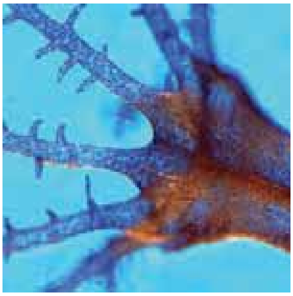
CORAL BLEACHING – A REVIEW OF THE CAUSES AND CONSEQUENCES

CHAPTER 4

4. CORAL BLEACHING – A REVIEW OF THE CAUSES AND CONSEQUENCES

The mass coral bleaching events that have occurred throughout the tropics over the last decade have provided unprecedented opportunity, and motivation, to study this phenomenon. As a result, knowledge about the causes and consequences of coral bleaching has increased substantially in recent years. This accumulating body of information is providing critical advances in our understanding and has generated new insights, which can assist reef managers to respond to the threat of coral bleaching. This section aims to provide a summary of recent developments in the science of coral bleaching, highlighting emerging knowledge and recent insights that are most relevant to reef managers.



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The zooxanthellae can be clearly seen as golden-coloured dots in this close-up image of a coral polyp. The symbiotic relationship with these tiny dinoflagellates enables corals to gain energy from sunlight

4.1 What is coral bleaching?

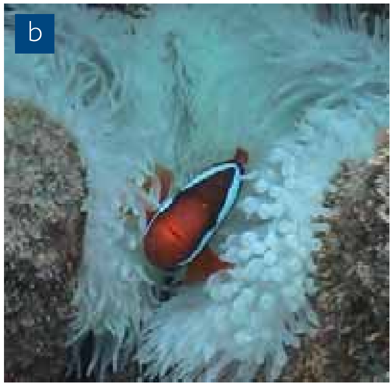
4.1.1 The coral-algal symbiosis

The great majority of corals live in a symbiotic relationship with zooxanthellae, a type of single-celled dinoflagellate algae. These microscopic algae live within the coral's tissues. Zooxanthellae produce energy-rich compounds through photosynthesis, providing a food source that is absorbed and used by the coral. In general, corals are highly dependent on this symbiotic relationship, receiving up to 90 per cent of their energy requirements in this way[17].

Bleaching is a stress response that results when the coral-algae relationship breaks down. The term 'bleaching' describes the loss of colour that results when zooxanthellae are expelled from the coral hosts or when pigments within the algae are degraded. Because the photosynthetic pigments found in zooxanthellae give corals most of their colouration, the loss of zooxanthellae renders the tissue largely transparent. The white of the calcium carbonate skeleton is then clearly visible through the un-pigmented tissue, making the coral appear bright white or 'bleached'[24]. Bleaching also occurs in other animals that are engaged in symbiotic relationships with zooxanthellae, such as foraminifera, sponges, anemones and giant clams.

Bleaching is a stress response that results when the coral-algae relationship breaks down

In some instances, coral bleaching will result in corals taking on a pastel shade of blue, yellow or pink rather than turning bright white. This is due to proteins produced by some corals, which tint the coral tissue and become the dominant pigment during bleaching, when zooxanthellae are absent[110, 111].



It isn't only corals that bleach; other organisms that have zooxanthallae, such as this (a) giant clam and (b) anemone can also bleach in response to thermal stress

4.1.2 The causes of coral bleaching

The primary cause of mass coral bleaching is increased sea temperatures[9,13,18,23,53]. At a local scale, many stressors including disease, sedimentation, cyanide fishing, pollutants and changes in salinity may cause corals to bleach. Mass bleaching, however, affects reefs at regional to global scales and cannot be explained solely by localised stressors operating at small scales. Rather, a continuously expanding body of scientific evidence indicates that such mass bleaching events are closely associated with large-scale, anomalously high sea surface temperatures[8,9,13]. Temperature increases of only 1-2°C can trigger mass bleaching events because corals already live close to their maximum thermal limits[9,23].

Mass coral bleaching affects reefs at regional to global scales – it is primarily caused by unusually high sea temperatures

The role of temperature and light. Increased temperatures cause bleaching by reducing the ability of the photosynthetic system in the zooxanthellae to process light. When temperatures exceed certain thresholds, incoming light overwhelms the photosynthetic apparatus, resulting in the production of reactive oxygen species that damage cellular structures[24,112]. Corals cannot tolerate high levels of these toxic molecules, and they must expel the zooxanthellae to avoid tissue damage. Because of the low tolerance of the photosynthetic process to high temperatures, even normal levels of sunlight are enough to damage the photosynthetic system of the zooxanthellae when temperatures exceed certain levels[23,113]. Furthermore, as light levels increase the amount of damage due to thermal stress increases as well[24].

The relationship between temperature and light in causing coral bleaching helps explain observations of reduced bleaching on shaded parts of coral colonies or in shaded reef areas[9,114,115]. It also suggests that the spatial extent and patterns of bleaching responses may be influenced by factors that determine the amount of solar radiation to which corals are exposed. These factors might include cloud cover[46], attenuation in the water column[116], stratospheric ozone[18] and shading by large landforms such as steep-sided shorelines[39].

Bleaching is reduced in shaded reef areas because light levels influence the amount of damage caused by temperature stress

Natural variations in turbidity may also play an important role in determining bleaching risk. A recent study of the patterns in underwater light levels on a coastal coral reef found that there were periodic intervals of low light levels due to cloud cover and sediment re-suspension (high turbidity), which were driven by large-scale pressure systems[117]. Such natural variability has strong implications for bleaching risk, and knowledge of these factors can be used to prioritise management effort to other factors that are amenable to management intervention.

4.2 Factors that confer resilience to coral bleaching

Resilience to bleaching is determined by the outcome of three key aspects of the bleaching process: resistance to bleaching, ability to survive the bleached state (tolerance) and rate of reef recovery after coral mortality. Understanding the factors that influence each of these steps is central to our ability to understand, and potentially manage, the factors that confer resilience to bleaching on corals.

Understanding the factors that determine variation in bleaching response of corals exposed to temperature stress provides an important basis for management actions in responding to the threat of bleaching

4.2.1 Factors that influence resistance

The variability that characterises bleaching events points to an important fact: individual corals vary in their responses to heat and light stress. Variability in bleaching response has been observed within individual coral colonies, among colonies of the same species, and between colonies of different species[23,118]. These taxonomic variations are further compounded by spatial patterns, with corals of the same species often showing different bleaching responses at different locations[18, 19, 79, 118]. These patterns have been observed at scales ranging from metres to thousands of kilometres. Knowledge of the factors, both external and intrinsic to individual corals, that determine whether corals bleach is an important basis for management actions in response to the threat of bleaching. Better understanding these factors is the central aim of an integrated research strategy being taken in the US territory of American Samoa as a management response to climate change (case study 9).

External factors. Externally, there is considerable variation in the environmental conditions experienced by coral colonies. This variation creates critical differences in exposure to heat, light or other stressors, leading to many of the patterns seen in bleaching responses. Some of this patchiness can be attributed to patterns in sea surface temperatures, especially at larger spatial scales[49]. Regional and local differences in weather can also cause differential heating of the water, while proximity to upwelling of cooler waters, mixing by currents and other large-scale processes can help keep temperatures below local bleaching thresholds. At smaller scales, the microenvironment of corals can also vary. Water currents and flow regimes increase water movement around corals, helping them to get rid of metabolic waste and toxic molecules[74], thereby potentially reducing their susceptibility to thermal stress.

Box 4.1 Coral taxa and resistance to mass bleaching

Bleaching resistance is highly variable among corals, as evidenced by the extremely variable responses of coral species to thermal stress. While some corals will show visible signs of bleaching after only one or two weeks at temperatures 1.5°C above the normal maximum, others at the same location will not bleach unless these temperatures persist for more than four to six weeks.

A strong hierarchy of resistance can be detected in diverse coral assemblages, such as those in the western Pacific and Indian Oceans[80] (Figure 4.1). Typically, fine-structured and fast-growing corals with thin tissue and good connections between polyps tend to be the most susceptible to bleaching. Tissue thickness has been shown to correlate with susceptibility to bleaching[123, 124], although the role and relative importance of these various traits remain to be thoroughly explored.

Common examples of corals with low resistance are the pocilloporids *and many* acroporids *(especially the branching and tabular growth forms), as well as the hydrocoral* millepora. *Species that are more resistant tend to be characterised by solid, massive skeletons, with thick tissue and slow growth rates, such as* porites, faviids, *and* mussids. *Interestingly, some of the species most often associated with inshore or turbid reef systems are among the most resistant to bleaching, such as* turbinaria[125].

RESISTANCE	GROWTH FORM	CORAL FAMILY	EXAMPLES
LOW	Fine branching	Pocilloporidae	*Seriatopora* *Stylophora* *Pocillopora*
	Branching, tabulate, encrusting/foliose	Acroporidae	*Acropora* *Montipora*
MEDIUM	Massive, brain	Faviidae	*Favia* *Favities* *Leptoria* *Goniastrea* *Platygyra*
	Massive, boulder	Poritidae	*Porites* *Goniopora*
HIGH	Various	Various	*Turbinaria* *Cyphastrea*

Figure 4.1 A generalised hierarchy of coral susceptibility to bleaching

Corals vary in their susceptibility to bleaching. While many factors influence bleaching resistance, the growth form or family of a coral provides a rough but reliable indication of its susceptibility to heat stress.

CASE STUDY 9

An integrated research strategy to assist management responses to climate change – American Samoa

Identifying the need for research

Resource managers increasingly struggle to determine local level responses to climate change. In the US territory of American Samoa, coral reef managers and scientists have identified climate change as a key and imminent threat to the health of the islands' fringing reef system. Physical dangers posed by wave action due to coral loss, increased or decreased rainfall, phase and community shifts on reefs, and sea level rise are just a few of the things that reef managers and policy-makers may have to contend with in coming years at this location. Residents of American Samoa have relied on the reef ecosystem for protection, food, goods and services for millennia. However, they are likely to face severe disruptions to lifestyle, public health hazards, and a decreased ability to be self-supportive if projected increases in the frequency and severity of bleaching eventuate.

In response, local policy-makers are facilitating climate-related research around the islands of American Samoa. It is hoped that data derived from these projects will give managers options for site-specific protection measures, such as Marine Protected Areas, targeted reductions in location-specific land-based sources of pollution, restrictions on use, and even, if appropriate, artificial propagation of coral.

Ofu Island in American Samoa

Ofu Island – a laboratory in the field

The most notable of the recent research initiatives within American Samoa is being conducted in the lagoonal system along the south shore of Ofu Island. This area is the focus of research aimed at determining whether some of the coral species residing there have adapted to bleaching stresses. The hydrography of the lagoon ensures that there is little, if any, flushing during low tides. It is during these times that temperatures and ultraviolet radiation (UV) around shallow water corals increase dramatically. The extreme temperature ranges that corals in Ofu can withstand on a regular basis indicate that this site may be a natural climate refuge[164]. The warmer water temperatures projected to accompany climate change are likely to result in calmer, clear water (due to stratification and the loss of UV blocking compounds in the water column itself). Knowledge about the characteristics that confer stress resistance to corals of Ofu lagoon can thus be used to understand the features that will help corals survive future thermal stress events in more open reef habitats.

Research projects

Four research projects have been developed by American Samoa in conjunction with various partners. In combination, they will provide valuable insights to guide management efforts aimed at helping American Samoan reefs survive future coral bleaching events.

Are some corals better prepared for climate change? MMA concentrations in Ofu lagoon corals (WWF /Emerald Coast Consulting).

This study examines the microsporine-like amino acid (MAA) concentrations in corals in the lagoons and near-shore (cooler, deeper) reefs of Ofu. Microsporine-like amino acids act as a kind of sunscreen, protecting corals from damaging UV light. Coral nubs are being collected from a combination of species found in all lagoons and paired with samples of the same species from outside of the lagoons, as well as from species only found in some lagoons. These samples will be compared to determine whether their history has imparted some selective advantage in terms of their capacity to deal with the thermal stress associated with future climate scenarios.

Nearshore hydrodynamic modeling for Marine Protected Areas (MPAs) in American Samoa (Eric Treml and Patrick Halpin, Duke University)

This research uses a spatially explicit, hydrodynamic modelling approach to address high-priority MPA management issues, such as coral bleaching, land-based sources of pollution, and over-fishing. The aim is to identify connections among the design of MPAs, long-term monitoring methods and the local needs of American Samoa. Working closely with the local marine management community, this research will result in the development of spatial management strategies and tools for coral reef protection and MPA site development.

Coral disease prevalence on the reefs of American Samoa (Greta Aeby, Hawaii Department of Land and Natural Resources)

This study addresses issues related to coral disease, coral bleaching and pollution and works to examine the relationships between water quality, coral bleaching and the susceptibility of organisms to disease. The goals of the research are to: (a) conduct a baseline assessment of the abundance and distribution of bleached and diseased corals and of crustose coralline algae at sites throughout American Samoa; (b) correlate the incidence of bleached and diseased colonies with environmental data, and (c) systematically describe gross and microscopic morphology of lesions in corals and crustose coralline algae. This work will help to develop a standardised nomenclature for identifying and classifying diseases. This is a particularly important task as the frequency of disease is expected to increase due to climate change and increases in land-based sources of pollution in reef areas worldwide[27].

Extrinsic and intrinsic factors affecting the resilience of corals to climate change and their use in designing marine reserve networks (Charles Birkeland, University of Hawaii)

This three-year study aims to determine the intrinsic and extrinsic factors that enhance the ability of a diverse set of corals (approximately 100 species) to resist environmental stressors, such as extreme upper temperature limits, temperature fluctuations, and low and high levels of dissolved oxygen. Intrinsic factors include: zooxanthellae types, microbial community composition, microsporine-like amino acid levels and genetic traits. Understanding these factors, and their relevance, will improve knowledge of ecosystem response to environmental factors, and of how future environmental conditions may affect community structure and functions. Such information will ultimately inform managers and scientists designing Marine Protected Areas and similar conservation strategies.

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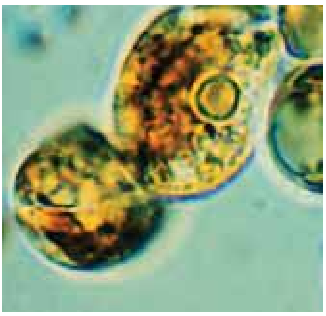
Other stresses in the external environment of corals can also have an affect on their susceptibility to thermal stress. Preliminary research indicates that synergies between temperature and other stressors, such as pollution, turbidity and sedimentation, changes in salinity or exposure to pathogens, may interact to trigger or exacerbate bleaching[41]. The role of pathogens in localised bleaching may also warrant further consideration, as recent studies have demonstrated the induction of bleaching by bacteria in certain corals from the Mediterranean and Red Seas[119, 120]. Further investigation of these issues, and confirmation of key mechanisms driving synergistic effects involving coral bleaching, have the potential to reveal opportunities for management interventions that could reduce bleaching impacts.

Internal factors. Intrinsically, both the genetic identity and the history of coral colonies and their zooxanthellae can contribute to variation in bleaching susceptibility[23, 121]. This may be observable in individual colonies, or the effect may be observable in the bleaching susceptibility of entire reef communities[122]. At the colony level, species characterised by branching or tabular growth forms and thin or well-connected tissue, tend to bleach more than species with massive growth forms and thicker or less-integrated tissues (see Box 4.1). Thicker tissue may shade zooxanthellae and increase resistance to bleaching[9, 123]. The ranking of common coral groups by bleaching susceptibility is remarkably consistent between sites on opposite sides of the world, suggesting that the properties of the animal host (above and beyond differences in zooxanthellae type) play an important role in determining the response of corals to thermal stress[80].



Genetic variation among individual zooxanthallae (shown here) influences the resistance of corals to heat stress and bleaching. Although corals may be able to shift the relative dominance of different varieties of zooxanthallae within their tissues in order to increase their resistance to bleaching, there are limits to the extent that corals can use this strategy to acclimatise to large temperature anomalies

The intrinsic characteristics of corals that enable them to adjust to elevated light levels also play a role in determining their resistance to bleaching. Coral polyps that have experienced higher light levels have been shown to be more resistant to bleaching when exposed to high water temperatures[115], suggesting that corals acclimatised to high light will be less likely to bleach in response to thermal stress. This implies that corals that have experienced (and survived) extreme environmental conditions in the recent past may be more resistant to bleaching stress in the future. However, the effects of historical exposure to light are subtle, and acclimatisation is unlikely to allow corals to withstand the large temperature anomalies that have triggered recent mass bleaching episodes[23].

Genetic variation in zooxanthellae is another intrinsic characteristic that could influence the bleaching resistance of corals (Box 4.2). Differences in thermal tolerance among varieties, or clades, of zooxanthellae suggest that coral hosts that have high densities of heat-tolerant algae may be less susceptible to coral bleaching[126]. Shifts toward more heat-tolerant populations of corals or zooxanthellae can be expected to arise from selective mortality of more sensitive genotypes during severe bleaching events. However, corals may also be capable of forming new symbioses with more tolerant zooxanthellae in response to changing temperature regimes (the Adaptive Bleaching Hypothesis)[127]; this possibility remains the focus of ongoing research and discussion (for example, Hoegh-Guldberg et al (2002)[113]).

Box 4.2 Zooxanthellae and resistance to mass bleaching

A characteristic that appears to be important in determining resistance of corals to bleaching is the type of zooxanthellae hosted. Numerous different types, or clades, of zooxanthellae have been recognised, and there is some evidence that they have different susceptibilities to thermal stress[128]. Many corals have multiple varieties of zooxanthellae within their tissue, and the relative proportion of the different varieties is variable. A recent experiment has revealed that some corals can vary the ratio of zooxanthellae clades, with a resulting improvement of their thermal tolerance[129]. This feature is akin to acclimatisation as it involves the use of pre-existing strategies within the coral-zooxanthellae association. If bleaching events increase in both severity and frequency in the future, this may play a small role in determining bleaching response patterns on larger spatial scales. As with other examples of acclimatisation, there is a limit to the extent that corals can use this strategy to shift their thermal tolerance.

Another possible mechanism by which corals could increase their thermal tolerance is to swap their zooxanthellae for more resistant varieties[127]. While this idea continues to be debated[113], it seems increasingly likely that changes in zooxanthellae populations are most likely to occur through shifts in the relative dominance of heat-tolerant varieties already within a coral's tissues, rather than by taking on new varieties. The potential for corals to adopt new varieties of zooxanthellae remains an area of active research.

The role of coral pigments in sheltering zooxanthellae from light stress is another area of active research that could help explain some of the differences in bleaching resistance[110, 111]. Fluorescent pigment granules (FPGs) are common in many corals, at least in the western Pacific. They are positioned within the coral's tissue to optimise the light environment for zooxanthellae, concentrating light in low-light habitats, and shielding zooxanthellae in high light conditions. In this way, corals with high concentrations of FPGs may be less vulnerable to bleaching when water temperatures reach stressful levels.

4.2.2 Factors that influence survival

Bleached corals are still living, and if temperature stress subsides soon enough, most are capable of surviving the bleaching event and repopulating their tissues with zooxanthellae. The mechanism by which corals regain their symbiotic algae probably varies among species. It may occur through uptake of new zooxanthellae from the water column, although the most likely process is multiplication of surviving zooxanthellae that remain in the bleached coral's tissues at very low levels. Even a coral that appears much bleached to the human eye can still retain as many as 100-1000 cells per cm^2 (normal densities are $1\text{-}2 \times 10^6$ per cm^2)[130].

Corals that survive bleaching events are still likely to suffer sub-lethal impacts, such as reduced rates of growth and reproduction and increased susceptibility to diseases

Corals that survive bleaching events can still suffer significant impacts. Reproduction of corals that have bleached and recovered, for example, is much lower than that of corals that have not bleached[26, 114, 131]. Growth of bleached corals is also reduced, probably due to the combined effects of the stress and the reduced supply of energy following decreased zooxanthellae densities[25]. Bleached corals may also have reduced immunity to pathogens, making them more susceptible to disease[27].

The condition, or health, of individual coral colonies is emerging as a particularly important factor in determining whether or not a bleached coral survives. Recent and ongoing studies predict that coral condition (as determined by its energy status or the size of its lipid stores) will affect mortality risk during and following a bleaching event[41]. Specifically, large energy stores are likely to help a coral survive the period of starvation associated with depleted zooxanthellae populations. With adequate energy stores, a healthy coral will be able to maintain itself while bleached, until zooxanthellae populations and photosynthesis can be restored. Similarly, coral species that rely more heavily on heterotrophy (feeding on organic material from the water column) for their energy supply[132], such as those on coastal reefs, are also more likely to be able to tolerate the loss of zooxanthellae.

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Without their energy-providing zooxanthallae, bleached corals essentially enter a period of starvation. The condition of a coral as it enters this state is an important factor determining whether the coral can survive a bleaching-induced 'famine'. Another factor influencing coral survival during bleaching is the coral's ability to feed on plankton and other organic matter in the water column by using its feeding tentacles, as shown here

Box 4.3 How managers can help corals survive bleaching

While extreme temperature stress is almost certain to result in widespread coral mortality, the effects of more moderate temperature anomalies are highly variable. When temperatures do not greatly exceed bleaching thresholds, the coral loses its zooxanthellae, but its tissue may not be directly damaged. Whether mortality follows bleaching in these circumstances is thought to be largely dependent on the coral's ability to endure starvation, or to supplement its energy requirements from food particles captured from the water column (heterotrophy).

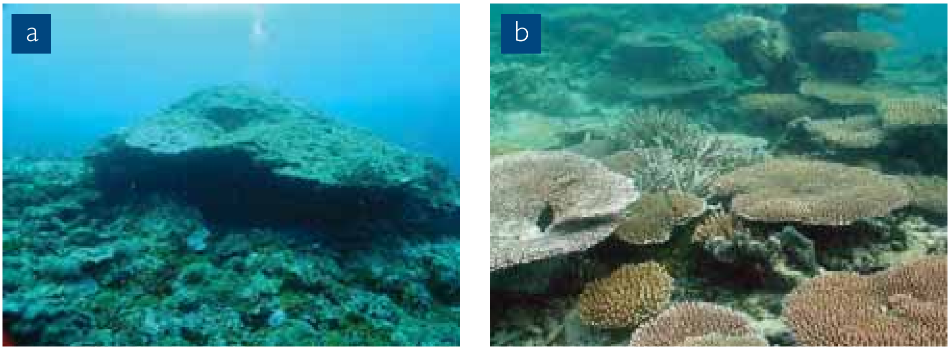
Some corals, especially species adapted to turbid environments, have been shown to rely heavily on heterotrophy. These corals may be less dependent on the energy provided by their zooxanthellae and thus less prone to starvation during a bleaching event. While the importance of heterotrophy to turbid-water corals has been demonstrated[132], its role in helping corals to survive bleaching requires further study. A better understanding of this issue may help managers identify coral communities that are at reduced risk of mortality from coral bleaching.

Coral health prior to exposure to heat stress may be the most important factor influencing colony survivorship during bleaching events. Most corals rely very heavily on the energy provided by their zooxanthellae, and bleaching effectively robs them of their main energy source. As a result, corals in the bleached state are beginning to starve, and their ability to endure this hardship is likely to be important in determining whether they survive. Like many animals, corals store surplus energy as lipids (fats). Corals in good condition will have relatively high lipid levels, endowing them with a buffer against periods of low energy supply. For this reason, it is thought that the condition of a coral at the time it bleaches may play a key role in determining whether it will be able to survive the period of starvation that follows. This implies that chronic stresses, such as water pollution or increased turbidity, which can negatively affect a coral's condition, could increase the risk of corals dying from the acute stress caused by bleaching. While these ideas have only recently begun to be examined for corals[41], they suggest that coral health should be considered as a priority focus for reef managers wanting to increase coral survival during moderate coral bleaching events.

4.2.3 Factors that influence recovery

Significant recovery can occur in only two to three years if mortality is minor (when there is an abundance of colonies that completely or partially survive the bleaching event). However, recovery of coral communities following severe mortality is likely to take much longer[5, 133, 134]. This is because reef recovery is a complex process influenced by multiple, interacting factors. On severely damaged reefs, recovery is dependent on the arrival of suitable coral larvae that have survived the bleaching event elsewhere, and their successful settlement, survival and growth[134]. Even assuming conditions favour recruitment, the recovery process is subject to the vagaries of larval supply and the many risks that confront the young coral, such as predation, smothering by sediments or algae, overgrowth by other corals, etc. In combination, these uncertainties mean that recovery of a site to an abundance, density and diversity of corals comparable to pre-bleaching conditions is a long-term prospect measured in terms of decades[133, 134].

A particularly sensitive step in the recovery process is larval recruitment. The production, settlement and survival of coral larvae is dependent on the availability of 'source' reefs to provide new larvae, good water quality to promote spawning, fertilisation and larval development, and suitable substrate for settlement and survival of coral larvae[45, 134].



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Reef recovery after severe coral mortality is a complex process influenced by multiple, interacting factors. These reefs in Palau demonstrate significant differences in their ability to recover. Both were severely affected by mass bleaching in 1998. Seven years after the event, only (a) minimal recovery is evident in one reef, while the (b) other has shown dramatic recovery of coral cover

Degraded water quality can affect the fertilisation success of corals[72, 135, 136], potentially placing severe limitations on the ability of coral communities to recover after bleaching-induced mortality. Water quality can also have a negative impact on recovery by encouraging algal growth, which in turn can reduce larval recruitment[44, 45]. Coral mortality allows an opening for frondose (leaf-like) and filamentous macroalgae ('seaweeds') to take on a more dominant role in reef ecosystems, often at the expense of coral recruitment[42, 45, 137]. This window of opportunity for algae following mortality events such as those associated with severe coral bleaching events means that the influence of nutrients in accelerating growth is more pronounced.

Recovery of severely damaged reefs is dependent on 'source' reefs to provide new larvae, good water quality, and suitable substrate. Where these conditions exist, new corals can settle and become established relatively quickly

The abundance of herbivorous fish populations is another critical factor influencing the success of recovery processes. In situations where herbivores have been heavily depleted through a combination of overfishing and disease, recovery of coral communities following disturbance has been greatly lengthened, or even stalled, resulting in a persistent shift from coral-dominated to algal-dominated reef for over a decade[82, 138].

Recovery can be even further compromised on reefs that are threatened by both degraded water quality and depleted herbivore populations. Increased nutrient levels greatly increase the potential for the excessive growth of algae that can occur when herbivory is reduced. Water quality and herbivore populations are each important, but in combination they become critical in determining the coral-algae balance after a disturbance[42, 45].

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Herbivores, such as grazing fishes, play a key role in maintaining the conditions that are required for the recovery of reefs damaged by coral bleaching

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Algae can overgrow established corals, or inhibit recruitment of new corals, when there are excess nutrients in the system or inadequate levels of herbivory

The importance of local processes highlights the pivotal role that effective management of local stressors can have in supporting the ability of reefs to recover from mortality associated with severe coral bleaching. In keeping with the example above, algal growth and herbivory could be optimised by limiting water pollution and fishing pressure. Furthermore, recent studies suggest that the 'source' of coral recruits is often from within the same or nearby reefs. Together, these insights emphasise the importance of managing local stressors when aiming to support the natural ability of reefs to recover from global stressors like bleaching events[11].

4.3 Can corals adapt to climate change?

The impact of mass coral bleaching on coral reef ecosystems over the long term will depend on the environmental changes that occur in tropical seas, the extent to which corals can acclimatise or adapt to changing conditions, and the ways in which repeat disturbances compound one another to shape coral reef ecosystems.

4.3.1 Future climates

Coral reefs are currently experiencing temperature regimes that exceed any they have experienced over at least the last 400 000 years[28]. Projections of temperature increases suggest that conditions will develop that are vastly different to those in which the majority of coral reefs have developed over the same time frame[11].

Global ocean temperature has increased by an estimated 0.6°C between the mid-1950s and mid-1990s. Some studies predict future increases in global sea temperatures of 1.4-5.8°C by 2100[8], suggesting that mass bleaching events, which may be induced at only 1-2°C above normal summer temperatures, are likely to be a much more frequent phenomenon in the future[9, 13, 28].

Projections of future sea temperature increase suggest that conditions will develop that are vastly different to those in which the majority of coral reefs have developed over the last 400 000 years

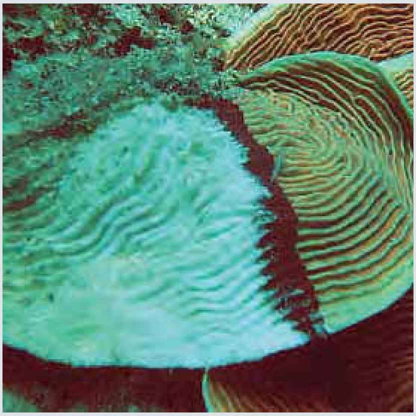
Oceanic currents and atmospheric conditions may also be affected by rising sea temperatures. Changes in the strength and direction of currents are likely to have a strong influence on local temperatures, while changes in atmospheric circulation may influence upwelling, precipitation patterns and the frequency and intensity of regional weather extremes[8]. All of these factors have the potential to increase the extent and severity of mass coral bleaching events. Importantly though, while the potential for these very significant changes is recognised, there remains substantial uncertainty about the direction, magnitude and location of changes in oceanic circulation due to climate change[13].

Potential effects of climate change on coral reefs. Climate change may influence coral reef ecosystems through processes such as mass coral bleaching, changes in the frequency or severity of storms[8], greater virulence of diseases[27], sea level rise[139], and reduced calcification rates in reef-building[20] (see Box 4.4). Of these, mass bleaching events are likely to be the most influential in determining future coral reef condition[13, 28]. By itself, mass bleaching has resulted in significant ecological impacts to coral reef areas unaffected by local stressors. For many other reefs, mass coral bleaching is an additional stress that exacerbates the impacts of local stressors[44]. The influence of mass bleaching events on coral reefs and, in particular, how it interacts with local stressors, will be one of the most important determinants of the future of coral reef ecosystems over the next 50 years[11].

Box 4.4 Coral reefs and climate change: implications beyond mass bleaching

Climate change threatens coral reef ecosystems in other ways aside from increasing the frequency and severity of bleaching impacts. Climate model projections indicate that we can also expect increases in sea level, greater incidence of coral disease and changes in ocean chemistry[13]. While the rates of coral reef growth are likely to keep pace with projections of sea level rise, shoreline inundation with rising water levels pose other risks. Among these are an increase in the export of sediments, nutrients and pollutants from flooded coastal areas. Animals that rely on the low-lying habitat provided by coral reef islands and cays, such as sea turtles and seabirds, are likely to be significantly affected, although these potential impacts are just beginning to be explored.

Many coral diseases increase in virulence at higher temperatures, suggesting greater prevalence of disease outbreaks as average sea temperatures increase. Diseases have already caused chronic coral mortality in many reef areas, such as the Florida Keys and the Caribbean, and reports of coral disease are increasing in other regions including the Great Barrier Reef and other Indo-Pacific locations.



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The impacts of mass coral bleaching will be compounded by other climate-related stressors. In particular, reduced calcification rates and increases in coral disease (shown here) are significant concerns. The incidence of coral disease can be expected to increase because disease virulence increases at higher temperatures and because the incidence of disease has been observed to increase following mass bleaching events, when corals are in a weakened condition

At a regional or global level, changes in ocean chemistry will result from changes in the earth's climate. In particular, dramatic increases in the levels of carbon dioxide (CO^2) in the earth's atmosphere are leading to a reduction in the pH of seawater, which in turn is decreasing the availability of carbonate ions. Reduced calcium carbonate saturation states of seawater are expected to significantly reduce the rates of calcification in key reef-building organisms such as corals and coralline algae[20, 140]. The implications of this for the ability of coral reefs to withstand storms and to maintain their role in shoreline protection are still being examined, but early indications are that these changes will be important, even if they manifest themselves only slowly or subtly. This has particular significance for the ability of coral reefs to maintain their roles in protecting shorelines from oceanic swells and supporting fisheries–both critical ecosystem functions in many tropical regions.

4.3.2 Can corals keep up?

Comparing projected sea temperature increases with existing coral reef temperature thresholds indicates that the frequency and severity of mass bleaching events can be expected to increase significantly. Studies on this issue have concluded that bleaching could become an annual event in coming decades as conditions that are known to have caused major mortality events in the past become more frequent[9, 28, 29]. However, these predictions assume that bleaching thresholds will not change over time, and do not allow for the effect of adaptation. The actual impacts on coral reefs will depend strongly on the capacity of corals to adapt and the rate at which they do so.

Adaptation. There is clear evidence of substantial variation in the resistance and survival of corals to bleaching, raising the possibility that these variations might be attributable to past adaptation. For example, corals of the same species may have a bleaching threshold of 28°C in the Galapagos but be able to tolerate temperatures over 34°C in the Persian Gulf. While these observations suggest that corals have historically had sufficient time and genetic variability to adapt, it is unknown whether they have the capacity to adapt fast enough to keep pace with current rates of change.

Studies that have compared future climate scenarios with current coral bleaching thresholds predict that the frequency and severity of mass bleaching events can be expected to increase significantly

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Adaptation involves genetic shifts in populations through selection of more resistant genotypes. This evolutionary process begins as soon as less resistant genotypes are killed. At that point, genotypes that are more resistant begin to make a greater contribution to the next generations of corals. However, the rate of adaptation depends on numerous factors, including the heritability of thermal tolerance, intensity of coral bleaching as a selective process, and the genetic structure of coral populations[11, 23, 28]. While there are differing degrees of optimism among recent studies, there is widespread agreement that the abundance and composition of reef communities will change substantially over coming decades, with large-scale degradation and losses of biodiversity possible in the longer term.

Acclimatisation. Acclimatisation refers to the ability of corals to make biochemical or physiological adjustments that increase their ability to withstand higher sea temperatures[23]. This mechanism occurs at the biochemical or cellular level, usually over time frames of hours or days. Physiological adjustments that give rise to acclimatisation may be highly ephemeral, lasting only as long as the stress, or they may be persistent, endowing a coral with the ability to withstand future stress (such as high temperatures during the following summer). Such adjustments, even short-term ones, usually come with costs, including the diversion of energy away from other processes (such as reproduction). Additionally, for acclimatisation to be effective it must outpace the rate of increases in temperature, which becomes decreasingly likely at the upper level of projected temperature rise.

Incorporation of more heat resistant zooxanthellae within coral tissues is one of the major mechanisms proposed for acclimatisation; however, the extent to which coral species can swap algal symbionts remains unclear. This mechanism, called the Adaptive Bleaching Hypothesis (after Buddemeier and Fautin[127]), proposes that corals may swap their zooxanthellae for a more tolerant type following exposure to sub-lethal thermal stress. This idea is a subject of continuing debate[113, 141].

Corals may also acclimatise to warmer conditions by altering the density or positioning of pigments within their tissue. These pigments, such as fluorescent pigment granules, can shade the zooxanthellae during thermal stress, reducing damage to the photosynthetic system and the risk of bleaching[43, 111]. Enhanced fluorescence seen in some corals that appear to be more resistant to bleaching may be evidence of the role of pigmentation in helping corals acclimatise to thermal stress.

Range-shifts in response to increasing sea temperatures. Coral populations may be able to adjust to increasing temperature regimes through migration of heat-tolerant genotypes. The large differences in the severity of bleaching suffered by corals exposed to otherwise similar conditions strongly suggest that corals differ in their inherent ability to resist bleaching. At least some of the properties that confer thermal tolerance to corals are likely to be heritable (genetically coded). This leads to the potential for larvae from heat-resistant corals to travel to reefs formerly dominated by less hardy genotypes, where they may settle and re-populate areas affected by bleaching-induced mortality. Over time, this could lead to heat-tolerant species or genotypes shifting their range into habitats previously dominated by other species.

The success of this process will depend on the existence and survival of heat-tolerant genotypes, and on connectivity among reefs. In addition, the location and extent of particular thermal realms is not likely to be static as the climate continues to change. This means that range-shifts would need to occur at rates that equal or exceed the rate of movement of thermal realms in order for this process to compensate for the loss of corals due to increasing temperatures.

The temperature sensitivity of corals, and the likely limitation in their rate of acclimatisation and adaptation, suggests that coral reefs are likely to have less live coral cover and lower biodiversity as a result of a warming climate

There have also been suggestions that coral reefs may expand into the subtropics as the temperature warms (see review by Coles and Brown[23]). However, there is a decrease in shallow-water areas and an increase in siliceous sediments further from the equator, creating conditions that are less suitable for reef development. Therefore, although changes in climate may result in more suitable temperatures for coral growth away from the tropics, higher latitude marine environments tend to have substrata that are much less suited to development of carbonate reef structures, resulting in limited potential for reef communities to move towards the poles.

4.4 Reefs and people in the future

There is now abundant evidence that corals are highly sensitive to increases in sea temperature[5, 9, 11, 13, 80]. Their ability to adjust, either through acclimatisation or adaptation, is limited or widely thought to be too slow to keep pace with even conservative climate projections[23, 28]. The implication of these conclusions is that coral reef ecosystems are destined for further change as sea temperatures continue to warm[9, 11, 23]. While there remains great uncertainty about the rate, extent and precise impacts of this deterioration, the future will almost certainly see degradation of reef systems and consequent losses in ecosystem services[9, 13, 23, 31, 37].

4.4.1 Ecological implications

Effects of mass bleaching on coral cover and biodiversity. The temperature sensitivity of corals, and the likely limitation in their rate of acclimatisation and adaptation, suggests that coral reefs are likely to have less live coral cover and lower biodiversity as a result of increases in the frequency and severity of mass bleaching events[11, 23, 28]. Among the coral species most likely to show declines in abundance immediately after a severe bleaching event are those that tend to be relatively fast growing and visually dominant, such as staghorn and tabular *Acropora*[19, 80, 115, 118]. The loss of these species is likely to have a noticeable impact on the aesthetics of many reefs, as well as altering the amount of habitat for many reef-dependent species[11]. While these species may also be among the quickest to recover by way of larval recruitment and rapid growth, it remains highly likely that differences in bleaching susceptibility among corals will result in significant shifts in the community structure of coral reefs. This change is likely to result in flow-on affects to other organisms, as many species, including a variety of fish and invertebrates, are dependent on the habitat provided by branching corals (Box 4.5).

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Reefs dominated by corals most sensitive to thermal stress, such as plate and staghorn *Acropora*, are more likely to suffer severe impacts from coral bleaching. Loss of these species is likely to have a noticeable impact on the aesthetics values of reefs as well as the amount of habitat available for many reef-dependent species

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The differential susceptibility of coral species to thermal stress can result in severe shifts in community composition. At this site in the Lakshadweep Islands, India, massive corals such as *Porites* are now the dominant members of the coral community. Prior to the 1998 bleaching event, these sites were dominated by staghorn *Acropora*

Differences in the ability of species to migrate and to adapt will further exacerbate changes in community structure due to differential mortality from severe bleaching. If bleaching events become increasingly frequent, the more susceptible species may have trouble re-establishing between bleaching events, leaving abundant space available for algal growth. Decreasing time intervals between bleaching events would also limit opportunities for resistant species to establish sustainable populations before temperatures increase again. While the exact change to reefs based on projected increases in the frequency and severity of mass bleaching are highly uncertain, recent modelling studies[9, 31, 47] report the possibility of extensive degradation.

Box 4.5 Implications of coral bleaching for reef biodiversity

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Coral bleaching also has implications for biodiversity. For example, the orange-spotted filefish rapidly disappeared from reefs around Okinawa after the 1998 coral bleaching event

Our understanding of the impacts of climate change on biodiversity is in its infancy. While the pathway and time course of this change is undefined, most experts agree that biodiversity will be affected to some extent by a rapid loss of reef-building corals resulting from major disturbances such as coral bleaching events. Given the strong relationships that characterise reef ecosystems, many other species are also vulnerable to the impacts of coral bleaching.

Organisms that depend on corals for food or shelter and which reproduce via external fertilisation may be most threatened by bleaching, with extinction becoming a real risk as the primary habitat provided by corals becomes rarer. The kinds of organisms most at risk include the obligate corallivores: those species that eat only corals. These species are directly dependent on the presence of coral for their existence and disappear quickly if coral is removed. The orange-spotted filefish (Oxymonacanthus longirostris) is an example; it rapidly disappeared from reefs around Okinawa after the 1998 bleaching event[142].

The response of the broader coral reef fish community to bleaching-induced losses of corals has proven more complex. Declines in some species (especially damselfishes that are strongly associated with branching corals) have been recorded following bleaching[63, 64, 143]*. In one recent study*[143]*, over 75 per cent of reef fish species declined in abundance, and 50 per cent declined to less than half their original numbers, following a devastating decline in coral cover caused in part by coral bleaching. However, the overall structure of fish communities in the Seychelles changed very little despite massive (threefold-twentyfold) decreases in live coral cover after the 1997-98 bleaching event*[64]*. Abundances of some fish have even appeared to increase following the loss of reef-building corals, with an overall increase in fish abundance observed after the 1998 mass bleaching event on Tanzanian reef systems*[63]*. These increases in fish populations appear to be caused by increases in herbivorous fishes, which may be responding to the greater availability of algae following reductions in coral cover.*

Other organisms are also likely to respond to changes in coral cover. For example, over 55 species of decapod crustaceans are associated with living colonies of a single coral species, Pocillopora damicornis[144, 145]*. Nine of these are known to be completely dependant on living pocilloporid coral colonies. Similarly, branching corals of the genus* Acropora *have 20 species that depend solely on the habitat they provide.*

Even under relatively conservative projections of sea temperature warming, many reefs previously dominated by a diverse assemblage of hard corals may give way to low-diversity, low-cover reef communities, reducing the ecosystem services upon which humans depend

Prospects for future coral reef condition. Even under relatively conservative projections, many reefs previously dominated by a diverse assemblage of hard corals may give way to low-diversity, low-cover reef communities. In the extreme, this may lead to algal-dominated reefs with low habitat complexity and limited scope for recovery by hard corals, all within 50 years. Although these projections may sound severe, they do not rely on catastrophic change. Rather, they assume, very conservatively, that reefs can recover between bleaching events as long as there are fewer than three massive mortality events per decade[28, 29]. Additionally, these projections do not consider the cumulative or synergistic effects of other stresses, such as water pollution or destructive fishing practices.

Reef recovery between mass bleaching events may be impeded by several factors (see Section 4.2.3 for information about factors that support reef recovery). Recovery processes can be substantially hindered by erosion of reef structures following coral mortality. The grazing of sea urchins in very high densities has led to erosion of reef structures in eastern Pacific reefs, such that the degraded state of reefs has persisted for two decades after the mass bleaching event of 1983[146, 147]. Projected reductions in the pH of upper ocean waters are likely to further encourage both biological and chemical erosion of reefs. Severe erosion can also lead to a shift toward an unstable substrate of coral rubble, making recovery from bleaching-induced coral mortality difficult[106]. The evidence from past mass bleaching events is that, while there are reports of active recovery from some sites, in general damaged reefs remain degraded compared to their pre-bleaching condition. It seems likely that the impacts of bleaching-induced mortality are likely to be evident for at least a decade at many locations.

While coral reefs are unlikely to be eliminated globally because of mass bleaching events, predicted declines in reef condition have serious implications. Reduced coral cover and degraded community structures are expected to reduce the suitability of coral reefs as habitat for many species, impacting the biodiversity and ecosystem services upon which humans depend. Although knowledge of the inter-dependencies is only beginning to accumulate, managers are becoming increasingly concerned about the effects of deterioration in reef condition on the human communities and industries that have come to rely on healthy ecosystems for their livelihood and lifestyle.

4.4.2 Social and economic implications

Impacts on fisheries. Changes in coral reef ecosystems resulting from bleaching are expected to translate into shifts in fish species composition and, possibly, reduced fishery catches[59, 148-151]. Coral reef ecosystems support fisheries by providing food and habitat for a diversity of species. Coral mortality from mass bleaching events leads to loss of reef structure and habitat, as dead coral skeletons erode and break down. This deterioration of the reef structure is probably not much different in nature from that caused by other disturbances, such as coral disease or outbreaks of the coral-feeding sea star *Acanthaster plancii*. However, the effects of coral bleaching events can extend over hundreds or thousands of kilometres[152], causing stress or damage on scales not normally experienced by coral reef ecosystems. Where significant coral mortality occurs, coral bleaching can result in dramatic decreases in the amount of habitat available for fish and other mobile reef species that depend on the structure provided by healthy coral reefs[64, 143].

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Changes in coral reef ecosystems caused by coral bleaching are expected to affect fisheries, especially small-scale and subsistence fisheries

Strongly coral-dependent fish species are expected to be the most affected by bleaching-induced coral mortality. Several species of fish are reliant on coral as a primary food source, and many other species use coral for shelter from predators. Post-bleaching declines in populations were recorded following the 1997-98 mass bleaching episode for several fish species that feed exclusively on corals[64, 142, 153], as well as for those that rely on coral for habitat, such as species of damselfishes that are strongly associated with branching corals[63, 64].

Coral-dependent fishes are important prey for larger species, many of which are targeted in coral reef fisheries. Bleaching events that result in widespread loss of physical habitat would be expected to have 'flow-on' effects for the higher trophic level predator fishes often targeted. Yet, while impacts on fish populations of the 1997-98 mass bleaching event have been clearly documented in several locations, evidence of impacts on fishery yields and income has been more difficult to document[44, 148, 154]. This may indicate that: (1) the expected relationship between loss of coral cover and predatory fish abundance is too simplistic; (2) functional redundancy at the study sites is, in the short-term, masking the likely impacts on higher-level predators in the long-term or (3) the relationship between fishers and the fishery resources are more dynamic and complex than expected (or a combination of these three factors).

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Fish species that are strongly dependant on corals for habitat or food, such as this damselfish on a reef at Pulau Pemanggil, Malaysia, are expected to be the most affected by bleaching-induced coral mortality. These coral-dependent fishes are important prey for larger species, many of which are targeted in coral reef fisheries

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Coral reef-based fisheries are the major source of food and income for coastal communities of tropical regions worldwide

Many reef-based fisheries are generalist in that they target a wide variety of species and sizes, and are partly subsistence-based. These characteristics make many reef-based fisheries both adaptable to changing conditions and able to be influenced by other external factors. Consequently, single cause-effect linkages may be difficult to discern. While the dynamic and adaptive nature of reef-based fisheries may make them more resilient to short-term decreases in fish stocks, they may also obscure indications of long-term risks to the sustainability of the fishery (see Section 2.4).

Impacts on tourism. Changes in coral reef ecosystems resulting from bleaching are expected to translate into economic losses to the tourism industry. The extent of the impact on tourism businesses varies with the flexibility of individual markets. For example, dive businesses that are based in population centres are likely to be more capable of responding to changes in reef quality caused by mass bleaching, because they may be able to shift from a focus on providing high quality dive sites for experienced divers to new divers expecting instruction or even to non-divers. By comparison, mass bleaching may significantly affect businesses based on taking divers to remote locations that are renowned for exceptional coral reef quality, but where options for business diversification are limited.

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Reef-based tourism plays a key role in many regional and national economies. Small-scale reef-oriented businesses, such as this ecotourism venture in the Philippines are vulnerable to deterioration in reef condition resulting from coral bleaching. Tourism businesses based on taking divers to remote locations renowned for exceptional coral reef quality are more likely to be negatively impacted by mass bleaching than operators based in population centres that may have more options for business diversification

Several recent studies have attempted to quantify losses resulting from coral bleaching on reef-based tourism industries. Estimates of the welfare loss between 1998-2001 from the 1997-98 mass bleaching event in Zanzibar, Mombasa, and the Seychelles are US$5.4 million, $6.4 million, and $9.7 million, respectively[37]. A recent study in Australia has estimated potential losses of US$95.5 million to US$293.5 million to the tourism industry by 2020 as a result of predicted deterioration in reef condition caused by coral bleaching[28].