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How fishes and invertebrates impact coral resilience

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Increasingly intense and frequent ocean heatwaves are causing widespread coral mortality. These heatwaves are just one of the many stressors — among for instance ocean acidification, nutrient pollution and destructive fishing practices — that have caused widespread decline of coral reefs over the past century. This destruction of reefs threatens the remarkable biodiversity of organisms that depend upon coral reefs. However, recent research suggests that many of the fishes and invertebrates that inhabit coral reefs may play an underappreciated role in influencing the resistance and recovery of corals to stressors, especially those caused by global climate change such as ocean heatwaves. Unraveling the threads that link these coral inhabitants to the corals' response to stressors has the potential to weave a more comprehensive model of resilience that integrates the plight of coral reefs with the breathtaking diversity of life they host. Here, we aim to elucidate the critical roles that coral-associated fishes and invertebrates play in mediating coral resilience to environmental stressors. By integrating recent research findings, we aim to showcase how these often-overlooked organisms influence coral resilience in the face of climate change.

While many corals feed on plankton, they are only able to thrive in nutrient-poor tropical waters because of their symbiosis with zooxanthellae — the microscopic photosynthesizing algae that live within the coral tissue and produce carbon for the coral in exchange for shelter and carbon dioxide. Extreme heat stress causes a breakdown of the coral–algae symbiosis, leading to the disappearance of the zooxanthellae (and their photosynthetic pigments), leaving corals bleached[1,2]. Bleaching can kill the coral. The majority of previous research seeking to understand the limits of the coral–zooxanthellae symbiosis has ignored the potential role of the wide diversity of fishes and invertebrates that live intimately associated with the coral, often living deeply embedded between their branches. However, recent studies in Australian and Polynesian waters have shown that corals living closely associated with small planktivorous damselfishes are less likely to bleach and can maintain high physiological performance and positive growth rates during and after simulated heatwaves[3,4] (Figure 1, top left). In contrast, corals without fish present underwent bleaching and had poorer physiological performance and stunted growth. This fish-induced increase in coral resilience is likely to occur because fishes change the nutrient environment of corals. Many reef fishes spend most of their day hovering above their coral homes feeding on plankton. They then retreat inside the coral to hide from predators or sleep at night, and during that time they excrete and egest ammonia-rich waste. Unlike nitrate, which is the typical form of nitrogen available in seawater, ammonia is a much easier form of nitrogen for zooxanthellae to process. Consequently, the presence of fish allows corals to sustain their zooxanthellae despite increased temperatures.

Another recent study[5] suggests fishes can similarly increase coral resilience to heat stress, though perhaps through a different mechanism. Territorial damselfishes that foster small gardens of turf algae are known to defend corals from predation[6]. Researchers showed that corals living within the territories of such farmerfish during a heatwave were a third less likely to die and twice as likely to recover. The authors hypothesize that fish increase coral resilience to heat stress by reducing coral predation. When corals are protected from predators by farmerfish, they do not need to retract their polyps as often to protect themselves. As a result, they are able to feed more on zooplankton, thus supplementing the nutrition provided by the zooxanthellae. Other recent research[7] shows that territorial damselfish increase the abundance of small mysid shrimps — crustaceans living in the water column on coral reefs and playing a crucial role in the food web and nutrient cycling[8]. This increase in abundance inside the fish territories has the potential to increase nutrients (via excretion by the shrimp) and possible food (if coral consume the shrimp), which can potentially benefit the corals during a heat wave. Thus, heterotrophic feeding can be crucial to coral nutrition and survival by compensating for the loss of zooxanthellae if the coral–algae symbiosis breaks down during a heatwave[9]. Collectively, this novel research highlights the potential role of coral-associated fishes in mediating the response of certain corals to marine heatwaves.

The importance of coral-associated animals extends beyond fishes to include a diversity of poorly studied invertebrates that live among the coral branches but rarely emerge and are often overlooked. Some of these species, such as guard crabs (*Trapezia*) and snapping shrimp (*Alpheus*), benefit corals and comprise an additional symbiotic mutualism with the coral — the crabs and shrimps eat the coral's lipid-rich mucus, and in exchange remove harmful sediments and protect the coral from predatory sea stars[10] (Figure 1, top right). A recent experiment[11] simulated future acidified conditions for corals living with and without obligate shrimps and crabs and found that the crustaceans reduced coral growth under benign laboratory conditions, demonstrating a cost to hosting the crustaceans. However, under acidified conditions, but without any other stressors, the corals incurred no net cost of hosting the crustaceans. Thus, acidification changed the relationship between coral and shrimp from parasitic to commensal, potentially allowing the coral to grow despite the more acidic environment. The mechanism

Figure 1. Macrosymbionts as powerful drivers of coral resilience.
Coral-associated invertebrates and fishes that affect coral growth, survival, and resilience. (Top left) The damselfish *Dascyllus aruanus* improves coral health by oxygenating water, subsidizing nutrients, removing sediment, and defending against predators, which can boost coral growth and provide resilience to ocean heatwaves (photo: Thomas Vignaud). (Top right) The coral crab *Trapezia rufopunctata* enhances coral health by defending against predators and aiding in the removal of sediment (photo: Thomas Vignaud). (Bottom left) The corallivorous snail *Coralliophila abbreviata*, which reduces coral resilience by increasing bleaching severity and post-bleaching tissue mortality (photo: Elizabeth Shaver). (Bottom right) Vermetid snails (*Ceraesignum maximum*) harm corals by reducing calcification, flattening colonies, and decreasing photosynthetic yield through its mucus nets, which impede water flow and alter chemical conditions.

for this change remains unknown. However, it is likely that other stressors, such as sedimentation[12,13], would further enhance the benefits of harboring the crustaceans. As with the effects of coral-associated fishes, these crustaceans are by no means a solution to the problems wrought by climate change. For example, under extreme heating, the cooperative relationship between crabs and shrimps can flip to an antagonistic one, in which the largest male crabs fight, kill and expel other crustaceans[14]. Because coral-associated invertebrates are hard to study, we lack a comprehensive understanding of how they are linked to coral resilience. In addition, beneficial effects are not limited to the species that live obligately with coral but can also be mediated by mobile species. For example, a recent experiment showed that a spider crab (*Mithrax spinosissimus*) increases the survival of young corals by 85% by reducing noxious macroalgae that compete with corals for space and light[15], thus promoting coral recovery after mortality events. Similarly, a recent study showed sea cucumbers mitigate coral disease by eating and processing the bacteria found in detritus in nearby sand[16]. These two new studies highlight the critical understudied role of invertebrate biodiversity in driving coral resilience that warrants future focus.

The benefits that these coral-associated animals provide are intriguing, and there may yet be additional benefits to uncover in the understudied diversity of fishes and invertebrate species that occupy corals. For example, a single coral colony of the cauliflower coral (*Pocillopora* spp.) at .01 m^3 can house more than 65 crustaceans and fishes from more than 20 species[17]. We know almost nothing about the natural history of most of these species, let alone an understanding of their link to coral resilience. Moreover, it is likely that there is a balance between beneficial and detrimental occupants affecting the coral. For example, a recent study[18] of Caribbean brain corals (*Pseudodiploria* and *Diploria* species), found that the presence of a parasitic snail (*Coralliophila abbreviata*) decreased the coral's ability to withstand and recover from a major ocean heatwave (Figure 1, bottom left). These snails may have the reverse effect of the fishes described above: instead of adding nutrients, they chronically drain the coral's energy reserves by slowly scraping away tissue, leaving it with few resources and causing its relationship with zooxanthellae to break down. Similarly, other coral-dwelling snails can influence coral resilience through an alternative pathway. For instance, the vermetid tube snail (*Ceraesignum maximum*), which uses mucus nets to feed on detritus and small zooplankton above living coral tissue, reduces growth of corals and the abundance of zooxanthellae, as well as the coral microbiome, all of which can lead to colony death[19] (Figure 1, bottom right). Such shifts in the coral bacterial communities and reductions in algal symbiont abundance likely have major ramifications for the corals' capacity to withstand warming. Therefore, additional research is critical because presently we do not know how these beneficial and detrimental species combine or interact to affect how corals respond to heatwaves or acidification, constraining our ability to predict the link between this understudied coral-associated biodiversity and coral resilience.

A new perspective is emerging on how fishes, invertebrates, and microalgae that occupy corals potentially affect coral resilience. Although the role of zooxanthellae has long been appreciated, we are only beginning to understand how these diverse macrosymbionts that occupy corals can affect the capacity of coral to resist and recover from climate-induced stress. Yet, it remains unclear what mechanism underlies these benefits and whether their effects can be generalized across different species of corals, fishes and invertebrates.

We are only starting to understand how coral occupants modify coral resilience to the multitude of stressors they face, including increased water temperature, disease, nutrient pollution, sedimentation and hypoxia. Fish and invertebrate occupants are of course no silver bullet for ameliorating effects of climate change on coral reefs; without a rapid reduction of global carbon emissions the effects of climate change on coral reefs are likely to be devastating. That said, these small, unstudied organisms have the potential to locally confer coral resilience, which may be particularly relevant to small scale restoration efforts. Looking forward, it is critical we build a deeper understanding of the basic biology of coral-associated organisms and incorporate the complex role of this diverse guild of organisms into our understanding of how coral reef ecosystems respond to environmental change. Ultimately, this broader more taxonomically inclusive perspective will improve our ability to accurately understand the resilience and adaptive capacity of this diverse ecosystem.

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DECLARATION OF INTERESTS

The authors declare no competing interests.

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