

Part II: Species and species groups

Chapter 5

Vulnerability of marine microbes on the Great Barrier Reef to climate change

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I make no apologies for putting microorganisms on a pedestal above all other living things. For if the last blue whale choked to death on the last panda, it would be disastrous but not the end of the world. But if we accidentally poisoned the last two species of ammonia-oxidisers, that would be another matter. It could be happening now and we wouldn't even know...

Tom Curtis (July 2006) in Nature Reviews Microbiology

5.1 Introduction

Global climate change will have a direct effect on the Great Barrier Reef (GBR) as discussed in previous and subsequent chapters. The primary effect of climate change will be a 1 to 3°C increase in global sea surface temperature along with sea level rises as predicted by Intergovernmental Panel on Climate Change (IPCC) models. Other associated effects include increased acidity and increased terrestrial inputs. The effects of climate change will have a significant impact on marine microbes, potentially altering microbial diversity, function and community dynamics. Although microbes constitute by far the largest diversity and biomass of all marine organisms, they are often ignored in discussions about the impacts of climate change (Figure 5.1). This is despite the fact that the vast microbial life on our planet plays a central role in either accentuating or mitigating the effects of climate change. Since microbes are central to the global cycles (including carbon, nitrogen and trace gases), changes to temperature, nutrient availability and environmental pH will have major impacts on microbial processes central to the climate debate. This chapter will discuss the exposure, sensitivity and impacts of climate change on marine microbes at global, regional and local scales, providing examples of observed impacts in marine ecosystems. In doing so, the adaptive capacity and vulnerability of marine microbes to climate change will be assessed. The background provided in this chapter emphasises the importance of marine microbes and outlines why they require greater appreciation in research effort and consideration in predictive climate models.

5.1.1 Tropical marine microbes

With more than a billion micro-organisms in a litre of sea water, the biodiversity of microbial communities (Figure 5.1) and the functional roles they play in the marine environment (Figures 5.2 and 5.3) are hugely significant. Limitations with traditional culture-based methodologies (generally only 0.1% to 1% of marine microbes can be recovered on culture media by conventional approaches) mean that the diversity, phylogeny and function of marine microbes have remained largely unexplored. However, with the advent of molecular techniques, we are now discovering a huge diversity of marine micro-organisms⁹⁰ and uncovering a wide range of previously unknown microbial functions^{35,52,43}. The functions and species composition of bacterial communities across the globe, including those of the GBR, may be adversely or positively affected by climate change. Shifts in microbial community structure may subsequently enhance or mitigate the effects of further climate change.

Marine microbes are highly abundant, with global oceanic densities estimated at 3.6×10^{29} bacterial cells⁹⁰, 1.3×10^{28} archaeal cells⁵⁸ and 4×10^{30} viruses⁹². Currently, estimates of marine bacterial diversity range from only a few thousand species⁴² to as many as two million distinct taxa¹⁹. Most analyses use a criterion of more than 97 percent sequence identity in the small subunit of ribosomal RNA to define a species or taxon. However, Fuhrman³³ points out that physiological and genomic differences may indicate a division on an even finer scale, suggesting that previous estimates of marine bacterial diversity may be too low³³. Additionally, recent research by Sogin et al.⁹⁰ examined microbial diversity in the North Atlantic and discovered that, while a relatively small number of microbes dominate, thousands of low-abundance microbes actually account for the majority of phylogenetic diversity. Sogin et al.⁹⁰ concluded that 'this rare biosphere is very ancient and may represent a nearly inexhaustible source of genomic innovation'.

Figure 5.1 Estimated number of marine species

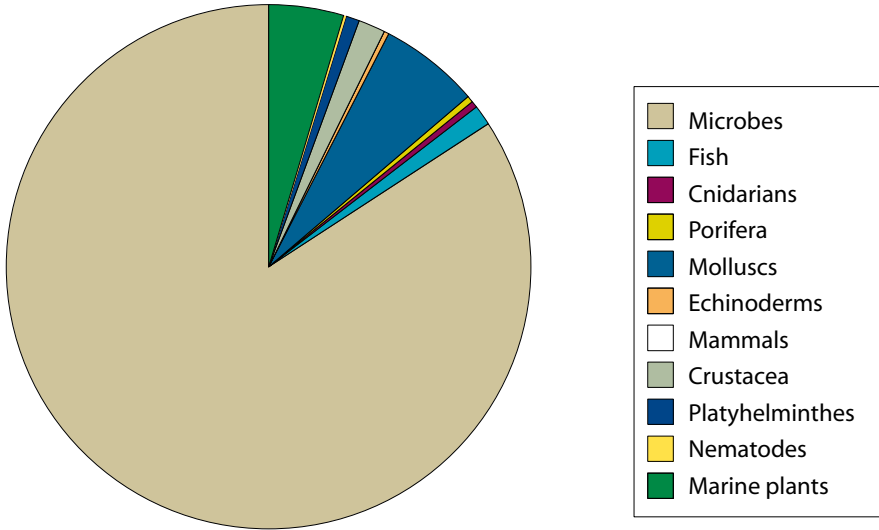


Figure 5.2 Ecological roles of marine microbes on the Great Barrier Reef

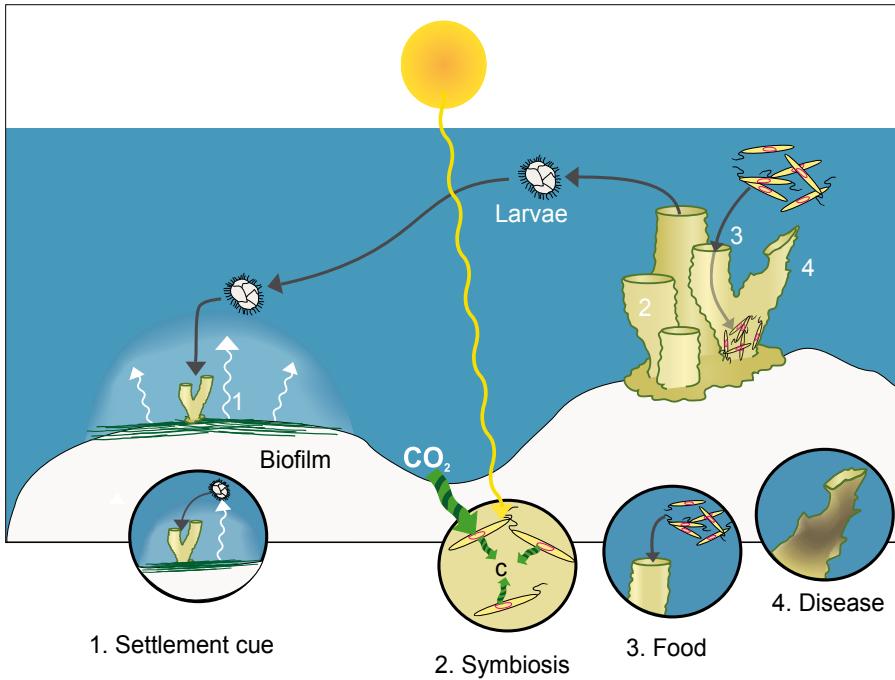
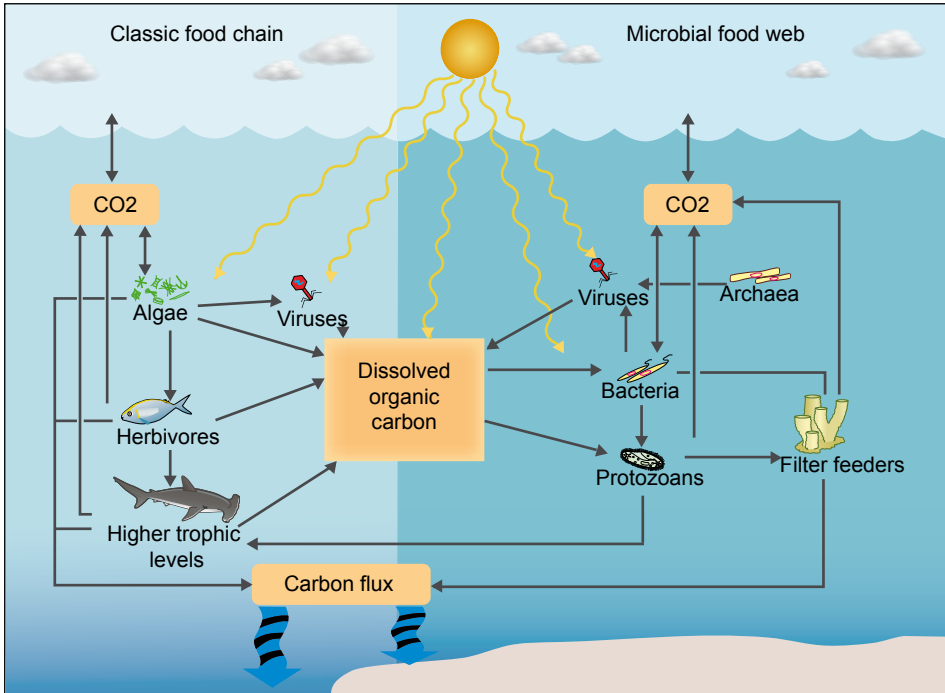


Figure 5.3 An overview of the classical food chain and microbial loop (Adapted from DeLong and Karl²⁴)



5.1.2 The functional role of marine microbes

5.1.2.1 Nutrient cycling

Changes in rates of bacterial photosynthesis or inorganic flux through the microbial loop can have major impacts on carbon cycling and on global climate. Bacteria are estimated to be responsible for 20 to 50 percent of marine primary productivity^{16,29} and perform fundamental roles in the degradation of organic matter. In the upper 500 metres of the ocean, microbes consume an estimated 75 percent of the sinking particulate organic carbon flux¹⁶. Marine microbes are also crucial to various bio-geochemical processes such as nitrogen fixation, chemolithoautotrophy, sulfate reduction and fermentation. Environmental perturbations that affect bacterial abundance or community composition are therefore likely to have large-scale effects on ecosystem function.

The traditional view of the marine carbon cycle was that eukaryotic organisms were the only important players in the transfer of carbon between trophic levels. Bacterial processes were largely ignored because bacteria were thought to be inactive and present in low numbers. It is now clear that this historical view of carbon flux from photosynthetic phytoplankton to herbivorous zooplankton to higher organisms is incomplete and the microbial loop needs to be considered in addition to this grazing food chain (Figure 5.3). This paradigm shift has come about over the past 30 years as



improvements in microbiological techniques for enumeration, measurement of growth and activity, and assessment of microbial diversity have revolutionised our understanding of marine microbiology²⁴. It is now clear that organic flux into bacteria is a major pathway through which, on average, one-half of oceanic primary production passes^{2,1}.

Archaea were traditionally thought to be restricted to extreme environments but are now known to be highly abundant in sea water^{22,34,25}. The Archaea comprise two major groups: the crenarchaeal Marine Group I, which dominates in deeper waters; and the euryarchaeal Marine Group II, which is more numerous in surface waters. Planktonic archaea are metabolically active and are able to take up inorganic carbon, contributing between 10 and 30 percent of total prokaryotic production in deep North Atlantic samples⁴⁸. The physiology of archaea in the marine environment is still poorly understood, but there is indirect evidence that marine crenarchaeotes might be capable of ammonia oxidation and may therefore play a role in nitrogen cycling⁹⁹. A recent study determined the natural distribution of radiocarbon in archaeal membrane lipids at two depths in the North Pacific, showing that the dominant metabolism at depth is autotrophy, whereas archaea in surface waters are predominantly heterotrophs⁵⁵. Although many questions on archaeal metabolism remain unanswered, it is now clear that crenarchaea in the oceans play major roles in both carbon and nitrogen cycling²³. The roles of pelagic archaea in the GBR have not yet been studied. However, it is likely that the GBR will have high numbers of the euryarchaeal Marine Group II archaea found in other shallow coastal regions.

The importance of marine viruses was not appreciated until the late 1980s but they are now known to be the most abundant biological entities in the sea. Bacteriophages cause bacterial mortality, creating a carbon cycle in which the dissolved organic matter assimilated by bacteria is released via bacterial lysis and metabolised by other bacteria, enhancing upper ocean respiration. Marine viruses are generally host specific and display a density-dependent mode of infection. Hence, they have considerable potential for altering bacterial community composition in the marine ecosystem. During algal blooms, marine viruses can infect the rapidly increasing population of algae, and viral lysis of microalgae can result in the release of large amounts of dimethylsulphide into the atmosphere¹²⁵. Dimethylsulphide triggers cloud formation, illustrating yet another mode of marine microbe and climate interaction.

In addition to marine environments, benthic environments are also host to microbial communities. Benthic environments in the GBR include muddy and sandy sediments, coral rubble and rock surfaces. Nitrogen fixation has been reported to occur in coral reef sediments¹⁵, with sediments surrounding Heron Reef containing ubiquitous and diverse nitrogen-fixing communities⁴⁹. The total bacterial communities in sediments are diverse, and their composition is influenced by biotic and abiotic factors such as wave energy and sediment depth⁴⁹. Sandy sediments in the vicinity of coral reefs can also contain high numbers of benthic microalgae⁴⁵. Studies in these environments and similar environments in other ecosystems consistently find that benthic surfaces and sediments are colonised by complex and diverse bacterial and archaeal communities. Benthic microbial communities are important in nutrient cycling, particularly under anaerobic conditions within sediments. Cycling processes in anaerobic estuarine and coastal sediments can include anaerobic methane oxidation by archaea and anaerobic ammonia oxidation by planctomycete bacteria^{97,94}.

5.1.2.2 Symbiosis

Symbiosis is considered a permanent association between organisms of different species. Marine microbes are involved in a variety of important symbiotic relationships with marine invertebrates from a range of taxa including sponges, cnidarians, molluscs, echinoderms and nematodes. Proposed symbiotic functions for marine microbes include: nutrition (through direct incorporation of dissolved organic matter in the sea water or translocation of photosynthate¹²¹, quorum sensing⁷⁰, assistance with reproductive processes⁶¹, assistance in chemical defence¹⁰¹, contribution to structural rigidity¹²¹, metabolism of a wide range of waste compounds¹¹⁹, and production of secondary metabolites⁸⁵. There are also many symbioses where the type of interaction between the host and its symbionts remains unknown. With such a broad range of functions, environmental conditions that affect the distribution or abundance of symbiotic marine microbes could have significant effects on host fitness and survival.

The best studied symbioses in GBR invertebrates are those between corals and their symbiotic zooxanthellae (Hoegh-Guldberg et al. chapter 10), and between sponges and their associated bacteria. In the case of sponges, more than 50 percent of the wet weight of the organism can be composed of bacteria. These are often remarkably complex symbioses with high microbial diversity, including novel species that have not been found in other ecosystems. There is evidence that some bacteria are ubiquitous in various sponges from different oceans and that some of the phylogenetic clades found in sponges are more similar to each other than to sequences found in other environments^{47,30,51}. For example, the bacterial genus *Poribacteria* has so far been found only in sponges, and these microbes have less than 75 percent sequence homology to previously known bacteria³¹. Many studies also report that sponges contain distinct microbial communities not found in the surrounding sea water^{108,47,95}. Taylor et al.⁹⁵ distinguished three types of sponge-associated bacteria: *specialists* found only on one host species, sponge associates found in multiple sponge species but not in sea water, and *generalists* from multiple hosts and the surrounding sea water.

In the intensively studied GBR sponge *Rhopaloeides odorabile*, the cultivated bacterial community is dominated by an alphaproteobacterium¹⁰⁸, close relatives of which were subsequently found in many other sponges from broad tropical locations^{96,68,30}. However, the total microbial community in *R. odorabile* as detected by molecular techniques contains a great diversity of bacteria¹¹⁰ as well as two archaea¹⁰⁹. The roles of many of the symbionts in this sponge remain enigmatic, although the culturable alphaproteobacterium appears to be linked to sponge health¹¹⁹. In other GBR sponge symbioses, the role of microbial symbionts is better understood. Autotrophic cyanobacterial symbionts can contribute to host nutrition through extracellular lysis and phagocytosis¹¹⁸ or by transfer of glycerol to sponge tissue¹²⁰. Considering the predominance of bacteria within sponges, the complexity of these symbioses and the evidence for vertical transfer of some sponge symbionts through larvae^{30,102}, it seems likely that bacterial symbionts play vital roles for their host sponges. Shifts in these microbial communities due to climate change are therefore likely to affect sponge health, growth rates and capacity for defence from predation and fouling.

Corals are associated with an abundant microbiota in addition to the *Symbiodinium* symbiosis discussed elsewhere in this volume (Hoegh-Guldberg et al. chapter 10). This includes bacteria in the coral surface microlayer^{83,69} and bacteria and fungi within the coral tissue^{63,27,84}. A diverse assemblage of archaea (including representatives of both the crenarchaeotes and euryarchaeotes) are also

associated with corals¹¹⁵. The coral *Pocillopora damicornis* from the GBR contains a diverse bacterial assemblage dominated by *Gammaproteobacteria*, including some strains closely related to *Vibrio shiloi* and *Vibrio corallilyticus*¹⁰, which are known causative agents of coral bleaching. As with sponges, there is some evidence that microbial populations associated with corals may be globally distributed¹⁰ and may have beneficial effects for the corals⁸⁴. If this is in fact the case, shifts in microbial communities caused by climate change are potentially an additional stressor for corals.

Microbial symbionts have been described in a range of other GBR invertebrates. The bivalve *Solemya terraeregina* from GBR reef sediments contain endosymbiotic bacteria in their gills⁶². The bacteria in *S. terraeregina* and in all other *Solemya* symbioses studied are *Gammaproteobacteria*, which are thought to fix CO₂ with energy obtained through the oxidation of reduced sulfur compounds. A marine gutless oligochaete from the GBR contains two bacterial endosymbionts just below the cuticle: a gammaproteobacterium that clustered with known chemoautotrophic endosymbionts, and an alphaproteobacterium and spirochaete distinctly different from all other chemoautotrophs²⁸. Symbiotic bacteria are also thought to play a role in reproduction of the GBR nudibranch *Dendrodoris nigra*. Presence of symbiotic bacteria in the vestibular gland and egg masses of this nudibranch may be important in breaking down the mucus layer and egg capsule during intercapsular development⁶¹.

5.1.2.3 Recruitment

For sessile animals such as corals, the choice of a suitable site for settlement is crucial for future survival. Physical and chemical cues are often critical factors in site selection for larval settlement^{76, 50}. Micro-organisms can play an important role in the induction of settlement and metamorphosis in many marine invertebrates, including shellfish such as oysters and abalone¹³, starfish⁵⁶, polychaete worms¹⁰⁰, hydroids⁷² and corals^{72, 113}. The best known source of chemical cues for corals are the crustose coralline algae, but it is clear that bacterial biofilms can also produce settlement and metamorphic cues^{46, 41, 77, 113}. Marine biofilms have been reported to induce metamorphosis in several classes of cnidarians, including Anthozoa (hard and soft corals)^{75, 46, 113}, Scyphozoa (jellyfish)¹¹ and Hydrozoa⁷¹. Environmental conditions that adversely affect the distribution and abundance of microbes involved in settlement and metamorphosis of reef invertebrates could therefore have large-scale effects on ecosystem structure and the distribution and reproductive fitness of some keystone species.

5.1.2.4 Disease

In recent decades, there has been a global increase in reports of disease in marine organisms⁶⁷. Disease epidemics have affected both vertebrate and invertebrate species including fish, seals, dolphins, shellfish (oysters, scallops, abalone and clams), starfish, sea urchins, sponges and corals (reviewed in Harvell et al.⁴⁴). Disease outbreaks have also affected seagrass, kelp and coralline algae populations⁴⁴. On the GBR, the incidence of disease has been most notable in corals^{57, 124, 10} and sponges¹¹². To date, at least eight different coral disease states have been described on the GBR, including pathogens that have had devastating effects on coral communities in the Caribbean (black band disease and white syndrome).

While it appears that the prevalence of marine disease has increased in recent years, this may be an artefact of increased awareness and detection. Determining whether prevalence is changing over time has been problematic due to an absence of baseline data for most marine organisms. Whether these reported disease outbreaks are due to new pathogens, changed environmental conditions or

enhanced 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 ecosystems.

To date, there are only six coral diseases for which the etiological agent has been described: bleaching of *Pocillopora damicornis* by the pathogen *Vibrio corallilyticus*⁶, black band disease¹⁸, white plague type II⁸², aspergillosis^{89,39}, white pox⁸⁰, and bleaching of *Oculina patagonica* by *Vibrio shilo*^{64,65}. In contrast, there are numerous diseases and 'syndromes' for which no causative agent has yet been identified (reviewed in Richardson⁸¹, Jones et al.⁵⁷, Bourne and Munn¹⁰). In fact, there is still some controversy about which species is responsible for forming the cyanobacterial mat in black band disease^{18,32}. The potential role of viruses in coral disease is also being investigated. Heat-shocked corals have been shown to produce numerous virus-like particles that are evident in animal tissue, zooxanthellae and the surrounding sea water²¹. In addition, these virus-like particles appear to induce cell lysis in non-stressed corals, suggesting the presence of an infectious agent. However, unequivocal transmission electron microscopy evidence for this has yet to be obtained. On the GBR, virus-like particles are abundant and correlate with the spatial dynamics of the bacterioplankton community⁸⁶. It has been suggested that virus-like particles on the GBR may significantly influence nutrient cycling rates and food-web structure⁸⁶.

Reports of global sponge disease have also increased dramatically in recent years (reviewed in Webster^{114,37,38,104,14,112}). These epidemics can have severe impacts on sponge populations and the ecology of reefs. Disease has decimated many sponge populations throughout the Mediterranean and Caribbean^{38,104}, and anecdotal reports suggest an increased prevalence of sponge disease on the GBR. However, a lack of baseline data makes it difficult to determine whether disease (which is a natural part of marine ecosystems) is actually increasing in prevalence. In almost all instances of sponge disease, the impact of infection on sponge tissue is described but there is a failure to isolate the causative agents. Putative pathogens have been identified for only two occurrences of sponge disease^{9,112}, and Koch's postulates have been confirmed in a single case¹¹². Despite the ecological importance of sponges, the study of sponge disease is in its infancy.

A wide range of factors is thought to contribute to disease outbreaks in the marine ecosystem. These include increasing seawater temperatures associated with climate change, anthropogenic pollution, nutrient enrichment, overharvesting and introduced species. Concomitant increases in many of these factors on the GBR make it difficult to attribute shifts in disease prevalence to any particular factor. There is some evidence from the Australian Institute of Marine Science Long-term Monitoring Program that coral disease events on the GBR are more common following periods of coral bleaching, adding weight to the argument that stressed environments have less resilience to disease.

Another scenario that warrants consideration is that disease may increase in cases where the host is particularly successful, and increases in host numbers result in an increased rate of contact between the infectious agent and its host. Conversely, reductions in the host population can result in the complete disappearance of diseases that are highly specific for that host⁶⁷.

5.1.3 Critical factors for marine microbes

Marine microbes respond very rapidly to changing environmental conditions, making them ideal bio-indicator organisms. Many prokaryotes also have the ability to rapidly evolve and respond to small perturbations in temperature by the expression of temperature-regulated genes. This has significant implications for resilience and pathogen virulence. Marine microbes also have strict physiological thresholds that make them sensitive to small perturbations in temperature, nutrients, salinity, oxygen and a range of anthropogenic contaminants. For these reasons, micro-organisms are ideal indicators for alerting us to climate change and other anthropogenic stressors in the marine ecosystem.

5.2 Vulnerability of marine microbes to climate change

5.2.1 Changes in El Niño Southern Oscillation and ocean circulation

Many marine pelagic microbes are ubiquitous in the ocean²⁶, hence, changes to oceanic circulation (such as a southern extension of the East Australian Current) are not expected to have significant direct impacts on populations. However, a shift in the geographic range of some GBR microbial populations may occur.

5.2.2 Changes in water temperature

5.2.2.1 Exposure – water temperature

The level of exposure to changing oceanic temperatures varies for different microbial niches. Pelagic microbes are highly exposed to even slight temperature shifts. However, some members of the benthic community (including microbes within biofilms) may be buffered from temperature shifts by virtue of their physical location beneath sediment or other organisms. Likewise, symbiotic and pathogenic microbes may be less exposed to changes in seawater temperature due to their location within host tissue.

5.2.2.2 Sensitivity – water temperature

The sensitivity to temperature of most pelagic, benthic and symbiotic microbes is extremely difficult to assess. Since precise temperature thresholds are known for only a few cultivated species, it is not possible to describe the sensitivity of the GBR microbial ecosystem as a whole. However, the sensitivity of pathogenic microbes to elevated temperatures has received considerable research attention. Elevated seawater temperatures can 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 resilience⁹¹. In particular, increased seawater temperature could potentially affect the overall health of marine organisms, thereby contributing to an increased or decreased incidence of disease on the GBR. 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 seawater temperature is potentially linked to a reduction in the health of the host organisms.

Alternatively, increasing temperatures may alter the virulence mechanisms of a pathogen, as is seen with the coral pathogen *Vibrio shiloi*. A great deal of research has been directed towards describing the virulence of this coral pathogen^{98,7,3,4,5}. These studies have characterised a wide range of virulence mechanisms that are stimulated under elevated seawater temperatures. These include chemotaxis and adhesion to a beta-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 production of superoxide dismutase to protect the pathogen from oxidative stress.

In sponges, it is possible that under adverse environmental conditions, such as high temperature and reduced water flow, normally non-pathogenic bacteria become capable of spongin degradation within live tissue³⁷. 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 seawater temperatures and reduced water flow, sponge pathogens may switch on virulence mechanisms, sponges may be unable to control proliferation of bacteria¹⁰⁴, or degeneration of sponge tissue may occur when exogenous bacteria replace the associated populations^{103,37}.

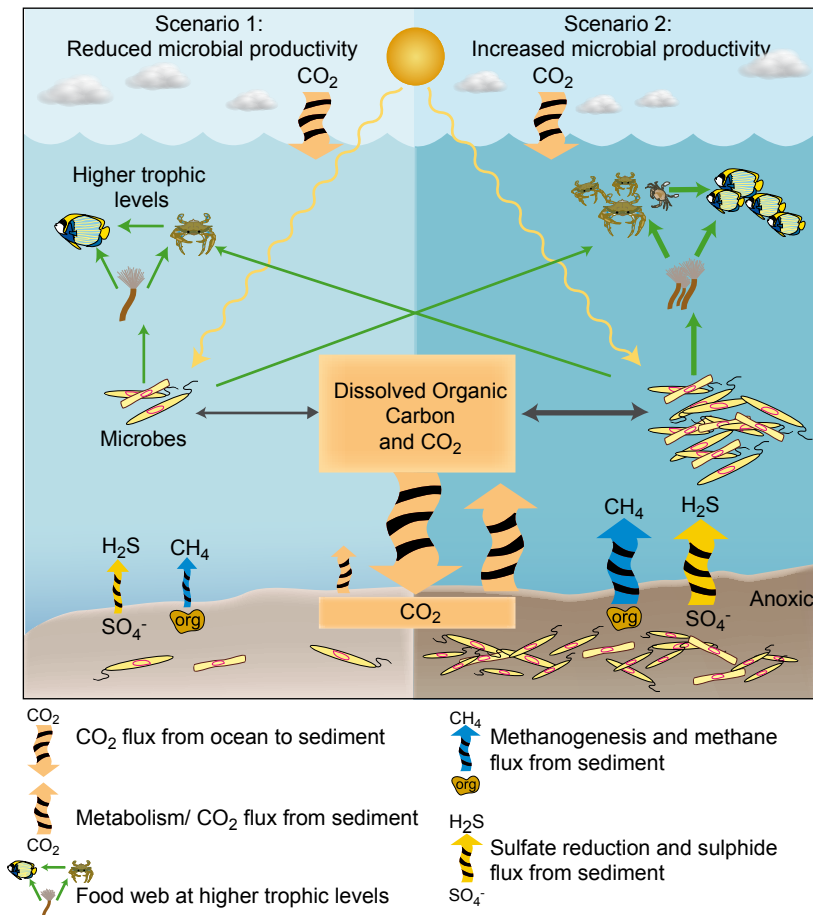
5.2.2.3 Impacts – water temperature

Nutrient cycle

An increase in seawater temperature of 1 to 2°C may have profound effects on the microbial loop. The composition of the microbial community is likely to undergo shifts in both numbers and species of bacteria that will affect the rates of carbon cycling in ways that we are not yet able to predict (Figure 5.4). For example, one can envision a scenario where a slight increase in water temperature in the GBR causes an increase in numbers and activity of pelagic bacteria, resulting in greater amounts of carbon passing through the microbial loop, and a concomitant reduction in carbon passing to higher trophic levels resulting in a reduction in fish numbers. A similar example from the eastern Mediterranean cites fish production being diminished by a dominant microbial loop¹²². Reduced numbers of fish that graze on macroalgae could ultimately result in a transition from coral-dominated to algal-dominated communities. Conversely, an increase in temperature may cause a shift to a less efficient bacterial community and a lower flux of carbon through the microbial loop with potentially the opposite effect on fish populations. The important point is that bacterial communities may be rapidly and profoundly affected by small shifts in temperature, with potentially major consequences for other reef organisms because of the importance of bacterial communities in carbon flux through the ecosystem.

If increased seawater temperature caused an increase in benthic bacterial productivity, there could be a concomitant increase in anaerobic processes as available oxygen is rapidly utilised (Figure 5.4). Since methanogenic archaea are present in anaerobic sediments, there is also the potential for an increase in methanogenesis if anaerobic zones in sediments are extended. This, in turn, would increase the total production of methane, which could be utilised by other microbes or fed back into the climate change cycle. Anaerobic methane oxidation is a process of global importance in marine sediments¹⁰⁶ and is performed by at least two phylogenetically distinct groups of archaea that are often observed in consortia with sulfate-reducing bacteria¹⁰⁵.

Figure 5.4 Potential productivity scenarios associated with climate change conditions



The long-term burial of organic carbon in sediments results in a net accumulation of oxygen in the atmosphere, thereby mediating climate change conditions¹¹⁷. Sediment microbial activity can play a fundamental role in determining whether particulate organic carbon is recycled or buried. Temperature regulation of the processes that lead to the microbial breakdown of complex particulate organic carbon could therefore influence the rates of overall carbon mineralisation. A study that examined carbon cycling in coastal anaerobic sediments reported a variable temperature response of the key functional microbial groups that mediate organic matter mineralisation¹¹⁷. In particular, the authors detected a temperature sensitivity of sulfate-reducing bacteria (whose activity dominates the anaerobic terminal metabolic pathway in marine sediments) greater than the temperature sensitivity of microbes involved in the hydrolysis/fermentation of complex organic matter¹¹⁷. This pioneering study showed that microbial processes involved in organic carbon breakdown were extremely sensitive to small changes in temperature, suggesting that global climate change may significantly influence the efficiency of organic carbon recycling in coastal ecosystems. While these results pertain to a temperate ecosystem,

it is conceivable that GBR microbes could respond in a similar way. However, knowledge of microbial community composition and temperature thresholds of individual species in GBR sediments is currently too limited to predict the response of key functional groups involved in organic carbon cycling.

Recruitment processes

Changes in microbial communities due to a 1 to 2°C increase in water temperature may alter production of morphogenic signalling compounds or responses of larvae to these compounds, which may have an effect on patterns of larval settlement and subsequent distribution of invertebrates. Alternatively, shifts in the community composition of benthic biofilms could adversely or positively affect microbial succession and subsequent recruitment of macro-organisms. This would have obvious implications for reef-building, maintenance and recovery processes. Limited knowledge of these processes and their probable complexity make it unlikely that these effects will be predictable.

Symbiosis

Considerable attention has been directed towards the impact of elevated seawater temperature on the symbiotic relationship between corals and zooxanthellae. However, almost no research currently exists on the impact of increasing seawater temperature on other reef microbial symbioses. It is likely that microbial symbionts have strict temperature thresholds, and a breakdown in symbiosis could result in host mortality, reduced host fitness, shifts in host geographic range, increased disease or an increase in predation or grazing. There is also the possibility that increased seawater temperatures may cause a shift from symbiotic to pathogenic function for some species.

Disease

Diseases have the potential to cause major impacts on population levels, biodiversity and community structure of coral reefs by causing shifts in the abundance of various groups. For example, in the GBR it is the fast-growing branching coral species (specifically the acroporids and pocilloporids) that are most susceptible to disease¹²⁴. In the Caribbean, populations of *Acropora palmata* were highly susceptible to disease in the 1980s, whereas the massive reef-building corals are currently most vulnerable to disease epidemics⁶⁷. Corals with varying morphologies provide different habitats for many different reef organisms, and an increase in disease occurrence in one morphological group could lead to dramatic changes in reef communities. A classic example of a complete phase shift in community structure as a result of disease happened in the Caribbean, where a disease epidemic in the dominant herbivore, the sea urchin *Diadema antillarum*, by an unidentified pathogen caused a shift from coral-dominated to algal-dominated reefs⁵³.

Elevated seawater temperature associated with El Niño – Southern Oscillation (ENSO) events has been implicated in interannual variation of Dermo disease in the Gulf of Mexico (a disease of the oyster *Crassostrea virginica* caused by the protozoan parasite *Perkinsus marinus*)⁹⁹. Dermo disease closely follows the ENSO cycle, with prevalence and infection intensity declining during El Niño events (cold, wet conditions) and rising during La Niña events (warm, dry conditions). This relationship between Dermo epidemics and ENSO suggests that it may be possible to predict disease outbreaks with climatic models, which could provide potential management strategies for oyster populations. Unfortunately, our current disease epidemiology datasets for the GBR (initiated for corals in 1998) are not yet extensive enough for valid correlations to be made with the ENSO cycle.

Predictions of how disease will affect marine communities are also complicated by the fact that stressors (such as increased temperature) may sometimes have a more negative impact on the pathogen than on the host⁶⁶, a scenario that would facilitate recovery of infected populations. It is therefore important to acknowledge that changing environmental conditions may increase or decrease the occurrence of disease.

At this point, it would be pertinent to briefly discuss the influence of climate on the abundance and ecology of human pathogens, which are ubiquitous in the marine environment, including the GBR. Pathogenic *Vibrio* species are responsible for the majority of non-viral infections related to shellfish consumption¹²⁶. Pathogenic vibrios thrive in warm waters of moderate salinity⁸⁷ and are closely associated with aquatic invertebrates⁷³. Altered climatic conditions may cause a shift in the geographic range of these pathogens, potentially resulting in increased risk of infection for humans. In addition, changes in plankton populations (in which vibrios are often commensals) would similarly affect the ecology of these pathogens. Ecological models have been developed to define the role of climate-related variables in outbreaks of cholera^{54,17,74,79}. These suggest that abiotic conditions including temperature, pH, salinity, Fe³⁺ and sunlight all favour the growth of *V. cholerae* and/or host plankton and result in increased pathogen virulence. Predicted climate change conditions such as elevated seawater temperature could potentially select for an increased prevalence or virulence of human pathogens in the GBR region.

5.2.2.4 Adaptive capacity – water temperature

The ‘rare biosphere’ of bacteria recently identified by Sogin et al.⁹⁰ may provide some resilience to environmental change. The enormous diversity of low-abundance populations suggests that there should be some capacity to take over ecological niches that become available due to environmental perturbations. Several ecological models predict a survival advantage for rare species since they are less affected by predation and direct competition with dominant species. As noted by Sogin et al.⁹⁰, the rare biosphere could ‘explain how microbial communities recover from environmental catastrophe’.

Pelagic and benthic microbes

There is the possibility of a shift in geographic range with an export of tropically acclimated species to southern temperate reef environments. Alternatively, microbes that are present as minor constituents of the total community could become major players if they are better adapted to new temperature regimes. As different microbes come to dominate the waters and sediments, shifts in the overall patterns of carbon and nitrogen cycling are conceivable. Given our current state of knowledge, it is not possible to predict the consequences of shifts in communities of bacteria and archaea in the water column and sediments.

Symbiosis

The high specificity of symbiotic microbial–invertebrate associations has been demonstrated by experiments with the bobtail squid *Euprymna scolopes*. This species of squid shows a preference for *V. fischeri* strains isolated from itself rather than from other species of squid or from the water column⁷⁸. This shows that intra-species variation can be important in these complex and subtle invertebrate–bacterium symbioses and that adaptive capacity would be considered low for such

intimate relationships. It is also possible that vertically transmitted symbionts may find refuge within their hosts in the face of elevated seawater temperature since they may be relatively immune from competition with bacteria in the surrounding seawater milieu. Of course, if the hosts are particularly susceptible to changing conditions and become extinct as a result of increased seawater temperature, vertically transmitted symbionts may be 'trapped' within the declining populations of the host and follow the host into extinction.

5.2.2.5 Vulnerability and thresholds – water temperature

The diverse and active microbial community has a major impact on nutrient cycling in marine waters. Small shifts in community composition could result in large changes in nutrient cycling. Increased seawater temperature could have significant impacts on microbial community composition and ecosystem function in the pelagic and benthic environments and affect the wide range of symbiotic and pathogenic relationships that currently exist on the GBR. However, the complexity of marine microbial communities and the nature of their interactions with nutrients make it impossible to predict the consequences of an increase in temperature of 1 to 2°C in waters of the GBR.

Despite the vulnerability of pelagic, benthic, symbiotic and pathogenic microbes to temperature, some resilience could potentially be conferred to the ecosystem by rapid genetic turnover, functional redundancy, expression of temperature-regulated genes and lateral gene transfer. Gene transfer is an important mechanism by which microbes can interact in the environment and facilitates the exchange of DNA that transforms other bacterial cells and enables populations to adapt or evolve. Prokaryotes have several possibilities to transfer genes including transduction, where genes are transferred by the activity of viruses. This results in the horizontal spread of genes within a community and may contribute to diversity. The 'insurance hypothesis' assumes that there are many species in an ecosystem that can perform the same or very similar functions¹²⁷. These redundant species can take over ecosystem functions once a dominant species becomes extinct or functionally obsolete. This insurance due to redundancy of species may result in a resilience of ecosystem functions. However, to date there is very little direct evidence of functional redundancy in the marine ecosystem.

5.2.3 Changes in ocean chemistry

5.2.3.1 Exposure – pH

As outlined for seawater temperature, most marine microbes would be highly exposed to changes in seawater chemistry.

5.2.3.2 Sensitivity – pH

The sensitivity of marine microbes to changes in pH has been examined primarily by observing growth rates and survival in a few cultivated species. The sensitivity of entire microbial communities, including effects of pH on microbial processes, requires further research to be fully elucidated.

5.2.3.3 Impacts – pH

Variable effects of reduced pH on marine micro-organisms have been reported.



Research studying the effects of CO₂ induced seawater acidification on the growth rates of marine microbes found that bacteria were so resistant to high concentrations of CO₂ that drastic impacts in terms of growth were observed only under conditions where the pH was below 5.5 to 6.0⁹³. The GBR is unlikely to experience a pH lower than 6.0 in the foreseeable future. These data suggest that the impacts of ocean chemistry on marine micro-organisms should be minimal or negligible. However, the study by Takeuchi et al.⁹³ focused on the effects of pH on bacterial growth rates but not on specific transformations that are mediated by marine micro-organisms (such as the nitrogen cycle).

Acidifying sea water causes an increase in the concentration of ammonium ions and a decrease in concentrations of ammonia. Ammonia-oxidising micro-organisms are central to the nitrogen cycle and will be adversely affected by acidification because they cannot oxidise the ammonium ions. This will have subsequent effects on the denitrifying and nitrifying bacteria in the marine ecosystem. There is evidence that marine nitrification rates are significantly reduced as sea water becomes more acidic^{118,107,36}, and the large-scale inhibition of nitrification and subsequent reduction of nitrite and nitrate concentrations could result in a decrease in denitrification. This, in turn, could lead to a build-up of nitrogen and unpredictable eutrophication phenomena.

5.2.3.4 Adaptive capacity – pH

The direct effect of pH on fundamental microbial processes (such as the nitrogen cycle) suggests that the adaptive capacity of the microbial system to pH will be quite low. However, further research on the impacts of acidification on microbial community dynamics and microbial function is required before this can be fully determined.

5.2.3.5 Vulnerability and thresholds – pH

The projected decline of 0.4 to 0.5 in ocean pH in the GBR by 2100 could have significant consequences on ecosystem function related to a direct impact on the nitrogen cycle and microbial loop. In addition, if important keystone microbial species are particularly sensitive and experience a shift in abundance or function due to altered ocean chemistry, this would obviously have larger implications for the wider microbial and tropical marine ecosystems.

5.2.4 Changes in light and ultraviolet light

Ultraviolet light is a powerful mutagen, interfering with accurate DNA replication and introducing errors during the cellular processes undertaken during DNA repair. A study that examined the effects of ultraviolet (UV) exposure on natural Antarctic phytoplankton and protozoans found that UV radiation altered the biomass and species composition of the community²⁰. The changes to size and availability of food to higher trophic levels could have major consequences by changing food-web structure and function and potentially influencing biogeochemical cycles. The expected increases in UV radiation with climate change could potentially impact on GBR microbial communities by increasing the rate of genetic change or causing shifts in community composition, with a decline in UV-sensitive species and an increased abundance of UV-tolerant species. This could have significant implications for the microbial loop and for pathogenic and symbiotic relationships (as identified in section 5.2.2.3).

5.2.5 Sea level rise

A rise of 0.1 to 0.9 metres in sea level by 2100 could increase fluxes of nutrients and pollutants into the marine environment and have direct impacts upon microbial communities as outlined in section 5.2.7. In addition, a rising sea level may facilitate the introduction of new microbes from terrestrial sources into the ecosystem. For example, *Aspergillus sydowii*, a pathogen of sea fans that has caused significant mortality in the Caribbean, has been identified in African dust samples transported thousands of kilometres from the Sahara to the Caribbean¹⁶.

5.2.6 Physical disturbance – tropical storms

Predicted increases in cyclone intensity could affect GBR microbial populations due to increased resuspension of bottom sediments and associated carbon and nutrients. This will have a direct impact upon the microbial loop (see section 5.2.7).

5.2.7 Rainfall and river flood plumes

5.2.7.1 Exposure – terrestrial inputs

It is foreseeable that more extreme flood events will increase nutrient and contaminant runoff into inshore areas, potentially altering microbial community composition and function.

5.2.7.2 Sensitivity – terrestrial inputs

Nitrogen stimulates pelagic microbial growth and thus has the capacity to influence photosynthetic rates and carbon dioxide levels. An increased concentration of nitrogen entering the GBR via river runoff and eutrophication would have significant implications for both micro and macro communities due to impacts on the microbial loop, symbiotic relationships and disease processes.

5.2.7.3 Impacts – terrestrial inputs

The nature of impacts from increased terrestrial inputs is extremely difficult to predict or model because of the complexity of the bacterial community. Bacterial activity can modify organic material even without large fluxes of organic material into bacteria¹. For example, the activity of slow-growing bacteria on the surfaces of small particulate material, termed 'marine snow', can result in production of large amounts of ectohydrolase enzymes that efficiently solubilise the organic particulate matter, releasing it into the surrounding water and reducing the sinking flux of carbon into deeper waters⁸⁸. A small shift in nutrient concentrations may change the bacterial communities performing this activity and select for communities that are either more or less efficient at this uncoupled solubilisation, with resultant changes in the flux of carbon through marine ecosystems even without marked changes in bacterial numbers or activities.

Similarly, the work of Bidle et al.⁹ showed that bacteria play an important role in solubilisation of silica from diatoms, thereby affecting the availability of free silica for new diatom growth. Some bacteria produce potent proteases that result in higher rates of silica dissolution and less transport of silica into the deep benthos, potentially resulting in higher diatom growth in the photic zone and greater rates of photosynthesis. Once again, a small shift in the bacterial communities, to favour bacteria with higher or lower rates of silica dissolution, could have profound effects on carbon cycling.

Nutrient enrichment may also increase the incidence and severity of marine epizootics, as evidenced by an increase in the severity of coral disease in the Caribbean after increased nutrient exposure¹². Increases in the concentration of inorganic nitrogen and phosphorous could affect disease dynamics by increasing pathogen fitness and virulence⁵⁹ or negatively impacting on host immunity.

5.2.7.4 Adaptive capacity – terrestrial inputs

In the microbial system, responses to terrestrial inputs could include changes in species composition, changes in growth rates, changes in gene expression, changes in physiological (enzyme) activity and changes in intimate associations (symbiosis and pathogens) with other organisms. Multiple species may fill similar physiological niches in the marine environment; hence, there is some potential for microbial community adaptation. However, for more-specific intimate associations such as those with symbionts and pathogens, it is impossible to predict the adaptive capacity with our current limited state of knowledge of these relationships.

5.2.7.5 Vulnerability and thresholds – terrestrial inputs

The complexity of the marine microbial loop, our limited knowledge of microbial associations with other reef organisms, and a lack of data on species or community thresholds make it impossible to assess the vulnerability and thresholds of GBR microbial communities to increased terrestrial input.

5.2.8 Linkages with other ecosystem components

5.2.8.1 Constraints to adaptation

With such limited data on how marine microbial communities respond to climate change parameters, it is difficult to accurately assess the overall constraints to adaptation. However, it would be reasonable to assume that concurrent stressors would have a more detrimental impact on the ecosystem and potentially constrain the adaptive capacity of marine micro-organisms. The high sensitivity and relatively short generation times of most marine microbes suggest that, in the absence of multiple stressors, microbes will be better able to adapt to chronic than to acute environmental perturbations.

5.2.8.2 Interactions between stressors

The complexity of the microbial loop and a lack of data on the functional role of many microbial species limit our ability to reliably assess the impacts of multiple stressors on GBR microbial communities. However, a study examining the effects of copper on a GBR sponge species showed that the community structure of sponge-associated bacteria was negatively affected by elevated copper concentrations and that a shift in the symbiotic community potentially caused a decline in sponge health¹¹. Although this is yet to be examined, it is foreseeable that increased seawater temperature and elevated nutrients and contaminants from river discharge could have similar and compounding effects on microbial symbioses and other GBR microbial communities.

5.2.8.3 Threats to resilience

Concurrent stressors are probably the most foreseeable threat to ecosystem resilience. For example, an increase in seawater temperature or nutrient load as a result of climate change has a detrimental effect on the health of many invertebrate species, making them more susceptible to disease and

increasing the potential for opportunistic bacterial species to become pathogenic. Other threats to resilience could include the introduction of pesticides or contaminants that impact on benthic microbial processes, and the introduction of new pathogens causing disease outbreaks.

5.3 Summary and recommendations

5.3.1 Major vulnerabilities to climate change

The projected increases in sea temperature, ocean acidification and terrestrial input are likely to be the primary climate change factors that will significantly impact marine microbial assemblages. The predicted impacts of these environmental shifts include changes to microbial community composition and function that may have significant implications for cycling within the microbial loop, recruitment, symbiotic relationships and disease. These are likely to have flow-on effects to higher trophic levels in the tropical marine ecosystem.

5.3.2 Potential management responses

In view of microbial abundance, diversity, interactions with reef invertebrates and influence on ocean chemistry, it is essential that ecosystem-based conservation models begin to incorporate micro-organisms.

While the effects of increased sea temperature will be difficult to mitigate from a GBR management perspective, there are a range of contributing environmental variables that could be amenable to management intervention. In addition to temperature-induced stress, marine microbial communities can be highly susceptible to other forms of anthropogenic pollution (such as elevated trace metals and nutrients). To illustrate this, case studies of copper-sensitive symbiotic microbes from a GBR sponge and the increased severity of coral disease under elevated nutrients were outlined. These examples highlight the importance of management strategies that aim to minimise stress to marine organisms (such as improving water quality and reducing nutrient loads). It is possible that this type of management approach could reduce the risk of disease outbreaks and the breakdown of symbiotic relationships in reef invertebrates.

5.3.3 Further research

As discussed in a recent review by DeLong and Karl²⁴, ‘a mechanistic understanding of the susceptibility of marine ecosystems to global environmental variability will require a comprehensive description of ... marine physical, chemical and biological interactions including thresholds, negative and positive feedback mechanisms and other nonlinear interactions’. In recent years, there have been important discoveries of previously unknown microbes, many of which have a significant impact on oceanic processes^{40,35,43}. An inadequate understanding of basic microbial community composition and function in the GBR means that considerable research effort is required to begin to accurately assess the effects of environmental change on pelagic, benthic, symbiotic and pathogenic microbes.



In particular, research priorities for the GBR should include:

- 1) **Examination of microbial processes** – including examining the role of microbes in carbon and nitrogen cycles.
- 2) **Examination of disease processes** – including examining disease aetiology and pathogen virulence so that managers can understand the conditions that promote the onset and transmission of disease.
- 3) **Examination of the effects of climate change conditions on microbial symbioses** – including examining the functional role of microbial symbionts and individual species thresholds so that the vulnerability of reef organisms to climate change can be comprehensively assessed.
- 4) **Examination of the effects of climate change conditions on biofilm formation** – including examining the role of biofilms in biogeochemical processes and metamorphic signaling to reef invertebrates.
- 5) **Metagenome sequencing of GBR seawater and sediment microbes** – such sequencing would facilitate the development of a comprehensive list of microbial inhabitants and their physiological potential, revealing patterns of biochemical interactions and habitat-specific correlations that could not be obtained by analysis of individual species. Most importantly, metagenome sequencing would assist interpretation of the evolutionary processes driving microbial adaptation and provide greater insight into how the microbial community is adapting to climate change.

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