Impact of global climate change on marine bacterial symbioses and disease

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Microbes constitute the largest diversity and biomass of all marine organisms, yet they are often ignored during discussions about the impacts of environmental change. This is despite the fact that, of all the organisms on the planet, it is the microbes that will play the largest fundamental role in either mitigating or exacerbating the effects of global climate change. Microbes will also be the first and fastest to shift their metabolic capabilities, host range, function and community dynamics as a result of climate change. Therefore, an understanding of microbial community composition and function in individual niche habitats is vital.

Within the marine ecosystem, microbes are involved in a variety of important relationships with invertebrates from a range of taxa including sponges, cnidarians, molluscs, echinoderms and nematodes. These obligate symbiotic relationships are vital for the continued health of the animal, with microbes providing many important functions including nutrition [1], reproduction [2], chemical defence and the production of secondary metabolites [3], structural support [4] and the metabolism of waste products from the host [5]. There are also many examples of symbioses where the nature of the relationship between the host and their symbionts is not yet understood. With such a wide range of functions, environmental conditions that disturb the distribution or abundance of symbiotic marine microbes could have significant effects on host fitness and survival.

In recent decades, there has been a global increase in reports of disease in marine organisms [6, 7]. Disease epidemics have affected both vertebrate and invertebrate species including fish, seals, dolphins, shellfish (oysters, scallops, abalone and clams), starfish, urchins, sponges and corals (as reviewed by Harvell and colleagues [8]). Disease outbreaks have also affected seagrass, kelp and coralline algae populations [8]. Whether these reported disease outbreaks are due to new pathogens, changed environmental conditions or improved detection mechanisms is a topic of current debate. In any case, environmental stress such as climate change, which compromises the physiological fitness of marine invertebrates and their symbionts and provides enhanced conditions for disease-causing microbes, will likely increase the prevalence of disease in marine systems.

Impact of climate change on symbiosis

With measurable increases in sea surface temperature (SST) over the last 30 years (see Lough in this issue), the severity and frequency of coral bleaching events have increased [9]. This has resulted in a large research effort directed towards understanding the impact of elevated SST on the symbiotic relationship between corals and zooxanthellae (see van Oppen & Burghardt in this issue).

However, there is a growing recognition that microbial partners other than the zooxanthellae represent an important component of coral symbioses. The coral 'holobiont', a term originally coined by Rowan [10], was more recently revived and modified [11, 12] to describe the symbiotic association of the coral host, its symbiotic zooxanthellae and all the other microbial partners closely associated with corals, including fungi, bacteria, archaea, and viruses. These, mostly prokaryotic, microbes all play important though poorly understood functional roles in coral health.

Recent trends in coral health research suggest that coral bacterial associations are destabilised as a result of environmental disturbance [13]. For example, Bourne and colleagues [14] demonstrated that, as corals bleached on a natural reef flat in response to elevated SST, the microbial community shifted to a *Vibrio* spp. dominated community. Post-bleaching, the coral associated microbial consortia returned to a community similar to pre-bleaching associations, providing further evidence for corals selecting and shaping their microbial holobiont partners and the significant impact of environmental change on these relationships.

Few studies have examined the impact of increasing SST on non-coral microbial symbioses in reefal systems. Similar to corals, microbial symbionts in other invertebrates are likely to have strict temperature thresholds and a breakdown in symbiosis is likely to result in reduced host health (even mortality) and fitness, shifts in hosts geographic range, increased disease or an increase in predation/grazing. There is also the possibility that increased SSTs may cause a shift from symbiotic to pathogenic function for some species. A recent example using a Great Barrier Reef sponge clearly demonstrates that elevated seawater temperatures can cause a shift in the microbial community and that this shift is attributed both to the loss of stable symbionts and the establishment of alien microbial populations, including potential pathogens (Figure 1) [15].

Impact of climate change on disease

The most comprehensive base-line data demonstrating changes in reef ecosystems due to disease are in the Caribbean, where changes in key reef organisms and coral cover [16, 17] are correlated with an unprecedented increase in coral diseases [18, 19]. While less

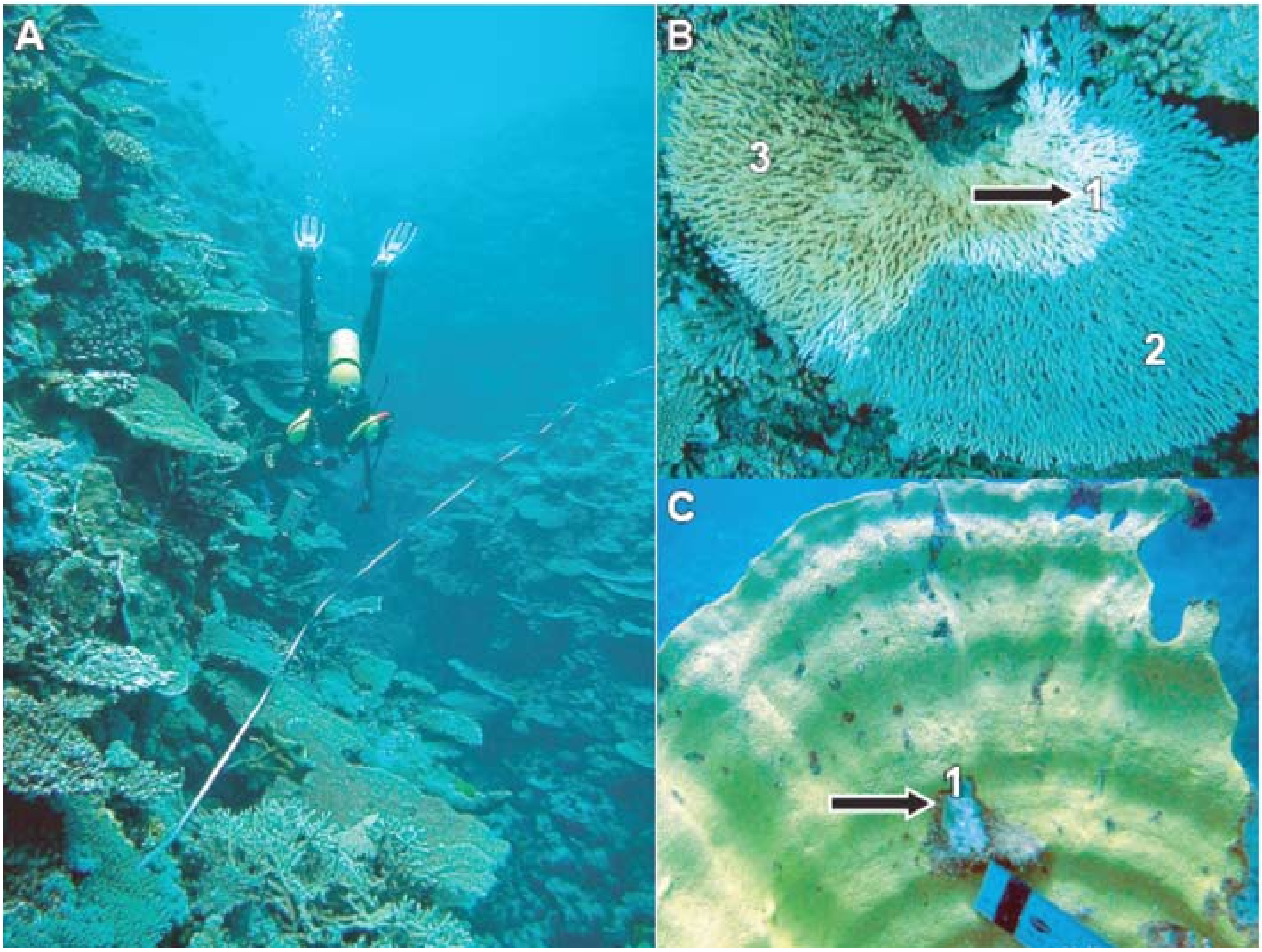

Figure 1. Great Barrier Reef examples.
(A) Transect line laid on a coral reef assessing health and disease prevalence (photo AIMS Long-term Monitoring Program).
(B) White syndrome on the coral *Acropora clathrata* (photo AIMS Long-Term Monitoring Program): 1. White lesion actively progressing across the plating colony; 2. Healthy coral tissue; 3. Dead coral skeleton over grown with algae.
(C) A diseased specimen of the Great Barrier Reef sponge *Ianthella basta* showing tissue lesions [1].

is known about other regions of the world, particularly the Indo-Pacific, there is some evidence that temperature stress is also causing a decline in reef health in our own backyard, the Great Barrier Reef [20, 21].

Climate change may affect the frequency and severity of disease outbreaks by increasing the prevalence and virulence of pathogens, facilitating invasions of new pathogens or reducing host resistance and resilience [22]. In particular, increased seawater temperature could potentially affect the overall health of marine organisms, thereby contributing to an increased or decreased incidence of disease. Also, as temperatures increase, oxygen levels decrease and metabolic rates increase, potentially leading to additional respiratory stress in some organisms. It is interesting that disease outbreaks appear to be caused by so many different types of pathogens – viruses, bacteria, fungi and parasites – suggesting that the increased incidence of disease associated with higher SST is potentially linked to a reduction in the health of the host organisms [23].

Alternatively, increasing temperature may alter the virulence mechanisms of the pathogen as is seen with the coral pathogen *Vibrio shiloi*. A large amount of research has been directed towards describing the virulence of this coral pathogen, as reviewed by Rosenberg & Falkovitz [24]. These studies have characterised a wide range of virulence mechanisms that are stimulated under elevated SSTs. These include chemotaxis and adhesion to a β-galactoside receptor in the coral mucus, penetration into epidermal cells, differentiation into a viable-but-not-culturable state, intracellular multiplication, production of toxins that inhibit photosynthesis and the production of superoxide dismutase to protect the pathogen from oxidative stress.

In sponges, it appears that under adverse environmental conditions such as high temperature and reduced water flow, normally non-pathogenic bacteria become capable of degrading the spongin skeletal fibres within live tissue [25]. The removal of bacteria and sponge excretion products by passive and active ventilation could also be reduced, facilitating bacterial proliferation and the onset of disease. Under conditions of high SSTs and reduced water flow, sponge pathogens may switch on virulence mechanisms, sponges may be unable to control proliferation of bacteria, or degeneration of sponge tissue may occur when exogenous bacteria replace the associated populations, as reviewed by Webster [26].

The prediction of disease outbreaks using climatic models was possible with Dermo disease of the oyster *Crassostrea virginica*, caused by the protozoan parasite *Perkinsus marinus* [27]. Dermo disease closely follows the El Niño southern oscillation cycle with prevalence and infection intensity declining during El Niño events (cold wet conditions) and rising during La Niña events (warm dry conditions). There is also some evidence that coral disease events are more common following periods of temperature stress and coral bleaching [20], adding weight to the argument that stressed environments have less resilience to disease. Unfortunately, our current disease epidemiology datasets for most marine species are not yet extensive enough for valid correlations to be made with other climate change conditions. Predictions of how disease will impact marine communities are also complicated by the fact that stressors (such as increased SSTs) may sometimes have a more negative impact on the pathogen than on the host [28], a scenario that would lead to recovery of infected populations. It is therefore important to acknowledge that changing environmental conditions may increase or decrease the occurrence of disease.

Conclusions

Our understanding about how climate change will impact upon the health of marine systems is in its infancy, and greater effort is needed to understand the 'normal' or 'acceptable' health status of these environments before they are irreversibly affected. Marine invertebrate symbioses represent a useful 'canary in the mine shaft' model for evaluating how climate change will impact on the overall coral reef ecosystem. Shifts in the microbial partners of these close symbiotic associations will provide an early indication of stress and impact. Diseases and disruptions to symbioses as a result of climate change have the potential to cause major impacts on population levels, biodiversity and community structure of marine ecosystems by causing shifts in the abundance of various groups.

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