Coral responses to climate change exposure

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Abstract
A brief historical narrative of coral responses to climate change exposures is followed by a review of evidence. I trace the history of investigations and summarize the findings from 112 multiple-site field studies that examined environmental exposure variables and coral bleaching and mortality response relationships. A total of 59 environmental variables in six topic areas were studied of which excess thermal exposure was the most common topic and variable. Investigations were broadly classified into two categories; those focused on either excess thermal stress thresholds (TM) or on continuous variables (VM). The TM investigations considered a total of 28 variables, but only $1.7 \pm 1.3$ (SD) variables per publication, and only 11% completed a variable selection process that competed variables for fit or parsimony. The 65 VM publications considered 59 variables, more variables per publication ($4.1 \pm 4.3$), and 43% of the studies followed a variable selection procedure. TM investigations received more citation and were most frequently used to identify future climate change impacts and sanctuaries. VM investigations often report excess heat threshold variables as weak single predictors of coral bleaching and mortality. Coral responses to exposure favors mechanisms of causation that are additive and interactive; specifically, the interactions between chronic and acute stresses within the geographic and habitat contexts of local environmental and coral genetic histories. Some of the potentially most important variables for predicting coral responses to exposure have seldom been studied or modeled. The implication is that the future status and health of coral reefs will be better than predicted by TMs. Moreover, impacts and sanctuaries are expected to be patchy and influenced by space, time, genetics, and taxa heterogeneity that will reflect a mix of avoidance, resistance, and recovery processes and their associated sanctuary locations.

1. Introduction
The goal of this paper is to briefly summarize the history and evaluate the current state of evidence for the influences of the environment on coral bleaching and mortality. Environmental and climate change forces that promote coral responses continues to be a difficult scientific problem (McClanahan et al. 2019, Suggett and Smith 2020). Global climate change, such as increasing carbon dioxide, latent heat, and acidification, are clearly on the increase and driving ocean physico-chemical conditions on multiple spatial scales (Skirving et al. 2019). While these metrics attract considerable attention, there are other less understood variables, such as dissolved oxygen, nutrients, and calcite concentrations, that are also changing on large scales (Vercammen et al. 2019, Donovan et al. 2020, McClanahan and Azali 2021). Additionally, the distribution patterns of the many potentially influential variables and their classification as chronic and acute is frequently missing (McClanahan 2020). Added to this complexity is the considerable spatial and temporal heterogeneity in local environmental conditions where corals live (Dixon et al. 2021, Donovan et al. 2021). Finally, there is the recent and evolutionary history of these environment-organism interactions and its consequences for specific elements of generic adaptation, or organismic acclimation and genetic and community change (Selmoni et al. 2020, 2021).
McClanahan et al 2020a). The difficulty of this problem for science is that the complexity is driven by scales of heterogeneity and their interactions, which makes it difficult to predict localized dysfunction in the coral-algae symbiosis (i.e. coral bleaching). It behooves those interested in the future of coral reefs to look back and consider the trajectory of investigation into the current state of this research, what we have learned, where we have had bias and blind spots, and where we need to go improve predictions and adaptation to future change.

1.1. Early science
Investigations into this complex global problem reflect many of the elements of early science—a description of the phenomenon, generation of hypotheses from observations, correlation and causation, and efforts to use natural variability or experiments to test alternatives and distinguish causation from correlation. The urgency of the problem has provoked the creation of models to predict bleaching both when it will occur and future outcomes. The scientific process has largely been underway since ~1985 (figure 1). Over these past ~35 years much has been learned. I argue here, however, that the science is still in its early stages and requires a critical examination of past research and the development of new directions to hasten a generation of improved predictive models. This review is, therefore, an effort to create a historical narrative summary and then to synthesize the main findings of bleaching and coral mortality impacts from the multiple field site studies of environment-coral interactions. Thereby, to contextualize the current state of this knowledge and to potentially promote a more empirically based climate-coral interaction paradigm. The results section is a review of evidence from 112 papers.

Prior to 1994, the coral bleaching literature was based on case studies from people working in field and laboratory conditions to evaluate coral health (Glynn 1996, Brown 1997). Field efforts were notably accelerated when the United States National Oceanographic and Atmospheric Association (NOAA) made their satellite or Earth-observing system data publicly available. This technology allowed access to measures of ocean-skin temperatures to combine with observations of whitened corals (bleaching) where symbiotic algae living in corals had declined. A first published connection between multiple field observation and satellite measurements was made in 1991, which resulted in the proposed ‘HotSpot’ (HS) metric of coral bleaching (Goreau and Hayes 1994). This metric appeared useful because both the exposure/sensitivity elements of stress were contained in the simple HS = MMM + 1 °C equation. That is, a potentially good proxy for local sensitivity was contained in the mean maximum monthly temperature denominator (MMM), element of the calculation. The acute threshold concept or the +1 °C was added to account for a potentially coral-centric tolerance to heat before the visible loss of symbionts. The cumulative sum of these anomalies over 84 days or 12 weeks formed the Degree-heating week (DHW) and the -months DHMs metrics, which have since been used frequently in ocean temperature data compilations. These metrics reflected a common early view that the loss of symbionts or bleaching was a rapid response that reflected a threshold-type behavior.

Corals were hypothesized to transition from normal to bleached state when temperatures exceeded the maximum summer +1 °C. Laboratory studies that manipulated temperatures and light were cited to support the +1 °C threshold decision (Glynn and D’Croz 1990, Jokiel and Coles 1990). However, symbiont densities in these studies did not decline abruptly, nor did corals change color appreciably with a +1 °C in increase. Glynn (1996), for example, concluded from experimental laboratory studies that +3 °C—+5 °C was required to markedly decrease symbiont densities in the Eastern Pacific Pocillopora damicornis. Jokiel and Coles (1977) did not report on symbiont density or color but reported rapid death of corals at +6 °C MMM in three Hawaiian species. In their subsequent study, they report +3 °C—4 °C to induce rapid change in symbionts that would visually be recognized as bleaching while emphasizing the modifying roles of PAR and UV light (Jokiel and Coles 1990). McLachlan et al (2020) summarized 255 laboratory studies of heat stress on corals and emphasized the considerable variability in responses arising from many limited-length manipulations of thermal stresses. They also criticize the highly limited number of locations and taxa used to date. Laboratory studies inform this review; but here I focus on results from field studies with multiple sites.

1.2. Emergence of the threshold models (TMs)
The earliest study in this evaluation chose a threshold method of >+1 °C or HS that was above the mean summer temperatures (Goreau and Hayes 1994). This metric appeared, in some limited cases, to coincide with field reports of coral bleaching. HSs and its modification as summed HSs or degree heating then became the most common metric for evaluating bleaching. Early investigations looked at some alternative thermal stress metrics, such as sea-surface temperature (SST) anomalies and Degree-heating days but found them to be highly correlated (Winter et al 1998, Glynn et al 2001). Few, however applied variable selection procedures to reduce autocorrelations and redundancy problems or compete the variables in terms of their fits to data. At the same time, the metrics of taxa and depth were evaluated and found to be significant but again alternatives were not tested for autocorrelation or eliminated by variable competition or selection processes (Hoegh-Guldberg and Salvat 1995). Winter et al (1998) added to the temperature variables in terms of three measures above
Figure 1. Timeline of numbers of coral-environmental exposure field study publications and studied variables grouped into six topics.
threshold (days, weeks, and months) and daily mean, maximum, minimum, and daily temperature ranges and found that they all were good predictors of bleaching. A $+2$ °C threshold was suggested as competent for explaining some observed variation in their Puerto Rican reefs.

Some early evaluations of the HS’s and DHW’s ability to detect bleaching and replicate this proposed MMM $+1$ °C, or the more integrative DHW metric, did not support the original proposal. For example, the two earliest studies concluded that bleaching was quite variable between locations and not induced at four DHW and might be as much as $>26$ DHW (Gleeson and Strong 1995, Podesta and Glynn 1997, Wellington et al. 2001). Nevertheless, the $\sim+2$ °C MMM threshold suggested in Puerto Rico (Winters et al. 1998) and $+1$ °C MMM in Moorea (Hoegh-Guldberg and Salvat 1995) were frequently cited to support the $+1$ °C HS usage and eventual convention.

Thereafter, most subsequent evaluations used the threshold concept and models (TM) with either the $>1$ °C threshold or the summation of cumulative temperatures above thresholds or the DHW and DHM metrics. For example, the NOAA working group settled on this $>1$ °C threshold but began to use a summation or four DHW for the presence of bleaching and eight DHW for ‘widespread bleaching and some coral mortality’ for observations up to 2002 (Liu et al. 2003). Eventually, these coral bleaching and mortality thresholds were commonly used to predict the future state of reefs (Liu et al. 2003, 2006, Donner et al. 2005). Yet, this decision may have been promoted by some early and highly cited bleaching papers (Hoegh-Guldberg 1999, Goreau et al. 2000) (figure 2). Many subsequent papers after this early science period assumed bleaching when DHW exceeded four DHW and mortality for $>8$ DHW (Heron et al. 2016, Van Hooidonk et al. 2016). It should be appreciated that not all early studies evaluated these thresholds but rather compared linear regressions fits of bleaching frequencies with a variety of temperature variables (Berkelmanns 2002, Berkelmanns et al. 2004).

Despite the high variability in estimated thresholds and weak coherence between studies, the HS concept and metric was developed and distributed as a satellite product of NOAA. For many

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**Figure 2.** Cumulative frequency of (a) published papers and (b) citations of environmental exposures—coral response field studies as total papers and as classified per the threshold model and variability models criteria.
reef investigators it was the dominant concept and associated metric to evaluate the impacts of climate change. Specifically, this followed from a future-projection climate model (Hoegh-Guldberg 1999) where a ‘tight association between warmer-than-normal conditions (at least +1 °C higher than summer maximum) and the incidence of coral bleaching’ was the basis for modeling future states. These models predicted that there would be annual bleaching events in the Caribbean, Asia, and the Great Barrier Reef by 2020. Using a similar set of threshold and reoccurrence assumptions, the demise of reef corals by thermal stress was predicted to occur in the southern Indian Ocean between 2010 and 2025 (Sheppard 2003). In contrast, most big data compilation studies indicate that Indian Ocean coral cover has been stable at 25%–35% with some declines and recovery after regional bleaching events in 1998, 2014, and 2016/17 (Donovan et al 2021, Obura et al 2021). This stability in coral cover does, however, hide the declines of thermally sensitive taxa, such as Acropora and Montipora, and geographic differences in disturbance and recovery times (McClanahan et al 2014, McClanahan et al 2020b). Despite the poor fits of excess heat TMs to field data, the threshold concept with some modifications is pervasive in the coral climate change literature. Responses to thermal thresholds were modified by taxa, depth, and locations, local acclimation, and genetic change to create a more nuanced conceptual model in 2003 (Hughes et al 2003). Cumulative excess heat and the assumption of linear or step-wise declines in coral cover over time are the standard ways to predict the future of coral reefs. These models largely predict major losses or ‘collapse’ of reef ecosystems in the next 30 years (Perry et al 2020, Cornwall et al 2021, Obura et al 2021, Dixon et al 2022).

1.3. The variability model (VM) alternative

Up to the mid 2000s, the concept of the SST thresholds modified by light, time, local sites, and taxa was the dominant model for describing coral bleaching (Dunne and Brown 2001). Apart from the study in Moorea, it was not until 2000 and onward when publishing field biologists started to classify bleaching regularly and systematically into categories of severity by taxa, and to consider other potential environmental variable on a larger intersite scale (Marshall and Baird 2000, McClanahan et al 2001, Berkelman 2002). For example, these types of VMs were initiated as part of the effort to understand bleaching between geographically associated sites (Spencer et al 2008, Berkelmanns 2002, Celliers and Schleyer 2002). There was a common consensus that differences between sites were driven by various habitat metrics, but this localized information created challenges for making large- and gross-scale predictions. Nevertheless, local exposure and modifying factors would be conceptually incorporated into some early large-scale models (Maina et al 2008).

Thereafter, evaluations of thermal metrics often included more modifying variables such as sites, exposures, depth, reef type, and an El Nino Southern Oscillation (ENSO) index (Spencer et al 2000). Spencer’s paper represented the first paper to evaluate a significant number of modifying variables without a central threshold concept and therefore the first study I classified as a VM paper. This early and subsequent menagerie of variables often indicated the investigator’s appreciation of the complexity of coral responses (table 1). Yet, they would lack a unified theory that could easily be incorporated into global climate change processes and models. Eventually, however, VM became equal to and more studied in recent times, although less cited cumulatively due to the high early citation of TM for making predictions (figure 2).

1.4. The first-generation global models

Once NOAA Coral Watch Alert settled on the >4 and >8 DHW thresholds, the future states of coral reefs could be modeled based on the rates of temperature rise provided by global-scale Intergovernmental Panel on Climate Change (IPCC) models (Donner et al 2005, Liu et al 2006). For example, combining the US government thermal thresholds products with IPCC SST rates of rise in the tropics suggested bleaching (i.e. >4 DHW) would occur every two years for over half the reefs by 2080 (Donner et al 2005, Donner 2009). At regional levels, the predictions were that many reefs in the Caribbean, Indian Ocean, Eastern and Central Pacific, and Southeast Asia would bleach and die every five years by 2021 or the time interval at which coral populations replacement by reproduction was expected (Sheppard 2003).

Thereafter, return time to these thermal threshold using mean SST rises and DHW became a common way to make global-scale predictions, often the time between two to eight DHW thresholds. While the amplitude and duration of excess heat are also likely options, the time interval between thresholds was the preferred metric. This choice has problems for accurate predictions, however, as subsequent global scale compilations have shown that duration and spatial extent, and not return time, are changing significantly over the current period of satellite measurements (Skirving et al 2019). While these three metrics may be correlated, it is more likely that return time frequencies are limited by the physical inertia of ocean circulation systems and only modified by warming relative to spatial extent and duration. Moreover, these TM predictions are quite sensitive to the SST variance because DHW thresholds are reached more frequently in regions with low SST summer and inter-annual variation. The first exploration of this historical threshold showed both advances
| Associations | Variable | Description/comment | Current scientific status | Percent of studies | References |
|--------------|----------|----------------------|---------------------------|--------------------|------------|
| Geography    | Site-reef| Specific sites with names | Between site variation always evident and driven by many local factors. | 35 | [3, 6, 7, 9, 45, 47, 48, 51, 55, 56, 57, 59, 61, 62, 63, 64, 71, 72, 75, 79, 80, 83, 88, 91, 92, 96, 98, 101, 102, 103, 104, 105, 106, 107, 108, 109, 110, 111, 112] |
| Latitude     | Global geography | Highest bleaching at 15–20° but coral responses depend on coral taxa composition, genetic diversity within taxa, and historical exposure. Thermal impacts influenced by latitude-dependent cyclones and rare thermal anomalies. | 15 | [13, 20, 40, 58, 64, 65, 74, 75, 77, 78, 90, 94, 98, 103, 104, 107, 109] |
| Longitude    | Global geography | Alters exposures to corals by frequency of exposure to inter-annual oceanographic oscillations. At small scale influenced by island exposure and modification of ocean currents, temperature distributions, and thermal stress. | 7 | [20, 40, 77, 90, 94, 103, 107, 109] |
| Ecoregion    | Spalding et al 2007 | Found to be the strongest predictor of resistance when combined with SST skewness. Skewness and TSA anomalies found to vary considerably by ecoregion. | 8 | [13, 40, 62, 64, 78, 94, 98, 106, 109] |
| Faunal Ocean Province Nation | Spalding et al 2007 | Responses similar to patterns for ecoregion. | 2 | [36, 94] |
| Habitat      | Depth | Meters below surface | Generally, bleaching decreases with depth but often reversed and interacts strongly with taxa, location, currents, and thermal stress. | 23 | [3, 6, 7, 17, 24, 39, 62, 64, 65, 71, 72, 74, 77, 78, 79, 85, 88, 90, 91, 92, 94, 101, 106, 107, 108, 109] |
| Reef habitats | Commonly used names for habitats and zones | Not a strong influence overall but interacts with currents, tides, exposure, and taxa. Coral cover most negatively affected by thermal anomalies on reef flats. | 12 | [19, 51, 53, 74, 77, 79, 84, 90, 92, 94, 103, 110, 112] |
| Exposure     | Windward versus leeward sides of reefs or islands | Windward and wave-exposed competitive corals most affected by thermal anomalies. | 10 | [6, 51, 53, 74, 77, 84, 91, 98, 103, 106, 109] |
| Reef type—atoll, barrier, fringing | | Island reefs more resilient than fringing reefs to thermal disturbances. | 4 | [6, 98, 109, 110] |
| Distance to shore | Distance from coral to land | Inverse relationship between distance to shore and bleaching. | 4 | [62, 72, 76, 85] |

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Table 1. (Continued.)

| Associations | Variable | Description/ comment | Current scientific status | Percent of studies | References |
|--------------|----------|----------------------|---------------------------|--------------------|------------|
| Isolation    | Isolation or connectivity to other reefs | Larval connectivity increased resilience. With tidal interactions affected abundance of weedy coral taxa. | 2 | [64, 100] |
| Excess thermal stress | DHW, DHM, DHD | Cumulative excess heat prior to bleaching in same year | Highly variable coral bleaching and mortality responses with many interacting factors including taxa, depth, region, waves, exposure, water quality, high spells, bimodality, time since previous stress, and others. Often has high covariance with other thermal stress metrics and low predictive accuracy. | 67 | [2, 4, 8, 11, 14, 16, 19, 21, 22, 23, 24, 25, 26, 27, 28, 30, 31, 32, 33, 37, 38, 40, 41, 42, 43, 44, 45, 46, 48, 51, 52, 53, 55, 56, 59, 61, 62, 63, 65, 66, 67, 71, 72, 73, 74, 75, 76, 77, 78, 80, 82, 83, 84, 85, 86, 88, 89, 90, 91, 92, 93, 94, 94, 96, 97, 101, 102, 103, 104, 105, 106, 107, 108, 109, 110, 111] |
| HotSpots or SST Anomalies (TSA) at various time and spatial scales | SST anomalies at various time and spatial scales | Similar and highly correlated to above degree-heating metrics. Yet, has higher predictive skill by removing the +1 above MMM threshold, which is not universal but regional. | 37 | [1, 4, 8, 9, 10, 11, 14, 15, 16, 17, 18, 19, 20, 22, 24, 32, 41, 54, 59, 64, 66, 68, 69, 70, 78, 79, 82, 86, 87, 90, 91, 94, 97, 99, 100, 103, 104, 106, 107, 108, 109] |
| Light or clouds, PAR | Photosynthetic active radiation | Interacts with temperature, UV, wind, currents, and ENSO. | 20 | [10, 12, 28, 31, 34, 38, 48, 50, 57, 58, 59, 60, 62, 64, 66, 69, 75, 82, 95, 104, 109, 112] |
| MMM-Maximum of monthly climatology at various time and spatial scales | Maximum of monthly climatology at various time and spatial scales | Historical often better than seasonal maximums at predicting bleaching. | 12 | [19, 46, 49, 54, 55, 59, 65, 67, 69, 70, 97, 104, 108] |
| Cumulative or inter-annual DHW/ anomalies | Cumulative over a longer time than a season | Coral cover or bleaching responses not clearly linearly related to cumulative heat stress. Some indication that there is a unimodal response between degree-heating metrics and coral cover. These is increased acclimation to these metrics over time. | 11 | [45, 48, 49, 65, 66, 67, 68, 74, 78, 95, 103, 104] |
| SST Maximum | Maximum on some scale of time | Can predict bleaching but also covaries with many other thermal stress variables. | 13 | [5, 19, 27, 28, 36, 46, 59, 61, 75, 78, 99, 104, 106, 108, 109] |
| ENSO/IOD indices | Ocean states or oscillations | Can significantly improve coral bleaching and may also depend on cloud cover. Many reports of bleaching during positive ENSO but not in all regions. | 10 | [6, 9, 30, 35, 59, 60, 67, 85, 97, 102, 108] |

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Table 1. (Continued.)

| Associations          | Variable                  | Description/ comment                     | Current scientific status                                                                 | Percent of studies | References                        |
|-----------------------|---------------------------|------------------------------------------|-------------------------------------------------------------------------------------------|--------------------|-----------------------------------|
| SST Mean              | Baseline temperature      | An important variable to know            |                                                                                           | 8                  | [5, 28, 59, 64, 67, 78, 91, 98, 104] |
| MMM variability       | Accounts for variability of maximum water temperature, i.e. SD | Improves bleaching predictions and variability between regions.                           |                                                                                           | 5                  | [29, 46, 65, 67, 78, 97]           |
| Acute—pre peak anomalies | Transient rise in temperatures before seasonal peak | Can increase acclimation to thermal stress. Bimodality and skewness are related measures, that appear to increase bleaching and thermal stress. Therefore, the various metrics may be difficult to distinguish. |                                                                                           | 6                  | [54, 59, 77, 79, 90, 94, 109]       |
| Upper percentile of temperature measures | Some evaluation of the percentage of the temperatures, i.e. 95% | Better accounts for SST variation between regions but presently not well evaluated.       |                                                                                           | 4                  | [19, 81, 86, 87, 103]              |
| Multivariate metric combining thermal stress | Combination of thermal variables using multivariate synthetic methods | These generally improve bleaching predictions and, in some but not all cases, coral cover and changes over time. |                                                                                           | 5                  | [28, 49, 60, 64, 81, 98]           |
| Light attenuation, turbidity | Light measured at seafloor | Appears to reduce coral recovery rates and therefore coral cover but relationships with bleaching not well understood. |                                                                                           | 5                  | [66, 91, 95, 104, 106, 109]        |
| Light, UV            | Ultraviolet, 290–400 nm | A potentially important metric for bleaching but seldom evaluated.                      |                                                                                           | 3                  | [104]                             |
| Modifying thermal stress | SST-SD/COV/Oscillations | SST variation associated with reduced bleaching or an increase in the threshold for bleaching. Variance metrics, such as SD, often covary and interact with many other variables that could be more influential resulting in variable predictive ability. Including variance metrics improves multi-variate models. |                                                                 | 15                 | [20, 23, 28, 34, 40, 44, 45, 64, 67, 77, 78, 90, 94, 98, 103, 104, 107] |
| Wind speed/-Doldrum index | Slow winds and currents associated with rapid rise in temperatures and bleaching. High winds associated with cyclones reduce bleaching. Low winds can reduce upwelling and nutrient delivery that have been suggested to increase bleaching. |                                                                                           | 13               | [12, 13, 26, 28, 50, 57, 58, 60, 62, 64, 74, 82, 86, 93, 104] |
| Chlorophyll-a         | Measure of phytoplankton density | Often associated with differential bleaching and changes in coral but difficult to separate from other effects that include currents, nutrients, light penetration, zooplankton, and others. |                                                                                           | 9                  | [28, 33, 39, 64, 66, 83, 91, 103, 104, 109] |

(Continued.)
| Associations        | Variable                  | Description/comment                                                                 | Current scientific status                                                                 | Percent of studies | References |
|---------------------|---------------------------|--------------------------------------------------------------------------------------|------------------------------------------------------------------------------------------|--------------------|------------|
| Kurtosis            | Can be at different time scales | Not a strong predictor of bleaching when evaluating SST prior to bleaching. Long-term time series SST data are a good predictor of coral cover and stress-tolerant taxa. Modest negative kurtosis associated with high cover and numbers of coral taxa. A good measure of chronic but not acute stress. Association with bimodality and potential impacts on coral needs investigation. | 8                   | [23, 40, 64, 65, 77, 90, 94, 98, 103] |
| Skewness            | Can be calculated at different time scales | Historical SST data negatively associated with coral cover and loss of cover. A good measure of historical acute stress. May be useful for predicting future states of coral. | 7                   | [23, 40, 64, 77, 90, 94, 98, 103] |
| Turbidity or suspended solids | Proxy data available from satellites | Reduces bleaching but also associated with lower coral cover. Mechanism of low coral cover may be lower recovery rates after disturbances. | 7                   | [53, 64, 76, 85, 104, 106, 109, 112] |
| Cyclones/hurricanes | Frequency or intensity     | Reduce localized bleaching but often strongly associated with low coral cover.      | 6                   | [26, 27, 64, 74, 76, 91, 106] |
| Ocean currents or water flow | Satellite, modelled or in situ measurements | Bleaching increases when currents slow and associated with doldrum conditions. Latitudinal and longitudinal currents may differ in their influence on bleaching and nutrients delivery. | 6                   | [20, 28, 58, 59, 82, 103, 104] |
| Wave energy         | Proxy data available from satellites | Variable relationships that may depend on wave interaction with taxa.             | 6                   | [74, 79, 83, 84, 91, 103, 106] |
| Daily temperature range | Maximum-minimum per day | Bleaching declines with increased daily variance prior to thermal anomalies and may also predict ability of corals to adapt to future warming. Evaluating relationships to historical SST population data and distributions, such as skewness, kurtosis, and anomalies, needed. | 5                   | [5, 43, 48, 57, 65, 95] |
| Rate of rise-inter-annual | Calculated prior to bleaching or coral cover change | Associated with higher bleaching globally but not strong in the WIO region. Also not associated with loss of coral cover after 1998. Likely due to higher bleaching in mid-latitudes where bleaching is more frequently reported, and SSTs are rising fastest. | 5                   | [28, 45, 49, 57, 78, 104] |
| Bimodality          | Various metrics can be evaluated for pre-bleaching and historical data | Both short and long-term metrics highly associated with bleaching and coral mortality. Relationship to kurtosis not well understood in terms of chronic versus acute stress metrics. | 4                   | [40, 77, 90, 94, 104] |

(Continued.)
| Associations | Variable | Description/comment | Current scientific status | Percent of studies | References |
|--------------|----------|---------------------|--------------------------|--------------------|------------|
| TSA          | variation or skewness or kurtosis | Various metrics of variation in degree-heating | A potentially good metric of frequency of thermal stress associated with bleaching. Less covariance with standard thermal stress metrics. | 4 | [64, 78, 103, 106, 107] |
| DHW          | variation as SD, skewness, or kurtosis | Various metrics of variation in degree-heating | A potentially good metric of frequency of thermal stress associated with bleaching. Less covariance with standard thermal stress metrics. | 4 | [77, 78, 103] |
| High spell duration |            | A few heat wave metrics | A strong variable in predicting bleaching that maybe an improvement on degree-heating metrics. | 4 | [77, 81, 90, 94] |
| Low spell duration |            | Duration of cool water | Weak single variable effect but interacts with high spell duration and longitude. | 3 | [77, 90, 94] |
| Nitrogen     | Water or tissue concentrations | | May interact with heat to increase bleaching but also associated with greater resistance to heat stress on large scale of central Pacific. | 3 | [92, 95, 109] |
| Salinity     | Seldom measured | | May add to thermal stress to increase bleaching. | 3 | [39, 108, 112] |
| Internal tides | Tidal induced cooling | | Interacts with taxa to cool water and reduce bleaching. | 2 | [51, 53] |
| Ocean current variation or skewness | Measure of rare changes in ocean | | Associated with coral mortality and loss of species. May also indicate variation in delivery of cold water and nutrients. | 2 | [82, 103] |
| Ocean height | Measure of ocean current impact on land | | Maybe a useful measure of the retention of water and resistance or impact of thermal anomalies over historical time. Needs more study. | 1 | [98] |
| Rate of rise-intra-annual | Spring to summer or 90 d prior to bleaching | | Associated with higher bleaching but not a strong factor | 1 | [65] |
| Coral and benthic community susceptibility or tolerance | Community metric that accounts for historical susceptibility of the taxa | Good predictor of bleaching and mortality in early studies but was reversed in 2016. Declines in susceptible taxa with SST variance metrics. Site susceptibility may become more variable over time with patch losses of susceptible taxa. | 9 | [24, 25, 28, 64, 74, 77, 90, 107, 111, 112] |
| Community multivariate metrics | Coral taxa composition | Similar to above | 7 | [24, 64, 77, 90, 94, 96, 105, 107] |
| Algal abundance and composition | Macroalgae main metric | Has been associated with higher and lower bleaching but may be site and environmental condition dependent. Negative correlations with coral cover at high macroalgal cover. | 4 | [80, 91, 103, 106] |
| Coral cover | Total or types of cover | Bleaching and mortality increase with coral cover but decline with cover of thermally resistant taxa | 4 | [20, 23, 79, 94] |

(Continued.)
and delays in the timing of repeated thermal exposures that depended on the region’s background SST variation (Donner 2009). Moreover, an inter-annual variation method does appreciably delay predictions of repeated threshold exposures by 5–12 years globally. This effect is strong in regions with low intra-annual variability, such as the western, or global coral biodiversity center, and central Pacific. On average, the +1 °C MMM threshold is equivalent to 2.45 standard deviations (SD) above the tropical climatological maximum but varies with regions (Donner 2009). Thus, +1 °C MMM often correlates with SST variation outside of the common experience of most corals, which should provide some predictive ability but less so if coral sensitivities to this exposure vary between locations.

A subsequent TM study suggested advances or delays in the timing of repeated bleaching that depended on the type of GCM used (Teneva et al 2012). All regions evaluated with high inter-annual variability were predicted to experience delays in repeated bleaching, which is likely to be a consequence of the underlying effect of variability on the threshold calculations relative to the rate of SST rise. Differences in the model’s projections were due to the inter-annual variation threshold used (i.e. 2.0 or 2.45 SDs), which was influenced by the window of the historical SST benchmark and spatial scale of the utilized temperature data. Thus, historical variability emerged here as an important proxy for future threshold-based bleaching and was highly influenced by the pool of data used to determine the proposed thresholds. For example, consider the potential influence of the number of ENSO events during the period of satellite measurements compared to those in the future. Also, whether the current and future SST data are measured and compiled at hourly, daily, weekly, or monthly intervals. Subsequent studies have shown the importance of daily SST ranges towards coral acclimation, but this high frequency is not measured by satellites (Safaie et al 2016). This temporal resolution is not obtainable from the satellite and shipboard sources. Therefore, high resolution SST monitoring is more challenging to obtain compared to some other important SST shape metrics like skewness and kurtosis that can reflect well acute and chronic stresses (McClanahan 2020, McClanahan and Azali 2021).

Global maps of two proposed thresholds and projected changes in temperature methods, based on either the summer or longer historical variation in MMM, found that neither had high predictive power (Donner 2011). Historical was, however, an improvement on summer-based predictions. Donner argued that correspondence between average intra-annual SST-SD and MMM + 1 °C can explain some of the correspondence between bleaching responses and various measures of temperature variation. Much of the tropics has an intra-annual SST-SD near 1 °C. Some exceptions are lower values (~0.5 SD) in the

Table 1. (Continued.)

| Associations | Variable                      | Description/ comment                                      | Current scientific status                                      | Percent of studies | References |
|--------------|-------------------------------|----------------------------------------------------------|---------------------------------------------------------------|--------------------|------------|
|              | Number of taxa               | Local site numbers and ecoregional compilations          | Bleaching lower in ecoregions with higher numbers of taxa. Improved predictions of bleaching in one region (Mariana Islands) using site-level data. | 4                  | [52, 78, 94, 107] |
| Human        | Watershed/crops/water quality| Various interacting metrics                               | Negative to neutral effect on bleaching and coral cover depending on nutrient/light interactions but some positive effects on cover of weedy and generalist taxa | 7                  | [33, 39, 64, 74, 76, 91, 92, 109] |
| influence    | Fisheries closures           | No-take                                                  | Variable bleaching and cover effects but coral cover generally higher in no-take areas where there is heavy fishing in surroundings | 6                  | [56, 74, 76, 77, 90, 91, 105] |
|              | Fisheries restrictions       | Mixed restrictions but often gear limits                 | Weak effect but interacts with taxa and other variables. Coral cover generally higher with more restrictions | 4                  | [74, 76, 77, 90, 105] |
|              | Human presence as distance   | Various metrics                                          | Reduced coral extension and cover near people                 | 4                  | [38, 44, 62, 74, 105] |
| or modification| Grazer abundance            | Mixed grazers                                            | Grazers associated with low coral cover                        | 2                  | [91, 106] |
western Pacific or Coral Triangle area and higher values (~2.0 SD) in East Africa and the northern and southern Caribbean. Donner concluded that if there was an appearance of a constant threshold for bleaching, it emerged because of the broad geographic similarity in the interannual variability in maximum SST. For example, two-thirds of the world’s reefs have inter-annual SST-SD between 1.73 and 2.94. This potentially makes for reasonable predictive skill for bleaching in most but not all tropical regions but only where coral sensitivities are similar.

1.5. Tests of skill and fit

Presence/absence data on coral bleaching was the main global source of data and being compiled at the ReefBase website to record bleaching observations. This database created the opportunity to evaluate the skill of the various predictions. Low predictive ability was reported in the first test evaluating 725 reported bleaching events over the first 25 years of the satellite record (1982–2006) using different MMM thresholds (Boylan and Kleypas 2008). Specifically, the standard MMM + 1 °C correctly predicted only 13.7% of the bleaching events. Lowering the threshold to MMM + 0.5 °C increased success slightly to 16.3%. Their second method set MMM to 2SD of the SST for the climatological maximum and slightly increased the predictive skill to 20.4%. Authors concluded that bleaching events using the >4 DHW threshold and in low intra-annual variability regions, such as the central Pacific, will be underestimated.

Another study using the four DHW bleaching threshold and bleaching records from 1990 to 2007 found a poor skill score with nearly equal false and true predictions for specific locations even when optimized (van Hooidonk and Huber 2009). Optimization was achieved globally at 6.1 DHW for presence/absence bleaching observations but thresholds could be quite variable between locations. For example, three locations in the Caribbean were optimized between 2.9 and 9.7 DHW. In a subsequent paper evaluating the global annual DHW time-to-threshold, a warmer excess heat threshold of DHW > 6 was used (Van Hooidonk et al 2013). This helped to identify reef locations that would reach this annual threshold earlier or later and to identify temporary climate sanctuaries. Given that optimization produced different thresholds for specific versus global optimization values, it seems future predictions based on generic or unoptimized thresholds will be inaccurate given these past failures. Local predictions are therefore likely to need local optimization to evaluate regional differences and better align with reported regional differences in coral sensitivity (McClanahan et al 2020a).

A similar TM study normalized the bleaching predictions using four threshold calculation methods to account for sparse observations (Logan et al 2012). The Bleaching Alert threshold was varied to get a more uniform frequency of 10% or once every 10 years, which resulted in a 31% predictive power and 8.3% false positive rate. The inter-annual variability method at a large scale had good prediction rate of 77% but also a false positive rate of 42%, or a more modest skill of 35%. Overpredicting bleaching was reported in most other studies, which might be explained by coral acclimation after establishing the original benchmark threshold (Logan et al 2014). However, given the qualitative and often anecdotal nature of the original MMM + 1 °C, there are other explanations. Van Hooidonk et al (2013) abandoned the MMM + 1 °C in favor of a simple MMM threshold and used the >6 DHW threshold for bleaching. Logan’s et al (2014) study also showed that using a large area should improve predictions as the probability of bleaching is likely to be captured as the area increases. Thus, the frequency may appear to be increasing as the sampled area increases and bleaching detected somewhere in the large area. Yet, the increasing spatial extent or duration over time has likely contributed to this false perception of increased frequency (Skirving et al 2019).

Metrics that measured the magnitude or amplitude but not the duration of the event also reduced the skill (Logan et al 2012). Duration of excess heat has increasingly been recognized as an important aspect of bleaching that is not currently distinguished in DHW because short acute and chronic heat can produce the same DHW value (Fordyce et al 2019, Genevier et al 2019, McClanahan et al 2019). Differentiating frequency, amplitude, and duration variables when evaluating bleaching responses is challenging (Oliver et al 2009). Nevertheless, more severe bleaching events were associated with ENSO events that had broad coverage, but their frequencies were not necessarily increasing over the 1973–2006 data compilation period. After 1998, mild bleaching was frequency reported but possibly attributable to more people stimulated to report their observations due to widespread publicity after the 1998 global bleaching event. Donner et al (2017) published a bleaching database updated until 2010 that increased observations to 7429 records. An additional update until 2016 contained an additional 1098 records but did not distinguish the elements of frequency, severity, extent, and uniformity (Oliver et al 2018). At the time of this writing, a database with 14 405 site observations collected between 1980 and 2020 was published (van Woensik and Kratochwill 2022). While compiling bleaching records in static national boundaries can reduce some of this unexplained variability (Hughes et al 2018), the sizes of national locations are large and still subject to reporting biases when duration and spatial extent are not readily distinguished from frequency.

The most recent evaluation of the national-level bleaching detection skill using presence/absence of mild and severe bleaching compilation of 100
countries over the 1982–2016 period concluded that the standard DHW is a poor predictor of bleaching (DeCarlo 2020). This method suggests CRW data may be the least accurate of commonly used SST databases. Improvements in accuracy occurred if the MMM is used rather than MMM + 1 °C and if the time window was narrowed from 12 to 9 weeks. As found in the Van Hooidonk and Huber (2009) study, the optimal global DHW was 6.3 but, when corrected to improve accuracy, it was reduced to 5.4 °C-weeks. There were, however, large differences between regions, with optimal skills ranging from a low of ~20% accuracy in the western Atlantic to a high of ~40% in the Indian Ocean. Additionally, thresholds may be changing over time, as the DHW > 4 threshold appeared to produce an increasing number of false alarms, particularly after 2000 (DeCarlo 2020). While a compilation of bleaching events in the Caribbean across the 2005 event, is often cited as support for the >4 and 8 DHW thresholds (Eakin et al. 2010), the data show high variability with ~30% of the corals bleaching at DHW = 0 and ~50% at DHW = 8. Coral mortality was also very patchy and not above 20% until ~12 maximum DHWs. Thus, considering all studies in total there is no discrete or generic global threshold for coral bleaching or mortality but rather high spatial and changing variability. For example, inclusion of an ENSO index in some studies improved predictions, possibly because light and cloudiness conditions change regionally with ENSO states, as found for the Great Barrier Reef in 2016 and globally (McGowan and Theobald 2017, Gonzalez-Espinosa and Donner 2021).

1.6. Multivariate models
A uniquely early multivariate study of bleaching combined 11 variables into 2 models of multi-variate exposure using a fuzzy-logic optimization method (Maina et al. 2008). Fits to four categories of Western Indian Ocean (WIO) bleaching reports showed all variables were significantly associated with bleaching, supporting the multivariate nature and complexity of bleaching. Bleaching intensity increased with the SST variables of maximum SST and DHW but also light as both photosynthetically active radiation (PAR) and ultraviolet (UV) as well as high zonal but low meridional surface currents. Bleaching declined most strongly with high SST variation with some influences of low wind speed and low slopes of interannual temperature rise. Importantly, while bleaching increased with the DHWs, the rate of background SST rise had the opposite influence. Increasing rate of rise in thermal exposure and subsequent bleaching and mortality is, however, a core assumption of standard TMs. The two multivariate model options fit modestly to some of the change in coral cover that were recorded in 16 Indian Ocean regions across the 1998 ENSO period. A similar level of success was found in predicting coral cover for a study using 20 variables, or the highest number among the 112 studies examined below (Zinke et al. 2018).

A subsequently larger study of the whole Indian Ocean post 1998 found that the above Global Stress Model performed quite well for immediate changes in coral cover ($r^2 = 0.50$) and coral community structure ($r^2 = 0.31$) based on ~2000 site × time replicates (McClanahan et al. 2015). The predictions weakened over time as, presumably, the coral communities recovered after 1998. In contrast, the more broadly used cumulative excess heat and time to threshold were quite weak predictors for these metrics of coral status ($r^2 < 0.05$). Many variables that modify bleaching and coral cover responses to thermal stress have not been included in global-scale predictions (table 1). Yet, there are many potentially useful exposure and modifying variables becoming increasingly available for analyses in global marine environmental databases (Vercammen et al. 2019, McClanahan and Azali 2021).

1.7. Coral sensitivity
Some models have considered the rates at which corals adapt to temperature increases to avoid future bleaching. For example, based on projected temperature change over the 21st century, an adaptive range of 0.88 °C–3.02 °C per century would be needed to eliminate the likelihood of the five year recurrent mild bleaching predictions (Teneva et al. 2012). Fifty percent of reefs will lie in the more modest range of 1.35 °C–1.82 °C per century. Epi-genetic driven acclimation rates of A. hyacinthus are on this scale and can occur over short periods of time (Palumbi et al. 2014). Moreover, some observation from transplantation studies shows that A. millepora in the Great Barrier Reef increased their temperature tolerance by 1.0 °C–1.5 °C due to symbiont shuffling (Berkelmans and van Oppen 2006). Symbiont-shuffling is, however, temporary, and likely to last no more than five years (Baker et al. 2013). Coral communities may also shift to less sensitive taxa after thermal disturbances, but this can have consequences for the coral cover and calcification processes (McClanahan et al. 2007, 2020b). In some systems, changes in taxa may also be quite temporary as sensitive taxa recover and quickly dominant (Gilmour et al. 2013). In other reef systems, less sensitive taxa persist with consequences for life history representation and the losses of cover and calcification (Darling et al. 2013, 2019, Edmunds et al. 2014, McClanahan 2020). A global synthesis of bleaching responses found an increase in the reported bleaching threshold for coral cover of 0.4 °C per decade (Sully et al. 2019). This acclimation rate may, however, be an early exposure response and not linearly sustainable over longer periods of time (McClanahan 2017).

Genetic change is likely to be the most important mechanism to reduce sensitivity in the long term and to maintain coral reef community composition.
and symbiosis. Early models of sensitivity based on symbiosis produced some realistic responses in line with the adaptive bleaching hypothesis (Ware et al 1996). These include an initial high sensitivity to small variations in mean warm temperatures, less sensitivity in subsequent warm anomalies, more tolerance of corals subjected to more variable conditions, patchy bleaching, and changing threshold-like responses. These responses required a generic coral model with multiple, vague, and low fidelity symbionts that have unique interactions and differential competitive advantages in different environments. Subsequent studies have found these attributes to vary among species but have also found the importance of the host coral taxa and coevolution for long-term changes in sensitivity to exposure (Bellantuono et al 2012a, Howells et al 2016, Laljennuse et al 2018). Thermal sensitivity is expected to vary with various coral morphologies and physiologies, life histories, and lead to considerable diversity of responses and adaptation rates (Wooldridge 2014, McClanahan et al 2020b). While there has been a focus on the symbiont-host interaction, there are multiple other life histories characteristics of corals that will be important influences on sensitivity and adaptation rates (Darling et al 2012, 2019, Van Woesik et al 2012, Torda et al 2017).

Thermal tolerance to early stressful exposure within a single species is a common example of plasticity in sensitivity. For instance, the dominant coral in windward reefs of Mauritius, A. muricata, have very different responses to aperiodic thermal stress dependent on whether larvae settled close to or far from shore. Offshore settlers showed lower thermal resistance than nearshore settlers in responses to inter-annual thermal anomalies (Louis et al 2016). Similar observations have been made on Stylophora pistillata where greater tolerance to episodic thermal stress is seen on leeward high temperature variability sites than exposed low-temperature variability seaward sides of reefs (Voolstra et al 2020). While a common observation, the coral communities in these nearshore or more variable environments are likely to be species depauperate, as the genetic/physiological acclimation responses are not common to all corals (McClanahan and Maina 2003). For example, Klepac and Barshis (2020) using transplantation studies found that, when exposed to high temperature variability, massive corals (Porites lobata) in the American Samoa failed to acclimate while branching S. pistillata did. This may explain the reversal in bleaching responses of massive Porites and branching Acropora reported on a very large geographic scale between early (pre-2010) and more recent, or 2016, thermal stresses (McClanahan et al 2020b). Many shallow nearshore locations have reported seawater temperatures change more than +1 °C daily without inducing, but rather protecting them from bleaching (Safaie et al 2016). Subsequent large replicate global studies indicate that removing this +1 °C threshold significantly improved predictions of bleaching (DeCarlo 2020). These findings further support the concept that bleaching responses are gradual and taxa-specific rather than a universally abrupt threshold change in coral symbionts and color. A future area of research is to investigate the variation in alleles and epigenetics conferring thermal tolerance among corals with different response patterns.

Nearly all models suggest that corals can adapt to the low carbon emission scenarios of <2 °C per 100 years (Donner et al 2005, Basket et al 2009, Teneva et al 2012, Logan et al 2014). Yet, models often use a hypothetical generic coral or the behaviors of a single dominant taxon, such as Acropora. Further, recent revisions of the Coupled Model Intercomparison Project (CIMP) suggest that warming is occurring faster and sooner than past estimates (Van Hooidonk et al 2020). Adaptation rates may differ based on the number of thermal-tolerance alleles, with increasing numbers of alleles slowing rates of adaptation (Bay et al 2017). Other factors include initial population sizes and the immigration rates of thermal tolerance genotypes. The number of thermal-tolerance alleles involved in studied corals seems to fall on the low end of 40–70 alleles, which suggests there are not too many to constrain adaptation (Bellantuono et al 2012b, Barshis et al 2013, Yetsko et al 2020). In contrast, coral’s high reliance on broadcast spawning and large and dispersed populations are more likely to limit rates of genetic change (Torda et al 2017). Thus, movements of corals from warm to cooler latitudes may be one of the primary ways that corals adapt (Nakabayashi et al 2019).

2. Methods/design section

Examination of the literature on specific exposure variables and coral responses presented here is focused on field-based studies of environmental interactions undertaken between 1984 and March 2020. Search terms used to identify papers were the combinations of coral AND bleaching, climate change, exposure, and stress. These word combinations were searched in Google Scholar (US) between January and March 2020. Identified papers were screened for the criteria of field studies with site replicates and local or satellite-based environmental measurement used for testing associations with either the bleaching or coral cover responses. Compiled papers were then examined for citations of previous research to undertake snowball searching of the papers that undertook similar investigations. This search and snowball process of inclusion and elimination was repeated multiple times over a three month period until no new titles were uncovered. Then, based on the above criteria, 112 papers were selected for extracting methods and results. These papers were then evaluated in term of extracting the stated
hypotheses, study period, geographic focus, topics, environmental variables, and the statistical procedures, methods to evaluate variables, test of significance, and the study’s conclusions. Citations at the time of the search were also extracted for evaluations of cumulative citations. Summary conclusions of the status of each variable is presented based on the consensus where the variables were examined (table 1). Some pooling of similar variables was undertaken, which resulted in an evaluation of 59 variables that could be classified into six topic groups based on the similarity of their biophysical associations.

I classified the publications as threshold papers if the core analysis were focused on variables with a threshold. TMs used a metric that required a variable, such as SST, to pass some pre-determined value for making a prediction of the response variables of either coral bleaching or coral cover. Papers classified as VMs could also use threshold variables, but they were included as part of an evaluation of other continuous variables that were examined for various response patterns and not chosen for having predetermined thresholds. Selected studies were evaluated for their association with the number of environmental variables. Principal component analyses (PCA) was used to evaluate the associations between studies by their usage of variables and topics. PCA is appropriate because the data are linear sums of the number of variables studied within each of the six topic areas. PCA normalizes the data, which helps to visualize and distinguish the 59 variables among the 112 investigations. In this case, the 59 variables were grouped according to their associations with the six categories described below. The analysis was performed in R version 4.1.2 using the PCA () function in FactoMineR package version 2.4 and visualized using the fviz_pca_biplot() function in factoextra package version 1.0.7 for the first two principal axes. Summaries of the literature in tables are presented for the total, TM, and VM categories as the PCA largely supported the original by-methods classifications.

I quantified the scientific stepwise process of variable selection and elimination used in these 112 field studies. In each paper, the steps in the selection processes reported were examined in terms of the initial selection to final presentation of statistical results. Therefore, for each paper the steps in variable selection could be distinguished as (a) chosen for evaluation, (b) pre-evaluated for testing as in correlation matrices and variation inflation factors (VIFs), (c) numbers of variables reduced for further statistical testing, (d) passing tests of significance, and (e) competed for fit or parsimony (i.e. Akaike information criterion (AIC) or \( r^2 \)) (table 2). The AIC provides a metric based on information theory to distinguish the strength of different or competing models (Burnham and Anderson 1998). These serial decisions were summarized as numbers and percentage of papers that utilized each of these five steps.

3. Review results

3.1. The history of variable evaluations

Compilations of the variables used to evaluate bleaching indicate that a total of 59 unique variables were evaluated among six overall topics (Supplemental table 1). These topics were geography (\( n = 6 \) variables), habitat (\( n = 6 \)), excess thermal stress (\( n = 15 \)), modifying thermal stress (\( n = 22 \)), coral and benthic community (\( n = 5 \)), and human influences (\( n = 5 \)).
Figure 3. Principal component axis of the number of 59 variables examined in 6 topic areas among 112 reviewed papers that examined coral responses of bleaching and mortality to environmental exposure. The 112 papers were classified prior to the PCA as either threshold of variability models based on whether the main variables evaluated were distinct threshold or continuous variables (see section 2). See supplement for citations associated with each numbered paper.

Summing the variables across all 112 studies gives an indication of the pervasiveness of the variables in the full study pool (Supplement). Excess thermal stress is the dominant topic, followed by geography, modifying variables, habitat, the coral benthic community, and human influences. Of these 112 studies, all 59 variables were studied in the 65 VM studies (figure 3). The remaining 47 TM publications studied a subset or 28 of the 59 variables.

In terms of their influence on bleaching or coral cover, studied variables indicate many influences and interactions (table 1). Many of these status conclusions are, however, based on a limited number of studies. Nevertheless, there is generally high variability and often weak support for associations of the common threshold metrics and coral bleaching and mortality. Significant interactions between excess heat and other variables are the consensus conclusions when viewed across these many studies. Some measure of excess thermal stress was studied in all papers with excess thermal stress and modifying variables, geography, and habitat as the four most studied topics in that order (table 2). The benthic community and human influence were studied in <20% of the publications and ~5% of the total number of variables.

Because many variables were seldom studied, these were a small percentage of the summed number of variables represented in all papers (supplementary table 1 (available online at stacks.iop.org/ERL/17/073001/mmedia)). Most single variables were not more than 5% of the total number of studied variables, which would make the coverage, generality, or widespread significance problematic. The most studied geographic element was a comparison between sites (51% of summed variables) with latitude as the second most studied variable. Depth was also the most common variable in the habitat topic (43%) followed by ocean exposure (18%). Excess and cumulative heat were the two most studied excess thermal stress variables (44%). There were many modifying variables, and few were consistently studied but temperature variation (13%) and wind (11%) were the most common. There were only a few coral and benthic community metrics evaluated, but susceptibility (33%) and community types (27%) were the most common.

Evaluating the studies by five-step variable selection procedure indicates that 91% of the papers evaluated more than one variable and those that did not were TM studies (table 3). TM models selected few or 1.7 ± 1.3 (SD) variables for study compared to 4.1 ± 4.3 for VMs. The high variation in VM variables reflects the right skew in these data with some papers evaluating many variables (i.e. 20 variables by Zinke et al 2018). Whereas the most variables evaluated by TM studies was eight (Claar et al 2018). Evaluating variables for redundancy and then testing them for correlations and VIFs prior to statistical evaluations was performed in only 25% of the papers and only 9% of the TM studies. Similarly, most studies (75%) considered variables that were not included...
in subsequent tests of significance. Seventy percent of the studies tested some variables for statistical significance but only 29% of the studies compared variables or models for competitive fits (i.e. greater variance explained) or parsimony (i.e. lower AIC values). Only 11% of the TM studies performed competition or parsimony tests compared to 43% of the VM studies. In general, the variables selection procedures were seldom systematic and, with some notable exceptions, poorly investigated. Excess thermal stress variables were assumed predictive without due selection procedures or subsequent critical statistical processes of evaluating variable redundancy and systematic elimination decisions.

### 4. Discussion

The perspective taken here is that the science of coral responses to environmental exposure is still an example of early science. Nevertheless, virtually all coral bleaching and climate change predictions for corals are based on mean temperatures, rates of rise, thresholds, and anomalies (Hoegh-Guldberg 1999, Sheppard 2003, Donner et al 2005, 2009, Logan et al 2014, McManus et al 2020, Dixon et al 2022). For example, a coral sanctuary geographic selection procedure evaluated 30 variables of which 23 were modifications of related threshold variables, which are highly correlated at the regional level (Beyer et al 2018). The more sophisticated models adjust future responses with the acclimation/adaptation of corals to mean temperature rises (Baskett et al 2010, Frieler et al 2013, Logan et al 2014). So, while these are reasonable assumptions, empirical studies examining a more diverse set of environmental parameters often find corals influenced most by variables not commonly modelled (Zinke et al 2018, McClanahan et al 2019). More recently, two large studies suggested that coral cover is more influenced by the variables of calcite and dissolved oxygen than common excess thermal stress metrics (Vercammen et al 2019, McClanahan and Azali 2021). This exemplifies the types of blind spots that can emerge when early provocative hypotheses capture the imagination of a scientific community. Consequently, there is a need for another generation of models that examines more environmental variables and specifically those metrics that have been shown in field studies to influence coral bleaching, mortality, and community change. Specifically coral cover and community change are understudied relative to the bleaching response, which may not be a good proxy for the desired management outcomes of coral persistence and ecological service provisions.

Well-established theories of chronic and acute stresses and life history responses are simplifying concepts that have not been fully examined and utilized to classify the complexity of reef environmental change. The concepts, therefore, provide a useful framework for making predictions and to assist evaluating the state of reefs. Stress theory is likely to better distinguish responses based on the life histories of the corals and not rely on composite metrics, such as coral cover, which is a simple but difficult variable to disarticulate from the many components of the community that constitute cover. Evaluating the distributions of environmental variables and life history responses in the chronic-acute framework will allow investigators to classify reefs and taxa by their environmental conditions. Then, to ask how life histories and proxies of ecosystem service are affected and distributed along chronic and acute stress axes. Chronic stresses will include important short-term elements, such as the daily to seasonal changes in tides, light, and temperatures. Chronic stress is also part of the history of a site at both ecological and evolutionary scales. Thus, this environmental and regional context is increasingly being understood as critical for evaluating acute responses to climate change that are often typified by large-scale coral bleaching and mortality (McClanahan 2020, McClanahan and Azali 2021).

While findings here and some large data compilations suggest a more adaptive and hopeful view of the future for corals in some reef environments, the persistence of these conditions in the face of increasing climate change is uncertain (Kleypas et al 2008, Frieler et al 2013, Hughes et al 2018, Skirving et al 2019). The probabilities of persistence can be clarified by evaluating, mapping, and including important thermal stress parameters in future projection models. The fate of corals may largely depend on the interaction between the resistance/acclimation effect of rising temperature variability and the recovery and resilience capacity of corals in various reef environments. Clearly, more

### Table 3. Summary of five-step selective process for variables and model selection used in statistical evaluations. The number of papers out of 112 studied and percent of total in parentheses. Papers classified as threshold and variability models.

| Five-step selective process                                                                 | All papers | Threshold model | Variability model |
|-------------------------------------------------------------------------------------------|------------|----------------|------------------|
| Greater than one variable chosen for evaluation,                                           | 102 (91)  | 37 (79)        | 65 (100)         |
| Variables pre-evaluated for correlations prior to testing                                 | 28 (25)    | 4 (9)          | 24 (37)          |
| Variables selected but not included in tests of significance evaluation                   | 84 (75)    | 37 (79)        | 47 (72)          |
| Selected variables tested for statistical significance                                    | 78 (70)    | 32 (68)        | 46 (71)          |
| Variables competed for fit or parsimony                                                   | 33 (29)    | 5 (11)         | 28 (43)          |
| Variables selected prior to tests of significance evaluation, mean ± SD                   | 3.1 ± 3.6  | 1.7 ± 1.3      | 4.1 ± 4.3        |
investigation is required to better understand the causes of the problem, identifying appropriate measurements and metrics, developing the most appropriate proxies, and evaluating their interactions with nearshore conditions. Otherwise, predictions and the consequences of future climate impacts will be poorly understood and possibly undermined by a poor connection between causative factors and the proxies of stress responses. The conditions of large environmental and field data sets and sophisticated artificial statistical intelligence are available, but these tools need to be embraced by investigators if an improved next generation of predictive models are to emerge.

Data availability statement

No new data were created in this study.

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Conflict of interest

I report no conflicts of interest.

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