The costs and benefits of environmental memory for reef-building corals coping with recurring marine heatwaves

Kristen T. Brown[1,2] and Katie L. Barott[1]*

[1]Department of Biology, University of Pennsylvania, Philadelphia, PA 19104 USA
[2]School of Biological Sciences, University of Queensland, St. Lucia, QLD 4072 Australia

*Corresponding author: kbarott@sas.upenn.edu

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Abstract

Marine heatwaves are occurring more frequently as climate change intensifies, resulting in global mass coral bleaching events several times per decade. Despite the time between marine heatwaves decreasing, there is evidence that reef-building corals can develop increased bleaching resistance across repetitive marine heatwaves. This phenomenon of acclimatization via environmental memory may be an important strategy to ensure coral persistence; however, we still understand very little about the apparent acclimatization or, conversely, sensitization (i.e. stress accumulation or weakening) of reef-building corals to consecutive heatwaves and its implications for the trajectory and resilience of coral reefs. Here, we highlight that not only will some corals become stress hardened via marine heatwaves, but many other individuals will suffer sensitization during repeat heatwaves that further exacerbates their stress response during repeat events and depresses fitness. Under current and predicted climate change, it is necessary to gain a better understanding of the acclimatization vs. sensitization trajectories of different species and individuals on the reef, as well as identify whether changes in bleaching susceptibility relates to physiological acclimatization, trade-offs with other biological processes, and ultimately coral persistence in the Anthropocene.

Introduction

The increasing frequency and severity of marine heatwaves driven by anthropogenic climate change threatens the very existence of coral reefs (Hughes, Kerry, Baird, et al. 2018; Smale et al. 2019), among the world's most biodiverse and productive ecosystems (Knowlton et al. 2010). A critical outstanding question in the field of coral biology with important societal implications is whether reef-building corals are capable of responding to the ongoing accumulation of heat in the ocean through adaptive and acclimatory mechanisms that promote survival into the future. Despite dramatic losses of living coral on reefs worldwide, there are rays of hope that coral reefs will persist. As marine heatwaves and resultant coral bleaching events have gone from rare to increasingly common occurrences, there is growing evidence that surviving coral communities are exhibiting higher bleaching thresholds (Brown et al. 2002; Gintert et al. 2018; Hughes, Kerry, Connolly, et al. 2018; Fisch et al. 2019; Hughes et al. 2021). In addition, corals in some habitats already exhibit elevated heat tolerance, as extreme conditions in their native environment has led to the evolution of higher thermal thresholds relative to nearby corals in more benign habitats (Palumbi et al. 2014; Schoepf et al. 2015). These adaptations have occurred over evolutionary time, yet there is extensive evidence that higher bleaching thresholds can also be gained within a coral's lifetime through phenotypic plasticity and acclimatization (Castillo et al. 2012; Palumbi et al. 2014; Barshis et al. 2018). These heat-tolerant corals may therefore become a node of resilience within coral communities as global temperatures continue to rise, as their ecological history has primed them with the toolkit needed to cope with heat stress. However, how the superimposition of heatwaves on top of already extreme thermal conditions affects these heat-tolerant corals is an important unanswered question, as these corals may already be living at the edge of their physiological limits (Camp et al. 2016; Klepac and Barshis 2020; Rathbone et al. 2021). Furthermore, now that marine heatwaves are occurring on a repetitive basis, there is less time for coral recovery and acclimatization between events, introducing the possibility that accumulation of heat stress with each additional heatwave may aggravate coral stress responses and preclude acclimatization. How many individuals and species follow these different trajectories in the face of repeating heatwaves is a critical determinant of coral survival and thus the persistence of coral reef ecosystems. Given this significance, more research is needed to determine whether corals acclimatize or accumulate stress to either their benefit or detriment, and to connect mechanisms across scales of biological organization (van Woesik et al. 2022) in order to better predict and conserve the future of coral reefs.

Environmental memory of prior heatwaves may increase heat tolerance of individuals and communities to subsequent heatwaves

Marine heatwaves are now occurring several times per decade and even in back-to-back years, leaving less time between events for corals to recover (Hughes, Anderson, et al. 2018). There is some evidence that with each marine heatwave, surviving corals have ‘environmental memory’ that can lead to development of stress tolerance through non-genetic mechanisms (e.g., changes in physiology, gene expression, and epigenetics; reviewed in (Hackerott et al. 2021)) as quickly as a year following exposure. Environmental memory has been qualitatively observed as decreased bleaching severity in a second marine heatwave compared to the level of bleaching observed during the initial marine heatwave, despite experiencing similar or greater heat exposure (Brown et al. 2015; Gintert et al. 2018; Hughes, Kerry, Connolly, et al. 2018; Fisch et al. 2019; Hughes et al. 2021). While encouraging, survivorship may not necessarily equate to high individual fitness or reef resilience. Across the same reefs that demonstrate less bleaching than expected, extensive mortality has led to a significant reduction in larval recruitment (Hughes et al. 2019) and the collapse of three-dimensionality and ecological function (Hughes, Kerry, Baird, et al. 2018). Further, corals of both bleaching-susceptible and bleaching-resistant phenotypes exhibit metabolic depression during heatwaves (Innis et al.

2021) and declines in reproduction (Levitan et al. 2014), highlighting that organismal effects transcend bleaching.

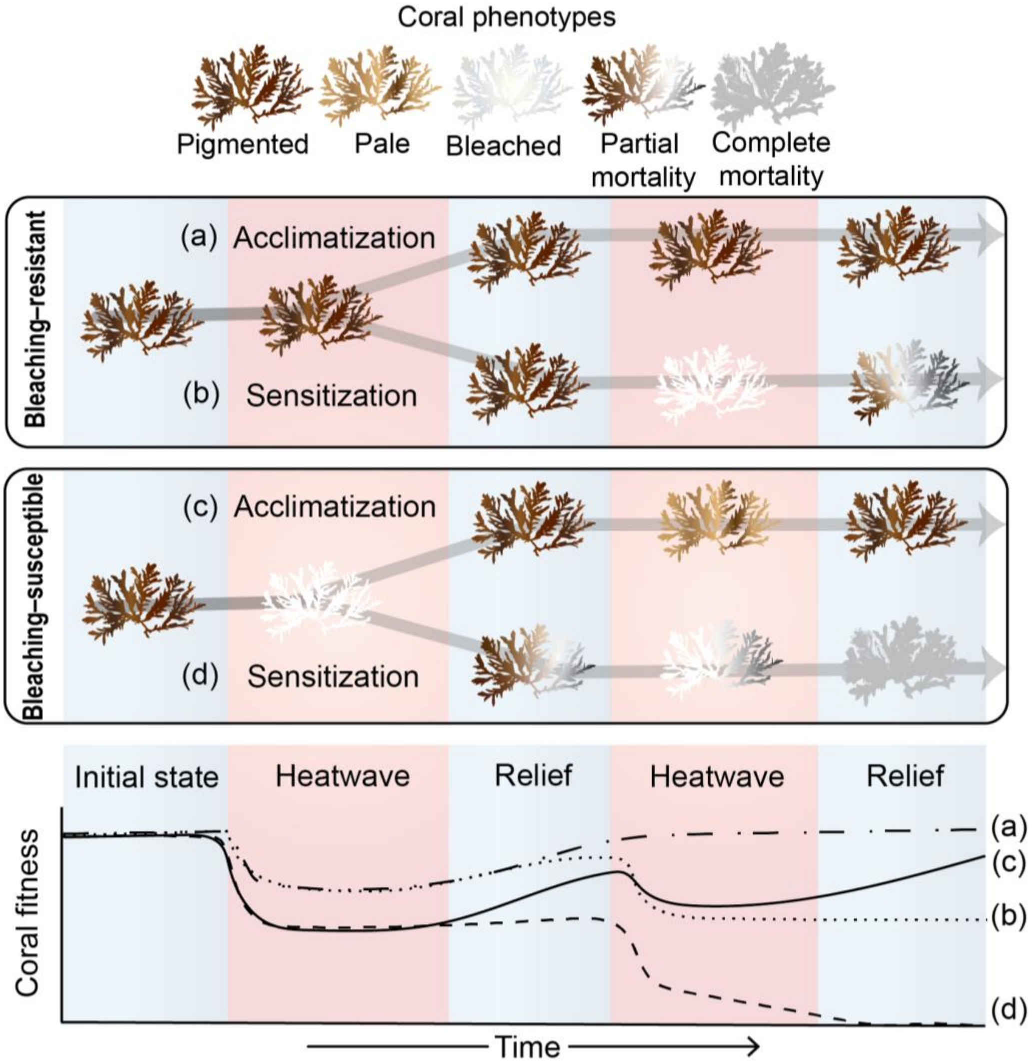

Figure 1. *Schematic of the influence of environmental memory of bleaching-resistant (a, b) and bleaching-susceptible (c, d) corals through repetitive marine heatwaves, with each initial phenotype following either an acclimatization (i.e. hardening) trajectory (a, c) or sensitization (i.e. weakening) trajectory (b, d). Bottom panel indicates coral fitness, a cumulative metric that accounts for changes in energy reserves, growth, reproduction, and survival.*

We propose that environmental memory can lead to four distinct trajectories for corals in response to repetitive marine heatwaves (Fig. 1). Coral trajectories are first distinguished by contrasting responses to the initial heat stress, with bleaching-resistant corals remaining pigmented and bleaching-susceptible corals losing their pigments. Each of these trajectories then bifurcates, as both phenotypes may exhibit contrasting downstream physiological responses in the aftermath of the initial heatwave: 1) positive (hardening; acclimatization) and 2) negative (weakening; sensitization). In bleaching-resistant corals, individuals often still exhibit signs of heat stress even in the absence of visible bleaching (e.g. metabolic depression; depleted energy reserves; reduced growth; lowered fecundity), and thus suffer an initial reduction in fitness (Fig. 1a, b). Bleaching-susceptible corals, on the other hand, suffer a significantly larger reduction in overall fitness following the loss of their endosymbiotic dinoflagellate algal symbionts (Symbiodiniaceae; herein referred to simply as algal symbionts) (Fig.1c, d). Once the heat stress subsides, corals of both bleaching phenotypes have the opportunity to recover their algal symbionts (for bleached corals) and replenish energy reserves (both phenotypes) from both auto- and hetero- trophic sources. However, not all individuals may recover at the same rate and as a result, there may not be enough time to reach the initial state prior to the next heatwave (i.e. incomplete recovery). Therefore, the onset of the second heatwave could lead to two distinct trajectories, where corals may either: a) demonstrate acclimatization to heat stress through the improved maintenance of algal symbionts and fitness (e.g., stress hardening) throughout the second heatwave (Fig. 1a,c); or b) experience a compounding of stress driven by an insufficient recovery, resulting in a heightened stress response during the second event (i.e., paling or bleaching) that may lead to partial to complete colony mortality and further reduced fitness following the second event (Fig. 1b,d). The beneficial acclimatization of the bleaching-susceptible corals (Fig. 1c) most closely resembles the current interpretation of coral environmental memory to heatwaves (e.g., (Hackerott et al. 2021)). Here, we add to that notion that corals will become stress hardened via marine heatwaves, and posit that many individuals may have insufficient resources for recovery and acclimatization, thus will suffer sensitization during repeat heatwaves that exacerbates the effects of heat stress and further depresses fitness. Species-specific responses to repeat heatwaves have identified coral species that tend to move along distinct trajectories (Table 1), with some able to withstand single heat stress events, but not repeat events (Fig. 1b), while other species are better able to withstand repeat events (Fig. 1a,c) (Grottoli et al. 2014; Thomas et al. 2019). These varying responses to individual and repeat heatwaves are likely driven by differences in life history traits of coral taxa, a better understanding of which may allow for improved predictions of community responses to repeat heatwaves. For example, coral species that are weedy, stress-tolerant, or generalists (sensu (Darling et al. 2012)) may be more likely to survive a single heatwave relative to fast-growing competitive taxa (e.g., branching and plating Acroporids) due to differences in reproductive strategies (e.g., brooding vs. spawning), algal symbiont associations (e.g., flexible vs. rigid) and/or morphological differences (e.g., thick vs. thin tissues; branching vs. massive morphologies) (Loya et al. 2001; Darling et al. 2012). However, species-specific responses to repeat heatwaves (i.e. acclimatization vs. sensitization) are complex (Table 1), and a better understanding of which traits and environmental histories are more likely to lead down which trajectory is needed.

Table 1. *Summary of observed bleaching and acclimatization trajectories of individual corals through at least two marine heatwaves.* *Individual coral species have been observed to follow both acclimatization and sensitization trajectories after exposure to repeat heatwaves. These species encompass many different life history strategies and include representatives found on reefs around the world. Initial phenotype indicates the bleaching phenotype observed during the first marine heatwave. Letters for each trajectory refer to Figure 1.*

Initial phenotype	Trajectory	Species	References
Bleaching-resistant	Acclimatization (a)	*Montipora capitata*[a,b] *Orbicella faveolata*[c] *Porites compressa*[a,b]	[a] (Innis et al. 2021) [b] (Ritson-Williams and Gates 2020) [c] (Fisch et al. 2019)
	Sensitization (b)	*Orbicella franksi*[d] *Siderastrea siderea*[d] *Stephanocoenia michelini*[d]	[d] (Neal et al. 2017)
Bleaching-susceptible	Acclimatization (c)	*Colastrea aspera*[e] *Colpophilia natans*[f] *Diploria labyrinthiformis*[f] *Montastraea cavernosa*[f] *Montipora capitata*[g]	[a] (Innis et al. 2021) [c] (Fisch et al. 2019) [d] (Neal et al. 2017) [e] (Brown et al. 2015) [f] (Gintert et al. 2018)

Initial phenotype	Trajectory	Species	References
		Orbicella annularis[f], *O. faveolata*[c,f], *O. franksi*[d] *Porites astreoides*[f], *P. compressa*[a], *P. evermanni*[h], *P. lobata*[h], *P. porites*[f], massive *P.* spp.[i,j] *Pocillopora meandrina*[h] *Siderastrea siderea*[d,f] *Stephanocoenia michelini*[d]	[g](Wall et al. 2021) [h](Sale et al. 2019) [i](Cantin and Lough 2014) [j](DeCarlo et al. 2019)
	Sensitization (d)	*Acropora aspera*[k], *A. formosa*[k], *A. humilis*[k], *A. millepora*[k], *A. nasuta*[k], *A. nobilis*[k], *A. palifera*[k], *A. pulchra*[k], *A. valida*[k] *Montipora capitata*[a,b], *M. digitata*[k] *Pocillopora damicornis*[k], *P. acuta*[b] *Porites compressa*[b], *P. cylindrica*[k], *P.* spp.[k]	[a](Innis et al. 2021) [b](Ritson-Williams and Gates 2020) [k](Ward et al. 2000)

It is also important to note that individuals within a single population can follow different trajectories (Matsuda et al. 2020), providing a source of adaptive variance (Drury et al. 2022). The proportion of individuals within a population that move along each trajectory will depend on the severity and duration of the initial stress event, the duration of the relief period (i.e., the time between heatwaves), and additional life history experiences that affect the time needed to recover to the initial pre-bleaching state, such as those that deplete energy reserves (e.g., reproduction, disease, predation, competition) or, conversely, promote heat tolerance (e.g., exposure to extreme habitats or sub-bleaching temperatures). For example, corals residing within extreme habitats are frequently exposed to temperatures above the local bleaching threshold (e.g., tidally dominated reef flats (Schoepf et al. 2020), enclosed lagoons (Camp et al. 2019), entire seas (Voolstra et al. 2021), and even locations of thermal power plant effluent (Jokiel and Coles 1974)), and often have higher heat tolerance than nearby corals. Corals can gain and maintain acclimatization to variable temperature regimes in as little as two years (Palumbi et al. 2014) and exposure to sub-bleaching stress weeks before a heatwave can be protective (Ainsworth et al. 2016). This suggests that corals can retain stress tolerance, particularly through non-genetic mechanisms such as phenotypic acclimatization, harboring stress-tolerant algal symbiont communities, changes in gene expression, and/or epigenetics (Palumbi et al. 2014; Schoepf et al. 2015; Kenkel and Matz 2016; Grottoli et al. 2017; Putnam 2021). Indeed, in many thermally variable habitats, corals have a reduced risk of bleaching during a heatwave relative to neighboring corals in more benign baseline thermal regimes (Safaie et al. 2018; Sully et al. 2019), and yet in other places, most corals in thermally variable habitats still bleach when exposed to heatwaves (Le Nohaïc et al. 2017; Schoepf et al. 2020; Ainsworth et al. 2021). Encouragingly, corals within thermally variable habitats appear to have a greater capacity to recover from bleaching (Camp et al. 2017; Schoepf et al. 2020), suggesting the environmental memory of daily exposure combined with memory of a heatwave may encourage corals along the acclimatization (i.e. hardening) trajectory. However, not all thermally variable habitats and temperature regimes are protective, and periods of extreme diurnal variability (i.e., daily amplitude >4°C) and severe heat stress (e.g., ≥8 degree heating weeks) has been shown to lower thermal tolerance (Schoepf et al. 2019; Klepac and Barshis 2020). Further, as the frequency and intensity of heatwaves increases, this protective mechanism is expected to be lost (Ainsworth et al. 2016), possibly shunting more individuals down the sensitization (i.e. weakening) trajectory (Fig. 1b,d). More work is clearly needed to understand the characteristics of protective thermal regimes in the field (e.g., magnitude and duration of heat stress, magnitude of diurnal variability, requisite recovery duration) and the capacity of individuals and communities already at the ceiling of their native range to respond to additional heat stress.

Integrating stress acclimatization and sensitization aspects of memory in understanding coral climate change responses

There are two important and complementary avenues for furthering our understanding of the causes and consequences of environmental memory in corals: 1) identify the biological mechanisms driving these differential responses (reviewed in (Hackerott et al. 2021)), and 2) assess the acclimatization/sensitization trajectories of individuals in the field over a long enough time frame to encompass multiple heatwaves and recovery periods to better understand demographic consequences (presented here). Long-term monitoring of individual trajectories is critical for understanding the diverse legacy effects of marine heatwaves and bleaching on coral responses, including growth, reproduction, and survival into the future, and for informing the interpretation of mechanistic studies. For example, while many studies may follow corals for between 6 to 12 months post-peak heat stress, coral calcification can take 1–4 years to recover to pre-bleaching levels (Cantin and Lough 2014; Gold and Palumbi 2018) and coral environmental memory can persist for up to a decade (Brown et al. 2015). Colony-level tracking is a particularly useful approach, and has been accomplished by: (i) following tagged or georeferenced corals that display bleaching-susceptible and/or bleaching-resistant phenotypes to reveal subsequent differences in calcification rates (Cantin and Lough 2014), energetics (Innis et al. 2021; Leinbach et al. 2021), reproductive success (Ward et al. 2000; Levitan et al. 2014; Fisch et al. 2019; Leinbach et al. 2021), mortality (Ward et al. 2000; Neal et al. 2017; Matsuda et al. 2020), and responses to subsequent stress (Ward et al. 2000; Neal et al. 2017; Fisch et al. 2019; Ritson-Williams and Gates 2020; Innis et al. 2021; Wall et al. 2021); (ii) examining corals across natural environmental gradients to better understand how multiple stressors exacerbate the impact of marine heatwaves on individual corals (Brown et al. 2002, 2015; Claar et al. 2020); and (iii) investigating coral bleaching recovery trajectories within both benign (thermally stable) and hardening (thermally variable) habitats in response to marine heatwaves (Gold and Palumbi 2018; Klepac and Barshis 2020; Schoepf et al. 2020). Following the same individuals or section of reef allows for a conclusive understanding of their heat stress response history (e.g., did they bleach or not, did they recover or not), removes the uncertainty associated with coral species identity, and eliminates any fine scale differences in environmental conditions (e.g., micro-environmental refugia that changes exposure to heat stress). It also allows us to determine if increased bleaching resistance gained via environmental memory leads to trade-offs with other processes (e.g. growth, reproduction, competition). It is important to note that it is becoming increasingly difficult to find a reef system that has not been impacted by marine heatwaves (Hughes, Anderson, et al. 2018), and this will become even more difficult as climate change intensifies (Hoegh-Guldberg et al. 2019). Therefore, special consideration should be placed on continuing and preserving long-term or historical datasets that incorporate data collected in periods of no thermal stress and/or prior to consecutive marine heatwaves. Furthermore, researchers should be careful to note the heat stress history of their study organisms, as this may significantly alter the interpretation of their results (Hughes et al. 2021). For example, the observation that massive corals lose heat tolerance in thermally variable habitats (Klepac and Barshis 2020), in contrast with branching corals from the same habitats (Palumbi et al. 2014), was likely confounded by the fact that the massive corals in that study had undergone an extreme heatwave (8 degree heating weeks) just weeks prior to the experiment (Gold and Palumbi 2018), whereas the branching corals in earlier studies had not. Thus, the massive corals may be as capable as branching corals to gain heat tolerance in variable thermal habitats, but because of their environmental memory, may have been on a sensitization trajectory (similar to Fig. 1b) that explains their poor performance. Experimental approaches complemented by robust understanding of the experimental corals' environmental history, such as working with corals with a known bleaching history (Morikawa and Palumbi 2019; Barott et al. 2021; Dilworth et al. 2021), may help improve ability to interpret experimental heat stress response experiments. Finally, identifying the thermal tolerance thresholds of individuals on different reefs (Voolstra et al. 2020, 2021) may also help researchers determine if bleaching-resistant corals have any additional ability to gain heat tolerance following simulated or *in situ* marine heatwaves.

Conclusions

The ongoing climate crisis has drastically altered the structure and function of coral reefs around the world. Mass coral bleaching events, triggered by marine heatwaves, have led to widespread coral mortality and severely impaired the ability of surviving corals to grow and reproduce for years, if not decades (Cantin and Lough 2014; Levitan et al. 2014; Hughes et al. 2019). It is possible that these ecosystems may never fully recover to their initial ecosystem state due to long-lasting physiological impacts, limited capacity for ecosystem-wide larval re-seeding, and the declining recovery time between marine heatwaves. Instead, ‘novel ecosystems’, defined as ecosystems where the composition and function has changed, are the current and future reality (Graham et al. 2014). In these novel ecosystems, it is critically important for managing reefs and promoting survival to determine if and how environmental memory of extreme heatwaves promotes higher heat tolerance via acclimatization into the future, or alternatively, results in cumulative stress that decreases heat tolerance. We should not assume that there are any extant naïve corals left on reefs (i.e., those that have not experienced thermal stress in their lifetime) and must contextualize our findings and conclusions considering the most recent marine heatwave. Current efforts to identify potential climate refugia, where certain reefs have a heightened chance of surviving projected climate change, represent an important avenue for future study and conservation (Beyer et al. 2018). In addition to entire reefs (e.g., parts of the Red Sea (Fine et al. 2013; Osman et al. 2018)), specific habitats, such as those that are thermally variable (e.g., (Oliver and Palumbi 2011; Woesik et al. 2012; Schoepf et al. 2015)), provide a natural laboratory to investigate how life-long exposure to daily, extreme temperatures influences coral thermal tolerance, and may serve as a source of heat resistant corals for dispersal/recolonization, trait-based restoration and/or assisted evolution (Van Oppen et al.

2015). However, more research is needed to determine if these corals can cope with ocean warming at the rate it is occurring when it is superimposed on top of the already extreme diel conditions. Promisingly, bleaching-resistant colonies appear to retain that phenotype across time and space following transplantation on the reef (Morikawa and Palumbi 2019; Barott et al. 2021). Unfortunately, efforts to experimentally prime corals with sublethal heat stress have not been effective at protecting corals from subsequent *in situ* heat stress (Dilworth et al. 2021; Henley et al. 2022). More work is clearly needed to better understand how environmental memory of heat stress influences coral responses to repetitive heatwaves, as well as how to harness that knowledge to identify individuals and reefs most at risk, in order to protect coral reefs into the future. As scientists, conservationists, and managers continue to investigate the potential for nature-based and assisted evolution solutions, global efforts to limit ocean warming to 1.5°C remains the only certain course of action to ensure a future for coral reef ecosystems.

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Conflict of interest

The authors declare no conflict of interest.

Data availability

No new data were generated or analyzed in support of this research.

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