

Opinion: Missing half the picture, focus on stony corals during bleaching events has left critical knowledge gaps in our understanding of reef-scale bleaching and recovery

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Stony corals make up the bedrock of coral reefs, but they are not the only benthic organisms that contribute to reef diversity. Sponges, ascidians, octocorals, anemones, macroalgae, and more add directly to the complexity and biodiversity of reefs (Figure 1). Additionally, they provide food and habitat for many mobile species including specialist to non-stony coral habitat builders (Pratchett 2007; Epstein and Kingsford 2019). The majority of studies on reef impacts focus on how stony corals have been affected and often include other groups only when they are negatively impacting stony coral health, such as competition with or overgrown of corals by algae or sponges (Coll et al. 1987; Lapointe et al. 2007; Clements and Hay 2023), or recruitment of stony coral larvae to coralline algae (Webster et al. 2011; Tebben et al. 2015; Tanvet et al. 2022). While it is important to understand how stony corals respond to stressors as they build the foundation of reef structures, it is also important to understand how all habitat building species may be affected in order to disentangle reef-scale dynamics. This includes soft bodied habitat formers, such as octocorals, anemones, and macroalgae, which leave little or no trace of mortality after an acute stress event (Steinberg et al. 2020) and therefore need to be surveyed and sampled as bleaching events unfold. Coral reef phase shifts, where reefs that are stony coral dominated become dominated by other taxa after disturbance events are becoming increasingly common (Norström et al. 2009; Bell et al. 2013; Baum et al. 2016), as such it is particularly important to understand how all habitat-forming taxa on reefs respond to heat stress in order to predict changes to future reef composition.

The most widespread stressor affecting coral reefs and gardens is climate change induced bleaching. Bleaching is the breakdown of symbiosis between the cnidarian host and its dinoflagellate endosymbionts which results in expulsion of symbionts and can lead to starvation of the host if temperatures do not return to within the tolerance limits for symbiosis (Jones 1997; Baker 2001). While tropical stony corals have been the main focus of coral bleaching studies both in the field and in manipulative experiments, other groups of cnidarians and even sponges also form symbiosis with photosynthetic organisms and can bleach (Pita et al. 2018; Steinberg et al. 2020, 2022). In addition, macroalgae, such as kelp and coralline algae, can experience adverse health effects during heatwaves that can lead to die-offs (Wernberg et al. 2016; Cornwall et al. 2019). As such, scientific focus on the effects of heatwaves on stony corals to the exclusion of other species has led to a lack of clarity on the dynamics of bleaching on the full reef environment.

For example, the first study to report octocorals bleaching in Lord Howe Island was published in 2022 (Steinberg 2022), despite several manuscripts being published about previous bleaching events from 1998 – 2011 (Harrison et al. 2011; Boulotte et al. 2016). In addition, in a search of the Web of Science Core Collection on 26 Sept 2023 using the topic keywords “Great Barrier Reef”, “bleach*”, and “coral*”

(supplemental material 1), where * is any letter combination, such as bleaching or bleached; then replacing “coral*” with “octocoral*”, “macroalgae*”, etc. only 21 of 975 contain the keyword “octocoral*” (supplemental material 2), 38 contain they keyword “macroalgae*” (supplemental material 3), 29 contain the keyword “anemone*” (supplemental material 4), and 28 contain the keyword “sponge*” (supplemental material 5). Even within the stony corals, different species, growth forms, and functional groups can respond quite differently during a bleaching event (Loya et al. 2001; Brandt 2009; Fabricius et al. 2011). Accordingly, studies that have examined the effects of heatwaves on reefs in non-stony coral species have found that these species respond differently to stony corals, and that there is significant interspecific variability (Goulet et al. 2008; Panithanarak 2015; Steinberg et al. 2022). Including non-stony coral species in reef-scale surveys, such as was done in the collaboration of Steinberg et al. (2022) and Moriarty et al. (2023), can help elucidate the reef-scale patterns of which species bleach, which die, and which are resistant to the negative impacts of heat stress.

In manipulative laboratory experiments of bleaching, the vast majority focus on stony corals, especially those that are considered to be vulnerable to bleaching (Bonesso et al. 2017; Gierz et al. 2020; McLachlan et al. 2020). Despite this, some interesting results in experimental heat stress of non-stony corals have helped us understand which species may or may not persist through heat stress in the field. For example, during manipulative bleaching of two Alcyonacean octocorals and one Xeniid octocoral, the Xeniid bleached and experienced animal cell apoptosis at much lower temperatures than other species (Strychar et al. 2005; Sammarco and Strychar 2013). As such, Xeniiids may die and dissociate from the reef surface before bleaching begins in other species, and so visual surveys may underestimate bleaching prevalence. In fact, octocorals may generally fare more poorly if they bleach, as the few studies that examine them have found that many die during or shortly after bleaching (Goulet et al. 2008; Sammarco and Strychar 2013; Steinberg et al. 2022). This is particularly interesting as octocorals often do not bleach as quickly as stony corals (Goulet et al. 2008; Steinberg et al. 2022), suggesting that despite a delay in the onset of bleaching, if the heat stress event is prolonged octocorals are likely to fare poorly. Unfortunately, we do not have enough evidence to fully back up this hypothesis, and additional evidence during bleaching surveys and manipulative bleaching experiments is required.

While some patterns have begun to emerge in octocoral responses to heat stress, in other groups these patterns are not as clear. Anemones retract into crevices when stressed, meaning that quantifying anemone bleaching during heat stress can be extremely difficult (Hill et al. 2014; Steinberg et al. 2022). Studies of anemone bleaching have found that anemones are capable of survival, but recovery can be prolonged (Hill et al. 2014; Frisch et al. 2019; Hayashi and Reimer 2020) and survival is not assured (Hobbs et al. 2013; Thomas et al. 2015). As many anemonefish species are threatened by loss or even prolonged retraction of their host anemones (Saenz-Agudelo et al. 2011; Hobbs et al. 2013; Howell et al. 2016; Frisch et al. 2019), and bleaching significantly reduces settlement of anemonefish larvae (Scott and Dixon 2016), understanding the responses of anemones to heat stress is integral to conservation of both anemones and anemonefish. Additionally, if anemonefish are lost because of retraction or death of anemones, surviving anemones will likely have lower survivorship even if conditions remain optimal as anemonefish provide critical services to their hosting anemones (Frisch et al. 2016). Understanding how symbiotic relationships such as these break down during bleaching is integral to maintaining reef biodiversity. Some work has been done in this vein on anemones and

anemonefish and on coral gobies that inhabit branching stony corals (Saenz-Agudelo et al. 2011; Froehlich et al. 2021), but has been so far overlooked in other hosts or with invertebrate symbionts.

Sponges are also underrepresented in the reef literature as compared to stony corals. Many sponges are symbiotic and can also undergo bleaching during heat stress (McMurray et al. 2011; Pita et al. 2018), and even those that are aposymbiotic are impacted by high temperatures (Pita et al. 2018). In the geological record after the end-Triassic coral mass extinction, sponges proliferated and become the dominant organisms on many reefs, which may happen again in the current extinction crisis (Bell et al. 2013). As such, it is particularly important that we understand the responses of sponges to bleaching events and whether they proliferate during the post-bleaching recovery period.

In the same vein, macroalgae are neglected in studies of coral reef bleaching despite being significant primary producers that can compete with coral for space or even become substrate for coral larval recruitment (Sandin and McNamara 2012; Tebben et al. 2015; Clements and Hay 2023). Though few studies have examined macroalgae through bleaching, some work has been done on the effects of macroalgae-coral interactions through bleaching. For example, Smith et al. (2022) found that macroalgae cover protected encrusting corals from bleaching stress, but inhibited recovery of all coral types. In addition, they found that macroalgae proliferated after bleaching, which may have further delayed recovery (Smith et al. 2022). As such, understanding the dynamics of macroalgal responses to heat stress and their interactions with other benthic groups can help us understand not only group-level responses, but also make reef-scale multi-species predictions. Finally, while some studies have found that coralline algae is crucial settlement media for coral larvae, and coralline algae can be killed by heat stress (Webster et al. 2011; Tebben et al. 2015; Tanvet et al. 2022), we have little information on the dynamics of coralline algae through coral bleaching events. Understanding how sponges and algae respond to heat stress is crucial to understanding the full dynamics of heat stress on reefs and their role in inhibition or facilitation of coral reef recovery.

Overall, by overlooking species that are not stony corals during bleaching we have limited our understanding of the consequences of heat stress on coral reefs, reef-scale capacity for recovery, and our ability to predict what recovered reef composition may be. Predicting if a reef that was originally dominated by stony and octocorals will likely become macroalgal or sponge dominated would be a boon for reef management and could assist in formulating management plans during the bleaching recovery period. I suggest that overall reef composition and health state of all major habitat-forming groups be included in surveys of heat stress on coral reefs. A partial example of this is the collaboration of Steinberg et al. (2022) and Moriarty et al. (2023), where they quantified full reef composition through bleaching and recovery at Lord Howe Island but did not monitor the health state of any groups outside of cnidarians. Secondly, I suggest that foundational studies of coral bleaching in stony corals (Cziesielski et al. 2019; Weis 2022), be replicated in other groups to bring our understanding of between- and within-group variation in heat stress susceptibility up to par with that of stony corals. Finally, future, cutting edge research into heat stress of habitat forming organisms should include multiple groups, which will allow us to understand how stony corals may fare against competing habitat formers. As bleaching events are expected to happen yearly by 2050 (Hoegh-Guldberg 1999), the time is now to undertake research that will allow us to manage reefs into the future.

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Figure 1: examples of habitat forming biodiversity on coral reefs. a) Mixed anemone and stony coral habitat at One Tree Island, QLD; b) mixed stony coral, octocoral, and algal habitat at Norfolk Island, NSW; c) a field of mixed branching stony corals and encrusting octocorals, One Tree Island, QLD; d) Mixed *Pocillopora* sp. And macroalgae habitat, Norfolk Island, NSW; e) mixed stony coral, octocoral, ascidian, sponge, and macroalgae habitat, Solitary Islands, NSW. All photos by John W. Turnbull, marineexplorer.org

