance. Time to recover was the best fitting correlate for either susceptibility [0.355, 4Ae] or mortality [0.490, 4Af]. Moreover, when we look at the grouped relative importance of factors for susceptibility [6c] and mortality [6d], timing of observations caused 21.1% and 30.1% of the variability in susceptibility or mortality, respectively, weather conditions caused 28.7% and 19.6% of the variability in susceptibility and mortality, respectively. Location explained 24% of the variability in susceptibility and 16% of mortality, while biological and ecological factors represented 15.1% and 22.7% of susceptibility and mortality, respectively.

Taxonomy was notably low on the spectrum of importance for noted factors in both zooxanthellae densities [Tables 1A, 2A] and bleaching susceptibility and mortality [Table 4A], so data were regrouped with *post hoc* analyses [Table 5] and restricted by taxonomic recordings, to re-analyze (Table 6A) as taxonomy is widely used to describe disturbance impacts in coral ecology. The data (Table 6A) still show high variability and higher importance of other factors. Notably, for families (Table 6Aa) and genera (Table 6Ab), the top 5 always included thermal stress accumulation, timing of observations, the ocean_subregion, and bleaching occurrence. The analyses for Species (Table 6Ac), however, showed a wild trend, where the greatest factor for susceptibility was whether the coral transmits algae to its offspring. For species [Table 6Ac], corals that do transmit algae to their offspring are highly significantly less susceptible than corals that do not transmit algae to offspring [Table 6A]. Intra-taxonomic resolution was not fully analyzed as this document moves towards the sentinel disturbance guilds, but, as an example, *Pocillopora damicornis* had a range of healthy zooxanthellae densities from $0.35x10^6$ cells/cm^2 [71] up to $10x10^6$ cells/cm^2 [72].

Post hoc results of [55] illustrate the change of perception in timing of observations and discrepancies due to the timing of observations for growth forms [Figure 5A] and growth forms through time (related to the onset of thermal stress) [Figure 6A]. When broken down by our time; the x-axis shows time and the y-axis shows the percent impacted, so we can monitor impacts through time. [Figure 6A] represents the change in perception of bleaching responses - susceptibility and mortality - caused by timing of observations (in months relative to thermal stress accumulation, for the pooled 20DHW thermal data, highest count). The peak bleaching susceptibility and mortality of branching corals occurs about 4-5 months, observations taken after this may underestimate susceptibility/mortality due to unknown cause of death (e.g. algal overgrowth from within where the tissues held in the porosity of skeletons have not won their way in competition back to the outside of the colony and are overwhelmed by the algae that are present to replenish the zooxanthellae populations). Massive colonies, however, reach a peak in susceptibility/mortality at about 8 months, but have been shown to have a high heat capacity (e.g. essentially concrete) and have been shown to retain heat stress for up to 3 years [73]. Biological factors will be fully explored in their own sections.

Thermal stress and timing of observations represent a relative importance of 40-58% of the variability in the dataset [Table 4Ac, 4Ad], and were thus explored by Tukey's *post hoc* to simplify for further analysis [Table 5A]. Temperatures and thermal stress were re-grouped into 'Thermal Stress Accumulation' which was partitioned into 3 levels, high medium or low [Table 5A, Figures 7A-9A]. The thermal stress accumulation categories removed all but one instance of a highly significant result, the 'Medium' category of Susceptibility, although there is still obvious importance within the categories [Table 5, a-d]. 'Timing of Observations' relative to Thermal Stress Accumulation are

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another *post hoc* data grouping [Table 5, a-d] and are separated by months since the onset of thermal stress into three categories, the beginning, middle, and end of events. The timing categories lower the overall variability, but in opposition to the thermal stress categories, *post hoc* analysis of the timing of observations seems to open more significance to be explored [Table 5A, a-d]. Location caused variability in the zooxanthellae densities [Tables 1 and 1A and 2A] and bleaching responses [Tables 3A and 4A] and represents some 16-24% of the variability in responses [Table 4Ac, 4Ad], so Tukey's *post hoc* was used to further explore this category [Table 5C, a-j]. The *post hoc* category of subregion within ocean basin removed some variation from location significance [Table 5AC, i-j] and will henceforth be used.

Table 4. Trait-structured constraints on symbiont cladal diversity across coral functional groups. Descriptive statistics of cladal counts (mean ± SE), sample sizes, and observed upper ranges are shown for skeletal architecture, reproductive mode, symbiont transmission, morphology, and genus. Cladal diversity is not continuously distributed but constrained within discrete, trait-defined bounds, indicating that symbiotic flexibility is biologically structured rather than uniformly available across coral lineages.

Field	Factor	Average Cladal Count	Counts	SE	Upper Range
Complexity of Skeleton	Complex	1.26	111	0.073	5
	Robust	1.17	156	0.037	4
Reproductive Mode	Brooder	1.60	5	0.245	2
	Spawner	1.37	68	0.115	5
Sexual Reproduction	Gonochoric	1.06	17	0.059	2
	Hermaphroditic	1.47	59	0.131	5
Transmission of Algae to Offspring	No	1.42	60	0.126	5
	Yes	1.43	7	0.297	3
Morphology	Branching	1.19	27	0.085	3
	Free living	1	6	0	1
	Massive	1.31	13	0.133	2
	Sub-massive	1.43	7	0.202	2
	Tabular	1	3	0	1
Genera	Acropora	1.57	37	0.2	5
	Cyphastrea	1	5	0	1
	Echinophyllia	1	6	0	1
	Echinopora	1.25	8	0.164	2
	Favia	1.29	7	0.184	2
	Fungia	1	9	0	1
	Galaxea	1.57	7	0.202	2
	Goniastrea	1.25	8	0.164	2
	Goniopora	1	6	0	1
	Hydnophora	1.6	5	0.245	2
	Leptoseris	1	5	0	1
	Lobophyllia	1.17	6	0.167	2
	Montastrea	1.33	6	0.211	2
	Montipora	1	17	0	1
	Pachyseris	1	5	0	1
	Pavona	1	6	0	1
	Platygyra	1	7	0	1
	Pocillopora	2	6	0.516	4
	Porites	1	10	0	1
	Psammocora	1	9	0	1
	Symphyllia	1	5	0	1
	Turbinaria	1.5	6	0.224	2

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Table 5. Skeletal complexity as a structural modifier of bleaching susceptibility, mortality, and recovery across thermal stress accumulation and observation timing. Average values of skeletal complexity are presented across low, medium, and high thermal stress accumulation, resolved by timing of observation relative to stress exposure (beginning, middle, end). Data were restricted to pair-wise susceptibility–mortality entries and *post hoc* grouped to minimize variance attributable to timing effects (see Table 5A; Figures 7A-9A); only observations with n ≥ 3 were retained. Values are ordered by thermal stress accumulation, timing of observation, and mortality, illustrating how skeletal architecture modulates bleaching outcomes through differential exposure, tissue integration, and survivorship under escalating thermal stress.

Thermal stress accumulation	Timing of observations	Complexity of skeleton	Susceptibility	±SE	n	Mortality	±SE	BEQ (S-M)/S
Low	Beginning	Complex	39.51	2.07	280	7.10	1.16	0.82
		Robust	40.60	2.00	271	4.95	0.96	0.88
	Middle	Complex	48.63	3.76	87	9.85	2.58	0.80
		Robust	35.67	3.52	89	3.09	0.77	0.91
	End	Complex	37.50	3.46	99	16.41	3.04	0.56
		Robust	33.76	3.07	108	7.74	1.62	0.77
Medium	Beginning	Complex	51.22	5.19	54	8.48	3.12	0.83
		Robust	37.78	3.25	107	3.01	0.87	0.92
	Middle	Complex	33.20	5.45	25	14.52	4.26	0.56
		Robust	29.86	5.06	36	3.28	1.14	0.89
	End	Complex	68.10	3.86	94	48.94	4.48	0.28
		Robust	64.34	3.90	80	41.70	4.54	0.35
High	Beginning	Robust	55.73	13.50	10	17.93	3.57	0.68
		Complex	42.45	14.12	11	3.57	9.28	0.92
	End	Complex	80.45	7.50	20	70.85	9.57	0.12
		Robust	100.00	0.00	20	58.54	10.81	0.41

Beyond the physical characteristics that provide the rules for bleaching responses on larger spatial scales [Tables 3A, 6A and 7A], the diversity of bleaching responses is consistently undermined by Biological factors outside of taxonomical categorization. The Biological factors account for 15.1% of the noise in the datasets in bleaching susceptibility [Table 4Ac], 22.7% for mortality [Table 4Ad], and 16% of the noise in the dataset for recovery [Table 3]. To further the view of these biological factors, *post hoc* results of bleaching responses [Table 4A] were used to form data groupings [Table 5D, a-d] for growth form to shift to a Level of Colony Integration (LCI) model, where low represents more solitary form corals, medium represents sub-massive, massive, and encrusting, and high represents more branching and tabular growth forms.

3.3.2. A Thermal and Time-Relative Matrixed View of Bleaching Responses

To examine how bleaching susceptibility, mortality and recovery vary jointly with thermal stress intensity and timing, *post hoc* regroupings [Table 5] were used to partition data into categories of Thermal Stress Accumulation (TSA) and Timing of Observations (TOB) relative to TSA, and these are matrixed [Tables 7-11 and 6A-10A] and are presented similar to the previous table pairs of Descriptive Statisticvs [Tables 7-11, 6A, 7A 8Aand 9A] alongside Tables of analytical statistics [Table 10A], to create dynamic equations for zooxanthellae densities [Tables 1A and 2A], susceptibility and mortality [Tables 7-11, 8A-10A] and recovery [Table 3]. While the analytical statistics are presented for all [Table 10A], the descriptive statistics [Tables 7-11, 8A and 9A] are organized by factors and then matrixed within TSA and TOB to gain insight into the underlying patterns.

Taxonomy through time and stress is shown in [Table 6A] for Families [Table 6Ai), Genera [Table 6Aii], and Species [Table 6Aiii]; however, it is outside the purveyance of the new aims of this document due to the low relative importance in finding variability in bleaching susceptibility and mortality [Tables 3A and 4A, which show taxonomy to represent <2-5% of overall variability in responses] or recovery [<7% relative importance of time to recover, Table 3]; moreover, when data

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were restricted to taxonomic recordings [Tables 4A] factors still showed greater significance. Furthermore, taxonomic ranking and bleaching quotients were variable through thermal stress accumulation and timing of observations [Table 6Ai, 6Aii, 6Aiii]. Factors of importance are presented within the matrixed TSA and TOB categories, and include Biological [Tables 4-9] which are represented by Complexity of Skeleton [Table 5], Reproductive Mode [Table 6], Sex [Table 7], the Transmission of Algae to Offspring [Table 8] and Colony Morphology [Table 9], Ecological factors [Table 9A] are represented by Depth, Habitat and Anthropogenic Input. Time was a major factor represented in various fashions, and bleaching occurrence is explored as a section of its own [Table 10], and other timing [Table 11]. The *post hoc* categories of locations (subregions within oceans) are shown through TSA and TOB [Table 12] and also have their own section.

Physical factors showed some consistencies through time [Tables 9A and 10A], Deeper depths (15-18m+) consistently had a higher bleaching quotient -overall bleaching susceptibility produced less mortality. Habitats followed a similar trend in that reef slopes had a BEQ closer to 1, which was also true for lesser events in the shallows; however, greater thermal stress accumulation overwhelmed shallower habitats with accumulation of stress and lead to overall reef health deterioration [Table 9A]. Non-polluted areas and polluted areas with management maintained more efficient bleaching responses, while polluted areas without protection fared worse [Table 9A].

Overview of Matrixed Descriptive Statistics

Thermal bleaching accumulation categories and timing of observations are summarized by paired observations and their explanatory powers [Figures 3A-5A]. Low Thermal Stress Accumulation [Figure 3A] shows that the explanatory power of susceptibility relates much stronger to mortality [Figure 3A, bottom; R^2 of 0.45) at the end of events; however, not that over half of the responses are not quantified by thermal stress nor the timing of observations relative to thermal stress, supporting the notion to explore phenotypic responses within these categories. Medium Thermal Stress Accumulation [Figure 4A] shows almost double the explanatory power of susceptibility relating to mortality (based on R^2 values) as timing of observations continue, such that at the end of events [Figure 4A, bottom] the correlation coefficient is 0.75. High Thermal Stress Accumulation [Figure 5A] also correlates susceptibility higher to mortality as the timing of observation lengthen, with an end explanatory power of 0.79 for just temperature and timing of observations relative to thermal stress accumulation. Notably, there is not a 1:1 relationship between thermal stress accumulation and timing categories, and that further implies [e.g. Figure 9] underlying mechanisms in biology and ecology that are ultimately influencing bleaching responses.

The overall trends in records (*n*) across the matrixed categories of thermal stress accumulation and timing of observations relative to thermal stress accumulation will be explored, as the results are unevenly distributed counts [e.g. Figures 7A-9A] and the factors of data analyses and restrictions for statistical analyses have changed the number of records in each overall matrixed category [Figures 7A-9A]. Notably, there are 618/1877 total records, or 33.33%of the total records that are in the beginning TOB of Low TSA, versus 94/1877 records, or 0.05% for the End (TOB) for all levels of TSA. From a broad scale of trends, the High TSA were less selective and generally induced higher mortality from susceptibility, while Low and Medium TSA had more observations and greater variability than High TSA [Table 10A]. In Low and Medium TSA, the rank-order of susceptibility, mortality, and the bleaching quotient are generally inconsistent and diverse through time [Table 10A], while, in contrast, observations of High TSA further detail the importance of noting and quantifying the variability and relativity of time. dependent on a different dimension of time, as the bleaching occurrence held the clearest contrasting results [Table 10A] and show that the first time a reef experiences an event, the bleaching efficiency quotient is 0.01, while the fifth time a reef has experienced TSA and bleached, the quotient is 0.98 – this reflects 100% susceptibility in both cases, but mortality is null at the end of the 5th experience of a heavy event, where it was once nearly 'absolute'. Note, that these, High TSA, End TOB, were the data with fewest records. In a trend somewhat similar to thermal stress accumulation, the Beginning (n=824) and Middle (n=293) of events

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had greater variability, while the End (n=464) timing of observations relative to the onset of thermal stress were more straightforward and less variable [Table 10A].

Low TSA [Table 10A} records (*n*=1449) were mostly at the onset of events (*n*=618), with fewer observations in the middle (*n*=186) or end (*n*=213). At the Beginning TOB of Low TSA [Table 10Aa], 20 factors were tested, with 9 being highly significant for susceptibility [Table 10Aai] and 2 highly significant correlations, habitat and generalization [Table 10Ai1]; moreover, mortality also had 9 significant factors of 20 [Table 10Aaii], with 3 factors significantly correlating to mortality, doldrums, decade, and the Level of Colony Integration [Table 10Aaii1]. In the Middle TOB of the Low TSA [Table 10Ab], 16 factors were studied, with 5 producing highly significant impacts on susceptibility [Table 10Abi] and 2 producing significant correlations [Table 10Abi1], subregion within Ocean, and months of observations. Mortality for the Middle of the Low TSA has 4 significant factors of 16 [Table 10Abii], relief from weather, habitat, subregion within Ocean, and depth, with no strongly significant correlations [Table 10Abii1]. The End TOB of the Low TSA [Table 10Ac] contained 18 factors, of which 5 were highly significant for Susceptibility [Table 10Aci] and 2 factors highly correlated [Table 10Aci1], Reef Type and ; while Mortality had 8 factors that were highly significant [Table 10Acii], and 2 that were highly corelated [Table 10acii1] subregion within ocean and Family.

Medium TSA [Table 10B] had observations (*n*=334) at the beginning (*n*=180), few in the middle (*n*=74) and most at the end (*n*=198).The Beginning TOB of the Medium TSA [Table 10B] explored 19 factors, of which 8 had a highly significant impact on susceptibility [Table 10Bai], and 2 factors that highly correlate, Months of Observations and subregions within Oceans [Table Bai1]; while, Mortality data had 2 significant factors [Table Baii]: subregion within Ocean and Family, and no highly significant correlates [Table Baii1]. The Middle TOB of the Medium TSA [Table 10Bb] had 9 factors with enough data to study. For susceptibility, two were significant [Table 10Bbi] and one correlated [Table 10Bbi1], bleaching occurrence; while mortality results [Table 10Bbii] had subregions within Ocean Basins and the Level of Colony Integration as highly significant, with the subregion within the Ocean as the only highly significant correlation [Table 10Bii1]. The End TOB of the Medium TSA [Table 10Bc] had 20 factors that were able to be studied, of which 8 were significant [Table 10Bci] and correlated [Table 10Bci1] to susceptibility, while 8 were significant [Table 10Bcii] and 6 correlated [Table 10Bcii1] for mortality.

High TSA [Table 10C] records (*n*=94) were lowest overall with the Beginning (n=24), Middle (*n*=19) and End (*n*=19) representing the least number of records within the matrix. The Beginning TOB of High TSA [Table 10Ca] studied 14 factors, with only one significant factor for susceptibility, depth [Table 10Cai] and no highly significant correlations [Table 10Cai1], while Mortality data showed 4 highly significant factors [Table 10Caii] with 3 highly significant correlations [Table 10Caii1], Months of Observations, Degree Heating Weeks, and Bleaching Occurrence. The Middle TOB of the High TSA [Table 10Cb] studied only 2 factors the data were so low and represented no highly significant relationship by ANOVA for either susceptibility [Table 10Cbii] or mortality [Table 10Cbii] nor highly significant correlations for susceptibility [Table 10Cbi1] or mortality [Table 10Cbii1]. The End TOB of the High TSA [Table 10Cc] had enough records to analyze 13 factors with 4 factors each highly significant for susceptibility [Table 10Cci] and mortality [Table 10Ccii] – three of which were shared, Bleaching Occurrence, Level of Colony Integration, and subregion within Ocean basin; whereas Susceptibility was also influenced by Family, and Mortality was also influenced by Depth. In addition, susceptibility of End TOB, High TSA correlated to the Level of Colony Integration [Table 10Cci1], while mortality highly correlated to bleaching occurrence and depth [Table 10Ccii1].

Systems Architecture of Bleaching Responses

Bleaching susceptibility [Figure 6] behaves like a distributed, additive system where many predictors contribute incrementally, and their influence is relatively stable across contexts [e.g. R^2 = 0.45]. Notably the 2 high standard errors [y-axis] are related to Complexity of Skeleton and Bleaching Occurrence, both of which host double digits worth of relative importance. In contrast, bleaching

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mortality [Figure 7] exhibits threshold-like behavior, where once critical conditions are exceeded, different rules govern outcomes. The strong relationship [R^2 = 0.81] shown between relative importance and uncertainty observed for mortality [Figure 7) indicates that dominant predictors are also highly context-dependent, consistent with a high-dimensional, adaptive system near a tipping point. By comparison, the absence of such scaling for susceptibility [Figure 6] suggests nonlinear collapse dynamics in which survival outcomes become decoupled from environmental gradients; this pattern is consistent with cryptic evolutionary filtering and partial mortality processes, whereby extreme stress selectively prunes vulnerable tissue and symbiont configurations while preserving resistant and resilience types.

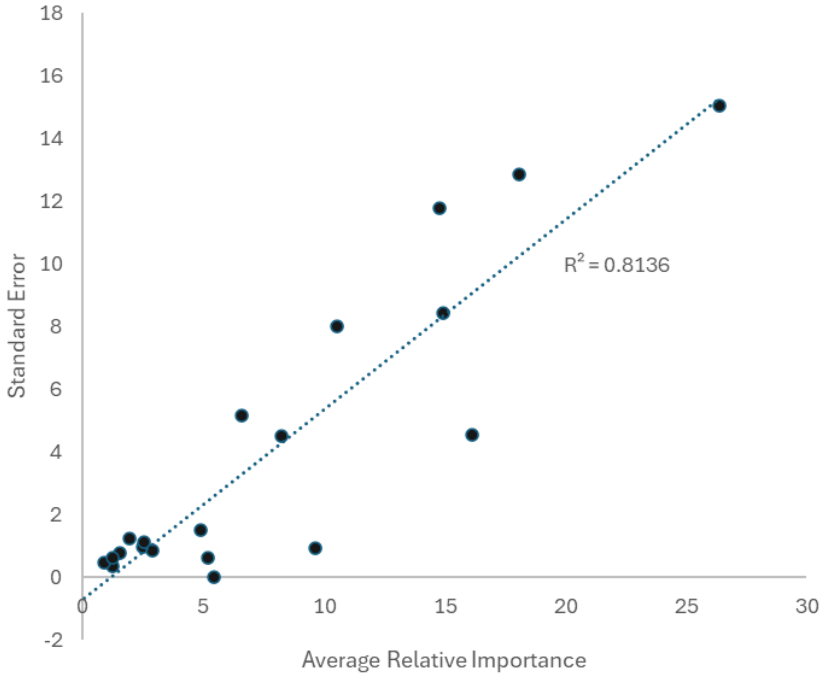

Figure 7. Relative importance scales more directly with impact on bleaching mortality than susceptibility. Summary of the relationship between average relative importance (ARI) of predictor variables and their standardized effect sizes on bleaching mortality. In contrast to susceptibility (Figure 6), mortality exhibits a stronger, more coherent scaling between explanatory importance and effect magnitude (R^2 = 0.81), indicating a narrower and more deterministic failure architecture. This pattern suggests that while susceptibility arises from multiple overlapping pathways, mortality reflects convergence onto a smaller subset of dominant drivers, consistent with threshold-mediated system collapse rather than distributed stress response.

3.3.3. Unravelling the Mechanisms of Bleaching Recovery

As both bleaching definitions [Tables 1A and 2A] and bleaching response metrics [Table 4A] correlate most strongly with recovery capabilities [Table 3e, 3f], these results indicate that bleaching susceptibility is inherently linked to recovery dynamics rather than just mortality alone. The processes governing the initial responses of bleaching cannot be fully interpreted without observing the outcome of recovery, as recovery itself is contingent upon the severity and structure of the initial response. The misalignment of cause and effect represents a persistent misperception of time in underlying assumptions and it mis-scales interpretation of bleaching studies as susceptibility is best understood not as a measure of weakness, but as a position along a fight-flight spectrum of sentinel disturbance strategies, where recovery capacity provides the appropriate functional context for interpretation. Therefore, a useful metric of exploring susceptibility may be understanding recovery and the fight or flight spectrum of sentinel disturbance guilds.

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During OISEO [42], I observed that the earliest bleaching corals exhibited multiple recovery pathways, including partial mortality, endolithic persistence, and post-disturbance tissue re-emergence [The Phoenix Effect, 43]. Approximately one-third of colonies that initially sloughed tissue and were presumed dead subsequently regenerated living tissue. This response was associated with perforated, high-complexity skeletons that permit tissue retention within skeletal refugia during unfavorable conditions [supported by pers. Comms. with Professors Andrew Baird and Scott Smithers], followed by recolonization of the skeletal surface once environmental conditions return to ambient levels. In contrast, corals lacking these architectural recovery mechanisms exhibited reduced capacity to retain symbiont diversity and were more likely to resist bleaching outright or experience higher partial mortality when stressed.

Taken together, these recovery pathways indicated that bleaching outcomes are constrained not only by the magnitude and duration of thermal stress, but by the structural integrity of the coral holobiont itself. Skeletal architecture functions as a physical decision framework that governs tissue retention, symbiont preservations, and the temporal buffering of stress, thereby determining whether bleaching leads to regeneration, partial mortality, or collapse. Recovery is therefore not an independent phase following disturbance, but an emergent property of architectural resilience that is expressed through time. This framing establishes structural complexity as a central mediator linking susceptibility, morality, and recovery, and provides the foundation for evaluating how biological design features regulate bleaching responses across spatial and temporal scales.

Recovery data [Table 3] seem reliant on relief from stress and geographical location; however, these data are severalfold fewer (n<150) than either the susceptibility (n>2200) or mortality data (n>1500). Average recovery times are noted [Table 7a] amongst variables and the ANOVA test showed 7 highly significant factors: Shelf position, Relief from weather, Thermal Stress Accumulation, Anthropogenic Input, Location, Habitat, and Genus. Sex (gonochorism or hermaphroditism) also significantly impacted recovery (Table 7b; $p<0.5$). Four factors had a highly significant ($p<0.001$) correlation with recovery [Table 7c], Shelf Position, Anthropogenic Pressure, Degree Heating Index, and Relief from Weather; while sex and location were both significant ($p<0.5$). Notably, weather contained 63.5% of the relative noise in the recovery data [Table 7d], while biology/ecology represented 16.0% of the variability, Location represented 13.8% of the variability, and taxonomy represented 6.7% of the variability. A generic dynamic equation would thus be:

Bleaching Recovery

$$y = \text{Weather } (63.5\%) + \text{Biology and Ecology } (16.0\%) + \text{Location } (13.8\%) + \text{Taxonomy } (6.7\%) \quad (1)$$

Fewer observations were available on recovery, yet these preliminary results [Table 7] show that the ability of corals to recover after a mass bleaching event is most dependent upon the relief from weather which cuts recovery time in half, although inner reef shelf positions average 4 times longer to recover than mid-shelf or outer shelf reefs [Table 7a]. Areas of known high Anthropogenic Input took twice as long to recover as areas of medium or low anthropogenic input [12 months compared to 6, Table 7a]. French Polynesia was notably quicker to recover [3.29 month average, Table 7a] than the other locations, with the Centre of Biodiversity taking an average of 10.33 months to recover from bleaching [Table 7a]. Moreover, the biological and ecological traits [Table 7] appear to be the mediators that determine the outcome for the individual coral within environmental conditions. The finding that Hermaphroditic corals and Spawners have slightly faster average recovery times compared to Gonochoric corals and Brooders, respectively, is consistent with investigating the role of the reproductive strategies to define the bleaching responses.

3.3.4. Quantitative Resolution of the Paradox of Efficiency vs. Mortality

The bootstrap paradox of coral bleaching arises when resampling-based statistical methods are used to infer biological outcomes from variables that are not causally ordered. In such systems, predictors and responses are recursively defined: the same observations are used to estimate

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uncertainty, establish significance, and infer biological meaning. When the underlying process is non-linear or state-dependent, this circularity can obscure real structure, producing the illusion of noise or contradiction rather than resolution. This paradox becomes especially apparent when analyzing coral bleaching, where susceptibility, mortality, and recovery are often treated as sequential stages of a single failure pathway. Under this assumption, high susceptibility is expected to predict high mortality, and recovery is implicitly interpreted as incomplete failure rather than a functional response.

When susceptibility, mortality, and recovery are examined as triplet data values, the limitations of this framework become evident. The Average Relative Importance (ARI) analysis of susceptibility and mortality (Figure 8) reveals a positive overall trend ($R^2 = 0.6322$), yet the presence of significant outliers demonstrates that high susceptibility is not a deterministic precursor of high mortality. This statistical divergence defines the operational space of the recovery system architecture: a regime in which organisms successfully decouple environmental stress from lethal outcomes through sentinel buffering mechanisms. The bootstrap paradox is further quantified by the relationship between recovery and susceptibility (Figure 9; $R^2 = 0.5784$). Traditional models often interpret total bleaching as a near-death state. However, these data (Figures 8–10) show that for many sentinel guilds, total susceptibility is not pathological but functional. Rapid expulsion of dysfunctional symbionts preserves skeletal and tissue architecture, enabling subsequent tissue regeneration—a process described here as the Phoenix Effect. Notable exceptions to this pattern include *Madracis decactis* and *Scolymia sp*., who exhibited 0% susceptibility and mortality, and 500% recovery following a bleaching event. In these cases, bleaching functioned as a temporal opportunity for maximal habitat expansion, reframing bleaching as an adaptive window rather than a failure state [72].

By redefining bleaching metrics not as predictors of death but as indicators of system efficiency, this analysis resolves the bootstrap paradox without requiring additional data. Instead, resolution emerges through constraining what the data are allowed to explain: pattern persistence rather than linear prediction across time, space, and biological scale. The predictive limitations of traditional bleaching metrics become starkly evident when analyzing the relationship between susceptibility, mortality and recovery across triplet data values. The Average Relative Importance (ARI) of susceptibility and mortality of this triplet database is shown [Figure 8], while susceptibility and mortality are related to recovery [Figures 9, 10, respectively]. Susceptibility and mortality have a positive trend [$R^2 = 0.6322$, Figure 8], although the significant outliers demonstrate that high susceptibility is not a deterministic precursor of high mortality. This statistical gap represents the primary operational space of the recovery system architecture – the sentinel protocols that successfully decouple environmental stress from lethal outcomes.

The bootstrap paradox is further quantified by the dependence of recovery upon susceptibility [$R^2 = 0.5784$, Figure 9]. Traditional models often view total bleaching as a state of near-death; however, these data [Figures 8-10], reveal that for many sentinel guilds, total susceptibility is a functional requirement for total recovery. By rapidly expelling dysfunctional symbionts the holobiont preserves its architectural integrity, allowing for subsequent tissue resurrection – the Phoenix Effect. Notable exception to this trend includes two cases of extreme resiliency in *Madracis decactis* and *Scolymia sp*., where they showed 0 susceptibility, 0 mortality, and 500% recovery after the event [72] showing bleaching was a temporal opportunity for maximum habitat coverage rather than a traditional disturbance.

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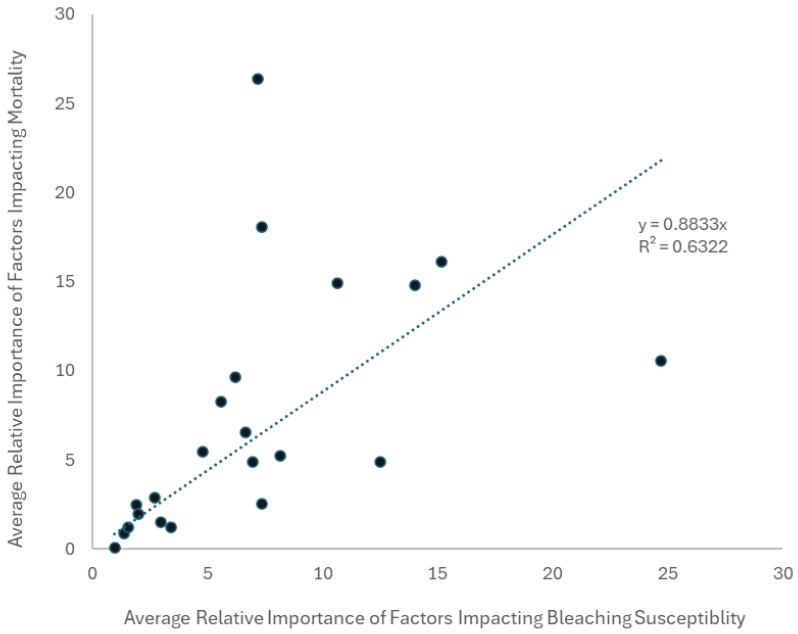

Figure 8. Data restricted to triplet values, examining the coupled relationship between bleaching susceptibility and mortality. Scatterplot shows the average relative importance of factors influencing bleaching susceptibility plotted against their corresponding importance for mortality, restricted to observations where susceptibility, mortality, and recovery were jointly reported. The strong positive relationship ($R^2 = 0.6322$) demonstrates that, within triplet-constrained datasets, susceptibility and mortality share coordinated signal, while retaining substantial variance among individual drivers. This highlights that predictive alignment emerges only when dimensional completeness is preserved, reinforcing the necessity of triplet-based interpretation in resolving bleaching outcomes.

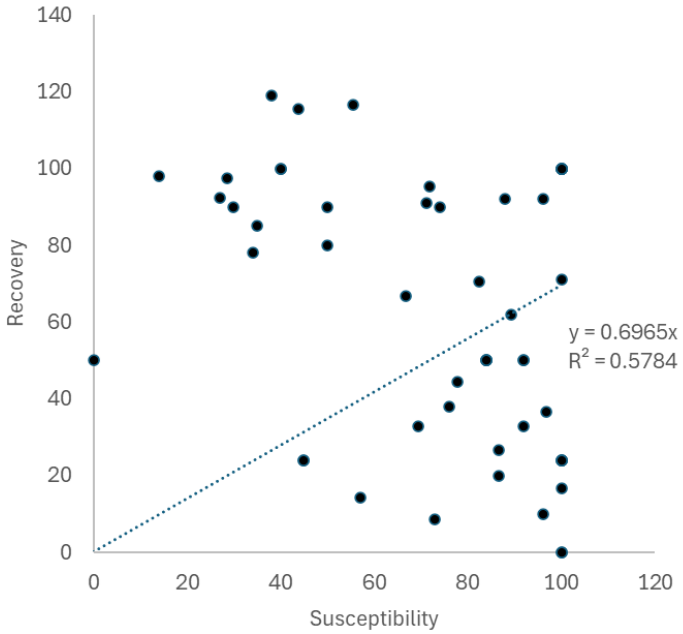

Figure 9. Relationship between bleaching susceptibility and recovery across triplet-restricted observations. Scatterplot shows recovery plotted against susceptibility for observations where susceptibility, mortality, and recovery were jointly reported. A positive but weakened relationship ($R^2 = 0.5784$) indicates that, unlike

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mortality, recovery does not scale linearly with susceptibility. High-susceptibility observations span a wide range of recovery outcomes, demonstrating decoupling between initial bleaching response and longer-term system reconstitution. This divergence highlights recovery as a distinct biological axis, governed by processes beyond immediate susceptibility to stress.

Finally, the weakest correlation within the triplet data is found between recovery and mortality [R2 = 0.3748, Figure 10]; this low predictive power reinforces the misperception of time inherent in current scientific discussion. Because 'mortality' is often recorded before the biological window for resurrection has fully closed, short-term or snapshot observations fail to account for the timing of recovery mechanisms, such as tissues hiding safe in endoskeletal refugia. The high degree of dispersion shown [Figure 10], validates the need for the BEQ as a more accurate metric for the holobiont's long-term survival architecture over static mortality counts.

Comparison of response predictors of bleaching susceptibility and mortality [Figure 14] show only partial correlation to mortality outcomes [R2 = 0.27]; the lower correlation indicates that factors governing bleaching onset substantially differ from those governing post-bleaching survival. Several predictors exerted strong influence on susceptibility [summarized in Table 4, 5-9], but weak influence on mortality, while others showed the inverse pattern, representing that bleaching does not represent a simple escalation toward death, but instead, marks a transition into distinct physiological regimes. This decoupling supports a phase-shift model in which bleaching functions as a stress detection and buffering response, while mortality reflects downstream filtering processes governed by internal host-symbiont architecture and tissue-level failure dynamics rather than external environmental gradients alone [which is consistent with Tables 5 and 6].

Table 6. Reproductive Modes as a structural modifier of bleaching susceptibility, mortality, and recovery across thermal stress accumulation and observation timing. Average values of skeletal complexity are presented across low, medium, and high thermal stress accumulation, resolved by timing of observation relative to stress exposure (beginning, middle, end). Data were restricted to pair-wise susceptibility–mortality entries and post hoc grouped to minimize variance attributable to timing effects (see Table 5A; Figures 7A-9A); only observations with n ≥ 3 were retained. Values are ordered by thermal stress accumulation, timing of observation, and mortality, illustrating how skeletal architecture modulates bleaching outcomes through differential exposure, tissue integration, and survivorship under escalating thermal stress.

Thermal stress accumulation	Timing of observations	Reproductive mode	Susceptibility	±SE	n	Mortality	±SE	BEQ (S-M)/S
Low	Beginning	Spawner	39.36	2.84	157	8.10	1.50	0.79
		Brooder	39.16	4.06	62	2.88	1.24	0.93
	Middle	Spawner	44.40	5.47	41	8.46	2.91	0.81
		Brooder	50.49	6.33	29	5.09	1.39	0.90
		Both	14	6.67	4	2.75	1.89	0.80
	End	Brooder	47.20	10.68	12	33.76	10.17	0.28
		Spawner	48.47	3.99	86	18.52	3.09	0.62
Medium	Beginning	Spawner	54.20	3.55	89	5.37	1.77	0.90
		Brooder	26.74	5.21	31	4.05	1.82	0.85
		Both	66.20	21.20	5	2.00	2.00	0.97
	End	Spawner	63.63	4.02	87	44.13	4.59	0.31
		Brooder	70.75	5.84	25	32.67	7.05	0.54
High	Beginning	Spawner	48.07	10.76	18	12.14	5.68	0.75
		Brooder	53.00	24.95	3	0.00	0.00	1
	End	Brooder	100.00	0.00	8	75.50	16.04	0.24
		Spawner	90.22	4.99	23	64.74	9.72	0.28

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Table 7. Mode of Sexual Reproduction as a structural modifier of bleaching susceptibility, mortality, and recovery across thermal stress accumulation and observation timing. Average values of skeletal complexity are presented across low, medium, and high thermal stress accumulation, resolved by timing of observation relative to stress exposure (beginning, middle, end). Data were restricted to pair-wise susceptibility–mortality entries and post hoc grouped to minimize variance attributable to timing effects (see Table 5A; Figures 7A-9A); only observations with n ≥ 3 were retained. Values are ordered by thermal stress accumulation, timing of observation, and mortality, illustrating how skeletal architecture modulates bleaching outcomes through differential exposure, tissue integration, and survivor-ship under escalating thermal stress.

Thermal stress accumulation	Timing of observations	Sex	Susceptibility	±SE	n	Mortality	±SE	BEQ (S-M)/S
Low	Beginning	Hermaphroditic	40.34	2.99	142	8.99	1.64	0.78
		Gonochoric	37.38	3.71	77	2.26	1.04	0.94
	Middle	Gonochoric	50.07	6.02	33	7.47	3.16	0.85
		Hermaphroditic	42.20	5.40	40	6.47	1.81	0.85
	End	Gonochoric	40.44	6.45	32	24.16	6.01	0.40
		Hermaphroditic	51.36	4.52	67	18.36	3.38	0.64
Medium	Beginning	Hermaphroditic	46.79	4.37	70	6.50	2.22	0.86
		Gonochoric	46.58	4.55	55	2.36	0.99	0.95
	End	Hermaphroditic	73.53	4.27	56	48.46	5.66	0.34
		Gonochoric	56.47	5.13	55	35.18	5.49	0.38
High	Beginning	Gonochoric	47.64	11.80	16	13.66	6.30	0.71
		Hermaphroditic	52.40	16.91	5	0.00	0.00	1
	End	Hermaphroditic	100.00	0.00	16	75.50	10.96	0.24
		Gonochoric	85.00	7.38	15	59.00	12.35	0.31

Table 8. Transmission of Algae to Offspring as a structural modifier of bleaching susceptibility, mortality, and recovery across thermal stress accumulation and observation timing. Average values of skeletal complexity are presented across low, medium, and high thermal stress accumulation, resolved by timing of observation relative to stress exposure (beginning, middle, end). Data were restricted to pair-wise susceptibility–mortality entries and post hoc grouped to minimize variance attributable to timing effects (see Table 5A; Figures 7A-9A); only observations with n ≥ 3 were retained. Values are ordered by thermal stress accumulation, timing of observation, and mortality, illustrating how skeletal architecture modulates bleaching outcomes through differential exposure, tissue integration, and survivorship under escalating thermal stress.

Thermal stress accumulation	Timing of observations	Transmission of algae to offspring	Susceptibility	±SE	n	Mortality	±SE	BEQ (S-M)/S
Low	Beginning	Yes	45.21	11.39	8	9.36	4.18	0.79
		No	61.32	3.67	68	7.20	2.42	0.88
		Both	66.20	21.20	5	2.00	2.00	0.97
	Middle	No	44.29	6.10	33	5.76	1.88	0.87
		Yes	48.35	7.59	22	2.39	0.60	0.95
	End	No	50.79	4.69	61	18.73	3.38	0.63
		Yes	39.76	7.27	23	14.29	5.49	0.64
Medium	Beginning	Yes	45.21	11.39	8	9.36	4.18	0.79
		No	61.32	3.67	68	7.20	2.42	0.88
		Both	66.20	21.20	5	2.00	2.00	0.97
	End	No	56.45	5.83	42	27.18	4.79	0.52
		Yes	50.30	6.54	25	19.38	6.25	0.61
High	End	No	82.50	13.89	6	63.17	18.49	0.23
		Yes	92.50	5.12	16	57.06	12.57	0.38

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Table 9. Level of Colony Integration as a structural modifier of bleaching susceptibility, mortality, and recovery across thermal stress accumulation and observation timing. Av-erage values of skeletal complexity are presented across low, medium, and high thermal stress accumulation, resolved by timing of observation relative to stress exposure (begin-ning, middle, end). Data were restricted to pair-wise susceptibility–mortality entries and post hoc grouped to minimize variance attributable to timing effects (see Table 5A; Figures 7A-9A); only observations with n ≥ 3 were retained. Values are ordered by thermal stress accumulation, timing of observation, and mortality, illustrating how skeletal architecture modulates bleaching outcomes through differential exposure, tissue integration, and survivorship under escalating thermal stress. Level of colony integration.

Thermal stress accumulation	Timing of observations	Colony integration	Susceptibility	±SE	n	Mortality	±SE	BEQ (S-M)/S
Low	Beginning	Low	25.45	4.39	43	0.95	0.46	0.96
		Medium	38.92	2.77	148	3.13	0.65	0.92
		High	37.71	2.75	169	13.50	1.97	0.64
	Middle	Low	30.79	13.94	7	2.69	1.34	0.91
		Medium	42.07	5.03	46	5.45	1.43	0.87
		High	55.62	5.95	37	20.00	5.53	0.64
	End	Low	31.70	12.53	9	16.52	9.00	0.48
		Medium	39.13	4.76	52	12.45	2.68	0.68
		High	55.33	5.61	50	28.60	5.19	0.48
Medium	Beginning	Low	38.39	4.87	18	1.28	0.76	0.97
		Medium	56.35	3.58	83	3.95	1.00	0.93
		High	34.70	6.33	37	10.08	4.27	0.71
	Middle	Medium	21.71	4.59	7	13.43	4.95	0.38
		High	42.25	12.71	8	42.25	12.71	0
	End	Medium	53.45	4.61	68	28.61	4.37	0.47
		High	72.62	4.40	60	51.73	5.70	0.29
High	Beginning	Medium	23.86	13.60	7	0.00	0.00	1
		High	58.61	10.47	17	21.32	8.92	0.64
	End	Medium	55.00	15.33	5	16.60	11.92	0.70
		High	97.22	2.78	36	82.49	6.17	0.15

Table 10. Bleaching Occurrence as a structural modifier of bleaching susceptibility, mortality, and recovery across thermal stress accumulation and observation timing. Average values of skeletal complexity are presented across low, medium, and high thermal stress accumulation, resolved by timing of observation relative to stress exposure (beginning, middle, end). Data were restricted to pair-wise susceptibility–mortality entries and post hoc grouped to minimize variance attributable to timing effects (see Table 5A; Figures 7A-9A); only observations with n ≥ 3 were retained. Values are ordered by thermal stress accumulation, timing of observation, and mortality, illustrating how skeletal architecture modulates bleaching outcomes through differential exposure, tissue integration, and survivorship under escalating thermal stress.

Thermal stress accumulation	Timing of observations	Bleaching occurrence	Susceptibility	±SE	n	Mortality	±SE	(S-M)/S
Low	Beginning	First	47.04	1.97	270	9.60	1.38	0.80
		Second	37.67	2.46	204	6.88	1.32	0.82
		Third	9.98	2.02	54	4.19	1.04	0.58
		Fourth	50.55	3.26	91	0.06	0.06	1
	Middle	First	54.35	3.02	124	8.09	1.97	0.85
		Second	14.28	2.51	38	5.43	1.72	0.62
		Fourth	28.13	5.90	25	3.48	1.62	0.88
	End	First	41.71	3.17	97	11.71	2.44	0.72
		Second	25.67	3.60	64	19.07	3.49	0.26
		Third	28.54	5.35	44	3.94	2.76	0.86
		Fourth	80.33	7.99	9	10.89	7.30	0.86
Medium	Beginning	First	56.53	3.91	58	8.76	2.89	0.84
		Second	24.00	4.06	31	9.42	2.27	0.61

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		Third	76.42	5.44	33	8.94	4.39	0.88
	Middle	First	22.47	3.08	57	12.70	3.00	0.43
		Second	68.44	6.04	18	9.44	3.41	0.86
	End	First	73.18	8.24	22	66.65	8.68	0.09
		Second	52.40	11.25	17	42.29	10.03	0.19
		Third	99.17	0.83	6	68.33	10.78	0.31
		Fourth	60.10	4.65	53	30.43	4.09	0.49
		Fifth	36.40	3.95	39	7.13	3.00	0.80
High	Beginning	First	41.62	9.21	21	9.52	6.56	0.77
		Second	97.33	2.67	4	54.65	6.88	0.44
	Middle	First	87.10	4.72	20	27.65	6.13	0.68
	End	First	100.00	0.00	31	98.74	0.90	0.01
		Second	58.75	11.87	12	34.00	12.46	0.42
		Fifth	100.00	0.00	7	2.14	0.51	0.98

Table 11. Average susceptibility and mortality values resolved by thermal stress accumulation phase, timing of observation, and ocean basin, using pair-wise susceptibility–mortality entries and post hoc groupings to minimize variance associated with timing and stress accumulation. Data are ordered by thermal stress accumulation and observation phase, revealing spatially structured differences in how susceptibility translates into mortality across regions. The (S–M)/S metric highlights basin-specific efficiency of mortality expression under comparable stress conditions.

Thermal stress accumulation	Timing of observations	Location	Susceptibility	±SE	n	Mortality	±SE	(S-M)/S
Low	Beginning	N. Indian	70.71	8.84	15	24.33	6.79	0.66
		N. Pacific	52.57	4.03	72	12.44	3.39	0.76
		S. Atlantic	45.26	5.99	28	2.11	1.79	0.95
		S. Pacific	27.95	3.09	121	0.05	0.04	1
		W. Indian	42.68	2.66	139	1.04	0.47	0.98
		W. Pacific	47.72	3.27	86	13.49	2.66	0.72
	Middle	N. Indian	24.81	4.64	49	17.09	4.64	0.31
		S. Atlantic	68.52	2.34	34	5.17	0.86	0.92
		S. Indian	54.07	4.38	54	0.30	0.24	0.99
		W. Atlantic	30.06	4.90	49	4.58	1.44	0.85
	End	E. Pacific	61.87	24.99	3	61.87	24.99	0
		N. Atlantic	30.21	6.04	15	15.54	2.62	0.49
		N. Indian	38.47	10.91	17	29.65	11.36	0.23
		N. Pacific	5.72	0.93	29	1.07	0.48	0.81
		S. Atlantic	0.00	0.00	4	0.00	0.00	***
		S. Indian	30.98	2.92	65	2.48	1.17	0.92
		S. Pacific	37.34	5.64	46	1.96	1.96	0.95
		W. Atlantic	57.33	7.92	18	26.02	6.07	0.55
		W. Indian	55.79	6.65	21	52.59	7.19	0.06
		W. Pacific	71.40	9.65	13	27.29	9.38	0.62
Medium	Beginning	E. Indian	0.00	0.00	4	0.00	0.00	***
		N. Pacific	31.84	10.49	13	5.38	2.34	0.83
		S. Atlantic	72.25	13.23	4	0.00	0.00	1
		S. Pacific	38.82	6.68	11	0.00	0.00	1
		W. Atlantic	32.43	2.79	114	2.85	0.73	0.91
		W. Indian	87.58	3.55	34	20.88	5.89	0.76
	Middle	E. Indian	19.23	2.67	40	6.35	1.97	0.67
		N. Pacific	61.35	6.46	23	13.35	4.51	0.78
		W. Indian	33.30	10.49	10	33.30	10.49	0
	End	E. Pacific	38.97	4.27	42	9.74	3.32	0.75
		N. Pacific	88.13	4.54	16	82.19	7.02	0.07
		S. Atlantic	74.75	4.92	4	0.00	0.00	1
		S. Pacific	74.00	17.11	4	51.00	18.89	0.31

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		W. Indian	26.67	13.33	3	0.00	0.00	1
High	Beginning	E. Pacific	50.53	8.77	25	16.74	6.52	0.67
	Middle	E. Indian	87.10	4.72	20	27.65	6.13	0.68
	End	E. Pacific	91.13	4.56	31	60.77	8.22	0.33
		N. Pacific	100.00	0.00	16	100.00	0.00	0

***Somehow this operation is currently undefined, although dividing by 0 is appropriate for health statistics.

Table 12. Regional comparisons linking symbiont density, bleaching susceptibility, mortality, and background variability. *Post hoc* analyses comparing locations across multiple dimensions of bleaching response. Data include correlations between zooxanthellae densities and bleaching outcomes (A), regional differences in healthy and bleached zooxanthellae densities (B), regional patterns of bleaching susceptibility and mortality (C), and contextualization of bleaching outcomes relative to natural variability and colony integration (D). Zooxanthellae densities are reported as $\times 10^6$ cells cm^{-2}; susceptibility and mortality are expressed as percent affected. All data were transformed prior to analysis (square-root transformation for proportional data; arcsine transformation for zooxanthellae densities). Standard error (±SE) is shown.

A) Correlation analyses linking symbiont density to bleaching outcomes across locations. Correlation analysis testing the relationship between zooxanthellae population density (healthy and bleached states) and bleaching observations (susceptibility and mortality) across locations. Results demonstrate a strong association between healthy and bleached symbiont densities, while relationships between density and bleaching outcomes are weaker and non-uniform, indicating that bleaching response is not a simple linear function of symbiont abundance alone

Factor	***n***	**Correlation coefficient**	**p**
Healthy and bleached	10	0.893	<0.001***
Healthy and susceptibility	10	0.346	>0.05
Healthy and mortality	10	0.431	>0.05
Bleached and susceptibility	10	0.059	>0.05
Bleached and mortality	10	0.191	>0.05
Susceptibility and mortality	10	0.500	>0.05

B) Mean zooxanthellae population densities for healthy and bleached corals by location. Mean (±SE) zooxanthellae population densities for healthy and bleached corals across geographic regions. Regional differences reveal substantial spatial structure in baseline symbiotic states, with some locations maintaining higher symbiont densities even under bleaching conditions, suggesting location-specific buffering or historical filtering of symbiotic stability.

Location	**Healthy**			**Bleached**		
	Average	**±SE**	***n***	Average	**±SE**	***n***
East Indian	7.06	1.02	20	1.34	0.32	12
East Pacific	4.63	0.71	57	1.32	0.27	42
North Atlantic	1.89	0.16	13	0.44	0.12	10
North Indian	2.81	0.52	38	0.33	0.19	3
North Pacific	2.29	0.17	38	0.33	0.19	3
South Atlantic	3.29	0.28	18	0.82	0.26	11
Southern Pacific	2.28	0.48	23	1.03	0.19	4
West Atlantic	2.43	0.20	63	0.48	0.08	48
West Indian	11.09	1.13	40	3.03	0.46	25
West Pacific	2.58	0.26	103	0.93	0.15	79

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C) Regional variation in bleaching susceptibility and bleaching-related mortality. Mean (±SE) bleaching susceptibility and mortality (%) across reef locations. Geographic patterns show that susceptibility and mortality are partially decoupled across regions, highlighting that high susceptibility does not uniformly translate to high mortality and reinforcing the role of regional context in shaping bleaching outcomes.

Location	**Susceptibility**			**Mortality**		
	Average	**±SE**	***n***	Average	**±SE**	***n***
East Indian	56.13	3.53	118	22.69	3.58	78
East Pacific	56.63	3.49	126	28.39	3.85	112
North Atlantic	58.89	5.90	34	13.71	2.62	17
North Indian	61.25	4.54	62	38.07	6.44	43
North Pacific	44.15	1.94	347	24.31	2.59	223
South Atlantic	58.76	3.56	59	3.51	0.68	50
Southern Pacific	35.30	2.16	254	1.65	0.82	182
West Atlantic	45.73	1.62	463	8.81	1.02	389
West Indian	56.23	2.19	288	30.65	2.36	277
West Pacific	49.65	2.65	144	20.50	2.90	116

D) Bleaching outcomes relative to natural variability and colony integration. Comparison of natural fluctuations (% loss from the mean), sublethal bleaching, and lethal bleaching across locations and levels of colony integration (LCI). Categories of natural variability are based on prior statistical thresholds (Tables 1 and 2). This comparison contextualizes bleaching responses relative to background variability, illustrating that lethal bleaching frequently exceeds expected natural fluctuation ranges, while sublethal bleaching often overlaps with them.

Factor		**Natural variation**			**Sublethal bleaching**			**Lethal bleaching**		
Location	LCI	Average	*n*	**±SE**	Average	*n*	**±SE**	Average	*n*	**±SE**
East Indian	Low	24.12	8	1.5	62	3	0	81.00	3	0.00
	Medium	29.00	9	7.5	53.75	6	3.91	85.00	6	0.00
East Pacific	Medium	25.64	36	2.24	51.14	21	3.28	80.52	21	3.36
	High	34.82	17	9.61	47.00	13	4.07	82.80	13	1.68
North Atlantic	Medium	45.40	5	12.00	51.83	9	3.92	78.69	9	4.77
North Indian	High	21.67	16	3.77						
North Pacific	Medium	26.00	3	0	48.06	5	3.64	83.38	5	6.66
	High	32.38	29	2.81	64.20	10	5.81	94.5	10	0.67
South Atlantic	High	8.71	14	2.68	55.00	9	10.87	78.9	9	6.21
South Pacific	High	19.06	17	4.92	56.50	4	3.50	83.75	4	0.25
West Atlantic	Medium	33.84	44	4.28	47.72	11	1.56	87.45	11	2.34
	High	20.40	15	5.44	37.47	7	2.24	77.17	7	4.24
West Indian	Medium	68.77	33	5.87	67.78	28	2.67			
	High	38.57	7	7.67	45.00	3	0.00	68.00	3	0.00
West Pacific	Low	3.00	9	1.50	57.00	6	12.52	73.00	6	8.94
	Medium	34.50	4	7.50	52.00	3	0.00	63.75	3	2.75
	High	19.01	78	2.24	59.26	52	2.23	79.04	52	1.29

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Table 13. The five biological drivers underlying Scleractinian "Phoenix" responses to mass bleaching. This table synthesizes the primary trait axes identified across the Results (skeletal complexity, reproductive mode, sexual reproduction strategy, symbiont transmission, and level of colony integration) into a unified conceptual framework explaining non-linear bleaching outcomes. For each driver, the mechanistic basis of influence and its ecological significance are summarized, illustrating how coral survival, mortality, and recovery emerge from interacting biological architectures rather than from thermal stress exposure alone. Together, these drivers define the functional pathways through which corals persist, reorganize, or fail following bleaching disturbance.

	Skeletal Complexity	**Reproductive Mode**	**Sexual Reproduction**	**Transmission of Algae to Offspring**	**Level of Colony Integration**
Mechanism of Influence	Provides micro-habitats and light-scattering properties within the calcium carbonate structure.	Distinguishes between different strategies of larval development and settlement.	Involves the specific methods of gamete exchange and genetic recombination.	Defines whether symbionts are passed directly from the parent (vertical) or acquired from the environment (horizontal).	The degree of physiological connectivity and resource sharing between individual polyps.
Why it Matters	It acts as an underlying expression mechanism of bleaching survival by creating internal refugia for zooxanthellae.	This trait serves as a biological driver that determines how a colony expressed resilience or vulnerability during a bleaching event.	It is a key component in the system architecture of mass bleaching responses, influencing long-term recovery patterns.	This is a critical survival mechanism that dictates the stability of the symbiosis across generations	High integration allows the colony to function as a unified system, pushing the "death" of the organism into a perpendicular state through resource redistribution.

Over half of the variation in bleaching susceptibility was explained by the top three predictors: Bleaching Occurrence (average relative importance -ARI- of 24.72%), ocean_subregion (ARI 15.19%), Complexity of Skeleton (ARI 14.04%), while Location (ARI 14.41%) and Relief from Weather (ARI 10.65%) also had a 'double digit' impact. In comparison, bleaching mortality had the top 3 host over of 60% of variation: Habitat (ARI 26.39%), Months of Observations (ARI 18.07%) and ocean_subregion (ARI 16.14%), and other 'double digit' factors included the Complexity of Skeleton (ARI 14.78) and Bleaching Occurrence (10.57%).Notably, location-related variables, Bleaching Occurrence and Complexity of Skeleton maintained importance for both Susceptibility and Mortality. Here the skeletal porosity of coral clades explained 14-15% of the relative importance in differences in bleaching susceptibility and mortality across the 9 matrixed categories of thermal stress accumulation and timing of observations relative to the thermal stress onset. Skeletal porosity is impressive for its number and consistency. By contrast, taxonomy ranged from 1-4% relative importance and was relatively more inconsistent than complexity of skeleton 0.63-0.87 standard error vs taxonomy which ranged from 0.77-2.73.

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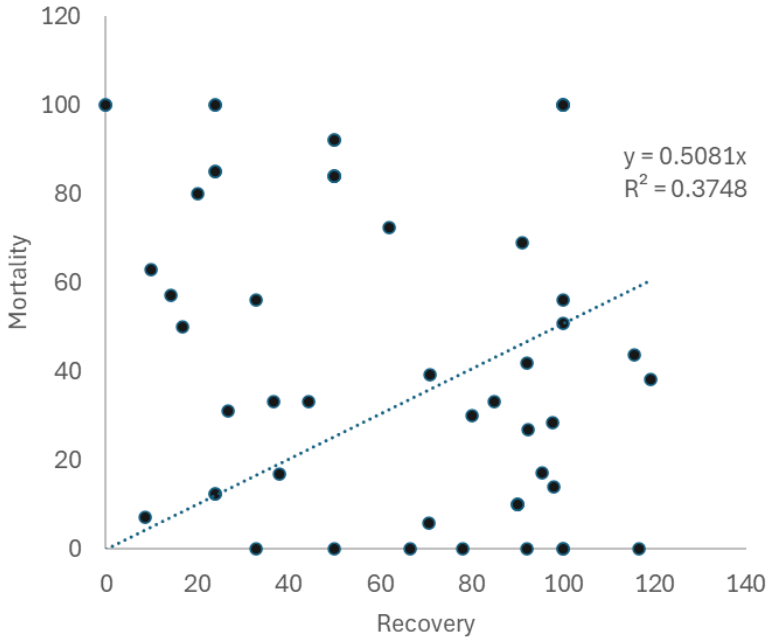

Figure 10. Relationship between recovery and mortality across triplet-restricted observations. Scatterplot shows recovery plotted against mortality for observations where susceptibility, mortality, and recovery were jointly reported. A moderate positive relationship (R^2 = 0.3748) indicates that higher mortality does not preclude recovery, nor does low mortality guarantee rapid system reconstitution. The broad dispersion of recovery values across the mortality axis demonstrates that recovery dynamics are partially decoupled from lethal outcomes, reinforcing recovery as an independent biological process rather than an inverse proxy of mortality.

3.3.5. Biological Drivers Undermining Bleaching Response Patterns

The residual variability in bleaching responses observed after accounting for timing and thermal stress accumulation [Figures 7A-9A] reveals a strong biological signature that cannot be explained by environmental forcing alone. This biological variability, consistently detected across bleaching susceptibility, mortality, and recovery metrics [Tables 3, 4A] alongside zooxanthellae densities [Table 1], represents the dominant unresolved component governing bleaching outcomes. Rather than reflecting noise or stochastic failure, these patterns indicate that coral-symbiont systems express structured, heritable response strategies that regulate bleaching as a functional survival mechanism. Recognizing bleaching as an outcome shaped by biological design – rather than solely by external stress magnitude – resolves the apparent paradox between ecological vulnerability and long-term geological persistence. By reframing susceptibility as a position along a spectrum of adaptive response strategies, this analyses shifts bleaching from a narrative of fragility to one of conditional resilience, rooted in phenotypic plasticity and co-evolved survival architectures.

Descriptive statistics of cladal representation across biological traits [Table 5] indicate substantial heterogeneity in baseline diversity prior to the application of environmental stress. Average cladal counts varied across skeletal complexity, reproductive modes, sexual system, symbiont transmission strategy, and morphology, with no single trait category overwhelmingly dominating representation. However, taxonomy and specifically genera, turned into a very fruitful data exploration for potential bleaching mechanisms [Table 5]. Counts were unevenly distributed among trait classes and taxonomy, reflecting both biological structure and sampling availability, but variability was consistently present across all categories. These baseline differences establish that biological diversity is intrinsic to the dataset before the influence of thermal stress or bleaching responses, providing necessary context for interpreting trait-mediated or genera-mediated effects observed in subsequent analyses.

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Skeletal Complexity as an Underlying Expression Mechanism of Bleaching Survival Mechanisms

Complexity of Skeleton is an ancestral trait to our fossil knowledge of Scleractinia. The co-evolutionary adaptation of half of Scleractinia (complex) to host endosymbiotic sponges and have porous skeletons. While the other half of Scleractinia has robust skeletons. Robust corals have evolved histidine systems, blood cells and other immune response systems such as photoprotectants (e.g. sunscreens) [74]. In contrast, Complex corals have the Phoenix effect, so having a complex skeleton affords one a vulnerability, but also pathways for recovery. This appears to us as a flight response, when in actuality, the coral is only susceptible as it can recover, but it is a gamble.

When susceptibility and mortality were examined jointly across thermal stress accumulation and timing of observations skeletal complexity consistently modulated bleaching outcomes [Tables 7 and 10]. Under comparable thermal stress regimes, complex and robust skeletal architectures exhibited divergent susceptibility, mortality and BEW values, particularly as observations progressed from the beginning to the end of thermal stress events. Differences between skeletal categories were low, medium, and high thermal stress accumulation with the magnitude of divergence increasing toward later observation periods. These patterns indicate that skeletal architecture influences the balance between susceptibility and mortality across temporal phases of bleaching, independent of stress intensity alone. The resulting BEQ values demonstrate that recovery potential and survival outcomes are contingent upon structural traits interacting with both the accumulation and timing of thermal stress exposure.

Together, these results [Tables 7 and 10] demonstrate that biological and architectural traits systematically shape bleaching responses event after accounting for thermal stress intensity and timing, highlighting intrinsic mechanisms that govern variability in susceptibility, mortality, and recovery.

Reproductive Mode as an Underlying Expression Mechanism of Bleaching Survival Mechanisms

Reproductive Mode contributed measurable variability to bleaching susceptibility and mortality across thermal stress accumulation and timing of observations [Tables 8 and 10A]. Across low thermal stress conditions, spawners and brooders exhibited comparable susceptibility early in events, while brooders consistently showed lower mortality values, resulting in higher BEQ values relative to spawners. As observations progressed toward the end of low-stress events, mortality increased in both reproductive modes, though brooders maintained a higher proportion of non-lethal responses.

Under medium thermal stress accumulation, divergence between reproductive modes became more pronounced [Tables 8 and 10A]. Spawners generally exhibited higher susceptibility values than brooders at both early and late observation periods, while brooders retained lower mortality despite comparable or elevated susceptibility. This pattern resulted in consistently higher BEQ values for brooders relative to spawners under medium stress conditions.

At high thermal stress accumulation, sample sizes were reduced; however, reproductive mode differences remained evident. Early observations showed brooders exhibiting zero recorded mortality despite elevated susceptibility, whereas spawners experienced measurable mortality. By the end of high-stress conditions, both reproductive modes exhibited high susceptibility and mortality, though brooders retained marginally higher BEQ values.

Across stress regimes, reproductive mode influences the balance between susceptibility and mortality more strongly than susceptibility alone, indicating that reproductive strategy contributes to variability in bleaching outcomes when environmental stress intensity and timing are held constant.

Mode of Sexual Reproduction as an Underlying Expression Mechanism of Bleaching Survival Mechanisms

Mode of sexual reproduction further refined bleaching outcomes by shaping the decoupling between susceptibility and mortality [Tables 9 and 10A]. Hermaphroditic taxa generally exhibited

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higher susceptibility than gonochoric taxa across stress categories, particularly under medium and high thermal stress accumulation; however, this increased susceptibility did not translate proportionally into mortality during early and middle observation periods. Instead, hermaphroditic corals frequently maintained higher BEQ values, indicating greater recovery potential despite extensive bleaching. This pattern supports the interpretation that elevated susceptibility in hermaphrodites reflects and adaptive shedding or reconfiguration response rather than intrinsic vulnerability.

By contrast, gonochoric taxa tended to show tighter coupling between susceptibility and mortality, especially toward the end of bleaching events. Under high thermal stress conditions, gonochoric corals experienced substantial mortality once susceptibility thresholds were exceeded, whereas hermaphroditic taxa retained a wider range of outcomes, including instances of complete susceptibility followed by partial or delayed mortality. These results suggest that sexual system influences the flexibility of pos0bleahcing trajectories, with hermaphroditism associated with prolonged survival and greater capacity for recovery following severe disturbances.

Transmission of Algae to Offspring as an Underlying Expression Mechanism of Bleaching Survival Mechanisms

Transmission of symbionts to offspring influenced bleaching outcomes primarily through its effects of bleaching efficiency rather than absolute susceptibility or mortality alone [Tables 10 and 10A]. Across low and medium thermal stress accumulation, taxa lacking vertical transmission generally exhibited higher susceptibility than those transmitting symbionts; however, this increased susceptibility was not consistently associated with higher mortality. As a result, non-transmitting taxa frequently maintained higher BEQs, particularly during early and middle observations periods, indicating effective de coupling of bleaching from lethal outcomes.

By contrast, taxa exhibiting vertical transmission tended to show longer susceptibility but a tighter coupling between susceptibility and mortality as stress accumulated, reflected in lower BEQ values under prolonged exposure. This pattern was most pronounced toward the end of bleaching events, where vertically transmitting taxa experienced comparable or elevated mortality relative to non-transmitting taxa despite reduced susceptibility. Under high thermal stress conditions, both strategies converged towards extreme outcomes, with susceptibility approaching saturation and BEQ declining sharply, indicating that symbiont transmission strategy does not confer resistance under severe stress but instead modulates the trajectory and timing of bleaching responses.

Taken together, these results suggest that vertical transmission functions less as a resistance mechanism and more as a constraint on post-bleaching flexibility. While inherited symbionts may stabilize early symbiosis, they appear to reduce the capacity for rapid symbiont turnover or restructuring during extreme disturbance, thereby limiting recovery pathways once bleaching thresholds are exceeded. This reinforces the interpretation that bleaching success is governed by architectural flexibility and recovery capacity rather than by symbiont fidelity alone.

Level of Colony Integration as an Underlying Expression Mechanism of Bleaching Survival Mechanisms

Level of Colony Integration exerted a strong and consistent influence on bleaching outcomes across thermal stress accumulation and timing of observation categories [Table 11 and 10A]. Across low and medium thermal stress, colonies with higher integration generally exhibited elevated susceptibility relative to poorly integrated colonies; however, this increased susceptibility did not scale proportionally to mortality. As a result, moderately to highly integrated colonies frequently maintained higher BEQ values during early and middle observation periods, indicating effective buffering of lethal outcomes despite pronounced bleaching responses.

As thermal stress accumulated and observations progressed toward the end of bleaching events, highly integrated colonies showed a marked decline in BEQ, reflecting increasing coupling between susceptibility and mortality. Under these conditions, mortality rose sharply in highly integrated

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colonies, suggesting that once internal buffering capacity is exceeded, failure propagates rapidly across the colony. In contrast, low-integration colonies displayed lower initial susceptibility and more variable mortality responses, resulting in intermediate BEQ values that were less sensitive to timing bit more heterogenous across stress regimes.

Under high thermal stress accumulation, differences among integration levels diminished, with BEQ collapsing across all categories as susceptibility approached saturation and mortality increased sharply. This convergence indicates that colony integration modulates the trajectory and timing of bleaching responses rather than conferring absolute resistance to extreme stress.

Overall, these results [Tables 11 and 10A] suggest that colony integration functions as double-edged architectural trait: enhancing internal resource sharing and recovery potential under moderate stress, while increasing vulnerability to cascading failure once physiological thresholds are exceeded. This pattern reinforces the interpretation that bleaching outcomes are governed by internal architecture and failure dynamics, rather than by external stress intensity alone.

3.3.6. The Impact of the Variability of the Underlying System Components of Time and Location on Bleaching Responses

Bleaching responses are not static properties of taxa or environments, but emergent outcomes of processes unfolding across space and time. As thermal stress accumulates and observations are made at different points along the disturbance – recovery continuum, the apparent magnitude and direction of bleaching susceptibility and mortality shift often producing contradictory interpretations when time is treated as a fixed variable rather than a dynamic system component.

The *post hoc* groupings for thermal stress and time [Table 5A] further impress the need for quantification of time as the effects of mass bleaching events vary over the course of time [Figures A7-A9, Tables 7-11 and 8A-10A]. Historically, the full picture of the durational impacts of bleaching has been misperceived due to the timing of observations relative to the physiological impacts felt by the organisms [Tables 7-11 and 8A-10A]. The impacts to massive and branching growth forms [represented in both medium and high levels of colony integration, Table 11] of bleaching events reflect a different story than one-off observations [Figures 5A and 6A]. For full durational studies, susceptibility is negligent through time between branching and massive growth forms, although mortality does vary [Figure 5A and 6A]. We have frozen time to their response [Figures 3 and 4] and we need to become aware and maintain mindfulness that actions change through time and relative perceptions provide bias.

Bleaching occurrence, defined as the number of bleaching events reported for a given location, exhibited on the strongest and most consistent relationships with bleaching responses [Tables 12 and 10A]. Susceptibility generally increased with the number of reported bleaching events, particularly under medium and high thermal stress accumulation categories, reflecting cumulative exposure effects. Mortality, however, showed nonlinear scaling with bleaching occurrence: early events were often associated with moderate mortality, while later events displayed either sharply elevated mortality or evidence of reduced mortality despite high susceptibility. This dispersion suggests selective filtering across repeated events, where vulnerable phenotypes are progressively removed, leaving more resilient configurations. Consequently, bleaching occurrence functions as both a stress-history metric and an emergent indicator of adaptive filtering across time.

Bleaching responses varied across locations, per the *post hoc* categories [Table 5A] of ocean_subregion [Tables 13, 10A]. Geographic location integrates multiple underlying drivers of bleaching responses, including regional thermal histories, basin-scale circulation, species composition and evolutionary exposure to stress. Consequently, location represents a composite variable through which temporal dynamics and biological filtering are expressed rather than an isolated causal factor. When bleaching responses were examined across ocean basins and subregions, substantial spatial heterogeneity emerged in both susceptibility and mortality patterns, particularly when resolved by timing of observations and relative thermals stress accumulation [Tables 13, 10A].

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These patterns indicate that bleaching responses are not uniform, but instead reflect region-specific trajectories shaped by repeated exposure, selective mortality, and differential recovery potential.

To contextualize biological and temporal patterns within broader spatial structure, bleaching responses were further examined across ocean basins and subregions. Location-based analyses [Table 14] revealed substantial geographic variability in zooxanthellae densities, bleaching susceptibility, and bleaching-related mortality indicating that spatial context contributes meaningfully to observed response distributions. Mean healthy zooxanthellae densities differed markedly among regions, corresponding reductions under bleached conditions, while susceptibility and mortality exhibited rather than uniform scalin with thermal stress alone.

When natural fluctuations were compared with sublethal and lethal bleaching outcomes across locations and levels of colony integration [Table 14e], bleaching responses consistently exceeded background variability, though the magnitude of divergence varied among regions. These patterns suggest that geographic location integrates long-term environmental histories and selective regimes that shape both baseline physiological states and responses to repeated thermal stress events. Within ocean basins, bleaching was significantly different (MANOVA, $F_{(2,178)} = 14.434$, $p<0.00$) from mean healthy zooxanthellae densities (which were not significantly different), although Tukey's *post hoc* showed a significant difference for bleached zooxanthellae densities from the Pacific Ocean compared to the Atlantic and Indian Oceans. Mean healthy and bleached zooxanthellae densities of pair-wise data for the Atlantic Ocean (n=31) healthy: $2.69x10^6$ (SE±$3.17x10^5$), bleached: $4.85x10^5$ (SE±$9.36x10^4$). For the Indian Ocean (n=19) healthy densities average $5.24x10^6$ (SE±$1.24x10^6$) and bleached densities were $1.01x10^6$ (SE±$2.65x10^5$). In the Pacific Ocean (n=128), healthy densities averaged $7.43x10^6$ (SE±$2.13x10^6$) and bleached densities averaged $2.78x10^6$ (SE±$3.89x10^5$).

4. Discussion

The results presented here challenge the prevailing tendency to interpret coral bleaching as a uniform, terminal outcome of stress and instead reveal bleaching as a structured, context-dependent system response. Across datasets spanning symbiont density, susceptibility, mortality, recovery and symbiont diversity, variability emerges not as noise or inconsistency, but as an intrinsic feature of how coral-algal symbioses respond to disturbances. Interpreting bleaching therefore requires moving beyond static definitions and isolated metrics toward a framework that accounts for dynamic trajectories, functional states, and architectural constraints.

This discussion synthesizes the results by shifting the interpretive focus from outcome-based classifications to system architecture. Rather than asking whether corals bleach or die under stress, the emphasis here is on how bleaching responses are expressed, constrained, and resolved across time. By integrating absolute and proportional measures of symbiont loss with recovery patterns and biological expression mechanisms, the results support a view of bleaching as a functional state embedded within a broader response spectrum, rather than an endpoint signaling irreversible failure.

Accordingly, the sections that follow first reinterpret commonly used indicators of coral health, then articulate bleaching as a functional, non-terminal state with direct implications for how responses are monitored and compared. The Discussion then extends this framework to examine the architecture of bleaching responses, including sources of variability, disturbance guilds, and phase shifts that occur without collapse. Finally, these patterns are situated within a deep-time ecological context, highlighting how persistence under repeated disturbance has shaped the response space observed in modern reef systems.

4.1. From Variability to System Architecture

Much of the foundational understanding of coral bleaching—what occurs, under what conditions, and how recovery is interpreted—has been shaped as much by methodological assumptions as by biological processes themselves. Observational constraints and proxy-based measurements have historically encouraged descriptive interpretations that blur distinctions between variability, dysfunction, and failure. The redefinition of coral bleaching presented here

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reflects a broader epistemological shift: the translation of qualitative descriptors into quantitative, operational criteria.

This shift is not merely methodological; it is foundational to scientific progress across disciplines. By converting qualitative phases of coral health into measurable fluorometric states, we demonstrate how subjective biological phenomena can be reframed to support reproducibility, comparative analysis, and mechanistic inference. Similar transitions have occurred elsewhere: ecological terms such as "stress," "resilience," and "recovery" are often used descriptively despite lacking standardized thresholds; in medicine, clinical diagnoses once reliant on symptom narratives are increasingly anchored to biomarkers; in psychology, constructs such as anxiety or well-being have moved from qualitative descriptions to psychometric and neurophysiological metrics. Even in physics, phenomena now formalized through nonlinear dynamics—such as turbulence or chaos—were initially characterized qualitatively before appropriate mathematical frameworks emerged.

The central limitation, therefore, is not the absence of data, but the absence of frameworks capable of translating observational language into dimensional, testable system states. In coral reef science, the coral–algal symbiosis has long been assessed through visual cues and pigment proxies, yet lacks a time-resolved, colony-integrated metric of physiological dysfunction. By introducing calibrated PAM fluorometry as a system-level diagnostic, this framework requires explicit consideration of baseline variability—what constitutes "normal" behavior in zooxanthellae populations and how natural fluctuations scale across time and disturbance regimes (Figures 1–5; Tables 2–4).

Interpreting Zooxanthellae Population Densities

Zooxanthellae densities have been observed to fluctuate with environmental parameters [42,60–62,75–77]. Seasonal variations occur such that the lowest mean density occurs during summer, while winter values may be up to 2-3 times higher; however, this appears to be dependent upon location (77); it has therefore been suggested that bleaching cannot be distinguished from these fluctuations. However, due to the slow progression of seasonal fluctuations in comparison to acute bleaching [77,79–81], if monitored consistently and routinely, bleaching is readily distinguishable from seasonal variations in zooxanthellae population densities. Furthermore, seasonal observations may be confounded by prolonged bleaching responses in massive, encrusting, and foliose colonies [82], which accumulate thermal stress (up to 3 years for *Porites lobata*, [75]), and their length of resistance is likely related to the level of colony integration and whether or not the colony can produce partial mortality [32].

Most factors studied had a negative impact on zooxanthellae population densities; however, both light and nutrient enrichments can have a positive impact on the population density. Light can potentially cause indistinguishable variation between healthy and bleached colonies due to variations in zooxanthellae pigmentation [83]. Most importantly, pollutants cause background, chronic stress that lowers baseline zooxanthellae densities and may make it harder to distinguish bleaching from natural variations, without consistent monitoring [42]. In this study, there was a marked and consistent trend with depth, with shallower sites (1-3m) generally having lower zooxanthellae densities than deeper sites (up to 20m). This pattern has been reported previously [69,74] and is a clear response to changes in light availability. As light becomes limiting, photosynthetic potential can be enhanced (up to a point) simply by increasing the concentration of zooxanthellae within surface tissues of the coral. It might be, therefore, that a similar pattern should be apparent when comparing along latitudinal gradients, though this will depend on the extent to which it is the total amount of light received, or the maximum amount of light received at any one time. The use of taxonomy to explore absolute densities of zooxanthellae densities was obscured by low records due to the variability in methods [Figure 2] and perhaps methods inherently have to be different for different corals, so that may all just be reflective of organismal diversity.

Nutrient enrichment (e.g. ammonia) was the only causal agent that increased mean zooxanthellae density [Figure 5]. [84] show that ammonia is regulated by urea in corals; such that

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indicator levels of urea can be measured in a field laboratory using a colorimetric kit designed for use with human blood plasma (which, if bought in bulk, costs 50 cents a test and takes 15 minutes to complete). The information from such data (as well as other environmental parameters measured from simple cost-effective water ecology kits) could be applied to management options. For instance, regulation of urea and ammonia (e.g. fish and invertebrate populations, [85]) will in turn regulate local coral populations. Therefore, areas that have lower urea concentrations should be protected to increase fish populations (thereby increasing zooxanthellae densities), while areas that have higher urea concentrations should be open to the public to help exploit fisheries and maintain ecosystem balance. This would require continued surveillance efforts and dynamic governance, because too much ammonia can cause bleaching [77,86–89], presumably because of overcrowding in the zooxanthellae population [90]. Moreover, the urea testing methods of [84], in collaboration with color sciences and chemistries could be a much more fruitful, common sense, cost-efficient pathway.

Bleaching of zooxanthellae may be defined as >55% reduction in zooxanthellae densities; where less than that may indicate that zooxanthellae have bleached pigments [77,79–81], that are more readily recoverable [91]. If the stress continues, corals are likely to bleach zooxanthellae (>55% loss), which takes weeks to months to recover [32,49,92–94]. A reduction of >78% of the zooxanthellae population suggests sustained bleaching that will likely lead to mortality if conditions persist [41], but this is also dependent upon the level of colony integration (e.g. concentration of stress in massive colonies producing partial mortality, [32]). If the MHZD is unknown, then sublethal bleaching may remain undistinguishable; however, lethal bleaching can be distinguished [81]. If the MHZD is known, then sublethal and lethal bleaching are clearly distinguishable from background variation.

Importantly, pollutants were the only categorical mechanism of bleaching (less the work of Leonard Muscatine [whom had a “skim the water for heat-stressed algae” method of discerning bleaching and likely discovered that impaired were bleached first) that reduced zooxanthellae densities within the realms of natural variation (e.g. the <45 flexibility of the proportional average while being monitored consistently): Moreover, nutrient enrichment was the only stressor that inflated population densities [Figure 1]. Colonies must be monitored consistently through time to observe the change in color and capture the impacts of pollution and natural variabilities in the area [Table 1]. This evidence suggests that perhaps a lot of what has been termed natural variations in palings/shadings of corals (and therefore variability in their algal densities and/or populations) are realistically sublethally stressed corals [42].

4.2. Bleaching as a Functional, Not Terminal, State

The simple version of the definition of bleaching is that it is a general stress response by the coral holobiont, which can be observed as either a fight or flight reaction based upon the strength and timing of the stressor [42]. Short term, high stress conditions elicit a flight response, where the colony expels photosynthetically healthy zooxanthellae in an effort to prevent further damage [39]. However, for longer-term chronic stress the colony fights the damage (through photoprotection and photorepair) then experiences photodamage, which leads to photoinhibition, which leads to chronic photoinhibition (free oxygen radicals begin to form) when the whole colony expels their chronically photoinhibited zooxanthellae [42]. This is essentially [36]’s photoinhibition model of coral bleaching, but at the level of the holobiont, not just molecular. *Post hoc* analyses of PAM Fluorometry measurements from [42] revealed objective definitions for each of these phases once methods are standardized [Table 2, Figures 3, 4].

Fluorometry measurements reveal differences in the responses of corals to environmental stress [42], though there are some complexities in interpreting changes in resulting measurements. The photoinhibition model of coral bleaching presented by [36] recognizes several distinct phases of chronic photoinhibition (or bleaching); i) photoprotection, ii) photorepair, iii) photodamage, and iv) photoinhibition. I found this sequence to occur at the level of the colony [Figure 4] when quenching was standardized to a mean coral, and I compared the variability from the proportional mean values of healthy corals to a particular colony in experimental conditions [42]. During this sequence F and

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Fm values remain constant during photoprotection and photorepair, but photosynthetic yields become highly variable during photodamage and photoinhibition [Table 2]. In the formative stages, quenching analyses are important in revealing photoprotection (i.e. xanthophyll cycling or heat dissipation) and photorepair occurring simultaneously, but with competing roles. Once colonies bleach, the photosynthetic yield again stabilises, but may increase or decrease as it shuffles, acquires or grows zooxanthellae. Increases in photosynthetic yields among bleached corals are counter-intuitive, but reflect selective expulsion of defective zooxanthellae [81,95], similar to what the zooxanthellae densities report, there is less fluctuation across zooxanthellae densities in bleached corals (8%, [Table 1]. The specific physiological processes that lead to photoinhibition remain unclear [96] but are likely to vary depending upon the relative contribution of high light, high temperature and/ or other adverse environmental conditions to the bleaching response.

This definition of bleaching is supported by field observations made during mass bleaching events by [29,81], and it supports the commonly used visual methods of determining bleaching, the colour card [31] and categorization by bleaching level (e.g. slightly, moderately or severely bleached, e.g. [40]). However, as [33] suggested, these categories may misrepresent what is happening and beg for longer measurements and consistency and I suggest that fluorometry should be used to determine accuracy, which is supported by the suggestion of [29] who highlight the necessity of in-depth observational studies of bleaching.

There are exceptions to the definition of bleaching, such as intra-colonial gradients, timing of observations/measurements, and other experimental protocol. Variations associated with intra-colonial causes, such as branch gradients, shade-light adapted sections of branches [29,98–100] and comparison between inner and outer branch densities [76] exceeded the threshold (ranged from 25-110%). Moreover, light can potentially cause indistinguishable variation between healthy and bleached colonies due to variations in zooxanthellae pigmentation [83]. However, [99] showed that the light and dark-adapted sections of branches lose the same percentage during bleaching. Therefore, if methods are applied and repeated correctly, bleaching should be distinguishable from within colony variation.

The timeframes of experiments had a significant impact on the mean zooxanthellae loss. Except for [42], where health was fixed and time was measured, all experiments tested the mean difference between healthy and bleached organisms after a given timeframe, a pre-determined end to the experiment. Further differences in estimates of zooxanthellae densities probably also relate to differences in experimental protocols. For instance, the time that corals are left to acclimate to aquarium conditions ranges from hours to weeks (although they were not fully recorded or analyzed, but see [60,61]. Another likely source of variation is the replication of homogenized subsamples, which ranged from 2-12. Importantly, methods to determine the number of algae have caused 1/3 of the variation (or 'noise') in the reported algal densities from the Zooxanthellae Density Meta-database [Table 2]. Intraspecific variation in the timing of the bleaching response [80,81] causes mean zooxanthellae densities (from randomization and replication) to appear to be slowly decreasing (e.g. [100]). However, bleaching is an acute response [supported by field observations of mass bleaching events [80,81,102,103].

Furthermore, the OISEO [42] measured the phenotypic plasticity in the timing of the bleaching response for two common and susceptible corals with contrasting life history traits, *Acropora nasuta* is a complex spawning coral (that does not transmit algae to its offspring) while *Pocillopora damicornis* is a robust brooding coral (that does transmit algae to its offspring), and there were obvious differences in responses between them. 1/3 of the *Acropora nasuta* experimental corals sloughed their tissue and held remnant patches within their porous skeletons that came back out from 3-4 weeks onwards in recovering conditions (e.g. observation of the mechanism for the Phoenix Effect [43,104] through their complex, porous skeletons, half of extant corals are complex; regardless of if they hermatypic or not; half of the global populace of corals can look dead, and arise from endoskeletal porosity to compete for surficial skeleton again against their greatest foes, the algae they farm [16].

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In OISEO [42], the Acroporids were also witnessed to uptake bioluminescent algae that were in the sea-flowed outdoor aquaria [31]. There were cohorts of bleaching responses in time, that best correlated with hybridization for *Acropora nasuta* and 2-3 other Acropora species [pers. obs. Bette Willis] and cryptic ecomorphs in the Pocilloporids [pers. obs. Sebastian Schmidt-Roach]. Additionally, one single branch of a single *Pocillopora damicornis* colony responded entirely differently from the rest, and even appeared to have a cryptic endolithic algae, which every Acroporid colony had during sampling while they were in recovery (I discarded them all because I was trying to get to the zooxanthellae counts and did not realize how rare it was to study recovery as I did at the time); this may have been an exhibition of chimerism [105].

The main impact to recovery seems a reflection of the closeness of reefs to anthropogenic stressors such as pollutants that lower baseline values of zooxanthellae densities, [Figure 6] and place more colonies in a sublethal state of bleaching which has less energy reserves to [106] to combat additional stressors [106–109]; however, when the reefs are given time to recover and then experience another mass bleaching event, the associated mortality for bleaching susceptible species is oftentimes less conspicuous [109–112].

New Framework Monitoring Protocol

If bleaching is interpreted as a functional system state rather than a terminal outcome, then monitoring approaches must make their underlying assumptions explicit. Much of the inconsistency in reported bleaching severity, susceptibility, and recovery across studies arises not from biological disagreement, but from unacknowledged differences in what is being measured, and how outcomes are defined. The following protocol outlines the minimum interpretive conditions required to assess bleaching responses within a structural framework:

(1) **Measurement consistency within individuals is required**. Comparisons of zooxanthellae population densities, symbiont assemblage composition and associated metrics must be conducted on comparable regions of the same organism across time. Sampling different branches, tissues, or colony regions without accounting for internal heterogeneity introduces variance that cannot be biologically interpreted as response. Functional assessment therefore requires repeated measurements anchored to consistent sampling locations; such that proportional change, recovery, or suppression reflects system behavior rather than spatial artifact.

(2) **Temporal alignment between stress exposure and biological response must be assumed explicitly.** Full bleaching responses are a temporally structured process, not instantaneous events. Monitoring protocols treat stress response exposure and observed response as synchronous collapse dynamic trajectories into static classifications. Assessments must therefore account for lagged responses, delayed recovery, and asynchronous expression across individuals. Failure to define the temporal window of observation renders comparisons of 'bleached' vs. 'unbleached' states biologically ambiguous [e.g. 50% successful estimate of mortality based on color alone, 42].

(3) **Chronic stressors must be distinguished from acute bleaching responses.** Long-term exposure to pollutants or sublethal stressors can suppress baseline zooxanthellae population densities and reduce population variability, producing conditions that superficially resemble bleaching. In these cases, low variance and reduced deviation from the mean should not be interpreted as stability or health – healthy is variable. Rather, chronically suppressed states represent energetically constrained systems that may be highly vulnerable to subsequent disturbance. Protocols that rely solely on absolute density thresholds risk conflating chronic suppression with acute bleaching.

(4) **Life history context constrains valid interpretations.** Monitoring protocols must be scaled to the life history and evolutionary context of the study organism. For long-lived, modular organisms such as corals, short observation windows are insufficient to resolve functional outcomes. Assumptions regarding recovery potential, persistence, and failure must therefore be

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stated explicitly, including the temporal scale over which observations are considered biologically meaningful.

(5) **Definitions of mortality must be operationally specific**. In modular organisms, visual tissue loss does not necessarily constitute organismal death. Remnant tissue reservoirs and endoskeletal refugia may retain the capacity for regeneration long after apparent bleaching or partial mortality. Monitoring protocols that do not account for these recovery pathways systematically underestimate persistence and misclassify functional states. Absence of visible tissue should not be assumed to indicate terminal failure without explicit justification (e.g. Robust or solitary coral).

Taken together, this protocol does not prescribe specific field methods or analytical tools. Rather, it establishes the interpretive assumptions required for bleaching assessments to be biologically comparable and mechanistically meaningful. Without these assumptions made explicit, bleaching classifications risk reflecting methodological inconsistency rather than true differences in system responses.

4.3. Exploring Bleaching Response Architectures

We have historically framed a disparaging interpretation of thinking that corals are extremely sensitive, vulnerable and weak organisms. However, rather than being weak, corals are cryptic survivors of mass extinctions, and their vulnerability represents a warning to us. It is therefore unnecessary to wait to see how these organisms adapt; we should first explore their co-evolutionary history with mass extinction events and consider how well-adapted they are and see the whole situation from a new light. As Thomas Kuhn noted, science is more likely to progress via a swift conceptual reorganization rather than slow, cumulative change.

Corals have cryptic ecomorphs [113], hybridization [114], chimerism [105], the Phoenix effect [42,43], the 'Naked Coral' Lazarus Effect [3], all of these mechanisms that represent both non-Mendelian genetics (cryptic linkages) and definitions of species that extend beyond strictly Darwinian frameworks. [17] showed that the animal tissues can survive acidification high enough to dissolve their skeletons and if returned to ambient conditions, the tissues can reassimilate minerals from the seawater and regrow their skeletons, a likely mechanism of the 'Naked Coral' and 'Lazarus Effect' [3].

We have been, in a way, measuring our own responses to coral disturbances. Coral bleaching is not a failure, but a co-evolved strategy for survival, represented by a disturbance guild spectrum (fight or flight responses) determined by life history and reproductive traits. Bleaching, in this view, is correlated best with recovery capabilities [Tables 7, 9, 10]. Representative resistant guild members include colonies with low levels of integration, robust skeletons, and that brood and transmit algae to offspring. The susceptible end of the disturbance guild spectrum includes corals that have various modes of recovering from bleaching, and bleach (susceptible, high integration of colony, complex skeletons, various reproductive traits, higher species diversity) can uptake zooxanthellae exogenously or farm from within from endolithic algae (also why competitive interactions are so fast to overwhelm colonies – the algae comes from within to overtake the colony, as the tissues can also do) and do not need to foster a genetic library, they are more apt to shuffle or bleach to acquire better clades (Adaptive Bleaching Hypothesis, 116. 117]).

4.3.1. Sources of Bleaching Response Variability

The Bleaching Response Meta-database and Zooxanthellae Density Meta-database together allow for transformation of taxonomic information into traits such as life history strategies and reproductive modes which can then be observed as sentinel disturbance guilds. The full spectrum of disturbance guilds needs further illumination; however, the polar ends of the disturbance guilds appear to be resistant or susceptible. The time it takes to bleach (susceptibility) varies by weather and timing, some life history and morphology [Figures 5A, 6A], while the time to recover is the strongest correlation with mortality from events [Table 3]. The resolved paradox is that if corals can recover

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quickly, they are more susceptible to bleaching and/or tissue sloughing; however, if corals would lose genetic diversity in their symbiont population or if they have few recovery mechanisms, then they resist bleaching and often produce partial mortality. The apparent paradox is that corals capable of rapid recovery are often most susceptible to bleaching, to avoid temporal thermal stress.

Coral reef science has incorrect assumptions on the levels of replication, scales of space and time and overall organismal dimensionality. The results of the ZDM analyses (Tables 1 and 2, and 3; Figures 1, 2, and 3] show how methods employed have blurred the answers when relating and comparing objective experiences. If major factors, such as the timing of observations relative to the onset of thermal anomalies, are entirely ignored and that is the basis of discussion, what is the point of that discussion, truly? One would not just have a report of susceptibility as mortality and recovery estimates are what shape community assemblages and determine how the population will survive. As noted within the ZDM and BRM, corals have highly variable modes of both asexual and sexual reproduction that influence the dynamics of their algal symbionts.

The susceptibility of local coral assemblages to mass bleaching episodes can also vary temporally, between successive bleaching events [53,117]. Most often, when reefs first bleach, heavy casualties result due to the loss of susceptible corals, such as Acropora and/ or Pocillopora [118], but the rates of mortality in subsequent bleaching events is oftentimes much less [119]. Reductions in the proportion of colonies that bleach and/ or die may reflect the selective removal of highly susceptible species from local coral assemblages, and/ or acclimation of individual colonies [67]. Corals that live in more dynamic environments also appear to cope better with bleaching, which suggests acclimatization or adaptation may operate to reduce bleaching susceptibility of individual colonies or populations, respectively [120,121]. Alternatively, areas that generally avoid thermal stress (i.e. upwelling) have a lower tolerance than areas that do not (i.e. non-upwelling) when exposed to doldrums and thermal stress [20].

The timing of the bleaching response appears highly dependent upon what best enables survival of genetic material (recovery). Therefore, bleaching susceptibility is dependent upon reproductive mode (e.g. Spawners are capable of acquiring new zooxanthellae, brooders are not,[122]), sex (hermaphrodite, gonochoric, e.g.[123]), maturity (smaller corals beneficial- more energy to invest and size allows higher mass transfer of free radicals, e.g. [44]), and the level of colony integration (how well affected areas are partitioned e.g. enabling partial mortality).Corals are well-adapted to bleaching. If intelligence were to be defined as creativity in survival, then corals are much smarter than us. Partial mortality, fission, fusion, tissue resurrection, polyp bail-out, etc.

There are known differences in bleaching susceptibility among different coral taxa (e.g., among coral genera; [19,23], although the hierarchy of bleaching susceptibility is not always consistent among different geographical locations. On the Great Barrier Reef (GBR), for example, Pocilloporidae corals, especially Stylophora and Pocillopora, are often the first to bleach and the most severely affected corals, whereas Fungiidae tend to be resistant to all but the most severe bleaching episodes (Figure 1). In French Polynesia, however, Pocilloporidae corals are much more resistant to bleaching compared to Acropora [124]; to the extent that recurrent bleaching is causing a shift towards Pocillopora-dominated coral assemblages [125].

4.3.2. Architectural Determinants of Deep Time Adaptations

While climate-change will undoubtedly cause, and is already having, major impacts on coral reef ecosystems [126,127], variation in the current and future capacity of corals to resist bleaching will lead to marked changes in community composition, prior to wholesale loss of these important habitat-forming organisms. The structure of future coral communities dictates what organisms will find them as suitable habitat. In many areas where branching corals, which provide structural integrity hence shelter to various organisms, are the dominant morphology, they are the most susceptible and often suffer the largest mortalities in relation to mass bleaching events [22,23,129,138,139]. In general, families of corals that are mostly characterized by branching growth forms (e.g., Acroporidae and Pocilloporidae) are considered to be most susceptible to bleaching and

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experience highest rates of mortality once bleached [32,104]. In contrast, families of corals that typically have massive morphologies (e.g., Faviidae, Mussidae, and Poritidae) appear resistant to increasing temperature, being among the last to bleach and more frequently experience partial, rather than whole colony mortality [32,43,46].

[Table 13] synthesizes the five primary architectural drivers underlying the Scleractinian Phoenix framework, illustrating how deep-time adaptive capacity emerges from the interaction of skeletal structure, reproductive strategy, symbiont transmission, and colony-level integration rather than any single trait in isolation. These dimensions represent orthogonal axes of biological organization that collectively shape bleaching response trajectories, recovery pathways and long-term persistence. Skeletal complexity governs the physical physiological stress is distributed, isolated, or amplified across the organism. Highly integrated colonies function as unified systems that may suppress variability but risk catastrophic failure, while modular colonies permit spatial decoupling of damage and recovery through fission, partial mortality, and tissue persistence.

Together, these drivers define a multidimensional response space within which bleaching manifests not as a binary outcome, but as a spectrum of functional states shaped by evolutionary history. The Phoenix response—characterized by apparent death followed by regeneration from remnant tissues—emerges where skeletal complexity, modular integration, and recovery-enabled reproductive strategies intersect. Table 13 therefore provides a mechanistic bridge between observed bleaching outcomes and the deep-time architectures that have allowed corals to persist through repeated environmental upheavals across geological history.

4.3.3. Sentinel Disturbance Guilds

The bleaching response architectures illustrated in Figure 1 define a set of Sentinel Disturbance Guilds, wherein coral taxa function as biological indicators of disturbance timing, intensity, and ecological consequence rather than as uniform victims of thermal stress. These guilds are not taxonomic groupings, but functional roles that emerge from the interaction of susceptibility, mortality, and recovery across time. As such, they provide an interpretive framework for understanding how coral assemblages register, absorb, and respond to environmental perturbation.

Vulnerable–terminal corals act as early-warning sentinels, exhibiting rapid bleaching and high mortality that signal acute stress events and system thresholds. Susceptible–recovery corals function as resilience sentinels, bleaching readily yet demonstrating survival through rapid regeneration, thereby revealing the capacity of reef systems to rebound following disturbance. Resistant corals serve as buffer sentinels, indicating the presence of intrinsic photoprotective or molecular mechanisms that prevent bleaching and stabilize community structure under stress. Finally, opportunistic or Phoenix corals operate as reorganization sentinels, increasing in abundance or performance following disturbance and signaling shifts in competitive landscapes and long-term community trajectories.

Together, these sentinel guilds demonstrate that bleaching responses encode information about both environmental forcing and biological strategy. Interpreting bleaching solely through metrics of prevalence or severity therefore obscures the functional signals embedded within differential outcomes. Recognizing sentinel guilds allows bleaching events to be read as structured ecological messages—revealing not only when stress occurs, but how reef systems reorganize in response across ecological and evolutionary timescales.

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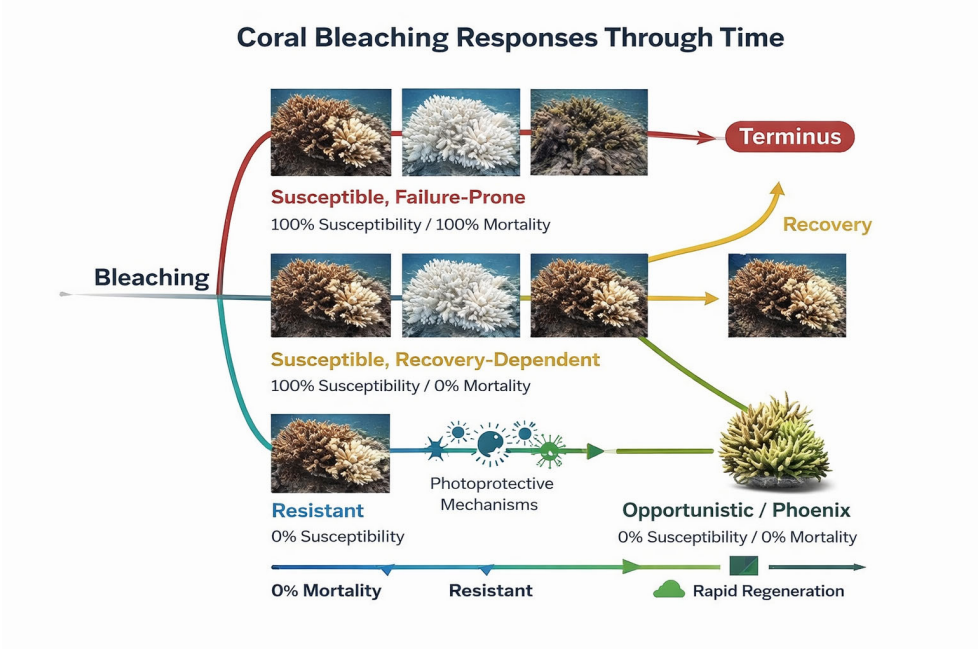

Figure 1. Coral bleaching response architectures across time: decoupling susceptibility, mortality, and recovery into distinct survival pathways. Rather than treating bleaching as a single continuum of severity, this conceptual model maps alternative state trajectories in which bleaching susceptibility does not deterministically predict mortality and recovery is an active, time-structured process. The schematic defines sentinel disturbance guilds—failure-prone, recovery-dependent, resistant, and opportunistic ("Phoenix")—that partition outcomes by trajectory (directionality through time) rather than by snapshot condition. This framework makes explicit the central inference of the manuscript: survival emerges from biological architecture and timing, not exposure alone.

[Figure 1] synthesizes bleaching outcomes as response architectures rather than linear severity states, explicitly decoupling susceptibility, mortality, and recovery. Traditional bleaching frameworks implicitly assume that high susceptibility predicts high mortality and that recovery represents a return to a pre-disturbance baseline. The trajectories illustrated here demonstrate that these assumptions are not supported when bleaching is examined as a process unfolding across ecological and evolutionary timescales. Four dominant response architectures emerge.

The vulnerable–terminal architecture is characterized by high susceptibility coupled with high mortality. Colonies following this pathway bleach rapidly, fail to maintain symbiont function, and experience extensive tissue loss that culminates in system collapse. These trajectories converge on a terminal state when recovery mechanisms are insufficient or overwhelmed, particularly under acute or repeated thermal stress.

In contrast, the susceptible–recovery architecture exhibits high susceptibility but low mortality. Colonies bleach readily, yet retain the capacity for rapid symbiont reacquisition, tissue regeneration, or energetic compensation. In this pathway, susceptibility reflects sensitivity to stress detection rather than physiological failure. Recovery is therefore not anomalous but constitutive of survival, rendering these corals vulnerable in appearance yet resilient in outcome.

The resistant–buffered architecture is defined by low susceptibility and low mortality. Colonies occupying this state avoid bleaching altogether through photoprotective and molecular buffering mechanisms, including heat-shock proteins, antioxidant pathways, proteomic stability, and symbiont regulation. Resistance here reflects a prevention strategy rather than post-disturbance repair, allowing colonies to maintain functional continuity through environmental perturbation.

Finally, the opportunistic or Phoenix architecture represents a distinct response in which colonies exhibit negligible susceptibility and mortality while demonstrating recovery gains

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exceeding pre-disturbance levels. These trajectories indicate that disturbance can catalyze reorganization, expansion, or competitive release rather than loss. Recovery in this context is not restorative but transformative, producing net positive change in biomass, tissue integration, or ecological dominance.

Critically, these architectures [Table 13, Figure 1] demonstrate that bleaching is not inherently pathological, nor is mortality its inevitable consequence. Susceptibility, mortality, and recovery operate on partially independent axes, shaped by life-history traits, symbiont dynamics, colony integration, and energetic strategies. The same bleaching stimulus may therefore produce fundamentally different outcomes depending on the architecture through which it propagates.

By framing bleaching as movement through alternative system pathways rather than progression toward failure, this model reconciles apparent contradictions in the literature, including cases where highly susceptible taxa persist, resistant taxa eventually decline, and opportunistic taxa increase in abundance following disturbance. These results support the interpretation of bleaching as a state transition within a complex adaptive system, rather than a singular endpoint, with implications for predicting reef futures under increasingly variable thermal regimes.

4.3.4. Phase Shifts Along Functional Disturbance Guilds

Significant spatial, temporal and biological variation in bleaching susceptibility among corals makes it unlikely that there will be wholesale loss of coral assemblages (cf. [126]), at least not in short to medium time scales (years to decades). Instead, bleaching is expected to drive reorganization of community structure, mediated through shifts in the relative abundance of functional disturbance guilds rather than uniform decline across taxa.

Branching and tabular corals, particularly Acropora and Pocilloporidae, which contribute disproportionately to habitat complexity on Indo-Pacific reefs, are generally among the most thermally sensitive taxa and often exhibit high mortality during early phases of thermal stress [13]. However, the apparent dominance of these taxa among early bleaching casualties reflects, in part, observation timing bias [Figures 5A and 6A]. Branching morphologies tend to bleach rapidly within the first few weeks to months of the onset of thermal stress [32,49], whereas massive and robust growth forms frequently exhibit delayed bleaching responses, sometimes occurring months after the initial thermal anomaly [74,76,82,130]. When temperatures remain above average into the following summer, massive growth forms become more susceptible than branching species [49,76,130–133] which suggests that massive growth forms accumulate thermal stress over time. If natural selection is occurring in coral populations due to selective removal of weak phenotypes or genotypes, we would expect a temporal decline in the proportion of coral colonies that bleach, or die, at a given temperature [67]. [117] compared the thermal histories and DHW's of several locations on the Great Barrier Reef with the observed effects during bleaching events and found that at some locations, thermal thresholds have increased throughout repeated bleaching exposure. When reefs are first reported to mass bleach heavy casualties often result due to the disproportionate loss of susceptible corals (e.g. branching *Acroporids* and *Pocilloporids*, [118]); however, the bleaching susceptible corals are, in many cases, also the fastest to recover from disturbance; and, there is a growing field of evidence for acclimatization and adaptation to local environmental conditions [22 71, 117].

Mass-bleaching episodes leads to increased bleaching resistance [53,67,136], which suggests that bleaching susceptibility will vary spatially with marked variation in thermal history and local environmental regimes. It is also clear that bleaching thresholds vary spatially for individual coral taxa [11], though it is not clear whether this leads to geographic changes in relative bleaching susceptibility, or if the entire assemblage is simply more resistant at locations exposed to generally higher or more frequent extreme temperatures [136,137].

The increasing incidence of climate-induced coral bleaching will not necessarily favour those corals that are resistant to bleaching [120,138]. Bleaching-susceptible species (e.g., Acropora) often have faster rates of recovery from disturbances, and could potentially increase in abundance, depending on the specific frequency versus severity of major bleaching events [11,119]. Accordingly,

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highly susceptible corals (e.g., Acropora) have become even more dominant in the aftermath of severe bleaching at some locations [127]. However, more research is necessary to test how changing environmental regimes will affect the underlying population dynamics and demographic rates of coral reef community assemblages.

Changes in community structure and diversity are caused by variability in the susceptibility, mortality, resistance and resilience to disturbance [74–76]. In many areas where branching corals, which provide structural integrity hence shelter to various organisms, are the dominant morphology, they are often the most susceptible and often suffer the largest apparent mortalities [Tables 3 and 4; 36, 37]. Massive and submassive corals are more resistant [Table 3, 4], although when conditions are too frequent and/or severe, as they were throughout the 1997-98 global mass bleaching event, mortality may result [77,78]. Smaller spawning corals (e.g. Acroporids) have increased resistance to bleaching, while adults are more susceptible; while the opposite trend appears to be true for brooding corals [37,79–84].

The structure of future coral communities dictates what organisms will find them as suitable habitat. In many areas where branching corals, which provide structural integrity hence shelter to various organisms, are the dominant morphology, they are the most susceptible and often suffer the largest mortalities in relation to mass bleaching events [22,23]. Massive and submassive corals are more resistant to coral bleaching events, although this is not always the case. For instance, in the Mesoamerican coral reef system [140], it was observed that larger coral colonies were more likely to experience partial mortality, while smaller coral colonies were more likely to die; moreover, that the most spatially dominant coral taxa were often the most susceptible to the lethal effects of bleaching. [130] showed that the dominant branching communities of Okinawan corals (*Seriatopora hystrix, Seriatopora caliendrum, Stylophora pistillata, Pocillopora damicornis*, and *Millepora intricate*) experienced local extinctions, while the less common corals were resistant and now dominant, such as massive and encrusting colonies of Porites, Goniastrea, Leptastrea, Platygyra, Favia, and Favites.

4.3.5. Scope, Constraints, and Interpretive Limits

The structure of coral assemblages will inevitably change as the frequency and intensity of mass bleaching events increase. Predicting the precise trajectories of these changes, however, requires careful distinction between susceptibility, mortality, and recovery, as well as recognition of the temporal scales over which these processes operate. This study does not attempt to forecast specific future community compositions; rather, it resolves how bleaching responses are structured biologically and how these responses translate into differential persistence across disturbance regimes.

A primary constraint in interpreting bleaching outcomes arises from species-specific and trait-mediated variation in recovery capacity following thermal stress. Corals experiencing bleaching are not uniformly impaired: colonies vary widely in energetic reserves, tissue integration, symbiont acquisition strategies, and structural modularity. As a result, apparent resistance or vulnerability is often contingent on observation timing, with early surveys emphasizing rapid bleaching responses and later surveys capturing delayed mortality or regeneration. Without accounting for this temporal offset, comparisons among studies risk conflating susceptibility with failure.

Anthropogenic stressors further complicate interpretation by lowering baseline physiological states prior to bleaching events. Pollutants, eutrophication, sedimentation, and overfishing reduce background zooxanthellae densities and energetic reserves, placing colonies into chronic sublethal stress states. Under these conditions, bleaching responses may reflect compounded stress exposure rather than intrinsic thermal sensitivity. Importantly, when reefs are afforded sufficient recovery intervals between disturbance events, subsequent bleaching episodes often produce lower apparent mortality among previously susceptible taxa, consistent with selective filtering and survivorship bias rather than uniform adaptation.

This study is explicitly limited to thermal stress–mediated bleaching responses and does not directly address interacting drivers such as disease dynamics, ocean acidification, or storm damage.

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While these factors undoubtedly influence coral vulnerability, the patterns resolved here suggest that modes of recovery scale predictably with susceptibility, regardless of disturbance source. Thus, the response architectures identified are expected to generalize across stressors, even if absolute outcomes differ.

Finally, interpretation of these results must remain grounded in scale. Ecological timescales capture bleaching as an acute crisis, whereas evolutionary timescales reveal bleaching as a recurrent filtering mechanism operating across deep time. This work does not argue that contemporary bleaching poses no risk to reef ecosystems; rather, it demonstrates that bleaching is not synonymous with system failure. The critical uncertainty lies not in whether corals possess mechanisms for persistence, but in whether disturbance frequency will exceed the recovery windows required for those mechanisms to operate effectively.

4.3.6. Deep Time Ecology and Future Implications

The most immediate threat is increased global sea-surface temperatures [10,21,140], which causes naturally occurring thermal anomalies (e.g., linked to El Niño) to more frequently exceed coral thermal tolerances, resulting in mass bleaching and climate models predict and additional 1.8-4^{o}C rise in tropical sea-surface temperatures over the coming century [10,12,142–152]. Mass bleaching has therefore been proposed as an early symptom of our planet's health, or sentinel habitat, not because it is novel, but because the rate at which thermal thresholds are now exceeded is accelerating beyond historical ecological baselines.

One proposed mechanism for buffering these accelerating thermal thresholds is the adaptive capacity of the algal symbionts. Numerous studies have demonstrated variability in symbiont composition, physiology, and thermal tolerance, suggesting that shifts in algal communities may modulate bleaching responses under thermal stress [70,71,110,116,117]. However, work addressing the adaptive capacity of the coral holobiont – the entire suite of organisms associated with a coral, including the organism itself, and the symbiotic, communalistic and microbial communities – is comparatively limited [53,57,113,152]. Given the long evolutionary history of corals and their symbiosis [1,3,7–11,15,16], and the well-established role of intermediate disturbance in mediating biodiversity [9], it is reasonable to infer that coral-algal systems have evolved a diversity of life history strategies shaped by repeated exposure to environmental perturbations. These strategies do not eliminate disturbance but instead distribute risk across biological organization and time.

When disturbance exceeds the capacity for risk to be distributed across biological organization and time, its consequences are expressed at broader ecological and biogeochemical scales. In the millennia following the loss of shallow-water reef systems, global impacts may emerge that mirror patterns observed during previous mass extinction events. These include population outbreaks of opportunistic r-strategists fueled by nutrient enrichment, coupled with increased decomposition that progressively depletes available oxygen. Under such conditions, decomposer activity can both accelerate mortality and ultimately become oxygen-limited itself, constraining ecosystem recovery and restructuring marine habitats in ways that persist long after the initial disturbance.

Under oxygen-limited and increasingly acidified conditions characteristic of mass extinction intervals, mortality is often inferred from the disappearance of visible structure rather than directly observed biological failure. Organic remains may be transformed into fossil beds or dissolved through ocean acidification – yet experimental handling of coral skeletons—including complete skeletal removal using strong acids for zooxanthellae density analyses—demonstrates that the loss of calcified structure does not necessarily equate to the loss of living tissue. As a result, the operational definition of "death" becomes ambiguous in organisms capable of cryptic persistence. Scleractinian corals, in particular, exhibit remarkable evolutionary continuity through mass extinction events, retaining ancestral skeletal architectures (e.g., complex versus robust porosity) across radiations that postdate extinction boundaries by tens of millions of years. These patterns suggest that apparent extinction at ecological scales may mask persistence and re-emergence at lineage scales and produce Lazarus effects [3].

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During mass extinctions, life dies. These remains can either be turned into fossil beds or dissolve due to ocean acidification. However, I and others have used 100% HCl to remove skeletons in the lab for zooxanthellae density processing and that had null impact on the tissue, hard to tell now if those samples were "dead". Death is truly unknown as these organisms have shown utterly magnificent cryptic evolution and perseverance – they can lose their skeletons, and perhaps just sink to where they no longer feel the environmental pressures and return to the surface on the other side of the mass extinction, into the massive radiation of species that began our knowledge of Scleractinia, already maintaining the ancestral cladal split of skeletal porosity (Complex vs. Robust) and notably, some 40 million years older than Rugosa and Tabulata Corals. Scleractinian corals did not attain dominance of the shallows until the extinction (questionably an endosymbiotic amalgamation with exogenic uptake of genomes, another adaptation of Modern Scleractinia) of Rugosa and Tabulata Corals at the end Permian Mass Extinction/Mass Radiation Turnover Event.

Empirical support for cryptic persistence and scale-dependent responses emerges from fine-resolution observations of bleaching and recovery dynamics. In the OISEO dataset [42] bleaching responses occurred in distinct temporal cohorts that correlated most strongly with hybridization in Acropora nasuta and several closely related Acropora species (pers. obs. B. Willis), as well as with cryptic ecomorphs in the Pocilloporids (pers. obs. S. Schmidt-Roach). Notably, bleaching and recovery responses were not uniform even within individual colonies: a single branch of a *Pocillopora damicornis* colony responded entirely differently from adjacent branches, including the apparent presence of a cryptic endolithic algal assemblage during recovery. Although these samples were not retained at the time, such divergence is consistent with chimerism and within-colony physiological compartmentalization. Across taxa, the most consistent difference among bleaching responses was not susceptibility but recovery capacity, with a subset of colonies sloughing tissue early while retaining remnant patches within porous, complex skeletons that re-expanded after several weeks under recovering conditions. These observations demonstrate that bleaching outcomes are structured across nested biological scales—tissue, branch, colony, and lineage—challenging the assumption that the coral "individual" represents a singular, temporally coherent unit.

The capacity for responses to be structured across nested biological scales is closely linked to skeletal architecture in Scleractinian corals. Approximately half of extant Scleractinian species exhibit complex, porous skeletal morphologies, irrespective of whether they function as hermatypic reef builders, and this condition represents the oldest known ancestral trait within the clade. Skeletal porosity permits remnant tissue to persist cryptically within endoskeletal spaces during periods of environmental stress, enabling later reoccupation of abandoned skeletal volume when conditions improve. In this context, organismal continuity becomes partially decoupled from external morphology, such that visible colony structure is an incomplete proxy for biological persistence. As a result, chronological age and spatial extent alone are insufficient descriptors of coral identity; a small fragment may represent a deeper evolutionary lineage than a large, visually intact colony. This architectural capacity effectively alters the temporal resolution at which survival and recovery are expressed, challenging conventional assumptions about organismal dimensionality in reef-building corals.

By deep-sea Scleractinian coral genomics, their origin is at least some 450 million years ago [8,15], yet they were already highly diverse and the ancestral trait of skeletal porosity (porous complex or dense robust skeletons) already existed in the first fossil findings [8]. Importantly, the calcium carbonate that the reef engineers attain from the seawater to begin this process precipitates out in the form of aragonite or calcite, depending on environmental conditions, both stochasticity in time and space; aragonite is a more unstable form (during Earth changes and in the shallows), while calcite is a very stable form of calcium carbonate (in more stable evolutionary periods and at depths). Notably, calcite has a double refractive property that maximizes light harvesting for photosynthesizers at depth [155], so mesophotic communities do flourish [156]. So, where there is light, the symbiosis does exist (and perhaps form a chemosymbiosis at depth, like stromatolites).

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Moreover, cryptic co-evolved traits between corals and their algal symbionts likely operate across biological scales that do not map cleanly onto classical Mendelian inheritance or organism-level selection. Life history and reproductive strategies among reef-building corals span a breadth that exceeds that of many more recently evolved taxa, encompassing sexual reproduction, asexual fragmentation, chimerism, and mixed symbiont transmission modes. This diversity of reproductive and developmental pathways suggests that evolutionary responses to disturbance may be distributed across multiple temporal and organizational scales simultaneously, rather than expressed through single, lineage-bound adaptive trajectories.

Restoration practices already exploit some of these properties. For example, complex corals that exhibit diminished endogenous timekeeping are fragmented and grown under sheltered conditions until energetic allocation shifts from growth to reproduction, after which colonies are outplanted to enhance larval production and genetic connectivity (e.g., Mote Marine Laboratory). Yet such interventions raise fundamental questions about organismal identity and dispersal. What constitutes the "individual" when a coral fragments, acclimates, adapts, reproduces sexually, or clones itself asexually? At what dimensional scale should survival and persistence be measured — a nubbin, a fragment, a colony, a genet, a reef, a genomic lineage, or an ocean basin?

Corals further complicate biological dimensionality through their skeletal architectures, which allow remnant tissue to persist cryptically within endoskeletal porosity during adverse conditions and later reoccupy abandoned skeletal space. In this sense, some corals exhibit functional persistence across environmental oscillations, with organismal continuity decoupled from visible morphology. A small branch fragment may be older, in evolutionary or genomic terms, than a massive colony, rendering chronological age an insufficient descriptor of biological persistence.

Studying such organisms therefore requires both methodological humility and expanded dimensional frameworks. Snapshot-based observation is insufficient to capture recovery trajectories, cryptic persistence, and latent survival mechanisms that are not anomalies but central features of reef biology. From this perspective, intermediate disturbance theory—long applied to ecological diversity maintenance—may operate analogously at evolutionary scales, where periodic mass extinction pulses function not solely as destructive forces but as diversity-generating filters that shape novel traits, symbioses, and adaptive pathways across geological time and dimensionality. The longstanding paradox of how corals appear highly susceptible on ecological timescales yet persist across geological intervals arises from mis-scaled interpretation: assessments of vulnerability are biased by assumptions about time, space, individuality, and death that are poorly suited to organisms whose persistence is distributed across tissues, colonies, genets, and lineages.

4.3.7. Formal Synthesis: A Unifying Interpretive Framework

With projected increases in frequencies and intensities of climate conditions, we should take every precaution and effort to not lose shallow water reefs, as it will be quite some time before a new version of coral comes up from the depths again and the Earth will very likely lose most of its albedo and surface habitability for millennia. Meanwhile, the cryptic survivors may rest in ocean trenches again to rise and re-acclimate to new minerals in the water and any other changed environmental considerations from the mass extinction. Corals and other survivors will radiate out and fill new niches since there will be plenty of opportunities as most other life will have likely died from surface conditions and dissolved from strong acidity or fossilized for future oil resources, as fossil fuels are renewable only on geologic timeframes far exceeding those of human or ecological recovery. Corals have survived more than we should hope to experience, we need shallow water coral reefs here on Earth for our survival, for our planet, the only hospitable planet that we know of, for its planetary albedo, the corals are prepared to survive full-fledged planetary acidification. I propose this work as a benchmark study for incorporating the relativity of time, organismal dimensionality, and lineage persistence into ecological interpretation. From this framework, I derive multiple theorems addressing the issues of mis-perceived time and mis-scaled interpretation, and their resolution

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through explicit quantification of temporal and biological assumptions, and not redefining terms, but sharpening their meanings.

Theorem 1. *The Issue of mis-perceived time and mis-scaled interpretation*

As seen in the literature for coral reef ecology, sometimes bad assumptions can get in the way of good science. The assumptions, though, had to be attained from a retro-active point of hindsight to capture the variability at the beginning, and is akin to an Ouroboros, where assumptions are validated by the same observations they are meant to explain. So, all of the information is correct, but it needs to be fine-combed and transformed for the assumptions of time and organismal dimensionality for assurance that interpretation falls within the purveyance of actual happenings.

Theorem 2. *The Unifying Field Theorem*

The correction for the issue of mis-perceived time or mis-scaled discussion – fine tooth combing the assumptions of data based on the end results. Forward-thinking Morality is what I call the responsibility of ensuring our interpretations don't misrepresent actual happenings of the past or future and are grounded in full assumptions for repeatability.

This unifying interpretive framework is not intended to resolve all open questions within coral reef ecology, nor to serve as a comprehensive theory of biological persistence. Rather, its value lies in clarifying how assumptions about time, scale, and biological organization shape scientific interpretation. By making these assumptions explicit, the framework provides a means to move forward with informed hindsight—allowing emerging ecological problems to be evaluated within a dimensional context appropriate to their underlying processes, including those not yet fully observed or defined.

4.3.8. Speculative Synthesis: A Unifying Interpretive Framework

The following synthesis explores the conceptual implications of the Unifying Interpretive Framework beyond the immediate empirical scope of this study. Rather than advancing predictive claims, this section is intended to illustrate how the framework may assist in organizing biological complexity across scales of time, space, and organismal integration.

Science itself is an evolving interpretive process, and evolutionary outcomes are often reconstructed as the accumulation of stochastic events. An alternative perspective, consistent with the framework proposed here, is that many biological trajectories may be constrained by structural and symbiotic necessities rather than randomness alone. For example, the coral polyp's internal skeleton, symbiotic partnerships, and modular growth reflect recurring solutions to energetic and environmental constraints rather than singular evolutionary accidents. Life gambles with the inevitability of time.

If life on Earth is viewed as a continuum shaped by shared ancestry and differentiated primarily by temporal, spatial, and symbiotic context, then ecological systems can be interpreted as emergent properties of larger organizing processes. Under this view, Earth's biosphere itself functions as an integrated system governed by cyclical drivers such as seasonality, tides, and biological rhythms. This perspective reframes ecology as the study of interacting temporal processes rather than isolated taxa or events.

Within this context, the framework offers a way to reconsider longstanding paradoxes in ecology, including resilience versus vulnerability and stability versus change. Apparent contradictions may arise not from biological inconsistency, but from mismatches between the temporal scale of observation and the processes being measured. By explicitly incorporating dimensionality and timing into interpretation, the framework provides a means to contextualize ecological responses that appear contradictory under static or single-event analyses.

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Finally, and explicitly speculatively, the framework invites consideration of whether some ecological and evolutionary dynamics operate within a form of bootstrap constraint, in which systems must reach particular levels of structural or symbiotic complexity before additional pathways become available. Under this view, biological innovation is not solely the product of incremental adaptation, but may also reflect threshold-dependent transitions that are only observable retrospectively.

Such a perspective does not imply determinism, nor does it advance predictive claims. Rather, it highlights how inevitability and contingency may coexist in biological systems constrained by time, energy, and organization. In cnidarians, repeated convergence on modularity, photosymbiosis, and architectural integration suggests that certain solutions may be repeatedly favored under shared boundary conditions, even as local outcomes remain context dependent.

More broadly, these considerations underscore the value of interpretive frameworks capable of accommodating nonlinearity, threshold effects, and scale dependence. The contribution of the present framework lies not in forecasting specific futures, but in providing conceptual structure for recognizing when apparent novelty, resilience, or collapse may instead reflect delayed emergence or reorganization within long-standing biological constraints.

These speculative extensions are presented to demonstrate the generative capacity of the framework and its potential to unify disparate ecological observations. They are not intended to assert empirical claims beyond the data presented here, but to offer a conceptual structure through which future research may explore complex adaptive systems with greater interpretive coherence.

5. Conclusions

We have insufficiently recognized the paleoecology, evolutionary biology, and the relativity of time, space, death, and dimensionality in coral systems. Corals clearly possess survival mechanisms that extend beyond conventional perceptual and conceptual frameworks. Historically, coral resilience has often been inferred from single-timepoint observations and limited follow-through on recovery dynamics, despite reef organisms having undergone extensive evolutionary filtering across environmental upheavals, including repeated mass extinction events. These histories have produced organisms capable of persistence through cryptic tissue reservoirs, modular fragmentation, symbiotic restructuring, and nonlinear recovery pathways that challenge traditional assumptions about individuality, age, and mortality.

Variability in the foundational methods used to estimate zooxanthellae population density has contributed to indistinguishable variation where clarity is required. Concurrently, anthropogenic pressures such as pollution and overfishing have lowered baseline symbiont densities in many reef systems. Mass bleaching events should therefore be understood not as isolated phenomena, but as emergent outcomes of interacting stressors operating across ecological and temporal scales. Cost-effective, standardized monitoring of water quality and environmental conditions remains an essential component of reef management, alongside continuous observation, adaptive governance, and improved integration of ecological feedback cycles into decision-making frameworks.

As oceans buffer atmospheric carbon dioxide through uptake, increasingly large-scale thermal anomalies are expected to drive recurrent mass bleaching via the expulsion of symbiotic dinoflagellates [21,111,112,118]. Resulting species losses may reduce not only taxonomic diversity but also ecosystem function, increasing the probability of phase shifts and structural reorganization [157,158]. When bleaching-associated mortality is severe, coral frameworks may degrade into rubble substrates, facilitating transitions away from coral-dominated states toward macroalgal dominance [160,161]. Such phase shifts are accelerated by both top-down and bottom-up processes, including herbivore removal [160] and eutrophication [162], which together suppress recovery potential and restructure reef assemblages [163,164].

The timing of bleaching responses appears strongly dependent on factors that enable the survival and transmission of genetic and symbiotic material during and after disturbance. Corals may therefore be simultaneously vulnerable on ecological timescales yet resilient across evolutionary

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ones. Drivers operating at the scale of individual colonies or local assemblages do not necessarily translate directly to population- or lineage-level outcomes, and vice versa. While additional stressors – including disease, ocean acidification, and storm activity – also influence vulnerability, this study focused specifically on thermal stress in relation to mass bleaching. Nevertheless, similar scale-dependent dynamics are likely to apply across multiple disturbance regimes.

Importantly, the effects of global climate change operate with temporal lags. Even under scenarios of reduced emissions, bleaching frequency and severity are expected to increase in the near term due to inertia within the climate system. The question therefore shifts from whether coral reefs can persist indefinitely under present conditions to how their biological and structural legacies may reorganize across human, ecological, and geological timescales.

Intermediate disturbance theory, when extended to evolutionary scales, suggests that pulses of disturbance—including historical mass extinctions—have contributed to the diversification of reef systems and associated traits, including symbiotic strategies. Over geological time, corals may retreat to deeper or more thermally stable refugia until surface conditions stabilize. On ecological timescales, however, sustaining reef function will require continued refinement of monitoring, management, and interpretive frameworks capable of integrating long-term biological constraints with short-term environmental change.

Ultimately, the value of the framework presented here lies not in predicting specific futures, but in improving our capacity to interpret resilience, collapse, and recovery as emergent properties shaped by time, scale, and biological organization.

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Abbreviations

The following abbreviations are used in this manuscript:

COTS	Crown of Thorn Seastars
ZDD	Zooxanthellae Density Database
ZDM	Zooxanthellae Density Meta-database
BRD	Bleaching Response Database
BRM	Bleaching Response Meta-database

Appendix A. Figures

The Method for Sample Size (Method SS [Figure 1] expressed as branch, colony, or fragment in [Figure 2]) used to determine mean zooxanthellae densities) caused the most variation in Mean Healthy Zooxanthellae Densities (MHZD). Tukey's *post hoc* tests showed three groups, with the values from core samples (n=17) $1.25x10^7$ (SE±$1.99x10^6$) being significantly higher than other sample sizes. The next highest MHZD came from colonies (n=124) MHZD: $4.78x10^6$ (SE±$188x10^5$) and fragments (n=35) MHZD: $3.96\ x10^6$ (SE±$7.63x10^5$). The final grouping had the lowest MHZD, and it contained: nubbins (n=28) MHZD: $2.73x10^6$ (SE±$5.62x10^5$), samples (n=16) MHZD: $2.38x10^6$ (SE±$2.40x10^5$), and branches (n=44) MHZD: $1.89x10^6$ (SE±$3.15x10^5$). Three methods to remove coral

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tissue (Methods TR, [Figures 1 and 2]) were generally applied in studies (decalcification, airbrushing and waterpiking) and caused significant variation in MHZD [Figures 1 and 2]. Tukey's *post hoc* tests showed significantly different results for MHZD from decalcified samples (n=152) MHZD: $5.41x10^6$ (SE±$3.55x10^5$) rather than picked/brushed. Airbrushing (n=41) produced higher MHZD: $3.51x10^6$ (SE±$6.73x10^5$) than waterpiking (n=146), which produced the lowest MHZD of $2.59x10^6$ (SE±$1.97x10^5$).

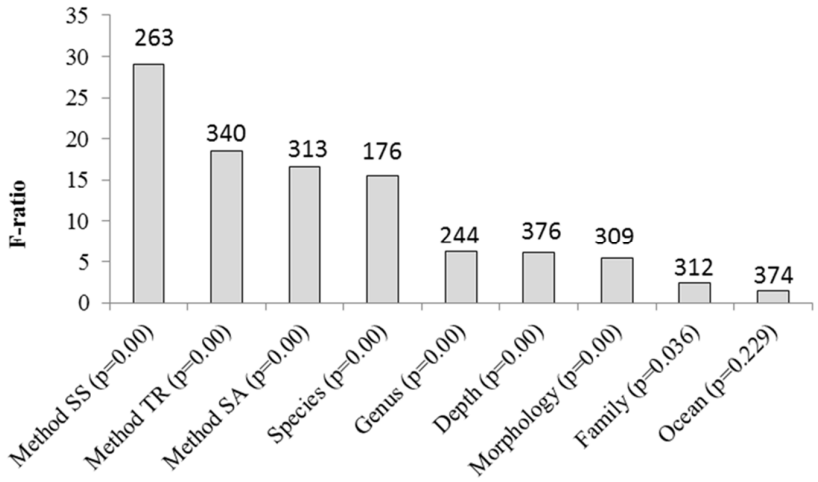

Figure A1. Zooxanthellae Density Database results showing the relative contribution (F-values) of different factors to variation in healthy zooxanthellae densities. Sample size (n) and associated p-values are indicated.

Methods of Surface Area (Method SA) determination (313/369 records, F=16.68) caused a significant amount of variation in mean zooxanthellae densities [Figure 1]. Tukey's *post hoc* revealed significantly higher results for leaf-area image analysis (n=11), which had a mean zooxanthellae density of $1.24x10^7$ (SE±$2.45x10^6$). Modification of the paraffin wax method (n=13) and calipers (n=140) were also separated by Tukey's *post-hoc*, but not significant; the mean healthy zooxanthellae density for the modified paraffin wax method was $5.90x10^6$ (SE ±$1.88x10^6$) and for calipers it was $4.95x10^6$ (SE±$2.81x10^5$). Mean healthy values from studies that calculated surface areas (mixture of graphing paper and vague descriptions, such as "measured") were $2.76x10^6$ (SE±$4.34x10^5$). MHZD that were normalized to coral polyps were $2.55x10^6$ (SE±$7.01x10^5$). Aluminum foil used for surface area determination produced MHZD of $2.66x10^6$ (SE±$2.50x10^5$). The original paraffin wax method produced mean values of $2.36x10^6$ (SE±$2.30x10^5$). For those interested, a separate ANOVA was run to compare the paraffin wax method with the modified version of this method, which produced significantly ($F_{(1,47)}$=4.577, $p<0.05$) higher estimates (the modified version). While methods obviously cause variations in the results, there is still conspicuous evidence of variability beyond methods. Two examples to highlight this variability include the range of estimates within a single study, for example the average healthy zooxanthellae density ranged from 0.67- 8.48×10^6 cell/cm^2 in the South China Sea using the same methods as the same time [69].

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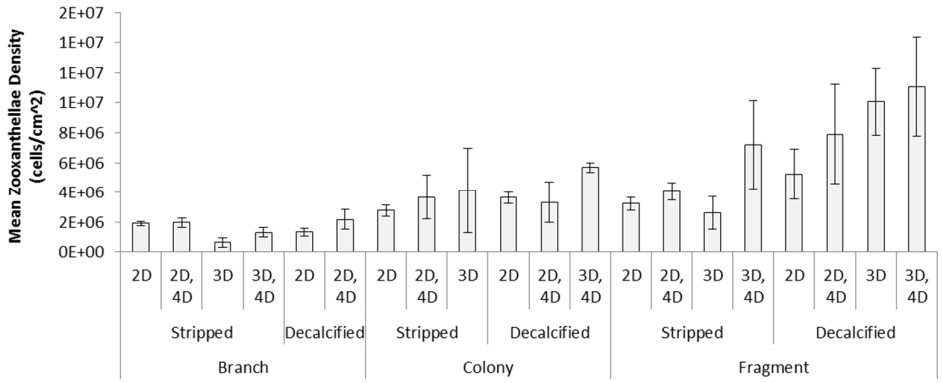

Figure A2. Mean healthy zooxanthellae densities resolved by methodological differences. Variation is partitioned by sample size (branch, colony, fragment), tissue processing method (stripped or decalcified), and sampling dimensionality (2D, 3D, or 4D, where 4D denotes repeated measures through time).

The species had a significant effect on mean zooxanthellae densities [Figure 1]. Tukey's *post hoc* showed three groups and showed a significant difference for *Goniastrea aspera* (n=9), which had the highest MHZD, $1.16x10^7$ (SE±$2.28x10^6$). The second grouping contained *Acropora nasuta* (n=38) MHZD: $6.00x10^6$ (SE±$1.54x10^5$), *Pocillopora damicornis* (n=57) MHZD: $4.22x10^6$ (SE±$2.4.x10^5$), and *Porites lutea* (n=6) MHZD: $4.62x10^6$ (SE±$1.94x10^{6**}$); however *A. nasuta* was the only coral not included in the third grouping, other than *G. aspera*. The third grouping contained most corals *Montastrea annularis* (n=15) MHZD: $2.74x10^6$ (SE±$3.17x10^5$), *Seriatopora hystrix* (n=7) MHZD: $2.79x10^6$ (SE±$5.33x10^5$), *Montastrea faveolata* (n=14) MHZD: $2.73x10^6$ (SE±$5.37x10^5$), *Porites cylindrica* (n=7) MHZD: $2.79x10^6$ (SE±$5.37x10^5$), *Acropora millepora* (n=14) MHZD: $2.15x10^6$ (SE±$2.39x10^5$), *Porites lobata* (n=8) MHZD: $2.82x10^6$ (SE±$1.90x10^6$), *Stylophora pistillata* (n=15) MHZD: $1.87x10^6$ (SE±$5.92x10^5$). Moreover, a healthy zooxanthellae density range for *Montastraea annularis* was 2.65-8.76$x10^6$ cells/cm^2 across studies. *Pocillopora damicornis* data were analysed separately with methods SS (Branch, Fragment, Colony), which yielded significantly different results. ($F_{(2, 58)}$ = 50.728, p<0.00). Tukey's *post hoc* separated each of the categories, with branches (n=11) having the lowest MHZD ($1.24x10^6$SE±$3.4x10^5$), fragments (n=11) having medium MHZD ($3.01x10^6$SE±$6.72x10^5$) and colonies (n=37) having the highest MHZD ($3.01x10^6$SE±$1.22x10^5$)

The genus had a significant effect on mean zooxanthellae densities [Figure.1]. Tukey's post-hoc, although not significant, separated the lower mean zooxanthellae densities of the genera Acropora, Pocillopora, Pavona, and Goniastrea. The average healthy zooxanthellae densities of genera are as follows (in decreasing order): *Favia* (n=6) $1.71x10^6$ (SE±$4.91x10^5$), *Montastrea* (n=28) $2.51x10^6$ (SE±$2.16x10^5$), *Montipora* (n=10) $2.78x10^6$ (SE±$6.45x10^5$), *Seriatopora* (n=8) $2.64x10^6$ (SE±$4.84x10^5$), *Porites* (n=31) $3.23x10^6$ (SE±$6.18x10^5$), *Acropora* (n=79) $3.91x10^6$ (SE±$2.49x10^5$), *Pocillopora* (n=64) $4.26x10^6$ (SE±$3.16x10^5$), *Pavona* (n=7) $5.18x10^6$ (SE±$2.07x10^{6**}$), *Goniastrea* (n=15) $8.78x10^6$ (SE±$1.92x10^6$).

The family had a significant effect on mean zooxanthellae densities [Figure 1]. Tukey's post-hoc test grouped Agariciidae and Oculiniidae as having higher (not significant) healthy zooxanthellae densities. Pocilloporidae (n=88) had the lowest zooxanthellae densities, which averaged $3.68x10^6$ (SE±$2.73x10^5$). Poritidae (n=36) had the second lowest mean zooxanthellae densities, $4.14x10^6$ (SE±$7.33x10^5$), while Acroporidae (n=90) had an average of $3.76x10^6$ (SE±$2.33x10^5$). Faviidae (n=61) averaged $4.43x10^6$ (SE±$6.17x10^5$). Agariciidae (n=17) and Oculiniidae (n=7) had average zooxanthellae densities of $6.73x10^6$ (SE±$1.99x10^6$) and $8.16x10^6$ (SE±$1.80x10^6$), respectively.

Growth form (n=309/369 records) caused significant variation amongst healthy corals [Figure 1]. Encrusting growth forms (n=10) had the highest mean zooxanthellae density, $5.41x10^6$ (SE±$1.46x10^6$), and was separated by Tukey's *post hoc*, but not significant. Branching corals (n=191) had an average zooxanthellae density of $3.59x10^6$ (SE±$1.71x10^5$), with high values (n=133) averaging $4.0x10^6$ (SE±$2.1x10^5$) and low values (n=133) averaging $3.3x10^6$ (SE±$2.1x10^5$). Massive corals had an average

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zooxanthellae density of $5.38x10^6$ (SE±$6.05x10^5$), with high values (n=35) averaging $6.73x10^6$ (SE±$1.09x10^6$) and low values (n=35) averaging 5.12x106 (SE±$9.22x10^5$). Foliose corals (n=15) had the lowest mean zooxanthellae density, $1.94x10^6$ (SE±$3.26x10^5$) and was separated by Tukey's *post hoc*, although non-significant.

Depth had a significant effect on mean zooxanthellae densities [Figure 1]; however, the relationship was such that corals decreased in zooxanthellae densities until >20m, where an increase is noted. Mean healthy zooxanthellae densities for <3m were $3.99x10^6$ (SE±$5.35x10^5$). Depths ranging between 3-6m had average zooxanthellae densities of $4.50x10^6$ (SE±$2.37x10^5$). From 7-10m, zooxanthellae densities averaged $2.48x10^6$ (SE±$4.80x10^5$). From 11-19m, zooxanthellae densities averaged $1.94x10^6$ (SE±$2.60x10^5$). And, zooxanthellae densities increased for depths >20m, which averaged $3.38x10^6$ (SE±$6.46x10^5$).

The ocean basin did not have a significant effect on MHZD [Figure 1]; although Tukey's *post hoc* tests showed that the Indian Ocean had higher average zooxanthellae densities. The Indian Ocean (n=65) had MHZD: $6.02x10^6$ (SE±$8.25x10^5$). The Pacific Ocean (n=155) had the highest MHZD: $6.94x10^6$, but also the highest standard error ±$1.89x10^6$. The Atlantic Ocean (n=55) had MHZD: $2.96x10^6$ (SE±$2.36x10^5$).

Appendix A.1. Examination of Absolute Healthy and Bleached Zooxanthellae Population Densities

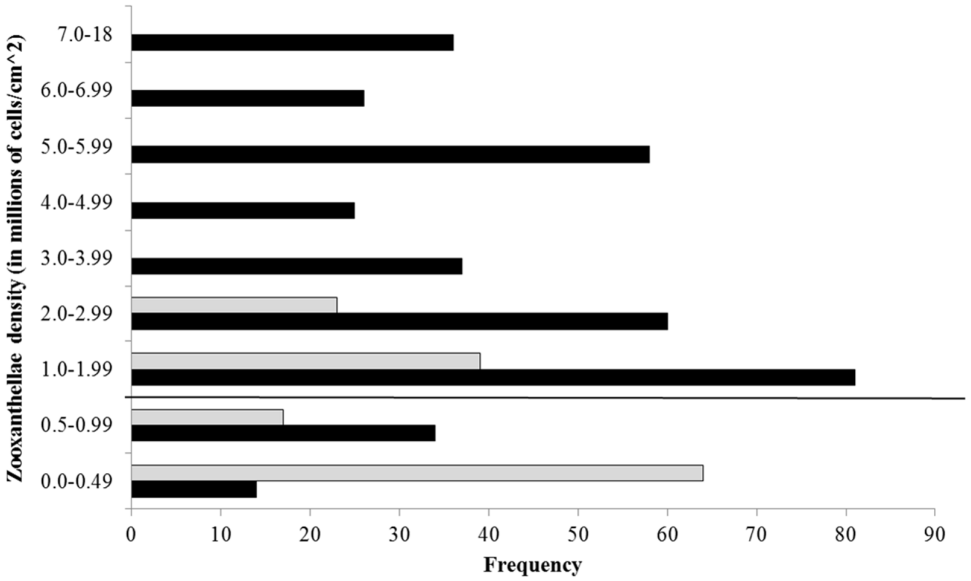

Figure A3. Frequency distribution of mean zooxanthellae densities for healthy (black) and bleached (gray) corals. The vertical line indicates 1.0×10^6 cells cm^{-2}, a commonly cited average healthy density.

Appendix A.2. Proportional Loss in Zooxanthellae Population Density by Cause of Bleaching

The proportional loss in zooxanthellae populations associated with sublethal paling and lethal bleaching were then analyzed through causal agents [Figure 6]. For the causal agent of sublethal bleaching ($F_{(4,151)}$ =12.074, p<0.001), Tukey's *post-hoc* showed that the percent loss associated with light, temperature and multiple stressors (most often representing temperature and another variable) was significantly higher than the percent loss associated with cold shock or pollutants (both of which are within 'natural variation'). For lethal bleaching ($F_{(4, 91)}$ = 6.466, p<0.000), the percent loss associated with cold-shock was significantly lower than the other causes and all collected by Leonard Muscatine. Pollution data came from 15 different studies that used variations on all methods. Only one of the records of sublethal bleaching data for pollutants reached the definition of sublethal bleaching, *Acropora spp.* (also Muscatine's work), the rest ranged from 8-53%. Zooxanthellae loss associated with

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sublethal ($F_{(5,182)}$ = 7.541, p<0.000) and lethal ($F_{(5, 117)}$ = 6.108, p<0.000) bleaching significantly increased with time and in both cases, Tukey's *post hoc* separated the lower mean values of one day experiments, which were significantly lower for sublethal stress.

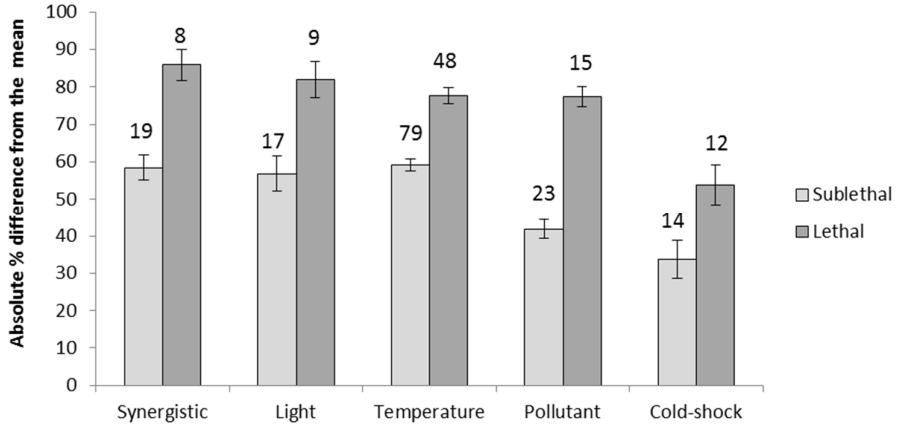

Figure A4. Absolute percent deviation from mean zooxanthellae densities associated with different stress causes. Error bars represent ±SE; sample size (n) is shown above bars.

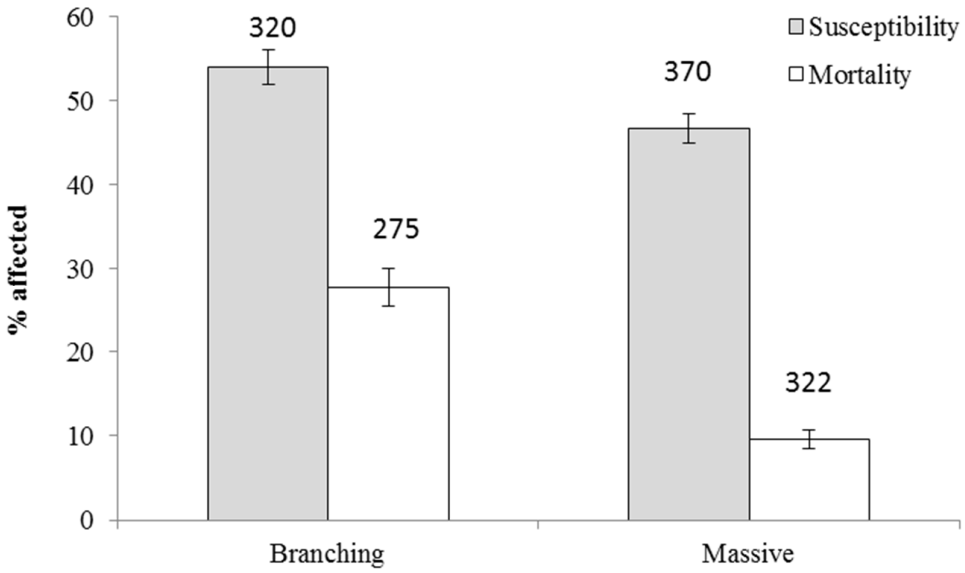

Figure A5. *Post* hoc results from McCowan et al. (2012) illustrating morphological and familial effects on bleaching susceptibility. Branching and massive morphologies do not differ significantly when pooled, but nested family-level responses reveal significant subgroup structure. Mortality patterns (not tested here) suggest lower lethal outcomes in massive colonies, consistent with partial mortality dynamics.

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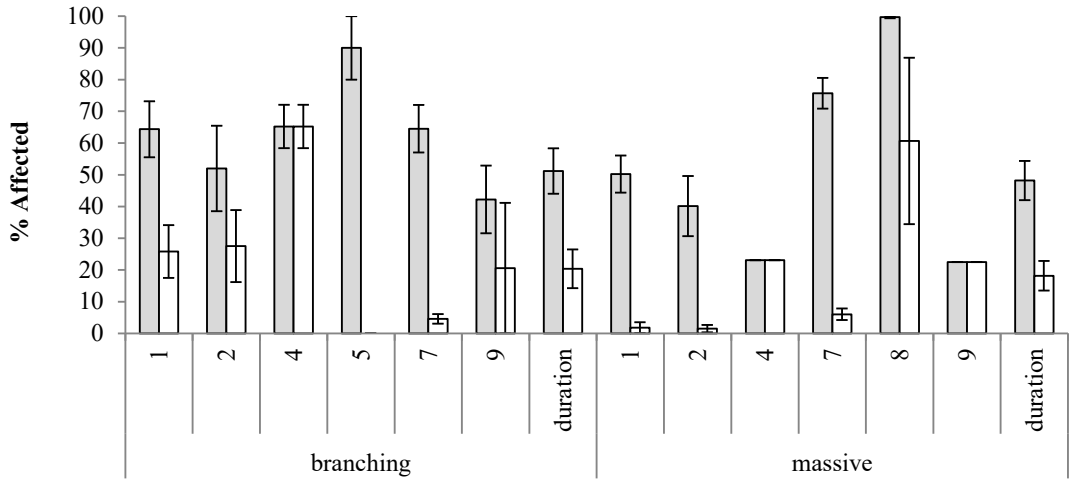
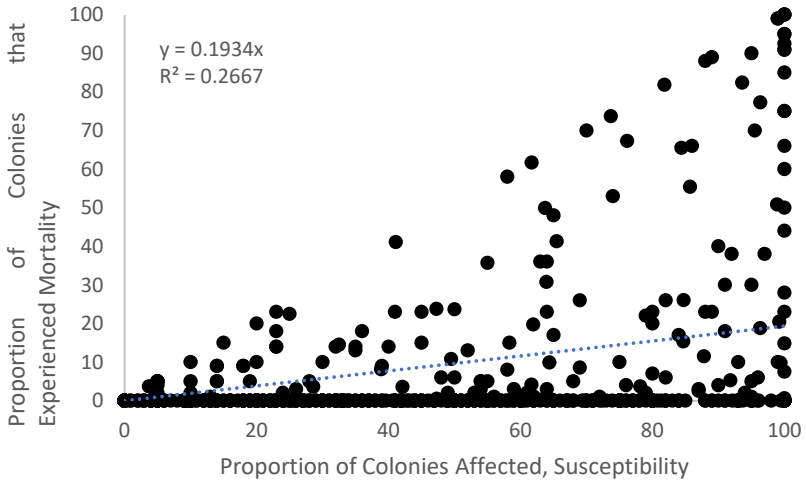
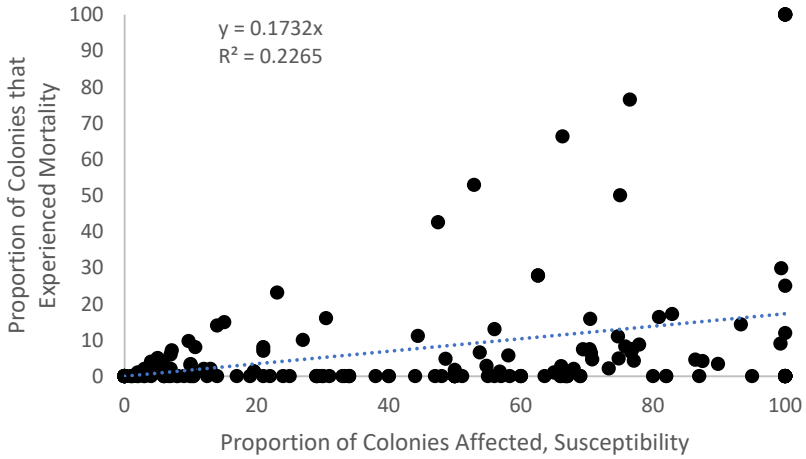


Figure A6. Temporal restructuring of bleaching susceptibility and mortality when resolved by timing of observations relative to thermal stress accumulation. Branching corals peak in susceptibility and mortality approximately 4–5 months post-stress, whereas massive corals peak later (~8 months), reflecting differences in heat retention and tissue integration.





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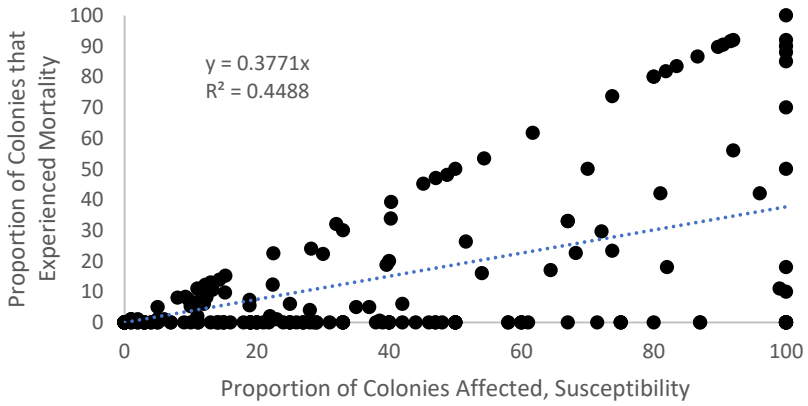
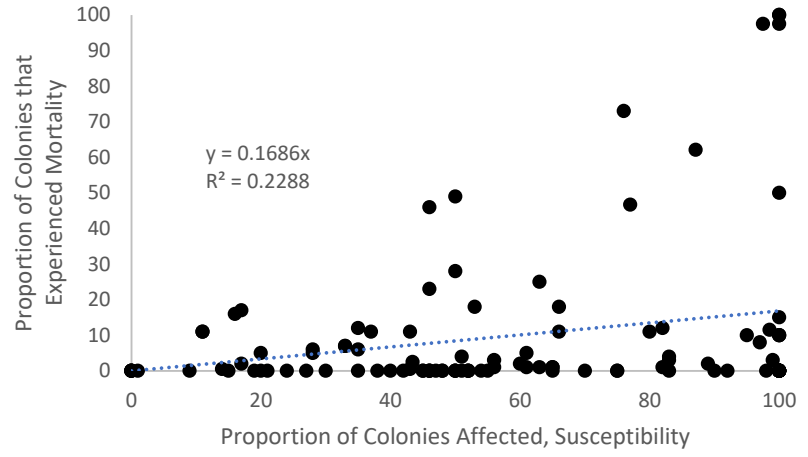
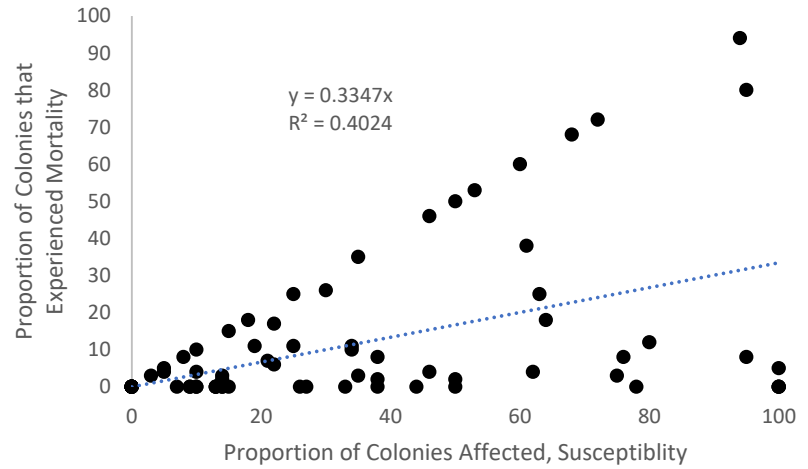


Figure A7. Paired bleaching susceptibility and mortality data during Low Thermal Stress Accumulation (DHW), resolved by timing of observations: Beginning (0–3 months), Middle (4–7 months), and End (8+ months). Linear fits assume a zero intercept; equations and correlation coefficients are shown.





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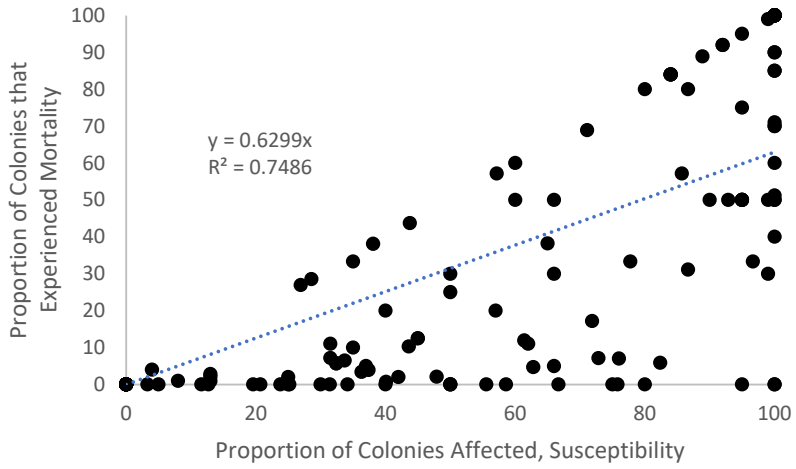
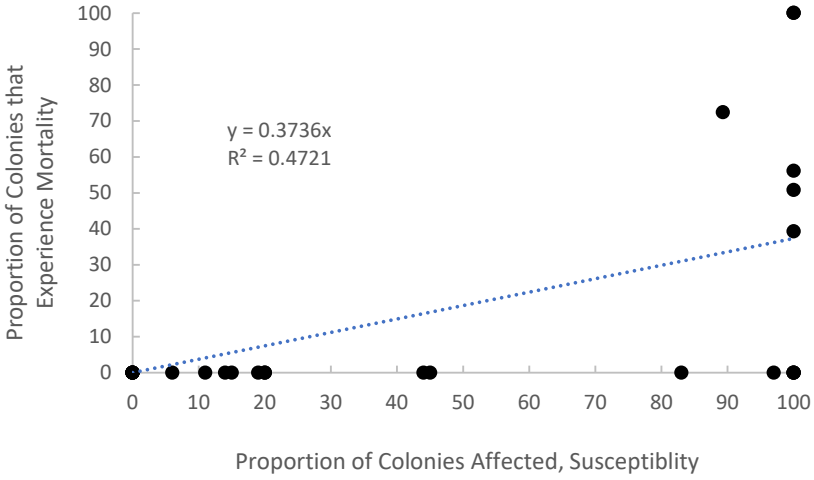
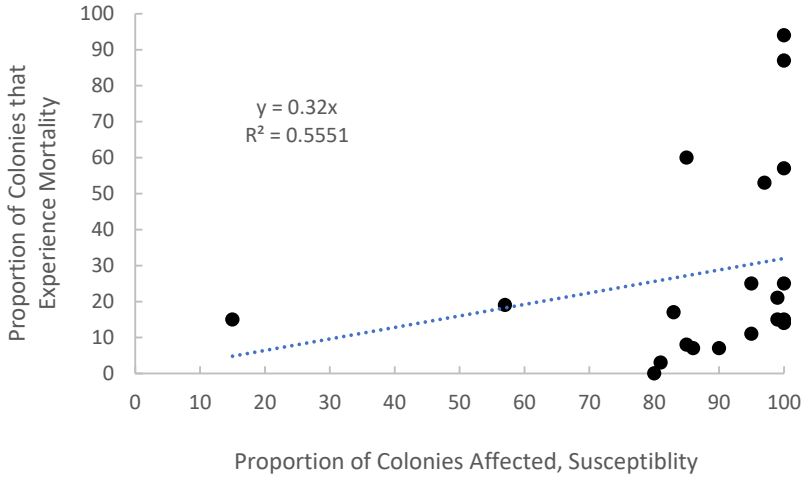


Figure A8. Paired bleaching susceptibility and mortality data during Medium Thermal Stress Accumulation (DHW), resolved by timing of observations relative to stress onset. Linear relationships illustrate how mortality expression varies with observation timing under moderate stress.





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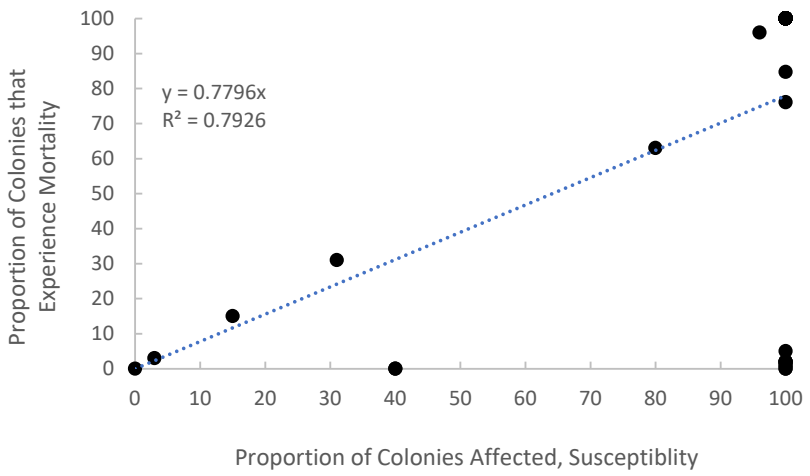

Figure A9. Paired bleaching susceptibility and mortality data during High Thermal Stress Accumulation (DHW), resolved by timing of observations. The dispersion of outcomes highlights non-linear mortality expression under extreme stress conditions.

Appendix B. Tables

Dynamic Equations for Absolute Zooxanthellae Densities

Records went from 369 for healthy values from the Zooxanthellae Density Database to 243 records of paired healthy and bleached values from the Zooxanthellae Density Meta-database. Pair-wise healthy and bleached zooxanthellae densities [Tables 1a and 2a], average declines in the zooxanthellae densities equaled 71% and linear regression showed a significant relationship (r^2= 0.509, $F_{(1, 186)}$ = 194, p<0.000). In lieu of an absolute density, which has been unachievable [Figures 2 and 3], I prepared descriptive and analytical statistics 1for dynamic equations. One may use the averages provided in [Table 1] as standards to fill in the blanks for expected results, whereby the completion of multiple independent ANOVAs [Tables 2b and 2e for healthy and bleached values, respectively] are completed to utilize the f factors to illustrate the amount of noise in the data from each given factor for a comparison of their relative importance in finding the true mean of the data [Table 2c and 2f for healthy and bleached values, respectively], and test for the data transparency (predictive power) comparing the explanatory power of the correlation coefficients {Tables 2d and 2g for healthy and bleached values, respectively]. Examples below:

Healthy Zooxanthellae density

y = Methods (43.2%) + Location (26.8) + Biology and Ecology (18.4%) + Taxonomy (11.6%) (1)

Bleached Zooxanthellae density

y = Methods (37.1%) + Biology and Ecology (29.2%) + Location (20.6%) + Taxonomy (13%) (1)

The general trends discussed above with the Zooxanthellae Density Database [Figures 1 and 2] remained similar to healthy fluctuations in zooxanthellae densities from the Zooxanthellae Density Metadatabase [Tables 1 and 2] , but as the Meta-database contained new factors to partition variance (including more methods information) and new *post hoc* groupings, there are differences (e.g. compare Figure 1 with Table 2a).

Major points of noted difference when comparing [Figure 1] and [Table 2a] include the Ocean Basin, which had been at the bottom of the list [Figure 1], turned into the second greatest cause of variability [Table 2a]. Ocean basin alongside subregion of the Ocean were the only factors in the top 5 that were not directly related to methods, although it could reflect methods used for local reef

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morphologies, as source authors were also in the top 5 (Table 1a); therefore, the two factors of Ocean basin and subregion were used to organize zooxanthellae data and bleaching response data for later comparisons. Moreover, morphology, a biological/ecological factor became the second largest factor affecting bleached zooxanthellae densities [Table 2e], which supports the hypothesis that intrinsic variability is paramount to how a coral responds to disturbance. These absolute values are revisited after the bleaching responses are analyzed to compare the zooxanthellae densities with the knowledge of the relative importances of factors to susceptibility, mortality and recovery of corals.

Table A1. Analysis of variance on data restricted to pairwise averages of healthy and bleached zooxanthellae population densities (n ≥ 5). All data were square-root transformed prior to analysis and organized by F-values.

A) Paired sample tests comparing average healthy and bleached zooxanthellae densities, including Pearson correlation and Student's t-test.

Test	Coefficient	n	p
Correlation	0.804	246	<0.001***
T-test	24.039	245	<0.001*** [1]

[1] ***Highly significant interaction.

B) ANOVA results identifying factors associated with variation in healthy zooxanthellae population densities.

Source	SS Type III	df	n	MS	F	p
Method for Tissue Removal	18.83	1	233	6.92	43.917	<0.001***
Ocean Basin	2.07	2	242	2.40	36.643	<0.001***
Source Author	16.53	13	178	2.74	33.700	<0.001***
Surface Area Determination	17.64	3	202	18.09	29.476	<0.001***
Subregion	20.70	3	245	6.67	22.716	<0.001***
Genus	15.00	12	230	6.44	19.130	<0.001***
Location	18.77	10	228	7.37	14.080	<0.001***
Replication	10.07	2	64	11.38	13.216	<0.001***
Transmission of Algae	1.45	2	210	6.21	12.886	<0.001***
Sex	18.17	1	227	7.61	12.620	<0.001***
Sample Size	19.22	6	242	6.30	11.512	<0.001***
Species	10.25	15	191	3.03	10.798	<0.001***
Morphology	1.92	2	242	7.41	9.759	<0.001***
Generalization	1.92	1	241	7.71	9.058	<0.01**
Reproductive Mode	16.39	2	221	6.93	8.793	<0.001***
Depth	14.29	3	154	8.20	7.716	<0.001***
Sampling Time	19.22	10	242	6.29	7.466	<0.001***
Family	18.78	6	238	6.79	7.438	<0.001***
Complexity of Skeleton	19.22	1	242	7.78	6.045	<0.05*
Decade	19.22	2	242	7.67	5.300	<0.01**

*Significant, **strongly significant, ***highly significant.

C) Relative importance of factors contributing to variation in healthy densities derived from B.

Grouped Factor	Grouped Relative Importance	Source	F	Relative Importance
Methods	43.2	Method for Tissue Removal	43.917	13.6
		Source Author	33.700	10.5
		Surface Area Determination	29.476	9.1
		Replication	13.216	4.1
		Sample Size	11.512	3.6
		Sampling Time	7.466	2.3

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Location	26.8	Ocean Basin	36.643	11.4
		Subregion	22.716	7.0
		Location	14.080	4.4
		Depth	7.716	2.4
		Decade	5.300	1.6
Biology and Ecology	18.4	Transmission of Algae	12.886	4.0
		Sex	12.620	3.9
		Morphology	9.759	3.0
		Generalization	9.058	2.8
		Reproductive Mode	8.793	2.7
		Complexity of Skeleton	6.045	1.9
Taxonomy	11.6	Genus	19.130	5.9
		Species	10.798	3.4
		Family	7.438	2.3

D) Pearson correlation tests among factors identified in B.

Source	n	Pearson's Correlation Coefficient	p
Location	229	0.471	<0.001***
Method for Tissue Removal	234	0.399	<0.001***
Subregion	246	-0.370	<0.001***
Replication	65	-0.351	<0.001***
Sampling Time	243	0.317	<0.001***
Sex	228	-0.230	<0.001***
Depth	155	-0.287	<0.001***
Morphology	243	0.237	<0.001***
Transmission of Algae	211	-0.217	<0.001***
Sample Size	243	0.199	<0.01**
Generalization	242	0.191	<0.01**
Source Author	179	0.162	<0.01**
Complexity of Skeleton	243	0.156	<0.05*
Ocean Basin	246	-0.150	>0.05*
Reproductive Mode	222	-0.112	>0.05
Surface Area Determination	203	0.096	>0.05
Genus	231	0.087	>0.05
Species	192	-0.063	>0.05
Family	239	0.030	>0.05
Decade	243	0.026	>0.05

*Significant, **strongly significant, ***highly significant.

E) ANOVA results for bleached zooxanthellae population densities.

Source	SS Type III	df	n	MS	F	p
Method for Tissue Removal	6.97	1	233	2.57	39.928	<0.001***
Morphology	3.61	3	473	6.51	28.142	<0.001***
Source Author	5.94	13	178	1.24	24.256	<0.001***
Transmission of Algae	0.56	2	210	2.23	21.238	<0.001***
Ocean Basin	0.72	2	242	2.61	18.494	<0.001***
Genus	5.90	12	230	1.38	17.608	<0.001***
Surface Area Determination	.046	3	202	2.47	15.341	<0.001***
Subregion	8.50	3	246	3.08	11.158	<0.001***
Location	6.94	10	228	2.24	9.166	<0.001***
Sex	6.94	1	227	2.95	8.980	<0.01**

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Species	4.01	15	191	1.35	8.072	<0.001***
Depth	5.14	3	154	2.96	7.610	<0.001***
Sample Size	7.22	6	242	2.59	7.117	<0.001***
Family	6.15	6	238	2.29	6.534	<0.001***
Sampling Time	7.22	10	242	2.54	5.266	<0.001***
Generalization	7.19	1	241	2.93	5.179	<0.05*
Decade	7.22	2	242	2.90	4.615	<0.05*
Reproductive Mode	6.70	2	221	2.94	4.485	<0.05*
Complexity of Skeleton	7.22	1	242	2.94	4.232	<0.05*
Replication	2.81	2	64	4.29	1.821	>0.05

*Significant, **strongly significant, ***highly significant.

F) Relative importance of factors contributing to variation in bleached densities derived from E.

Grouped Factor	Grouped Relative Importance	Source	F	Relative Importance
Methods	37.1	Method for Tissue Removal	39.928	16.1
		Source Author	24.256	9.8
		Surface Area Determination	15.341	6.2
		Samples Size	7.117	2.9
		Sample Time	5.266	2.1
Biology and Ecology	29.2	Morphology	28.142	11.4
		Transmission of Algae	21.348	8.6
		Sex	8.980	3.6
		Generalization	5.179	2.1
		Reproductive Mode	4.485	1.8
		Complexity of Skeleton	4.232	1.7
Location%	20.6	Subregion	11.158	4.5
		Ocean Basin	18.494	7.5
		Location	9.166	3.7
		Depth	7.610	3.1
		Decade	4.615	1.9
Taxonomy	13.0	Genus	17.608	7.1
		Species	8.072	3.3
		Family	6.534	2.6

G) Pearson correlation tests among factors identified in E.

Source	n	Pearson's Correlation Coefficient	p
Location	229	0.426	<0.001***
Method for Tissue Removal	234	0.379	<0.001***
Source Author	179	0.276	<0.001***
Subregion	246	-0.260	<0.001***
Transmission of Algae	211	-0.220	<0.001***
Replication	65	-0.206	<0.001***
Sex	228	-0.196	<0.001***
Surface Area Determination	203	0.185	<0.001***
Depth	155	-0.185	<0.05*
Morphology	243	0.167	<0.01**
Reproductive Mode	222	-0.157	<0.01**
Generalization)	242	0.145	<0.01**
Complexity of Skeleton	243	0.131	>0.05
Ocean Basin	246	0.114	<0.05*

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Species	192	-0.092	>0.05
Decade	242	-0.054	>0.05
Genus	231	0.039	>0.05
Family	239	-0.031	>0.05
Sampling Time	243	0.014	>0.05
Sample Size	243	-0.003	>0.05

*Significant, **strongly significant, ***highly significant.

Table A2. Inter- and intra-specific variation in healthy zooxanthellae population densities. Data are restricted to species with n > 20 overall and n ≥ 3 per factor. Panel A shows interspecific variation; Panels B–F show intraspecific variation for Acropora millepora, Coelastrea aspera, Orbicella annularis, Pocillopora damicornis, and Stylophora pistillata, respectively. Healthy densities are reported as $\times 10^6$ cells cm^{-2}; standard error is shown as $\times 10^5$ cells cm^{-2}. Data are ordered by F-ratio values.

A) Average values of healthy and bleached zooxanthellae population densities

Healthy	**±SE**	***n***	**Bleached**	**±SE**	***n***
3.70	2.69	243	1.00	0.83	243

[1] ***Highly significant interaction.

B) Taxonomy and average healthy and bleached zooxanthellae densities

Factor	**Source**	**Healthy**	**±SE**	***n***	**Bleached**	**±SE**	***n***
Family	Acroporidae	1.89	2.12	55	0.50	0.60	55
	Agariciidae	7.57	1.69	16	2.51	5.45	16
	Faviidae	4.04	4.28	74	1.28	1.80	74
	Oculinidae	11.24	16.76	7	1.63	4.91	7
	Pocilloporidae	3.20	4.16	58	0.84	1.11	58
	Poritidae	3.45	9.85	31	0.64	1.66	31
Genus	Acropora	1.49	1.00	45	0.39	0.48	45
	Agaricia	1.30	4.25	8	0.52	1.93	8
	Cladocora	3.32	3.68	6	0.95	2.46	6
	Coelastrea	8.15	10.66	11	3.00	2.44	11
	Montastrea	1.82	4.71	6	0.75	1.57	6
	Montipora	3.73	9.02	10	1.02	1.85	10
	Oculina	11.12	19.77	6	1.73	5.68	6
	Orbicella	2.40	1.46	45	0.53	0.83	45
	Pavona	12.92	8.31	6	5.00	0.45	6
	Pocillopora	4.28	6.90	31	0.82	1.36	31
	Porites	2.93	8.66	30	0.63	1.71	30
	Seriatopora	2.95	3.81	13	1.31	3.39	13
	Stylophora	1.03	1.61	14	0.43	0.69	14
Species	Acropora millepora	1.58	1.31	24	0.54	0.07	24
	Acropora muricata	1.25	2.77	7	0.21	0.00	7
	Agaricia lamarcki	1.48	6.95	5	0.60	3.18	5
	Cladocora caespita	3.32	3.68	6	0.95	2.46	6
	Coelastrea aspera	8.15	10.66	11	3.00	2.44	11
	Montastrea cavernosa	1.82	4.71	6	0.75	1.57	6
	Oculina patagonica	11.12	19.77	6	1.73	5.68	6
	Orbicella annularis	2.30	1.63	27	0.54	1.15	27
	Orbicella faveolata	3.08	4.01	10	0.45	1.51	10
	Orbicella franksi	1.86	1.84	8	0.59	1.97	8
	Pocillopora damicornis	3.34	4.24	26	0.57	0.98	26
	Porites cylindrica	3.36	3.06	5	1.06	0.85	5

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	Porites lobata	3.26	1.35	19	0.64	2.60	19
	Porites lutea	1.45	6.87	5	0.22	1.20	5
	Seriatopora hystrix	2.95	3.81	13	1.31	3.39	13
	Stylophora pistillata	1.03	1.61	14	0.43	0.69	14

C) Location and variation in healthy and bleached zooxanthellae population densities

Factor	Source	Healthy	±SE	n	Bleached	±SE	n
Decade	1980's	1.45	3.11				14
	1990's	4.98	7.40	54	1.35	2.14	54
	2000's	3.49	2.86	175	0.94	0.91	175
Ocean Basin	Atlantic	2.29	1.36	69	0.53	0.70	69
	Indian	7.67	8.26	37	1.82	1.98	37
	Pacific	3.35	3.67	137	1.02	1.23	137
Subregion	East	5.59	8.06	54	1.32	2.22	54
	North	1.72	2.77	25	0.47	1.66	25
	South	4.18	4.91	15	0.88	1.93	15
	West	3.54	3.24	152	1.13	1.30	152
Location	Bahamas	2.61.	2.16	27	0.39	1.16	27
	Costa Rica	0.88	0.69	9	0.11	0.37	9
	Florida	1.81	1.91	10	0.44	1.19	10
	Great Barrier Reef	2.56	3.32	79	0.93	1.47	79
	Jamaica	1.51	1.63	21	0.59	0.89	21
	Japan	0.72	1.27	10	0.20	0.66	10
	Kenya	3.36	3.06	5	1.06	0.85	5
	Mediterranean Sea	7.22	1.52	12	1.34	3.18	12
	Mexico	3.38	3.08	9	0.75	2.88	9
	Panama	6.63	1.21	30	1.70	3.54	30
	Thailand	10.06	1.13	17	2.65	2.30	17

D) Biological and Ecological factors and variation in healthy and bleached zooxanthellae densities

Factor	Source	Healthy	±SE	*n*	Bleached	±SE	*n*
Depth	<3m	2.90	2.39	36	1.04	1.75	36
	<6m	5.51	9.76	31	0.85	1.51	31
	<9m	6.37	10.53	40	1.77	3.54	40
	<12m	1.91	3.61	5	0.38	0.58	5
	<15m	1.76	2.02	19	0.21	0.76	19
	>15m	1.82	2.37	24	0.78	1.25	24
Transmission of Algae to Offspring	Both	8.15	10.66	11	3.00	2.44	11
	No	3.12	3.38	108	0.82	1.14	108
	Yes	3.08	3.96	92	0.78	0.88	92
Morphology	Branching	2.54	2.34	119	0.68	0.620	119
	Encrusting	6.24	15.90	13	1.20	3.30	13
	Massive	4.65	4.74	111	1.32	1.57	111
Generalization	Generalist	3.10	2.85	150	0.90	1.05	150
	Specialist	4.70	5.22	92	1.18	1.32	92
Sex	Gonochoric	5.65	7.46	65	1.57	2.35	65
	Hermaphroditic	2.92	2.28	163	0.80	0.70	163
Reproductive Mode	Botha	5.13	6.50	31	1.51	2.31	31
	Brooder	1.80	2.25	34	0.73	1.53	34
	Spawner	3.54	3.43	157	0.96	1.09	157
Complexity of Skeleton	Complex	3.33	4.53	104	0.86	1.22	104
	Robust	3.98	3.25	139	1.11	1.11	139

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E) Methods used and variation in healthy bleached zooxanthellae population densities

Factor	Source	Healthy	±SE	*n*	Bleached	±SE	*n*
Method for Tissue Removal from skeleton	Pick	3.29	2.63	213	0.90	0.85	213
	Decalcify	8.83	1.07	21	2.42	2.20	21
Sample Size	Branch	1.46	0.96	50	0.49	0.52	50
	Colony	3.32	6.91	36	1.23	2.98	36
	Core	8.96	1.31	18	2.06	3.14	18
	Fragment	4.27	7.00	59	1.27	2.08	59
	Nubbin	4.87	5.61	12	1.10	1.14	12
	Sample	2.76	1.82	46	0.52	1.21	46
	Subsample	4.94	9.89	22	1.15	2.00	22
Sampling Time	<1 day	2.15	2.27	38	0.63	0.97	38
	<1 week	2.92	4.07	45	1.15	1.77	45
	<2 weeks	1.54	2.32	12	0.57	1.25	12
	<1 month	2.25	2.58	27	0.94	1.96	27
	<1.5 months	2.95	6.22	17	0.77	2.49	17
	<3 months	4.01	12.59	18	0.84	2.46	18
	<4 months	7.06	26.02	8	2.76	1.11	8
	<6 months	3.02	4.00	9	0.94	2.13	9
	<1 year	4.93	9.06	11	0.69	1.09	11
	<2 years	9.10	12.24	31	2.03	3.24	31
	>2 years	2.43	2.00	27	0.24	0.64	27
Surface Area Determination	Calipers	4.30	5.51	25	1.00	2.39	25
	Foil	2.38	2.93	89	0.61	0.83	89
	Image Analyzer	13.91	12.11	11	3.14	6.81	11
	Wax	4.05	5.35	78	1.15	1.57	78
Replication	<6	7.42	9.60	36	2.01	2.94	36
	<8	13.25	15.66	8	1.87	2.80	8
	≥8	3.24	7.70	31	1.25	3.23	31
Source Author	Berkelmans	1.39	0.99	18	0.36	0.39	18
	Brown	10.06	11.28	17	2.65	2.30	17
	Centeno	0.88	0.69	9	0.11	0.37	9
	D'Croz	1.27	2.14	17	0.30	1.11	17
	Fitt	1.96	1.83	37	0.25	0.47	37
	Flores-Ramirez	3.38	3.08	9	0.75	2.88	9
	Hill	4.59	2.50	7	1.19	1.60	7
	Hoegh-Guldberg	1.09	2.07	12	0.36	0.66	12
	Hueerkamp	13.65	8.92	13	3.54	4.30	13
	Jones	4.78	1.16	19	2.04	5.13	19
	Mercurio	0.98	0.43	6	0.21	0.02	6
	Rodolfo-Metalpa	7.32	2.03	9	1.63	3.77	9
	Visram	3.36	3.06	5	1.06	0.85	5
	Warner	1.88	2.32	9	0.77	1.52	9

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Table A3. Inter- and intra-taxonomic variation in bleaching susceptibility and mortality using paired susceptibility–mortality records. Panel A shows inter-familial variation (n > 50 per family), Panel B inter-generic variation (n > 40 per genus), and Panel C inter-specific variation (species with n > 20 and n ≥ 3 per factor). ANOVAs were used to partition variance within each taxonomic level; data are ordered by F-values.

A) Average values for factors that cause inter and intra-specific variation

	Source	Healthy	±SE	n
Species	Acropora millepora	2.06	1.59	40
	Coelastrea aspera	10.23	1.21	20
	Orbicella annularis	2.91	2.92	34
	Pocillopora damicornis	2.52	2.77	49
	Stylophora pistillata	1.92	4.12	36
Ocean	Atlantic	2.91	2.51	40
	Indian	6.93	1.01	35
	Pacific	2.11	1.63	104
Replication level	Branch	1.81	1.58	63
	Colony	2.75	3.09	32
	Core	9.54	1.59	17
	Fragment	2.48	6.94	16
	Sample	2.65	2.34	27
Location	Bahamas	2.57	2.95	12
	Florida	2.07	2.48	6
	Great Barrier Reef	2.11	1.70	61
	Hawaii	1.70	3.21	13
	Jamaica	3.49	6.25	14
	Japan	1.55	5.60	8
	Mexico	2.92	3.16	6
	Pacific	7.73	1.60	4
	Panama	2.74	6.55	16
	Red Sea	2.96	7.99	17
	Thailand	10.68	1.30	18
Method for tissue removal	Airbrush	2.53	2.29	60
	Decalcification	6.24	9.36	38
	Waterpik	2.52	2.54	72
Method for surface area	Calculated	2.31	3.13	10
	Callipers	5.19	1.00	29
	Foil	2.41	3.74	41
	Image analyser	5.11	2.09	7
	Paraffin Wax	2.11	1.99	64
	Modified Paraffin Wax	3.60	6.24	9
Time	< 1 day	2.81	3.51	45
	< 1 week	5.13	8.64	29
	< 2 weeks	4.30	1.82	4
	< 1 month	1.62	1.91	26

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	< 2 months	1.63	1.93	18
	< 3 months	1.85	5.27	4
	< 6 months	3.98	7.33	11
	< 9 months	3.25	3.03	10
	< 1 year	2.84	9.54	11
	< 2 years	6.64	2.60	5
	> 2 years	5.13	1.62	16
Cause	Aerial exposure	9.77	18.95	3
	Ammonium enrichment	1.45	2.35	16
	Depth	3.53	5.45	28
	High light and temperature	4.98	7.91	18
	Light	2.75	7.26	19
	One sample	3.27	12.07	5
	Pollutant	1.38	8.87	6
	Seasonal variation	4.59	16.04	15
	Temperature	2.81	3.92	68
Subregion	East	2.74	6.55	16
	North	2.54	4.62	33
	South	1.90	2.43	24
	West	3.82	3.96	106
Depth	< 3m	2.38	4.07	43
	< 6m	2.38	2.99	43
	> 6m	3.18	3.81	25
Replicate counts	< 6	4.53	1.03	15
	> 6	2.95	6.55	25

B) Variation in healthy zooxanthellae population densities of Acropora millepora

	Source	Healthy	±SE	n
Replication level	Branch	1.69	1.29	27
	Colony	3.25	3.03	10
	Population	1.39	1.99	3
Cause	Depth	1.62	1.51	15
	High temperature and light	2.87	3.48	3
	Pollutant	1.49	0.78	3
	Seasonal variation	3.25	3.03	10
	Temperature	1.39	1.47	9
Method for surface area	Callipers	2.49	1.74	3
	Foil	1.47	2.33	3
	Wax	2.07	1.82	34
Method for tissue removal	Airbrush	2.07	1.83	34
	Decalcification	2.49	1.74	3
	Waterpik	1.49	0.78	3

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C) Variation in healthy zooxanthellae population densities of Coelastrea aspera

	Source	Healthy	±SE	n
Replication level	Colony	6.07	6.05	4
	Core	11.63	16.80	13
Time	< 1 month	8.85	11.34	14
	> 1 year	13.46	27.60	6
Cause	Aerial Exposure	9.77	18.85	3
	High light and temperature	8.70	19.28	5
	Temperature	10.56	22.63	6
Replicate counts	3	9.77	18.85	3
	6	10.00	31.39	3

D) Variation in healthy zooxanthellae population densities of Orbicella annularis

	Source	Healthy	±SE	n
Method for surface area	Callipers	5.51	9.20	6
	Foil	2.31	1.96	21
Cause	Depth	4.99	6.52	9
	High light and temperature	2.16	3.62	4
	Temperature	2.08	1.45	20
Depth	< 3m	2.27	4.91	3
	< 6m	2.36	3.99	4
	< 15m	2.11	1.56	14
	< 18m	1.53	2.73	3
	< 24m	3.93	1.76	3
	> 24m	5.51	9.20	6
Time	< 1 week	1.86	1.91	6
	< 1 month	3.93	1.76	3
	< 6 months	4.72	8.63	8
	< 1 year	2.37	4.18	3
	> 2years	2.16	2.01	12
Replicate counts	< 8	3.93	1.76	3
	> 8	2.59	4.17	5
Subregion	North	2.07	2.48	6
	West	3.10	3.55	27
Location	Bahamas	2.57	2.95	12
	Florida	2.07	2.48	6
	Jamaica	3.49	6.25	14
Method for tissue removal	Airbrush	2.16	3.62	4
	Decalcification	3.93	1.76	3
	Waterpik	2.91	3.55	27
Replication level	Colony	1.97	3.31	5
	Core	2.74	4.76	4
	Sample	2.40	2.32	17

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E) Variation in healthy zooxanthellae population densities of Pocillopora damicornis

	Source	Healthy	±SE	n
Method for surface area	Calipers	1.64	3.83	11
	Wax	2.56	5.06	21
Subregion	East	2.74	6.55	16
	North	1.54	2.27	3
	South	1.48	2.64	17
	West	4.59	2.50	7
Cause	Ammonium Enrichment	1.41	2.29	10
	High light and temperature	4.83	0.96	6
	Light	2.03	6.03	6
	Seasonal Variation	0.77	1.74	3
	Temperature	2.82	6.53	16
Method for tissue removal	Airbrush	3.45	5.59	20
	Decalcification	1.64	3.83	11
	Waterpik	1.77	2.27	9
Time	< 1 day	2.75	5.50	10
	< 1 week	3.97	6.79	5
	< 2 months	1.70	2.40	14
	< 3 months	1.85	5.27	4
	< 1 year	3.02	1.32	8
Depth	< 3m	1.79	3.03	13
	< 6m	2.16	1.73	5
	< 9m	2.77	8.17	13
Replication level	Branch	2.57	3.26	24
	Colony	2.93	8.05	13

F) Variation in healthy zooxanthellae population densities of Stylophora pistillata

	Source	Healthy	±SE	n
Ocean	Indian	2.96	7.99	17
	Pacific	0.98	1.20	19
Depth	< 3m	1.10	1.30	15
	< 6m	0.97	3.29	5
	< 9m	0.61	1.64	4
	> 9m	2.81	1.03	3
Location	Great Barrier Reef	1.03	1.61	14
	Japan	0.85	0.71	5
	Red Sea	2.96	7.99	17
Subregion	North	2.48	6.43	22
	West	1.03	1.61	14
Time	< 1 day	2.95	8.57	16
	< 1 week	0.91	1.32	14
	< 2 weeks	1.50	2.46	6

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Cause	Ammonium enrichment	1.04	3.04	5
	Light	3.08	1.03	13
	Pollutant	1.27	1.45	3
	Temperature	0.96	1.99	11
Method for surface area	Calculated	1.41	1.71	4
	Foil	2.48	9.49	15
	Image Analyser	2.70	7.13	4
	Wax	1.21	1.89	9

Table A4. Variation in bleaching susceptibility and mortality attributable to (A) taxonomy, (B) location, (C) biological/ecological traits, (D) timing of observations, and (E) temperature. Values are shown alphabetically; only categories with n > 10 are included. No constraints were imposed on the database.

A) Taxonomy and average proportional susceptibility and mortality to mass bleaching events

Factor	Source	(S-M)/S	Susceptibility			Mortality		
			Average	±SE	*n*	Average	±SE	*n*
Family	Acroporidae	0.50	54.7	1.89	367	27.2	2.27	290
	Agariciidae	0.69	51.7	3.31	137	16.2	2.93	112
	Astrocoeniidae	0.53	36.1	9.44	13	17.0	9.39	11
	Dendrophyllidae		41.1	13.96	11			
	Diploastraeidae	0.58	35.7	7.68	27	15.0	7.90	20
	Euphyllidae	0.65	42.8	5.04	46	15.1	5.24	36
	Fungiidae	0.77	40.0	3.82	77	9.2	3.08	66
	Lobophyllidae	0.97	36.1	4.51	45	1.16	0.54	38
	Meandrinidae	0.86	30.7	4.96	35	4.4	2.18	30
	Merulinidae	0.80	47.8	1.87	333	9.7	1.28	268
	Milleporidae	0.33	56.4	4.96	60	37.7	6.53	48
	Montastraeidae	0.94	42.0	6.32	27	2.7	1.52	21
	Mussidae	0.78	45.4	2.83	144	10.2	2.12	120
	Pocilloporidae	0.57	47.3	2.45	229	20.4	2.80	164
	Poritidae	0.64	41.4	2.15	273	14.9	2.05	214
	Psammocoridae	0.84	54.7	8.58	21	8.6	5.66	15
	Siderastreidae	0.93	57.7	4.02	58	4.0	1.73	48
Genus	Acanthastrea	0.97	44.7	7.08	16	1.4	1.00	12
	Acropora	0.44	60.1	2.45	230	33.8	3.06	188
	Agaricia	0.80	60.4	4.42	60	11.9	3.51	49
	Astreopora	0.94	38.7	5.08	17	2.5	1.83	13
	Colpopyllia	0.78	52.1	6.41	21	11.3	4.31	16
	Cyphastrea	0.41	28.1	8.92	17	16.6	8.61	13
	Diploastrea	0.58	35.7	7.68	27	15.0	7.90	20
	Diploria	0.67	56.4	8.67	20	18.7	7.45	15
	Echinophyllia	1	20.6	7.20	10	0	0	10
	Echinopora	0.61	35.3	7.07	25	13.7	5.96	21
	Favia	0.90	47.1	5.04	37	4.7	3.28	30
	Favites	0.75	51.5	5.79	33	12.7	5.00	23
	Fungia	0.83	56.5	5.73	31	9.5	5.23	23
	Galaxea	0.74	36.2	5.71	29	9.5	4.58	24
	Goniastrea	0.84	47.8	7.08	27	7.7	4.38	24
	Goniopora	0.87	38.1	8.03	25	5.0	4.66	21
	Hydnophora	0.68	40.7	6.68	24	13.0	5.19	21

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	Leptoria		27.5	9.64	11			
	Lobophyllia		43.0	11.06	11			
	Madracis	0.39	10.9	3.40	21	6.6	3.90	17
	Meandrina	0.92	36.0	7.82	13	2.7	2.24	12
	Millepora	0.35	55.6	5.00	59	36.4	6.54	47
	Montastrea	0.94	44.4	4.89	43	2.8	1.17	31
	Montipora	0.65	44.9	3.79	91	15.8	3.64	64
	Mycetophyllia	0.50	32.6	12.32	11	16.4	11.06	11
	Orbicella	0.84	65.6	3.85	50	10.4	2.11	44
	Pavona	0.52	43.4	5.59	51	20.9	5.85	40
	Platygyra	0.75	51.3	5.07	45	13.0	4.33	35
	Pocillopora	0.54	47.2	2.82	162	21.8	3.41	114
	Porites	0.60	42.4	2.32	235	16.8	2.31	183
	Psammocora	0.85	55.7	8.58	21	8.6	5.66	15
	Pseudodiploria	0.88	48.9	4.80	34	5.9	2.19	30
	Seriatopora		75.1	9.39	12			
	Siderastrea	0.92	56.1	4.15	53	4.7	1.93	44
	Stephanocoenia	0.54	35.0	10.19	12	16.17	10.34	10
	Stylophora	0.73	61.4	8.18	23	16.4	9.67	14
	Symphyllia	0.95	37.9	9.50	15	2.0	1.37	12
	Turbinaria		41.1	13.96	11			
Species	*Acropora cervicornis*	0.77	36.6	7.90	21	8.3	5.62	16
	Acropora hyacinthus	0.25	68.1	13.78	10	51.3	14.22	10
	Acropora palmata	0.78	39.7	8.49	18	8.6	4.64	14
	Agaricia agaricites	0.80	68.9	6.62	22	13.8	6.24	19
	Agaricia tenuifolia	0.58	37.9	8.74	12	16.0	9.51	11
	Colpophyllia natans	0.73	48.5	7.32	17	12.9	4.78	14
	Diploria labyrinthiformis	0.64	51.5	8.91	18	18.7	7.45	15
	Favia fragum	0.98	46.9	7.77	13	0.9	0.63	12
	Meandrina meandrites	0.91	34.8	8,40	12	3.0	2.44	11
	Montastrea cavernosa	0.94	42.0	6.32	27	2.7	1.52	21
	Montipora capitata		31.4	11.14	13			
	Orbicella annularis	0.87	66.9	4.36	35	8.9	2.16	32
	Orbicella faveolata		70.2	7.29	12			
	Pavona varians		52.0	11.32	11			
	Platygyra daedalea	0.69	69.9	6.54	14	21.4	7.69	14
	Pocillopora damicornis	0.38	48.3	6.57	36	30.0	8.28	25
	Pocillopora elegans		62.5	12.26	10			
	Pocillopora meandrina		19.8	5.40	21			
	Pocillopora verrucosa	0.56	71.2	9.55	10	31.2	13.25	10
	Porites astreoides	0.95	45.1	6.19	30	2.2	0.78	26
	Porites compressa		2.5	1.29	10			
	Porites lobata	0.79	23.3	6.32	26	4.9	3.19	24
	Porites porites	0.77	56.8	6.92	24	13.3	4.15	21
	Pseudodiploria strigosa	0.91	48.9	6.04	25	4.4	1.72	22
	Siderastrea siderea	0.93	60.7	4.98	34	4.4	2.47	31

B) Location and average proportional susceptibility and mortality to mass bleaching events

Factor	Source	(S-M)/S	Susceptibility			Mortality		
			Average	±SE	*n*	Average	±SE	*n*
Ocean Basin	Indian	0.82	47.9	1.46	556	8.4	0.88	456
	Pacific	0.84	53.4	1.46	556	8.4	0.88	456
	Atlantic	0.60	44.2	1.22	872	17.8	1.34	634

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Subregion	Central		43.6	11.47	10			
	East	0.62	43.0	1.72	450	16.4	1.80	309
	Northeast	0.49	63.7	7.59	24	32.6	9.67	18
	North	0.55	70.6	4.64	36	31.9	9.88	15
	Northwest	0.16	67.3	3.76	108	56.3	4.39	94
	Southeast	1	15.3	2.61	101	0.0	0.00	58
	South	0.95	45.7	1.89	286	2.4	0.77	258
	Southwest	0.94	58.8	3.56	59	3.5	0.68	50
	West	0.64	50.4	1.12	970	18.2	1.09	825
Country	Andaman Sea	0	90.9	2.48	53	90.9	2.48	53
	Barbados		61.7	6.44	28			
	Belize	0.89	35.8	2.75	99	4.0	1.57	82
	Brazil	0.93	57.8	3.70	55	3.8	0.72	46
	Costa Rica	0.78	52.7	4.21	60	11.8	3.56	50
	Curacao	0.98	36.9	8.82	15	0.7	0.73	15
	Dominica	0.80	46.5	4.20	44	9.4	2.69	44
	Florida Keys		79.4	5.62	17			
	French Polynesia	0.96	48.9	2.84	138	1.9	1.08	111
	Great Barrier Reef	0.59	49.7	2.65	144	20.5	2.90	116
	Grand Cayman	0.94	83.2	11.22	12	4.9	2.60	12
	Hawaii	1	15.8	2.63	103	0.0	0.00	58
	Indonesia	0.73	46.1	2.78	172	12.5	2.09	172
	Jamaica	0.96	27.8	4.07	67	1.2	0.77	63
	Japan	0.13	76.8	5.13	49	66.5	6.07	45
	Kenya	0.56	57.8	3.05	93	25.7	3.31	91
	Maldives		72.9	4.05	14			
	Martinique	0.52	49.7	8.13	15	24.0	6.84	15
	Mauritius	0.79	14.9	2.30	71	3.2	0.82	71
	Meso-American Reef	0.60	38.4	7.73	17	15.5	2.62	15
	Palau	0.52	31.8	2.44	133	15.2	7.16	23
	Panama	0.48	54.2	7.83	32	28.0	7.99	30
	Persian Gulf		71.4	5.39	43			
	Papua New Guinea	0.63	51.4	7.66	16	18.8	7.72	11
	Puerto Rico		63.6	11.08	14			
	Rodrigues	0.97	43.7	7.10	15	1.3	0.91	15
	Seychelles	0.32	52.7	7.09	24	35.6	7.73	21
	Singapore	0.69	20.1	3.51	21	6.3	2.59	21
	South Africa	0.96	42.2	2.49	147	1.6	0.63	147
	Thailand	0.70	90.9	3.04	35	27.0	6.66	32
	Tioman Island	0.65	18.3	4.17	19	6.4	3.07	19
	Tobago	1	53.4	7.72	16	0.0	0.00	16
	United Arabian Emirates	0.37	29.4	11.04	14	18.4	12.03	11
	US Virgin Islands	0.69	48.1	3.19	120	15.0	2.37	115
Location	Eastern Indian	0.60	56.1	3.53	118	22.7	3.58	78
	Eastern Pacific	0.50	56.6	3.49	126	28.4	3.85	112
	Northern Atlantic	0.77	58.9	5.90	34	13.7	2.62	17
	Northern Indian	0.38	61.3	4.54	62	38.1	6.44	43
	Northern Pacific	0.45	44.1	1.94	347	24.3	2.59	223
	Southern Atlantic	0.94	58.8	3.56	59	3.5	0.68	50
	Southern Indian	0.96	42.3	2.48	148	1.6	0.63	147
	Southern Pacific	0.95	35.3	2.16	254	1.6	0.82	182
	Western Atlantic	0.81	45.7	1.62	463	8.8	1.02	389
	Western Indian	0.46	56.2	2.19	288	30.6	2.36	277

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	Western Pacific	29.2	49.7	2.65	144	20.5	2.90	116
Continental Shelf Position	Inner	0.73	61.6	3.66	70	16.5	3.69	61
	Middle	0.41	68.1	6.95	26	40.5	7.74	24
	Outer	0.86	41.0	3.22	99	5.6	2.72	65

C) Biological factors and average proportional susceptibility and mortality to mass bleaching events

Factor	Source	(S-M)/S	Susceptibility			Mortality		
			Average	±SE	*n*	Average	±SE	*n*
Complexity of Skeleton	Complex	0.60	49.2	1.22	902	19.5	1.27	715
	Robust	0.75	45.0	1.14	940	11.4	0.94	745
Level of Colony Integration	High	0.45	52.0	1.72	518	28.8	1.91	425
	Medium	0.79	46.9	1.57	491	10.0	1.03	430
	Low	0.78	37.2	3.20	103	8.2	2.28	88
Transmission of Algae to Offspring	Both	0.75	48.7	9.87	20	12.1	6.77	20
	No	0.67	54.2	1.77	421	18.1	1.60	374
	Yes	0.67	44.6	2.25	260	14.5	2.05	216
Morphology	Branching	0.44	50.2	1.84	443	28.0	2.05	359
	Columnar	0.63	55.9	9.33	22	20.6	8.24	20
	Encrusting	0.80	36.3	3.60	80	7.2	2.32	66
	Free-living	0.72	40.3	7.07	23	11.2	5.98	22
	Massive	0.79	47.3	1.66	434	10.1	1.09	378
	Submassive	0.79	43.8	4.88	57	9.3	3.12	52
	Tabular	0.40	65.1	5.38	53	39.2	6.32	46
Generalization	Generalist	0.71	47.6	1.45	629	13.7	1.17	531
	Specialist	0.49	50.6	2.40	286	25.9	2.50	250
Sex	Gonochoric	0.68	49.4	335	2.00	15.6	1.78	294
	Hermaphroditic	0.63	51.6	471	1.71	19.3	1.62	407
Reproductive Mode	Both	0.75	44.3	9.46	22	11.0	6.19	22
	Brooder	0.71	49.3	2.45	211	14.3	2.15	175
	Spawner	0.63	51.7	1.53	589	19.2	1.44	518

D) Ecological factors and average proportional susceptibility and mortality to mass bleaching events

Factor	Source	(S-M)/S	Susceptibility			Mortality		
			Average	±SE	*n*	Average	±SE	*n*
Anthropogenic Input	No	0.87	44.1	2.20	200	5.8	1.13	195
	Yes, but protected	0.90	38.5	4.30	60	4.0	1.86	58
	Yes	0.39	60.8	6.46	27	37.0	7.06	27
Anthropogenic Pressure	No	0.54	53.7	7.07	22	24.5	5.91	22
	Yes	0.87	44.1	2.20	200	5.8	1.13	195
Dominant Topography	Acropora	0.67	36.5	6.32	37	11.9	4.67	36
	Acropora and Montipora	0.32	80.3	4.62	30	54.5	7.26	30
	Acropora cervicornis	0.58	74.7	7.34	19	31.3	6.70	19
	Acropora hyacinthus	1	50.2	7.92	16	0.0	0.00	16
	Montastrea	0.58	57.4	7.36	19	24.1	6.00	19
	Pavona and Pocillopora	0.83	31.3	3.96	31	5.2	2.57	31
	Pocillopora	0.56	58.5	7.77	22	25.8	9.44	19
	Porites	0.65	60.5	7.47	17	21.2	7.71	17
	Porites and others	0.38	49.4	5.98	33	30.7	5.66	31

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Depth	<3 m	0.79	27.2	4.07	57	5.6	2.30	53
	<6 m	0.42	60.3	3.50	131	34.9	3.84	129
	<9 m	0.95	43.4	2.44	165	2.4	0.76	165
	<12 m	0.71	49.9	1.96	283	14.6	1.63	260
	<15 m	0.75	59.8	5.13	43	15.1	4.60	38
	<18 m	0.80	46.5	4.20	44	9.4	2.69	44
	>18 m	0.72	38.7	3.31	100	10.9	2.33	961
Habitat	Bay	0.40	35.0	4.06	64	21.0	6.03	35
	Lagoon	0.34	56.3	7.30	23	36.9	7.59	21
	Reef Crest	0.93	24.3	3.96	60	1.6	1.07	57
	Reef Flat	0.09	75.6	6.12	36	68.6	7.34	34
	Reef Slope	0.86	42.8	3.15	121	5.8	1.83	103
Polluted	No	0.92	45.0	2.69	144	3.7	1.11	142
	Yes	0.7	43.0	3.78	82	12.9	2.95	82
Reef Type	Barrier Reef	0.59	49.7	2.65	144	20.5	2.90	116
	Patch Reef	0.61	45.7	1.58	456	17.8	1.59	370
	Subtropical	0.96	41.9	2.66	133	1.8	0.69	133
	Supratropical	1	45.2	6.98	14	0.0	0.00	14

E) Timing and average proportional susceptibility and mortality to mass bleaching events

Factor	**Source**	**(S-M)/S**	**Susceptibility**			**Mortality**		
			Average	**±SE**	***n***	**Average**	**±SE**	***n***
Timing of Observations	0-3 months	0.83	42.2	1.03	1068	7.0	0.67	825
	4-7 months	0.74	47.1	1.90	346	12.2	1.42	294
	>7 months	0.40	54.9	1.73	484	32.8	1.90	465
Month of observations relative to the onset of thermal anomalies	<1 month	0.83	53.9	2.90	128	9.1	2.11	114
	1-2 months	0.86	38.2	1.26	655	5.4	0.73	504
	2-3 months	0.83	53.0	2.92	145	9.0	2.27	111
	3-4 months	0.73	39.2	3.04	140	10.4	2.20	96
	4-5 months	0.41	45.8	3.72	81	27.2	4.75	55
	5-6 months	0.86	39.5	3.57	97	5.4	2.03	97
	6-7 months	0.77	47.4	3.38	118	11.1	1.98	92
	8-9 months	0.38	44.5	5.06	73	27.8	4.66	71
	9-10 months	0.85	31.9	2.90	68	4.7	1.77	68
	10-11 months	0.36	52.2	8.12	22	33.3	6.62	22
	>11 months	0.35	62.1	2.09	313	40.2	2.49	296
Decade	1980's	0.40	67.1	3.60	121	40.2	4.78	88
	1990's	0.66	51.9	1.13	910	17.5	1.12	776
	2000's	0.81	38.2	1.38	584	7.3	0.87	476
	2010's	0.53	47.6	1.84	429	22.5	2.16	295
Recovery time (months)	<3 months	0.74	43.1	5.41	55	11.3	3.63	55
	3-12 months	0.85	47.2	3.39	74	7.0	2.32	70
	12-24 months	0.19	87.9	2.73	22	71.0	5.70	22
Bleaching Occurrence	First bleaching	0.65	54.9	1.07	932	19.0	1.14	757
	Second	0.67	35.8	1.21	655	11.7	1.06	470
	Third	0.81	41.1	2.93	165	7.9	1.75	139
	Fourth	0.56	59.9	2.14	234	26.3	2.5	220
	Fifth	0.81	46.0	4.01	58	8.8	2.96	49

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F) Physical factors and average proportional susceptibility and mortality to mass bleaching events

Factor	Source	(S-M)/S	Susceptibility			Mortality		
			Average	±SE	*n*	Average	±SE	*n*
Thermal Stress Accumulation	0-30 DHW	0.75	42.2	0.84	1601	10.7	0.65	1315
	>30 DHW	0.52	79.5	2.53	158	38.1	3.55	147
Degree Heating Week Index (DHW)	0-10	0.91	43.6	3.12	126	4.0	1.70	96
	11-20	0.78	40.0	1.00	1074	8.6	0.68	931
	21-30	0.58	47.7	1.73	401	19.8	1.82	288
	31-40	0.74	81.3	3.22	59	20.9	4.64	50
	41-50	0.50	71.0	4.86	62	35.4	5.36	60
	>50	0.28	91.1	4.28	37	65.7	7.37	37
Annual Temperature Range	≤3	0.92	56.8	3.93	54	4.4	2.10	47
	3.1-4.0	0.77	25.2	2.20	106	5.9	5.88	17
	4.1-5.0	0.79	43.1	2.75	142	9.4	1.56	142
	5.1-6.0	0.72	48.7	2.63	166	13.4	2.52	166
	>6.0	0.40	83.6	10.15	11	49.9	11.81	11
Peak Temperature (above mean monthly, °C)	<1	0.93	28.3	4.92	45	2.1	1.19	45
	1-1.9	0.66	46.7	3.44	75	15.7	3.00	67
	2-2.9	0.53	54.3	2.23	274	25.5	2.18	248
	3-3.9	0.91	49.6	2.04	209	4.4	0.92	209
	4-5.9	0.50	59.0	7.40	22	29.6	9.82	20
	>6	0.50	73.9	4.77	54	36.6	10.38	15
Relief or exacerbation of physical stress	No relief	0.68	73.1	3.66	79	23.6	4.16	76
	No relief and Doldrums	0.39	46.8	3.35	142	28.5	3.36	137
	Relief	0.80	45.4	1.85	335	9.3	1.31	319
	Relief and Doldrums	0.84	52.8	3.29	68	8.7	2.18	68
Cloud Cover/Storm	No	0.55	53.9	2.45	247	24.1	2.37	239
	Yes	0.76	44.9	2.56	179	10.8	1.89	163
Upwelling	No	0.53	48.3	3.21	144	23.0	2.97	142
	Yes	0.83	48.1	2.11	224	8.1	1.43	224
Doldrums	No	0.52	68.3	7.51	27	32.8	7.69	24
	Yes	0.59	47.5	2.26	256	19.3	2.11	251
Leeward/Windward	Leeward	0.70	42.1	2.59	112	12.8	2.09	112
	Windward	0.61	63.1	7.26	13	24.4	8.18	10

Table A5. Restriction of post hoc analyses from all records to paired susceptibility–mortality data. Factors shown include (A) thermal stress accumulation, (B) timing of observations, (C) location, and (D) growth form. Asterisks denote significance (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$).

A) Factors associated with variations in estimates of susceptibility to mass bleaching events

Source	SS Type III	df	*n*	MS	F	p
Thermal Stress Accumulation*	267.066	1	1758	0.138	172.769	<0.001***
Degree Heating Index**	267.466	5	1758	0.137	39.994	<0.001***
Bleaching Occurrence*	324.008	4	2043	0.148	38.448	<0.001***
Decade**	324.008	3	2043	0.151	33.735	<0.001***
Subregion**	324.008	8	2043	0.146	23.095	<0.001***
Timing of Observations*	295.925	2	1897	0.153	21.189	<0.001***
Country**	296.466	31	1914	0.118	20.182	<0.001***
Relief from Physical Stress*	105.637	3	669	0.148	15.520	<0.001***
Annual Temperature Range**	65.407	4	478	0.122	15.307	<0.001***
Habitat	53.116	4	303	0.148	15.098	<0.001***

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Recovery	22.650	2	150	0.128	14.193	<0.001***
Months of Observations**	294.000	11	1889	0.146	12.668	<0.001***
Shelf Position	25.790	2	194	0.119	12.051	<0.001***
Ocean Basin**	324.008	2	2043	0.157	9.982	<0.001***
Peak Temperature**	102.300	5	678	0.142	9.725	<0.001***
Depth	119.339	6	822	0.137	9.513	<0.001***
Location*	323.562	10	2042	0.152	9.147	<0.001***
Transmission of Algae to Offspring	118.282	1	700	0.167	8.950	<0.01**
Level of Colony Integration*	192.431	2	1111	0.171	7.919	<0.001***
Clouds/Stormy Weather**	71.90	1	425	0.167	6.483	<0.05*
Doldrums**	47.764	1	282	0.166	6.335	<0.05*
Dominant taxa	34.475	8	223	0.130	6.254	<0.001***
Species	71.165	24	480	0.122	5.340	<0.01**
Complexity of Skeleton	292.282	1	1841	0.158	5.220	<0.05*
Morphology**	192.341	6	1111	0.170	4.058	<0.001***
Genus	259.843	37	1632	0.149	3.899	<0.001***
Anthropogenic Input*	38.114	2	286	0.131	3.545	<0.05*
Family	302.905	16	1902	0.156	3.456	<0.001***
Reproductive Mode	139.803	1	821	0.170	3.199	>0.05
Sex	118.804	1	821	0.144	2.650	>0.05
Reef Type	104.075	3	787	0.132	1.660	>0.05
Generalization	168.780	1	914	0.185	0.748	>0.05
Anthropogenic Pressure**	28.085	1	221	0.127	0.710	>0.05
Pollutants**	32.422	1	225	0.144	0.471	>0.05
Upwelling**	56.378	1	367	0.154	0.064	>0.05

B) Factors associated with variations in estimates of mortality from mass bleaching events

Source	SS Type III	df	n	MS	F	p
Thermal Stress Accumulation*	178.988	1	1461	0.112	144.065	<0.001***
Timing of Observations*	227.967	2	1583	0.124	130.470	<0.001***
Recovery Time	23.176	2	146	0.085	64.911	<0.001***
Degree Heating Index**	178.988	5	1461	0.103	56.784	<0.001***
Habitat	43.400	4	249	0.098	54.519	<0.001***
Subregion**	249.592	8	1634	0.128	40.393	<0.001***
Level of Colony Integration*	152.856	2	942	0.150	39.704	<0.001***
Anthropogenic Pressure*	21.477	2	279	0.061	38.522	<0.001***
Months of Observations**	224.857	11	1575	0.113	38.024	<0.001***
Decade**	249.592	3	1634	0.144	35.630	<0.001***
Anthropogenic Input**	13.962	1	216	0.057	30.969	<0.001***
Location*	249.530	10	1633	0.130	29.397	<0.001***
Upwelling**	47.361	1	365	0.1320	29.871	<0.001***
Country**	215.033	31	1539	0.088	29.807	<0.001***
Ocean Basin***	249.592	2	1634	0.149	22.211	<0.001***
Complexity of Skeleton	209.574	1	1459	0.141	25.103	<0.001***
Reef Type	88.178	3	666	0.122	20.862	<0.001***
Generalization	125.061	1	780	0.156	20.282	<0.001***
Peak Temperature**	80.630	5	603	0.115	20.186	<0.001***
Shelf Position	20.995	2	149	0.113	19.360	<0.001***
Depth	100.204	6	784	0.112	19.716	<0.001***
Clouds/Stormy Weather**	66.379	1	425	0.167	18.830	<0.001***
Pollutants	15.868	1	223	0.171	14.440	<0.001***
Morphology**	152.856	6	942	0.150	14.387	<0.01**
Relief from Physical Stress*	90.368	3	645	0.133	12.686	<0.001***
Bleaching Occurrence*	249.592	4	1634	0.149	10.511	<0.001***

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Dominant Taxa	36.509	8	217	0.129	9.340	<0.001***
Annual Temperature Range**	45.074	4	382	0.110	7.629	<0.001***
Family	227.860	16	1507	0.142	6.822	<0.01**
Genus	200.483	37	1276	0.146	3.573	<0.01**
Species	39.719	24	394	0.088	3.342	<0.01**
Reproductive Mode	113.360	1	714	0.158	3.199	>0.05
Doldrums**	47.134	1	274	0.171	2.841	>0.05
Transmission of Algae to Offspring	90.930	1	609	0.149	2.770	>0.05
Sex	4.908	1	714	0.007	0.0477	>0.05

C) Grouped factors and the relative percent importance associated with the variation in estimates of coral susceptibility to mass bleaching events

Grouped Factor	Grouped Relative Importance	Source	F	Relative Importance
Timing	30.1%	Decade	33.735	12.43%
		Recovery	14.193	5.23%
		Months of Observations	12.668	4.67%
Weather	28.7%	Degree Heating Index	39.994	14.74
		Annual Temperature Range	15.307	5.64%
		Peak Temperature	9.725	3.58%
		Cloudy/Stormy Weather	6.483	2.39%
		Doldrums	6.335	2.33%
Location	21.4%	Subregion	23.095	8.51%
		Country	20.182	7.44%
		Ocean Basin	9.982	3.68%
Biology and Ecology	15.1%	Complexity of Skeleton	5.22	1.92%
		Depth	9.513	3.51%
		Transmission of Algae to Offspring	8.950	3.30%
		Habitat	5.444	2.01%
		Morphology	4.058	1.50%
Taxonomy	1.7 %	Species	5.340	1.97%
		Genus	3.899	1.44%
		Family	3.456	1.27%

D) Grouped factors and the relative percent importance associated with the variation in estimates of coral mortality from mass bleaching events

Grouped Factors	Grouped Relative Importance	Source	F	Relative Importance
Timing	21.1%	Recovery Time	64.911	9.56%
		Months of Observations	38.024	5.60%
		Decade	35.630	5.25%
Weather	19.6%	Degree Heating Index	56.784	8.36%
		Upwelling	29.871	4.40%
		Peak Temperature	20.186	2.97%
		Clouds and Stormy Weather	18.830	2.77%
		Annual Temperature Range	7.629	1.12%
Biology and Ecology	22.7%	Complexity of Skeleton	25.103	3.70%
		Habitat	20.825	3.07%
		Generalization	20.282	2.99%
		Depth	19.716	2.90%

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		Pollutants	14.440	2.13%
		Morphology	14.387	2.12%
Location	16.0%	Subregion	40.393	5.95%
		Country	29.807	4.39%
		Ocean Basin	22.211	3.27%
Taxonomy	2.0%	Family	6.822	1.00%
		Genus	3.573	0.53%
		Species	3.342	0.49%

E) Correlation of factors with average susceptibility to mass bleaching events

Source	*n*	Pearson's Correlation Coefficient	p
Recovery	151	0.355	<0.001***
Degree Heating Index**	1759	0.284	<0.001***
Shelf position**	195	-0.282	<0.001***
Thermal Stress Accumulation*	1759	0.258	<0.001***
Peak Temperature	679	0.212	<0.001***
Months of Observations*	1890	0.166	<0.001***
Doldrums**	283	-0.148	<0.05*
Timing of Observations*	1898	0.147	<0.001***
Relief from Physical Stress*	670	-0140	<0.001***
Decade**	2044	-0.127	<0.001***
Annual Temperature Range**	479	0.123	<0.01**
Weather**	426	-0.123	<0.05*
Country**	1915	-0.121	<0.001***
Transmission of Algae to Offspring	701	-0.112	<0.01**
Level of Colony Integration*	1112	0.111	>0.001***
Habitat	304	0.088	>0.05
Genus	1633	-0.072	<0.01**
Reef Type	788	-0.070	>0.05
Sex	806	0.067	>0.05
Family	1903	-0.063	<0.01**
Anthropogenic Pressure**	222	0.057	>0.05
Complexity of Skeleton	1842	-0.053	<0.05*
Ocean	2044	-0.051	<0.05*
Subregion	2044	0.049	<0.05*
Anthropogenic Input*	287	0.049	>0.05
Depth	823	-0.047	>0.05
Pollution	226	-0.046	>0.05
Species	481	-0.038	>0.05
Dominant Taxa	224	-0.034	>0.05
Location*	2043	-0.033	>0.05
Bleaching Occurrence*	2044	-0.032	>0.05
Generalization/Specialization	915	0.029	>0.05
Reproductive Mode	822	0.025	>0.05
Upwelling	368	0.013	>0.05
Morphology	1112	0.006	>0.05

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F) Correlations of factors to average mortality from mass bleaching events

Source	n	Pearson's Correlation Coefficient	p
Recovery	147	0.490	<0.001***
Months of Observations**	1576	0.393	<0.001***
Degree Heating Index**	1462	0.391	<0.001***
Thermal Stress Accumulation*	1462	0.371	<0.001***
Timing of Observations	1576	0.370	<0.001***
Anthropogenic Pressure**	217	0.355	<0.001***
Anthropogenic Input*	280	0.343	<0.001***
Upwelling**	366	-0.275	<0.001***
Shelf Position	150	-0.256	<0.01**
Pollution**	224	0.247	<0.001***
Weather**	402	-0.212	<0.001***
Relief from Physical Stress*	646	-0.182	<0.001***
Annual Temperature Range**	383	0.162	<0.01**
Level of Colony Integration*	943	-0.160	<0.001***
Morphology**	943	-0.160	<0.001***
Generalization/Specialization	781	0.159	<0.001***
Habitat	250	-0.155	<0.05*
Country**	1540	-0.135	<0.001***
Location*	1634	-0.131	<0.001***
Complexity of Skeleton	1460	-0.130	<0.001***
Family	1508	-0.119	<0.001***
Doldrums**	275	-.101	>0.05
Species	395	-0.098	>0.05
Ocean**	1635	0.091	<0.001***
Genus	1277	-0.085	<0.001***
Decade**	1635	-0.071	<0.01**
Reproductive Mode	715	0.067	>0.05
Transmission of Algae to Offspring	610	-0.067	>0.05
Depth	785	-0.065	>0.05
Bleaching Occurrence*	1635	-0.032	>0.05
Sex	715	-0.025	>0.05
Peak Temperature**	604	0.013	>0.05
Dominant taxa	218	-0.003	>0.05

Table A6. Average taxonomic values derived from paired susceptibility–mortality records after post hoc grouping to reduce variance associated with thermal stress accumulation and observation timing (see Table 10A).

A) ANOVAs (i and iii) and descriptive statistics (ii and iv) for inter-familial variation in bleaching susceptibility (i and ii) and mortality (iii and iv).

i) Bleaching susceptibility - where n>50 for each family and n ≥ 5 for factors

Source	SS(Type III)	df	n	MS	F	p
Thermal stress accumulation	182.053	2	1095	0.156	35.905	<0.001***
Bleaching occurrence	213.121	4	1227	0.161	24.720	<0.001***
Ocean_subregion	212.574	11	1222	0.147	21.231	<0.001***
Timing of observations	205.053	2	1193	0.167	16.978	<0.001***
Relief from weather	60.127	3	406	0.139	9.570	<0.001***

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Habitat	48.313	7	250	0.160	8.498	<0.001***
Level of colony integration	138.745	2	726	0.187	8.130	<0.001***
Species	87.156	44	469	0.126	6.095	<0.001***
Transmission of algae to offspring	90.565	2	505	0.176	5.228	<0.01**
Genus	`199.376	38	1111	0.162	4.083	<0.001***
FAMILY	213.121	6	1227	0.171	3.674	<0.01**
Dominant taxa	22.823	7	142	0.149	2.645	<0.05*
Shelf position	65.446	6	462	0.139	2.210	<0.05*
Sex	103.911	1	570	0.182	1.663	>0.05
Complexity of skeleton	212.751	1	1226	0.173	1.445	>0.05
Anthropogenic Input	25.554	3	173	0.157	1.303	>0.05
Depth	70.637	4	469	0.150	1.284	>0.05
Generalisation	129.022	1	643	0.20-1	1.241	>0.05
Reproductive mode	105.887	2	578	0.183	1.228	>0.05

*Significant, **strongly significant, ***highly significant.

ii) Bleaching-related mortality- where n>50 for each family and n ≥ 5 for factors

Source	SS(Type III)	df	n	MS	F	p
Timing of observations	172.975	2	1193	0.123	109.773	<0.001***
Thermal stress accumulation	127.812	2	1095	0.101	85.998	<0.001***
Habitat	38.317	7	250	0.080	33.614	<0.001***
Ocean_subregion	189.248	1	1222	0.120	33.054	<0.001***
Bleaching occurrence	189.565	4	1227	0.143	26.125	<0.001***
Level of colony integration	120.787	2	726	0.156	24.858	<0.001***
Anthropogenic Input	13.428	3	173	0.056	23.419	<0.001**
Relief from weather	44.711	3	406	0.096	21.318	<0.001***
Complexity of skeleton	189.502	1	1226	0.152	18.628	<0.001***
Generalisation	110.218	1	643	0.168	14.564	<0.001***
Shelf position	57.561	6	462	0.108	12.672	<0.001***
FAMILY	189.565	6	1227	0.148	9.277	<0.001***
Depth	62.523	4	469	0.129	5.091	<0.01**
Dominant taxa	22.332	7	142	0.133	4.658	<0.001***
Reproductive mode	100.046	2	578	0.1722	3.222	<0.05*
Transmission of algae to offspring	80.916	2	505	0.159	2.700	>0.05
Species	60.851	44	469	0.112	2.734	<0.001***
Genus	176.381	38	1111	0.151	2.589	<0.001***
Sex	99.134	1	570	0.174	0.081	>0.05

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A) Averages for inter-familial variation in bleaching susceptibility (i) and mortality (ii), ordered by F values of ANOVAs

*ii*i) Bleaching-related mortality- where n>50 for each family and n ≥ 5 for factors

Source	SS(Type III)	df	n	MS	F	p
Timing of observations	172.975	2	1193	0.123	109.773	<0.001***
Thermal stress accumulation	127.812	2	1095	0.101	85.998	<0.001***
Habitat	38.317	7	250	0.080	33.614	<0.001***
Ocean_subregion	189.248	1	1222	0.120	33.054	<0.001***
Bleaching occurrence	189.565	4	1227	0.143	26.125	<0.001***
Level of colony integration	120.787	2	726	0.156	24.858	<0.001***
Anthropogenic Input	13.428	3	173	0.056	23.419	<0.001**
Relief from weather	44.711	3	406	0.096	21.318	<0.001***
Complexity of skeleton	189.502	1	1226	0.152	18.628	<0.001***
Generalisation	110.218	1	643	0.168	14.564	<0.001***
Shelf position	57.561	6	462	0.108	12.672	<0.001***
FAMILY	189.565	6	1227	0.148	9.277	<0.001***
Depth	62.523	4	469	0.129	5.091	<0.01**
Dominant taxa	22.332	7	142	0.133	4.658	<0.001***
Reproductive mode	100.046	2	578	0.1722	3.222	<0.05*
Transmission of algae to offspring	80.916	2	505	0.159	2.700	>0.05
Species	60.851	44	469	0.112	2.734	<0.001***
Genus	176.381	38	1111	0.151	2.589	<0.001***
Sex	99.134	1	570	0.174	0.081	>0.05

B) ANOVAs for inter-generic variation in bleaching (i) susceptibility and (ii) mortality

i) Bleaching susceptibility - where n>40 for each genus and n ≥ 5 for factors

Source	SS(Type III)	df	n	MS	F	p
Bleaching occurrence	127.755	4	728	0.150	31.678	<0.001***
Thermal stress accumulation	108.071	2	635	0.153	31.519	<0.001***
Ocean_subregion	127.755	12	728	0.128	23.602	<0.001***
Timing of observations	122.590	2	702	0.165	21.635	<0.001***
Level of colony integration	102.982	2	549	0.177	17.241	<0.001***
Habitat	36.723	6	179	0.139	15.097	<0.001***
Transmission of algae to offspring	58.713	1	338	0.167	13.570	<0.001***
Species	64.990	29	353	0.116	8.082	<0.001***
Relief from weather	31.971	3	215	0.139	6.166	<0.001***
GENUS	127.400	7	726	0.169	5.146	<0.001***
Dominant taxa	13.548	5	89	0.126	4.639	<0.01**
Depth	42.484	5	312	0.130	3.717	<0.01**
Shelf position	33.815	5	251	0.133	1.635	>0.05

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Anthropogenic input	8.753	3	78	0.110	1.582	>0.05
Reproductive mode	69.176	1	395	0.175	0.870	>0.05
Sex	68.715	1	395	0.174	0.404	>0.05
Generalisation	87.553	1	442	0.198	0.176	>0.05

ii) Bleaching mortality - where n>40 for each genus and n ≥ 5 for factors

Source	SS(Type III)	df	n	MS	F	p
Thermal stress accumulation	99.721	2	635	0.122	91.828	<0.001***
Habitat	32.078	6	179	0.049	80.867	<0.001***
Timing of observations	127.290	2	702	0.149	75.719	<0.001***
Generalisation	81.014	1	442	0.171	32.106	<0.001***
Ocean_subregion	138.023	12	728	0.132	27.512	<0.001***
Level of colony integration	103.917	2	549	0.175	23.467	<0.001***
Relief from weather	36.411	3	215	0.144	13.596	<0.001***
Bleaching occurrence	138.023	4	728	0.177	13.640	<0.001***
Depth	53.287	5	312	0.145	12.273	<0.001***
Anthropogenic input	7.958	3	78	0.082	7.478	<0.001***
GENUS	137.823	7	726	0.179	7.122	<0.001***
Reproductive mode	74.791	1	395	0.187	6.973	<0.01**
Shelf position	44.202	5	251	0.1598	6.724	<0.001***
Dominant taxa	15.100	5	89	0.131	6.311	<0.001***
Transmission of algae to offspring	57.933	1	338	0.169	6.096	<0.05*
Sex	74.791	1	395	0.188	4.143	<0.05*
Species	48.129	29	353	0.110	3.886	<0.001***

C) ANOVAs for inter-species variation in bleaching (i) susceptibility and (ii) mortality

i) Bleaching susceptibility (where n>20) for each species and n ≥ 5 for individual records)

Source	SS(Type III)	df	n	MS	F	p
Transmission of algae to offspring	21.933	1	156	0.126	18.592	<0.001***
Ocean_subregion	25.818	6	192	0.091	16.081	<0.001***
Bleaching occurrence	26.753	4	198	0.116	9.059	<0.001***
Relief from weather	5.588	2	50	0.090	6.980	<0.01**
Thermal stress accumulation	24.528	2	184	0.126	6.233	<0.01**
SPECIES	26.753	7	198	0.115	5.833	<0.001***
Timing of observations	26.300	2	195	0.129	5.211	<0.01**
Sex	26.753	1	198	0.133	4.195	<0.05*
Complexity of skeleton	26.753	1	198	0.134	3.200	>0.05
Anthropogenic input	6.737	3	100	0.064	2.790	<0.05*
Depth	8.299	4	101	0.080	1.632	>0.05
Shelf position	6.752	1	84	0.080	1.095	>0.05

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Dominant taxa	1.288	2	18	0.075	0.564	>0.05
Habitat	1.473	1	57	0.026	0.780	>0.05
Level of colony integration	26.753	1	198	0.136	0.166	>0.05
Reproductive mode	26.753	1	198	0.136	0.014	>0.05

ii) Bleaching mortality - where n>20 for each species and n ≥ 5 for factors

Source	SS(Type III)	df	n	MS	F	p
Timing of observations	15.062	2	195	0.054	42.565	<0.001***
Level of colony integration	15.481	1	198	0.069	28.246	<0.001***
Thermal stress accumulation	13.777	2	184	0.068	10.936	<0.001***
Reproductive mode	14.705	1	198	0.075	10.789	<0.01**
Relief from weather	3.419	2	50	0.053	8.534	<0.01**
SPECIES	15.841	7	198	0.066	6.016	<0.001****
Anthropogenic input	6.874	3	100	0.060	5.932	<0.01**
Location	14.003	6	192	0.063	5.880	<0.001***
Complexity of skeleton	15.481	1	198	0.076	5.810	<0.05*
Sex	15.481	1	198	0.076	5.499	<0.05*
Bleaching occurrence	15.481	4	198	0.076	2.401	<0.05*
Depth	7.395	4	101	0.071	1.844	>0.05
Transmission of algae to offspring	13.048	1	156	0.084	1.156	>0.05
Habitat	1.473	4	57	0.026	0.780	>0.05
Dominant taxa	1.476	2	18	0.090	0.227	>0.05
Shelf position	4.985	1	84	0.060	0.173	>0.05

Table A7. Average values of ecological factors matrixed by thermal stress accumulation (Low, Medium, High) and timing of observations relative to stress onset (Beginning, Middle, End). Data are restricted to paired susceptibility–mortality records with n ≥ 3. Error represents standard error. Values are ordered by thermal stress accumulation, observation timing, and mortality.

A) Variation in bleaching-related susceptibility and mortality due to thermal stress accumulation

a. Overall variation in susceptibility and mortality due to thermal stress accumulation

Factor	SS (Type III)	df	*n*	MS	F	p
Susceptibility	235.725	2	1449	0.151	57.743	<0.001***
Mortality	174.188	2	1449	0.103	121.648	<0.001***

b. The 'Low' category of thermal stress accumulation (0-19 weeks)

Factor	SS (Type III)	df	*n*	MS	F	p
Susceptibility	149.950	1	1019	0.341	0.341	>0.05
Mortality	74.552	1	1019	0.073	10.261	<0.01**

c. The 'Medium' category of thermal stress accumulation (20-39 weeks)

Factor	SS (Type III)	df	*n*	MS	F	p
Susceptibility	53.651	1	334	0.136	62.518	<0.001***
Mortality	47.720	1	334	0.143	0.184	>0.05

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d. The 'High' category of thermal stress accumulation (40+ weeks)

Factor	SS (Type III)	df	*n*	MS	F	p
Susceptibility	14.701	1	94	0.141	11.114	<0.01**
Mortality	26.844	1	94	0.256	11.973	<0.01**

B) Variations in bleaching susceptibility and mortality due to the timing of observations relative to the onset of thermal stress

a. Overall variation in susceptibility and mortality due to the timing of observations relative to the onset of thermal stress

Factor	SS (Type III)	df	*n*	MS	F	p
Susceptibility	237.725	3	1449	0.161	5.568	<0.01**
Mortality	174.188	3	1449	0.109	51.418	<0.001***

b. The 'Beginning' category of timing of observations relative to the onset of thermal stress (0-3 months)

Factor	SS (Type III)	df	*n*	MS	F	p
Susceptibility	129.953	3	824	0.153	9.469	<0.001***
Mortality	54.999	3	824	0.066	3.503	<0.05*

c. The 'Middle' category of timing of observations relative to the onset of thermal stress (4-7 months)

Factor	SS (Type III)	df	*n*	MS	F	p
Susceptibility	43.908	3	293	0.144	4.873	<0.01**
Mortality	28.758	3	293	0.088	11.650	<0.001***

d. The 'End' category of timing of observations relative to the onset of thermal stress (≥8 months)

Factor	SS (Type III)	df	*n*	MS	F	p
Susceptibility	85.133	4	464	0.172	8.691	<0.001***
Mortality	112.005	4	464	0.217	14.211	<0.001***

C) Variations in bleaching susceptibility and mortality due to location

a. Overall variation in susceptibility and mortality due to location

Factor	SS (Type III)	df	*n*	MS	F	p
Susceptibility	323.562	10	2042	0.152	9.147	<0.0001***
Mortality	249.530	10	1633	0.130	29.397	<0.001***

b. 'Eastern Indian' category

Factor	SS (Type III)	df	*n*	MS	F	p
Susceptibility	20.845	5	117	0.103	18.088	<0.001***
Mortality	11.427	5	77	0.064	21.347	<0.001***

c. 'Eastern Pacific' category

Factor	SS (Type III)	df	*n*	MS	F	p
Susceptibility	23.828	5	125	0.156	6.612	<0.001***
Mortality	26.291	5	111	0.157	12.306	<0.001***

d. 'Northern Atlantic' category

Factor	SS (Type III)	df	*n*	MS	F	p
Susceptibility	3.508	1	32	0.077	14.585	<0.01**

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e. ‘Northern Indian’ category

Factor	SS (Type III)	df	*n*	MS	F	p
Susceptibility	9.558	6	57	0.111	5.822	<0.001***
Mortality	9.898	5	40	0.196	3.118	<0.05*

f. ‘Northern Pacific category

Factor	SS (Type III)	df	*n*	MS	F	p
Susceptibility	52.525	4	345	0.125	19.418	<0.001***
Mortality	48.449	4	222	0.143	30.464	<0.001***

g. ‘Southern Atlantic’ category

Factor	SS (Type III)	df	*n*	MS	F	p
Susceptibility	66.861	13	454	0.132	5.127	<0.001***
Mortality	29.618	13	387	0.065	6.051	<0.001***

h. ‘Southern Pacific’ category

Factor	SS (Type III)	df	*n*	MS	F	p
Susceptibility	40.794	5	247	0.111	24.866	<0.001***
Mortality	2.533	5	179	0.012	6.520	<0.01**

i. ‘Western Indian’ category

Factor	SS (Type III)	df	*n*	MS	F	p
Susceptibility	47.656	7	285	0.067	61.703	<0.001***
Mortality	60.043	7	274	0.093	54.061	<00.001***

j. ‘Western Pacific’ category)

Factor	SS (Type III)	df	*n*	MS	F	p
Susceptibility	15.159	2	143	0.102	0.038	>0.05
Mortality	16.565	2	114	0.134	5.476	<0.01**

D) Variation in bleaching susceptibility and mortality due to the growth form or morphology of the coral

a. Overall variation in bleaching susceptibility and mortality due to the growth form

Factor	SS (Type III)	df	*n*	MS	F	p
Susceptibility	192.341	6	111	0.170	4.058	<0.001***
Mortality	152.704	6	940	0.1650	14.564	<0.001***

b. ‘High’ category of the level of colony integration (branching, columnar, and tabular)

Factor	SS (Type III)	df	*n*	MS	F	p
Susceptibility	90.835	1	464	0.196	0.254	>0.05
Mortality	85.834	1	378	0.227	0.930	>0.05

c. ‘Medium’ category of the level of colony integration (massive and submassive

Factor	SS (Type III)	df	*n*	MS	F	p
Susceptibility	71.473	1	490	0.146	0.971	>0.05
Mortality	35.442	1	428	0.083	0.475	>0.05

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d. 'Low' category of the level of colony integration (encrusting and free-living)

Factor	SS (Type III)	df	*n*	MS	F	p
Susceptibility	15.234	1	102	0.150	0.320	>0.05
Mortality	6.707	1	87	0.078	0.075	>0.05

Table A8. Average taxonomic values derived from paired susceptibility–mortality records following post hoc grouping to reduce variance from thermal stress accumulation and timing effects (see Table 10A).

a. Families

Thermal stress accumulation	Timing of observations	Family	Susceptibility	±SE	n	Mortality	±SE	(S-M)/S
	Beginning	Milleporidae	37.51	8.75	13	19.26	10.00	0.49
		Acroporidae	44.04	3.28	122	10.73	2.08	0.76
		Pocilloporidae	42.95	4.40	76	10.07	2.78	0.98
		Euphyllidae	37.36	9.19	10	8.80	6.66	0.76
		Agariciidae	42.26	5.99	33	6.06	4.02	0.86
		Merulinidae	43.76	2.93	105	5.18	1.30	0.88
		Montastraeidae	28.37	0.00	7	4.35	0.00	0.85
		Poritidae	31.81	3.27	95	3.94	1.36	0.88
		Mussidae	37.89	5.55	34	0.74	0.68	0.98
		Siderastreidae	60.63	8.27	13	0.65	0.58	0.99
		Alcyonacae	40.40	14.88	5	0.40	0.24	0.99
		Lobophyllidae	38.83	8.46	12	0.25	0.25	0.99
		Fungiidae	40.52	7.09	23	0.22	0.22	0.99
		Diploastraeidae	18.53	10.83	7	0.00	0.00	1
		Meandrinidae	15.54	9.08	7	0.00	0.00	1
		Dendrophylliidae	0.75	0.75	4	0.00	0.00	1
	Middle	Milleporidae	54.90	18.35	5	29.41	17.91	0.46
		Acroporidae	49.74	5.62	32	13.04	5.21	0.74
		Poritidae	49.90	7.00	26	11.07	4.35	0.78
		Alcyonacae	51.00	28.88	3	6.00	6.00	0.88
		Mussidae	45.26	6.83	21	5.05	2.38	0.89
		Agariciidae	24.00	12.06	3	3.67	3.67	0.85
		Fungiidae	23.25	11.52	8	4.50	1.93	0.81
		Merulinidae	34.45	5.71	35	2.71	1.17	0.92
		Siderastreidae	55.91	9.90	12	2.05	0.71	0.96
		Pocilloporidae	27.71	10.95	7	1.14	0.46	0.96
Low		Lobophyllidae	34.50	13.81	8	0.75	0.75	0.98

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		Euphyllidae	26.17	11.44	6	0.67	0.42	0.97
	End	Agariciidae	38.33	11.39	12	22.46	9.71	0.41
		Acroporidae	45.59	5.31	47	17.51	4.69	0.62
		Poritidae	30.86	7.24	23	15.30	6.14	0.50
		Mussidae	28.35	10.35	11	13.39	4.79	0.53
		Euphyllidae	30.39	9.16	9	12.49	9.80	0.59
		Merulinidae	39.43	4.58	49	9.64	2.27	0.76
		Pocilloporidae	38.37	7.98	20	9.45	5.95	0.75
		Milleporidae	9.40	9.40	3	8.00	8.00	0.15
		Siderastreidae	37.78	6.24	5	7.10	3.38	0.81
		Fungiidae	12.32	3.69	11	1.00	1.00	0.92
		Lobophyllidae	29.55	8.01	11	0.00	0.00	1
	Beginning	Acroporidae	58.21	10.41	17	22.15	9.09	0.62
		Milleporidae	37.31	13.49	8	13.06	12.08	0.65
		Pocilloporidae	7.00	2.98	9	6.94	5.19	0.01
		Meandrinidae	33.08	6.14	12	5.50	4.07	0.83
		Merulinidae	64.93	6.66	29	4.21	1.94	0.94
		Poritidae	35.95	9.87	11	3.41	1.69	0.91
		Mussidae	28.42	4.31	31	2.13	1.02	0.93
		Siderastreidae	63.80	8.18	10	1.60	0.91	0.97
		Montastreidae	65.17	13.59	6	1.00	1.00	0.98
		Agariciidae	45.38	11.47	13	0.77	0.77	0.98
		Fungiidae	32.85	6.91	13	0.00	0.00	1
	Middle	Acroporidae	34.73	8.93	11	21.73	7.44	0.37
		Poritidae	36.13	8.57	8	14.13	7.53	0.61
		Pocilloporidae	55.00	17.09	4	13.25	8.44	0.76
		Fungiidae	48.67	14.50	3	6.00	2.52	0.88
		Agariciidae	24.00	12.06	3	3.67	3.67	0.85
		Euphyllidae	40.40	20.28	5	3.00	3.00	0.93
		Lobophyllidae	22.75	6.26	4	2.50	2.50	0.89
		Merulinidae	24.63	6.37	19	1.84	0.65	0.93
		Mussidae	37.50	23.94	4	0.50	0.50	0.99
	End	Diploastraeidae	96.67	3.33	3	96.67	3.33	0
		Fungiidae	83.77	8.20	6	78.22	13.68	0.07
		Acroporidae	84.79	5.34	30	74.93	6.78	0.12
		Euphyllidae	86.00	12.00	4	73.50	24.50	0.15
		Merulinidae	75.87	7.99	20	50.26	9.01	0.34
		Mussidae	70.83	6.95	16	44.47	9.44	0.37
		Agariciidae	65.28	7.63	25	37.19	7.86	0.43
		Poritidae	54.46	8.67	23	33.26	8.88	0.39
Medium		Pocilloporidae	57.87	7.04	23	32.30	8.54	0.44

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		Milleporidae	48.67	12.74	5	31.56	19.58	0.35
		Siderastreidae	46.16	14.75	7	15.48	10.98	0.66
		Meandrinidae	27.98	15.50	6	10.84	7.00	0.61
		Psammocoridae	43.90	16.66	3	1.13	1.13	0.97
	Beginning	Milleporidae	59.75	23.24	4	50.00	28.87	0.16
		Psammocoridae	48.83	26.58	4	30.80	18.32	0.37
		Agariciidae	48.86	18.72	7	5.61	5.61	0.89
		Pocilloporidae	52.40	16.91	5	0.00	0.00	1
		Poritidae	31.25	23.11	4	0.00	0.00	1
	Middle	Poritidae	87.00	1.53	3	24.67	17.67	0.72
		Merulinidae	83.87	10.87	8	24.62	7.07	0.71
	End	Acroporidae	100.00	0.00	4	100.00	0.00	0
		Milleporidae	100.00	0.00	8	100.00	0.00	0
		Pocilloporidae	100.00	0.00	16	73.05	0.00	0.27
		Poritidae	85.46	7.68	13	72.00	8.42	0.16
		Agariciidae	32.67	23.9	3	27.00	4.93	0.17
High		Psammocoridae	100.00	0	4	0.50	0.29	0.99
Thermal stress accumulation	Timing of observations	Genus	Susceptibility	±SE	n	Mortality	±SE	(S-M)/S
	Beginning	*Millepora*	37.51	8.75	13	19.26	10.00	0.49
		Pavona	34.71	11.62	11	18.19	11.55	0.48
		Stylophora	74.50	11.76	9	14.22	11.16	0.81
		Acropora	47.82	4.29	71	13.52	3.17	0.72
		Pocillopora	38.11	4.93	54	11.48	3.43	0.70
		Dipsastraea	48.36	22.18	3	9.47	5.14	0.80
		Galaxea	37.36	9.19	10	8.80	6.66	0.76
		Hydnophora	37.65	8.38	13	8.78	6.31	0.77
		Echinopora	39.68	9.58	9	8.66	5.89	0.78
		Lobophyllia	25.33	15.34	3	8.33	7.36	0.67
		Cyphastrea	10.28	10.28	6	7.20	3.64	0.30
		Montipora	35.90	6.39	37	6.49	2.76	0.82
		Favites	37.38	7.10	8	6.08	3.19	0.84
		Platygyra	33.26	7.94	11	6.12	3.15	0.82
		Orbicella	76.49	5.48	16	5.85	3.70	0.92
		Porites	32.29	3.61	80	4.68	1.60	0.86
		Astreopora	41.09	8.79	7	4.64	3.29	0.89
		Seriatopora	97.75	2.25	4	4.50	4.50	0.95
		Leptoria	51.00	15.79	5	2.00	2.00	0.96
		Goniastrea	30.20	8.30	10	1.50	0.97	0.95
Low		*Montastraea*	27.55	4.79	12	0.83	0.83	0.97

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	Siderastrea	60.63	8.27	13	0.65	0.58	0.99
	Fungia	60.90	10.87	10	0.50	0.50	0.99
	Favia	40.84	7.03	13	0.46	0.39	0.99
	Diploria	66.70	23.61	3	0.00	0.00	1
	Colpophyllia	62.55	12.92	4	0.00	0.00	1
	Agaricia	52.26	6.94	19	0.00	0.00	1
	Acanthastrea	51.67	13.54	3	0.00	0.00	1
	Symphyllia	34.80	17.00	5	0.00	0.00	1
	Goniopora	34.71	10.39	11	0.00	0.00	1
	Pseudodiploria	32.33	9.52	10	0.00	0.00	1
	Echinophyllia	26.00	13.45	3	0.00	0.00	1
	Diploastrea	18.53	10.83	7	0.00	0.00	1
	Madracis	5.40	2.77	5	0.00	0.00	1
	Turbinaria	0.75	0.75	4	0.00	0.00	1
Middle	*Millepora*	54.90	18.35	5	29.41	17.91	0.46
	Montipora	53.33	7.67	4	16.83	16.49	0.68
	Acropora	46.97	7.96	21	16.67	7.26	0.65
	Porites	47.74	7.90	21	13.70	5.24	0.71
	Orbicella	47.00	19.65	4	11.46	7.19	0.76
	Pseudodiploria	61.10	10.54	7	5.02	1.59	0.92
	Coelastrea	18.67	6.74	3	3.67	2.33	0.80
	Platygyra	36.29	13.36	7	3.57	3.57	0.90
	Agaricia	59.86	16.38	7	3.09	1.42	0.95
	Siderastrea	47.59	9.87	10	2.46	0.79	0.95
	Diploastrea	17.68	6.15	4	2.43	2.43	0.86
	Montastraea	45.54	17.93	5	2.86	2.86	0.94
	Diploria	23.40	6.58	5	2.20	2.20	0.91
	Acanthastrea	58.67	27.34	3	2.00	2.00	0.97
	Coeloseris	33.00	15.71	4	2.00	2.00	0.94
	Colpophyllia	33.00	15.71	4	2.00	2.00	0.94
	Favia	48.64	13.69	7	1.55	1.04	0.97
	Pocillopora	37.80	12.73	5	1.20	0.58	0.97
	Galaxea	23.33	21.36	3	0.67	0.67	0.97
	Echinopora	17.50	16.19	4	0.50	0.50	0.97
	Goniopora	52.00	27.15	3	0.00	0.00	1
	Astreopora	49.00	10.69	3	0.00	0.00	1
	Echinophyllia	25.00	15.54	4	0.00	0.00	1
End	*Pavona*	56.68	21.35	5	35.73	20.89	0.37
	Hydnophora	32.92	16.46	3	32.68	16.35	0.01
	Agaricia	45.50	19.17	3	30.30	10.33	0.33
	Acropora	56.08	7.09	31	26.06	6.62	0.54
	Porites	36.93	8.65	18	19.55	7.58	0.47
	Orbicella	65.89	10.33	7	18.96	2.51	0.71

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		Pseudodiploria	36.10	15.48	3	17.53	7.87	0.51
		Galaxea	32.64	11.05	7	16.06	12.45	0.51
		Echinopora	13.59	13.59	4	13.34	13.34	0.02
		Platygyra	52.32	9.81	7	13.17	8.50	0.75
		Pocillopora	46.90	9.58	14	12.92	8.40	0.72
		Millepora	9.40	9.40	3	8.00	8.00	0.15
		Favites	23.59	3.20	4	4.96	3.28	0.79
		Montipora	21.71	6.64	7	2.14	1.83	0.90
		Astrea	64.00	20.22	5	0.00	0.00	1
		Goniastrea	58.33	22.05	3	0.00	0.00	1
		Acanthastrea	35.67	5.93	3	0.00	0.00	1
		Astreopora	22.33	10.71	3	0.00	0.00	1
		Favia	21.67	5.84	3	0.00	0.00	1
		Fungia	16.64	8.24	4	0.00	0.00	1
		Echinophyllia	9.33	4.70	3	0.00	0.00	1
		Goniopora	1.67	0.88	3	0.00	0.00	1
		Mussismilia	0.00	0.00	3	0.00	0.00	***
	Beginning	*Acropora*	59.88	12.77	13	24.73	11.82	0.59
		Eusmilia	38.33	14.24	3	16.33	16.33	0.57
		Montipora	52.75	18.07	4	13.75	5.30	0.74
		Millepora	37.31	13.49	8	13.06	12.08	0.65
		Favites	86.25	13.75	4	12.50	12.50	0.86
		Madracis	7.88	3.23	8	7.81	5.80	0.01
		Stephanocoenia	51.00	28.88	3	6.00	6.00	0.88
		Colpophyllia	34.25	5.53	4	4.50	2.87	0.87
		Orbicella	49.11	8.64	9	4.00	2.66	0.92
		Porites	35.95	9.87	11	3.41	1.69	0.91
		Goniastrea	86.20	8.57	5	3.20	2.96	0.96
		Coeloseris	100.00	0.00	4	2.50	2.50	0.97
		Platygyra	83.75	11.43	4	2.50	2.50	0.97
		Coelastrea	82.50	17.50	4	2.50	2.50	0.97
		Siderastrea	63.80	8.18	10	1.60	0.91	0.97
		Meandrina	46.00	6.16	4	1.50	1.19	0.97
		Pseudodiploria	46.71	6.19	7	1.29	0.64	0.97
		Montastraea	65.17	13.59	6	1.00	1.00	0.98
		Agaricia	23.75	7.07	8	0.00	0.00	1
		Mycetophyllia	4.00	4.00	5	0.00	0.00	1
	Middle	*Montipora*	45.33	24.85	3	36.00	22.07	0.21
		Porites	39.25	5.44	4	24.75	13.46	0.37
		Acropora	19.83	7.61	6	14.67	8.63	0.26
	End	*Diploastrea*	96.67	3.33	3	96.67	3.33	0
		Acropora	86.72	6.70	22	79.33	7.45	0.09
Medium		*Montipora*	93.50	6.50	4	77.50	22.50	0.17

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		Stephanocoenia	56.25	23.66	3	47.92	28.94	0.15
		Agaricia	86.84	6.14	9	37.26	10.94	0.57
		Favites	71.56	14.07	3	36.00	31.13	0.50
		Millepora	48.67	12.74	5	31.56	19.58	0.35
		Porites	52.48	8.84	22	30.32	8.77	0.42
		Pavona	45.43	11.34	10	28.63	13.82	0.37
		Pocillopora	57.44	7.90	18	27.72	9.17	0.52
		Pseudodiploria	61.43	7.69	3	26.44	15.75	0.57
		Orbicella	64.73	13.91	6	18.52	6.55	0.71
		Siderastrea	46.64	12.78	8	16.67	9.58	0.64
		Psammocora	43.90	16.66	3	1.13	1.13	0.97
	Beginning	*Millepora*	59.75	23.24	4	50.00	28.87	0.16
		Psammocora	48.83	26.58	4	30.80	18.32	0.92
		Pavona	59.40	24.26	5	7.86	7.86	0.87
		Pocillopora	52.40	16.91	5	0.00	0.00	1
		Porites	31.25	23.11	4	0.00	0.00	1
	End	*Millepora*	100.00	0.00	8	100.00	0.00	0
		Acropora	100.00	0.00	3	100.00	0.00	0
		Porites	85.46	7.68	13	72.00	12.30	0.16
		Pocillopora	100.00	0.00	14	69.20	11.94	0.31
High		*Psammocora*	100.00	0.00	4	0.50	0.29	0.99

b. Genera

1. Species

Thermal stress accumulation	Timing of observations	Species	Susceptibility	±SE	n	Mortality	±SE	(S-M)/S
Low	Beginning	*Diploastrea heliopora*	43.88	22.98	5	41.94	23.77	0.04
		Pocillopora verrucosa	58.98	13.52	6	21.35	13.93	0.64
		Orbicella faveolata	97.67	2.33	3	20.00	20.00	0.80
		Platygyra daedalea	47.36	8.48	3	17.44	7.85	0.63
		Pocillopora damicornis	28.24	11.57	11	11.87	5.75	0.58
		Hydnophora exesa	92.50	7.50	4	3.75	3.75	0.96
		Acropora hyacinthus	24.13	6.71	7	3.57	2.83	0.85
		Orbicella annularis	75.83	4.57	12	2.80	1.02	0.96
		Dipsastraea favus	23.40	6.58	5	2.20	2.20	0.91
		Montipora digitata	51.50	26.86	4	1.65	1.46	0.97
		Siderastrea siderea	60.90	8.72	11	0.77	0.68	0.99
		Porites astreoides	33.79	7.88	11	0.18	0.18	0.99
		Diploria labyrinthiformis	66.70	23.61	3	0.00	0.00	1

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	Colpophyllia natans	62.55	12.92	4	0.00	0.00	1
	Agaricia agaricites	58.63	10.65	8	0.00	0.00	1
	Porites porites	40.52	11.31	7	0.00	0.00	1
	Agaricia tenuifolia	38.68	12.75	5	0.00	0.00	1
	Favia fragum	34.82	7.69	6	0.00	0.00	1
	Pseudodiploria strigosa	32.22	10.65	9	0.00	0.00	1
	Montastraea cavernosa	28.37	4.35	7	0.00	0.00	1
	Meandrina meandrites	25.70	14.35	4	0.00	0.00	1
	Acropora palmata	8.93	7.03	3	0.00	0.00	1
	Madracis mirabilis	5.33	3.93	3	0.00	0.00	1
	Montipora flabellata	0.65	0.38	4	0.00	0.00	1
	Porites lobata	0.27	0.19	11	0.00	0.00	1
	Montipora capita	0.00	0.00	5	0.00	0.00	***
	Montipora patula	0.00	0.00	5	0.00	0.00	***
	Pocillopora ligulata	0.00	0.00	7	0.00	0.00	***
	Pocillopora meandrina	0.00	0.00	6	0.00	0.00	***
	Porites compressa	0.00	0.00	7	0.00	0.00	***
	Porites evermanni	0.00	0.00	6	0.00	0.00	***
Middle	*Porites porites*	47.45	13.67	6	11.91	5.29	0.75
	Orbicella annularis	47.00	19.65	4	11.46	7.19	0.76
	Pseudodiploria strigosa	57.30	14.85	5	4.62	2.22	0.92
	Coelastrea aspera	18.67	6.74	3	3.67	2.33	0.80
	Agaricia agaricites	88.91	6.68	3	3.62	2.16	0.96
	Montastraea cavernosa	40.25	22.12	4	3.57	3.57	0.91
	Acropora palmata	41.48	14.56	4	3.48	2.63	0.92
	Siderastrea radians	43.60	14.39	4	3.14	1.10	0.93
	Favia fragum	50.88	19.00	4	2.71	1.64	0.95
	Porites astreoides	42.44	16.36	7	2.37	1.28	0.94
	Siderastrea siderea	50.25	14.35	6	2.00	1.14	0.96
	Acropora cervicornis	16.38	11.52	4	0.00	0.00	1
End	*Acropora digitifera*	80.33	19.67	3	74.33	25.67	0.07
	Porites nigrescens	85.21	10.53	4	60.69	19.28	0.29
	Galaxea astreata	85.90	4.90	3	54.08	25.27	0.37
	Acropora aspera	94.17	5.83	6	50.00	22.36	0.47
	Acropora eurystoma	79.82	16.34	3	49.79	22.57	0.38
	Acropora hyacinthus	64.56	14.89	9	45.89	14.70	0.29
	Stylophora pistillata	66.67	33.33	3	42.67	29.78	0.36

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Acropora valida	66.00	22.68	3	38.00	31.26	0.42
Porites panamensis	58.80	19.17	6	33.45	21.05	0.43
Isophyllia sinuosa	78.57	14.87	3	28.38	16.50	0.64
Pocillopora damicornis	52.75	8.72	24	27.09	8.08	0.49
Montipora aequituberculata	32.50	22.87	4	26.25	24.61	0.19
Psammocora stellata	59.06	22.99	5	24.84	15.39	0.58
Pavona gigantea	34.58	20.24	4	24.75	22.33	0.28
Pocillopora elegans	67.81	12.37	9	24.30	14.33	0.64
Pocillopora verrucosa	68.03	10.06	9	23.50	12.10	0.65
Acropora millepora	77.33	22.67	3	20.00	6.43	0.74
Madracis decactis	19.20	11.77	5	19.20	11.77	0
Acropora gemmifera	75.00	14.60	4	18.75	18.75	0.75
Agaricia tenuifolia	41.97	9.70	10	17.59	10.37	0.58
Favia pentagona	40.89	13.49	3	17.50	3.09	0.57
Favites abdita	74.17	17.34	6	16.67	10.54	0.78
Orbicella faveolata	70.77	9.64	9	15.83	6.31	0.78
Platygyra daedalea	68.02	6.75	13	15.73	5.61	0.77
Diploria labyrinthiformis	47.82	10.64	13	15.44	6.89	0.68
Coelastrea aspera	60.75	15.06	8	15.13	12.21	0.75
Porites porites	54.43	7.39	20	14.00	4.31	0.74
Colpophyllia natans	50.63	7.87	13	13.92	5.05	0.72
Coeloseris mayeri	83.33	16.67	6	13.33	11.45	0.85
Gardineroseris planulata	23.88	13.21	6	13.00	10.30	0.46
Dipsastraea favus	43.77	16.34	4	12.68	4.85	0.71
Eusmilia fastigiata	26.25	15.19	4	12.25	12.25	0.53
Acropora cytherea	21.00	21.00	3	12.00	12.00	0.43
Pavona varians	40.78	13.65	8	11.40	10.09	0.72
Acropora palmata	36.98	9.50	12	10.03	5.33	0.73
Pseudodiploria clivosa	48.69	7.17	7	11.35	7.72	0.77
Stephanocoenia intersepta	41.13	14.30	6	10.29	7.31	0.75
Orbicella franksi	31.03	21.41	3	9.87	9.87	0.68
Dichoenia stokesii	22.47	8.05	5	9.82	7.38	0.56
Orbicella annularis	66.37	4.63	30	9.49	2.26	0.86
Goniastrea retiformis	78.33	16.41	6	9.17	6.64	0.88
Acropora cervicornis	29.57	8.62	15	8.89	5.98	0.70
Agaricia agaricites	66.21	8.21	14	8.04	4.40	0.88
Galaxea fascicularis	25.07	6.17	4	7.55	4.21	0.70

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		Pavona cactus	45.67	17.93	6	7.20	6.45	0.84
		Siderastrea radians	46.81	11.19	7	6.56	4.54	0.86
		Porites lutea	31.82	8.15	8	6.48	4.17	0.80
		Porites furcata	67.17	8.86	4	5.92	4.05	0.91
		Siderastrea siderea	54.91	5.35	28	4.89	2.72	0.91
		Pseudodiploria strigosa	46.66	6.47	21	4.60	1.79	0.90
		Montipora digitata	43.80	22.18	5	3.91	2.53	0.91
		Porites lobata	21.92	7.09	23	3.55	3.04	0.84
		Montastraea cavernosa	31.56	6.33	17	3.36	1.85	0.89
		Meandrina meandrites	32.67	10.00	10	3.29	2.67	0.90
		Madracis mirabilis	7.67	3.04	6	2.75	2.65	0.64
		Pocillopora eydouxi	21.32	7.88	6	2.33	2.33	0.89
		Porites astreoides	40.79	6.67	25	2.29	0.81	0.94
		Favia fragum	43.55	8.15	11	0.98	0.68	0.98
		Pocillopora meandrina	14.85	8.83	9	0.23	0.23	0.98
		Astrea curta	64.00	20.22	5	0.00	0.00	1
		Manicina areolata	49.03	4.96	3	0.00	0.00	1
		Dendrogyra cylindrus	30.00	20.00	5	0.00	0.00	1
		Montipora flabellata	0.65	0.38	4	0.00	0.00	1
		Montastraea capitata	0.00	0.00	5	0.00	0.00	***
		Montipora patula	0.00	0.00	5	0.00	0.00	***
		Pocillopora ligulata	0.00	0.00	7	0.00	0.00	***
		Porites compressa	0.00	0.00	7	0.00	0.00	***
		Porites evermanni	0.00	0.00	6	0.00	0.00	***
Medium	Beginning	*Acropora aspera*	100.00	0.00	4	50.00	28.87	0.5
		Isophyllia. sinuosa	56.67	23.33	3	9.33	9.33	0.84
		Madracis decactis	15.33	15.33	3	7.67	7.67	0.50
		Madracis mirabilis	13.33	1.76	3	5.50	5.25	0.59
		Porites astreoides	39.75	15.62	4	5.25	4.03	0.87
		Porites porites	57.67	23.85	3	4.67	3.28	0.92
		Colpophyllia natans	34.25	5.53	4	4.50	2.87	0.87
		Dichocoenia stokesii	29.33	12.13	3	3.67	3.67	0.87
		Coeloseris mayeri	100.00	0.00	4	2.50	2.50	0.97
		Platygyra daedalea	83.75	11.43	4	2.50	2.50	0.97
		Meandrina meandrites	44.67	8.51	3	2.00	1.53	0.96
		Siderastrea siderea	64.22	9.14	9	1.78	1.00	0.97

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		Pseudodiploria strigosa	51.50	7.73	4	1.50	0.96	0.97
		Orbicella annularis	44.86	9.96	7	1.71	1.55	0.96
		Montastraea cavernosa	65.17	13.59	6	1.00	1.00	0.98
		Pseudodiploria clivosa	40.33	10.65	3	1.00	1.00	0.98
		Acropora palmata	17.50	9.19	4	0.63	0.47	0.96
	End	*Diploastrea heliopora*	96.67	3.33	3	96.67	3.33	0
		Pocillopora damicornis	51.48	19.00	4	31.25	23.02	0.39
		Porites lutea	30.33	30.33	3	30.33	30.33	0
		Orbicella annularis	78.09	8.03	4	26.03	6.99	0.67
		Agaricia agaricites	88.75	5.15	4	25.00	14.43	0.72
		Siderastrea siderea	69.72	18.30	3	25.00	25.00	0.64
		Porites lobata	51.30	17.14	4	17.50	17.50	0.66
		Pocillopora elegans	35.77	14.53	3	4.90	1.27	0.86
		Pavona cactus	24.67	7.45	3	1.30	1.30	0.95
High	Beginning	*Psammocora stellata*	48.83	26.58	4	30.80	18.32	0.37
		Pocillopora damicornis	53.00	24.95	3	0.00	0.00	1
	End	*Pocillopora damicornis*	100.00	0.00	6	67.33	20.66	0.33
		Pocillopora elegans	100.00	0.00	4	51.00	28.29	0.49

Table A9. Average values of ecological factors matrixed by thermal stress accumulation and timing of observations, using paired susceptibility–mortality records (n ≥ 3). Data are ordered by stress accumulation, observation timing, and mortality; error represents standard error.

A) Depth (in descending order)

Thermal stress accumulation	Timing of observations	Depth (metres)	Susceptibility	±SE	n	Mortality	±SE	(S-M)/S
Low	Beginning	0-3m	47.00	5.84	26	0.31	0.22	0.99
		3-6m	69.80	8.17	19	31.45	7.28	0.55
		6-9m	43.31	5.43	35	1.69	1.43	0.96
		9-12m	53.67	3.33	79	10.53	2.42	0.80
		12-15m	43.50	6.60	19	0.02	0.02	1
		>15m	43.40	6.52	28	2.34	2.34	0.95
	Middle	0-3m	26.50	7.31	26	18	7.06	0.32
		6-9m	58.07	3.58	69	1.36	0.44	0.98
		9-12m	42.38	5.07	34	4.08	0.78	0.90
		>15m	27.08	5.76	26	3.34	1.56	0.88
	End	0-3m	6.93	1.53	14	1.36	0.63	0.80

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		3-6m	42.40	5.45	54	9.92	3.38	0.77
		6-9m	30.98	2.92	65	2.48	1.17	0.92
		9-12m	18.72	7.74	18	10.56	5.55	0.70
		12-15m	45.92	8.92	13	21.87	7.74	0.52
Medium	Beginning	3-6m	20.33	3.53	3	0.00	0.00	1
		6-9m	74.80	8.84	12	35.40	10.93	0.53
		9-12m	57.91	6.36	12	5.83	2.50	0.90
		15-18m	45.47	4.16	43	7.33	1.71	0.84
		>18m	46.67	2.91	3	0.00	0.00	1
	End	0-3m	72.50	15.88	4	48.75	20.93	0.33
		3-6m	55.54	10.38	7	13.19	9.61	0.76
		9-12m	47.32	4.73	49	16.25	3.61	0.66
		12-15m	95.00	2.89	4	95.00	3.54	0
		>15m	48.87	5.82	34	29.89	5.37	0.39
High	Beginning	9-12m	68.38	11.24	13	19.29	10.66	0.72
		12-15m	96.43	3.57	3	55.93	9.56	0.42
		>15m	9.44	3.13	9	0.00	0.00	1
	End	3-6m	100.00	0.00	20	89.44	6.73	0.11
		9-12m	78.75	13.74	8	50.76	16.56	0.36
		12-15m	72.50	14.11	8	1.38	0.60	0.98

B) Habitat

Thermal stress accumulation	Timing of observations	Habitat	Susceptibility	±SE	n	Mortality	±SE	(S-M)/S
Low	Beginning	Lagoon	44.50	8.78	15	26.17	7.62	0.41
		Fringing reef	55.30	4.09	51	12.99	3.13	0.77
		Subtropical	45.36	10.01	14	4.21	3.55	0.91
		Fore reef	22.51	4.93	40	2.04	1.51	0.91
		Back reef	23.58	4.34	39	0.26	0.15	0.99
		Reef slope	59.44	4.69	36	0.03	0.02	1
		Patch reef	29.00	5.51	39	0.00	0.00	1
	Middle	Reef flat	52.91	13.81	11	40.09	14.47	0.24
		Fringing reef	68.52	2.34	34	5.17	0.86	0.92
		Patch	28.13	5.90	25	3.48	1.62	0.88
		Subtropical	54.07	4.38	54	0.30	0.24	0.99
	End	Fringing	54.24	5.90	40	21.85	4.77	0.60

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		Subtropical	30.98	2.92	65	2.48	1.17	0.92
		Reef Crest	30.26	8.51	14	0.00	0.00	1
		Reef Slope	23.02	8.77	14	0.00	0.00	1
Medium	End						20.93	0.33
		Reef flat	72.50	15.88	4	48.75		
		Lagoon	76.00	7.08	20	39.25	7.79	0.48
		Patch reef	49.44	5.08	40	25.75	4.92	0.48
		Gulf	43.82	5.41	19	12.71	5.92	0.71
		Fringing reef	24.19	7.53	14	4.29	3.62	0.83
High	End	Reef flat	100.00	0.00	16	100.00	0.00	0
		Gulf	90.00	6.00	4	80.40	3.04	0.11
		Bay	75.71	15.47	7	47.14	18.66	0.38
		Reef slope	26.67	13.33	3	0.00	0.00	1

C) Anthropogenic input

Thermal stress accumulation	Timing of observations	Pollution	Susceptibility	±SE	n	Mortality	±SE	(S-M)/S
Low	Beginning	No	57.26	8.15	22	11.14	4.02	0.81
		Yes	46.09	6.05	34	5.26	2.98	0.89
	Middle	Yes	28.13	5.90	25	3.48	1.62	0.88
		No	54.07	4.38	54	0.30	0.24	0.99
	End	Yes	45.92	8.92	13	21.87	7.74	0.52
		No	30.98	2.92	65	2.48	1.17	0.92

D) Shelf position

Thermal stress accumulation	Timing of observations	Shelf position	Susceptibility	±SE	n	Mortality	±SE	(S-M)/S
Low	Beginning	Middle	60.25	14.56	6	54.75	22.35	0.09
		Lagoon	62.29	14.19	7	25.57	9.67	0.59
		Gulf	78.09	11.19	8	23.25	8.22	0.70
		Inner	55.94	4.22	47	10.56	1.54	0.81
		Fringing	38.79	3.44	64	3.34	0.42	0.91
		Outer	59.44	4.69	36	0.03	0.00	1
		High Latitude	45.17	6.98	14	0.00	0.00	1

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Table A10. ANOVA results for paired susceptibility–mortality data stratified by thermal stress accumulation: (A) low, (B) medium, and (C) high. Each category is further subdivided by timing of observations relative to stress onset (Beginning, Middle, End). Not all combinations were available due to data limitations.

A) Low Thermal Stress Accumulation

a.) The beginning of the low degree heating week category (0-19 Degree Heating Weeks

i. Factors associated with variation in estimates of susceptibility to mass bleaching events

Factor	SS (Type III)	df	*n*	MS	F	p
Relief from Weather	25.543	2	180	0.094	41.271	<0.001***
Bleaching Occurrence	91.851	3	618	0.131	28.900	<0.001***
Location	90.222	18	607	0.086	25.651	<0.001***
Species	25.534	18	146	0.058	15.329	<0.001***
Generalization	44.546	1	257	0.166	13.095	<0.001***
Habitat	37.089	6	233	0.128	10.502	<0.001***
Ocean_subregion	90.669	6	614	0.136	10.100	<0.001***
Months of Observations	91.168	3	616	0.144	7.344	<0.001***
Transmission of Algae to Offspring	35.151	1	192	0.759	4.679	<0.05*
Level of Colony Integrations	58.041	2	359	0.959	3.478	<0.05*
Shelf Position	20.798	7	195	0.142	3.357	<0.01**
Dominant Topography	8.958	5	53	0.139	3.326	<0.05*
Genus	73.722	27	479	0.138	3.061	<0.001***
Depth	24.165	5	205	0.114	2.389	<0.05*
Degree Heating Index	91.851	1	618	0.148	1.995	>0.05
Family	83.758	14	562	0.147	1.628	>0.05
Anthropogenic Input	9.641	2	55	0.173	1.321	>0.05
Sex	34.428	1	218	0.158	0.407	>0.05
Complexity	83.034	1	550	0.151	0.139	>0.05
Reproductive Mode	34.428	1	218	0.159	0.088	>0.05

1. Correlation of factors with average susceptibility to mass bleaching events (only significant results reported)

Factor	*n*	Perason's Correlation Coefficient	p
Habitat	234	0.235	<0.001***
Generalization	258	-0.221	<0.001***
Relief from Weather	181	0.199	<0.01**
Transmission of Algae to Offspring	192	-0.155	<0.05*
Bleaching Occurrence	619	-0.087	<0.05*

ii. Factors associated with variation in mortality associated with mass bleaching events

Factor	SS (Type III)	df	*n*	MS	F	p
Ocean_subregion	39.813	6	614	0.055	19.112	<0.001***
Habitat	10.39	6	233	0.032	18.720	<0.001***
Shelf Position	12.740	7	195	0.055	17.715	<0.001***
Depth	13.693	5	205	0.049	15.907	<0.001***
Level of Colony Integration	24.579	2	359	0.064	14.353	<0.001***
Sex	12.527	1	218	218	12.023	<0.01**
Anthropogenic Input	3.617	2	55	0.047	11.728	<0.001***
Months of Observations	39.832	3	616	0.062	11.052	<0.001***
Dominant Topography	4.482	5	53	0.050	8.264	<0.001***
Reproductive Mode	12.527	1	218	0.056	7.221	<0.01**
Transmission of Algae to Offspring	11.294	1	191	0.160	4.679	<0.05*
Species	3.168	18	146	0.018	2.778	<0.001***
Family	34.557	14	562	0.059	2.632	<0.01**

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Complexity	32.168	1	550	0.058	2.243	>0.05
Genus	32.809	27	479	0.066	1.553	<0.05*
Degree Heating Index	39.860	1	618	0.065	0.517	>0.05
Generalization	13.024	1	257	0.051	0.397	>0.05

1. Pearson's correlation coefficients for significant results of ANOVA factors vs. mortality

Factor	*n*	Pearson's Correlation Coefficient	p
Doldrums	79	-0.504	<0.001***
Decade	615	-0.273	<0.001***
Level of Colony Integration	360	0.264	<0.001***
Sex	219	0.229	<0.01**
Reproductive Mode	219	0.179	<0.01**
Transmission of Algae to Offspring	192	-0.155	<0.05*
Ocean	619	0.100	<0.05*
Family	563	-0.099	<0.05*
Subregion	617	0.086	<0.05*
Location	608	-0.080	<0.05*

b. The Middle Timing of the Low Degree Heating Week category

i. Factors associated with variation in susceptibility and mortality of corals to mass bleaching events

Factor	SS (Type III)	df	*n*	MS	*F*	p
Months of Observations	27.022	3	186	0.119	14.729	<0.001***
Ocean_subregion	27.014	3	185	0.120	14.627	<0.001***
Habitat	27.022	3	186	0.125	11.226	<0.001***
Anthropogenic Input	12.008	1	78	0.140	9.075	<0.01**
Depth	7.956	3	154	0.121	8.072	<0.001***
Complexity	25.868	1	175	0.144	5.448	<0.05*
Degree Heating Index	27.022	1	186	0.142	5.376	<0.05*
Relief from Weather	14.177	2	109	0.122	4.728	<0.05*
Level of Colony Integration	13.856	2	89	0.149	1.985	>0.05
Reproductive Mode	10.218	2	73	0.317	1.865	>0.05
Family	25.339	10	171	0.145	1.419	>0.05
Sex	9.803	1	72	0.136	0.942	>0.05
Genus	13.445	10	95	0.148	0.607	>0.05
Species	3.368	4	29	0.128	0.349	>0.05
Transmission of Algae to Offspring	7.672	1	54	0.144	0.230	>0.05
Generalization	10.939	1	77	0.144	0.050	>0.05

1. Correlation of factors with average susceptibility to mass bleaching events, only significant results reported

Factor	*n*	Pearson's Correlation Coefficient	p
Ocean-subregion	186	-0.326	<0.001***
Anthropogenic Input	79	-0.325	<0.01**
Months of Observations	187	0.324	<0.001***
Relief from Weather	110	0.199	<0.05*
Complexity	176	-0.174	<0.05*
Degree Heating Index	187	0.168<	<0.05*

ii. Factors associated with variations in coral mortality from mass bleaching events

Factor	SS (Type III)	df	*n*	MS	F	p
Relief from Weather	7.056	2	109	0.037	42.001	<0.001***
Habitat	7.607	3	123	0.039	25.630	<0.001***

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Ocean_subregion	11.915	3	185	0.054	12.890	<0.001***
Depth	7.956	3	154	0.044	9.959	<0.001***
Level of Colony Integration	8.477	2	89	0.90	3.466	<0.05*
Anthropogenic Input	7.961	1	79	0.098	2.957	>0.05
Months of Observations	12.185	3	186	0.064	2.806	<0.05*
Generalization	3.638	1	77	0.049	2.654	>0.05
Family	11.853	10	171	0.066	1.966	<0.05*
Species	0.698	4	29	0.023	1.388	>0.05
Transmission of Algae to Offspring	1.499	1	54	0.028	0.648	>0.05
Degree Heating Index	12.185	1	186	0.066	0.640	>0.05
Genus	8.161	10	95	0.082	1.426	>0.05
Reproductive Mode	3.638	2	73	0.051	0.137	>0.05
Sex	3.610	1	72	0.051	0.043	>0.05

1. Pearson's correlation results for significant results of ANOVA factors vs. mortality; only significant results reported

Factor	*n*	Pearson's Correlation Coefficient	p
Anthropogenic Input	79	0.327	<0.01**
Level of Colony Integration	90	0.260	<0.05*
Habitat	124	-0.239	<0.01**
Complexity	176	-0.171	<0.05*
Location	184	-0.167	<0.05*
Depth	155	-0.161	<0.05*

c. The End Timing of the Low Degree Heating Week category

i. Factors associated with variation in estimates of susceptibility to mass bleaching events

Factor	SS (Type III)	df	*n*	MS	F	p
Bleaching Occurrence	30.513	3	213	0.127	9.795	<0.001***
Ocean_subregion	30.513	8	213	0.108	9.793	<0.001***
Reef Types	14.624	2	107	0.118	9.247	<0.001***
Relief from Weather	18.463	1	122	0.142	9.108	<0.01**
Recovery (months)	12.929	4	57	0.150	8.274	<0.001***
Shelf Position	13.701	2	70	0.164	7.753	<0.01**
Species	103.222	75	582	0.128	4.124	<0.001***
Months of Observations	30.513	2	213	0.139	3.013	<0.05*
Level of Colony Integration	20.918	2	110	0.185	2.649	>0.05
Genus	23.245	25	155	0.133	1.815	<0.05*
Depth	11.156	3	167	0.144	1.617	>0.05
Family	28.951	10	200	0.140	1.486	>0.05
Sex	17.052	1	96	0.177	1.437	>0.05
Habitat	4.624	2	30	0.150	1.368	>0.05
Transmission of Algae to Offspring	14.121	1	83	0.170	1.285	>0.05
Complexity of Skeleton	29.026	1	203	0.143	0.883	>0.05
Generalization	13.055	1	99	0.187	0.211	>0.05
Reproductive Mode	16.607	1	95	0.177	0.001	>0.05

1. Correlation of factors with susceptibility to mass bleaching events; only significant results reported

Factor	*n*	Pearson's Correlation Coefficient	p
Recovery (months)	58	0.383	<0.01**
Reef Type	108	-0.367	<0.001***
Relief from Weather	123	-0.265	<0.01**
Complexity	214	0.197	<0.01**
Species	583	-0.088	<0.05*

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ii. Factors associated with variations in coral mortality associated with mass bleaching events

Factor	SS (TypeIII)	df	*n*	MS	F	p
Habitat	1.564	2	39	0.150	196.399	<0.001***
Anthropogenic Input	4.725	1	79	0.040	39.372	<0.001***
Ocean-subregion	21.507	8	213	0.108	34.933	<0.001***
Reef Type	10.148	2	107	0.073	16.991	<0.001***
Recovery (months)	3.948	4	57	0.034	16.056	<0.001***
Months of Observations	21.507	3	213	0.092	7.737	<0.001***
Bleaching Occurrence	21.507	3	213	0.093	7.247	<0.001***
Complexity of Skeleton	20.148	1	203	0.097	5.321	<0.05*
Depth	11.156	3	167	0.063	5.746	<0.01**
Shelf Position	8.417	2	7	0.108	4.850	<0.05*
Reproductive Mode	12.662	1	95	0.128	3.896	<0.05*
Species	65.683	75	582	0.095	2.509	<0.001***
Level of Colony Integration	14.957	2	100	0.134	1.981	>0.05
Genus	17.777	25	155	0.112	1.279	>0.05
Family	20.117	10	200	0.100	1.216	>0.05
Transmission of Algae to Offspring	9.316	1	83	0.112	0.934	>0.05
Relief From Weather	5.069	1	122	0.042	0.873	>0.05
Sex	12.763	1	96	0.133	0.740	>0.05
Generalization	13.055	1	99	0.153	0.005	>0.05

1. Pearson's correlation results for significant results of ANOVA factors verses mortality; only significant results reported

Factor	*n*	Pearson's Correlation Coefficient	p
Habitat	31	-0.69	
Anthropogenic Input	80	0.579	<0.001***
Reef Type	108	-0.469	<0.001***
Location	214	0.291	<0.001***
Months of Observations	214	0.240	<0.001***
Depth	164	0.211	<0.01**
Complexity of Skeleton	204	-0.160	<0.05*
Species	583	-0.122	<0.01**

B) Medium thermal stress accumulation

a. The Beginning timing of the medium thermal stress accumulation category

i. Factors associated with variation in coral susceptibility to mass bleaching events

Factor	SS (Type III)	df	*n*	MS	F	p
Bleaching Occurrence	31.317	2	179	0.105	61.133	<0.001***
Ocean_subregion	31.372	5	179	0.110	22.132	<0.001***
Relief from Weather	5.456	2	52	0.072	12.674	<0.001***
Months of Observations	31.740	3	180	0.149	11.941	<0.001***
Reproductive Mode	18.644	2	124	0.131	10.136	<0.001***
Level of Colony Integration	19.780	2	137	0.132	7.395	<0.01**
Species	10.007	19	84	0.053	6.546	<0.001***
Transmission of Algae to Offspring	15.083	2	104	0.133	5.664	<0.01**
Complexity of Skeleton	27.845	1	160	0.170	4.556	<0.05*
Family	28.079	12	165	0.137	4.373	<0.001***
Genus	21.113	22	137	0.101	4.233	<0.001***
Depth	6.324	3	72	0.079	3.598	<0.05*
Generalization	23.446	1	141	0.164	2.895	>0.05
Sex	19.304	1	124	0.1577	0.025	>0.05

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1. Correlation of factors with average susceptibility to mass bleaching events

Factor	*n*	Pearson's Correlation Coefficient	p
Relief from Weather	53	-0.396	<0.01**
Months of Observations	181	-0.381	<0.001***
Ocean_subregion	180	0.373	<0.001***
Transmission of Algae to Offspring	105	-0.307	<0.01**
Reproductive Mode	125	0.216	<0.05*
Family	166	-0.169	<0.05
Complexity of Skeleton	161	-0.167	<0.05*

ii. Factors associated with variation in coral mortality to mass bleaching events

Factor	SS (Type III)	df	*n*	MS	F	p
Ocean_subregion	10.611	5	179	0.110	22.132	<0.001***
Relief from Weather	6.847	2	52	0.109	6.357	<0.01**
Complexity of Skeleton	7.774	1	160	0.047	5.808	<0.05*
Months of Observations	10.625	3	180	0.055	5.244	<0.01**
Depth	5.145	3	72	0.066	2.849	<0.05*
Family	8.928	1	65	0.049	2.340	<0.001***
Level of Colony Integration	6.831	2	137	0.049	1.903	>0.05*
Reproductive Mode	5.996	2	124	0.049	0.203	>0.05*
Bleaching Occurrence	10.586	2	179	0.059	1.919	>0.05*
Species	4.522	19	84	0.050	1.302	>0.05*
Genus	8.546	22	137	0.064	0.877	>0.05*

1. Pearson's correlation results for significant results of ANOVA factors verses mortality; only significant results reported

Factor	*n*	Pearson's Correlation Coefficient	p
Relief from Weather	53	0.316	<0.05*
Months of Observations	181	-0.238	<0.01**
Ocean-subregion	180	0.197	<0.01**
Complexity of Skeleton	161	-0.188	<0.05*

b. The Middle timing of the Medium thermal stress accumulation category

i. Factors associated with variation in coral susceptibility to mass bleaching events

Factor	SS (Type III)	df	*n*	MS	F	p
Bleaching Occurrence	9.085	1	74	0.078	43.055	<0.001***
Ocean_subregion	8.529	2	72	0.079	18.933	<0.001***
Genus	0.990	3	13	0.053	2.880	>0.05
Depth	0.929	1	8	0.104	1.904	>0.05
Level of Colony Integration	1.454	1	14	0.107	0.534	>0.05
Months of Observations	9.033	2	72	0.128	0.363	>0.05
Complexity of Skeleton	6.765	1	60	0.114	0.328	>0.05
Family	6.820	8	60	0.118	0.725	>0.05
Relief from Weather	1.655	1	14	0.127	0.056	>0.05

1. Pearson's correlation results for significant results of ANOVA factors verses mortality; only significant results reported

Factor	*n*	Pearson's Correlation Coefficient	p
Bleaching Occurrence	75	0.609	<0.001***
Ocean_subregion	73	0.352	<0.01**

ii. Factors associated with variation in coral mortality to mass bleaching events

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Factor	SS (Type III)	df	*n*	MS	F	p
Level of Colony Integration	5.608	2	72	0.058	13.306	<0.001***
Ocean_subregion	5.608	2	72	0.064	8.739	>0.001***
Complexity of Skeleton	3.188	1	60	0.047	8.146	<0.01**
Family	3.201	8	60	0.043	2.905	<0.01**
Genus	1.380	3	13	0.108	0.943	>0.05
Relief from Weather	1.963	1	14	0.146	0.412	>0.05
Depth	1.017	1	8	0.141	0.222	>0.05
Bleaching Occurrence	5.716	1	74	0.078	0.005	>0.05

1. Pearson's correlation results for significant results of ANOVA factors verses mortality; only significant results reported

Factor	*n*	Pearson's Correlation Coefficient	p
Ocean_subregion	73	0.435	<0.001***
Complexity of Skeleton	61	-0.348	<0.01**

c. The End Timing of the Medium thermal stress accumulation category

i. Factors associated with variation in coral susceptibility to mass bleaching events

Factor	SS (Type III)	df	*n*	MS	F	p
Relief from Weather	10.071	2	78	0.071	32.847	<0.001***
Ocean_subregion	30.800	6	198	0.104	17.265	<0.001***
Degree Heating Weeks	23.168	1	136	0.157	12.834	<0.001***
Dominant Taxa	18.981	6	113	0.106	11.877	<0.001***
Shelf Position	14.660	2	96	0.126	11.002	<0.001***
Bleaching Occurrence	30.800	4	198	0.131	10.184	<0.001***
Anthropogenic Input	4.479	2	48	0.068	10.175	<0.001***
Recovery	5.392	5	54	0.061	7.883	<0.001***
Sex	17.356	1	110	0.149	7.650	<0.01**
Generalization	19.780	1	125	0.151	7.404	<0.01**
Level of Colony Integration	23.630	2	136	0.164	5.199	<0.01**
Depth	12.024	4	91	0.112	5.026	<0..01**
Months of Observations	30.800	3	198	0.147	4.726	<0.01**
Species	3.953	8	30	0.092	2.629	<0.05*
Family	28.576	13	176	0.145	2.607	<0.01**
Genus	18.579	13	118	0.136	2.394	<0.01**
Reproductive Mode	17.293	1	110	0.156	0.510	>0.05
Transmission of Algae to Offspring	14.899	1	96	0.156	0.510	>0.05
Complexity of Skeleton	28.268	1	173	0.164	0.446	>0.05

1. Pearson's correlation results for significant results of ANOVA factors verses susceptibility; only significant results reported

Factor	*n*	Pearson's Correlation Coefficient	p
Relief from Weather	79	-0.680	<0.001***
Anthropogenic Input	49	0.552	<0.001***
Species	31	-0.430	<0.05*
Location	199	0.422	<0.001***
Shelf Position	97	-0.399	<0.001***
Genus	119	0.422	<0.001***
Recovery	55	0.310	<0.05*
Degree Heating Weeks	137	0.295	<0.01**
Family	177	-0.257	<0.01**
Sex	111	0.256	<0.01**
Level of Colony Integration	137	0.250	<0.01**
Generalization	126	0.237	<0.01**

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Months of Observations	199	-0.216	<0.05*
Depth	92	-0.215	<0.05*
Dominant Taxa	114	-0.191	<0.05*

ii. Factors associated with variation in coral mortality to mass bleaching events

Factor	SS (Type III)	df	*n*	MS	F	p
Ocean_subregion	48.146	6	198	0.113	39.002	<0.001***
Anthropogenic Input	7.213	2	48	0.066	31.311	<0.001***
Recovery	11.352	5	54	0.087	16.257	<0.001***
Bleaching Occurrence	48.146	4	198	0.187	15.858	<0.01**
Dominant Taxa	20.743	6	113	0.105	15.242	<0.001***
Generalization	31.185	1	125	0.226	13.697	<0.001***
Degree Heating Weeks	26.455	1	136	0.181	10.996	<0.01**
Depth	11.826	4	91	0.107	5.913	<0.001***
Level of Colony Integration	33.428	2	136	0.230	5.519	<0.01**
Sex	27.557	1	110	0.242	4.875	<0.05*
Months of Observations	48.146	3	198	0.231	4.600	<0.01**
Family	43.792	13	176	0.199	4.397	<0.001***
Transmission of Algae to Offspring	24.100	1	96	0.244	3.931	<0.05*
Genus	29.940	13	118	0.193	3.860	<0.001***
Species	5.873	8	30	0.1557	2.114	>0.05
Reproductive Mode	27.156	1	111	0.245	1.003	>0.05
Complexity of Skeleton	42.057	1	173	0.246	0.791	>0.05

1. Pearson's correlation results for significant results of ANOVA factors verses mortality; only significant results reported

Factor	*n*	Pearson's Correlation Coefficient	p
Anthropogenic Input	49	0.745	<0.001***
Relief from Weather	79	-0.680	<0.001***
Location	199	0.488	<0.01**
Genus	119	-0.428	<0.001***
Dominant Taxa	114	-0.343	<0.001***
Family	177	-0.331	<0.001***
Generalization	126	0.315	<0.001***
Recovery	55	0.310	<0.05*
Degree Heating Weeks	137	0.222	<0.01**
Months of Observations	199	-0.235	<0.05*
Level of Colony Integration	137	0.222	<0.01**
Sex	111	0.207	<0.05
Transmission of Algae to Offspring	97	-0.199	<0.05*
Bleaching Occurrence	199	-0.188	<0.01**

C) High thermal stress accumulation (>40 DHW)

a) The beginning of the high thermal stress accumulation

i) Factors associated with variation in estimates of susceptibility to mass bleaching events

Source	SS(Type III)	df	n	MS	F	P
Depth	5.718	2	23	0.129	11.686	<0.001***
Months	5.359	1	22	0.182	8.370	<0.01**
Degree heating weeks	6.049	1	24	0.209	5.999	<0.05*
Ocean_subregion	6.049	1	24	0.209	5.999	<0.05*
Bleaching occurrence	6.049	1	24	0.209	5.999	<0.05*
Level of colony integration	5.718	1	23	0.219	4.166	>0.05

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Generalization	5.273	1	20	0.262	1.138	>0.05
Complexity of skeleton	5.273	1	20	0.268	0.653	>0.05
Family	5.718	4	23	0.285	0.273	>0.05
Genus	5.255	4	21	0.292	0.255	>0.05
Sex	5.273	1	20	0.275	0.198	>0.05
Reproductive mode	5.273	1	20	0.275	0.160	>0.05
Species	1.530	1	6	0.300	0.104	>0.05
Transmission of algae to offspring	4.485	1	18	0.263	0.029	>0.05

1) Correlation of factors with average susceptibility to mass bleaching events (only significant results reported)

Source	n	Pearson's correlation coefficient	p
Months of observations	23	0.534	<0.01**
Depth	24	-0.528	<0.01**
Degree heating weeks	25	-0.455	<0.05*
Bleaching occurrence	25	0.455	>0.05
Location	25	-0.455	>0.05

ii) Factors associated with variation in estimates of mortality associated with mass bleaching

Source	SS(Type III)	df	n	MS	F	p
Months of observations	1.941	1	22	0.002	1109.104	<0.001***
Degree heating weeks	4.254	1	24	0.125	10.993	<0.001***
Ocean_subregion	4.254	1	24	0.125	10.993	<0.001***
Bleaching occurrence	4.254	1	24	0.055	17.715	<0.001***
Depth	3.985	2	23	0.126	5.273	<0.05*
Transmission of algae to offspring	1.856	1	18	0.093	3.060	>0.05
Generalisation	1.903	1	20	0.087	2.848	>0.05
Family	3.939	4	23	0.137	2.459	>0.05
Level of colony integration	3.939	1	23	0.161	2.422	>0.05
Genus	3.853	4	21	0.151	2.116	>0.05
Species	0.963	1	6	0.136	2.097	>0.05
Complexity of skeleton	1.903	1	20	0.091	1.915	>0.05
Sex	1.903	1	20	0.093	1.477	>0.05
Reproductive mode	1.903	1	20	0.096	0.760	>0.05

1) Pearson's correlation tests for significant results of ANOVA factors versus mortality (only significant results reported)

Source	n	Pearson's correlation coefficient	p
Months of observations	23	0.991	<0.001***
Degree heating weeks	25	-0.569	<0.001***
Bleaching occurrence	25	0.569	<0.001***
Location (country)	25	-0.569	<0.01**
Depth	24	0.146	>0.05

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b) The middle of the high thermal stress

i) Factors associated with variation in estimates of susceptibility to mass bleaching events

Source	SS(Type III)	df	n	MS	F	p
Complexity	0.935	1	19	0.01	0.313	>0.05
Family	0.683	1	10	0.076	0.007	>0.05

ii) Factors associated with variation in estimates of mortality associated with mass bleaching events

Source	SS(Type III)	df	n	MS	F	p
Complexity	1.478	1	19	0.080	0.482	>0.05
Family	0.503	1	10	0.056	0.018	>0.05

c) The end of the high degree heating week category

i) Factors associated with variation in estimates of susceptibility to mass bleaching events

Source	SS(Type III)	df	n	MS	F	p
Bleaching occurrence	4.202	2	49	0.048	20.007	<0.001***
Level of colony integration	2.831	1	40	0.051	16.849	<0.001***
Ocean_subregion	4.202	2	49	0.052	16.510	<0.001***
Family	2.868	5	47	0.030	10.442	<0.001***
Depth	3.449	3	35	0.065	7.096	<0.01
Sex	1.399	1	30	0.042	4.691	<0.05*
Generalization	1.405	1	31	0.042	3.750	>0.05
Relief from weather	2.161	2	27	0.069	3.257	>0.05
Months of observations	4.202	1	49	0.083	2.493	>0.05
Genus	1.140	4	41	0.026	1.907	>0.05
Reproductive mode	1.399	1	30	0.046	1.379	>0.05
Transmission of algae to offspring	1.324	1	21	0.063	0.930	>0.05
Thermal stress accumulation	4.202	1	49	0.086	0.887	>0.05

1) Correlation of factors with average susceptibility to mass bleaching events

Source	n	Pearson's correlation coefficient	p
Level of colony integration	41	0.549	<0.001***
Depth	36	-0.508	<0.01**
Complexity of skeleton	40	0.393	<0.05*
Sex	31	-0.373	<0.05*
Ocean_subregion	50	-0.288	<0.05*

i) Factors associated with variation in estimates of mortality to mass bleaching events

Source	SS(Type III)	df	n	MS	F	p
Bleaching occurrence	12.936	22	49	0.067	72.448	<0.001***
Depth	10.771	3	35	0.137	15.479	<0.001***
Level of colony integration	9.483	1	40	0.178	14.215	<0.001***

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Ocean_subregion	12.936	2	49	0.174	13.571	<0.001***
Relief from weather	4.498	2	27	0.103	9.396	<0.05
Genus	10.887	4	41	0.179	5.945	<0.01**
Family	12.066	5	47	0.168	5.929	<0.05*
Months of observations	12.936	1	49	0.257	2.345	>0.05
Generalization	8.546	1	31	0.267	1.979	>0.05
Sex	8.411	1	30	0.280	1.083	>0.05
Complexity of skeleton	10.940	1	39	0.281	0.929	>0.05
Reproductive mode	8.411	1	30	0.287	0.344	>0.05
Transmission of algae to offspring	6.464	1	21	0.321	0.113	>0.05
Thermal stress	12.936	1	49	0.269	0.080	>0.05

1) Correlation of factors with average mortality to mass bleaching events

Source	n	Pearson's correlation coefficient	p
Bleaching occurrence	50	-0.764	<0.001***
Depth	36	-0.702	<0.001***
Level of colony integration	41	0.517	<0.01**
Family	48	-0.339	<0.05*

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