ANNUAL REVIEWS

Annual Review of Marine Science

Standardized Methods to Assess the Impacts of Thermal Stress on Coral Reef Marine Life

Christian R. Voolstra,[1] Rachel Alderdice,[1] Luigi Colin,[1]
Sebastian Staab,[1] Amy Apprill,[2]
and Jean-Baptiste Raina[3]

[1] Department of Biology, University of Konstanz, Konstanz, Germany;
email: christian.voolstra@uni-konstanz.de

[2] Department of Marine Chemistry and Geochemistry, Woods Hole Oceanographic Institution, Woods Hole, Massachusetts, USA

[3] Climate Change Cluster, University of Technology Sydney, Ultimo, New South Wales, Australia; email: jean-baptiste.raina@uts.edu.au

Annu. Rev. Mar. Sci. 2025. 17:193–226

First published as a Review in Advance on August 8, 2024

The *Annual Review of Marine Science* is online at marine.annualreviews.org

https://doi.org/10.1146/annurev-marine-032223-024511

Keywords

coral reef, climate change, bleaching, standardization, meta-analysis, meta-organism, holobiont

Abstract

The Earth's oceans have absorbed more than 90% of the excess, climate change–induced atmospheric heat. The resulting rise in oceanic temperatures affects all species and can lead to the collapse of marine ecosystems, including coral reefs. Here, we review the range of methods used to measure thermal stress impacts on reef-building corals, highlighting current standardization practices and necessary refinements to fast-track discoveries and improve interstudy comparisons. We also present technological developments that will undoubtedly enhance our ability to record and analyze standardized data. Although we use corals as an example, the methods described are widely employed in marine sciences, and our recommendations therefore apply to all species and ecosystems. Enhancing collaborative data collection efforts, implementing field-wide standardized protocols, and ensuring data availability through dedicated, openly accessible databases will enable large-scale analysis and monitoring of ecosystem changes, improving our predictive capacities and informing active intervention to mitigate climate change effects on marine life.

INTRODUCTION

Climate change is one of the most pressing challenges facing humanity, with far-reaching consequences for ecosystems worldwide (Bellard et al. 2012). The increase in greenhouse gas emissions due to human activities has led to a steady and continuous rise in global temperatures. The Earth's oceans, in particular, are experiencing profound changes as a result of rising temperatures, leading to shifts in ocean currents; altered weather patterns, including extreme events (e.g., heatwaves, hurricanes, and floods); rising sea levels; ocean acidification; and changing salinity patterns, among other effects (Doney et al. 2012). These changes have severe implications for marine ecosystems, including disruptions in species distributions, altered reproductive cycles, and changes in primary productivity, with cascading effects throughout the food web (Doney et al. 2012). More directly, however, thermal stress poses a significant threat to the health and survival of marine life, given that it disrupts metabolism, growth, and reproduction and leads to decreased fitness, population declines, and species migration (Pinsky et al. 2013).

Stony corals and the reef ecosystems they build are sensitive to a range of environmental stressors (e.g., changes in water quality, light, and oxygen levels) but are particularly susceptible to the effects of climate change. Indeed, ocean acidification impedes coral calcification (Kleypas 2011), and thermal stress, in the form of extreme or prolonged heat events, causes coral bleaching, which is now considered the main driver of current reef decline (Hughes et al. 2018a). Bleaching describes the physical whitening of coral tissue due to the loss of endosymbiotic algae that provide photosynthates covering the energetic needs essential to coral survival (Hoegh-Guldberg & Smith 1989). Coral cover has decreased dramatically over recent decades, with current estimates suggesting a loss of 50% since the 1950s (Eddy et al. 2021). During the third global coral bleaching event alone (2014–2017), an estimated 35% of reefs experienced significant coral mortality (Eakin et al. 2022). Most recently (April 15, 2024), it was announced that the world is experiencing its fourth global bleaching event (ICRI 2024), the second in the last 10 years, the consequences of which have yet to fully unfold (Raimer et al. 2024).

Corals are the engine and the architect of reef ecosystems that provide a habitat for more than a third of all described marine multicellular species (Fisher et al. 2015). The reefs that corals form are biodiversity reservoirs, with largely unmapped biosynthetic potential (Paoli et al. 2022). Besides their ecological importance, close to a billion people rely on coral reefs for their livelihood, as a source of income, to provide food, or to protect shorelines (Kittinger et al. 2012). Thus, studying the effects of thermal stress on corals and coral reef marine life in general is paramount to accurately forecast the trajectory of coral reefs at large and the many marine species that depend on them, including many economically and ecologically important pelagic fishes.

The application of standardized methods facilitates such efforts and allows for the cross-species, cross-system (meta-)analyses needed to effectively predict ecosystem responses and inform conservation strategies. The objective of this review is to examine the array of standardized methods available to assess the impacts of thermal stress on marine life and to determine how to maximize their utility. By evaluating the current state of knowledge and highlighting advancements in technology and scientific understanding, this review aims to contribute to the refinement and development of standardized approaches in this field. We discuss the general importance of standardization, assess the availability and applicability of standardized methods, and highlight method-specific considerations to best assess the impacts of thermal stress on marine life. While we focus on corals and reef ecosystems in light of the pressing need to accelerate research to mitigate the impacts of climate change, the standardized methods discussed are broadly applicable in marine research. We therefore present how the conclusions drawn here extend beyond the realm of corals and reef ecosystems. Through this review, we aim to synthesize existing knowledge, identify gaps, and propose future directions to improve our ability to assess and manage the impacts of thermal stress on marine ecosystems.

THE RESPONSE OF CORALS TO THERMAL STRESS

Laboratory experiments and field studies started investigating the effects of temperature and thermal stress on marine organisms long before the recent rise in sea surface temperatures (SSTs) (Mayer 1914). These pioneering studies helped define the metabolism and ecological niches of many marine species. As the effects of climate change have imposed a new imperative in marine sciences, it is more important than ever to characterize how marine organisms respond to ocean warming and heatwaves. Decades of studies on reef-building corals—arguably among the most sensitive marine organisms to climate change—uncovered that their responses to thermal stress are diverse and affected by processes occurring at multiple biological scales.

At the molecular and cellular scales, thermal stress impairs a wide range of processes in corals and their endosymbiotic algae, Symbiodiniaceae (Helgoe et al. 2024, LaJeunesse et al. 2018). In coral cells, common responses to heat stress, such as downregulation of cell division and upregulation of cell death, protein degradation, protein folding, oxidative stress, and immune responses, have been reported from transcriptomic and proteomic studies (DeSalvo et al. 2008, Mayfield et al. 2018). In the algal symbiont cells (Symbiodiniaceae), heat stress negatively affects photosynthetic efficiency and can damage the photosynthetic machinery (Warner et al. 1999), but there is little evidence for changes at the gene expression level (Barshis et al. 2014, Voolstra et al. 2021b). It has long been hypothesized that the oxidative stress arising from disrupted algal photosynthetic and host–algal mitochondrial electron flow triggers the expulsion of Symbiodiniaceae cells from coral tissues (Baird et al. 2009, Lesser 1997). Yet recent evidence suggests that this process is unlikely to be the primary driver of coral bleaching (Dungan et al. 2022, Schlotheuber et al. 2024). Indeed, thermal stress impacts the metabolic fluxes between the symbiotic partners (Rädecker et al. 2021), slowing down the vital translocation of photosynthates from Symbiodiniaceae (Hughes et al. 2010) and curtailing the control of the symbiosis by the cycled nutrients long before the physical whitening, i.e., expulsion of the algal cells (Cui et al. 2023; Rädecker et al. 2021, 2023).

At the species and population scale, the coral thermal stress response is strongly affected not only by the intensity and duration of the thermal regime but also by the rate of heating (Middlebrook et al. 2010, Palumbi et al. 2014). An additional level of complexity comes from intraspecific variability in thermal tolerance. Such variability can be derived from associations with different Symbiodiniaceae (DeSalvo et al. 2010, Sampayo et al. 2008) and other microbial symbionts (Ziegler et al. 2017) as well as genetic variations in the coral host (Fuller et al. 2020). Variability in thermal tolerance occurs not only within but also between coral populations, sometimes separated by only hundreds of meters (Kenkel et al. 2013, Oliver & Palumbi 2011). Indeed, corals living in environments experiencing large daily fluctuations are typically more resistant to acute heat stress than those inhabiting more thermally stable environments (Castillo et al. 2012, Oliver & Palumbi 2011, Voolstra et al. 2020). Finally, differences in thermal stress responses also occur between corals inhabiting different reef regions (Evensen et al. 2022, Fine et al. 2013, Osman et al. 2018). Over such large spatial scales, patterns of coral thermal tolerance often align with local temperature regimes (Jokiel & Coles 1990); in other words, corals are acclimated or adapted to their regional (summer) climate. Upper thermal limits can differ by up to 8°C between the hottest reefs in the world, in the Persian-Arabian Gulf, and more temperate subtropical reefs, in line with differences in their mean summer maximum temperatures (Howells et al. 2022).

Comparisons of coral bleaching events have revealed that the thermal tolerance of many coral populations has increased over time (Fox et al. 2021), and a recent global analysis has confirmed this trend (Sully et al. 2019). Indeed, the onset of bleaching occurred at SSTs approximately 0.5°C warmer between 2007 and 2017 than in the previous decade (Sully et al. 2019). Yet we do not know whether this difference is caused by (*a*) the selective mortality of thermally susceptible individuals, populations, or species, resulting in coral assemblages that are more resistant, or (*b*) the acclimatization or adaptation of communities to increasing temperatures. General shifts from sensitive to tolerant species assemblages following bleaching have previously been reported, arguing for the former (Hughes et al. 2018b).

All of these important insights on coral thermal stress responses have been derived from experimental approaches and field monitoring. Hundreds of studies have used manipulative experiments to characterize these responses, but their thermal profiles, setups, and parameters were often not consistent or not properly documented (McLachlan et al. 2020). It is therefore possible that the large variability in thermal stress tolerance reported within and between populations (Evensen et al. 2022, Voolstra et al. 2021b), reef habitats (Kenkel et al. 2013, Voolstra et al. 2020), seasons (Berkelmans & Willis 1999), and species (Evensen et al. 2022) may not be fully due to biological causes. To help resolve the extent of variance attributed to biological differences, a core reporting approach of the experimental setup, conditions, and results is required to provide structure, increase transparency, and capitalize on the increasing number of thermal stress studies. Such standardized reporting will allow researchers to efficiently perform meta-analyses in order to identify susceptible and tolerant coral and more quickly devise solutions for conservation and restoration (Grottoli et al. 2021).

EXPERIMENTAL APPROACHES TO ASSESS CORAL THERMAL STRESS

Thermal stress experiments generally involve subjecting organisms to specific temperature regimes to simulate naturally occurring or projected conditions. Here, we consider thermal stress in the context of coral bleaching and present the standardization practices already implemented and those that are desirable to improve reproducibility and cross-study comparison (Grottoli et al. 2021). Importantly, most of the experimental design or reporting considerations and the underlying principles are not restricted to corals but can be applied to a broad range of marine organisms. We start by describing key parameters to consider when designing thermal stress experiments—such as heating rates, thermal profiles, and target temperatures—and providing specific recommendations for in situ, remote, and experimental conditions to maximize the relevance and comparability of their findings. We then present the different experimental platforms available to elucidate the impact of thermal stress on corals.

Experimental Design Considerations

This section presents important methodological considerations for heat-stress experiments, which will help improve our understanding of the coral thermal tolerance spectrum and response.

Target temperatures. In thermal stress experiments, temperatures are often based on in situ or satellite SST measurements of the reef collection site (Cziesielski et al. 2019). Target temperatures are typically set to 1–2°C above the long-term mean summer maximum [the so-called maximum monthly mean (MMM)], in line with the temperatures observed to induce a bleaching response in situ (Jokiel & Coles 1990). From an ecological perspective, bleaching takes time, and therefore degree heating weeks (DHWs) are used as a measure of bleaching probability. The DHW variable combines the intensity and duration of heat into a single metric that indicates how much thermal stress has accumulated in an area over the past 12 weeks (3 months) by adding up any temperatures exceeding the bleaching threshold (1°C above MMM) during that time. When the DHW reaches 4°C-weeks, significant coral bleaching is likely, especially in more sensitive coral species. Recent increases in the frequency and intensity of in situ heat-stress events, however, challenge this general notion, with heat stress being so extreme that shorter accumulation time frames or smaller thresholds may need to be considered (Brown et al. 2023, Leggat et al. 2019, Szereday et al. 2024), besides uncertainties pertaining to the offset between satellite-derived SST estimates and in situ temperature data (Gomez et al. 2020). In addition, certain coral populations are recognized for their exceptionally high thermal tolerance with respect to absolute temperatures (Evensen et al. 2021) as well as their ability to withstand temperatures above their local MMM (i.e., relative thermal tolerance). Such corals include those from the northern Red Sea, particularly the Gulf of Aqaba, which can withstand >5°C above their MMM (Fine et al. 2013, Savary et al. 2021), a temperature range typically lethal to corals elsewhere. Thus, prior to any large-scale experimental work, pilot studies to empirically assess coral responses to a range of temperatures are recommended to identify an optimal bleaching temperature and avoid unintended coral mortality over the experimental duration (Evensen et al. 2021, McLachlan et al. 2020).

Heating rate and duration. To reach target temperatures, a ramp is typically integrated into the thermal profile (McLachlan et al. 2020). The pace of the ramp-up can impact the onset and severity of coral bleaching, with differences of only 0.5°C per day eliciting variable phenotypic and physiological responses (Middlebrook et al. 2010). Natural bleaching events typically develop over weeks to months, with slow gradual heating rates ranging from approximately 0.1°C to 0.5°C per day (Spady et al. 2022). By comparison, coral heat-stress experiments, irrespective of the duration, have applied a wide range of heating rates, from ≤1°C per hour to 1°C per week (McLachlan et al. 2020, Schoepf et al. 2019). The range of heating rates partially stems from different ecological considerations, where a heating rate of 0.5–1°C per hour is based on the thermal fluctuations that corals can withstand on reef flats (Berkelmans & Willis 1999) or summer thermal spikes, which are increasingly challenging corals (Sully et al. 2019). By comparison, rates of 1–2°C per week reflect the dynamics of previous bleaching events to accommodate corals from thermally stable environments (Middlebrook et al. 2010). The tendency toward faster heating rates reflects the greater number of shallow-water corals studied and the focus on coral stress responses to thermal spikes (McLachlan et al. 2020). When multiple temperature treatments are used, the heating rates should be adjusted to take the same time, focusing on the extent of heat accumulation rather than the differences in ramp-up rate (Grottoli et al. 2021, Voolstra et al. 2020). Importantly, fast heating rates reaching extreme temperatures (>5°C above MMM) can deviate from the typical bleaching response and elicit rapid tissue loss and mortality within days (Evensen et al. 2021, Leggat et al. 2019). In addition to contextualizing the employed heating rate, studies assessing the impact of different or fluctuating heating rates on coral responses during short- and long-term experiments are warranted (Evensen et al. 2021, Voolstra et al. 2020).

Whether corals recover or die following bleaching depends largely on the extent of heat accumulation experienced, i.e., both the rate and duration of the heating event (Kayanne 2017, Liu et al. 2014). The DHW metric considers both factors (see above) and can explain more than 50% of the variance in coral bleaching severity observed across large spatial scales (Hughes et al. 2018a). Inevitably, DHWs are more easily interpreted in longer-term experiments. However, as short-term heat-stress experiments accommodate more rapid testing and are becoming increasingly popular (Evensen et al. 2023, Klepac et al. 2024), the DHW metric can also serve as an ecologically relevant point of reference for short-term acute heat-stress assays. On more refined timescales, degree heating days (DHDs) and degree heating hours (DHHs) have also been recently applied and can detect greater diel variability that may contribute to differences in coral thermal tolerance and bleaching (Szereday et al. 2024, Wyatt et al. 2019). Reporting on the extent of heat accumulation with consideration of the rate and duration in heat-stress experiments holds great promise for supporting a valuable cross-study metric, allowing comparisons of data from short-term acute and more longer-term heat-stress experiments.

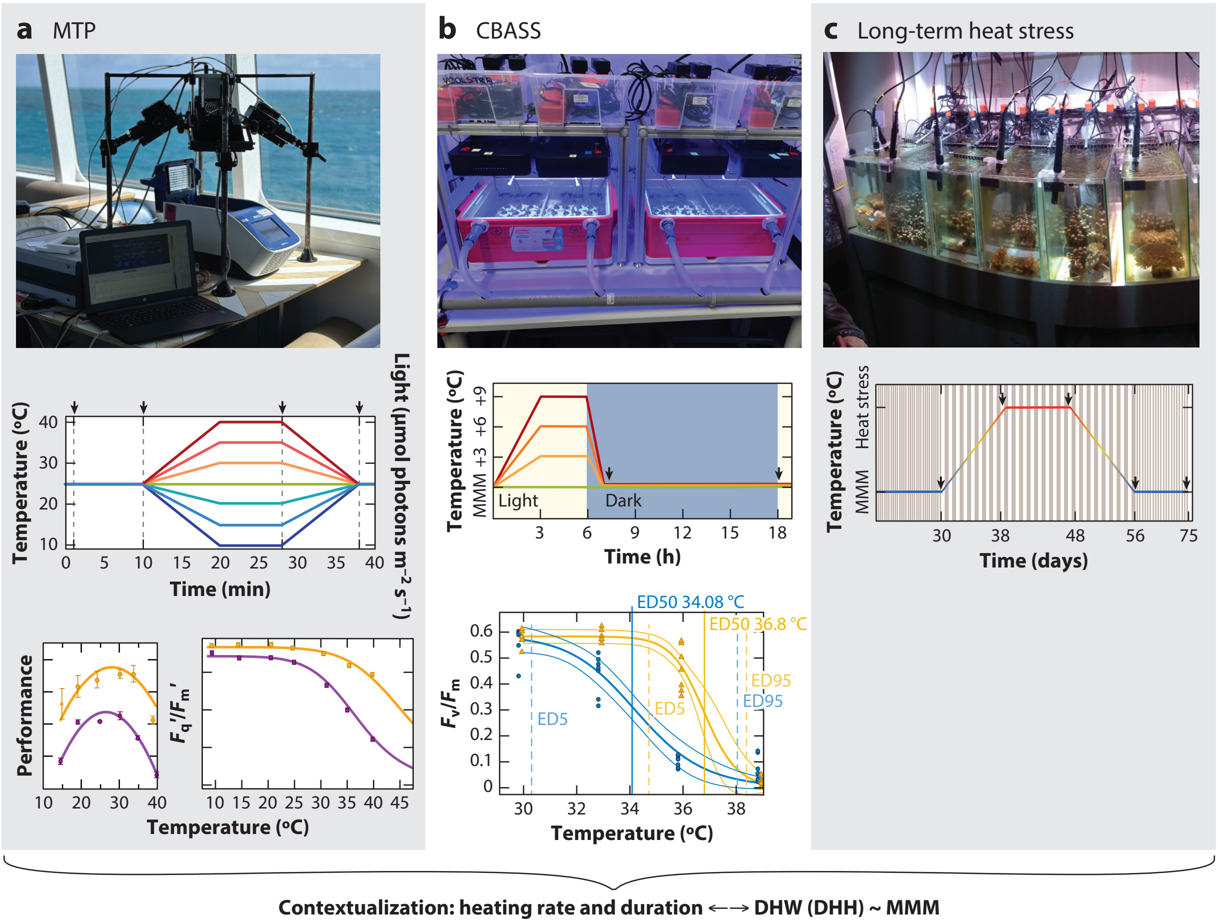
Thermal profiles. Heat-stress experiments generally consist of temperature profiles that follow a heat-hold (ramp-up to target temperature and hold) or heat-pulse (heat ramp-up, heat-hold, heat ramp-down) pattern, the latter of which includes either a single cycle of heat-holds at various target temperatures or repeat cycles of a single heat-hold temperature to assess the impact of thermal stress on corals (Grottoli et al. 2021, Morikawa & Palumbi 2019, Voolstra et al. 2020) (**Figure 1**). In heat-stress experiments that employ heat-pulse temperature profiles, the cycle of heat ramp-up, heat-hold, and heat ramp-down is often followed by a recovery phase that lasts longer than the heat cycle itself. Thermal cycles allow incorporation of natural diurnal cycles and exposure to heat stress during ecologically relevant daylight hours (with overnight reprieves) and are preferred in heat-stress experiments (McLachlan et al. 2020). It is also of value to mimic the precise thermal regimes found in different reef habitats, but this requires an initial characterization of local conditions over an appropriate period of time.

Other abiotic factors. Natural coral bleaching is not caused solely by heat stress (Suggett & Smith 2020). Experimental studies have reported that coral bleaching can occur in response to other abiotic stressors, such as deoxygenation (Alderdice et al. 2021), low water flow (Nakamura & van Woesik 2001), high-intensity white light or UV radiation (Brown 1997), and cold temperatures (Hoegh-Guldberg & Fine 2004). The large range of environmental conditions contributing to bleaching and their potential combined effects indicate that results derived from single-stressor experiments may not accurately represent coral responses in their natural environment. More studies are now integrating multiple stressors to determine whether they exhibit cumulative or antagonistic effects on bleaching susceptibility (Alderdice et al. 2022, McLachlan et al. 2020). Typically, combined stressors will worsen the coral's capacity to respond and manage the stress response (Alderdice et al. 2022, Ban et al. 2014). Conversely, in cases of high water flow (Nakamura & van Woesik 2001), high salinity (D'Angelo et al. 2015, Osman et al. 2018), or low light levels (via self-shading, turbid waters, or high cloud cover) (Tagliafico et al. 2022), the coral heat-stress response appears to be alleviated. Such counteracting factors have been acknowledged in regions referred to as thermal refugia (Osman et al. 2018, Schoepf et al. 2020, Tagliafico et al. 2022). Therefore, considering as many of these factors as possible within the heat-stress experiment or from the source reef will be critical for identifying specific variables contributing to coral bleaching susceptibility or resistance. An overview of the recommended in situ, remote, and experimental conditions to measure and report is provided in **Table 1**.

Experimental Platforms

This section details the experimental avenues used to elucidate the impact of thermal stress on corals, as well as the recently introduced standardized acute thermal assays that allow for the rapid diagnosis of thermal thresholds.

Model organisms. Despite extensive research, the mechanisms underpinning coral symbiosis establishment or breakdown, and what could prevent or mitigate them, remain to be fully resolved. Limitations stem from the practical challenges of working with coral holobionts and their highly complex associations with Symbiodiniaceae, bacteria, archaea, protists, and viruses (Rohwer et al. 2002, Voolstra et al. 2021a). The development of different model organisms is now playing a significant role in addressing these challenges and knowledge gaps (Baumgarten et al. 2015, Puntin et al. 2022). Such model organisms are typically more easily maintained, bred, and manipulated (e.g.,



	MTP	CBASS	Long-term heat stress
Duration	37.5 min	18 h	Days to weeks
Thermal stress type	Thermal performance curve	Heat pulse with multiple temperatures and overnight reprieve (day on the reef)	Typically heat ramp-up and heat-hold
Protocol	Standardized	Standardized	No standardized thermal profiles
Application	Photosynthetic organisms	Photosynthetic organisms (commonly)	Universal
Measurements	Oxygen and chlorophyll *a* fluorescence (bio-optical)	Photosynthetic efficiency and bleaching scoring (commonly)	Suite of physiological variables (e.g., photosynthetic efficiency, coral whitening, and tissue biomass)
Installation, deployment	Mobile, rapid	Mobile, rapid	Fixed, static
Analysis	Thermal optima and limits	ED50 thermal threshold, ED5 breakpoint, ED95 thermal limit, ED5–ED95 decline width, recovery capacity (7 h versus 18 h)	Onset of bleaching, recovery time, legacy effects
Other aspects	Small specimen size; requires fluorometer, custom well plates with oxygen sensors, and gradient thermocycler	Any continuous variable that changes with thermal stress suitable for ED50 thermal threshold determination (e.g., coral whitening, tissue biomass); possibility of pilot studies for optimal temperature range	Opportunity to mimic ecologically relevant bleaching process and assess recovery; possibility of acclimation to rearing condition; long-term experiments are subject to external variations/fluctuations

(*Caption appears on following page*)

Figure 1 (*Figure appears on preceding page*)

Experimental platforms to assess the impacts of thermal stress on marine life. Thermal stress experiments generally involve subjecting organisms to specific temperature regimes. Given the advent of recurrent bleaching over recent decades, short-term heat-stress experiments have dramatically increased in popularity for their ability to assay a large number of specimens in a short time and at site. (*a*) The most recent addition is the portable multi-taxa phenotyping (MTP) system, which has a runtime of 37.5 min (England et al. 2024). The thermal profile consists of a 10-min hold at ambient temperature, a 10-min ramp-up, a 7.5-min hold at target over a large temperature range (15–38°C), and a 10-min ramp-down. This profile is intended to capture different performance metrics pre- and post-stress using a combination of light and temperature stress conditions that allow modeling of thermal optima and limits. The rapid nature of this experimental platform is accompanied by a substantially downsized specimen that requires prior testing to ensure that variables such as oxygen levels are maintained and not subjected to unwanted drawdown. (*b*) The Coral Bleaching Automated Stress System (CBASS) was officially inaugurated in 2020 (Voolstra et al. 2020) with the addition of the standardized thermal tolerance threshold metric ED50 [the temperature at which the measured trait (e.g., photosynthetic efficiency) is half the initial value, i.e., 50% lower compared with the baseline] in the subsequent year (Evensen et al. 2021) (see the sidebar titled A Standardized Empirical Metric for Thermal Tolerance). Standardized thermal thresholds are based on log-logistic regression modeling of loss of photosynthetic efficiency over temperature (i.e., dose–response curves). The system and various variants thereof have since then experienced a highly popular uptake in the recent literature, providing a standardized platform and analytical framework to compare thermal thresholds in relation to set (the physiological state of the organism, e.g., healthy, compromised, or stressed) and setting (the external environment, e.g., biotic/abiotic factors and climate history). CBASS assays consist of standardized 18-h thermal profiles that are intended to mimic a reef-day. The profiles comprise a 3-h ramp-up, a 3-h heat-hold, a 1-h ramp-down, and an 11-h nighttime reprieve for four different flow-through tanks probing temperatures of the local maximum monthly mean (MMM) (control) and three increments thereof (typically +3–4°C, +6°C, and +9°C), which is intended to capture a broad response and bleaching spectrum (Evensen et al. 2022, 2023; Voolstra et al. 2020). Comparison of ED50s after ramp-down and after overnight reprieve can provide insight regarding the ability to recover, which may reflect differences in resilience (Savary et al. 2021). (*c*) Long-term heat-stress experiments are more variable by design and can run from days to weeks to months (Grottoli et al. 2021). The heating rates are typically much slower (approximately 1°C/day) than those in short-term experiments and more closely resemble in situ warming rates, thus eliciting ecologically pertinent bleaching responses and empirical determination of the heat-hold bleaching threshold temperature. However, the heating rates are typically consistently increased throughout the day and night, with a subsequent heat-hold at the bleaching temperature (no nighttime reprieve). Thus, although it is claimed that long-term heat-stress experiments better reflect naturally occurring bleaching events, the consistent heating rate and the absence of overnight cooling are not representative of natural conditions. Similar to the slow heating rate, the gradual process of recovery can be followed over time and can even be combined with a subsequent heat stress to study putative legacy effects. The different experimental platforms and designs can be contextualized through the heating rate and duration of the various thermal profiles, which allows the calculation of, for instance, degree heating hours (DHHs) or degree heating weeks (DHWs) as a comparative denominator. Additional abbreviations: ED5, temperature at which photosynthetic efficiency decline is initiated; ED95, temperature at which photosynthetic efficiency decreases below 95% of the initial (baseline) level. Photo in panel *a* by Hadley England; photos in panels *b* and *c* by Christian R. Voolstra.

into aposymbiotic states) than reef-building corals and are valuable substitutes for experimental work, reducing the impact of direct sampling from reefs.

Cnidarian models (e.g., different sea anemones and hydrozoans) have advanced our understanding of the interactions between coral holobiont members, including cnidarian–dinoflagellate (Rädecker et al. 2023), cnidarian–bacteria (Costa et al. 2021, Dörr et al. 2023), cnidarian–virus (Brüwer & Voolstra 2018), and dinoflagellate–bacteria (Xiang et al. 2022) relationships. For example, the ability of bleached hosts to acquire new algal symbionts was demonstrated more than 20 years ago using the model sea anemone Aiptasia, an umbrella term comprising several genotypes, strains, and likely lineages under the species now described as *Exaiptasia diaphana* (Kinzie et al. 2001). Natural or induced shuffling of algal symbionts to nonnative thermotolerant coral species has now been reported in reef-building corals as a strategy to enhance thermal tolerance (Quigley et al. 2023) or assist recovery after environmental stress events (Cunning et al. 2015). Similarly, beneficial symbiotic relationships between cnidarians and bacteria were proposed in the pioneering work with the hydrozoan *Hydra* sp. (Fraune & Bosch 2007, Fraune et al. 2015) and hypothesized and confirmed shortly thereafter in coral (Reshef et al. 2006, Ziegler et al. 2017). This led to the notion that changes in the animal (coral) microbiome can support environmental adaptation at large (Reshef et al. 2006, Voolstra & Ziegler 2020). This in turn instigated the premise of

A STANDARDIZED EMPIRICAL METRIC FOR THERMAL TOLERANCE

Standardized empirical heat-stress testing has enabled the ranking of corals based on their relative thermal tolerance (Evensen et al. 2022, Savary et al. 2021, Voolstra et al. 2020). The CBASS approach determines standardized thermal tolerance thresholds using the ED50 value derived from a dose–response curve (log-logistic regression) (Iakovleva & Voolstra 2023), corresponding to the temperature at which the measured thermal tolerance trait (e.g., photosynthetic efficiency) is half the initial value, i.e., 50% lower compared with the baseline (Evensen et al. 2021, 2023). The ED50 value is a physiology-based standardized metric that is contextualized to the climatology of the local reef, since the baseline temperature of the CBASS assay corresponds to the MMM climate variable (Evensen et al. 2021, 2023; Voolstra et al. 2020), considered an in situ thermal safety margin (Coles et al. 1976, Jokiel & Coles 1990). Thus, the ED50 temperature, which typically lies several degrees Celsius above the MMM, provides a standardized, comparable heat-stress tolerance threshold. Importantly, it must be considered within the constraints of the CBASS approach and not be equated to in situ thermal thresholds.

The MMM in turn directly connects to DHW through the HotSpot variable (Goreau & Hayes 1994): A coral bleaching HotSpot value is the positive difference between the measured daily global 5-km satellite SST and the MMM to pinpoint the occurrence of bleaching heat stress exceeding the long-term climatology. In turn, the daily global 5-km DHW is a 12-week accumulation of HotSpots (to reflect the sensitivity of corals to accumulating heat stress over time), whereby only HotSpot values of at least +1°C (i.e., MMM +1°C) are considered, with finer-scale approaches being applied more recently (Szereday et al. 2024).

Following the dose–response curve using the CBASS approach (**Figure 1*b***) also enables researchers to extract the breakpoint temperature at which photosynthetic efficiency decline is initiated (i.e., the ED5). This indicates the relative sensitivity to heat stress, with more sensitive corals reaching their breakpoints at lower temperatures (compare the blue and yellow dose–response curves in **Figure 1*b***). Further, the temperature at which the photosynthetic efficiency decreases below 95% of the initial (baseline) level (i.e., the ED95) can be considered the absolute thermal limit, at which physiological function (e.g., photosynthetic efficiency) is effectively lost. The steepness of the slope (decline width = ED95 − ED5) may further reflect how fatally corals bleach (with possible recovery or not), following either a gradual (blue line in **Figure 1*b***) or a steep (rapid) (yellow line in **Figure 1*b***) decline after their breakpoint. Indeed, more thermally tolerant central Red Sea corals followed a plateau-and-plummet curve suggestive of sustained tolerance over a broad temperature range, but at the cost of a rapid demise once they pass their tipping point. In contrast, northern Red Sea corals exhibited an early-but-slow-decline curve, reflective of a measured response in direct relation to the heat-stress exposure level (Evensen et al. 2022, Voolstra et al. 2021b). Such inference of stress response strategies may help better predict coral trajectories in the future. Thus, in addition to the ED50 temperature, the ED5, the ED95, and the shape of the dose–response curve (decline width) provide further information and correlate the physiological response to climate metrics (Gomez-Campo & Baums 2024, Tiwari et al. 2021, Voolstra et al. 2021b).

microbial therapy (probiotics) as an active intervention to counter the effects of thermal stress and increase resilience in coral (Apprill et al. 2012, Peixoto et al. 2017, Santoro et al. 2021, Voolstra et al. 2021a).

The above examples underline that work on model organisms and the target species they represent can and should be conducted in parallel to inform and advance each other. By definition, model organisms may be extremely useful to study certain processes but remain very limited for others. For instance, Aiptasia is a great model to study the mechanistic underpinnings of coral–Symbiodiniaceae relationships due to their association with similar Symbiodiniaceae (Baumgarten et al. 2015, Wolfowicz et al. 2016), tractable manipulation (Rädecker et al. 2018, 2023), and experimental accessibility by means of a translucent tissue and the absence of a skeleton

Table 1 Key contextual and experimental heat-stress data allowing for contextualization and standardization

Type of data	Variable	Significance	Measurement/method	Considerations
Sample metadata	Collection date	The sampling date determines the temperature regime (seasonality), which affects physiology (acclimation).	Calendar	Metadata should ideally include the day, month, and year (and even the time of day, which is relevant for diel cycles), but at minimum must include the month and year.
	Collection site	The collection site provides long-term climate context (see the rows on remote environmental metadata below), contextualization to and comparison with other studies, and a spatial perspective on coral thermal stress response.	Latitude and longitude	Cell phones allow accurate location mapping. A coordinate format compatible with Google Maps should be used.
	Sampling depth	Light and temperature (variability) attenuate with depth, affecting coral physiology and thermal thresholds.	Dive watch or depth logger	Light attenuates exponentially in the first 10 m of seawater (by approximately 10% for each additional meter of depth); the differences are most pronounced in the first 10 m.
Remote environmental metadata	MMM	Corals are adapted to their MMM; bleaching commonly occurs if coral are exposed to temperatures 1–2°C above their MMM for extended periods of time.	MMM, available as part of CRW (NOAA 2024c; **ftp://ftp.star.nesdis.noaa.gov/pub/sod/mecb/crw/data/5km/v3.1_op/climatology/nc/**)	Pilot experiments may be performed to empirically determine an optimal bleaching temperature and avoid unintended coral mortality.
	SSTA	Reef sites where the weekly SST is greater than the long-term averaged weekly SST may experience sublethal thermal stress priming.	SSTA, available as part of CoRTAD (NOAA 2024a)	
	TSA	Reef sites where the weekly SST is greater than the maximum long-term averaged weekly SST may exhibit thermal stress legacy effects.	TSA, available as part of CoRTAD (NOAA 2024a)	
	DHW	Heat accumulation (intensity and duration) is reflected by the DHW metric, which reflects the sum of temperatures exceeding the bleaching threshold (1°C above MMM) over the past 12 weeks.	DHW, available as part of CRW (NOAA 2024c)	Significant coral bleaching is expected at ≥4 DHW.
	LSD index	The LSD index integrates light in the form of photosynthetically active radiation and temperature in the form of SST into one bleaching metric (Skirving et al. 2017).	LSD, available as part of CRW (NOAA 2024d)	This index may be more accurate in predicting the onset and severity of coral bleaching events compared with heat accumulation metrics alone.

(*Continued*)

Table 1 ***(Continued)***

Type of data	Variable	Significance	Measurement/method	Considerations
In situ environmental metadata	Temperature	Similar to collection date, in situ temperature contextualizes the experimental temperature setting (e.g., the offset between in situ and heat-stress control temperature).	Dive watch or temperature logger (e.g., HOBO logger or CTD)	Long-term in situ temperature logging provides an offset to remote-based temperature data. In situ temperature provides higher spatial resolution than satellite-based temperature (CRW has a spatial resolution of 5 km^2).
	Light	Light levels and solar radiation affect bleaching susceptibility and ability to recover.	Light logger (e.g., LI-COR, HOBO, or Apogee logger)	Light thresholds of corals are not routinely determined, but measuring in situ light conditions at the collection site is a good starting point. UV levels are relevant for outdoor experiments but are rarely considered.
	Turbidity	Suspended particles can scatter light and reduce the amount of light reaching corals, thus affecting bleaching susceptibility.	Turbidity sensor (CTD) or Secchi disk	The method used depends on the budget and required accuracy. High turbidity can be associated with lowered bleaching susceptibility, but high sedimentation can exert stress on corals.
	DO	Low DO levels can lower bleaching thresholds and exacerbate thermal stress (Alderdice et al. 2022).	DO sensor (as handheld device or on CTD)	DO levels <2 mg L^{-1} are considered hypoxic, but thresholds can vary across species. DO levels are not commonly measured or monitored.
	Chlorophyll	Phytoplankton density in the water column indicates nutrient status, which affects bleaching susceptibility (Wiedenmann et al. 2012).	Chlorophyll sensor (on CTD)	
	Habitat type	Reef topography/geomorphology associates with specific environmental conditions (e.g., flow rate, light exposure, and temperature variability).	Note-taking while diving or Allen Coral Atlas (**https://allencoralatlas.org**)	
	Reef state/ condition	Species abundance and diversity indicate reef health, which may affect thermal resilience.	Transects (video or photograph surveys)	The proportion of live coral cover versus dead skeletons can reflect whether corals originate from a degrading, recovering, or thriving reef. Analysis can be standardized using machine learning tools (e.g., CoralNet or ReefCloud).

(*Continued*)

Table 1 ***(Continued)***

Type of data	Variable	Significance	Measurement/method	Considerations
Experimental metadata (based on Grottoli et al. 2021)	Experiment date	The offset between collection data and experiment data determines physiological status (e.g., acclimation period).	Calendar	Metadata should ideally include the day, month, and year (and even the time of day, which is relevant for diel cycles), but at minimum must include the month and year.
	Heating rate	The pace of heat ramp-up affects coral bleaching severity.	Time taken to reach heat-stress temperature	The impact of heating rate can differ between species.
	Duration	The duration of the experiment affects the extent of heat-stress accumulation.	Duration of experiment (minutes to hours to days)	
	Thermal profile	Heat cycling and heat-hold reflect different degrees of ecological relevance.	Temperature sensors connected to chiller/heater to control thermal profile; temperature loggers (e.g., HOBO loggers) for recording	Researchers should consider subjecting organisms to heat stress during the most ecologically relevant daylight hours. Characterization of local conditions provides guidelines for thermal profile.
	Light regime	The diel light cycle and light intensity/quality affect coral physiology.	Light logger (e.g., LI-COR, HOBO, or Apogee logger)	Light intensity is often unconsidered or low in heat-stress experiments. There should be ≥250–600 μmol photons m^{-2} s^{-1} during the daytime heating phase. A mix of blue and white light is typically used to reflect in situ light intensity in reefs.
	Flow rate	Sufficient and consistent flow prevents stagnant water, which avoids gradients of temperature, pH, oxygen, biological waste, and excess microbial growth, all of which affect coral bleaching susceptibility.	Measurement of rate of inflow volume over time (e.g., liters per hour) extrapolated to water turnover rate	Submersible pumps promote circulation, which is important for acute thermal stress experiments, where the impact of low flow can manifest rapidly.

(*Continued*)

Table 1 (*Continued*)

Type of data	Variable	Significance	Measurement/method	Considerations
Organismal responses	Bleaching phenotype	The health of photosynthetic endosymbiotic algae is directly linked to the health of coral (Muscatine 1990), making the bleaching phenotype a key indicator of the coral stress response.	Pigmentation scoring against color scale reference, which indicates the level of whitening Photosynthetic efficiency F_v/F_m (dark-acclimated maximum quantum yield of photosystem II) (Warner et al. 1996) using PAM fluorometry, which indicates the fraction of light energy converted into chemical energy during photosynthesis Chlorophyll *a* levels measured using a spectrophotometer, which indicate the health and density of Symbiodiniaceae inside coral tissue Measurement of Symbiodiniaceae cell density using a hemocytometer, flow cytometer, or qPCR, which indicates bleaching level	Pigmentation scoring via photographic imaging supports taxonomic records of coral samples, colony size estimation, and identifying visible stress responses such as tissue loss under extreme stress; researchers should consider using before-and-after heat-stress images to address inherent coloration differences between samples or colonies. Photosynthetic efficiency is a highly standardized, rapid measurement that is unaffected by coloration and reflects overall coral health (happy algae, happy coral). A combination of multiple bleaching phenotype metrics is desirable to avoid relying on a single variable.
	Behavior	Certain behaviors can impact stress tolerance thresholds and vary across species.	Heterotrophic feeding rates (prey per polyp over time) Polyp or tentacle expansion Mucus production	High heterotrophic feeding rates can offset lower autotrophy (Rädecker et al. 2021). For sessile marine organisms, such as corals, even subtle tissue motions affect the physiology of the organism by promoting nutrient and gas exchange into and within tissues (Pacherres et al. 2020).
	Energy budget	Tracking how energy resources are allocated across physiological processes can help to gauge the health of the organism under stress.	Specimen incubation to measure respiration, photosynthesis, and calcification rate by quantifying changes in oxygen or total alkalinity of incubation water over time For longer-term experiments, growth rates assessed using caliper measurements, scaled photos, or 3D photogrammetry	Durations of incubations vary according to the metabolic rate of different organisms or treatments. Researchers should consider the allometric scaling of differently sized specimens.

(*Continued*)

Table 1 (*Continued*)

Type of data	Variable	Significance	Measurement/method	Considerations
	Biomass/ sample size	The loss of protein biomass in an organism is indicative of its stress level. For many physiological variables, measurements need to be normalized to fragment size to allow for comparison.	Total soluble protein content using commercial kits Total tissue content via dry weight or water displacement methods Surface area using wax dipping, geometric approximation, 3D scanning, or photogrammetry	
	Biomarkers	Biomarker levels or expression allows assessment of heat-stress severity, providing a means of comparison across samples or studies. Accurate biomarkers allow researchers to predict, monitor, and diagnose stress resilience. Biomarkers can signify heat stress prior to visual manifestation. Symbiodiniaceae species contribute to coral thermal tolerance and thus are biomarkers for gauging thermal tolerance. The microbiome is indicative of stress level and thermal tolerance (Boilard et al. 2020, Ziegler et al. 2017).	Enzymatic assays that reflect oxidative stress or apoptosis Gene expression, based mostly on RNA sequencing analysis of the coral host to identify differentially expressed genes or regulated pathways Visual/spectral fluorescent or colorful protein analysis Symbiodiniaceae profiling via ITS2 sequencing (meta-barcoding) Microbiome community profiling via 16S ribosomal RNA gene meta-barcoding	Establishing baseline enzyme activity levels and accounting for natural variability are essential for distinguishing stress-induced changes from background variation; assays are usually performed using commercial kits, which can help promote a level of standardization. The highly variable nature of gene expression and experimental design makes the identification of universal gene biomarkers challenging. Fluorescent/colorful host proteins are photoprotective and promote bleaching recovery (Bollati et al. 2020). Universal primers and the SymPortal analytical framework support standardization and facilitate cross-study comparisons. Bacterial community assemblage can be highly dynamic and thus potentially highly sensitive biomarkers. Stressed corals typically exhibit high alpha and beta diversity.

Abbreviations: CoRTAD, Coral Reef Temperature Anomaly Database; CRW, Coral Reef Watch; CTD, conductivity, temperature, and depth sensor; DHW, degree heating week; DO, dissolved oxygen; ITS2, internal transcribed spacer 2; LSD, light stress damage; MMM, maximum monthly mean; PAM, pulse amplitude modulation; qPCR, quantitative polymerase chain reaction; SST, sea surface temperature; SSTA, sea surface temperature anomaly; TSA, thermal stress anomaly.

(Jacobovitz et al. 2021, Roberty et al. 2024). Yet calcification is arguably a key process affecting coral biology that cannot be considered using Aiptasia. To study such coral-specific processes, coral models such as *Stylophora pistillata* are employed (Moya 2006, Voolstra et al. 2017, Zoccola et al. 2015), in addition to the more recently introduced *Galaxea fascicularis* or *Acropora tenuis*, which offer laboratory-based induction of spawning, aposymbiotic states, asexual generation of clonal lines (i.e., isolated polyps), and coral cell lines (Kawamura et al. 2021, Puntin et al. 2023). Noncoral model organisms can further be employed for large-scale screenings to limit the use of coral resources; for example, Aiptasia is now being used to fast-track functional screening for microbes that affect coral thermal tolerance and serve as candidates for probiotics (Dörr et al. 2023), given its association with similar bacteria (Costa et al. 2021, Röthig et al. 2016). Overall, the further development and experimental interrogation of cnidarian model organisms (e.g., Aiptasia), coral model organisms (e.g., *G. fascicularis*), and corals in their native reef habitat need to be advanced in parallel to complement insights gained and to establish real-world applicability of active interventions (Voolstra et al. 2021a, 2024).

Mesocosms. In short-term experimental setups, biotic and abiotic seasonal and stochastic fluctuations are rarely considered. Yet such fluctuations can also contribute to coral bleaching and disease susceptibility (Vega Thurber et al. 2014, Pogoreutz et al. 2017, Ziegler et al. 2017), highlighting the need to establish finely regulated control and filtering systems for longer-term heat-stress experiments. The development of coral reef mesocosms with advanced control systems has been effective in establishing more stable ecosystem-level aquaria by incorporating filter feeders (e.g., bivalves) and other reef organisms (e.g., fish and invertebrates) for automated but more natural nutrient and mineral cycling, gaseous fluctuations, and fouling control (Wiedenmann 2012). Such stable experimental mesocosms have coral growth rates that are similar to or faster than those on reefs (Forsman et al. 2015) and maintain the diversity of their algal symbiont population (Smith et al. 2009), facilitating long-term rearing in which model genotypes can be tracked across different experimental treatment regimes (Wiedenmann 2012). Mesocosm studies have provided key insights regarding the contribution of bacteria to thermal bleaching and recovery, as they allow for controlled experiments and treatments that may be considered too complex or harmful to be carried out in situ, such as microbiome manipulations (Santoro et al. 2021) or pollutant exposure (Silva et al. 2019). Induction of coral spawning (Craggs et al. 2017) has also been successful within reef mesocosms, providing an important year-round coral stock, the ability to experimentally assess different life stages of the coral holobiont, and support for assisted gene flow efforts (Hagedorn et al. 2021). Importantly, the use of mesocosms can help to elucidate basic principles or narrow down the parameter search space in a less complex and less variable environment that can then inform field trials and be further validated in experiments in situ (Delgadillo-Ordoñez et al. 2024).

In situ experiments. Studying the heat-stress response of marine organisms in situ enables researchers to capture the complexity of environmental and/or biological interactions and characterize the response heterogeneity within populations and communities. Transect sampling or video surveys can help capture these aspects (including species abundance and diversity) and contextualize whether corals originate from a degrading, recovering, or thriving reef. In situ environmental measurements (e.g., of temperature, light regime, and turbidity) are important to identifying accurate conditions for laboratory-based experiments and resolving differences between reef locations. Water bodies that represent natural laboratories characterized by strong regional temperature gradients (Berumen et al. 2019, Voolstra et al. 2021b), extreme conditions (Camp et al. 2019), or contrasting thermal histories (Brown et al. 2023) are increasingly being utilized to identify key drivers of coral thermal tolerance variance and traits subject to natural selection. In situ tracking of tagged (and preferably mapped) coral colonies within well-characterized reefs is undoubtedly key in understanding whether measured responses in experiments are a consequence of prior severe or sublethal (likely priming) stress events and the extent of possible acclimation (Brown et al. 2023).

To more accurately determine the acclimation potential of corals, it is important to consider the differences between acclimation due to seasonality and that resulting from extreme marine heatwaves. Seasonality can significantly regulate physiological, behavioral, and morphological traits and consequently alter the thermal threshold of coral (Berkelmans & Willis 1999). Whether the extent of seasonal adjustment determines the capacity and pace at which a coral can acclimate or must adapt to extreme conditions remains unclear (Lachs et al. 2023). Therefore, there is a need to characterize the scale at which organisms adjust to their thermal environment across seasons versus years in controlled and natural settings. Short-term acute thermal assays are typically mobile experimental platforms that were motivated by the notion that bringing the lab or experiment to the reef may allow researchers to determine thermal thresholds that are unaltered by long-term rearing conditions or acclimation following collection. They also allow for opportunistic experimental inquiry at sites where bleaching events emerge, thus evading the risks, uncertainties, and efforts associated with in situ experiments that rely on proper prognosis where thermal stress events emerge or unfold, as discussed below.

Short-term acute thermal assays. Short-term acute thermal assays are becoming an increasingly popular type of heat-stress experiment due to their mobility, rapidity, and standardization (Evensen et al. 2023, Klepac et al. 2024, Voolstra et al. 2020). These assays commonly expose organisms to thermal profiles with either different heat-hold temperatures or repeated cycles at a predefined thermal stress temperature, with high standardization of experimental conditions (Grottoli et al. 2021, Morikawa & Palumbi 2019, Oliver & Palumbi 2011, Voolstra et al. 2020). Without such standardization, phenotypes cannot be directly compared across studies due to the different experimental conditions and measured biological traits and the absence of an empirical quantitative metric (McLachlan et al. 2020). To remedy this, there has been a collective effort to improve the comparability of coral thermal stress testing and to create a standardized point of reference (Evensen et al. 2023; Grottoli et al. 2021; McLachlan et al. 2020; Voolstra et al. 2020, 2021a). Implementation of standardization in experimental procedures and reporting is critical to establish effective tools for high-throughput screening, interexperiment comparability, and monitoring of coral thermal tolerance within restoration programs (Alderdice et al. 2024, Grottoli et al. 2021, Klepac et al. 2024).

Leading this effort thus far is the Coral Bleaching Automated Stress System (CBASS) (Evensen et al. 2023, Voolstra et al. 2020), which provides a standardized experimental platform (in terms of design, analysis, and reporting) for rapid phenotyping of coral thermal threshold diagnostics using 18-h-long short-term acute heat-stress assays to derive the ED50 metric, corresponding to the temperature at which the measured thermal tolerance trait (e.g., photosynthetic efficiency) is half the initial value, i.e., 50% of the baseline (**Figure 1**). As outlined above, any thermal stress response will always be a function of the length and intensity of the heat stress applied. As such, standardized thermal tolerance thresholds (i.e., ED50 values) should not be equated to absolute thermal tolerances (or limits) in the wild but instead used as a means to compare corals across species, environments, climate histories, and so on (see also the sidebar titled A Standardized Empirical Metric for Thermal Tolerance). Notably, however, better coral performance in short-term acute thermal assays could be equated to reduced in situ bleaching susceptibility and improved restoration outcomes in studies thus far (Klepac et al. 2024, Morikawa & Palumbi 2019, Voolstra et al. 2020).

By design, CBASS aims to follow a natural diurnal cycle and subject corals to heat stress during ecologically relevant daylight hours (Evensen et al. 2023, Voolstra et al. 2020). Other experimental setups used for short-term acute heat-stress assays, such as the semi-portable SeaSim in a Box (National Sea Simulator, Australian Institute of Marine Science), have also adopted CBASS-type approaches (Marzonie et al. 2023). The incorporation of additional stressors, such as deoxygenation (Alderdice et al. 2022) or pathogenic bacteria (Dörr et al. 2023), highlights how such a standardized framework can also identify factors in addition to heat stress that impact thermal thresholds. CBASS has focused on detecting and ranking the variance in coral thermal thresholds between populations or regions (Cunning et al. 2021, Evensen et al. 2022, Voolstra et al. 2020) but also has the capacity for more fine-scale differentiation, such as ranking of coral colonies (genotypes) within a population and comparison of said ranking over time or across seasons (see the sidebar titled A Standardized Empirical Metric for Thermal Tolerance). Evidence of prior thermal stress legacy effects that affect present thermal thresholds (Dörr et al. 2023, Evensen et al. 2022) suggests the possibility of detecting thermal acclimation. Whether coral rankings based on short-term acute thermal assays can be directly compared with rankings from prolonged gradual heat assays or in situ bleaching (and mortality) is under investigation. So far, similar physiological states and bleaching outcomes have been demonstrated between acute and chronic heat-stress exposures (Evensen et al. 2021, Voolstra et al. 2020), but not in all cases (Klepac et al. 2024). These differences highlight the need to establish a standardized long-term experimental design that includes a range of coral species, which may be disproportionately impacted by the high heating rates applied in short-term acute assays (Sahin et al. 2023).

Another experimental platform, the multi-taxa phenotyping (MTP) system (England et al. 2024), was more recently developed, with a focus on high-throughput screening that enables very rapid (<1 h) phenotyping of thermal optimum performance boundaries (**Figure 1**). Notably, both CBASS and the MTP system are capable of assessing a broad range of marine organisms and cover two different aspects of thermal stress—thermal tolerance (CBASS) and thermal optima (MTP system) (see also the sidebar titled A Standardized Empirical Metric for Thermal Tolerance). These two metrics are complementary, providing comprehensive insight into the capacity for organisms to persist under climate change.

REMOTE SENSING AND MONITORING

While heat-stress experiments are helpful to assess organism-specific responses and mechanisms of stress and tolerance, longer-term monitoring before, during, and after stress events is key to evaluating the impacts of warming and climate change on the larger coral reef ecosystem. These ecosystem measurements are central to our understanding of coral reef recovery or decline. As corals are the framework builders of reefs, they impact biological, chemical, geological, and physical processes that are central to the ecosystem, and therefore monitoring extends beyond the corals and includes various ecosystem members and components. Coral reef ecosystem monitoring takes the form of measurements by divers, autonomous in situ instruments, and remote aircraft or satellites (Apprill et al. 2023, Obura et al. 2019). In addition to data recording, integration of measurements into the context of the environment (e.g., storms and groundwater input), human activities (e.g., land use, vessel traffic, and protection), and climate and ocean processes (e.g., carbon dioxide emission levels and the El Niño–Southern Oscillation) provides the opportunity to model scenarios and build a predictive framework to help inform conservation and policy decisions (Donner et al. 2018). Ideally, monitoring programs make measurements that feed into the core areas of ecosystem functioning: calcium carbonate production (i.e., reef accretion and erosion), herbivore–algae interactions, predator–prey interactions, and nutrient cycling (Brandl et al. 2019). However, the reality is that time, feasibility, and budget are major factors that feed into the ability to construct and carry out long-term monitoring efforts. Here, we describe monitoring methods based on diver in situ, autonomous in situ, and remote/satellite ex situ measurements.

Diver in situ monitoring is common on reefs worldwide. These measurements focus on visual observations by divers as they follow a transect line or rove around an area while recording data about the benthic and pelagic organisms. Divers may also swim with video cameras, which allows them to record data more quickly and reconstruct the reef in 3D a posteriori, often termed structure from motion or 3D photogrammetry (Burns et al. 2015, McCarthy et al. 2022). Image characterization and classification are conducted either by humans or, increasingly, by a combination of humans and artificial intelligence/machine learning (e.g., CoralNet or ReefCloud; Lozada-Misa et al. 2017). Finally, divers may also collect samples of water, sediment, or organismal tissue for a variety of applications, including microbiome, metabolome, and population genetics analyses or other health assessments.

Autonomous in situ monitoring involves moored or drifting autonomous sensors or samplers that capture data about the reef without the need for divers. Autonomous measurements can provide increased temporal and even spatial coverage compared with diver-based measurements and allow for the capture of rarer processes or events. Common autonomous sensors include temperature and light (e.g., HOBO Pendant Temperature and HOBO Pendant Light Data Loggers) as well as those that incorporate pH, oxygen, nutrients, and chlorophyll (e.g., EXO Sondes). All of these parameters provide important insight into reef features and processes, which can vary on diel and event-related time spans (e.g., storms). Single instruments are now capable of registering and relaying real-time in situ measurement of multiple variables. One notable example is the Spotter platform (a basketball-sized buoy) (Sofar 2024), which is available free of charge through the philanthropic organization Aqualink (Aqualink 2024) or available for purchase. These buoys can measure waves, wind, temperature, and atmospheric pressure at the water surface in real time. Below the surface, they can record sea levels, subsurface temperature, turbidity, acidity, $p\mathrm{CO}_2$, video, and audio. The buoy then transmits the data through a satellite link and incorporates it into a freely available web app, providing access to data from buoys across the world.

Besides physical variables, rates of reef metabolism, photosynthesis, respiration, and calcification are all central to the ecosystem and can be measured using custom-built gradient exchange and eddy covariance methods (Apprill et al. 2023). Fish and invertebrates on reefs use sound as a common means of communication, and tracking reef sounds provides insights into biodiversity and processes. Commercially available sound recorders include the SoundTrap (Jones et al. 2022) and HydroMoths (Lamont et al. 2022) and are well suited for long-term deployment with near-continuous recordings. Autonomous underwater vehicles are starting to be employed for visual monitoring and have the potential to carry instruments and thus become an integrated sampling platform for reef monitoring (Teague et al. 2022).

Remote ex situ monitoring, also known as satellite monitoring, relies on automated remote sensing to record and extrapolate environmental factors such as SST, sea surface height, surface winds, and ocean color with high spatiotemporal resolutions. Satellite-deployed sensors can measure a range of environmental parameters, the most prominent being SST, which enables the calculation of DHW (see above), but reef geomorphology, shallow reef areas, bathymetry, live coral cover, and bleaching occurrence can also be recorded and mapped (Mumby et al. 2004). Applications such as NOAA's Coral Reef Watch (CRW) blend highly resolved temporal measurements (i.e., every 15 min) from multiple satellites (i.e., four geostationary and two polar orbiting), providing a nearly global daily map of SST measurements with a 5-km^2 resolution (Liu et al. 2014). This spatiotemporal resolution is significantly finer than the heritage CRW's twice-weekly global 50 km^2. With the growing consensus on the relevance of short-term diel changes on reefs (Pineda et al. 2013, Safaie et al. 2018, Voolstra et al. 2020) overlaid by long-term climate trends, high temporal resolution of climate and weather data is fundamental to assess the effects of such variability/fluctuations on a larger scale. Yet fine-scale bleaching differences matter greatly in understanding why some colonies bleach and others do not. As a consequence, even the 5-km^2-pixel resolution is not fine enough to resolve the bleaching trajectory of single colonies, between-species heterogeneity, or microhabitat differences (Yadav et al. 2023).

Besides SST, NOAA's more recently developed Coral Reef Temperature Anomaly Database (CoRTAD) (NOAA 2024a) provides further variables, such as (the frequency of) thermal stress anomalies (TSAs) and (the frequency of) SST anomalies (SSTAs), which correlate with the bleaching susceptibility of coral taxa (Sully et al. 2019). In addition, NOAA's Coral Reef Information System (CoRIS) Geoportal (NOAA 2024b) provides benthic habitat maps, marine observational data, and biological survey data that can further be integrated with in situ experimental data to inform correlations among climate, weather, and biological response. Notably, real-time in situ measurements (e.g., from the Spotter platform; see above) provide the finest spatiotemporal resolution to yield the most accurate predictions, which are advantageous for early warning systems and real-time heatwave tracking.

Given the impact of climate change on subsurface and deeper ocean thermal properties, new hyperspectral sensors with improved capabilities that go beyond SST at the air–sea interface are being developed and continue to improve (Donlon et al. 2002, Freeman et al. 2010). Simultaneously, heuristic (rule-following) and meta-heuristic (strategy-guided) algorithms are constantly pushing toward a more accurate estimation of SST and ocean subsurface temperature. Hydrodynamic models are also helpful to combine and illustrate how atmospheric forcing, currents, and reef terrain impact the residence times of water, which are directly related to the temperature, salinity, and nutrient conditions impacting corals. One example is the Regional Ocean Modeling System (ROMS) (Shchepetkin & McWilliams 2005), which can be used to incorporate the impact of larger-scale oceanographic processes on coral reefs and can be used in conjunction with in situ and satellite measurements. Another example is the Allen Coral Atlas (**https://allencoralatlas.org**; Lyons et al. 2022), an online platform that integrates multiple datasets and products in order to facilitate monitoring of coral reefs at a global scale. The products contained in the Allen Coral Atlas use high-resolution satellite imagery (10 m^2 pixel) and advanced analytics to map bathymetry, reef extent, coral habitat, turbidity, and bleaching prevalence (Lyons et al. 2022).

Coral reefs undergo constant cycles of disturbance and recovery. Monitoring allows us to track these events over time to determine whether the level of disturbance is outside the natural variability. Establishing baseline levels is crucial for distinguishing between natural variability and changes induced by external factors. Due to the complexity of coral reef ecosystems and the natural cyclicality of their natural habitat, disentangling the compounded effect of multiple types of disturbance proves complicated. New methods of monitoring, such as environmental DNA (eDNA) and remote sensing techniques, may allow researchers to track species composition and abundance in reef environments in the near future. Reef water microbial communities are increasingly recognized for their comprehensive ability to reflect reef, oceanographic, and human-based inputs on environments (Terzin et al. 2024). These microbial communities comprise the majority of eDNA in the environment, and the inclusion of microbial monitoring approaches alongside the current coral reef monitoring framework will improve our ability to rapidly detect changes occurring in coral reefs. In addition to microorganisms, eDNA approaches can be used to estimate the biodiversity and species abundance of reef biota and may help overcome some of the challenges inherent to traditional labor-intensive surveys because they are fast, simple to use, and relatively cheap and can be standardized, thereby reducing reliance on taxonomic expertise (West et al. 2020).

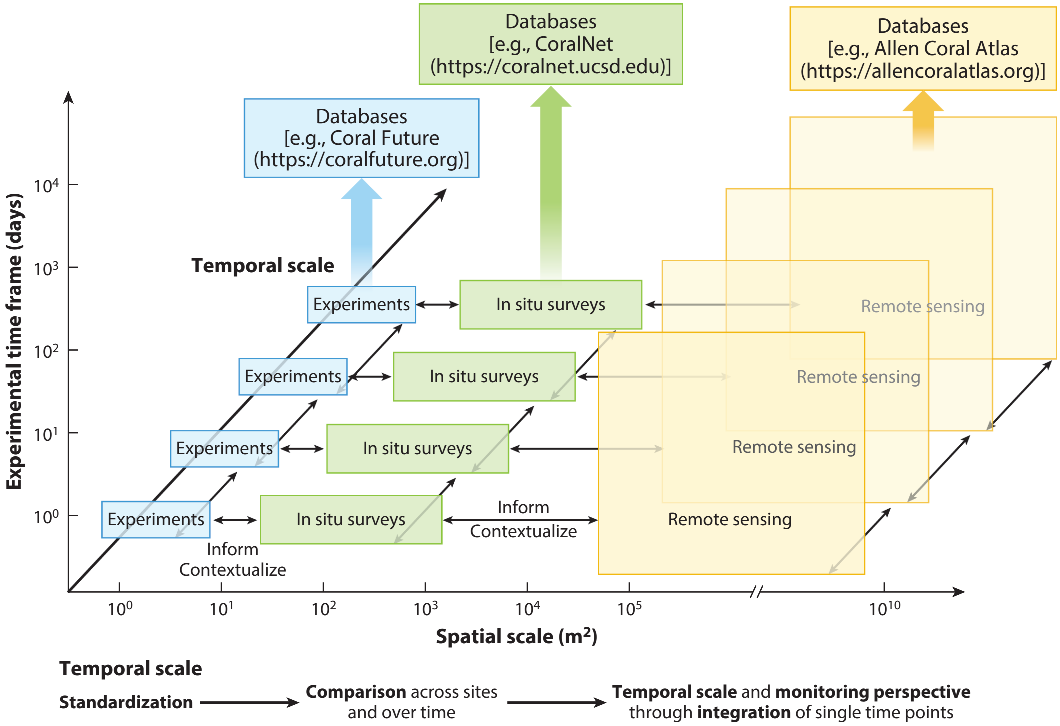


Figure 2

The value of standardization in integrating thermal stress data over time, moving from snapshots to time-integrated observations. Experiments typically depict the response of specimens collected at a specific point in time at a specific location and themselves cover a time frame of days (*y* axis). Experiments can be informed or contextualized (*black arrows*) by reef surveys and remote sensing data to integrate a broader spatial scale (*x* axis). However, only standardization allows the integration of data across studies, thus providing an emergent temporal scale that is otherwise unavailable (*z* axis). Experimental, reef survey, environmental, and remote sensing data should be stored in global databases [e.g., Coral Future (**https://coralfuture.org**) for experimental data, CoralNet (**https://coralnet.ucsd.edu**) for in situ surveys, and the Allen Coral Atlas (**https://allencoralatlas.org**) for remote sensing] for universal access and cross-linking.

A holistic approach incorporating remote sensing of environmental parameters with in situ observation of ecosystem indicators and experimental data will result in improved protection and management of coral reefs (**Figure 2**). By extending observation in a long-term setting, we can develop a comprehensive understanding of coral adaptive capacity and resistance to thermal stress in the context of environmental and ecosystem dynamics. When long-term data are integrated with remote monitoring models, new prediction tools can be developed, such as the NOAA CRW Satellite Bleaching Alert (SBA), to inform conservationists, policymakers, and other stakeholders. In essence, long-term monitoring programs have the ability to contextualize discrete studies and uncover patterns that would be missed by shorter-term observations, proving them fundamental to assessing the cumulative effects of thermal stress on marine life within the larger environmental and ecosystem context (**Figure 2**).

FROM HINDSIGHT ANALYSIS TO FORWARD PREDICTION

Advances in technology and scientific understanding have significantly contributed to more detailed and accurate information on thermal conditions, organismal responses, and ecosystem-level effects. The development and refinement of standardized methods incorporating and utilizing these new capabilities can further contribute to more precise and comprehensive data, leading to better-informed conservation and management strategies for marine ecosystems and the development of novel mitigation measures. In this section, we discuss key advances in specific fields and how they may impact our abilities to monitor coral reefs, predict future stress events, and modify management strategies.

Genomic and Environmental DNA Approaches to Large-Scale Assessments of Biodiversity, Genetic Diversity, and Genetic Adaptive Potential

Genetic and genomic approaches will undoubtedly play essential roles in future monitoring and forecasting capabilities because they can easily be scaled up and standardized. In recent years, improvements in sequencing platforms and associated reductions in sequencing costs have induced a shift from the study of a handful of single nucleotide polymorphisms (SNPs) that may be indicative of thermal stress responses to the sequencing of transcriptomes and, most recently, entire coral (meta-)genomes (Fuller et al. 2020, Robbins et al. 2019). Whole-genome sequencing is increasingly used to characterize adaptive genetic variation because it allows the correlation of specific phenotypes, e.g., thermal resistance, to specific genomic loci across environmental gradients (Fuller et al. 2020). These techniques will undoubtedly continue to enhance our understanding of how corals and other marine organisms may acclimate or adapt to changing thermal conditions; they may also identify important loci for thermal tolerance, determine the adaptation rate of populations to thermal stress, and, in combination with more targeted approaches, identify and elucidate the role of microorganisms that contribute to coral holobiont resilience (Hume et al. 2016, Jin et al. 2016, Ziegler et al. 2017).

Expanding the use of eDNA in coral reefs also holds great promise. Studies in other systems often amplify short fragments of mitochondrial DNA for rapid and accurate species identification. Due to the slow mitochondrial sequence evolution of reef-building corals (Shearer et al. 2002), nuclear markers are preferable, such as the ribosomal gene array [small subunit (SSU) ribosomal RNA, internal transcribed spacer 2 (ITS2), and large subunit (LSU) ribosomal RNA], but reference databases are needed to ensure taxonomic fidelity (Arrigoni et al. 2017). Standardization toward a universal taxonomic marker, optimized universal primers, and a common analytical framework can fast-track discoveries, interstudy comparability, and meta-analyses, as has been established for the Symbiodiniaceae coral symbionts through the SymPortal framework (Hume et al. 2019) in conjunction with the SYM_VAR_5.8S2/SYM_VAR_REV primer pair for highly specific and sensitive amplification of the Symbiodiniaceae ITS2 region (Hume et al. 2018). The biomass of corals is highly correlated with their surface area, which likely determines the rate at which they shed DNA into the surrounding seawater (Nichols & Marko 2019). Recent studies have confirmed that visual estimates are indeed linked to the abundance of coral eDNA (Alexander et al. 2020, Nichols & Marko 2019, West et al. 2020). Multimarker approaches provide even more comprehensive results, allowing the detection of not only scleractinian corals but also cryptobenthic species often missed by visual surveys (Alexander et al. 2020, West et al. 2020). eDNA approaches can, therefore, robustly capture the diversity and abundance of specific species or generate more holistic biodiversity estimates. However, the use of eDNA in coral reef monitoring should be heavily standardized to reach its full potential. Based on parameters proposed in other aquatic environments (Rees et al. 2014), researchers should ideally collect the same volume of water (e.g., 2 L) in triplicate, filter samples as soon as possible using the same type of filter (e.g., polycarbonate or polyethersulfone) and pore size (e.g., 0.2 μm), store them in the same way (e.g., refrigerated or at room temperature in a storage buffer), and extract DNA using the same kind of kits. As outlined above, samples should be amplified using the same universal or species/genus-specific primers and compared against a reference database specifically curated for reef organisms. If standardized procedures are implemented, eDNA may provide a cost-effective way to generate biodiversity inventories, with repeated temporal sampling allowing biodiversity shifts to be assessed at the ecosystem scale, providing new opportunities for scaling up and standardizing coral reef monitoring efforts.

In addition to biodiversity monitoring, eDNA may ultimately be used to obtain population genetic information. Indeed, studies in other systems have revealed the potential of eDNA to assess the genetic diversity of individual species (Adams et al. 2019). Yet several challenges still need to be addressed to confidently determine real genetic variation using eDNA, including the difficulty of assigning sequences to individuals, amplification issues resulting in the loss or erroneous inflation of allelic diversity, and the exacerbated impact of DNA degradation on nuclear DNA (Adams et al. 2019). To overcome some of these issues, stringent and standardized thresholds should be applied when filtering and analyzing eDNA data, together with the sequencing of controls and multiple replicates, which will help discriminate sequencing errors from rare alleles. In addition, instead of using eDNA to try to resolve population genetic questions to the level of individual organisms, this tool could be used to compare genetic variability at the population level, providing a cost-effective way to quantify standing genetic variations for targeted alleles.

Other eDNA approaches, such as electrochemical biosensors, can be deployed directly in the environment and do not involve any downstream extraction, amplification, or bioinformatic analyses. With such biosensors, oligonucleotide probes are attached to the surface of an electrode, and the hybridization of the target DNA to the probes creates an electronic signal that is recorded (Menon et al. 2020). Electrochemical biosensors can be highly specific and compact and cost only a few dollars to manufacture. They have therefore been used extensively for disease diagnostics and in the food safety industry (Menon et al. 2020). However, these sensors have a short shelf life and are not as sensitive as other eDNA methods, and detection can be impacted by changes in pH and temperature (Menon et al. 2020), two variables that can fluctuate rapidly in the marine environment. Nevertheless, recent attempts to use biosensors in coral reefs have allowed the in situ detection of DNA from specific coral predators (Wang et al. 2023) and coral probiotics (Wang et al. 2024), indicating a promising avenue for future research.

Citizen Science and Collaborative Initiatives

Citizen science initiatives and collaborative monitoring programs involve members of the public in the collection of scientific data. These initiatives have a long history in terrestrial ecology through biodiversity censuses such as Audubon's Christmas Bird Count, which has been running since 1900. In marine systems, the large number of active recreational scuba divers (approximately 6 million worldwide) has prompted the development of many citizen science projects in recent years. Such projects often use a standardized methodology and can take several shapes, from global surveys of benthic composition and coral cover (Reef Check; **https://www.reefcheck.org**) to specific reporting of coral bleaching (e.g., to CRW; NOAA 2024e), as well as a myriad of regional initiatives centered around monitoring and restoration (Becken et al. 2019). Citizen science projects can overcome some of the economic challenges linked to data collection, as they are equivalent to millions of dollars of in-kind contributions per year (Theobald et al. 2015). This large workforce can therefore substantially increase the scope of data collection efforts both spatially and temporally, allowing for broad coverage and long-term monitoring of coral reefs.

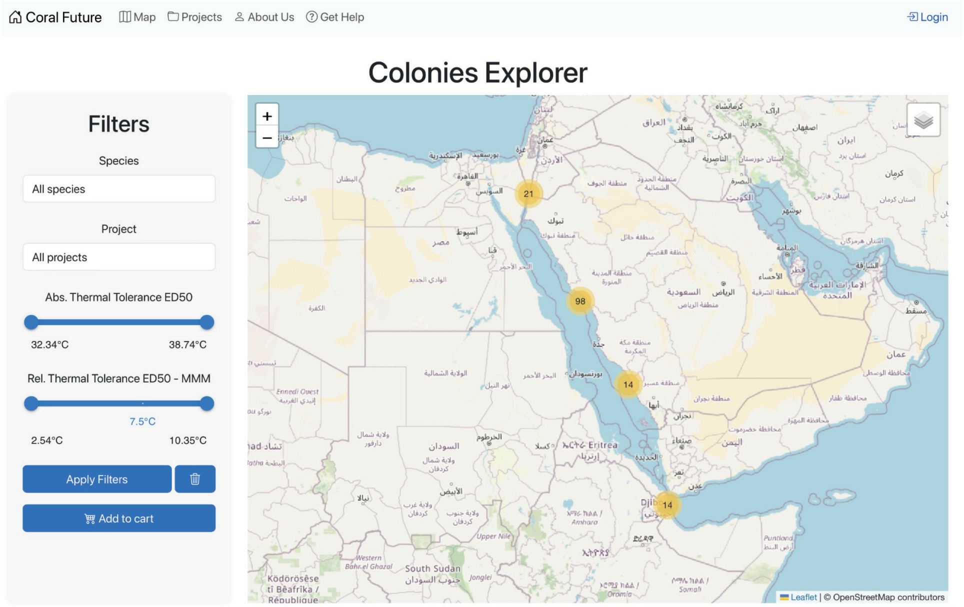
The robustness of the datasets generated by multiple citizen science projects, such as Reef Check and Reef Life Survey, is well documented (Done et al. 2017, Hodgson 1999). Using standardized approaches and appropriate training, data collected by volunteers are typically indistinguishable from those collected by scientists (Done et al. 2017). Data from Reef Check have been used to assess global patterns of coral bleaching over 20 years (Sully et al. 2019) and to design marine protected areas (MPAs) (Lau et al. 2019). In addition to the scientific and reef management benefits, these initiatives typically increase the environmental awareness and scientific education of the public (Hesley et al. 2023). Despite the reliability and scale of the data generated by these standardized approaches, data from only a handful of initiatives have been used in peer-reviewed publications thus far. Similarly, the collection of these data is often not integrated in the long-term management of MPAs (Theobald et al. 2015), which means that the potential impact of citizen science initiatives on both scientific research and management stakeholders is not fully realized.

Future Directions

Novel approaches need to be tested and implemented to more robustly predict organismal responses to thermal stress and climate change and to guide future conservation and restoration decisions (Voolstra et al. 2021a). One of the current bottlenecks is the difficulty of integrating data across biological scales, which is key to accurately predicting the outcomes of future thermal stress events (**Figure 2**). One way to integrate processes across biological (i.e., molecular, cellular, organismal, or population) and spatial (i.e., microhabitat, reef, region, or oceanic basin) scales is through hierarchical modeling (van Woesik et al. 2022). This type of modeling can account for the natural nesting of genes within individual corals, corals within habitats, habitats within reefs, reefs within regions, and regions within oceanic basins. With such models, the effect of a specific thermal stress event on an individual coral colony is dependent on the sum of processes occurring at different hierarchical levels. In other words, it allows us to consider that the impact of thermal stress is context dependent, closely mimicking natural sources of variability. Other powerful approaches, such as ecophysiological modeling, can be used to predict how the performance of organisms (e.g., metabolic rate, reproductive output, growth, and survival) is affected by thermal stress. Finally, the integration of genetic information into predictive models offers a very promising avenue to estimate future adaptive processes and their effect on population persistence (Bay et al. 2017, Logan et al. 2021, Matz et al. 2020).

The use of artificial intelligence in coral reef sciences and conservation is also particularly promising. More specifically, machine learning algorithms can recognize specific patterns through exposure to large training datasets. In recent years, machine learning has been used for automated estimation of benthic composition from in situ images (González-Rivero et al. 2020) and the identification of reef refuges and habitats suitable for the development and protection of coral species using remote sensing data (da Silveira et al. 2021) or benthic surveys, seawater quality, and physiological data (Mayfield et al. 2022). In addition, recent tools such as VirFinder (Ponsero & Hurwitz 2019) and Coracle (Staab et al. 2023) have used marine microbiome datasets to predict the viral origin of DNA sequences and determine the association between bacterial community members and coral thermal tolerance, respectively. Results from these approaches are impacted by the type of databases used (Mioduchowska et al. 2022). Therefore, using well-curated, ecosystem-specific databases can improve the quality and reproducibility of results (Lobanov et al. 2022).

Large databases are often developed independently of one another, but the explosion of multiomics datasets, as well as remote sensing and in situ data, calls for easier integration of different data types. This could be achieved through dedicated standardized and central databases that would expand access to data, guarantee their quality level, and provide templates allowing for more consistent data to be generated (**Figure 3**). These databases could be integrated through universal identifiers that cross-link more specialized databases (e.g., databases of eDNA, omics, citizen science surveys, or telemetry) under a common umbrella, following the FAIR (findability,



Species: All species

Project: All projects

Abs. Thermal Tolerance ED50: 32.34°C – 38.74°C

Rel. Thermal Tolerance ED50 - MMM: 2.54°C – 10.35°C (7.5°C)

Figure 3

Coral Future (**https://coralfuture.org**), a centralized, global database to access standardized coral thermal tolerance data. In addition to the importance of standardized methods to assess the impacts of thermal stress, the underlying data need to be stored in global databases for universal access, ideally with cross-reference identifiers to other databases and published studies. This not only addresses the issue of data inaccessibility—due to either a lack of expert knowledge about how to retrieve certain data or a lack of visibility when the data are stored in supplemental material or repositories or published in textual format—but also enables meaningful metadata analyses to identify novel factors contributing to thermal stress and resilience. The image shows a screenshot of the Coral Future centralized database, which stores standardized coral thermal tolerance data [ED50 values, corresponding to the temperature at which the measured thermal tolerance trait (e.g., photosynthetic efficiency) is half the initial value, i.e., 50% lower compared with the baseline] from acute thermal stress experiments [using the Coral Bleaching Automated Stress System (CBASS)]. The filters on the left-hand side allow researchers to quickly conduct powerful queries to answer questions such as where the most thermally tolerant coral are found (absolute thermal tolerance) or what the thermally most resilient species is globally (relative thermal tolerance). Answers to these questions can then be contextualized to the accompanying environmental conditions or long-term climate history. The value of centralized databases increases with the number of study data they hold, which in turn relies on the commitment and input of researchers, thus highlighting the importance of collaboration and data sharing.

accessibility, interoperability, and reusability) principles for data management (Wilkinson et al. 2016). Such a centralized system containing multiple specific databases would support different needs and generate positive feedback, promoting the collection of standardized data and the creation of standardized workflows.

BEYOND CORALS: APPLYING STANDARDIZED METHODS TO MARINE LIFE

Although coral reefs often epitomize the impact of climate change on ecosystems, the harmful effects of thermal stress are pervasive in the marine environment, affecting organisms ranging from bacteria to whales (Smith et al. 2023). Physiological impacts of thermal stress have been particularly investigated in aquaculture organisms (i.e., commercially important fishes and shellfish), but other foundation species, such as seaweeds and seagrasses, have also been well studied in recent years (Bennett et al. 2022). Importantly, the lessons learned from reef-building corals in terms of desirable method standardization (**Table 1**) are broadly applicable to all sessile marine species. Some additional considerations impact vertebrates and motile invertebrates, such as the size of the experimental tanks, the number of individuals per tank, the implementation of measures to reduce stress responses to captivity, the use of standardized endpoints (e.g., critical thermal maximum, lethal temperature, or onset of spasms), and the development of comparable estimates between different life stages. As with reef-building corals, discrepancies in methodology and endpoints to estimate thermal tolerance have long been recognized in fishes and motile invertebrates, limiting comparisons between studies and extrapolations to the natural environment (Chown et al. 2009, Lutterschmidt & Hutchison 1997). To this end, a framework incorporating the effects of the intensity and duration of the stressor on the organisms—the thermal tolerance landscape (similar to DHW in corals)—can reduce the effect of methodological differences and provide more robust thermal tolerance estimates across a wide range of marine species (Rezende et al. 2014). As a general rule, it may be worthwhile to bear in mind that virtually any scientific approach benefits from standardization. While standardized methods are commonplace in the medical field, they are admittedly more complex to implement in ecological settings. Yet, by increasing the reproducibility and comparability of the data, widespread standardization in marine sciences will catalyze new findings, allow for the tracking of management outcomes at larger scales, and more accurately inform future actions. Importantly, employing standardized methods does not come at an extra cost, which will hopefully foster their wide adoption in the marine field.

SUMMARY POINTS

1. Thermal stress experiments have a long history in marine research, but amid the climate emergency, there is an urgent need to characterize the response of organisms and the long-term trajectory of ecosystems.
2. Standardized methods are critical to ensure interstudy comparability, allowing researchers to generalize findings and scale up data collection efforts.
3. Contextualization of experiments, in situ surveys, and remote sensing using metadata also provides a form of standardization, reconciling similarities and differences between datasets.
4. By increasing the reproducibility and scale of data collection, standardized methods can help researchers, policymakers, and conservation practitioners make informed decisions to mitigate the effects of climate change on our oceans.

FUTURE ISSUES

1. Global ecosystem-specific databases with consistent data reporting, labeling, and formatting (i.e., data standardization) that will facilitate universal data access, retrieval, and comparison are urgently needed.
2. The integration of different types of thermal stress data across biological scales (i.e., from genes to ecosystems) will connect large-scale, long-term processes (e.g., climate)

and their effects on small-scale, short-term responses (e.g., bleaching susceptibility and mortality).

3. Novel standardized experimental approaches (e.g., short-term acute thermal assays) will produce comparable data, allowing researchers to contrast or consolidate patterns over large spatial scales, while new analytical tools (e.g., machine learning approaches) will analyze big data and allow for discovery of nonlinear relationships.
4. Automated inventorying and monitoring (e.g., of environmental DNA) will accurately assess standing genetic and biological diversity to pinpoint reef sites of high conservation value and to monitor conservation and restoration success through tracking of maintained or increased genetic and biological diversity.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

C.R.V. and R.A. are supported by the Paul G. Allen Family Foundation (Global Search project). C.R.V. and L.C. are supported by the Deutsche Forschungsgemeinschaft (project 458901010). C.R.V. and S.S. acknowledge funding from the King Abdullah University of Science and Technology (KAUST, grant OSR-2021-NTGC-4984). J.-B.R. is supported by an Australian Research Council Fellowship (FT210100100).

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