


Timing matters: survey timing during extended heat stress can influence perceptions of coral susceptibility to bleaching

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Abstract The frequency and duration of episodic ocean warming events are increasing, threatening the integrity of coral reefs globally. Interspecific differences in susceptibility to heat stress result from variable capacities of corals to resist bleaching or to persist in a bleached state. During shorter bleaching events, stress responses occur rapidly and the “window” for detecting bleaching is tightly constrained. However, during longer bleaching events, we argue that the timing of surveys can radically influence results, which need to be interpreted with care. For example, although “heat-resistant” corals may survive prolonged bleaching events, they have a greater chance of being recorded as having bleached because they can persist for longer in a bleached state. This could lead to erroneous conclusions about their vulnerability to heat stress compared with taxa that bleach and die rapidly. Therefore, as bleaching events lengthen, it is vital to consider not only temperature at the time of sampling, but also the accumulation of heat stress over the entire warming event. We present a simplified conceptual framework and an example from the Central Pacific to emphasize the importance of survey timing to perceived susceptibility of coral taxa to bleaching.

Keywords Coral bleaching · Coral mortality · Heat stress · Ecological monitoring · Symbiodiniaceae · Coral life histories

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Coral bleaching events are increasing in frequency and severity worldwide at an alarming rate (van Hooidonk et al. 2013; Heron et al. 2016). The corollary of this dramatic increase is that recovery intervals separating major bleaching events have diminished (Hughes et al. 2018). Additionally, coral bleaching events have recently shifted from heat stress exposures between 4 and 12 °C-weeks on average (Hoegh-Guldberg 2011), to exceeding exposures of 24–35 °C-weeks in some locations (Claar et al. 2018; Boyle et al. 2017; Brainard et al. 2018). Climate change models predict that these thermal stress events will continue to increase this century (Cai et al. 2014). This underscores the importance of understanding how different coral species respond to episodic heat stress events, in order to determine which species and reefs will persist, and therefore how the structure and diversity of overall coral communities will be impacted over the coming decades.

Corals can exhibit marked intra- and interspecific differences in their responses to heat stress events, with some colonies succumbing quickly to bleaching and death and others able to endure longer periods at elevated temperatures either in the fully pigmented or bleached state (Marshall and Baird 2000). Species-specific response differences, which may be attributed to coral life history traits (Darling et al. 2012; Madin et al. 2016) such as colony growth rate (Gates and Edmunds 1999) and investment in energy storage (Loya et al. 2001; Rodrigues and Grottoli 2007), have given rise to the concept of “winners” and “losers” (Loya et al. 2001). Because areas with thermally sensitive coral species tend to bleach more readily and more frequently than those with thermally tolerant coral species (Marshall and Baird 2000), species-specific responses can significantly alter the relative abundance of coral taxa at individual reefs toward thermally tolerant species, over the course of one or multiple bleaching events

(Loya et al. 2001; Grottoli et al. 2014; Yadav et al. 2018). Due in part to variability in coral species composition, the effect of pulse heat stress events on coral reefs varies across scales, with susceptibility of corals varying among regions, islands, and reefs.

Typically, slow-growing mounding corals (e.g., massive *Porites*) are resistant to bleaching and are considered to be stress-tolerant (Loya et al. 2001; Darling et al. 2012). Conversely, fast-growing, branching coral species (e.g., *Pocillopora* and *Acropora*) are thermally sensitive and susceptible to bleaching (Loya et al. 2001; Darling et al. 2012; Putnam et al. 2012). Stress-tolerant corals are therefore generally “winners” and thermally sensitive species “losers” during thermal stress (Gleason 1993; Edwards et al. 2001; Loya et al. 2001; Hongo and Yamano 2013). However, recent monitoring studies (Chou et al. 2016) and rapid coral bleaching assessments in the Indo-Pacific Ocean during the 2015–2016 El Niño event have documented cases where this pattern appears to be reversed, with greater frequencies of bleaching observed in “stress-tolerant” species, such as *Porites*, than in putatively thermally sensitive species. In this perspective piece, we examine the question: Why are “heat-resistant” corals sometimes observed to bleach more than “heat-sensitive” corals? We acknowledge that some seemingly counterintuitive observations in bleaching patterns of *Acropora* and *Porites* may reflect the capacity of these species for acclimation (Guest et al. 2012). We do not discount observed changes in bleaching frequency due to acclimation, and we agree that species-specific rates of acclimation and adaptation fundamentally impact bleaching resilience (Pandolfi et al. 2011). Instead, we propose an alternative survey-dependent mechanism to explain counterintuitive bleaching observations that does not depend upon coral acclimation or adaptation. We suggest that because coral species and colony-specific holobiont assemblages exhibit variable capacities to resist bleaching or to persist in a bleached state during prolonged heat stress events, the timing of bleaching surveys can influence perceptions of coral species’ susceptibility to bleaching.

Species-specific bleaching responses

We frame our discussion around two evolutionarily and physiologically distinct coral taxa (i.e., one idealized heat tolerant, e.g., massive *Porites*; and one idealized heat sensitive, e.g., *Pocillopora*) for simplicity while recognizing that, on natural reefs, these strategies are more realistically represented by a gradient of potential responses. Heat-sensitive coral species may be able to retain their symbionts (or symbionts avoid being expelled; Silverstein et al. 2017) for a short time. However, once a sensitive

coral starts to bleach, a combination of physiological factors (Putnam et al. 2017); including thin tissues and limited energy reserves (Loya et al. 2001) (but see Lesser 2013), and a higher probability of containing thermally tolerant but potentially opportunistic symbionts (Putnam et al. 2012; Silverstein et al. 2017), mean that it can persist in the bleached state for only a limited amount of time before either recovering or dying (Baird and Marshall 2002; Jones 2008). Since thermally sensitive coral species are generally more likely to bleach, when a researcher surveys a reef during a short duration bleaching event, they would most likely predominantly observe bleaching of these sensitive species. In contrast, heat-tolerant species can generally resist bleaching for longer than thermally sensitive corals (Putnam et al. 2012). For example, in heat-tolerant massive *Porites*, this is due in part to a more evolutionarily derived symbiosis between *Porites* and Symbiodiniaceae of the genus *Cladocopium* (C15; LaJeunesse 2005; LaJeunesse et al. 2018) as well as a higher food storage capacity within their thick tissues (Loya et al. 2001). Additionally, corals with thick tissues may be pre-conditioned to disturbances by environmentally mediated priming, where internal (i.e., within-tissue) variability of physiochemical conditions allows microscale acclimation that prepares corals for external stress (Putnam et al. 2017). Furthermore, *Porites lobata* can increase heterotrophy and potentially dissolved organic carbon (DOC) uptake, which facilitates the maintenance of energy reserves during bleaching (Levas et al. 2013). These characteristics allow thick-tissued corals to resist, persist in, and recover from the bleached state over longer periods than thermally sensitive corals, making them generally less likely to bleach during “normal” (i.e., short-term) thermal stress events. After heat stress subsides, thermally tolerant corals are generally able to recover (either fully, or with partial tissue loss), unless heat stress is extreme, although recovery may take longer than in thin-tissued corals (Gleason 1993). These taxa-specific bleaching patterns have been observed consistently on reefs around the globe, making recent observations of reversed bleaching dynamics appear conspicuous.

Bleaching observations during extended heat stress events are survey timing dependent

With limited resources, local bleaching surveys and broad-scale monitoring efforts are often constrained to a single survey time point during the course of a heat stress event (Marshall and Baird 2000; Berkelmans et al. 2004; Zapata et al. 2010; Kelmo and Attrill 2013). Many coral bleaching studies also have been reactive, with sampling occurring only after the onset of widespread coral bleaching across the reef, at sites without any data on the “pre-heat stress”

coral community composition. Costs and complex logistics of ecological monitoring exacerbate these constraints in remote reef locations. When bleaching events are short lived, it is likely that single surveys can accurately summarize the impacts of heat stress. However, as cool season reprieves diminish (Heron et al. 2016) and bleaching events become longer, multiple monitoring surveys for each event likely will be needed to accurately quantify the impacts of heat stress. If multiple surveys during a bleaching event are not feasible due to logistical constraints, explicit consideration of survey timing with respect to heat stress is imperative so that the impact of bleaching can be accurately quantified and compared across studies and regions (Claar et al. 2018).

We now consider how a change in the timing of bleaching surveys could influence perceived species-specific bleaching responses during an extended heat stress event. We assume that monitoring in this example is reactive (i.e., all surveys occur after the onset of bleaching). This is often the case, even in repeatedly monitored sites, as researchers are interested in documenting bleaching patterns and prevalence and increase sampling efforts in response to a bleaching event. Before heat stress begins, we assume that effectively all existing corals are healthy, and negligible bleaching is observed (Fig. 1). This assumption may not hold for reef ecosystems, since changes in coloration and minor bleaching (< 25% of a coral colony) may occur due to seasonal variability (Gates 1990).

This, along with other simplifying assumptions herein, should be carefully considered when applying this conceptual framework to real ecosystems. If researchers surveyed the reef at the onset of heat stress (Fig. 1, time point A), they would document minimal bleaching of sensitive species (e.g., *Pocillopora*; depending on the dominant symbiont or local host/holobiont characteristics), as well as either some or no bleaching of thermally tolerant species (e.g., *Porites*). Observers would record no recent mortality at this time point. At the peak of heat stress (Fig. 1, time point B), the prevalence of bleaching in thermally sensitive corals may appear very similar to the onset of heat stress (Fig. 1, time point A). However, if time point B represents a significant amount of heat stress, the underlying symbiont community structure of affected corals may have already shifted. By this point, *Pocillopora* corals with thermally sensitive symbionts, genotypes, or phenotypes may have already started to die, while those with thermally tolerant symbionts, genotypes, or phenotypes may begin to bleach. If the reef was surveyed only at this time point one might erroneously conclude that thermally tolerant corals are as, or more, sensitive to heat stress than thermally sensitive ones since colonies of both types would be bleaching. By time point C, most heat stress has dissipated from the system (since a DHW of 0 indicates no accumulation of heat stress for 12 full weeks), and most thermally sensitive corals will have reached their end status; that is, if they are going to survive the event, they will have regained their

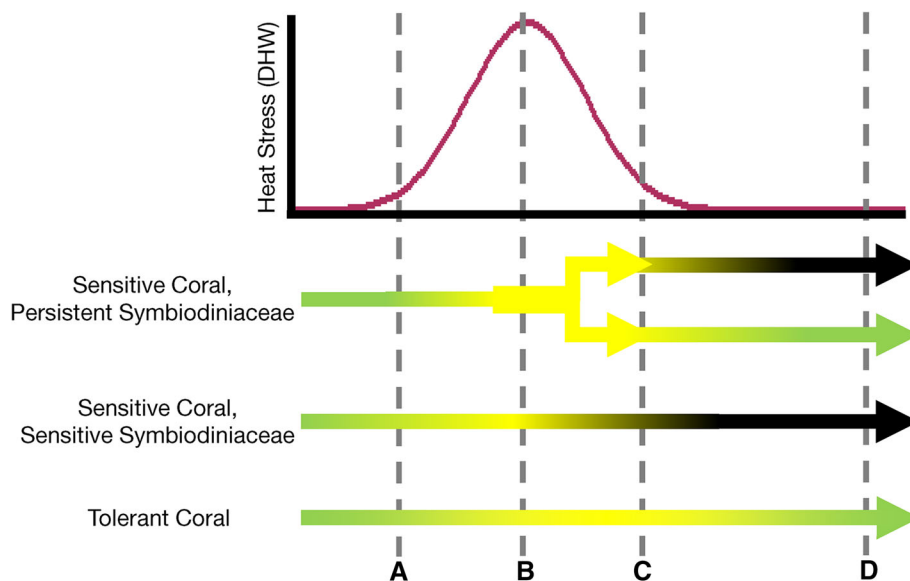


Fig. 1 Potential trajectories of coral bleaching, survival, or mortality for three model coral types over the course of a prolonged heat stress event (measured in degree heating weeks (DHW, °C-week)): i) a sensitive coral (e.g., *Pocillopora*) in symbiosis with persistent Symbiodiniaceae (e.g., *Durussodium*, previously *Symbiodinium* clade D), ii) a sensitive coral (e.g., *Pocillopora*) in symbiosis with a less persistent Symbiodiniaceae (e.g., *Cladocopium*, previously

Symbiodinium clade C), and iii) a thermally tolerant coral (e.g., *Porites lobata* or *Platygyra daedalea*). Trajectories are color coded as follows: green represents a healthy, unbleached coral; yellow represents a bleached coral colony; black represents a colony that died. Letters (A–D) denote four potential sampling time points during the heat stress event

symbionts; otherwise, they will have exhausted their energy reserves and died. Thermally tolerant coral species may still be bleached at time point C, relying on either heterotrophic feeding or energy reserves to maintain biological function. If the reef was surveyed only at this time point, it could lead to the incorrect conclusion that thermally tolerant coral species were more affected by the heat stress than thermally sensitive ones (i.e., if the thermally sensitive colonies that died are not recorded at all in surveys, and thermally tolerant colonies are recorded as being bleached). This scenario also highlights the importance of recording not only bleached corals, but also recent mortality. Finally, the outcome of the bleaching event (Fig. 1, time point D) records either survival or mortality of each of sensitive and tolerant corals. Therefore, depending on the time point the survey takes place (and whether recent mortality is recorded), results may appear counter to expectations from laboratory studies presented above.

The importance of survey timing was also emphasized by a previous study in which repetitive bleaching surveys were conducted during the 1997/1998 El Niño (surveyed 6, 10, 14, 20, 28, and 40 weeks after bleaching began; Baird and Marshall 2002). This study found that 6 weeks after bleaching began, when all living *Acropora* were bleached and massive corals (e.g., *Porites*, *Platygyra*) were only nominally affected, that 70% of the previously abundant *Acropora hyacinthus* population was already dead. Between six and ten weeks after bleaching began, more *Acropora* died, but others had completely recovered. Within this same period, bleaching increased across the community and more than half of the massive corals became severely bleached. Fourteen weeks after bleaching began (when temperatures dropped to the seasonal average), *Acropora* had reached their end status (i.e., fully recovered, or dead), but many massive colonies remained bleached for several months after. Without baseline data, the loss of a large proportion of *Acropora* colonies could have been missed. Furthermore, if sampling had only taken place at any one of these time points, the conclusions drawn would not have shown the complete picture of coral species-specific responses during this bleaching event. For example, at 10 or 14 weeks into the event, if baseline abundance or recent mortality was not recorded, one might have erroneously concluded that *Acropora* were not affected but that massive corals were. By surveying bleaching at multiple time points during this event, the authors accurately captured the dynamics of bleaching and mortality and provided a foundation for future work.

Specific example—Kiritimati Island during the 2015–2016 El Niño

A more recent example of the importance of survey timing comes from a study of coral bleaching, mortality, and survival during extended heat stress on Kiritimati atoll over the course of the 2015–2016 El Niño event, in which we observed what at first appeared to be counterintuitive species-specific bleaching patterns (Fig. 2). We note that this example is unusual compared to previous bleaching events, in that this is the first record of a year-long continuous heat stress event. While not representative of most coral bleaching events to date, the extended nature of this heat stress event underscores the importance of bleaching survey timing, as heat stress events continue to lengthen under climate change. After two months of heat stress (reaching DHW = 11.8 °C-weeks; approximately halfway between Fig. 1, time points A and B), many heat-tolerant corals (e.g., *Platygyra daedalea*, *Porites lobata*, *Dipsastrea matthaii*) were mostly or fully bleached, while thermally sensitive corals (e.g., *Pocillopora grandis* and *Montipora aequituberculata*) still appeared fully pigmented (Fig. 2). If we had surveyed this atoll's reefs only on this one occasion, we might have concluded that Kiritimati has extraordinarily resistant *Pocillopora* and *Montipora* (or extraordinarily sensitive Merulinids, e.g., *Platygyra* and *Dipsastrea*). However, when we returned after ten months of heat stress (peak DHW = 24.7 °C-weeks; sampling just before Fig. 1 time point C), we found nearly the opposite pattern: mass mortality of the thermally sensitive species and many colonies of thermally tolerant species that had either persisted in the bleached state or recovered to full pigmentation (Fig. 2). These patterns (with example photographs in Fig. 2) were observed at many sites around the atoll. Subsequent sampling in late 2016 and 2017 revealed that indeed many colonies of these thermally tolerant species had survived the event.

This study also underscored the importance of sampling before a bleaching event for accurate documentation of coral mortality and changes to overall coral community composition. For example, large table *Acropora* were present at several of our sites prior to the heat stress event. While these *Acropora* were variably bleached two months into the heat stress event (adjacent colonies exhibited all states between full “healthy” coloration and severe bleaching), they were all dead after ten months of heat stress. Since it is difficult to determine a coral's “time of death” from a skeleton (as turf and/or macroalgae are quick to overgrow exposed coral skeleton), it is vital to have quantitative pre-bleaching estimates of taxa-specific cover. These baseline measurements are particularly important during prolonged bleaching events, because as the duration

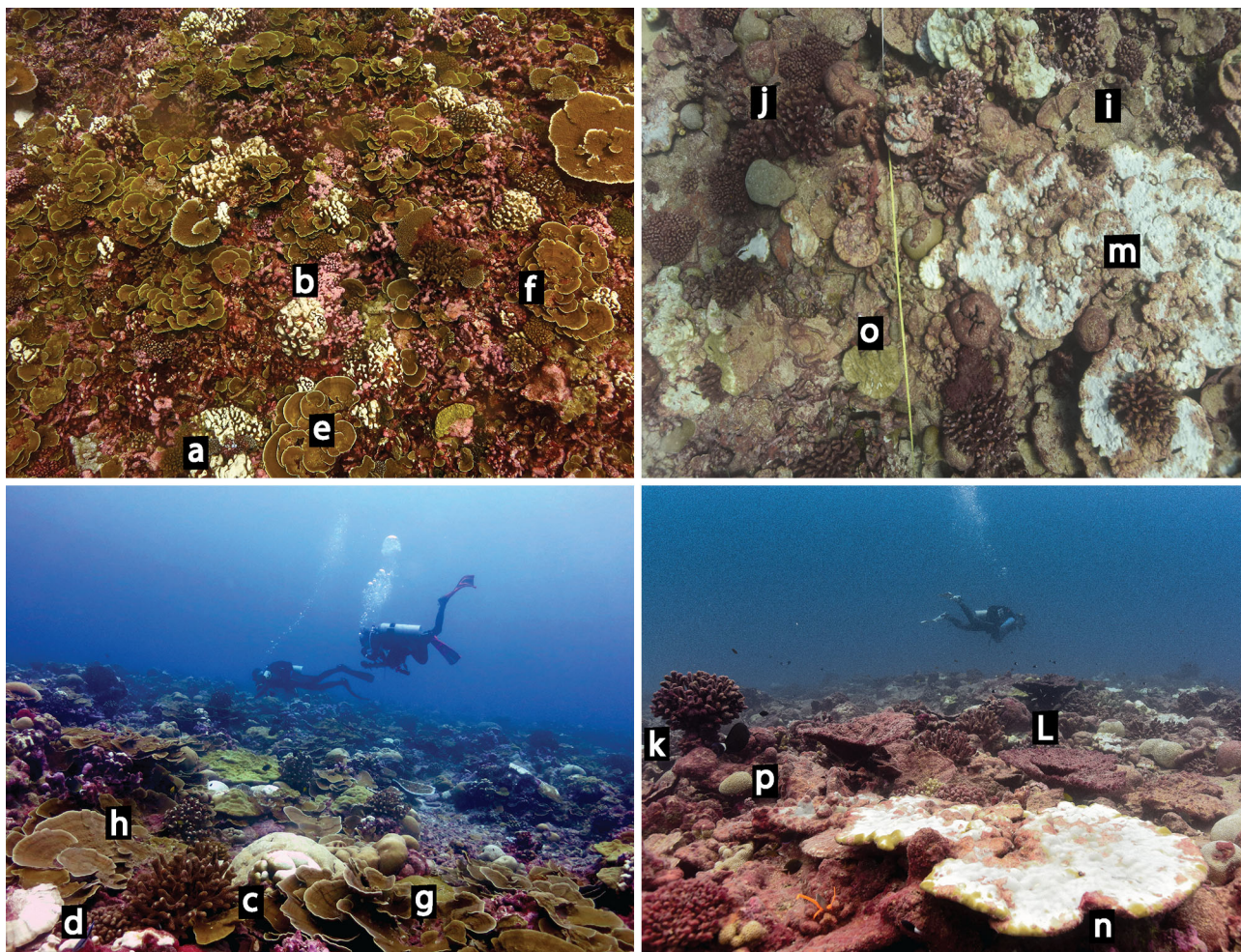


Fig. 2 Example images from the 2015–2016 El Niño bleaching event on Kiritimati Island. This extended bleaching event lasted for over ten months and reached 24.7 °C-weeks. Left panels: Two months after heat stress began, July 2015 (~ 11.8 °C-weeks), showing bleaching massive corals (a, b: *Goniastrea stelligera*; c: *Dipsastraea speciosa*, *Astreopora* sp.; d: *Porites lobata*) adjacent to apparently healthy

branching and plating corals (e–h: *Montipora aequituberculata*); Right panels: Near the end of the bleaching event (nine months after heat stress began, March 2016) showing dead branching and plating corals (i: *M. aequituberculata*, j, k: *Pocillopora grandis*, l: *Acropora* sp.), and bleaching (m, n: *P. lobata*) and recovering/apparently healthy (o: *P. lobata*, p: *Platygyra daedalea*) massive corals

and severity of warming increase, the possibility of local extirpation of entire coral taxa also increases, erasing knowledge of the historical state. Long-term coral reef monitoring programs, such as that of the National Science Foundation's Long-term Ecological Research (LTER) site at Moorea, French Polynesia (e.g., Adam et al. 2011; Holbrook et al. 2018), NOAA's Pacific Reef Assessment and Monitoring Program (Kenyon et al. 2006; Brainard et al. 2018), and the AIMS Long-Term Monitoring Program (LTMP) on the Great Barrier Reef (e.g., Sweatman et al. 2004), are of critical importance in this regard. These extensive data sets record baseline dynamics against which responses to acute disturbances can be compared, providing vital insights into underlying biological and ecological mechanisms of community change.

We suggest that counterintuitive observations in species-specific bleaching patterns may be emerging due to a mismatch between the frequency of ecological bleaching surveys and the fundamental shift in the severity of thermal stressors facing coral reefs today. As the temporal extent of bleaching events expands, timing of surveys will increasingly influence observed trends in species-specific bleaching. In conclusion, we propose that timing of coral bleaching monitoring influences observations and species-specific conclusions. If unaccounted for, the timing of coral monitoring will become a more commonly confounding factor in bleaching studies, as pulse heat stress events become prolonged and more intense on a global scale. We recommend that, if at all possible, repeat surveys should be conducted throughout the course of long bleaching events,

as well as following recovery. At minimum, we recommend researchers report the amount of accumulated heat stress at the time of sampling (DHW) compared to the overall event (i.e., at what point in the timeline of the overall heat stress event the survey was conducted), and explicitly consider this factor when interpreting the results of their bleaching surveys. Additionally, recent coral mortality should be recorded in the field when possible and compared to baseline coral abundances to ensure that changes outside of the bleaching survey are not missed. Ideally, long-term surveys can establish accurate baselines before bleaching events and can be used to detect overall changes in response to episodic thermal stress. Careful consideration of survey timing will minimize spurious conclusions and maximize the amount of knowledge extracted from coral bleaching studies.

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Compliance with ethical standards

Conflict of interest All authors declare that they have no conflict of interest.

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