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Madeleine J. H. van Oppen
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Coral Bleaching

Patterns, Processes, Causes and Consequences

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Cover illustration: Coral reefscape after a coral bleaching event at Halfway Island in the southern Great Barrier Reef, showing both bleached and unbleached corals side by side and some of the motile organisms that rely on a healthy reef ecosystem. (Photo Ray Berkelmans)

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Chapter 1
Introduction: Coral Bleaching - Patterns, Processes, Causes and Consequences

J.M. Lough and M.J.H. van Oppen

In 1769 when James Watt patented his improvement of the steam engine invented by Thomas Newcomen, the atmospheric concentration of the main greenhouse gas, carbon dioxide (CO_2), was ~280 ppm. A year later, Joseph Banks sailing on James Cook's *Endeavour* along the Great Barrier Reef, Australia, described with awe: "A Reef such a one as I now speak of is a thing scarcely known in Europe… a wall of Coral rock rising almost perpendicularly out of the unfathomable ocean". By 2006 the atmospheric concentration of CO_2 had increased 36% from the late eighteenth century to 381 ppm (WMO Greenhouse Gas Bulletin, http://www.wmo.ch/pages/prog/arep/gaw/gaw_home_en.html). During the intervening years inventors, engineers, scientists, politicians and entrepreneurs transformed the ways in which the world produced and transported goods, changed societies from agricultural to industrial and manufacturing bases and, most importantly, created and sustained the ever-increasing demand for energy consumption based on fossil fuels – the Industrial Revolution. By 1979 (when the first observations of mass coral bleaching were recorded) the atmospheric CO_2 concentration was 337 ppm. Article 2 of the 1992 UN Framework Convention on Climate Change (http://www.globelaw.com/Climate/fcc.htm) agreed to: "stabilization of greenhouse gas concentrations in the atmosphere at a level that would prevent dangerous anthropogenic interference with the climate system. Such a level should be achieved within a time frame sufficient to allow ecosystems to adapt naturally to climate change" – by then the atmospheric CO_2 concentration was 356 ppm. This was based on recognized concern that: "human activities have been substantially increasing the atmospheric greenhouse gases" and that this "will result in an additional warming of the Earth's surface and atmosphere and may adversely affect natural ecosystems and humankind." The first (1990), second (1995), third (2001) and fourth (Solomon et al. 2007; Parry et al. 2007) Assessment Reports of the Intergovernmental Panel on Climate Change provided mounting evidence of a changing world climate that, with increasing confidence, could be unequivocally attributed to enhanced greenhouse gases due to human activities. These reports also provided evidence that some impacts of climate change on natural ecosystems were already observable and, by the 2001 Assessment, coral reefs were identified as one of a number of "unique and threatened systems" (McCarthy et al. 2001). Human activities since the late eighteenth century have, unwittingly, led to already observable biological responses (coral bleaching) on one of

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the world's most charismatic ecosystems – coral reefs. This is in addition to what has been termed the "coral reef crisis" where direct local and regional human pressures on coral reef environments (such as over-fishing, destructive fishing, decline in water quality due to land-use changes, nutrient and chemical pollution and development on coasts, mining of coral, etc.) have caused declines in the health of many of the world's coral reef ecosystems (e.g., Wilkinson and Buddemeier 1994; Hughes et al. 2003; Buddemeier et al. 2004).

Tropical coral reefs are the most biologically diverse of marine ecosystems "equalling in beauty and excelling in grandeur the most favourite parterre of the curious florist" (Matthew Flinders, October 1802). They are complex ecosystems at all levels from their geological history, growth and structure, biological adaptation, evolution and biogeography, community structure, organisms and ecosystem metabolism and physical regimes. Coral reefs lay down enormous amounts of calcium carbonate to form massive reef structures that are able to withstand the forces of erosion and create diverse habitats for many organisms. Despite their relatively small area (estimated at only 0.1–0.5% of the ocean floor), coral reefs contain about one-third of the world's marine fish and reef fish account for ~10% of fish consumed by humans. Tens of millions of people in over 100 countries with coral reefs along their coastline depend on the economic and social goods and services provided by these rich ecosystems (Moberg and Folke 1999), valued at U.S.$ 375×10^{12}/year (Pandolfi et al. 2003).

At the heart of these complex ecosystems is an obligate symbiosis between the coral animal and single-celled photosynthetic algae (zooxanthellae) living in the coral tissue. Photosynthetic products provide the coral host with cheap energy. The zooxanthellae also play a role in light-enhanced calcification of scleractinian corals (Barnes and Chalker 1990), allowing the rapid calcification necessary to form reef structures. In return the algae obtain protection and essential nutrients (e.g., nitrogen, inorganic carbon; Davies 1984) from their coral host. The photosynthetic pigments within the algae give the corals their deep brown colour.

Coral bleaching is the term used to describe the loss by the coral animal of all or some of their symbiotic algae and photosynthetic pigments – with the result that the white calcium carbonate skeleton becomes visible through the now translucent tissue layer. Coral bleaching is not a new phenomenon due to global warming. Corals are known to bleach in response to a range of environmental stresses (e.g., low salinity, pollution, unusually high or low water temperatures). In the past, however, such occurrences of bleaching were only observed on small spatial scales in response to localized stresses. What is new and now clearly related to global warming due to the enhanced greenhouse effect is an increase in frequency of large-scale, mass coral bleaching events where entire reefs are affected.

Warming ocean temperatures in the vicinity of coral reefs are linked to the enhanced greenhouse effect and are already having observable consequences for coral ecosystems. Other aspects of projected climate change will also impact coral reefs. Although in some cases less certain (see Parry et al. 2007; Lough 2008; Hoegh-Guldberg et al. 2007) these include:

- More intense tropical cyclones which are a source of localized physical destruction on reefs
- Changes in regional rainfall and river flow regimes with likely more extreme rainfall events and more intense droughts that could affect the periodic extent of freshwater onto reefs
- A gradual rise in sea level that will affect light penetration and also the availability (increase and decrease) of suitable areas for corals to live
- Changes in large-scale and regional atmospheric (e.g., El Niño–Southern Oscillation (ENSO) events; prevailing weather patterns) and ocean circulation patterns that will affect connectivity between reefs
- Changes in ocean chemistry due to about one-third of the excess atmospheric carbon dioxide being absorbed by the oceans, which is lowering their pH and this, in turn, is decreasing the ability of marine calcifying organisms such as corals to form their skeletons and shells

These rapid climate changes are occurring against a backdrop of near-worldwide reef degradation due to local human activities (Hughes et al. 2003; Kleypas and Eakin 2007). In an ideal world, these localized sources of stress to coral reefs should be minimized to enhance the resilience of these remarkable ecosystems to global climate change.

This book fills a vacant niche by bringing together available scientific information on coral bleaching at different space and time scales from the deep geological record through to future projections. By focussing on the many facets of the coral bleaching phenomenon (the most immediate consequence of a changing climate for coral reefs) it builds upon several recent reports and books that highlight the vulnerability of coral reefs in a changing climate (e.g., Salm and Coles 2001; Grimsditch and Salm 2006; Phinney et al. 2006; Aronson 2007; Johnson and Marshall 2007).

The geological history and evolution of the critical coral–algal symbiosis at the heart of coral reefs is introduced by Stanley and van de Schootbrugge (Chap. 2). Oliver et al. (Chap. 3) assess the quality of the largely anecdotal observations of coral bleaching events in space and time and how the reliability of such observations (in the absence of globally widespread and standardized observations) can compromise our ability to determine significant changes in the frequency and occurrence of coral bleaching events. The observational record of the physical environment of coral reefs (particularly sea surface temperatures, SSTs) is much better than the biological record of coral bleaching events. Eakin et al. (Chap. 4) demonstrate how tropical SSTs are warming, the links between unusual warming and ENSO events and the now sophisticated remote sensing products that allow identification of oceanic “hotspots” and conditions conducive to coral bleaching in near-real time. The various tools available for detecting and observing coral bleaching are discussed by Spalding (Chap. 5). These range from remote sensing to the detail necessary in the field extending from whole reefs to individual colonies and, most importantly, the necessity for follow-on surveys to determine the consequences of a coral bleaching event. The possible role that the now recognized diversity of algal symbionts play in conferring thermal resilience on corals is considered by van Oppen et al. (Chap. 6). This also highlights the developing application of genetic analyses to determine algal symbiont diversity and their spatial patterns. Having undergone several bleaching events, is it possible that corals can increase their thermal tolerance? This is addressed by Berkelmans (Chap. 7) who also considers the relationship between thermal bleaching thresholds and the threshold that draws the line between coral's recovery or mortality. McClanahan et al. (Chap. 8) consider the range of consequences of coral bleaching events for corals and erect algae (the sessile benthos of a reef). They tease out the observed range of responses that varies between taxa and also through longer-term effects on reproduction, growth and the incidence of disease, etc. The complex structure of tropical coral reefs, built as a result of the coral–algal symbiosis, provides a habitat for many other motile reef organisms. Pratchett et al. (Chap. 9) assess the consequences of a coral bleaching event for these associated reef organisms and how these effects operate on both short and long time scales. Predicting what might happen to coral reefs in the future depends on understanding coral reef processes and reliably estimating how coral reef climates may change as global climate continues to warm. Donner et al. (Chap. 10) discuss how well current large-scale climate models can provide such information and the possible range of future climates for coral reefs. The findings of the various chapters are synthesized in Chap. 11.

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Chapter 2
The Evolution of the Coral–Algal Symbiosis

G.D. Stanley Jr. and B. van de Schootbrugge

2.1 Introduction

Scleractinians extract calcium (Ca^{2+}) and carbonate (CO_3^{2-}) from seawater to construct aragonite skeletons and have come to dominate present-day well lit, shallow-water coral reefs, evolving into a diverse array of growth forms with complicated corallum morphologies. Symbiotic dinoflagellate algae of the genus *Symbiodinium* (zooxanthellae) invade a wide variety of calcified and non-calcified marine invertebrates and have developed abilities to avoid the host's immune systems and evolve mutualistic associations. Scleractinian corals are a good example of zooxanthellae symbiosis. Ecologically distinguishing between zooxanthellate and azooxanthellate species, corals able to switch between these two categories are exceedingly rare. While azooxanthellate species may occupy some parts of the shallow-water reef, they prosper best in cold and deep water settings when adequate nutrients are available. Zooxanthellate corals dominate in tropical to subtropical, shallow-water reefs, producing large colonies and massive framework structures. Together with calcareous algae and other organisms, they foster an incredible diversity of marine life in low-nutrient environments. Current tabulations of scleractinians reveal 778 zooxanthellate versus 706 azooxanthellate species (Cairns 2007). The rapid calcification abilities and metabolic advantages conferred by photosymbiosis allow zooxanthellate scleractinians to dominate, grow rapidly, and construct reefs in oligotrophic waters of the tropics (Hallock 1997, 2001). Although we have a rich fossil record of scleractinian corals beginning some 245 Ma (million years ago), we have little information about the evolution of their algal symbionts.

The algal symbionts now partnering with corals likely evolved from a single adaptive radiation (Wood 1999). The discovery of at least six different clades (and many subclades) of *Symbiodinium* inhabiting different scleractinian hosts (Rowan 1998; LaJeunesse 2002; Statt et al. 2006), living at different depths and light intensities, and multiple clades of these symbionts infesting the same coral species, challenges a simplistic idea of symbiont co-evolution with their host. Corals acquire their symbionts by both vertical (from the parental colony) and horizontal (from the environment) modes but horizontal transmission by most broadcast spawners provides the greatest opportunity for recombination with their coral partners (Little et al. 2004).

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Furthermore, potential reshuffling of algal symbionts in response to global warming is hypothesized to have produced adaptive responses to bleaching (Fautin and Buddemeier 2004). Goulet (2006), however, challenged these assumptions as a general phenomenon, finding only a minority of corals able to host a single clade of *Symbiodinium*; but results from Mieog et al. (2007) contradict this finding.

This paper summarizes the early evolution of scleractinians and photosymbiosis. This theme has relevance for the bleaching phenomenon and the symbiotic relationship that has evolved between coral and zooxanthellae. The theme of photosymbiosis is certainly not limited to corals, as many other marine organisms (including non-calcifying ones) have developed similar symbioses. Indeed the phenomenon appears to be a pervasive theme in most ancient reefs, extending back to the middle Paleozoic when reefs were constructed by now-extinct rugose and tabulate corals as well as stony sponges (Copper 1989). The capacity of many species of living scleractinians for rapid and sustained skeletal growth is linked to light-enhanced calcification, a process long known to be associated with symbiotic zooxanthellae (Goreau and Goreau 1959). Although the exact physio-chemical processes and precise pathways by which the zooxanthellae increase calcification is not resolved (Marshall 1996; Goreau et al. 1996; Carlson et al. 1996; Gattuso et al. 1999), algal symbiosis certainly is the force behind the fast metabolism and rapid calcification rates of many zooxanthellate corals, especially reef-building species.

When did this ecological relationship evolve in the ancestors of modern corals and how has it changed through time? Wells (1956) assumed an original zooxanthellate ecological condition for the earliest Triassic scleractinian corals after which, in the Early Jurassic, some species assumed a deeper-water azooxanthellate ecology. Stanley (1981) proposed an alternative idea that the earliest scleractinians were initially azooxanthellate but, late in the Triassic, co-evolved a symbiosis with algal partners. The timing of this event was based, in part, on an absence of reef-building in Middle Triassic corals and the commencement of an adaptive radiation among Late Triassic corals. This coincided with the volumetric increase in reef complexes of the warm-water Tethys (Flügel 2002). It has been questioned whether Triassic and Jurassic corals actually are comparable to modern zooxanthellate counterparts in terms of reef-building and ecology (Leinfelder 2001; Flügel 2002; Stanton 2006) and it has been suggested that the photosymbiosis was not as “efficient” as in corals that emerged in the Cenozoic (Rosen 2000; Perrin 2002) when many progenitors of modern corals appeared.

2.2 Detecting Photosymbiosis in the Fossil Record

Because fossil scleractinian skeletons do not preserve the algal symbionts, their former presence is deduced by a variety of indirect methods, such as colony size and shape, corallite size and level of integration, the edge zone, and the nature of the skeleton (Coates and Jackson 1987; Rosen 2000; Stanley 2003). Measurement of annual growth bands and stable isotopes also holds promise in recognizing fossil zooxanthellate corals. Cowen (1988) inferred by such indirect methods that many extinct reef organisms, extending back over 500×10^6 years, were photosymbiotic. These included Cambrian archeocyathids, large calcified sponges (stromatoporoids), and Cretaceous rudistid bivalves. Although the basis of these assessments has not gone without challenge (Wood 1999), it seems certain that photosymbiosis opened new metabolic pathways; and enhanced calcification rates figure importantly for the success of many ancient reefs, especially those of the Mesozoic (Stanley 1992, 2006).

Colony shape, corallite size, and corallum complexity correlate well with living photosymbiotic corals and other hypercalcifying organisms. This is especially true of the platy growth habit (Rosen et al. 2000). Other features, such as thin tissue syndrome and the presence of pennular structures in the skeleton, have also been suggested as indicative of photosymbiosis (Wood 1999). Stolarski (2003) suggested that the regularity of mineral/organic phase alternations in thickening deposits among nano-structural aspects of the skeleton might distinguish zooxanthellate species from azooxanthellate counterparts. Stable isotope ^{13}C and ^{18}O fractionation in the skeletons of living zoxanthellate species differentiates them from azooxanthellate counterparts (Swart 1983). Scleractinian corals also produce discrete, periodic (annual) skeletal growth bands. The presence of these bands among ancient reef organisms provides estimates of growth rates and examples in Silurian to Devonian reef-building corals and stony sponges (stromatoporoids) were used to infer photosymbiosis (Copper 2002).

2.3 Mesozoic Reefs and Coral Evolution

In the early history of Mesozoic corals, the first calcified members of the living order Scleractinia made their debut in the fossil record 237 million years ago, soon after the start of the Middle Triassic and during an interval of warm climate and expanded carbonate shelves and reefs (Fig. 2.1). These first reefs of the Mesozoic were constructed by sponges, bryozoans, calcified algae, and non-colonial invertebrates. This was the recovery phase of reefs, long after the world's greatest mass extinction at the end of the Permian (Erwin 2006). The long interval of the Early Triassic was marked by a general absence of metazoan reefs and the suppression of carbonate deposition except in rare areas such as south China (Lehrmann 1999). Because the Early Triassic is a whole geologic epoch, largely without corals and metazoan reefs, it is a rather enigmatic interval. It testifies not only to the magnitude of the end-Permian mass extinction but also to the idea that adverse effects continued to suppress reefs and much of marine life for some $8–10\times10^6$ years. Scleractinians appeared around the world in the Middle Triassic interval (Fig. 2.1) and appear unrelated to ancient orders of Paleozoic corals, all of which perished in the end-Permian extinction. Scleractinians are thus separated from the last Paleozoic corals by a considerable time-gap. They also differ from these in composition (Paleozoic corals secreted calcite rather than aragonite), a different symmetry, and different patterns of septal insertion. The taxonomic diversity and corallum complexity of these earliest Triassic corals, coupled with their abrupt appearance and temporal isolation from Paleozoic corals, suggest a prior history as soft-bodied, anemone-like forms that left no fossil record. This is the "naked coral" hypothesis (Stanley and Fautin 2001) that was recently confirmed by molecular analyses (Medina et al. 2006) and by decalcification experiments in living corals (Fine and Tchernov 2007; Stanley 2007).

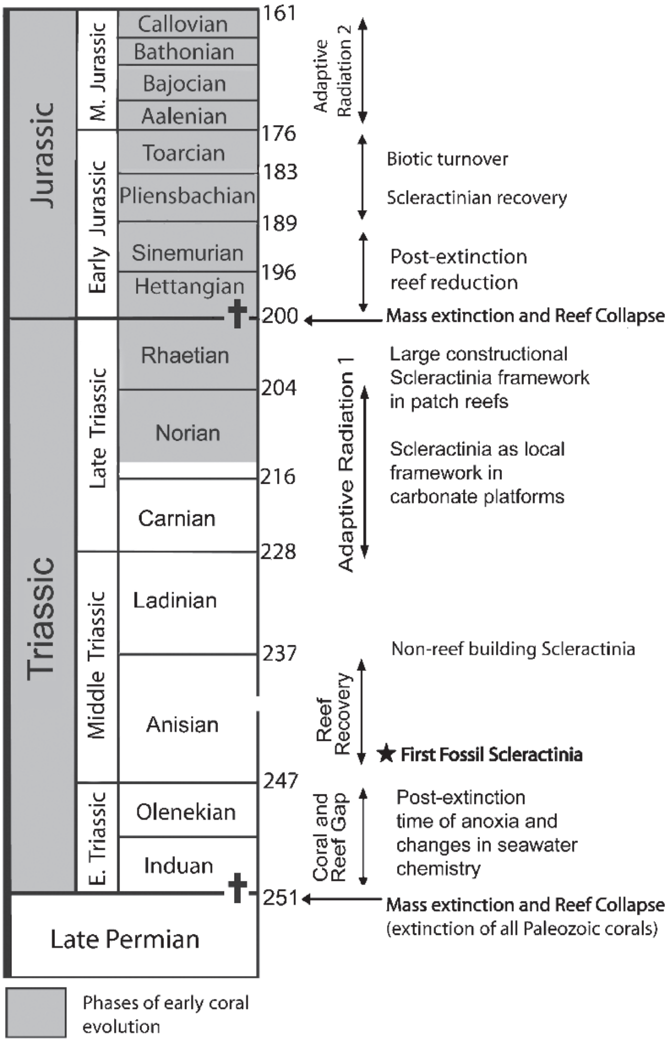

Fig. 2.1 Signposts and key highlights in the evolution of scleractinian corals during the early Mesozoic. The smallest subdivisions of the time column are stages discussed in the text. Geologic time in millions of years (*Ma*) is given to the right of the column

Although diverse and complex in corallum morphologies, the earliest scleractinians of the Middle Triassic interval did not build reefs and appear to have inhabited non-reef settings, while calcareous algae, foraminifers, bryozoans and non-colonial invertebrates produced carbonate complexes. The Late Triassic witnessed a sea-level rise, climatic warming, the emergence of large platform complexes, and an adaptive radiation among corals (Fig. 2.1). Explanations for the emergence of scleractinian corals as a framework-building component of reefs, along with calcified sponges, hydrozoans, and calcified algae, have occupied considerable discussions (Flügel 2002; Stanley 2003). Prior to the Late Triassic, scleractinians were mostly merely reef dwellers and did not participate in the construction of reefs. The emergence of scleractinians within this ecological reef guild during the Late Triassic was suggested by Stanley (1981) to equate with the co-evolution with zooxanthellae.

To test the hypothesis of photosymbiosis, geochemical approaches employing stable isotope analyses were applied to pristine solitary and colonial Late Triassic coral species from the Tethys. These provided the most compelling evidence that Late Triassic corals were zooxanthellate (Stanley and Swart 1995) – a finding corroborated by the isotopic composition of the organic matrix (Muscatine et al. 2005). Identification of biochemical markers of zooxanthellate symbiosis in the mineralizing matrices of living corals (Cuif et al. 1999) suggests that molecular compounds may help discriminate zooxanthellate corals in the fossil record.

Within Late Triassic time (Carnian–Norian transition) we find a biotic turnover at lower taxonomic levels among both sponges and corals that might indicate a small-scale mass extinction (Stanley 1988). Large colonial corals evolved more complex corallites in the succeeding “Norian–Rhaetian global reef bloom”. This correlates with the start of a 200×10^6 year prevalence of platy scleractinian growth, indicating a photosymbiotic response to reduced light illumination (Rosen et al. 2000). Coral-dominated reefs are especially well known from reef complexes in the Alpine regions of central Europe (Flügel 2002). During this reef bloom the latitudinal range of reefs expanded and warm climatic conditions are indicated. It has, however, been questioned whether Triassic corals constructing the reefs really were comparable to modern zooxanthellate species in terms of reef-building and ecology (Flügel 2002; Stanton 2006). Certainly these early coral species had ecologies somewhat different from extant species.

A mass extinction is stamped clearly in the geologic record of Late Triassic reefs (Fig. 2.1), especially in the region of the ancient shallow Tethys. The cause of this end-Triassic mass extinction, one of the “big five” of the Phanerozoic, has been variously related to the eruption of flood basalts and release of aerosols and greenhouse gases, sudden release of methane hydrates, and even a meteorite impact (Tanner et al. 2004) triggering major perturbations of the Earth’s global carbon cycle. The end of the Triassic coincides with evidence of a major reef collapse (Hallam and Goodfellow 1990).

The first two stages of the succeeding Lower Jurassic record a time of global reef reduction representing an interval of some $4–5\times10^6$ years when nearly all Triassic coral species died out. In the following stages of the Lower Jurassic, despite a Tethys anoxic event at the end of the Early Jurassic (Toarcian), there is evidence of recovery and biotic turnover leading to a renewal of coral and reef diversity during the Middle to Late Jurassic (Beauvais 1984). During the Middle and Late Jurassic, coral, sponge, and microbial reefs are known but it was during this period that corals again became principal builders of shallow reefs, while in deeper water settings, siliceous sponges and microbiobial deposits predominated (Leinfelder 2001). Some deeper water coral biostromes show evidence of an ecology quite different from the nutrient-limited model of coral reefs today (Insalaco 1996). The end of the Jurassic was marked by a small-scale biotic extinction but it was only slightly felt among reef communities. For nearly 30×10^6 years of the Early Cretaceous uniquely adapted rudistid bivalves evolved and coexisted in reefs along with corals, sponges, and other organisms.

Rudistids were amazingly adapted, gregarious bivalves that lived on reefs and were remarkably diverse. They mimicked corals in shape, close packing, and interlocking margins and they attained huge sizes, showing evidence of photosymbiosis (Cowen 1988). They came to dominate and construct build-ups in the shallow-water setting of the warm tropical Tethys from the Middle to Late Cretaceous time. This rudistid dominance coincided with global warming in a super greenhouse interval of high sea surface temperature (Johnson et al. 2001). Ironically, throughout the latest Cretaceous interval of maximum rudistid development, scleractinians were present and actually increased in diversity (Kiessling and Baron-Szabo 2004). While corals appeared to have lost their former dominance and abilities to build reefs, they nevertheless continued to prosper, especially in deeper, down-slope settings. The shallow-water guild was taken by rudistids. The end of the Cretaceous witnessed the demise of all rudistids and coincided with a warm greenhouse supercycle of high CO_2. Corals survived the devastating Cretaceous–Paleogene mass extinction while rudistids did not. Cretaceous zooxanthellate-like corals, especially those with complex corallum morphologies, were more severely affected by the extinction, relative to azooxanthellate taxa. Following the mass extinction, zooxanthellates appeared to have survived across the boundary (Rosen 2000) but preferentially more azooxanthellate corals are found in the succeeding Paleogene period (Kiessling and Baron-Szabo 2004). Post-extinction scleractinians diversified and appear to have recovered sooner than in previous mass extinctions.

Following the marine perturbations of the Paleocene–Eocene thermal maximum, coral reefs again prospered. The Cenozoic record of corals and reefs reveals the persistence of coral reef frameworks, starting in the Middle Eocene with an Oligocene diversity plateau after which coral extinctions occurred (Perrin 2002). The Neogene offers cases of reef expansion and provides evidence for the evolution of modern scleractinian genera. Compared with their ancient ancestors, late Cenozoic to Holocene reef-building scleractinians are enigmatic. In spite of their apparent fragility, they reveal amazing resilience in the face of plate tectonic upheavals and exhibit resistance to sea-level eustasy and major climatic changes. Answers to this enigma could come from discovered genetic variation and adaptive potential of various clades of zooxanthellae that evolved recently and now inhabit living reef corals (Little et al. 2004). Could the adaptive flexibility conferred by the shuffling of zooxanthellate clades have opened new adaptive potentials between host and symbiont, driving the evolutionary success of late Cenozoic and modern corals? The conclusions presented above, regarding the inefficiency of many Mesozoic zooxanthellate-like scleractinians for reef building (Leinfelder 2001; Flügel 2002), compared with Cenozoic to Holocene examples, might be explained by the idea that these ancient scleractinians had not yet evolved the adaptive repertoire with their zooxanthellate partners.

The gaps following mass extinctions represent the crisis "aftermath" among reef ecosystems of the Mesozoic. They were lengthy intervals ranging from 10^6 years to as much as 8×10^6 years in duration. Recovery clearly took considerable geologic time. As previously mentioned, many workers have equated this with perturbations in photosymbiosis partnerships. The eventual renewal of photosymbiosis among surviving scleractinian groups could explain at least some of the trends observed in the fossil record of reefs, although other factors certainly were also at play (Wood 1999).

2.4 The Suessiaceae: Late Triassic Dinoflagellate Symbionts?

The proliferation of scleractinian corals appears to have proceeded in concert with the Carnian–Norian (230–210 Ma) radiation of modern dinoflagellates (MacRae et al. 1996), which are the main photosymbionts in modern reef ecosystems. In the following we briefly discuss the evidence for a possible evolutionary relationship between Triassic dinoflagellates and corals.

In a seminal paper on the recognition of animal–algal symbiosis in the fossil record, Cowen (1983) was adamant that: "Direct evidence of symbiosis (discovery of the symbionts themselves) is highly unlikely in the fossil record. No symbionts are embedded in hard tissues of [the] host". A possible, and surely not the only, exception may be observed in the Late Triassic to Early Jurassic interval, where we find fossilized dinoflagellate cysts that belong to the family Suessiaceae, order Suessiales (Fig. 2.2). Fossil dinoflagellate cysts are distinguished and classified based on the number and arrangement of para-plates on the cyst-wall that are known to reflect the plate tabulation on the cell-wall in the motile stage (Fensome et al. 1999). Apart from being practically the oldest unequivocal dinoflagellate body fossils, members of the Suessiaceae share a unique para-tabulation of seven to ten latitudinal and two cingular para-plate series (Bucefalo Palliani and Riding 2000), which is strikingly similar to plate tabulation patterns observed in present-day *Symbiodinium*. Based on this similarity it has been suggested that Triassic Suessiaceae were symbionts of the earliest scleractinian corals (Bucefalo Palliani and Riding 2000).

Although it is tempting to attribute the proliferation of scleractinian corals during the Late Triassic to co-evolution with dinoflagellate symbionts, many questions remain. Cowen (1983) noted that: "Symbionts escape or decay or are ingested on the death of the host and would in any case be impossible to distinguish from free-living species even if preserved." The fossil record of Triassic suessiacean dinoflagellate species is reconstructed from the encysted life-cycle stage that must have developed independently from their coral hosts, during a free-living stage in the water column. Extant *Symbiodinium* is known to survive in the water column, where it does “re-infect” the embryos of coral species that do not transmit their symbionts vertically (Smith and Douglas 1987). However, in contrast to Triassic suessiacean dinoflagellates, *Symbiodinium* does not produce cysts that would allow it to become fossilized. Even though it will be virtually impossible to tie individual Triassic Suessiaceae to single Triassic coral species, there is much indirect evidence to suggest a link existed between Suessiaceae and early Scleractinia. Paleogeography may also hold a key (Fig. 2.2). A good match exists between the paleobiogeographic distribution of Late Triassic reefs and suessiacean dinoflagellates (Bucefalo Palliani and Riding 2000). For most of the Late Triassic, coral reefs were bimodally distributed across the equator from 40°N to 40°S (Kiessling 2001). This reef distribution is mimicked by the distribution of suessiacean cysts (Fig. 2.2), which are most abundant from Austria (Morbey and Dunay 1978) to Australia (Backhouse et al. 2002). Nearly all reported occurrences of Suessiaceae cysts are from sediments interbedded

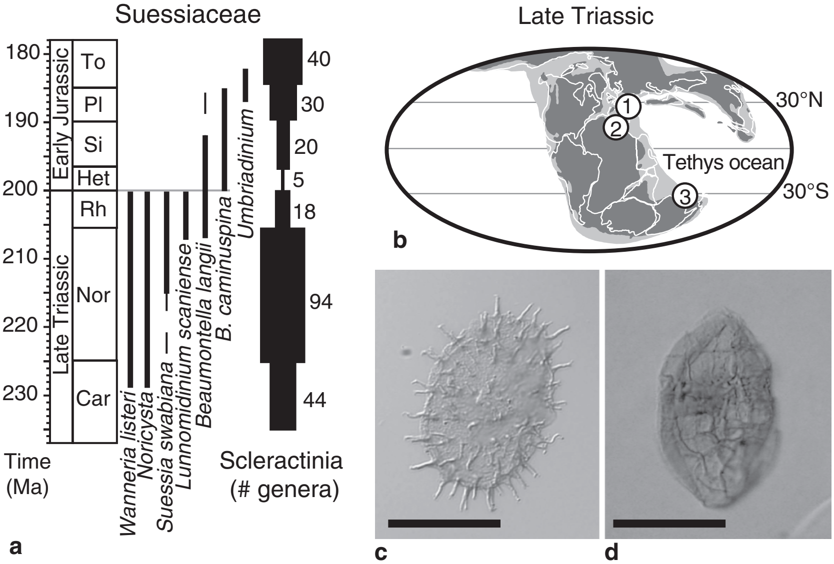

Fig. 2.2 **a** Late Triassic to Early Jurassic timescale with range chart showing most important Suessiales and scleractinian coral diversity. Coral data from Stanley and Beauvais (1994) and Flügel (2002). Stages: CAR, Carnian, NOR, Norian, *RH* Rhaetian, *HET* Hettangian, *SI* Sinemurian, *PLI* Pliensbachian, *TOA* Toarcian. **b** Late Triassic paleogeography showing the one-world continent of Pangea (modified after Scotese Paleomap Project 2000). Map shows reef sites with suessiacean dinoflagellate cysts: *1* Austria, *2* Libya, *3* NW Australia. Note the co-occurrence of reefs and Suessiaceae dinoflagellates between 30°N and 30°S and along the edges of the Tethyan Ocean. **c** *Beaumontella langii. Beaumontella* was the only genus that survived the end-Triassic mass-extinction event. This dinoflagellate cyst was obtained from the earliest Jurassic in the Mingolsheim core, SW Germany (van de Schootbrugge, unpublished data). *Bar* 20 µm. **d** *Suessia swabiana*. This specimen is from the latest Triassic in the FFC-1 core from southern Sweden. Photograph from Lindström and Erlström (2006), reprinted with permission of the authors and Elsevier Science. *Bar* 20 µm

with reef limestones. The oldest suessiacean genus *Noricysta* has been found in shales interbedded with Upper Carnian reef limestones in the Swiss Alps (Hochuli and Frank 2000). The best example, however, has been described from Ocean Drilling Program cores (ODP Leg 122) obtained from the Wombat Plateau, off the northwestern coast of Australia (Fig. 2.2). There, *Suessia* and *Wanneria* are the dominant dinoflagellate species occurring in massive *Astraeomorpha–Retiophyllia* reef build-ups (Brenner 1992).

The genus *Beaumontella* (Fig. 2.2) occurs abundantly in the uppermost Triassic of northwest Europe and is the only suessiacean genus that survived the end-Triassic mass-extinction event (200 Ma). The Triassic–Jurassic boundary mass-extinction event wiped out more than 95% of all scleractinian coral species (Flügel and Senowbari-Daryan 2001; Flügel 2002) and coral reef build-ups are extremely rare during the beginning of the Jurassic (Stanley 2001, 2003). *Beaumontella* also occurs abundantly in Lower Jurassic shallow marine sediments (van de Schootbrugge et al. 2007) and it may thus be hypothesized that *Beaumontella* thrived in response to severe environmental stress. Interestingly, the highly spinose cysts of *Beaumontella* resemble *Polarella glacialis,* the only extant suessialean dinoflagellate known to build cysts (Montresor et al. 1999).

The last suessiacean cyst genus, *Umbriadinium*, is known from uppermost Pliensbachian (185 Ma) sediments in Italy (Bucefalo Palliani and Riding 1997). By this time scleractinian corals, with clear Triassic characteristics, had started a renewed radiation (Fig 2.1). Suessiacean dinoflagellate cysts have not, however, been identified in sediments younger than the Toarcian stage, representing the Early Jurassic Toarcian (Bucefalo Palliani and Riding 2003), leaving a gap of more than 180×10^6 years in our understanding of coral–algal photosymbiosis.

One explanation for the disappearance of the Suessiaceae from the fossil record is that they lost the ability to produce fossilizable cysts or stopped making cysts altogether. An alternative, more easily testable, hypothesis is that scleractinian corals during the Jurassic and Cretaceous did not rely on symbiosis with dinoflagellates (i.e. *Symbiodinium*) and this was re-invented during the Cenozoic. There are many independent lines of evidence to suggest that Late Triassic photosymbiosis between corals and dinoflagellates evolved in response to oligotrophic conditions (Riedel 1991). Middle Jurassic scleractinian corals that appeared after the Toarcian bottleneck are markedly different in taxonomic composition from those of the Late Triassic (Beauvais 1984). According to Leinfelder (2001), Jurassic reef corals lived mostly in mesotrophic waters of high siliciclastic influx and their zooxanthellate symbiosis was speculated to have been not as “effective” for metabolism and calcification as modern reef corals. Many scleractinian corals that fared well in the aftermath of the end-Cretaceous mass-extinction event (65 Ma), were inferred to have lived in highly turbid waters, suggesting that they were azooxanthellate (Kiessling et al. 2005). Molecular phylogenetic analyses indicate that *Symbiodinium* evolved after the Cretaceous–Paleogene boundary (Shaked and de Vargas 2006) and that they diversified rapidly during the Miocene (LaJeunesse 2005). This coincides closely with the time when modern coral reefs took shape (Perrin 2002).

2.5 Geological Perspectives on Current Coral Bleaching

Present-day coral reefs exist within narrow limits of temperature, light, and seawater aragonite saturation states. In the broad perspectives of geologic time, we are in an icehouse supercycle with an ocean favoring the precipitation of aragonite. Current climate change may be prematurely moving us into enhanced greenhouse conditions and subjecting coral reefs to added stresses (Hoegh-Guldberg 2005). Thermal stresses caused by rising temperatures have triggered numerous mass bleaching events among living photosymbiotic corals (Chap. 3). Bleaching events signal a breakdown of symbiosis but the long-term repercussions for reefs and their capacity for adaptation and quick recovery have not been resolved. The fossil record, therefore, may assist.

Reef patterns observed throughout much of the Phanerozoic, following major mass extinctions, include episodes of relatively sudden collapse followed by extended reef eclipses, usually accompanied by decreased metazoan carbonate production. This has been succeeded by slow reef recoveries, leading eventually to new reef ecosystems. The geologically “sudden” response in many reef ecosystems to mass extinction and the extended post-extinction reef eclipse following reef collapse have direct relevance to current problems of coral bleaching. While difficult to detect bleaching in the fossil record, crises recorded in many reef ecosystems of the past certainly would have adversely affected photosymbiosis and ancient bleaching is a logical consequence. This appears to have been the case for corals during the end-Triassic when more than 95% of coral species, most judged zooxanthellate, died out (Stanley and Swart 1995) and during the Cretaceous–Paleogene event when an estimated 45% of coral species died out (Kiessling and Baron-Szabo 2004). During warm intervals of the Cenozoic (e.g. Eocene, Miocene) zooxanthellate corals were able to expand their ranges into higher paleolatitudes than those of the present day.

Although time-scales of paleoecological change within ancient reefs cannot be resolved with the resolution available for their Holocene counterparts, stresses associated with global mass extinction on ancient reefs most certainly involved bleaching and disruption of photosymbiosis. In some cases global warming is implicated but for others cooling is more likely. Several workers were quick to equate the sudden collapse of ancient reef ecosystems following mass extinctions to the breakdown of symbiosis (Talent 1988; Copper 1989; Rosen and Turnšek 1989; Stanley 1992; Perrin 2002), although this idea has not gone without challenge (Rosen 2000).

The fossil record chronicles the rise, fall, and recovery of reefs. It is a sobering record because of the longevity of post-extinction global reef gaps and the length of time before reef recovery. Intervals when reefs are either entirely absent or greatly reduced range from 10^6 years to as much as 10×10^6 years in duration. The length of time for recovery has implications for the current environmental crisis. Put into perspectives of the current biotic marine crisis, in which humans are both directly and indirectly involved, the implications are bleak for the future evolution of reefs (Myers and Knoll 2001). Although evolution is not predictable, meaningful estimates on diversity trends and rates of recovery following mass extinctions, are emerging from the fossil record. A study of the role of zooxanthellate photosymbiosis in the geologic past may provide new insights into both successes and failures on living coral reefs. The integration of biology and the fossil record, especially ecology, molecular biology, and life history of both corals and symbionts, offers potentials to better understand the current coral reef problems, including the bleaching phenomenon.

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Chapter 3
Coral Bleaching in Space and Time

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3.1 Introduction

Coral reefs are facing a range of serious anthropogenic threats that may significantly alter their ecological composition and reduce their capacity to deliver essential ecosystem services. Human influences such as destructive fishing, terrestrial runoff, pollution, and uncontrolled coastal development have a direct and immediately apparent impact on reefs. However the impacts of human-induced climate change are increasingly being seen as a more pernicious and intractable problem to resolve which probably requires concerted social action at a global scale and over many generations (Hughes et al. 2003). Large-scale bleaching of reef corals, resulting in mass mortality, has emerged as a critical global threat to coral reefs and is clearly attributable to thermal stress. Thermal stress on coral reefs has clearly increased over the past century (Chap. 4). As global temperatures continue to rise, largely due to anthropogenic greenhouse gas emissions, the threat to coral reefs is expected to increase significantly.

Predictions based on climate models and thermal tolerance of corals suggest regular widespread catastrophic bleaching within the next 15–25 years (Hoegh-Guldberg 1999; Donner et al. 2005; Chap. 10). However, climate models deal with large-scale atmospheric and oceanic processes, which in themselves are highly complex with many parameters and feedback loops that are difficult to quantify. There is additional uncertainty in foreseeing human trajectories of resource use and change. Predictions of the impacts of climate change are thus uncertain even over large (ocean basin) scales. At the scale of coral reefs this uncertainty is compounded further by the physical and biological complexity of coral reef environments. Physical complexities include currents, tides, bathymetry, depth, water quality, 3D habitat structure, and weather, all of which can affect the temperature and light environment and hence the susceptibility of corals to bleaching. Biological complexities include the variable responses of coral species, the interaction of corals with their diverse and differentially susceptible symbionts, interactions with pathogens, acclimatization, and adaptation processes (Chap. 7). Coral mortality and reef recovery depend on numerous local factors, human use, and conservation. It follows then that the degree of destruction and the permanence of the impacts are uncertain over

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large spatial scales and that the extent and severity of coral bleaching actually observed may not be as simple as predicted from climate models. These uncertainties increase as scales become smaller. Many of these complexities may never be fully understood; however much can be learnt from studying spatial and temporal patterns in bleaching records. An analysis of past records is, therefore, useful in identifying large-scale spatial and temporal patterns in coral bleaching and identifying key data gaps and data deficiencies which can be addressed in the future.

In the following analysis we investigate the spatial and temporal patterns of coral bleaching that can be detected in the ReefBase global database of bleaching records. In particular we address the following questions:

1. Can discrete global bleaching events be identified from the records of bleaching?
2. How many global events have occurred in the past three decades?
3. Are major bleaching events increasing in frequency and intensity?
4. Is background (low-level) bleaching increasing in frequency and extent?
5. Are there any clear spatial patterns of coral bleaching at global, regional, and subregional scales?
6. Do the observed periods of significant global bleaching correspond with the periodic occurrence of El Niño–Southern Oscillation (ENSO) events?

3.1.1 Early Bleaching Records (Pre-1982)

The earliest confirmed record of reef-wide bleaching due to thermal stress is probably that of Yonge and Nicholls (1931). They mention that, during a period of high summertime temperatures at Low Isles (Great Barrier Reef; GBR) in 1929, many corals died and several corals (particularly *Goniastrea* spp., *Favia* spp.) were observed to have lost their zooxanthellae and turned white. Some weeks later these corals were observed to be recovering their colouration, and histological inspection revealed that they had lost and then started to recover their zooxanthellae populations.

Shinn (1961) notes that *Acropora cervicornis* that had been transplanted to an inshore site in the Florida Keys bleached on their upper surfaces during periods of maximum summertime temperatures. This was not, however, a normal habitat for these corals and no observations of bleaching in normal populations were recorded. Goreau (1964) is probably the first person to publish a specific report on mass bleaching of corals in the reefs around Port Royal, Jamaica, during the aftermath of Hurricane Flora in 1963. He concluded, however, that the main cause of this bleaching was low salinity following heavy rains and floodwaters, rather than the high temperatures associated with current mass bleaching events. It is also possible that the report by Mayer (1914), in which he refers to corals not exposed to the air being "injured" after exposure to several hot calm days, represents a bleaching event. There is no mention, however, in his paper of loss of colour or bleaching. There is a total of 26 records of coral bleaching before the first well documented global-scale coral bleaching event of 1982–1983.

Coffroth et al. (1990), Williams and Bunkely-Williams (1990), Glynn (1991, 1993), and Goreau and Hayes (1994) have compiled records of much earlier mass coral mortality, dating back to 1876. These earlier reports provide details for specific sites in terms of the pattern and extent of mortality and the probable causes. Factors other than high temperatures (e.g. aerial exposure, freshwater, "dark water") are most often used to explain the mortality and in these cases there is no firm evidence to suggest that the cause of the mortality was high temperatures and that corals had bleached prior to dying.

3.1.2 Bleaching Records from 1982 Onwards

It was not until the global bleaching event of 1982–1983, first documented by Glynn (1983, 1984) that widespread bleaching and mortality was recognized as a major phenomenon that could impact coral status and health at regional and global scales. The interest generated by Glynn's early papers on bleaching in the Eastern Pacific led to anecdotal reports from a wide range of sites across the world in subsequent years. These early reports were compiled by Brown (1987), Glynn, (1990, 1991, 1993), Williams and Bunkley-Williams (1990), and Goreau and Hayes (1994). More recent summaries of coral bleaching records were published by a number of authors (Wilkinson 1998, 2000, 2002; Wellington and Glynn 2007).

In the late 1990s the World Conservation Monitoring Center and the WorldFish Center (then called ICLARM) both developed databases that compiled published and unpublished records of coral bleaching from throughout the World. In 2001 these datasets were combined and updated into a single database which is maintained by WorldFish as part of its ReefBase database on coral reefs. The dataset is available through the ReefBase website (www.reefbase.org).

The ReefBase bleaching database includes virtually all records in the published literature, as well as unpublished records communicated directly to ReefBase and the National Oceanic and Atmospheric Administration (NOAA) Coral Reef Watch (http://coralreefwatch.noaa.gov/) and those published on the coral list-server maintained by NOAA's Coral Health and Monitoring Network (http://coral.aoml.noaa.gov/). Despite increasing interest and commentary on global patterns of coral bleaching, this comprehensive dataset has not previously been analysed in any detail.

The majority of available bleaching records consist of descriptive accounts of the location of bleaching and, with varying degrees of detail, an assessment of the extent and severity of bleaching. Water depth and coral species affected are often not recorded. In a small number of cases, formal surveys using quantitative or semi-quantitative measurements provide estimates of the percentage of coral that bleached.

The minimum information in each bleaching record in the database is the date of observation, location, bleaching severity, and source of the information. Bleaching severity is a categorical variable. Table 3.1 shows the different categories, their descriptions and notes on how verbal reports have been translated into one of the categories.

Table 3.1 Coral bleaching categories used in ReefBase

Code	Category	Description	Notes
0	No bleaching	No bleaching observed	For quantitative surveys, no bleaching is recorded if the percentage of live coral cover bleached is less than 1%
−1	Bleaching (unknown severity)	Bleaching recorded	Bleaching observed but no information on severity. For the purposes of analysis this category is converted to 2 – moderate bleaching
1	Mild bleaching	Up to 10% of coral cover bleached	If no estimate of % of bleached corals or coral cover is provided then terms such as “light”, “mild”, “scattered”, “occasional” are used to identify this category
2	Moderate bleaching	10–50% of coral cover bleached	If no estimate of % of bleached corals or coral cover is provided then terms such as “significant”, “common”, “frequent”, “moderate” are used to identify this category
3	Severe bleaching	More than 50% of coral cover bleached	If no estimate of % of bleached corals or coral cover is provided then terms such as “heavy”, “abundant”, “severe” are used to identify this category

A total of 5215 records of coral bleaching in the ReefBase bleaching database were analysed, as of February 2007. Because many of these records provided information for adjacent areas within the same location, the data were first summarized by averaging all records from a single named place. This process reduced the number of records to 2808 records. Only a small number of records (<1%) did not include information on bleaching severity. Most of these were reports for early bleaching events prior to the major bleaching event of 1997–1998. For the purpose of the analysis, these records were reclassified as “moderate bleaching” since it is most likely that these early reports related to bleaching of more than 10% of coral cover. Very few (less than 3%) reports of mild bleaching were recorded in the database prior to 1997.

While the ReefBase bleaching database contains the most comprehensive archive of coral bleaching records and while all records are referenced either to a publication or a formal source, analysis of these records presented a number of problems. First, the records of severity are often quite subjective. This issue was addressed by grouping all records into a small number of broad categories. Second, some records of bleaching may be duplicates of other records of the same event reported by other sources. While some duplicates are likely to persist, we attempted to eliminate this through careful screening, and by grouping all records that relate to a single site into a single “site record”.

Finally, the number of reports received can vary both as a function of the severity and extent of bleaching, but also as a result of increased numbers of observers with an interest in bleaching. This “reporting effect” represents an important potential sampling bias that cannot be discounted or completely eliminated. While there are no data on the extent of this reporting effect, it is likely that the total number of potential observers of bleaching and the proportion of these who would be motivated to report on bleaching have both increased over the past two decades as field-based coral studies have increased and media attention on the destruction of coral reefs from bleaching and climate change has grown. Despite these sources of bias, we believe that a cautious and conservative analysis of the bleaching records can yield important insights into the extent of coral bleaching in space and time, the relationship between bleaching and climate variability, and change at regional and global scales.

3.2 Global Patterns of Coral Bleaching

3.2.1 Temporal Patterns

3.2.1.1 Site Records

There are two very clear patterns that can be seen when examining all levels of bleaching severity (Fig. 3.1). First, there is a clear increase in the number of sites reporting bleaching in the past decade. Second, several dramatic peaks of one or two years duration show the episodic nature of bleaching.

The trend of increasing bleaching occurrence is driven largely by mild bleaching records and, to a lesser extent, by moderate bleaching records (Fig. 3.1a). If only severe bleaching records are considered then this trend nearly disappears. This is

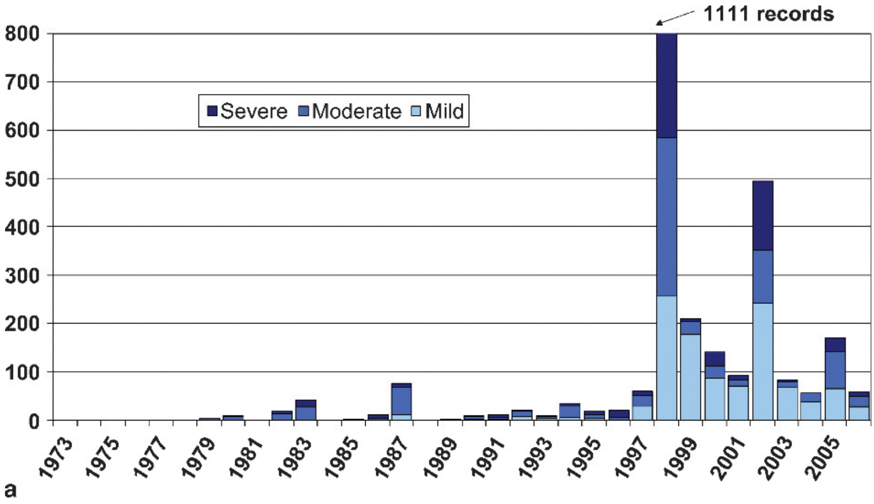
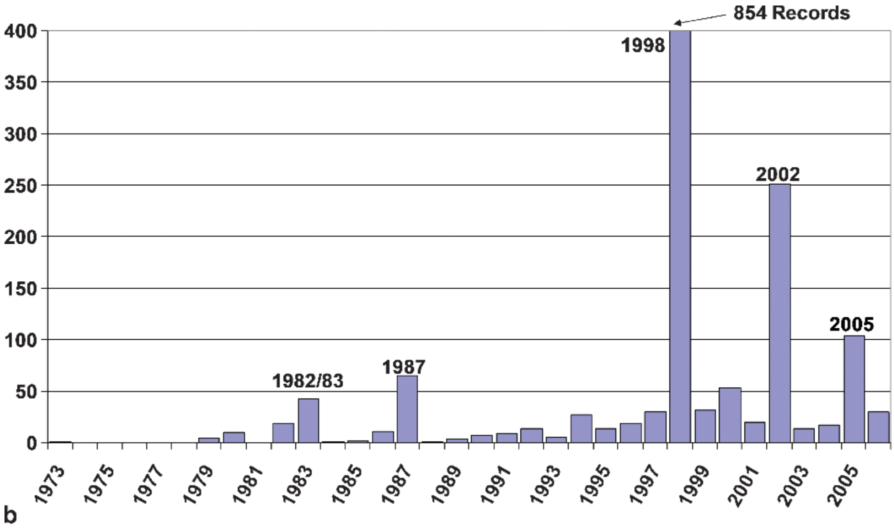


Fig. 3.1 Number of coral bleaching records in ReefBase by site and year for: **a** mild, moderate, and severe bleaching, **b** moderate and severe bleaching, and **c** moderate and severe bleaching, excluding Great Barrier Reef sites



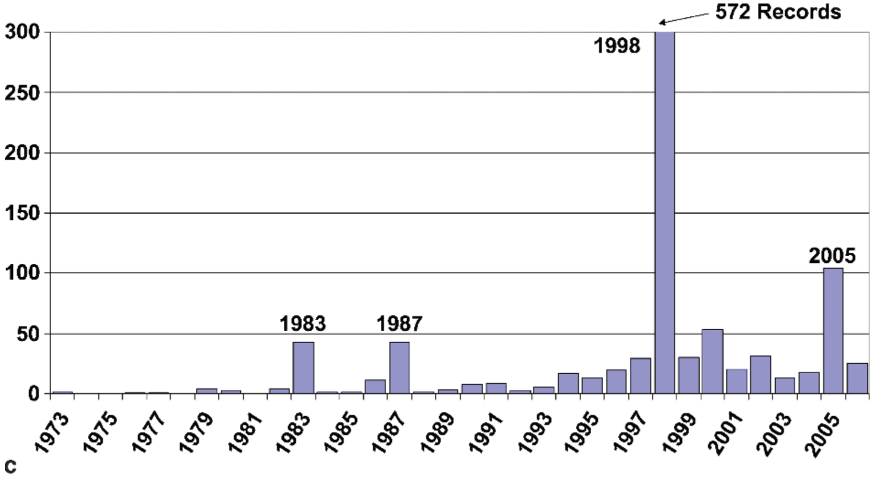


Fig. 3.1 (continued)

especially apparent when viewed as the proportion of bleaching events classified as severe (Fig. 3.2). While the increase in mild bleaching could be due to an increase in chronic low-level stress to corals it is also possible that the increased awareness of coral bleaching (particularly after 1998) has led to increased reporting of small amounts of bleaching that largely went unreported before then.

There are five clear peaks of varying magnitude that can be clearly identified: 1982/83; 1987; 1998; 2002, and 2005. If only severe and moderate bleaching events are considered, the same peaks remain (Fig. 3.1b). In 1998 and 2002 a very large number of sites were surveyed on the GBR, using aerial survey techniques, and this has contributed to the disproportionately large peaks for these years. If the GBR

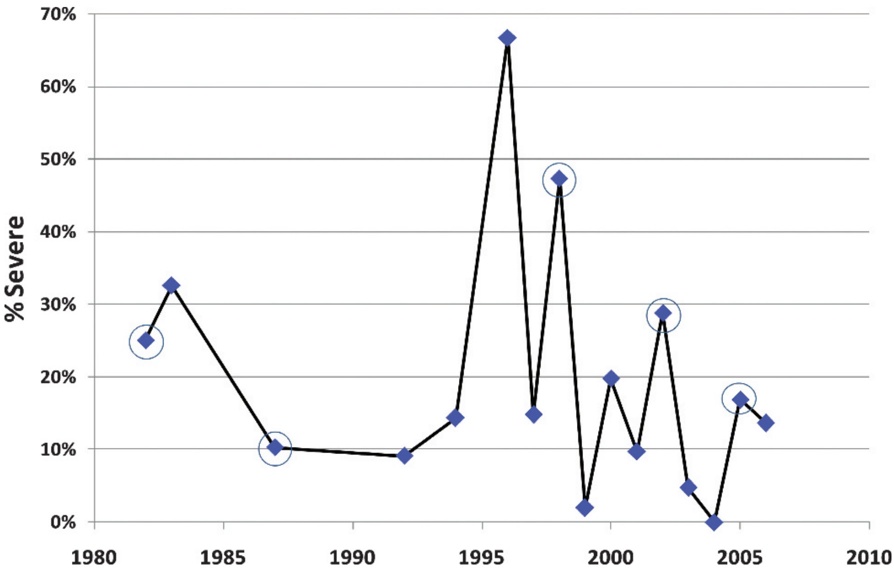


Fig. 3.2 Proportion of bleaching records classified as severe from ReefBase since 1982. *Circles* indicate years of major bleaching

records are eliminated from the graph, then the 2002 peak disappears (Fig. 3.1c), but all others remain.

3.2.1.2 Country Bleaching Records

Some countries have devoted much greater effort to monitoring and reporting bleaching than others. For instance, intensive aerial surveys of the GBR in 1998 and 2002 resulted in over 600 site records in these years. In other countries the total number of bleaching site records in a major bleaching year (1998) ranged from one to 45, with most countries having fewer than ten records. To reduce the distortion caused by this bias in sampling effort between countries, we looked at the presence or absence of bleaching per country and then examined trends in the number of countries reporting bleaching in any year.

The same two general patterns observed for site records are also apparent in the results for number of countries reporting bleaching (Fig. 3.3a). There are several clear peaks corresponding to major bleaching years and there is a very noticeable increase in the number of bleaching reports over time. The same peaks are evident as in Fig. 3.1. However, the peak for 2002 is missing in this case since the majority of bleaching occurred in one country (Australia). There is also a clear trend of increasing bleaching frequency over the past three decades. Again this trend is less distinct when only severe bleaching records are considered (Fig. 3.3b).

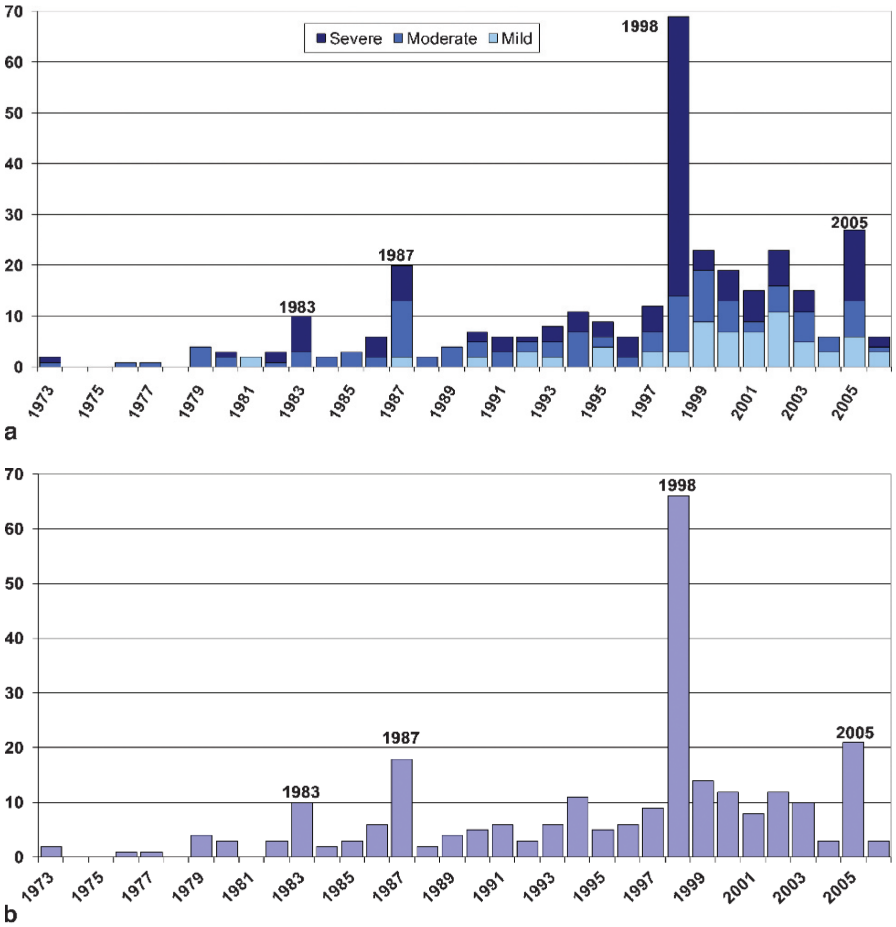


Fig. 3.3 Number of countries reporting bleaching in ReefBase by: **a** country and year and **b** country and year restricted to moderate or severe bleaching

3.2.2 *Spatial Patterns in Bleaching Reports*

As indicated in Fig. 3.1b, there are five distinct peaks in coral bleaching between 1973 and 2006. The spatial distribution of these records for each of these peak-bleaching periods (Fig. 3.4) shows that the 1997–1998 El Niño and 1998–1999 La Niña stand out as the most severe and spatially extensive period of coral bleaching so far recorded and provides the best opportunity to examine the spatial distribution of globally distributed bleaching. Bleaching records were submitted during 1998 from around the world, with the possible exception of the western Pacific, which has comparatively few records. Many western Pacific sites did bleach, however, during the 1998–1999 La Niña. No bleaching was recorded in 1998 from the

Fig. 3.4 Distribution and intensity of bleaching from records in ReefBase for the global bleaching years: **a** 1982–1983, **b** 1987, **c** 1998, and **d** 2005, and **e** the spatially restricted event of 2002. *Red dots* Severe bleaching, *yellow dots* moderate bleaching, *blue dots* mild bleaching, *green dots* no bleaching. Reef areas in *orange*

Solomon Islands, Hawaiian Islands, and New Caledonia. In French Polynesia, only mild to moderate bleaching was reported.

The lack of bleaching records from the Pacific in 1998 may predominantly be due to under-reporting. Comparatively few reports are available from most areas; the entire area from the Marshall Islands down to Tuvalu has no records at all and much of Melanesia experienced very low or no bleaching. The records of bleaching in Samoa may be due to an extreme low tide event rather than thermally induced bleaching. Given the high level of awareness of bleaching by the end of 1998 and the significant efforts of scientists to compile bleaching records for this particular event (e.g. Wilkinson 1998), it is likely that this relative absence of bleaching is real and may due to the fact that the Pacific islands are far from any continental land masses and less subject to the unseasonable increases in sea temperatures which occur on shallow continental shelves. During other years, however, severe bleaching has been recorded in the Pacific (e.g. Hawaii in 1996, Papua New Guinea and Fiji in 1999 and 2000). This suggests that local conditions can still produce thermal stress and bleaching, even in open oceanic areas.

In 1987, bleaching was also quite widespread, although the Pacific, Southeast Asia, and the Middle East are very poorly represented. In other years of major bleaching the distribution is less even. For instance in 1982–1983, the eastern Pacific was clearly the most severely affected region, while in 2002 and 2005 the GBR (see Sect. 3.3) and the Caribbean (Wilkinson and Souter 2008), respectively, were the clear focal areas for severe bleaching.

3.3 Great Barrier Reef

3.3.1 Time Series

Figure 3.5 shows that over the past 25 years, there are two major peaks in bleaching site records on the GBR, corresponding to the bleaching events of 1998 and 2002. These peaks are disproportionately high due to the intensive surveys conducted by Berkelmans and Oliver (1999) and Berkelmans et al. (2004). While the number of records is very low in the early years, there appear to be periods when significant bleaching was observed. In total there are eight discernable bleaching peaks. These bleaching years include 1980, 1982, 1987, 1992, 1994, 1998, 2002, and 2005. The proportion of these GBR bleaching events classified as severe has varied through the record, with no real trend (Fig. 3.2b). Anecdotal reports suggest that there may also have been a bleaching event sometime in the 1970s, but the year, extent, and intensity are unknown (Oliver 1985)[1].

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[1] Oliver (1985) also states that "bleaching at Magnetic Island was not nearly as extensive in 1983 compared with 1982". This indirect reference to a bleaching event in 1983 is in fact a typographical error. It should have been a reference to the 1980 bleaching event.

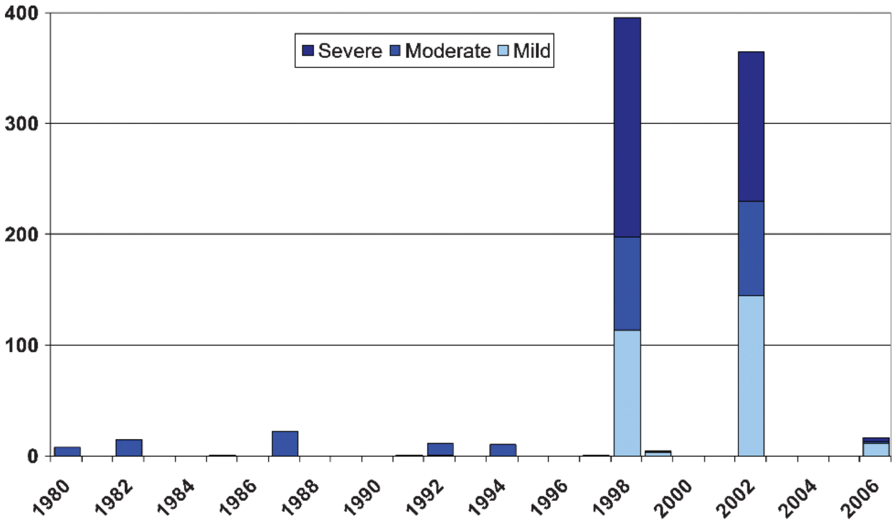

Fig. 3.5 Number of records of coral bleaching on the Great Barrier Reef

Extensive in-situ and satellite temperature data over the past 15 years also suggest that there were at least two "near-bleaching" years when bleaching thresholds were approached and noticeable paling commenced at a number of sites. These years include 1995 when Michalek-Wagner and Willis (2001) noted a mild bleaching event at Orpheus Island and early 2005 when mild bleaching was reported for several reefs on the GBR.

3.3.2 Spatial Patterns

The most striking similarity between the 1998 and 2002 beaching events on the GBR is the higher incidence and severity of bleaching on inshore reefs compared with offshore reefs (Berkelmans et al. 2004; Fig. 3.6). The same general pattern seems to hold in some of the other GBR bleaching events, particularly the mild bleaching events of 1992 and 1994, which affected predominantly inshore sites. The reasons for this pattern are not clearly understood but a number of plausible explanations, singly or in combination, may contribute to the observed effect. First, inshore shallow waters have a smaller volume and hence a reduced thermal capacitance compared with deeper offshore waters. Second, inshore waters may have a reduced ability to mix with cooler deeper water simply because the waters are warm for the full depth of the water column. Third, inshore corals are generally more darkly pigmented compared with their offshore relatives due to reduced light availability (higher turbidity) and higher nutrient loadings. The higher pigment density has been shown to increase solar absorption and raise the effective temperature experienced by corals

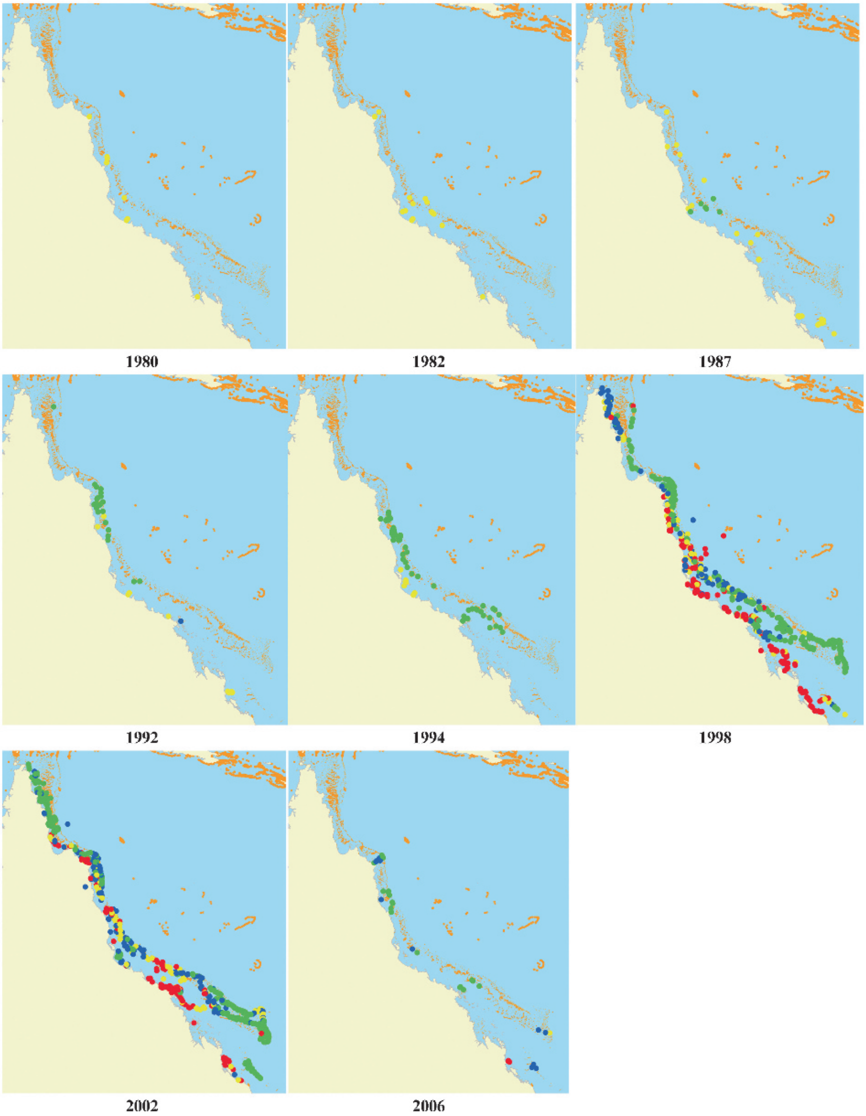

Fig. 3.6 Great Barrier Reef bleaching records. The maps for 1998 and 2002 include aerial survey data. Colours as per Fig. 3.4

by up to 1.5°C, exacerbating the bleaching risk for inshore coral communities (Fabricius 2006). Since anthropogenic impacts are also concentrated inshore, the clear management imperative to mitigate against additional stresses is doubly important in inshore environments. Good land management practices (river catchment, coastal development) and prudent fisheries management, especially for herbivorous fisheries, are particularly important priorities for management in these areas (Salm and Coles 2001; Marshall and Shuttenberg 2006).

3.4 Relationships with El Niño–Southern Oscillation Events

It is clear from Fig. 3.7 that the link between moderate–severe bleaching and powerful El Niño events is fairly strong at a global scale. Of the four global bleaching events identified above, three (1983, 1987, 1998) occur during or just after the most significant and sustained dips in the Southern Oscillation Index (SOI) since 1982/83 when attention first focussed on the phenomenon. The fourth bleaching event (2005) coincides with the second lowest dip in the SOI in the past 50 years, although it was very brief. During 1973 and 1978, similar sustained dips in the SOI are evident. The absence of coral bleaching during these periods may be due to lack of awareness and reporting. It is also possible that rising global temperatures are bringing corals closer to their bleaching thresholds and periods of warming during low SOI became sufficient to induce bleaching only after the 1978 phase shift (Trenberth and Hurrell 1994; Mantua et al. 1997). However some bleaching was indeed observed in 1973 and there are other unconfirmed reports on the GBR of significant bleaching in the early 1970s, The 1982–1983 bleaching is lower than expected given the intensity of the SOI phase, however this is probably due to reduced reporting. It was the first major bleaching event to receive widespread publicity; and scientific attention increased dramatically for subsequent bleaching events and El Niños.

On the GBR (Fig. 3.8) the relationship between El Niño events and coral bleaching is less straightforward. While the 1987 and 1998 events occurred during the height of El Niño phases, the 1982, 2002, and 2006 events occurred when the SOI was neutral. In 1982 this was just prior to a significant decline in the SOI, while in 2002 and 2006 bleaching occurred prior to less significant but still noticeable period of negative values.

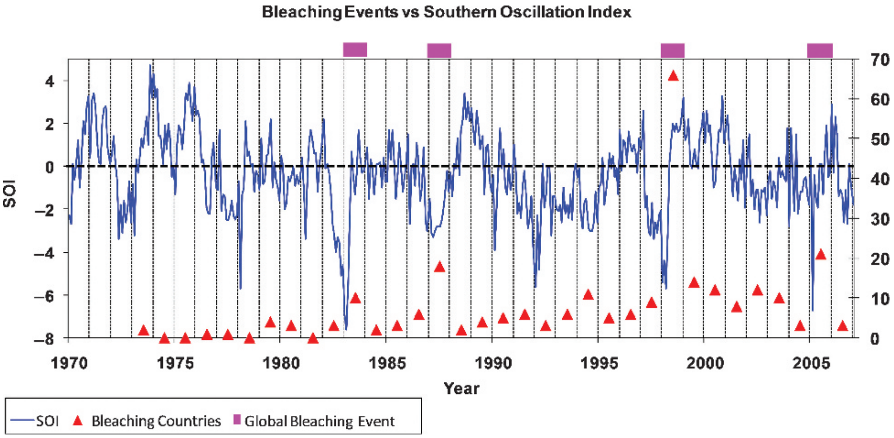

Fig. 3.7 Global bleaching events and the Southern Oscillation Index (*SOI*). The *shaded bars* at the top indicate years when global bleaching events occurred. *Solid triangles* show the number of countries which reported moderate to severe bleaching in each year

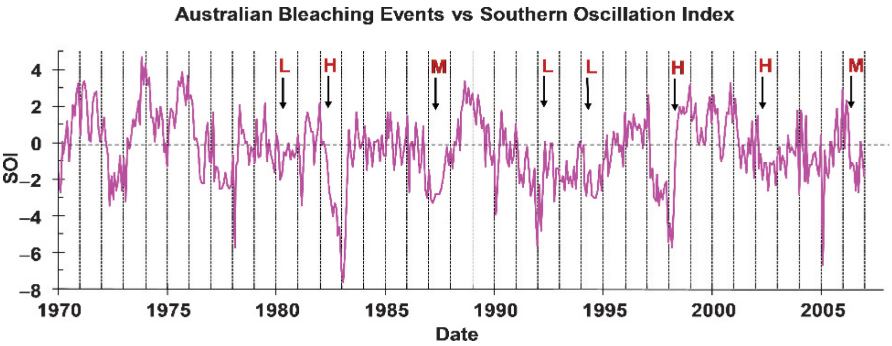

Fig. 3.8 Australian bleaching events and the SOI. *L*, *M*, *H* arrows indicate light, moderate, heavy bleaching events, respectively

3.5 Discussion

The results presented here represent the most comprehensive record of coral bleaching available on a global level. They provide a clear quantitative record of bleaching frequency and periodicity for the past three decades. We have identified four periods (1983, 1987, 1998, 2005) that can be called global bleaching events in terms of bleaching frequency and intensity and the number of countries affected.

Most authors who recently reviewed global patterns of coral bleaching (e.g. Glynn 1996, 2000, 2002; Wilkinson 1998) did not attempt to formally identify specific global events other than the 1982–1983 and 1998 events. In an early review, Williams and Bunkley-Williams (1990) clearly identified 1987 as a global bleaching event but this has received comparatively little attention since then. The most recent global event identified in our analysis (2005) received extensive media coverage; and formal reports are only now appearing in the scientific literature at the time of writing (Donner et al. 2007; Manzello et al. 2007; Whelan et al. 2007).

Goreau and Hayes (1994) and Glynn (1996, 2000, 2002) in their reviews of bleaching indicated that bleaching has increased in frequency since it was first reported at a global level in 1983. Other authors predicted an increasing frequency of occurrence based on climate models and specific bleaching thresholds (Hoegh-Guldberg 1999; Donner et al. 2007).

Our results clearly show an increase in the number of bleaching reports during the past three decades, with a major increase in the past decade after the 1998 event. The graphs in Fig. 3.1 suggest that, in the past decade, there was a low level of bleaching in all years, but these are easily differentiated from years with major bleaching episodes. Our data do not enable us to completely differentiate between true increases in bleaching frequency and increases in reporting effort. However, on the GBR and in much of the Caribbean, the level of scientific research and monitoring, together with the dedicated efforts of key institutions to record all bleaching events since 1983, makes it unlikely that major events have gone unreported. The same applies for many major coral reef areas around the world. Thus the major peaks in bleaching records are likely to be real phenomena, while the increase in annual background bleaching is more difficult to interpret. When we look only at major peaks in bleaching records, then at a global level we can clearly differentiate four global events. This is too small a number to quantitatively determine whether the frequency of severe events is increasing.

We conclude that there is insufficient evidence in the global database of bleaching records to either support or refute the hypothesis that major bleaching events are increasing in frequency. There is some evidence that low-level background bleaching has increased. A separate, but related issue is whether the intensity of bleaching is increasing. If this were the case, we would expect to see an increase in the proportion of severe bleaching reports, either on a year to year basis, or from one major bleaching event to the next. As can be seen in Fig. 3.2, the data do not indicate any such increase in the proportion of severe bleaching. This finding contrasts with data that show clear increases in both the frequency and intensity of bleaching-level thermal stress (Chap. 4). One potential reason is that the corals that survive severe events, such as 1998, are more capable of surviving subsequent thermal stress. A corollary is that severe bleaching events reduce diversity, removing the more thermally sensitive corals.

At the regional level, the spatial distribution of bleaching and the severity of bleaching on the GBR during the 1998 and 2002 bleaching events correlated strongly with thermal stress patterns (Berkelmans et al. 2004). Apart from the strong inshore–offshore effect, bleaching in these two events was patchy over scales of tens of kilometres, reflecting patterns in local weather and oceanography. As a result, many local-scale differences were evident between years. This makes prediction and scenario modelling particularly challenging at locals scales and highlights the need for a detailed understanding of the oceanographic environment and appropriate tools to draw inferences from diverse data sets (Wooldridge and Done 2004; Skirving et al. 2006; Wooldridge et al. 2006). A positive implication from this patchiness is that there is likely to be a proportion of reefs that will not bleach in successive events, giving affected reefs longer to recover. The Palm Islands in the central inshore GBR are a case in point. Coral cover was reduced by >50% at many sites dominated by *Acropora* spp. and, having avoided the 2002 event, recovery in this genus is well advanced after ten years.

The relationship between ENSO events and coral bleaching is highlighted repeatedly in the literature. In the eastern Pacific the relationship between El Niño and coral bleaching is both dramatic and unambiguous (Glynn 1984, 2000, 2002; Wellington and Glynn 2007). At a global level there is also a strong correspondence between the four major bleaching events and the occurrence of major negative deviations in the SOI (Fig. 3.5). This suggests that there are likely to be at least some links between the oceanographic and meteorological changes that accompany El Niño events. Not all teleconnections between the core canonical events of El Niño and thermal anomalies on coral reef areas have been clearly identified. Huppert and Stone (1998) suggest that additional stochastic triggering events may explain records of bleaching in non-El Niño years, and presumably also why no bleaching is recorded in some locations during El Niño years. Additionally, some regions of the western Pacific often cool down during El Niño events but warm up during La Niña events (e.g. Fiji, Papua New Guinea; Chap. 4). These sites show greater thermal bleaching during La Niña years.

On the GBR the records show a less direct correlation between negative SOI deviations and bleaching events, although the proximity of major bleaching to these deviations is very suggestive. The SOI may therefore be a poor direct indicator of ENSO events at a local or sub-regional scale even though it is possible that many of the GBR bleaching events are indirectly caused by ENSO-related anomalies. The reversals of normal ocean current directions, particularly in the equatorial Pacific during ENSO, events has a profound but indirect influence on local weather conditions. The nature and timing of the effects may be highly variable in different locations and from one event to another. For example, the western Pacific is generally cooler during an El Niño event which in theory suggests a low chance of bleaching. However, El Niño conditions in Australia generally bring drought and long periods of cloud-free, doldrum-like conditions. When this coincides with the austral summer, local heating of shallow inshore waters occurs. This would explain the observed inshore–offshore bleaching pattern during major bleaching events. El Niño weather patterns operate at regional scales and affect reef provinces only when they coincide with the regional summer. The GBR probably avoided a major bleaching event in 2005 only because ocean current anomalies returned to normal just before the austral summer.

Despite its limitation, the database of bleaching records in ReefBase is highly valuable for quantifying major bleaching events. Its utility could be greatly increased if monitoring and reporting effort could be standardized. This would enable smaller-scale patterns of milder bleaching events to be reliably detected, thus providing early verification of predicted increases in bleaching frequency due to climatic temperature increases. It would also provide much needed ground truth data for the bleaching HotSpots detected by satellite data (Chap. 4). Two key improvements in the bleaching reporting are standardization in the measurement of bleaching intensity and standardization in the number, location, and timing of bleaching surveys. The first issue was addressed by Oliver et al. (2004) and Marshall and Schuttenberg (2006). The adoption and use of a standard reporting protocol would greatly increase the reliability of bleaching records. The second issue will require a much greater level of coordinated effort by coral reef scientists and reef-users. Existing global networks such as the Global Coral Reef Monitoring Network and Reef Check are well placed to promote the regular reporting of bleaching conditions (both presence and absence) from standard locations; and we hope that these can encourage greater monitoring and reporting as a priority.

Overall, we conclude that the existing observations of coral bleaching enable us to confirm that severe bleaching events occurred at a global level on four recent occasions. Also, we have demonstrated that these events occurred in close temporal proximity to a strong negative deviation in the SOI. While there is no clear increase in the frequency or intensity of major global bleaching events, the number of bleaching records has clearly increased during the past three decades. However, increased vigilance and reporting of mild bleaching by an ever-increasing number of researchers and conservation-minded divers is confounding efforts to definitively separate changes in bleaching frequency from changes in reporting.

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Chapter 4
Climate Variability and Change: Monitoring Data and Evidence for Increased Coral Bleaching Stress

C.M. Eakin, J.M. Lough, and S.F. Heron

4.1 Introduction

Coral reefs live within a fairly narrow envelope of environmental conditions constrained by water temperatures, light, salinity, nutrients, bathymetry and the aragonite saturation state of seawater (Buddemeier and Kinzie 1976; Kleypas et al. 1999; Hoegh-Guldberg 2005). Their natural environment, at the interface of land, sea and the atmosphere, can vary quickly and potentially be stressful. Reef organisms have, over millions of years, evolved strategies to cope with occasional environmental disturbances (such as tropical cyclones). Given sufficient time between disturbances, damage or destruction would normally be followed by recovery and regrowth (Buddemeier et al. 2004). As documented in numerous scientific studies and reports, the world's coral reefs are "in crisis" as a result of direct local- and regional-scale human impacts on their environment. These impacts include overfishing, destructive fishing practices, changed land-use that increases sediment, nutrient and pollutant flows into reef waters, and poorly designed coastal development. This ecosystem degradation is largely occurring in the many tropical countries whose increasing populations are heavily dependent on coral reefs yet have insufficient resources to develop appropriate, sustainable management practices (Wilkinson 2004). Coral reefs are now confronted with additional global-scale stresses due to the introduction of enhanced greenhouse gases that are rapidly changing coral reefs' environmental envelope through both ocean acidification and increased thermal stress due to climate change (Hoegh-Guldberg et al. 2007).

There are several aspects of global climate change that are already impacting the environments of coral reef ecosystems (Chap. 1). The most immediate is rising sea surface temperature (SST) that is correlated with an increased frequency of mass coral bleaching reports since the early 1980s (Glynn 1993; Chap. 3). Pioneering studies in the 1970s demonstrated just how close (within 1–2°C) reef-building corals were living to their upper thermal tolerance limits before bleaching occurred (Coles et al. 1976; Jokiel and Coles 1977; Glynn and D'Croz 1990). The threshold for bleaching becomes critical during the seasonal SST maximum. Maximum SSTs at 1000 reef locations average 29.5°C, but range from 28.2°C to 34.4°C (Kleypas et al. 1999). These studies and others have identified that temperature thresholds at

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which corals bleach vary with the ambient water temperatures on each reef, such that corals have adapted to their local environmental conditions over long timescales (Chap. 7).

The first, most alarming, reports of mass coral bleaching events were not immediately linked with unusually warm global SSTs, although a connection eventually was made with El Niño warming (Glynn 1983, 1984). This was largely due to the lack of reliable, long-term records of SSTs and other environmental variables in the vicinity of coral reefs. Gradually, as more mass bleaching events occurred and observations improved, the link was made with unusually warm SSTs (Brown 1987; Glynn 1990, 1991, 1996). Unfortunately, the reporting of bleaching events is still incomplete in many parts of the world and the ability to tease out causal relationships between bleaching and environmental conditions is confounded by two simultaneous factors: (1) the rising thermal stress and (2) the recent increase in monitoring and reporting (Chap. 3). Nevertheless, the evidence that mass bleaching of coral reefs might be linked to global climate change due to enhanced greenhouse gas emissions (Smith and Buddemeier 1992; Brown 1997), which was considered unconvincing in the early 1990s (Glynn 1993), is now considered incontrovertible (Hughes et al. 2003).

This chapter focuses on the changing physical environment of coral reef ecosystems and especially SSTs that are responsible for most mass coral bleaching events. We use long-term climatic datasets to document SST changes near coral reefs over the past 150 years (future scenarios are considered in Chap. 10). SST conditions conducive to coral bleaching are considered in the context of observed global-scale ocean warming and climatic variability (e.g., El Niño–Southern Oscillation or ENSO). Since the 1980s, satellite-based observations of the oceans have dramatically increased our capability to observe ocean variations globally and provide the basis for identifying bleaching conditions in near-real-time. We describe the application of satellite-based SST and other products to detect and monitor environmental conditions related to coral bleaching events.

4.2 Data for Understanding Thermal Stress and Bleaching Patterns Worldwide

To date, no dataset provides continuous coverage spanning modern satellite and instrumental observations back through multiple decades or centuries. However, good data do exist at various temporal and spatial scales. For this study, two primary datasets are used: (1) century-length reconstructions generated from available instrumental observations of global SST and (2) modern near-real-time satellite observations and reanalyses of these records. Because both of these data are calibrated from similar instrumental datasets from recent years, both are considered to accurately represent large-scale patterns of thermal conditions that influence coral reefs.

4.2.1 Century-Length Global SST Reconstructions from Instrumental and Paleoclimatic Data

Unfortunately, continuous observations of physical parameters have been taken at only a limited number of reef sites and for no more than a couple of decades. Observations from other parts of the global ocean are not much more complete. The need for long records of SSTs has driven the development of new local to global ocean observing systems, satellite observations and algorithms to reconstruct past SSTs from instrumental data that are heterogeneous in space and time. Two such reconstructions efforts have developed at the Hadley Centre of the UK Meteorological Office [Hadley Centre sea Ice and Sea Surface Temperature (HadISST) data] and the National Climatic Data Center of the US National Oceanic and Atmospheric Administration [NOAA: Optimum Interpolation Sea Surface Temperature analysis (OISST) and Extended Reconstructed Sea Surface Temperature (ERSST) data]. Both organizations have developed global, gridded SST fields at a variety of temporal and spatial scales that are available online (Reynolds and Smith 1994; Rayner et al. 1996, 2006; Reynolds et al. 2002; Smith and Reynolds 2003, 2004; HadISST data available at: http://www.hadobs.org/; OISST and ERSST data available at: http://www.cdc.noaa.gov/PublicData/). While the methods used in developing these data sets are similar, users should examine each one to select the methods that best meet the needs of the application.

Paleoclimatic data also extend our understanding of climate patterns into the past (Jones and Mann 2004). Massive coral skeletons contain a rich archive of past climatic and environmental conditions in coral reef environments, which can be extracted, for example, using the ratios of stable isotopes ($\delta^{18}O/^{16}O$) or trace metals (Sr/Ca) in annual growth bands (Gagan et al. 2001; Felis and Patzold 2003). One approach reconstructed temperature fields from coral $\delta^{18}O$ data (Evans et al. 2002), but unfortunately there is no organization that is regularly updating this record with data from more recently collected coral cores. One problem noted by Evans et al. (2002) is the sparse array of available data that increases the error in global reconstructions. The other approach is to use regional composites or sets of records to characterize the patterns seen in particular ocean basins (Bradley et al. 2003; Grottoli and Eakin 2007) or to use nearby records if they exist. Both of these approaches have demonstrated that high-resolution paleoclimatic records can provide useful extensions of instrument-based reconstructions of tropical SSTs, but we now need new, longer paleo-records to significantly improve these historical perspectives on coral reef climates (Lough 2004).

4.2.2 Satellite Observations of SST and Thermal Stress

Polar-orbiting satellites provide near-real-time observations across the globe. A trade-off to their global coverage is relatively low spatial (1 km to tens of kilometers) and temporal (at best, four times each day) resolution. NOAA's Coral Reef

Watch (CRW) uses polar-orbiting satellite data to observe SSTs and other parameters that influence the health of coral reefs. The primary suite of CRW satellite products include near-real-time satellite global 0.5° (approx. 50 km) night-time SSTs and anomalies, coral bleaching HotSpots, and coral bleaching Degree Heating Weeks (DHW), updated twice each week (Fig. 4.1; Liu et al. 2006). These satellite data products are available online in graphical formats and as data files for the period from late-2000 to the present (CRW 2007; http://coralreefwatch.noaa.gov/). Animations of SST, SST anomaly, HotSpot and DHW charts over the most recent two, four and six months are also available. Other products, such as the Tropical Ocean Coral Bleaching Indices (Virtual Stations) webpage, the SST time series for selected reef sites and automated Satellite Bleaching Alert e-mails are especially targeted to provide needed information to coral reef resource managers and scientists. The current suite of near-real-time products were developed based on earlier monthly analyses of satellite and in situ SST data (Montgomery and Strong 1994; Gleeson and Strong 1995; Strong et al. 1997; Goreau et al. 2000).

4.2.2.1 HotSpots

The coral bleaching HotSpot (Fig. 4.1c) is the positive anomaly of temperatures that exceed the maximum monthly mean (MMM) for each 50-km pixel, thus identifying regions that are currently undergoing thermal stress. The SSTs and monthly climatology are derived from the Polar-orbiting Operational Environmental Satellite (POES) Advanced Very High Resolution Radiometer (AVHRR) night-time SSTs. The MMM climatology for each pixel, indicating the expected summer maximum temperature, is based on the period 1985–1993 with 1991–1992 excluded due to volcanic aerosol contamination. NOAA/NESDIS developed the satellite coral bleaching HotSpot product in 1996 based on the “ocean hot spots” concept introduced by Goreau and Hayes (1994) from analyses by Atwood et al. (1992) and experiments by Glynn and D’Croz (1990). HotSpots were produced experimentally over 1997–2002 and became CRW’s first operational product in September 2002.

4.2.2.2 Degree Heating Weeks

While the HotSpot product is extremely useful, it only provides an instantaneous measure of thermal stress. Corals respond to the cumulative thermal stress to which they are exposed. By accumulating the positive anomalies of SST above the maximum monthly mean, NOAA’s DHW index provides a measure of the cumulative thermal stress that corals experience (Fig. 4.1d). The DHW product was produced experimentally starting in 2000 and became operational in September 2003. Following Glynn and D’Croz (1990) and Atwood et al. (1992), the threshold for bleaching was established to be 1°C above the expected summer maximum temperature; and the DHW is calculated by summing all HotSpot values $\geq 1°C$ in each pixel over a 12-week period (Liu et al. 2003; Skirving et al. 2006a). In most cases, HotSpot values $<1°C$ do not result in widespread coral bleaching. This high-pass

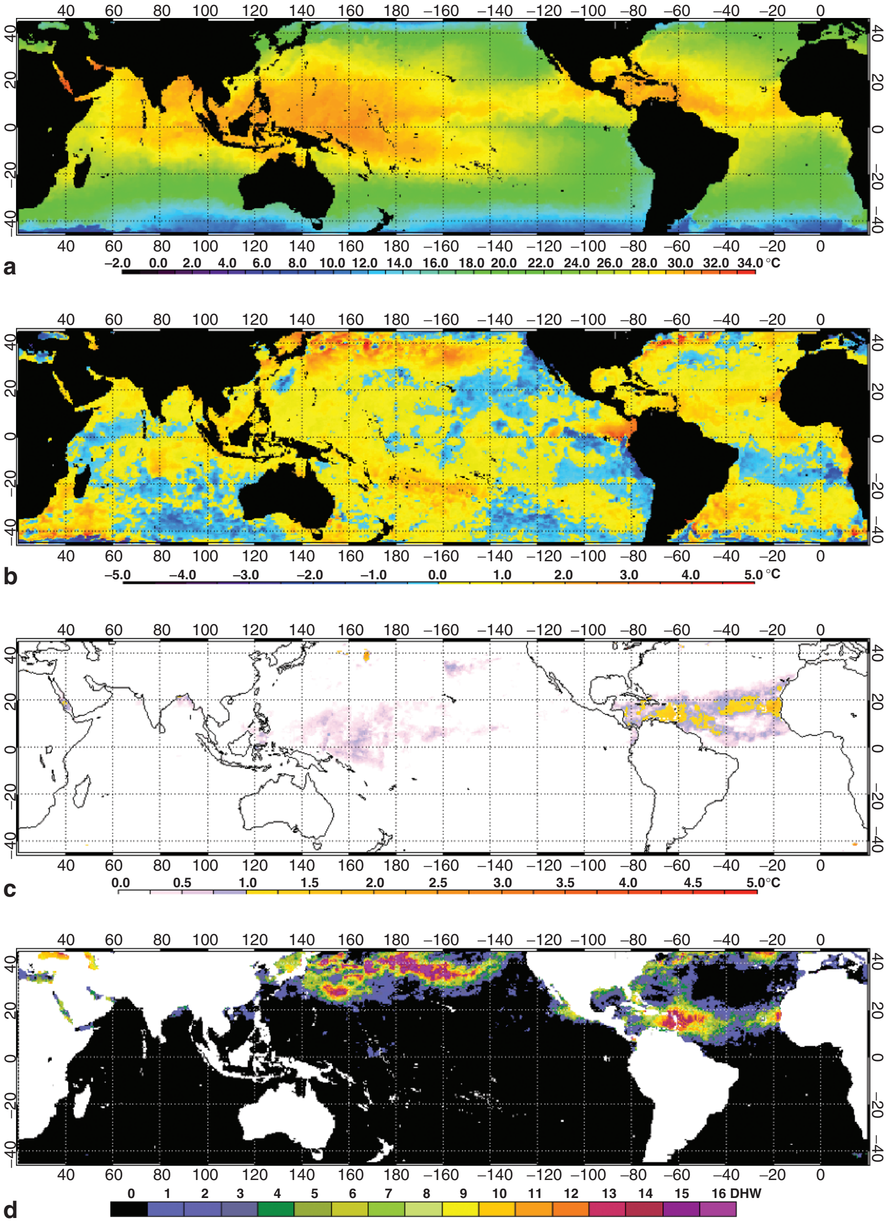

Fig. 4.1 NOAA Coral Reef Watch near-real-time satellite global 50 km night-time product suite for 22 October 2005: **a** sea surface temperatures (SST), **b** SST anomalies, **c** coral bleaching HotSpots and **d** coral bleaching Degree Heating Weeks (DHW)

clipping filter reduces runaway accumulations that can result when SSTs remain very close to the maximum monthly mean for long periods of time, a condition often encountered in equatorial mid-Pacific regions. A value of 2 DHW is equivalent to 2 weeks of HotSpot values of 1°C or 1 week of HotSpot values of 2°C and so forth. NOAA issues a coral bleaching alert via e-mail when values near a reef reach DHW values ≥4°C-weeks (Alert level 1). Significant coral bleaching is expected to occur 1–3 weeks after reefs begin to experience DHW values ≥4°C-weeks. Mass bleaching and the onset of coral mortality are expected after reefs experience DHW values ≥8°C-weeks (Alert level 2).

To date, the DHW index has been a nearly perfect, but conservative, predictor of bleaching around the world. For 23 of the 24 virtual stations monitored, bleaching has been reported in all cases when NOAA has issued a coral-bleaching alert. Recently, non-bleaching reports suggested a likely false alert in Oman (Coles, personal communication), probably resulting from an error in the climatology. There are a limited number of other regions (e.g., Gulf of Panama) where errors in the climatology have been identified. As a conservative predictor, many local-scale bleaching events are not predicted by the DHW index. However, the DHW index reliably provides the large- to basin-scale information needed for coral reef managers and scientists to anticipate mass bleaching.

4.2.2.3 Reprocessed Satellite Observations of SST

In addition to the operational near-real-time satellite observations, retrospective analyses of satellite SST data have been produced and periodically updated. The Pathfinder ver. 5.0 dataset (NOAA 2007; http://www.nodc.noaa.gov/sog/pathfinder4km/) provides daily global SST data at approximately 4 km resolution (Global Area Coverage) for the period 1985–2006. The Pathfinder product cannot run operationally, but it provides new value in that the data are reprocessed with the benefit of hindsight to reduce systematic bias and short-term errors that result from clouds and other atmospheric contamination of the SST signals (Kilpatrick et al. 2001). From the Pathfinder source data, an SST archive was produced at 0.5° (50 km) and half-weekly resolution, mimicking the methods for the near-real-time SST product (see Sect. 4.2.2). Using this dataset and following the methodology for the NOAA Coral Reef Watch product suite, SST anomalies [i.e., the difference between the SST and the climatology (average) value at a location and for that time of year], HotSpots and DHWs were constructed (as described previously). This 22-year record allows us to examine recent global and regional trends in SST anomaly and thermal stress. A new Pathfinder-based climatology has been developed to improve the near-real-time CRW products.

4.2.2.4 Bleaching Weather: A New Doldrums Product

While basin-scale coral bleaching occurs as a result of large-scale climatic phenomena, local weather patterns greatly influence bleaching variability among sites within the basin. Three related factors that influence local bleaching patterns are temperature, light and water-column mixing. One parameter that exerts a common influence to all of these is wind. When wind speeds drop, reduced vertical mixing, evaporative cooling and sensible heat transfer all increase the likelihood of high temperatures and light penetration (Dunne and Brown 2001; Mumby et al. 2001a; Skirving and Guinotte 2001; Obura 2005). Additionally, low winds can increase stratification in the water column, resulting in enhanced photo-degradation of colored dissolved organic material and, thereby, reducing shading (Manzello et al. 2006). CRW has developed an experimental Doldrums product using the NASA SeaWinds scatterometer onboard the QuikSCAT satellite that provides 0.25° (approx. 25 km) resolution wind fields for 90% of the Earth's ocean surface every 24 h (Perry 2001). The current experimental product identifies regions where multi-day average wind speeds have remained below 3 m/s and records the persistence (doldrums-days) of such conditions (Fig. 4.2; CRW 2007; http://coralreefwatch.noaa.gov/satellite/doldrums/). NOAA expects to use this product to augment SST-based algorithms to help detect conditions suitable to coral bleaching.

4.2.2.5 Future Products

To further refine its satellite product suite, CRW is developing products to monitor additional parameters that influence bleaching and coral reef health. Some parameters that further address the needs described in Sect. 4 include ocean surface solar insolation, cloud cover and turbidity. These will directly address parameters that influence the quantity and quality of light that reaches reef corals. Most are

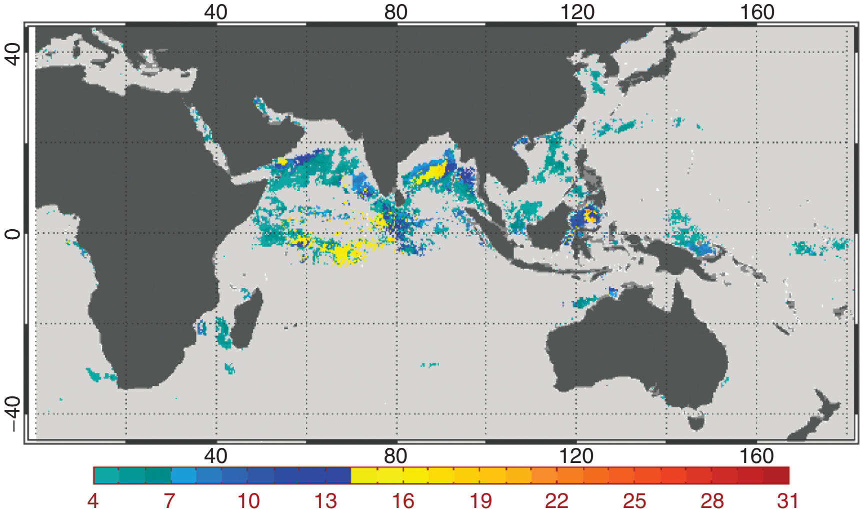

Fig. 4.2 NOAA Coral Reef Watch near-real-time satellite 25 km doldrums product for 24 April 2005 in the Indian Ocean region. The color scale indicates the number of days over which the multi-day mean QuickScat winds remained below 3 m/s

likely to use geostationary satellites rather than the polar-orbiting satellites that CRW uses today. Geostationary satellites provide more frequent sampling and better measures of variability and patterns throughout the day, but with coverage limited to part of one hemisphere. International data sharing agreements will hopefully provide access to data for most coral reef areas.

Also, CRW is working on improving the spatial and temporal resolution of its global data products. However, finer resolution in both space and time comes at a price, including an increased need to gap-fill cloudy regions and the greater influence of chaotic variability in coastal SSTs. Geostationary satellite data or blended geostationary–polar data may aid in this effort. Two such high-resolution efforts are already underway. In 2007, a joint project between the Great Barrier Reef Marine Park Authority (GBRMPA) and the Australian Commonwealth Scientific and Industrial Research Organization (CSIRO) released a 2-km product suite for Australia's Great Barrier Reef (GBR) that includes SST, positive SST anomaly, heating rate and degree heating day products (Maynard et al. 2008; CSIRO at http://www.cmar.csiro.au/remotesensing/gbrmpa/ReefTemp.htm). The Institute for Marine Remote Sensing at the University of South Florida is developing 1-km SST and degree heating week products for Florida and the Caribbean (Muller-Karger, personal communication). These efforts will help define the requirements and limitations to developing global high-resolution SST products. Additionally, NOAA is researching the application of global climate model-derived SSTs to forecast conditions that are conducive to coral bleaching weeks to seasons in advance. Similar GBR-only forecasting is under development by the Australian Bureau of Meteorology and GBRMPA.

4.3 Tropical SST Trends Since the Nineteenth Century

The SST maxima reached during recent mass coral bleaching events were unprecedented in the available instrumental records at a range of coral reef sites (Hoegh-Guldberg and Salvat 1995; Brown et al. 1996; Winter et al. 1998; Lough 1999, 2000a; Mumby et al. 2001b; Wellington et al. 2001; Eakin 2007; Wilkinson and Souter 2008). A number of correlated indices of local thermal stress and other contributors to bleaching have been identified: absolute SST maximum, SST maximum anomaly, heating rate, number of days above a particular threshold, etc. (Podesta and Glynn 1997; Liu et al 2006; Strong et al. 2006; Maynard et al. 2008).

Here we used global compilations of monthly SSTs averaged over 1° latitude–longitude boxes to assess large-scale variations and trends in the tropical oceans and typical patterns associated with ENSO events, 1870–2005 (HadISST 1.1; Rayner et al. 2003). Such data are extremely useful for providing long-term perspectives on the changing tropical ocean climate in relation to coral bleaching events (Sheppard and Rayner 2002; Barton and Casey 2005; Sheppard and Rioja-Nieto 2005). It should, however, be recognized that these large-scale averages can disguise the considerable small-scale thermal variability on coral reefs (Potts and Swart 1984) and can significantly underestimate the real water temperature ranges experienced by corals. For example, monthly HadISST data in the vicinity of offshore Myrmidon Reef in the central GBR indicates an annual range of 5–6°C, matching the 5°C annual range of daily-average SSTs recorded by an automatic weather station (http://www.aims.gov.au/pages/facilities/weather-stations/weather-index.html). However, the recorded variation between observed daily maxima and minima was ~9.5°C (Lough 2001). Furthermore, the modelling inherent within reconstructed SST datasets can also introduce errors in seasonal signals – a predecessor of the HadISST data (GISST 2.2) indicates an annual range of 2–3°C in monthly SSTs for the same location.

4.3.1 Tropical SST and Global Temperature Trends

The instrumental record of global land and sea temperatures (Fig. 4.3a) illustrates the significant warming that has occurred since the end of the nineteenth century (Brohan et al. 2006). Average temperatures for the most recent 30-year period, 1976–2005, are +0.5°C warmer than the first 30-year period of the record, 1871–1900 – a significant change in climate (i.e., the average expectation of weather). This warming also has occurred in the tropical oceans (30°N to 30°S) with maximum SSTs (Fig. 4.3b) averaging +0.4°C warmer in the most recent 30-year period compared with the late nineteenth century. Paleoclimatic data from a pan-tropically distributed set of 32 coral records confirm that the twentieth century oceans are warmer and fresher than the previous two centuries at most sites (Fig. 4.4; Grottoli and Eakin 2007).

Significant linear trends over the 135-year HadISST reconstruction yielded a +0.7°C warming for the global temperature series and +0.5°C for the tropical SST series. The major bleaching year of 1998 was, at the time, the warmest year on record for global temperatures and tropical maximum SSTs. Continued warming over the next seven years produced warmer global temperatures and major bleaching in the Caribbean in 2005 (Shein 2006; Eakin 2007; Wilkinson and Souter 2008). The increasing concentrations of greenhouse gases in the atmosphere trap more energy in the global climate system and this is causing warming of the system that is now affecting both the surface ocean and penetrating into deeper waters (Barnett et al. 2005; Levitus et al. 2005). This global-scale warming has been, and is projected to be, amplified in continental interiors compared to the oceans and at higher latitudes compared to the tropics (IPCC 2001, 2007a).

The trends in the HadISST dataset indicate that the tropical oceans have warmed ~70–80% of the global average value. A rise in maximum SSTs has occurred throughout the tropical oceans, with greatest warming in the southern Atlantic, Indian Ocean and parts of the central and eastern tropical Pacific and less warming in the north-central and south-central Pacific (Fig. 4.5).

Evidence from reef cores covering the past three millennia (Aronson et al. 2002) and observations of the bleaching-induced death of centuries old, slow-growing and thermally more resistant *Porites* corals (Mumby et al. 2001b) strongly suggests that

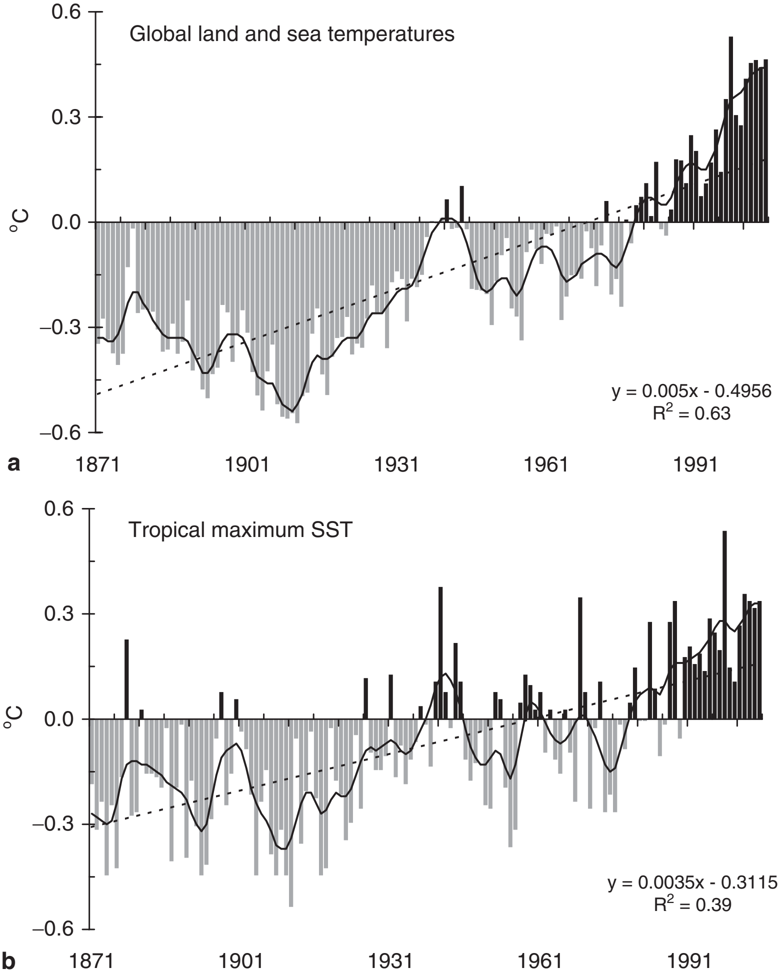

Fig. 4.3 **a** Global land and sea annual temperatures anomaly (data from Climate Research Unit, http://www.cru.uea.ac.uk/cru/info/warming/). **b** Tropical (30°N–30°S) annual maximum SST anomalies (HadISST data from British Atmospheric Data Centre, http://badc.nerc.ac.uk/home/index.html). Both **a** and **b** show annual values, 1871–2005, as anomalies from 1961–1990 mean; *thick line* is 10-year Gaussian filter emphasising decadal variability; linear trend is also shown

we have reached unprecedented thermal environmental conditions on coral reefs. Additionally, bleaching mortality of branching corals allowed corallivorous crown of thorns starfish, *Acanthaster planci*, to reach unprotected massive corals in Panama in 1983 for the first time in almost 200 years. The age of these massive corals was then used to estimate the return frequency of El Niño events to reefs in Pacific Panama (Glynn 1985). All of these data sources point to the likelihood that the recent severe El Niño events and the ocean temperature increases of the past 50 years are unique in at least the past few centuries.

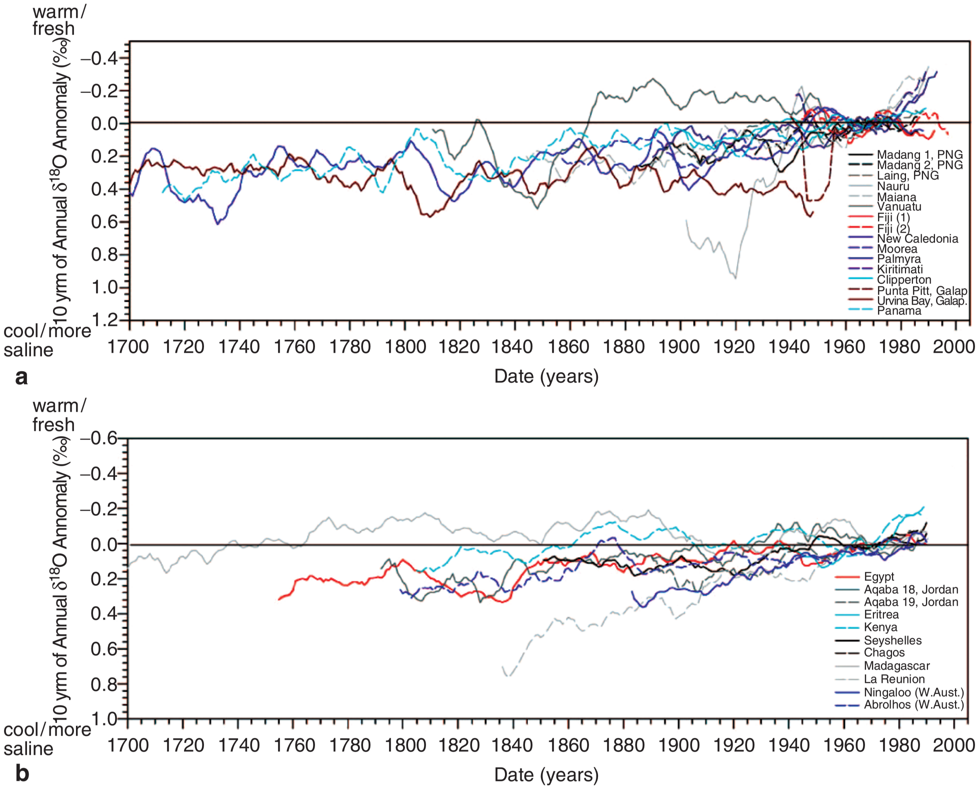

Fig. 4.4 10-year running mean annual coral δ^{18}O stable oxygen isotope anomalies: **a** Pacific Ocean, **b** Red Sea and Indian Ocean. All records normalized to the 1962–1979 period and centered on the fifth year of each 10-year period (from Grottoli and Eakin 2007). *Galap* Galapagos, *PNG* Papua New Guinea, *W. Aust.* Western Australia

4.3.2 Regional Trends in Thermal Stress

The 22-year satellite record (see Sect. 4.2.2.3) was used to examine the global and regional trends in SST anomalies at 50 coral reef sites that bleached during 1997–1998 (Lough 2000b). Grouping these 50 sites into five geographic regions, annual average SST anomalies for each region are shown in Fig. 4.6. The slopes of trend lines (Table 4.1) for each region over the 22-year record consistently range within 0.23–0.26°C/decade, with the exception of reef sites in the Pacific Ocean for which the trend is 0.18°C/decade. While not significantly different from the other regions, the lower trend in the Pacific Ocean anomaly may be important for the ability of

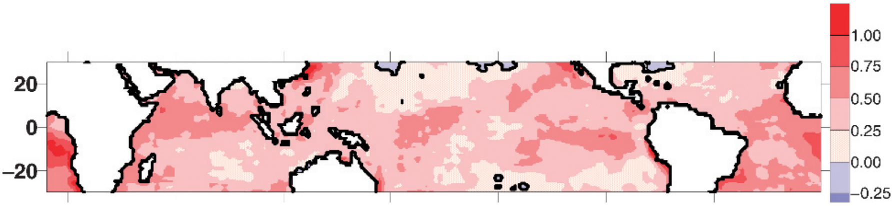

Fig. 4.5 Difference in average annual maximum SST, 1976–2005 minus 1871–1900, using 0.5°C contour intervals (HadISST data from British Atmospheric Data Centre, http://badc.nerc.ac.uk/home/index.html)

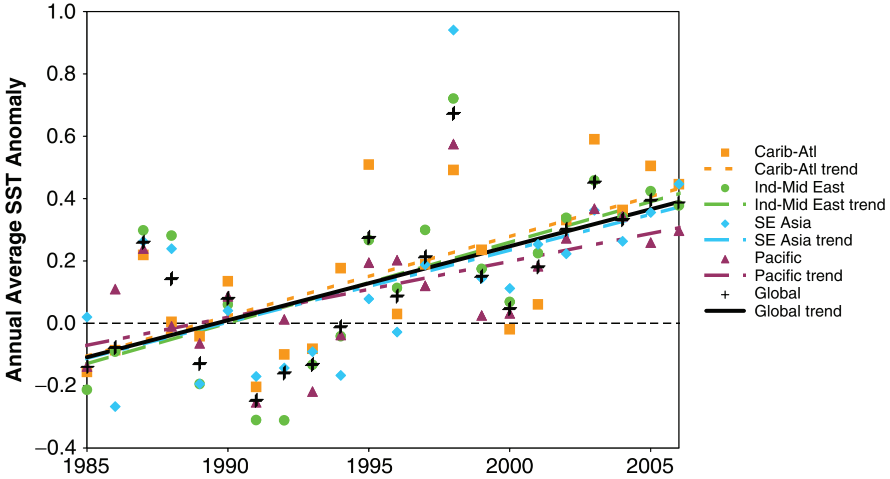

Fig. 4.6 SST annual anomalies and trends, 1985–2006, averaged for each year for the indicated sets of coral reef sites from the Pathfinder reanalysis of the 22-year satellite record: 50 global coral reef sites that bleached in 1998 (*black pluses*, *solid line*), 18 sites in Indian Ocean and Middle East (*green circles*, *dashed line*), 9 sites in southeast Asia (*blue diamonds*, *dash-dot line*), 11 sites in Pacific Ocean (*purple triangles*, *dash-dot-dot line*) and 12 sites in the Caribbean and Atlantic Ocean (*orange squares*, *dotted line*). The *black thin-dash line* shows the zero trend. Trend values for each line listed in Table 4.1

Table 4.1 Trends (and standard errors; *S.E.*) in SST anomalies across five geographic regions from the Pathfinder reanalysis of the 22-year satellite record, 1985–2006 (as displayed in Fig. 4.6). The SST anomaly values are averaged across specific reef pixels within each region and for each year

Region	Number of reef pixels	Trend in SST anomaly (°C/decade)	S.E. in trend (°C/decade)
Global	50	0.237	0.061
Indian Ocean and Middle East	18	0.261	0.074
Southeast Asia	9	0.232	0.078
Pacific Ocean	11	0.181	0.056
Caribbean and Atlantic Ocean	12	0.257	0.061

corals to thermally adapt and survive through climate change (Donner et al. 2005). The global rate of increase in SSTs is already at the rate predicted for the twenty-first century by global climate models where emissions are not reduced below current levels (2–4°C/century; IPCC 2007a). Further considerations of the impacts of future climate change on the bleaching of corals are discussed in Chap. 10. Comparing the annual global and regional average SST anomalies (Fig. 4.6) shows that, while the values are fairly consistent across the globe within each year, there are important spatial patterns of SST anomaly that change through time. The role of large-scale patterns in regional bleaching events is discussed in Sect.4.3.3.

Typical SST conditions that result in coral bleaching include not just unusually high maximum SSTs but also sustained warmer waters over a number of weeks. The NOAA DHW index (see Sect. 4.2.2.2) is a highly accurate predictor of such conditions. The record of NOAA's DHWs over 1985–2006 (Sect. 4.2.2.3) for 50 coral reef sites that bleached during 1997–1998 show increasing thermal stress throughout the 22-year period (Fig. 4.7). In this record, 1998 stands out as the year with the greatest cumulative reef thermal stress both globally (Fig. 4.7a) and in the Indian Ocean, southeast Asia and the Pacific Ocean (Fig. 4.7b, c, d). The exception to this pattern is the Caribbean/Atlantic (Fig. 4.7e) where thermal stress in 2005 greatly exceeded that of prior years.

The longer-term context of the increasing cumulative thermal stress on coral reefs shown by the satellite data can be determined using a degree-month index developed from multi-century records of reconstructed SST data. Similar to NOAA's DHWs, degree heating months sum the monthly anomalies above the long-term average monthly maximum and have been used to analyze climate model outputs for future bleaching potential (Lough 2000b; Donner et al. 2005). Using the HadISST and NOAA ERSST data based on SST anomalies from the same time period, indices were created for the same 50 coral reef sites discussed above for the period January 1871 to October 2006. With the exception of the 1877–1878 El Niño event, the regionally averaged degree-month values show very low thermal stress until the latter half of the twentieth century (Fig. 4.8a). 1998 was the most extreme year in terms of cumulative reef thermal stress when averaged over all 50 reef locations and for coral reef regions of the Indian Ocean, southeast Asia and the Pacific Ocean (Fig. 4.8a–d), consistent with the satellite record. Thermal stress in the Caribbean (Fig. 4.8e) peaked in 2005; however, the Caribbean region showed

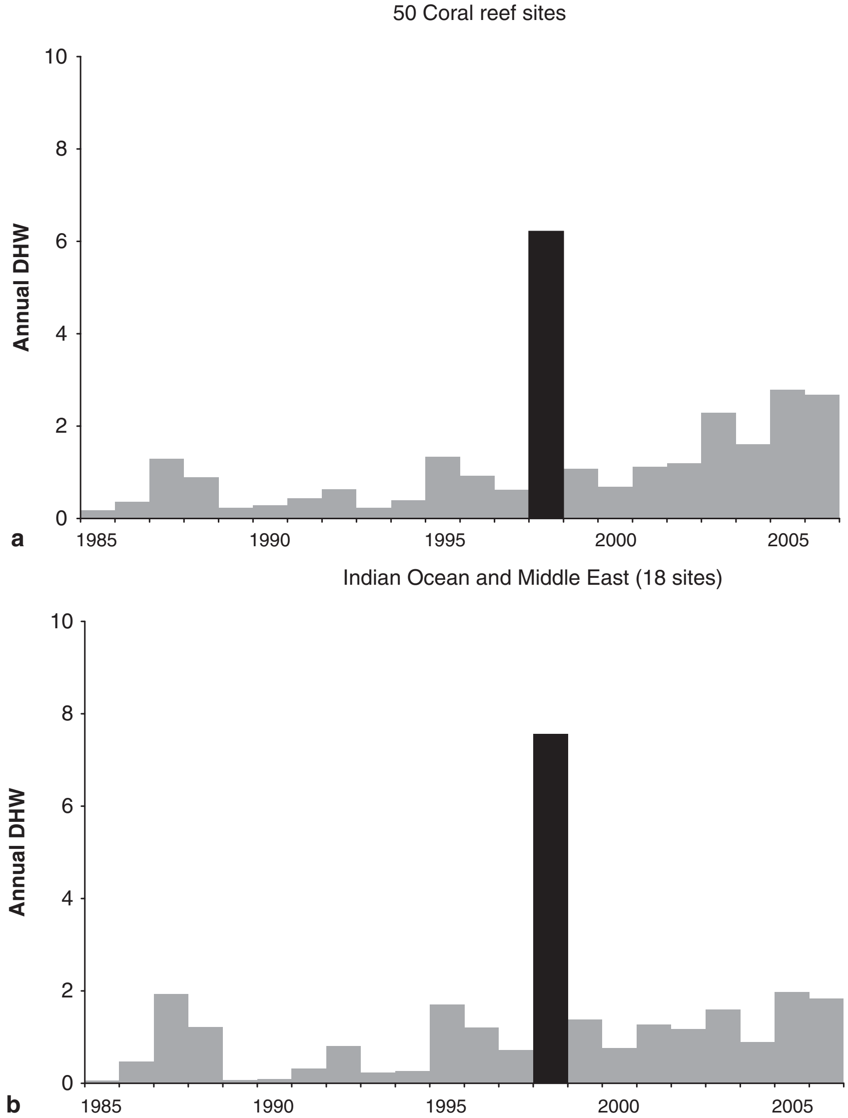

Fig. 4.7 Annual Degree Heating Week (*DHW*) indices, 1985–2006, averaged over the indicated number of 50 km Coral Reef Watch pixels for each region: **a** 50 coral reef sites that bleached in 1998, **b** 18 sites in Indian Ocean and Middle East, **c** 9 sites in southeast Asia, **d** 11 sites in Pacific Ocean and **e** 12 sites in the Caribbean and Atlantic Ocean (http://coralreefwatch.noaa.gov). Moderate bleaching has been shown to occur at DHW ≥ 4°C-weeks; severe bleaching occurs at DHW ≥ 8°C-weeks. *Black bar* shows most extreme year in 22-year record

significant thermal stress beginning decades earlier than the other regions (c.f., Lough 2000b; Barton and Casey 2005). It is unclear how much of the severe degradation of coral reefs in the Caribbean over recent decades resulted from this early increase in thermal stress (Gardner et al. 2003).

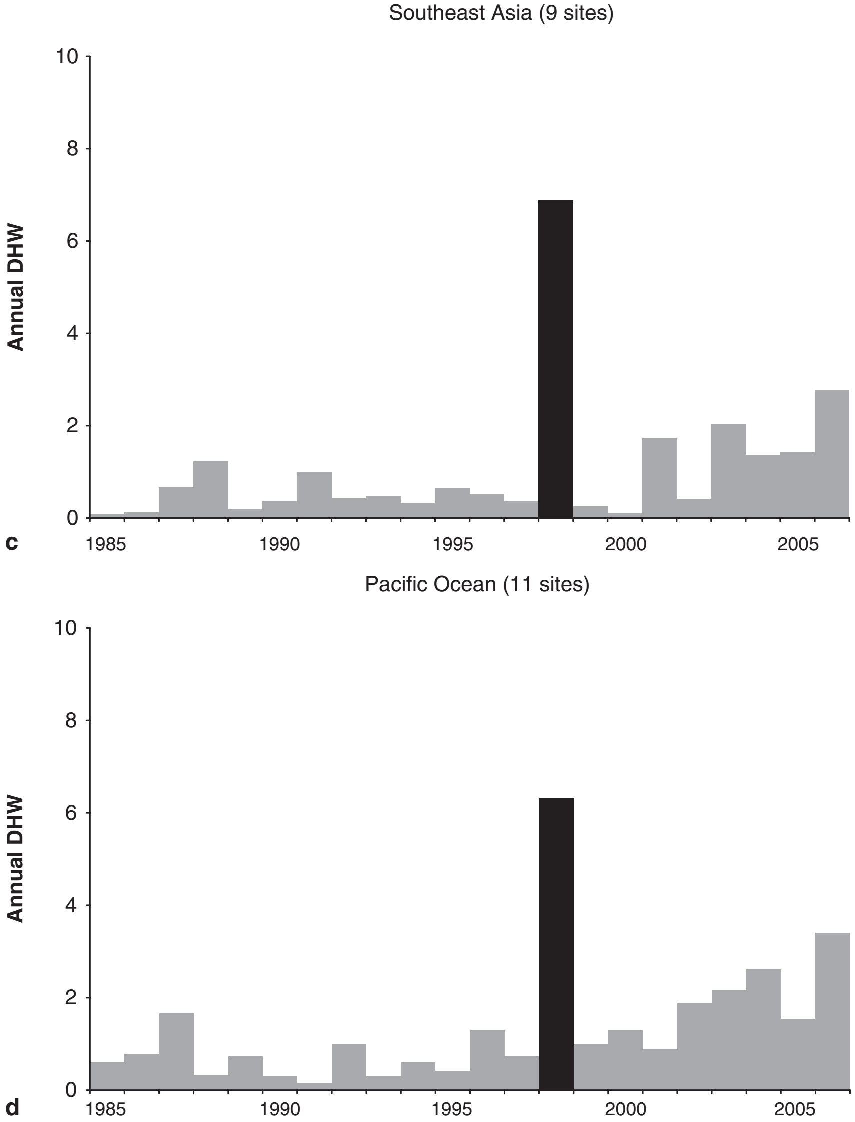

Fig. 4.7 (continued)

4.3.3 *Role of El Niño–Southern Oscillation and Other Large-Scale Patterns*

El Niño–Southern Oscillation (ENSO) events are the major source of short-term climatic variability within the tropical ocean-atmosphere system (McPhaden 2004). It was the major 1982–1983 El Niño event that first triggered warnings of a link between ENSO and mass coral bleaching events (Glynn 1983; Williams and

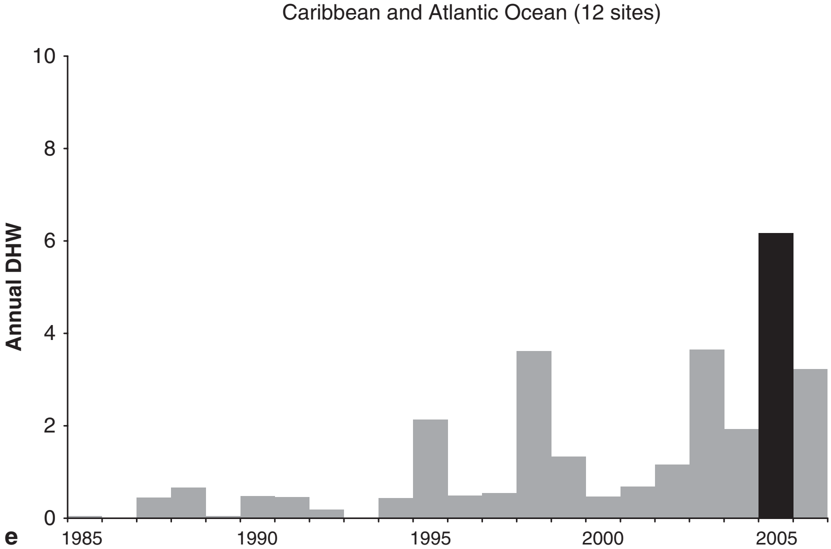

Fig. 4.7 (continued)

Bunkley-Williams 1990). The 1997–1998 El Niño event (coinciding with what was then the warmest year on record; Fig. 4.3a) was the other of the two most extreme El Niño events on record (Wolter and Timlin 1998; McPhaden 1999) and coincided with the greatest thermal stress at many coral reef sites (Figs. 4.7a, 4.8a). Over 15% of the world's reefs died and many reefs suffered over 90% bleaching in 1998 (Wilkinson 2000). ENSO events do not cause mass coral bleaching but instead increase the likelihood of anomalously warm SSTs in particular regions that result in coral bleaching. Major and minor ENSO years can be seen in the increased anomalies in Fig. 4.6 (i.e., 1987–1988, 1994–1995, 1997–1998, 2002–2003; but note the absence of signal for the 1991–1992 event). Mass coral bleaching can occur in the absence of ENSO extremes when other climate anomalies cause regional warming: e.g., GBR in early 1982 (Coffroth et al. 1990), Moorea in 1994 (Hoegh-Guldberg and Salvat 1995), Hawaii in 1996 (Jokiel and Brown 2004) and the Caribbean in 2005 (Eakin 2007; Wilkinson and Souter 2008).

Here we define the phases of ENSO by the Southern Oscillation Index (SOI), calculated as the difference in standardized sea-level pressure at Darwin, Australia and Tahiti, French Polynesia (Troup 1965; obtained from the Australian Bureau of Meteorology, at: http://www.bom.gov.au/climate/soihtm1.shtml). This index was used to identify 20 El Niño events, 20 La Niña events and 20 years of ENSO-neutral

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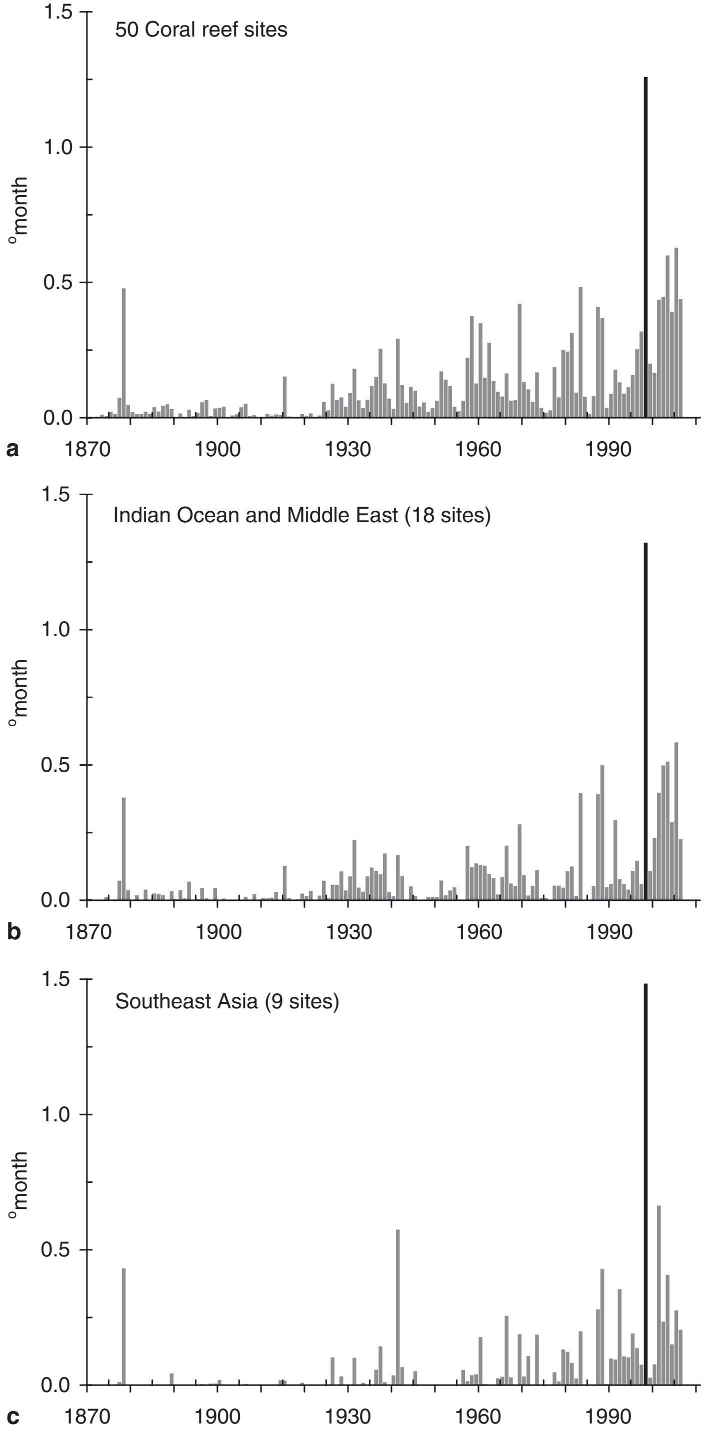
Fig. 4.8 Annual degree heating month indices (°*month*), 1871–2006, from HadISST and Reyn_SmithOIv2 data, for: **a** 50 coral reef sites that bleached in 1998, **b** 18 sites in Indian Ocean and Middle East, **c** 9 sites in southeast Asia, **d** 11 sites in Pacific Ocean and **e** 12 sites in the Caribbean and Atlantic Ocean. Data are available from http://www.aims.gov.au/pages/research/coral-bleaching/thermal-stress/thermal-stress-indices.html. *Black bar* shows most extreme year in 136-year record


50 Coral reef sites
°month
1.5
1.0
0.5
0.0
a
1870
1900
1930
1960
1990
Indian Ocean and Middle East (18 sites)
°month
1.5
1.0
0.5
0.0
b
1870
1900
1930
1960
1990
Southeast Asia (9 sites)
°month
1.5
1.0
0.5
0.0
c
1870
1900
1930
1960
1990

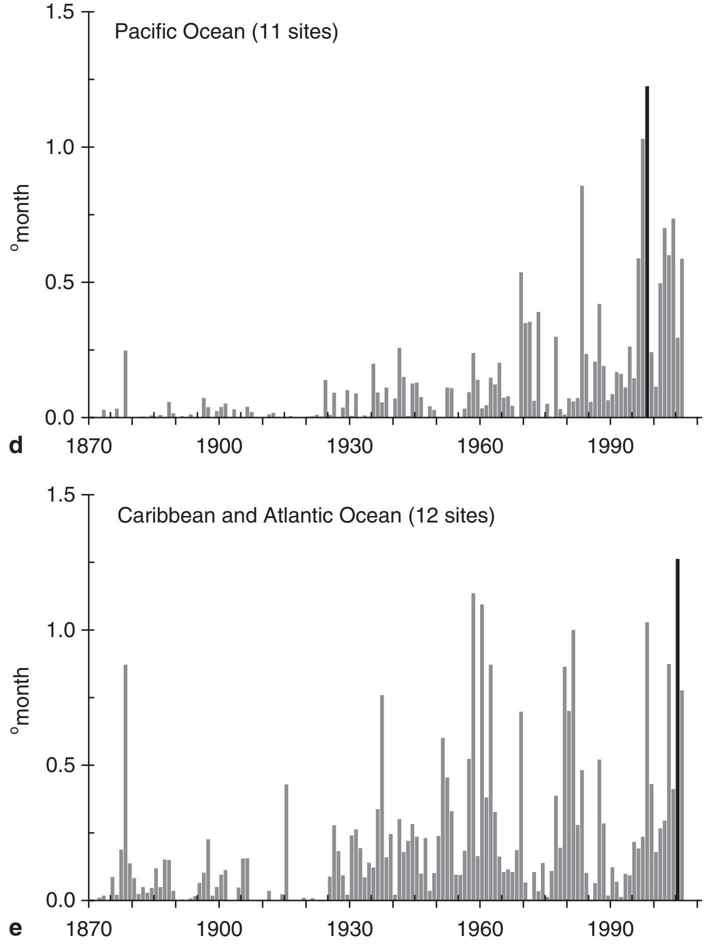


Fig. 4.8 (continued)

conditions from the upper, lower and middle percentiles, respectively, of the annual May–April values over the period 1871–2005. Monthly maxima were then averaged for each set of 20 years for both the target year and the following year (year *t* and year *t*+1; e.g., 1982 and 1983) for the tropical oceans. For each 1° latitude–longitude box, the average values for the 20 El Niño years and 20 La Niña years were tested for significant difference from the average of the 20 ENSO-neutral years.

The two extreme phases of ENSO, El Niño and La Niña, typically evolve over 12–18 months and are associated with distinct and different ocean–atmosphere circulation patterns in the core region of the central and eastern equatorial Pacific (McPhaden 2004). Typically for the two years spanning an El Niño event (e.g., 1982–1983, 1987–1988, 1997–1998), large areas of the tropical oceans have significantly warmer maximum SSTs than in ENSO-neutral years (Fig. 4.9a, b). Fig. 4.9b shows why, for example, many Caribbean bleaching events occur in the

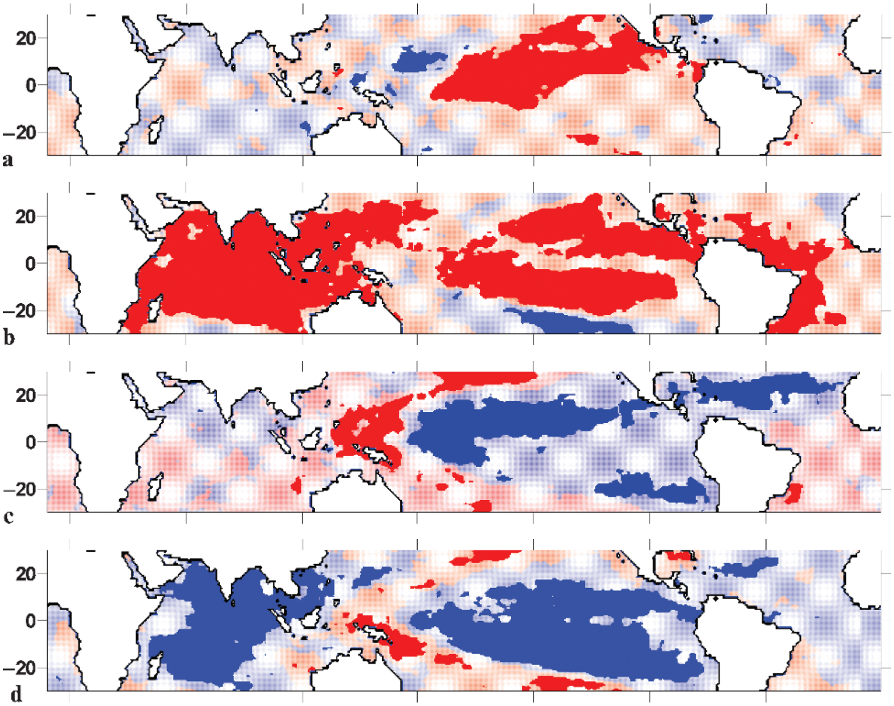


Fig. 4.9 Significantly (at 5% level) warmer (*red*) or cooler (*blue*) annual maximum SST difference: **a** El Niño year *t*, **b** El Niño year *t*+1, **c** La Niña year *t* and **d** La Niña year *t*+1. Average values calculated for 20 El Niño events, 20 La Niña events and tested for significant differences from 20 ENSO-neutral years. The groups of years were identified from the Troup (1965) SOI updated by the Australian Bureau of Meteorology

second year of an El Niño event. Conversely during the two years spanning a La Niña event, large areas of the tropical oceans have significantly cooler maximum SSTs than in ENSO-neutral years (Fig. 4.9c, d). An interesting exception is the region in the western equatorial Pacific lying along the South Pacific Convergence Zone where waters tend to be warmer during La Niña years and coral reefs experienced mass bleaching not in 1997–1998 but during the ensuing 1998–1999 La Niña (Wilkinson 2002). In general though, the risk of warmer than normal maximum SSTs and thus bleaching is greater during El Niño events for many of the world's coral reefs and this risk is much lower during La Niña and ENSO-neutral years. There is still debate as to whether the characteristics of recent ENSO events have changed (Trenberth and Stepaniak 2001) and how ENSO characteristics may change with continued global climate change (Philip and van Oldenborgh 2006). The important point for future mass bleaching on coral reef ecosystems is that even if temperature anomalies resulting from ENSO events remain within the range observed during the past 150 years, the warming of baseline maximum SSTs (Fig. 4.3b, 4.4, 4.6) increases the probability that waters overlying reefs will reach or exceed critical temperature thresholds for bleaching.

The ENSO system is not the only climatic pattern that influences ocean temperatures, and accordingly, the risk of coral bleaching. Oceanic SST variations also result from other longer-term modes including the Pacific Decadal Oscillation (Mantua et al. 1997) and the Atlantic Multidecadal Oscillation (AMO; Schlesinger and Ramankutty 1994), which show return periods on the order of 25 years and 65 years, respectively. These oscillations have typically been observed in periodic variations of temperature anomalies in the northern parts of their respective oceans. The Indian Ocean Dipole (Saji et al. 1999) is considered an aperiodic variation of SST anomalies between the eastern and western tropical Indian Ocean. Using an 18-year satellite time-series, Strong et al. (2006) observed a pattern shift in short-term SST trends during the latter half of the 1990s. Generally neutral trends across the Pacific Ocean transitioned to warming in the western Pacific and to cooling in the eastern Pacific; the tropical Indian Ocean moved from neutral to warming conditions; and warming trends in the northern and tropical Atlantic Ocean were enhanced. This pattern shift is likely a reflection of the superposition of short- and long-term climate variabilities.

Many authors have suggested that ocean temperature increases due to global climate change, especially in combination with natural variability such as ENSO, have and will continue to increase the frequency and severity of coral bleaching events (Williams and Bunkley-Williams 1990; Hoegh-Guldberg 1999; Eakin 2007). NOAA and NASA analyses revealed that global temperatures in 2005 surpassed 1998 as the warmest year on record (combined land and ocean global climate records; Shein 2006). This resulted in the most severe and widespread coral bleaching and mortality ever seen in the Caribbean (Eakin 2007; Wilkinson and Souter 2008). The anomalously warm North Atlantic temperatures that caused the 2005 Caribbean bleaching were only slightly related to ENSO and AMO. Trenberth and Shea (2006) used an attribution analysis to separate the anomaly in 2005 North Atlantic temperatures into its component climate patterns. They found that 0.45°C of the 0.9°C warming was due to the monotonic rise in global SSTs, 0.2°C due to after effects of the 2004–2005 mild El Niño and 0.1°C due to AMO. Donner et al. (2007) suggest that twentieth century anthropogenic warming, on top of the natural modes of variability, increased the probability that the Caribbean would experience the level of thermal stress observed in 2005 by an order of magnitude, compared with the natural modes alone. Their projections of future SST (including anthropogenic warming) suggest that, in the absence of acclimatization or adaptation by coral organisms, stress levels like those seen in 2005 will be experienced almost biannually by the 2030s.

4.4 Other Local Environmental Variables

Large-scale SST anomalies in the tropical oceans (Sect. 4.3.1) are the principal drivers of conditions that result in mass coral bleaching. At the local scale, the occurrence and intensity of bleaching can be highly variable both within a coral colony, between coral colonies, within a reef and between reefs in a region (Hoegh-Guldberg 1999). These variations are in addition to the differential susceptibility of different coral species to thermal stress (Marshall and Baird 2000). Other physical factors that operate locally can either enhance or suppress the impacts of higher-than-normal regional SSTs and thus the intensity of coral bleaching. Observations that corals often bleach more on their upper surface than at the sides clearly implicates light as an additional factor and frequently the local weather conditions that cause intense warming of the water column (low winds, low cloud amount, still waters; Skirving et al. 2006a) allow increased light penetration to the coral's surface (Coles and Jokiel 1978; Salm and Coles 2001). Increased cloudiness can mitigate bleaching even when SSTs are unusually warm (Mumby et al. 2001a). Lowered salinity due to a major flood event appears to have increased the intensity of coral bleaching on nearshore reefs of the central GBR in 1998 (Berkelmans and Oliver 1999). There can also be considerable local-scale variations in SSTs within and between reefs that can affect bleaching occurrence and intensity (Nadaoka et al. 2001; Berkelmans 2002; Berkelmans et al. 2004). Such local-scale SST variations can be related to water movements such as upwelling, mixing, tidal range and wave energy, shading and exposure that reduce the local thermal stress (Salm and Coles 2001; Skirving and Guinotte 2001; Skirving et al. 2006b). Although often small in scale, identification and enhanced protection of such bleaching resistant sites may be critical for recovery of adjacent bleaching-damaged coral populations (Marshall and Schuttenberg 2006; Skirving et al. 2006b).

4.5 Summary

We now have strong evidence of how global climate change due to the enhanced concentration of atmospheric greenhouse gases already has caused significant coral bleaching. This threat of future warming is so strong that coral bleaching has been highlighted among the greatest threats to ecosystems brought about by anthropogenic climate change (IPCC 2007b). Warming of the tropical oceans has raised the baseline SSTs where coral reefs live much closer to their upper thermal limits, so that weather conditions or interannual variability are more likely to raise SSTs above these limits than similar weather conditions did 100 years ago. The risk of unusually warm maximum SSTs also varies with the ENSO cycle, so that the risk of conditions conducive to bleaching further increases for much of the tropical oceans during ENSO events. This allows us to use El Niño conditions as an analogue for potential future climatic conditions. What remains is to determine if corals are capable of evolving physiological adaptations to thermal stress rapidly enough to cope with the combination of natural variability and climate change – a now ongoing, uncontrolled experiment that could result in the extinction of many corals.

Our ability to identify, monitor and predict SST conditions that can lead to coral bleaching has improved dramatically since the first reports of mass bleaching events in the early 1980s. This allows near-real-time monitoring and identification of potential bleaching conditions throughout the world's coral reefs. Of course, monitoring alone cannot prevent coral bleaching or mortality. It can, however, enable scientists and managers to be alert to bleaching and to document the intensity, impact and follow-on effects more comprehensively than was possible 10–20 years ago (Chap. 5). It also allows managers to take actions to help protect reefs at times when bleaching makes them more vulnerable to other stressors (Marshall and Schuttenberg 2006; Obura et al. 2006). Understanding linkages between the physical environment and biological processes on coral reefs improves our knowledge of the bleaching phenomenon, its ramifications and potential management responses. This helps managers develop and test management approaches to protect corals from mortality at the time of bleaching events. It also allows identification of "bleaching-resistant" corals, reefs and regions that should be targeted for enhanced protection. Resilient reefs may provide important refugia for coral reef organisms as climate continues to change and increasingly stress the world's reefs. The health of many of the world's coral reefs already has been severely compromised by local human-induced impacts. Climate change impacts at least add to local impacts and may act synergistically with them. In addition to the other consequences of a rapidly warming, enhanced greenhouse world (ocean acidification, more intense tropical storms, etc.), the observed increase in mass coral bleaching events does not bode well for the near- and long-term future of these vital ecosystems.

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Chapter 5
Detecting and Monitoring Coral Bleaching Events

M. Spalding

5.1 Introduction

Over the past 30 years coral bleaching has become a widespread phenomenon and is now seen by many as one of the most distinct manifestations of climate change impacts on natural ecosystems. In Chap. 3, Oliver et al. showed the evidence for the global extent of coral bleaching events in recent years. This is most dramatically illustrated with the 1998 event, linked to an El Niño, which led to bleaching in almost every coral reef region and to widespread mortality in some areas.

Quantifying the scale of such events presents particular challenges. In situ underwater observation is clearly of limited utility due to the magnitude of observation required – few reefs are within easy reach of research institutions, let alone dive shops, while detailed and regular observation may be necessary if an event is to be noted, let alone studied.

As an extreme example of the problem, the 1998 coral bleaching event caused mass mortality throughout the Seychelles (Spencer et al. 2000) and the Maldives (McClanahan 2000; Edwards et al. 2001). The Chagos Archipelago or British Indian Ocean Territory consists of a vast area of coral reefs in the same broad vicinity as these island groups, but no underwater observations were made at this time. Indeed almost a year later the UK government and their senior fisheries advisors (who have a boat on permanent patrol in the islands) suggested that the Chagos reefs had not bleached. It was only the observation of a bleached coral in the background of a photograph taken by an engineer doing work on a military base that enabled the case to be made for a post hoc assessment (M. Spalding, personal observation). The subsequent survey noted “near total” mortalities of the hard corals down to 15 m throughout this archipelago (Sheppard et al. 2001).

There is a need, then, for remote and ideally near continuous observation to ensure that an event as dramatic as the near total loss of reef corals across a region the size of England cannot pass by unnoticed in the future. At the same time, finer-scale observations of bleaching events may prove to be of critical value in understanding mechanisms and in determining management responses (West and Salm 2003). Fine-scale observations may clarify patterns of differential survival (deep vs shallow; lagoon or sheltered bays vs current-swept reef slopes) and support a better understanding of processes. At even finer resolutions the patterns of survival or of

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recovery also require observation at levels right down to the polyp and indeed within the cell.

5.2 Broad-Scale Approaches

5.2.1 Remote Sensing of Bleaching Events

At the broadest scales there is a need to be able to observe coral bleaching over very wide areas, in all localities across the planet. The only effective means of "seeing" reefs at these broad scales is using remote sensing with satellite platforms or aerial surveys. Bleached corals can hardly be mistaken in the field, but this also translates to a very distinctive spectral signature that may be visible from remote platforms (Holden and LeDrew 1998; Call et al. 2003).

In reality, the practical challenges of remote detection of coral bleaching remain considerable. Coral reefs present highly heterogeneous substrates – even up close, most are a complex patchwork of coral, algae, sponges and other surface cover. All but the highest resolution remote sensing platforms are sampling areas (pixels) that include a very broad mix of reflecting surfaces. This challenge is further compounded by the influence of differing depths of water column – in clear waters it is possible for the differentiation of marine features to 20 m, but it is a challenge to differentiate many features beyond that. And with most reef corals growing on sloping substrates, considerable variation in depth and reflectance can occur, even within the space of individual pixels.

The most widely used remote platforms for general reef mapping are those that allow coverage of relatively large areas relatively cheaply, typically Landsat and SPOT, although the higher resolution of IKONOS clearly enables more accurate feature assessment and classification (Andréfouët et al. 2003; Mumby et al. 2004).

Coral bleaching can be a short-lived phenomenon; and its spatial appearance can vary considerably. Some bleaching events are comprehensive and tightly synchronised (i.e., most species fully bleached at the same time) and these are likely to be easier to detect, particularly in areas of high coral cover. Where only some colonies are bleached, or where the loss of colour in bleached colonies is only partial, detection becomes increasingly challenging.

High spatial resolution is undoubtedly the most critical factor in helping to disaggregate the complex patchwork of substrate which typifies most coral reefs. Further improvement in bleaching detection ability can be achieved with finer spectral resolution (i.e., more and narrower widths of wavelength bands in the sensor); and with improved radiometric resolution (increasing the possible number of grey levels in the image). Temporal return is also critical: corals can shift from bleached to recovered in just a few weeks and dead corals become overgrown with algae in even shorter time-frames. Differential susceptibilities by different species or in different depths means that the "peak" of a bleaching event may only last a few days, although more typically it will last 2–4 weeks. With regular cloud-cover in the tropics a return of, say, 2 weeks for a sensor may be insufficient to capture a bleaching event.

The challenge of using satellite platforms, even high-resolution systems, is thus considerable. Andréfouët et al. (2002) tried to assess the optimum resolution for remote sensing of bleached corals using aerial photographs taken during the 1998 bleaching event and subjecting these to interpretation at varying resolutions. The authors noted a rapid tailing off of detection ability with resolutions increasing from 10 cm. As a crude guide, resolutions closest to that of the mean colony size will be most accurate, but resolution up to 1 m may still give some ability both to detect bleaching and to estimate variance between locations. At their study sites on the Great Barrier Reef, Andréfouët et al. (2002) also compared satellite-derived images taken before, during and after the 1998 bleaching using 20 m and 10 m resolution imagery, but showed a complete inability to detect even the fairly major bleaching of 1998.

Others had more success with these sensors. Philipson and Lindell (2003) showed at least basic detection of a very large-scale bleaching event in Belize using the 24 m resolution IRS LISS-III platform and suggested that much better detection should be possible with, for example IKONOS. Elvidge et al. (2004) showed very good detection with IKONOS imagery on the Great Barrier Reef, but point to the need for a pre-bleaching reference image. Yamano and Tamura (2004) and Graham et al. (2006) were also able to show detection of severe bleaching at Ishigaki Island in Japan, but only in shallow, coral-rich areas. The overall conclusion from these efforts is that bleaching detection at regional to global scales is still not possible. Improvements in availability of high-resolution imagery, notably reduction in the cost of imagery, may help but there are calls for new sensors to specifically target and improve spectral resolution for those wavelengths that might be able to differentiate marine features (Philipson and Lindell 2003).

The finer resolution of aerial photography offers much improved performance compared with current satellite platforms, but at considerably increased cost and with considerable challenges in surveying more remote reef systems. Some of the most extensive aerial survey work has been conducted by Ray Berkelmans in overflights over large parts (almost 25%) of the Great Barrier Reef during the bleaching events of 1998 and 2002 (Berkelmans and Oliver 1999; Berkelmans et al. 2004). This work was undertaken from a fixed-wing aircraft at a height of 160 m. These surveys covered over 2000 km of coast and provided critical information on two very large bleaching events that could not have been gathered either from satellite or field-based observations.

These same studies also showed that the timing of such surveys is critical. The best predictor of maximum bleaching levels was found to be the maximum sea surface temperature (SST) over a 3-day period, rather than estimates of longer periods of perhaps less extreme temperature anomalies (Berkelmans et al. 2004). Of course this may not be the case everywhere, but it presents further challenges to those seeking to accurately measure maximal levels of bleaching.

5.2.2 Remote Sensing of Indicators of Bleaching Likelihood

Proxy measures of likelihood of bleaching have been available for some years using very low resolution data on SST. Using night-time only SST records at 50 km resolution, the National Oceanic and Atmospheric Administration (NOAA)'s National

Environmental Satellite, Data, and Information Service (NESDIS), with its Oceanic and Atmospheric Research offices, developed a number of tools to predict bleaching likelihood (Strong et al. 1997; Strong et al. 2004; NOAA/NESDIS 2006; Chap. 4). Using data generated from an Advanced Very High Resolution Radiometer (AVHRR), SST measures are gathered twice weekly in near-real-time. These have been used to generate, inter alia, a measure of coral bleaching HotSpots (which are simply areas where the SST is at least 1°C above the mean maximum summertime temperature) and degree heating weeks (DHW), which is an index that summarises both longevity of anomaly and strength (size of temperature deviation).

It must be recognised that SST and DHW can only provide approximate pointers to conditions conducive to coral bleaching. Even so, both have shown themselves to be valuable predictors, particularly for the more extreme events. Numerous studies have shown their general validity (Sheppard 1999; Spencer et al. 2000) while a number of more specific experiments have been undertaken to improve and refine recording (see, e.g., http://coralreefwatch.noaa.gov/satellite/publications.html). McClanahan et al. (2007) compared the NOAA data with SST data available from the Joint Commission for Ocean and Marine Meteorology (JCOMM) and found the latter, which is satellite-derived but with corrections based on buoy and ship-based observations, to have a slightly better predictive capacity. As our knowledge of the thresholds for bleaching in different areas improves, the predictive capacity of such measures may be further improved (see also Chap. 4).

Various modifiers appear to strongly influence the role of SST in determining bleaching likelihood even at broad scales. Wooldridge and Done (2004) were able to further refine the predictive capacity of such approaches using a Bayesian belief network approach and found that bleaching susceptibility of the Great Barrier Reef in 2002 could be best predicted with a combination of: "site's heat stress in 2002 (remotely sensed), acclimatization temperatures (remote sensed), the ease with which it could be cooled by tidal mixing (modeled), and type of coral community present". McClanahan et al. (2007) also show a significant influence of past bleaching impact, reducing the bleaching likelihood in some areas.

During an actual warming event, the occurrence or degree of bleaching is further influenced by a range of other factors such as solar insolation and sea state, while different corals typically show different susceptibilities to bleaching (Marshall and Baird 2000; McWilliams et al. 2005). The important role of solar insolation at broad scales was further corroborated by observations of heavy and near continuous cloud-cover during critical periods of high temperature, which may have prevented bleaching in the Society Islands (Mumby et al. 2001) and in Mauritius (Turner 1999).

Even with refined models, summary data at 50km resolution is clearly insufficient to show the fine-scale patterns of variation which certainly occur. Berkelmans et al. (2004) observed changes at a scale of tens of kilometres, indicating local-scale variance, perhaps linked to oceanographic or weather patterns (e.g., upwelling or persistent cloud-cover adjacent to islands). Proximity to land will have further influence on water temperatures and bleaching likelihood – through direct shading by high terrestrial features, through runoff and through influences on water flows – but these will not be picked up in very low resolution SST data. Others have noted even finer-scale variance in bleaching tolerance or survivorship linked to shading, aspect, or water flows (Spencer et al. 2000; West and Salm 2003).

At very broad scales, SST data provide a useful indicator of bleaching likelihood, and it seems that various refinements could further improve such models. At the same time, however, the finer-scale variance in bleaching events needs to be documented and understood. Such patchiness may be of critical importance in both recovery and adaptation (Grimsditch and Salm 2006).

5.2.3 Summary of Remote Sensing Tools

- There are considerable challenges to using satellite sensors. Generally, very fine resolution is critical, and clearly detection will be better in areas where coral cover is high. There are, as yet, no broadly accepted tools.
- Aerial photography is highly successful not only in detection, but in quantifying and mapping bleaching impacts.
- Perhaps the most reliable tool is the use of temperature anomalies with AVHRR data. The coral bleaching HotSpots and DHW statistics provide powerful measures that also have the advantage of being consistent and comparable between regions and over time.
- These same data are also used in post hoc studies as a proxy measure of presumed impacts.

5.3 Field-Based Observation

Almost all bleaching monitoring is based on in situ observation by scientists and trained volunteers. Standardised reef monitoring techniques provide the basis for most assessments of how much coral has bleached and where.

More challenging, but at least as important, are the questions of differential survivorship, the identification of apparently resistant locations, species, or colonies and the gathering of associated environmental information to understand processes and mechanisms for bleaching and bleaching avoidance.

Good resources are widely available, describing the broad array of coral reef monitoring techniques (see, e.g., English et al. 1997; Hill and Wilkinson 2004) while subtle themes and variations are devised for almost every study that is published. Broadly, it can be seen that approaches sit on a spectrum of broad to narrow spatial coverage which is countered by a reverse spectrum of low to high accuracy:

1. Rapid semi-quantitative assessments. These can be gathered on directed or undirected swims, or using manta tows. They enable the assessment of large areas and thus also offer great strengths when considering the wider patterns of bleaching versus non-bleaching. This is a powerful tool for identifying low-level

bleaching and for getting a general picture but is obviously very weak for numerical studies and spatial or temporal comparisons.

2. Fixed transects. Longer transects offer some advantages of relatively large spatial coverage, while allowing some more accurate quantification. The accuracy of quantification is greatly increased using video transects although processing time is obviously increased. Standardised methods (often at permanently marked locations, or fixed depths and reef zones) enable comparison over time, but may restrict more exploratory survey approaches.
3. Quadrats, photo-quadrats and line point intercept approaches. These clearly give highest levels of accuracy, but there are considerable costs in terms of reductions in sampling area.

In developing a monitoring protocol, researchers must consider available resources and funding (over time). Ideally a nested sampling approach may be devised with some elements of monitoring across a range of scales. This allows more qualitative statements to be made about the overall impacts on the reef system, while allowing more quantitative rigour in fixed localities.

As with all monitoring, there is a requirement for repeat surveys and researchers must build continuing observation into their plans. Repeat surveys six months after peak bleaching may be critical for ascertaining levels of recovery and or mortality. Ongoing mortality may, however, continue even longer from associated coral disease impacts. Monitoring should be designed to assess not only impact but also ongoing recovery, including coral recruitment and growth.

The development of fixed sampling sites is clearly valuable in assessing trends over time, but the need for a broad and representative coverage of sites across an entire reef system, which is always important, should be of particular concern. Bleaching still remains poorly understood; and researchers may miss critical opportunities if their sampling sites do not adequately capture the patterns observed after the onset of a bleaching event.

5.3.1 Describing Bleaching

During any bleaching event, a coral's colours fade gradually. In many cases individual colonies show patterns of varying bleaching intensity across their surface: for example, those surfaces receiving greater levels of solar insolation often show greater bleaching, while vertical surfaces may be unbleached. A bleaching event may end with the gradual recovery of the coral, with subtle increases in colour over time. In other cases, part or all of the colony may die. In the field it is possible to overlook the subtle differences in colour and texture between a very recently dead coral, with a fine haze of filamentous algae, and a recovering coral. Such differentiation may be impossible in post hoc laboratory analysis of photo or video images.

In describing the bleaching pattern the most common metric is simply that of percent bleached. In contrast to remotely sensed studies, this term almost always refers to the proportion of the hard coral cover which is bleached rather than the proportion of the total substrate. Comparison between studies is sometimes challenged by poor reporting and inconsistency in dealing with variance in the form of the bleaching. Such problems may be avoided by differentiating and quantifying: (1) full bleaching of entire colonies, (2) patchy bleaching (including evidence of photosensitivity or sidedness) and (3) partial bleaching where some colour is still maintained.

Attention is typically focused on scleractinian corals, however many zooxanthellate species show similar responses and it may be worth including observations of bleaching in these (*Millepora*, *Heliopora*, soft corals, sea anemones). These should, however, not be included in more general estimates of percent bleaching.

Finally it is worth noting that, in some areas, notably in the Caribbean, partial bleaching in at least some species is highly prolonged (Lang et al. 1992). Continued monitoring should highlight this phenomenon. It may, however, also present challenges – obscuring the "peak" bleaching point and possibly leading to underestimation of the scale and extent of a single bleaching event or even failure to make clear connections with the original environmental drivers behind the event.

5.3.2 Assessing Mortality

With ever more frequent and larger temperature anomalies (Chap. 10) it is increasingly likely that coral mortality will be an important part of any bleaching event. Thus, bleaching related mortality must be incorporated into any monitoring regime.

Mortality may also be important in determining the magnitude of the peak bleaching impact, especially in locations where it may be difficult to time a survey to coincide with peak bleaching. There is, of course, a risk that mortality may be related to non-bleaching and here the contextual framework of the surrounding reef environment, coupled with the experience of the observer, may be critical. Dead corals are rapidly overgrown and can, within weeks, become highly altered (Lang et al. 1992). In the context of an ongoing bleaching event it is, therefore, relatively simple to differentiate recently dead corals from those that have been dead for some months or years; and there are many instances when it may be reasonable to assume that such death is bleaching-related.

Bleaching related mortality can be estimated even some time after the event in the more extreme cases. This was the case in the Chagos Archipelago, which was only surveyed one year after a suspected major bleaching event – here the context was provided both by the SST observations from the time and by the impacts in adjacent reef systems, including the Maldives and Seychelles. It was clear that the "near-total" loss of hard corals on these reefs was directly related to an unobserved massive bleaching event (Sheppard et al. 2002).

Semi-quantitative approaches may also be important. The semi-quantitative categorisation of results gathered from different surveys are, in many areas, the only means available to place bleaching and other impacts into an historical perspective (Winter et al. 1998).

5.3.3 Broader Patterns Across the Reef

Many of the traditional monitoring approaches, as already mentioned, give little space for a standardised approach to documenting patterns of survival over broader scales than the transect or quadrat. Work so far suggests that such patterns may be of critical importance and may show up variable survival both within reefs and across broader scales. This problem is compounded by the otherwise quite sensible desire among reef ecologists to standardise sampling techniques. This has led to most ongoing reef-monitoring programmes (many of which have been usefully adapted to survey for bleaching) remaining fixed on "standard" reef zones, at fixed (usually quite shallow) depths down the reef front. Often excluded from such studies are: channels, isolated or lagoon bommies, current-swept "promontories", deeper reef slope areas (below 30 m), or coral patches across the reef flat.

As bleaching becomes more frequent, a growing number of anecdotal reports suggest that there are indeed differential patterns of impact in different parts of the reef system and that these may offer critical refugia or centres for adaptation and recovery. Effort should be made to incorporate such locations into monitoring systems, but even post hoc descriptions of differential bleaching patterns can be valuable. Researchers should be encouraged to note any variance in bleaching intensity ("although not quantified, bleaching appeared to be more/less severe in lagoons/reef channels/deeper waters/close to land, etc.") or even the lack of such variance ("patterns of bleaching appeared to be very similar in…"). Such qualitative information may provide a valuable guide to future research and to managers.

5.4 Colony Scales and Finer

At the level of the coral colony, as already mentioned, there is variation in the intensity and appearance or morphology of a bleaching event between species and even between adjacent colonies. At these scales it may be important to establish repeat sampling of colonies and methods, therefore, may likely require the clear identification of individual colonies. Baird and Marshall (2002) used a simple categorisation of degree of colony bleaching as follows: no bleaching, 1–10% bleached, 11–50%, 51–99%, 100% bleached, dead; and they placed all pale (but still partially coloured) colonies in the 1–10% bleached category. Such a system may be more widely applied, although it may need some revision for Caribbean reefs where partial loss of colour appears to be much more widespread. Siebeck et al. (2006) provided a useful tool for describing degree of colour change which may improve consistency of monitoring through time, although it should be noted that this has so far only been used on five species and there was some degree of inter-observer error.

Describing patterns across a colony can also be important and can lead to advances in understanding processes and patterns of resilience. Sidedness of a bleaching occurrence is quite common and can often be linked to high solar radiation. Typically, bleaching may commence on those coral surfaces receiving the highest levels of solar radiation. More complex patterns have also been observed, notably by Brown et al. (2002a, b), where faces of corals that had undergone prior exposure to high solar insolation were subsequently more resilient to a high-temperature-related bleaching event.

At the level of colonies it is also possible to measure and assess recovery, including sub-lethal impacts on growth and reproduction. Baird and Marshall (2002) looked at growth rates in four species, by regular return-sampling to over 100 separate colonies during and after a bleaching event. They also looked at the reproductive potential, taking coral samples for laboratory analysis both before and after the known spawning period and assessing development of gametes and presence of fertilized eggs.

Measurements of photosynthetic activity can now be undertaken with relatively non-invasive techniques. Although many studies still involve the removal of specimens to adjacent laboratories (Brown et al. 2000), submersible tools do exist (Ralph et al. 1999; Warner et al. 1999; Fitt et al. 2001) for in situ measurement. Lombardi et al. (2000) used a fast repetition rate fluorometer to show variance in fluorescence yields from corals at different stages of bleaching, or recovery, while Hochberg et al. (2005) showed that a good estimate can be made of pigment densities using detailed recordings of optical reflectance spectra.

Working at the scale of polyps, cells and algal symbionts always requires a shift of effort from the field to the laboratory; and here we only provide a brief review of typical methods used on wild-sampled corals. Considerably more work of this nature has been developed using laboratory-cultured corals and this work is clearly important in refining techniques. It does not, however, constitute monitoring of natural bleaching events.

Assessing zooxanthellae densities can be done on tissue prepared for microscope counts. There is clearly some challenge in obtaining material from the field and in fixing it to ensure the collection and handling of the tissue does not influence the results. Some studies use a Water Pic to remove soft tissue, with the subsequent isolation of zooxanthellae by centrifugation (Warner et al. 1999). Others use coral cores which must then be decalcified before homogenisation (Le Tissier and Brown 1996).

Histological examination allows investigation of the distribution of zooxanthellae within a polyp. It provides some picture of the internal mechanisms of bleaching, with differential patterns of zooxanthellae loss and degradation typically observed in different tissues and at different stages of bleaching. Such patterns (for example the existence of a reservoir of algae in the base of the polyp) may give some indication of the ability of polyps to recover should environmental conditions improve (Brown et al. 1995; Le Tissier and Brown 1996).

Assessing chlorophyll concentrations is another useful measure and field studies use both spectrophotometry (Le Tissier and Brown 1996) and high-performance liquid chromatography (HPLC) (Ambarsari 1997; McDougall et al. 2006; Apprill et al. 2007). Unlike HPLC, spectrophotometry cannot discern chlorophyll-a-like compounds and can thus lead to higher chlorophyll readings than would be expected (McDougall et al. 2006).

It is now clear that different clades of zooxanthellae offer differing levels of thermal tolerance and hence different abilities to resist bleaching (Rowan et al. 1997; Baker et al. 2004; Chap. 6), although it appears that not all corals can host multiple clades (Goulet 2006). The identification and quantification of different clades require the extraction and isolation of zooxanthellae DNA and sequence analysis (Rowan and Knowlton 1995; Fabricius et al. 2004; Apprill and Gates 2007). Some work also shows differential acclimatization of the corals themselves to bleaching, suggesting a number of molecular biomarkers which might be valuable in measuring levels of adaptive thermotolerance in both corals and zooxanthellae (Downs et al. 2000; Brown et al. 2002a, b).

From an environmental perspective, the monitoring of these different algal clades may provide a critical understanding of existing resistance to future bleaching events and even the ongoing patterns of acclimatization in recovering corals (LaJeunesse 2002; Baker et al. 2004; Thornhill et al. 2006). Such work requires not only the very finest scale molecular techniques in assessing zooxanthellae diversity, but also broader-scale sampling to understand the distribution of clades between species, across the reef profile, between adjacent reefs and across much wider spatial scales (van Oppen et al. 2005; Garren et al. 2006).

5.5 Temporal Contexts

Although the primary purpose of this chapter is to provide an overview of the monitoring methods of bleaching events themselves, it must be pointed out that monitoring *either* side of a bleaching event is invaluable. Knowledge of a pre-bleaching state – of prior conditions of coral cover, variation across the reef system, prior bleaching events, “natural”, seasonal or recurring bleaching observations and (at a finer scale) “natural” backgrounds of zooxanthellae and photosynthetic function – can provide an invaluable reference in understanding any bleaching event. Similar monitoring protocols can and should be used post hoc in an attempt to document rates of recovery and patterns of recovery and further to document shifts in community structures, or zooxanthellae clades.

Monitoring changes in growth and reproductive success (Baird and Marshall 2002) may identify sub-lethal impacts of prior bleaching events; or conversely may uncover other processes that could hinder or expedite recovery. Changes in disease incidence may also provide some measure of underlying sub-lethal effects (Miller et al. 2006; Bruno et al. 2007). Others have quantified recruitment, counting new colony densities and identifying to species where possible (Sheppard et al. 2002);

this gives an indication of rates and patterns of recovery in different areas and may provide a pointer to possible shifts in community structure.

5.6 Connecting Across Scales

We have described means of assessing and monitoring bleaching from global scales to patterns within individual colonies; and each of these approaches is valuable. It is also important, however, to be able to link spatial scales. Global and regional patterns are helping to inform the science of global change and are also strengthening the hands of policy makers in seeking to address climate change.

Broad scales help provide a context for field observations; and they support informed extrapolation to areas where there have been no field studies. Field studies provide texture to the global patterns, enabling a better understanding of patterns of resistance and resilience which may help in the wider interpretation of coral reef futures and are also helping policy-makers in the challenges of planning for uncertain futures. Clear examples of such applications for planning and conservation are being provided with the promotion of resilient networks of marine protected areas (Grimsditch and Salm 2006; Marshall and Schuttenberg 2006; see also http://www.reefresilience.org/). But it is only with the finest-scale studies that we can begin to understand the mechanisms of bleaching and the variance in response which will be so critical in understanding future impacts. Once again, connecting across spatial scales provides further texture to our picture of the many facets of the phenomenon of coral bleaching. Perhaps most striking in this regard are the observations of variance in zooxanthellae clades over both space and time (with the possibility of related or independent patterns in the coral-host resistance/susceptibility), providing what may be critical clues into the future for coral reefs in a warming world.

It is also critical to consider patterns across time-scales. “Monitoring” implies ongoing observation and understanding the temporal component is important in determining long-term futures for both coral reefs and those who rely on them. It is important that bleaching events are not seen in isolation. Bleaching impacts appear to be significantly affected by the location and impact of prior events. There also appear to be quite significant non-lethal impacts affecting long-term survivorship. Mortality is a frequent component of bleaching events and must be accurately assessed alongside the growth and recruitment of the remaining corals.

Finally, researchers must be encouraged to place their own research within a wider context. Bleaching as a global phenomenon cannot simply be reported in one-off reports in local or national contexts. Although valuable, such reports in isolation may be misleading. Researchers should consider existing methodologies before devising new ones. If they choose to develop or refine their own approaches, they should at least consider how their own work can be directly compared with the work of others. In the reporting process they should indeed make such comparisons, providing a regional and temporal context for their own work.

The challenges of summarising a vast literature and burgeoning array of methods into wider regional and global assessments are considerable (see Chap. 3). Such reporting needs to be continued and indeed strengthened; and researchers should be encouraged to contribute to global monitoring schemes. Such a broader review greatly helps in developing our understanding of the global threats posed by coral bleaching; it will support more informed considerations of management responses; and it will in all likelihood provide yet stronger arguments to governments and to civil society on the urgent need to tackle the ultimate causes of climate change.

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Chapter 6
Bleaching Resistance and the Role of Algal Endosymbionts

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6.1 Introduction

Scleractinian corals and octocorals form endosymbioses with single-celled dinoflagellate algae in the genus *Symbiodinium* (commonly referred to as zooxanthellae). This association is obligate in most coral species, with the coral host deriving a large proportion of its energy budget from the algal endosymbionts (Muscatine and Porter 1977), although nutritional dependence on zooxanthellae is generally lower in octocorals (Fabricius and Klumpp 1995). The zooxanthellae also play a vital role in light-enhanced calcification of scleractinian corals (Barnes and Chalker 1990; Moya et al. 2006). In healthy corals, zooxanthellae occur at extremely high densities of >10^6 cells cm^{-2} of coral surface. During bleaching events, the symbiosis breaks down and zooxanthellae are lost from coral tissues. Consequently, the coral starves unless zooxanthella densities are recovered rapidly and/or the coral has the ability to meet its energy demands through heterotrophy (Grottoli et al. 2006).

Zooxanthella symbioses are established via horizontal or vertical (i.e., maternal) transmission. Approximately 85% of corals are horizontal transmitters that produce gametes free of zooxanthellae (Fadlallah 1983; Babcock and Heyward 1986; Harrison and Wallace 1990). In this case, zooxanthellae must be acquired de novo from the environment in each generation, at the larval or early juvenile stage. Most broadcast spawning corals show horizontal symbiont transmission, although there are some that transmit zooxanthellae directly to the oocytes (e.g., *Montipora* spp., *Porites* spp.). In contrast, the majority of brooding corals show vertical transmission, releasing internally brooded larvae that already harbour zooxanthellae. A small proportion of brooding corals have horizontal symbiont transmission, an example being *Isopora palifera*.

Symbiodinium was long considered to be a monotypic genus with a world-wide distribution (Taylor 1974). However, in the early 1980s it became evident that the species *Symbiodinium microadriaticum* Freudenthal comprises a highly diverse group of organisms (Schoenberg and Trench 1980; Blank and Trench 1985, 1986). This was confirmed more recently by molecular analyses (for reviews, see Baker 2003; Coffroth and Santos 2005; Stat et al. 2006) and detailed morphological analyses (LaJeunesse 2001). Despite the existence of subtle morphological differences

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between some *Symbiodinium* species, however, most zooxanthellae are morphologically extremely similar when examined using light microscopy. Therefore, the identification of *Symbiodinium* has relied primarily on genetic methods.

6.2 Genetic Diversity of *Symbiodinium*

Eight phylogenetic lineages or clades (A–H) have been distinguished based on nuclear small and large subunit ribosomal DNA (nrDNA) as well as chloroplast large subunit ribosomal DNA; and the relationships among six of these clades have been verified by analyses of mitochondrial *cox1* and chloroplast *psbA* DNA (Baker 2003; Coffroth and Santos 2005; Barbrook et al. 2006; Pochon et al. 2006). Estimates from molecular clocks calibrated based on a "universal" dinoflagellate rate of sequence evolution for large subunit nrDNA (Tchernov et al. 2004) or on vicariant events and host fossil dating (Pochon et al. 2006), suggest that the genus originated between 65×10^6 and 50×10^6 years ago. Hence, corals associate with a suite of evolutionarily highly divergent symbionts in six of the eight known clades (A–D, F, G) of *Symbiodinium*, including the most basal lineage A and several derived lineages. Each of the clades comprises many *Symbiodinium* strains or types, sometimes referred to as sub-clades or phylotypes (although the latter is used by some authors to denote the eight main clades A–H). Here we will use the terms "type" to indicate taxonomic entities below the level of the eight known clades, and "clones" or "genotypes" to denote genets within a type. Diversity below the level of the clade is usually assessed using the internal transcribed spacers (ITS1, ITS2) of the nrDNA (Hunter et al. 1997; Baillie et al. 2000a; LaJeunesse 2001; van Oppen et al. 2001), the rDNA 23S gene (Santos et al. 2002) or the *psbA* non-coding region (Moore et al. 2003) of the chloroplast DNA (cpDNA), and microsatellite flanking regions (Santos et al. 2004). The delineation of species boundaries in *Symbiodinium* is an issue of much debate and not easily resolved, although several authors have proposed distinct ITS or cpDNA sequences as representing different species. The investigation of intra-specific levels of genetic diversity is still in its infancy (but see examples using allozymes (Schoenberg and Trench 1980), DNA fingerprinting (Goulet and Coffroth 2003a), random amplified polymorphic DNA (Baillie et al. 2000b) and microsatellites (Santos et al. 2001, 2003b; Magalon et al. 2006).

The few studies in which the diversity and spatial structure of *Symbiodinium* populations were examined using high resolution markers showed very dissimilar results. In the Caribbean gorgonian, *Pseudopterogorgia elisabethae*, ~96% of the 575 surveyed colonies from 12 populations harboured a single *Symbiodinium* clone (Santos et al. 2003a). Furthermore, extreme population structure was observed over spatial scales ranging from a few to ~450 km, with 66–100% of colonies within 10 of the 12 surveyed populations harbouring the same clone; only in a few cases were genotypes shared among populations. In contrast, Magalon et al. (2006) found up to four *Symbiodinium* clones within single colonies of the scleractinian coral, *Pocillopora meandrina,* from the Tonga and Society archipelagos in the South Pacific, a greater extent of allele sharing among populations and significant genetic differentiation only at scales greater than ~200 km. *Symbiodinium* populations harboured by colonies of the soft coral *Sinularia flexibilis* from the Great Barrier Reef (GBR) harboured between two and six clones; and up to 14 clones were found within colonies from Torres Strait populations, with significant genetic differentiation existing among populations at scales ranging from tens to 100s of kilometres (Howells et al. 2008). There appears to be no correlation between the number of *Symbiodinium* genotypes present within individual colonies and either the mode of symbiont transmission, the specificity of the symbiosis, or the extent of spatial structure observed. *P. elisabethae* and *Sinularia flexibilis*, for example, show horizontal transmission and strong symbiont specificity, while *P. meandrina* transmits algal symbionts directly to its offspring (Hirose et al. 2001) and also shows relatively high symbiont specificity [at least two distinct symbiont C1 clones have been identified in the South Pacific (Magalon et al. 2006) and on the GBR (LaJeunesse et al. 2004a)]. The pattern emerging from these limited data is that genetic diversity within Caribbean *Symbiodinium* types is lower than within Pacific populations. However, studies of a much wider range of taxa are required before the veracity of this pattern can be assessed.

6.3 Biogeographic Patterns in *Symbiodinium* Diversity

Among scleractinian corals, *Symbiodinium* distributions vary considerably between the Caribbean and the Indo-Pacific (Baker and Rowan 1997; Baker 2003; LaJeunesse et al. 2003). At shallow depths (<7 m) in the tropics, members of *Symbiodinium* clades A–D are common in the tropical western Atlantic (Caribbean), with individual coral species typically hosting members of one of these clades, but sometimes hosting members of up to three additional clades. In contrast, at similar depths in the tropical Indo-Pacific, scleractinian corals are dominated by members of clades C and D (Fig. 6.1a–d, Table 6.1). The generalist symbiont types within clade C (i.e., the more ancestral types C1 and C3 *sensu* LaJeunesse, C3 equivalent to van Oppen C2) are present in both Caribbean and Pacific hosts, suggesting that they arose prior to the closure of the Isthmus of Panama (LaJeunesse 2005). The high diversity within clade C seen in both oceans is thought to have independently evolved through a series of adaptive radiation events (LaJeunesse 2005).

The apparent similarity between tropical Caribbean scleractinian symbioses and their counterparts from the temperate Indo-Pacific and Mediterranean led to speculation that the closure of the Isthmus of Panama and subsequent cycles of glaciations in the northern hemisphere led to cooler and more variable temperature regimes in the tropical western Atlantic which, in turn, selected for *Symbiodinium* that are more typical of temperate hosts (Baker and Rowan 1997; Baker 2003). A Caribbean radiation of clade B also dates to this period (LaJeunesse 2005), supporting the idea that environmental change during the Plio–Pleistocene transition drove the patterns of association (Baker and Rowan 1997; Baker 2003; LaJeunesse et al. 2003).

As with the scleractinians, *Symbiodinium* distribution among octocorals varies between major ocean basins (van Oppen et al. 2005a). Overall diversity is greatest in the western Pacific and the GBR where, at the clade level, the symbiosis is dominated

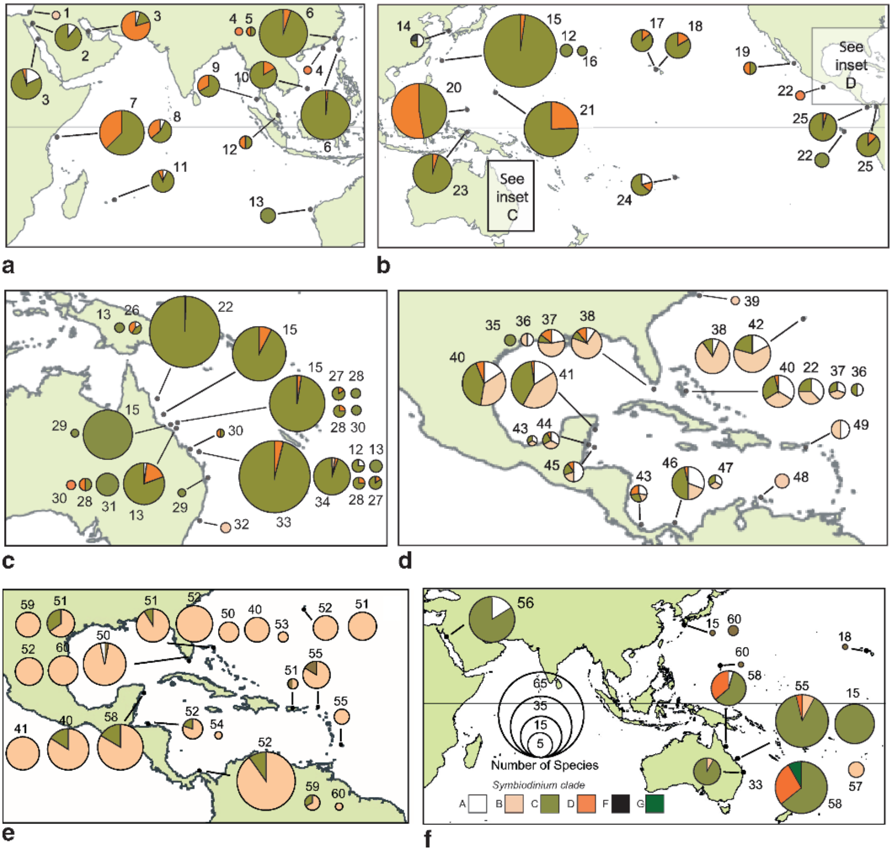

Fig. 6.1 Geographic distribution of *Symbiodinium* clades in scleractinian corals in: **a** west Pacific, Indian Ocean, Red Sea and east Mediterranean, **b** central to east Pacific, **c** east Australia, **d** west Atlantic; and in octocorals in: **e** west Atlantic, **f** Pacific and Red Sea. Numbers adjacent to pie charts are literature sources, as listed in Table 6.1.

primarily by *Symbiodinium* clade C, with a substantial number of hosts also having clade D. Clades A, B and G are also reported from soft corals on the GBR, although occurrences of these taxa are rare (Fig. 6.1e, f). Within the Red Sea, soft coral symbioses are dominated by *Symbiodinium* clade C and to a lesser extent Clade A (Barneah et al. 2004). In the Caribbean and Bermuda, soft corals harbour predominantly *Symbiodinium* clade B, with some species containing *Symbiodinium* clade C. Within octocorals, symbiont distribution does not appear to vary with depth as observed in some scleractinians. Both general reef surveys (LaJeunesse 2002; LaJeunesse et al. 2003; van Oppen et al. 2005a) and studies which specifically examined symbiont diversity over depth (Goulet and Coffroth 2003b, 2004) failed to detect any depth pattern in symbiont distribution.

Table 6.1 Literature sources used for Fig. 6.1

Pie Chart No.	Reference(s)
1	M. Fine, unpublished data
2	Karako-Lampert et al. 2004
3	Baker et al. 2005
4	Chen et al. 2003
5	Chen et al. 2005a
6	Chen et al. 2005b
7	Baker et al. 2004, unpublished data
8	Visram and Douglas 2006
9	M. Goodson et al., unpublished data
10	Huang et al. 2006
11	McClanahan et al. 2005
12	Loh et al. 2001
13	van Oppen et al. 2001
14	Rodriguez-Lanetty et al. 2003
15	LaJeunesse et al. 2004a
16	Rodriguez-Lanetty and Hoegh-Guldberg 2002
17	Rowan and Powers 1991a, b
18	LaJeunesse et al. 2004b
19	Iglesias-Prieto et al. 2004
20	Fabricius et al. 2004
21	Pochon et al. 2001
22	Baker 1999
23	van Oppen 2004
24	Darius et al. 1998, 2000
25	Baker 1999, Glynn et al. 2001
26	Ulstrup et al. 2006
27	van Oppen et al. 2005a
28	Ulstrup and van Oppen 2003
29	Rodriguez-Lanetty et al. 2001
30	Berkelmans and van Oppen 2006
31	Little et al. 2004, van Oppen 2004
32	Baker 1999, Loh et al. 1998, Rodriguez-Lanetty et al. 2001
33	LaJeunesse et al. 2003
34	Loh et al. 1998, 2001
35	Wilcox 1998
36	Thornhill et al. 2006a
37	Thornhill et al. 2006b
38	Baker et al., unpublished data
39	Rowan and Powers 1991b
40	LaJeunesse 2002
41	Banaszak et al. 2006
42	Savage et al. 2002a
43	Garren et al. 2006
44	Warner et al. 2006
45	Baker et al., unpublished data, McClanahan et al. 2003

(continued)

Table 6.1 (continued)

Pie Chart No.	Reference(s)
46	Baker 1999, 2001
47	Rowan and Knowlton 1995, Rowan et al. 1997, Toller et al. 2001a
48	Diekmann et al. 2003
49	Rowan and Powers 1991b
50	Coffroth, unpublished data
51	Holland 2006
52	Goulet and Coffroth 2004
53	Santos et al. 2004
54	Kirk and Coffroth, unpublished data
55	LaJeunesse database, at http://www.auburn.edu/~santosr/sd2_ged.htm
56	Barneah et al. 2004
57	Strychar et al. 2005
58	van Oppen et al. 2005b
59	Pochon et al. 2004
60	Santos et al. 2003b

Differences in symbiont diversity between the Atlantic and Pacific also influence the patterns of host and symbiont biodiversity in these two ocean basins. LaJeunesse et al. (2003) suggested that, although the total number of *Symbiodinium* types may be greater in the Indo-Pacific than in the Caribbean (due in large part to the enormous diversity of *Symbiodinium* in clade C), the ratio of symbiont to host diversity may be higher in the Atlantic than in the Pacific. This effect is mostly a result of the additional diversity within clades A and B that contribute to symbiont pools in the Atlantic.

6.4 Physiological Differences among Genetically Distinct *Symbiodinium* Types

The role of symbiont identity and diversity in terms of fitness of the coral host has only been superficially explored. To a large extent, physiological characteristics of distinct zooxanthella types have been inferred from correlative studies. For example, zonation of *Symbiodinium* clades over light gradients within colonies and between shallow and deep colonies of *Montastraea annularis*, *M. faveoloata* and *M. franksi* suggests that these symbionts have distinct light sensitivities (Rowan and Knowlton 1995; Rowan et al. 1997; Toller et al. 2001a). Observations of patchy bleaching within *Montastraea* colonies during a natural bleaching event further suggest that bleaching tolerances of *Symbiodinium* clades A–C differ substantially (Rowan et al. 1997). Toppled *M. annularis* colonies showing a cline of *Symbiodinium* B and C along an irradiance gradient re-established their original zonation patterns with respect to light in the newly oriented colonies over a six-month period (Rowan et al. 1997). In combination, these studies suggest that coral–algal associations can vary temporally and be controlled by environmental factors (see also Sect. 6.5).

Similar patterns of depth zonation in zooxanthella types were observed for the Caribbean species *Acropora cervicornis, Stephanocoenia intersepta, Porites astreoides* and *Diploria strigosa* (Baker et al. 1997; Baker 2001). When corals were transplanted from deep to shallow habitats, high light stress following transplantation caused a portion of the transplanted colonies to bleach. Corals that showed a depth zonation in symbiont type recovered with the zooxanthella types typical for conspecific colonies from the shallow environment, rather than their original deep-water types, while coral species that showed no depth zonation in symbiont type recovered with the same symbionts that were harboured at depth. Although these results suggest that bleaching may provide an opportunity for changes to occur in the *Symbiodinium* communities inside the host tissues in favour of one that is better adapted to the changed environmental conditions (Baker 2001), further tests are required to establish this, as Thornhill et al. (2006b) documented a change in the absence of visible bleaching in some colonies. These authors also hypothesized that Caribbean *Symbiodinium* clade D is tolerant of high light and stress in general. Brown et al. (2002) found clade D to be dominant in corals on a reef flat in Thailand, also suggesting that *Symbiodinium* D is relatively tolerant of high light. In contrast, intra-colony zonation patterns of clades C and D in *Acropora valida* (Ulstrup and van Oppen 2003) and the high abundance of clade D in corals from turbid reef environments on the GBR (van Oppen et al. 2001, 2005a) led to the hypothesis that clade D is better adapted to low-light environments. The sub-tropical coral, *Oulastrea crispata,* forms a stable symbiosis with *Symbiodinium* clade D in turbid non-reefal environments of China, where annual water temperatures fluctuate between 12°C and 35°C (Chen et al. 2003). This is concordant with Indo-Pacific *Symbiodinium* D being shade-adapted and also suggests members of this clade can withstand low temperatures. Populations of the coral *Acropora palifera* in southern Taiwan harbour a mix of C and D zooxanthellae, with clade D decreasing in relative abundance with seasonally increasing seawater temperatures (Chen et al. 2005a).

In contrast to evidence from these two studies, which classify clade D zooxanthellae as tolerant to both low and widely varying temperatures, clade D has been observed more commonly in corals inhabiting warm waters in a variety of regions globally (Baker et al. 2004, 2005; Fabricius et al. 2004; Ulstrup et al. 2006). The observation that C-corals bleached while D-corals were healthy during the 1997/1998 bleaching event in the far eastern Pacific (Baker et al. 2004) confirms that at least some *Symbiodinium* D are tolerant to high temperatures. An apparent increase in the abundance of clade D following major bleaching events was also taken as evidence that D-corals are more thermally tolerant compared with other coral–algal associations (Glynn et al. 2001; Baker et al. 2004; van Oppen et al. 2005b). In summary, corals harbouring clade D appear to be tolerant to a range of stresses, being either eurythermal, with thermal tolerances encompassing both high and low temperature extremes, or thermal tolerance varying among potentially different types within clade D.

Experimental data on the physiological characteristics of distinct zooxanthella types are far more limited (Table 6.2). Cultured zooxanthella strains can differ considerably in physiological characteristics, such as photo-acclimatory responses to changes in irradiance or growth rates (Iglesias-Prieto and Trench 1994, 1997;

Table 6.2 Physiological performance of *in hospite*/cultured/freshly isolated zooxanthellae of known genetic identity. *Symbiodinium* types in italics refer to LaJeunesse's nomenclature (LaJeunesse 2001, 2002) and those in bold to van Oppen's nomenclature (van Oppen et al. 2001)

Host	*Symbiodinium* type	Symbiotic state of zooxanthellae	Physiological characteristic	Reference
Montastraea faveolata	*B1*, *C7*	*In hospite*	C7 loses capacity for diel recovery of photoinhibition earlier than B1 during short-term elevated temperature stress	Warner et al. 2006
Porites astreoides	*A4a*	*In hospite*	High resistance to photodamage during non-stress and high-temperature stress conditions	Warner et al. 2006
Palythoa caribaeorum	*C1*, *D1a*	*In hospite*	No differences in thermal tolerance	Kemp et al. 2006
Acropora millepora	**C2, D**	*In hospite*	D-corals have higher thermal tolerance than C2-corals	Berkelmans and van Oppen 2006
A. millepora, *A. tenuis*	**C1, D**	*In hospite*	C1-juveniles grow 2–3 times faster than D-juveniles	Little et al. 2004
A. millepora	**C1, D**	*In hospite*	Photosynthetic capacity (rETR$_{MAX}$) 45% greater in *Symbiodinium* C1 than in *Symbiodinium* D, resulting in doubling of ^{14}C photosynthate (energy) incorporation into juvenile coral tissue.	Cantin et al. 2008
A. tenuis	**C1, D**	*In hospite*	C1-juveniles have higher thermal tolerance than D-juveniles	Abrego et al. 2008
Pocillopora damicornis, *P. verrucosa*	C, D	*In hospite*	D-corals are not photosynthetically impaired by experimental high temperature, while C-corals are	Rowan 2004
P. verrucosa, *Pavona gigantea*	*D1*, *C1c*, respectively	*In hospite*	D1 is "sun-loving", C1c is "shade-adapted"	Iglesias-Prieto et al. 2004
Aiptasia pallida	A, B	*In hospite*	A-anemones have higher photosynthetic rates than B-anemones at elevated temperatures	Goulet et al. 2005
Stylophora pistillata	C	*In hospite*	Heat sensitive	Tchernov et al. 2004
Montipora samarensis	C	*In hospite*	Heat tolerant	Tchernov et al. 2004
54 species, including hydrozoans, anemones, gorgonians, scleractinians	A, B, C, D	Cultured, *in hospite*	In culture, clade A symbionts produce mycosporine-like amino acids (MAAs) whereas clade B, C, D, and E symbionts do not. *In hopite*, all zooxanthella types examined (members of clades A-D) produce MAAs.	Banaszak et al. 2000, 2006

Unknown	B, A	Cultured	Both heat-sensitive and heat-tolerant strains within clades A and B	Tchernov et al. 2004
Cassiopeia xamachana, *Montipora verrucosa*, *Zoanthus sociatus*	*S. microadriaticum* (*A1*), *S. kawagutti* (*F1*), *S. pilosum* (*A2*), respectively (*Symbiodinium* genetic identity from LaJeunesse 2001)	Cultured	Three types have different photosynthetic characteristics and differ in their photo-acclimatory capabilities that correlate with their ecological distribution when endosymbiotic	Iglesias-Prieto and Trench 1994
Cassiopeia xamachana, *Cobdylactis gigantea*, *Aiptasia pallida*, *Meandrina meandrites*	*A1*, *A1.1*, *B1*, *F2*, respectively	Cultured	A1.1 has most limited capacity to acclimate to high light levels. B1 and A1.1 have greatest thermal sensitivity, F2 and A1 show high degree of thermal tolerance	Robison and Warner 2006
Cassiopeia xamachana, *Montipora verrucosa*, *Pocillopora damicronis*, *Cassiopeia* KB8, *Zoanthus sociatus*, *Tridacna gigas*, *Aiptasia pulchella*	A, C, B, A, A, A, B, respectively	Cultured	Different growth rates at three temperatures among types within clade A; some types showing increased growth, some decreased growth and some no change in growth with increasing temperature	Kinzie et al. 2001
Agaricia sp., *Montastraea cavernosa*, *M. franksi*, *Oculina diffusa*, *Porites astreoides*, *Aiptasia pallida*, *Bartholomea annulata*, *Condylactis gigantea*, *Cassiopeia xamachana*	A, B, C	Freshly isolated	PI curves are not uniform for all members of one clade and not consistently different between clades	Savage et al. 2002b

Kinzie et al. 2001). However, photo-physiological responses are known to differ significantly between *in hospite* and isolated zooxanthellae (Ralph et al. 2001; Bhagooli and Hidaka 2003) and it is unclear how these data from zooxanthella cultures relate to the natural, symbiotic situation. Compared with *Symbiodinium* clade C, experimental studies of clade D *in hospite* suggest that it is more thermally tolerant (Rowan 2004; Berkelmans and van Oppen 2006), more thermally sensitive (Abrego et al. 2008) and more light-loving (Iglesias-Prieto et al. 2004). There are two (not mutually exclusive) explanations for these seemingly contradictory findings on the physiological performance of *Symbiodinium* clades C and D. First, it is likely that physiological diversity exists not only among *Symbiodinium* clades, but also among types within clades (Kinzie et al. 2001; Tchernov et al. 2004). Second, either host factors or the interaction between host and symbiont may cause the same *Symbiodinium* types to behave very differently in different host species (Goulet et al. 2005; Abrego et al. 2008; Mieog et al., unpublished data). Thus, the physiologic responses of corals to environmental change may not be due to the plasticity of the coral or the algal symbiont within the coral, but due to plasticity in the holobiont itself, i.e., the same host can manifest different physiologies and responses depending on the host–symbiont pairing (Baker 2003; Goulet et al. 2005: Stat et al. 2006).

6.5 Shifts in Symbiont Communities as a Mechanism to Cope with Environmental Change?

Initial uptake of symbionts by juvenile colonies is mostly non-selective, allowing for a mix of symbiont types to establish symbioses with a single host colony. Subsequently, one symbiont typically increases in abundance (Kinzie 1974; Coffroth et al. 2001; Little et al. 2004). Little et al. (2004) hypothesized that the non-selective uptake of symbionts during early ontogeny and the maintenance of multiple symbiont types throughout life is an adaptive trait, as it permits changes in the relative abundance of symbiont types with distinct physiological characteristics within a single coral host. This may be a mechanism for the holobiont to acclimatize to perturbations in the environment (Buddemeier and Fautin 1993; Ware et al. 1996; Buddemeier 1999). Superficially, this hypothesis seems to be contradicted by the observation that some corals exhibiting strong symbiont specificity and temporal stability at adulthood also take up a range of symbiont types and clades shortly after settlement (Coffroth et al. 2001; Goulet and Coffroth 2003a). It is feasible, however, that this trait is selectively neutral in such corals and has, therefore, not been lost through evolution. Furthermore, this phenomenon may be related to the fact that immunity is suppressed during the first ~2–4 months of a coral's life (Frank et al. 1997; Nozawa and Loya 2005); and the suppression of immunity itself may have selective advantages during early ontogeny in both corals with symbiont specificity and those without. It is also possible that specificity does not result in the total exclusion of heterologous symbionts at this early developmental stage, but is expressed as lower densities and a different pattern of localization of heterologous compared with homologous symbionts inside the host tissues (Rodriguez-Lanetty et al. 2004, 2006). Finally, even though multiple types are initially acquired, some selectivity is exhibited in that not all symbiont types (strains) are taken up (LaJeunesse 2001; Coffroth unpublished data).

Scleractinian corals exhibit varying degrees of symbiont specificity, with some taxa establishing symbioses with a wider range of symbionts and other host taxa being relatively specific. Some corals are able to establish and maintain stable symbioses with a range of evolutionarily divergent *Symbiodinium* types (simultaneously within a single colony or separately in individual colonies). Key examples are *Montastraea annularis, M. faveolata* and *M. franksi* in the Caribbean (Rowan and Knowlton 1995; Rowan et al. 1997; Toller et al. 2001a) and *Acropora millepora* on the GBR (van Oppen et al. 2001; Berkelmans and van Oppen 2006). Other corals exhibit high specificity/fidelity to one or a few closely related *Symbiodinium* types, at least within geographic regions (populations in distinct geographic regions may have evolved specificity for a different symbiont type). This is believed to be the most common type of symbiosis (LaJeunesse 2005), however, the prevalence of symbiosis specificity is likely to have been overestimated for several reasons. First, specificity of the coral–algal symbiosis is generally inferred from small sample sizes. For example, *Montastraea franksi* was initially reported to harbour clade C only (Rowan and Knowlton 1995), but was later found to associate with members of clades B, C and D (Toller et al. 2001a; Thornhill et al. 2006b). Second, most coral colonies are dominated by a single *Symbiodinium* type (Goulet 2006), but it is likely that one or more additional types (from the same or a different clade) are maintained at such low densities that these have generally gone undetected by the genetic methods applied (LaJeunesse 2001; Santos et al. 2001; Goulet and Coffroth 2003a; Ulstrup and van Oppen 2003; Mieog et al. 2007). Third, it is unknown how many coral species show "sequential specificity", as was observed for *Acropora tenuis* on the GBR (Little et al. 2004). Juveniles of this species become dominated by *Symbiodinium* clade D ~2–4 months after initial non-selective uptake of zooxanthellae (Little et al. 2004). However, adult colonies are dominated by members of clade C (van Oppen et al. 2001, 2005a), suggesting that a change in dominant clade from D to C symbionts must take place between the age of ~6 months and adulthood. Finally, coral host species that form a symbiosis with host-specialized *Symbiodinium* types often simultaneously harbour additional symbionts that are common within the reef region [e.g., *Stylophora pistillata* on the GBR (LaJeunesse et al. 2003; van Oppen et al. 2005b) or *Montipora* spp. (van Oppen 2004)].

Changes in the dominant symbiont types harboured by single coral colonies may occur through changes in the relative abundance of zooxanthella types that are already present in the host tissues (a process coined "shuffling"; Baker 2003) or by uptake of new symbiont types from the environment (a process called "switching"; Baker 2003). For scleractinian corals, available evidence suggests that the temporal window for symbiont uptake is relatively narrow (Little et al. 2004), but is at least ~2 months (Mieog et al., unpublished data). Evidence for exogenous uptake of a new zooxanthella type by corals is only available for a Caribbean soft coral (Lewis and Coffroth 2004) and it is not known whether adult uptake occurs in other species.

Despite our ignorance of the exact mechanism responsible, it has been shown that the types of symbionts dominating coral tissues can change over time. For example, some colonies of *Montastraea annularis*, *M. franksi* and, to a lesser extent, *M. faveolata*, displayed changes in the *Symbiodinium* types dominating their tissues over a 6-year survey period in the Florida Keys. As no changes were observed in populations from the Bahamas, it was suggested that changes in populations from the Florida Keys were linked to the greater environmental fluctuations that occur there (Thornhill et al. 2006b). A considerable increase in the occurrence of *Symbiodinium* clade D after the 1997/1998 bleaching event was detected in populations of *M. annularis*, but a reversion to pre-bleaching zooxanthella community composition took place over a number of years. Transplantation of colonies of the GBR coral, *Acropora millepora,* from two cooler reefs (a southern GBR and a mid-shelf reef in the central GBR) to a warm inshore reef was followed by severe bleaching of all transplanted colonies during the following austral summer ~6–11 months after transplantation (Berkelmans and van Oppen 2006). The transplants from the mid-shelf reef recovered with the *Symbiodinium* type they originally harboured (type C2*), but the transplants from the southern location recovered with a different zooxanthella type (clade D) than the one previously dominating their tissues (type C2). With this change from *Symbiodinium* C2 to D, the thermal tolerance limit of these corals increased by 1.0–1.5°C, while the transplants from the mid-shelf reef that did not change zooxanthella type maintained exactly the same thermal stress response as before. The authors hypothesized that shuffling rather than switching is the most likely mechanism responsible for the change, as clade D zooxanthellae occur in low abundance in the corals from the southern reef. In addition, the difference in the extent of bleaching between the two transplanted populations (the transplants from the southern reef that changed zooxanthella type bleached more severely than the ones from the mid-shelf reef) may have triggered a change in the one population but not in the other (Toller et al. 2001b). Finally, populations of the coral *Acropora palifera* in southern Taiwan show annual fluctuations in the relative abundance of *Symbiodinium* clades C and D (Chen et al. 2005a), suggesting that symbiont shuffling occurs in response to seasonal changes in the environment.

In contrast to the patterns of change in response to environmental conditions described above, temporally stable coral–algal associations have also been documented for both spawning and brooding species. Thornhill et al. (2006b) observed no significant changes in the zooxanthella communities within individual colonies of the broadcast spawners, *Acropora palmata*, *A. cervicornis* and *Siderastrea siderea,* over a period of 6 years, despite diversity in symbiont types. The brooding species *Agaricia agaricites*, *Porites astreoides* and *Siderastrea radians* showed complete spatial and temporal symbiont fidelity to one *Symbiodinium* type over a 3–4 year period, despite significant visual bleaching of the *A. agaricites* colonies in 2005 (Thornhill et al. 2006a). Zooxanthella types harboured by colonies of the gorgonian coral, *Plexaura kuna,* remained unchanged over a 10 year period, both across different habitats and after transplantation (Goulet and Coffroth 2003b). The same results were obtained for the scleractinian corals, *Pocillopora verrucosa* and *Pavona gigantea,* 1 year after transplantation to a different depth (Iglesias-Prieto et al. 2004).

The brooding coral, *Oulastrea crispata,* also showed no change in its symbiont community over a 1 year survey period (Chen et al. 2003).

6.6 Prediction of Changes in *Symbiodinium* Diversity and Distribution over the Next Century

The data summarized above show that changes in the dominant symbiont type within individual coral colonies can occur. It is not, however, clear how many coral species or populations have the ability to change their symbiont community, how rapidly these changes can occur and the nature and strength of the cue that triggers the change. Although experimental data are limited, a growing body of evidence supports the notion that a change in the dominant symbiont type is accompanied by a change in the physiological response of the holobiont (Little et al. 2004; Berkelmans and van Oppen 2006). Goulet et al. (2005) showed that the same clone of *Aiptasia pallida* responds differently to elevated temperatures with different clades of *Symbiodinium*. Those harbouring *Symbiodinium* clade A had higher photosynthetic rates than those with *Symbiodinium* clade B at elevated temperatures. Berkelmans and van Oppen (2006) showed that shuffling from clade C to D zooxanthellae in *Acropora millepora* colonies increases thermal tolerance by 1.0–1.5°C. Although this is a huge ecological advantage in the short term and may delay the impact of increasing seawater temperatures, it is unlikely to allow corals to keep pace with increasing sea water temperatures as a consequence of global warming over the next century (Berkelmans and van Oppen 2006; IPCC 2007). Moreover, shuffling from C to D in this coral species comes at a cost of reduced growth (Little et al. 2004) and possibly reduced fecundity and competitive ability.

At this stage it is difficult to make realistic predictions of future changes in the composition of symbiont types harboured by reef corals. In the short term, corals with flexible symbioses may shuffle or switch symbionts; and an increase in the abundance of thermally tolerant symbiont strains (such as some of the clade D symbionts) is expected with an increasing frequency of bleaching conditions. Those host–symbiont pairings that are incapable of switching or shuffling may, however, become (locally) extinct, leading to a loss in the diversity of symbionts and corals on many reefs, unless these are able to adapt to the changed environmental conditions. The potential to adapt to increasing sea surface temperatures depends mainly on the extent of heritable genetic variation for heat tolerance, the generation time of the coral host and algal endosymbionts and the strength of selection. Reliable estimates for these parameters are unavailable, but generation times are likely to be long for corals. Nevertheless, due to the enormous population sizes and rapid turn-over of zooxanthella populations *in hospite*, the frequency of somatic mutations in these algal symbionts may be significant in terms of adaptive evolution. Selection on genotypes that differ physiologically (e.g., those that have undergone an advantageous mutation) has been shown to lead to extremely fast changes in relative abundances of those genotypes in *Chlorella* (Meyer et al. 2006). Finally, virtually nothing is known about the population structure and dynamics of *Symbiodinium*. To examine whether bleaching events represent bottlenecks for zooxanthella populations and whether thermally tolerant strains can spread across reef systems, population genetic approaches should be employed in future research.

6.7 Conclusions and Major Knowledge Gaps

- Zooxanthellae play an important role in determining the physiological performance of corals, but the relative contribution of the host versus symbiont to bleaching resistance in different coral–algal associations is still poorly understood
- Zooxanthellae exhibit much diversity within phylogenetic clades. Many of these intra-cladal variants ("species") may exhibit different physiological tolerances; the role that these may play in response to bleaching remains to be fully investigated
- Within our range of detection, many corals appear to harbour a single dominant clade. However, genetically distinct symbionts have been detected at lower abundance within coral colonies; and the role of these "cryptic" symbionts is still unknown
- Symbiont shuffling is an important mechanism by which some (but definitely not all) coral species can increase their thermal tolerance. On its own, however, this may be insufficient to cope with increasingly higher seawater temperatures as a result of global warming
- The adaptive potential of corals to climate change is still unknown

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Chapter 7
Bleaching and Mortality Thresholds: How Much is Too Much?

R. Berkelmans

7.1 Introduction

A considerable number of studies have investigated the link between coral bleaching events and environmental factors. Whilst localized bleaching events can have many causes (Dove and Hoegh-Guldberg 2006), widespread bleaching events have, almost without fail, been demonstrably linked to unusually warm temperatures often in conjunction with increased light. Prior to the 1990s, there was a paucity of representative instrumental temperature data to link with observations of mass coral bleaching (Chap. 3). However, temperatures beyond the envelope normally experienced by corals have always been implicated as the cause of mass bleaching. For example, as early as 1914 Alfred Mayer wrote:

"Thus on July 21–22, 1911, at Tortugas, Florida, after several hot, calm days, the shallow water over Bird Key Reef rose to 33° to 38°C and Dr L. R. Cary observed that large numbers of *Diadema, Octopus, Fissurella*, and other molluscs and small fishes were killed in considerable numbers over extensive areas, and the corals were injured even when not exposed to the air" (Mayer 1914).

Finding a suitable metric for temperature, light and other meteorological variables that adequately predicts bleaching and can be universally applied has proven much more challenging. In theory, a bleaching threshold for a particular coral species at a particular location is a function of absolute temperature, light and exposure time (Fitt et al. 2001). Ideally, it also incorporates possible additional stress factors such as salinity (Coles and Jokiel 1992), water quality (Marshall and Schuttenberg 2006) or mitigating factors such as water motion (Nakamura and van Woesik 2001; van Woesik and Koksal 2006). However, constructing and applying such a multivariate model for predicting impending bleaching events is highly problematic and impractical. The problems include the difficulty in establishing the model parameters for each species, the applicability of laboratory-derived values to real-world field conditions and the availability of representative real-time data for variables such as underwater light, water motion and water quality parameters. As a result, a more parsimonious approach needs to be considered. Published papers on bleaching thresholds and predictors are invariably empirically derived using correlations between bleaching events and environmental factors. The developed relations often involve

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multi-species coral assemblages, use a single parameter and simple metrics of readily available data, and are either location specific or "best-fit" approximations applied over large spatial scales (from tens to 1000s of kilometres). Consequently, "bleaching thresholds" have taken many different forms and are not easily applied to other locations, nor are they comparable between locations. Examples of the kinds of bleaching indices include satellite-derived sea surface temperature (SST) metrics such as monthly means (Goreau et al. 1993; Brown et al. 1996), anomalies above monthly means (e.g. "HotSpots" and "ReefTemp"; Goreau and Hayes 1994; Strong et al. 1997; Maynard et al. 2008; Chap. 4), "degree-heating-weeks" or "degree-heating-days" (Gleeson and Strong 1995; Maynard et al. 2008; Chap. 4) and maximum 3-day temperature (Berkelmans et al. 2004). For indices derived from in situ data, examples include maximum daily SST (Jones et al. 1997; Winter et al. 1998), monthly means (Podestá and Glynn 2001), weekly means and anomalies (Vargas-Ángel et al. 2001), degree-days (Podestá and Glynn 2001), days above certain temperatures (Winter et al. 1998), coefficient of variation of SST (Sammarco et al. 2006) and time–temperature curves (Berkelmans 2002a; Manzello et al. 2007). Thus, although highly diverse, each of these indices has merit for its own application driven by specific research questions, local conditions and responses, the spatial and temporal scale of interest and using the best locally available data.

The spatial and temporal scale of interest is an important factor in determining which metric to use as a bleaching threshold. "HotSpots" and "Degree-heating-weeks" are operational web-based products produced by NOAA at a global scale (http://www.osdpd.noaa.gov/PSB/EPS/SST/climohot.html; Chap. 4). One of the best features of these products is the "global view" of bleaching risk. The downside is that globally applied algorithms inherently suffer from error (i.e., false positive or negative bleaching predictions) at local/regional scales (e.g., McClanahan et al. 2007). Regionally applied algorithms for satellite-derived SSTs such as "ReefTemp" Maynard et al. 2008, which is specific for the Great Barrier Reef (GBR), should reduce error rates but this is as yet untested. On the other end of the spectrum, highly localized (reef-specific) bleaching indices such as time–temperature curves (Berkelmans 2002a) offer little spatial overview, but potentially highly accurate bleaching predictions. Because these are "calibrated" to local conditions and responses, they can potentially also be extended to defining mortality thresholds for selected coral taxa. Used together, the satellite- and in situ-derived products can offer both locally accurate bleaching and mortality predictions and wider spatial interpolation of likely thermal stress.

Time–temperature curves were first developed for 13 reefs on the GBR following the 1998 bleaching event (Berkelmans and Oliver 1999; Berkelmans 2002a). Since then there has been another GBR-wide bleaching event in early 2002 and a localized but intense bleaching event in early 2006, which affected the southern GBR (GBRMPA 2006). The purpose of this chapter is to:

- Evaluate the appropriateness of in situ temperature in modelling bleaching thresholds and determine what improvement in predictive capacity could be gained by incorporating solar radiation and other environmental data into a model, using Magnetic Island in the central GBR as a case study

- Review and evaluate the accuracy of the time-integrated bleaching thresholds for the GBR which were constructed after the 1998 bleaching event, with the benefit of an additional 7 years of SST data and in light of the 2002 and 2006 bleaching events
- construct mortality thresholds for coral taxa at specific sites which suffered high mortality (>50%) during the 1998, 2002 and 2006 bleaching events on the GBR

7.2 Methods

7.2.1 Statistical Modelling

The physiological response of corals to bleaching is, in large part, a function of the amount of light (photosynthetically active radiation, PAR; ultra violet, UV) received after high temperatures have damaged the carbon-fixing processes of the zooxanthellae (Jones et al. 1998). To determine the relative influence of solar and UV radiation, SST and a number of other potential weather variables in explaining past coral bleaching events at Magnetic Island, a statistical exploratory model was constructed using classification trees. Classification trees examine the effects of predictor variables one at a time on a categorical response variable (e.g., bleaching) using a hierarchical system of splits, each one resulting in more homogeneous groups (De'ath and Fabricius 2000). Trees are an alternative to traditional statistical methods used with categorical response variables such as logistic regression and discriminant analysis and are often preferred because they can be used with a variety of data types, they can handle missing data and have the ability to uncover patterns and associations missed by traditional linear models (De'ath and Fabricius 2000). The categorical regression trees (CRT) exhaustive search algorithm of computing univariate splits was used since it deals with missing data better than other algorithms by using surrogates (Breiman et al. 1984). A 10-fold cross-validation was performed on the final tree model with a learning data set to evaluate the robustness of the model with larger data sets. Statistical analyses were performed using SPSS software ver. 15.0.

The onset and intensification (if these occurred in separate months) of bleaching (dependent variable) were tested against 17 potential explanatory variables. These included monthly mean, minimum and maximum SST (calculated from daily averages), total monthly global radiation (measured horizontal and 19° off horizontal – the angle of maximum quantum exposure for Magnetic Island), total monthly UV-A radiation, maximum and minimum monthly air temperature, mean monthly relative humidity and dew point (9 a.m. and 9 p.m.), monthly total rainfall and evaporation, and monthly total wet and sunshine hours. Data covered the summer months from December to March between 1991 and 2004 and included four bleaching events: 1992, 1994, 1998 and 2002. SST data were obtained from SeaTemps, a long-term sea temperature monitoring program on the GBR (www.aims.gov.au/pages/facilities/adc/seatemps.html). Weather data were obtained from

Allunga Exposure Laboratories (global and UV radiation, rain, wet hours), a materials testing facility ~20 km south of Magnetic Island and the Australian Bureau of Meteorology (air temperature, dew point, humidity, evaporation, sun hours) at the Townsville airport, ~8 km south of Magnetic Island. The efficacy of using weather data 20 km away from the study site was tested by comparing two related variables: monthly global radiation (measured at Allunga Exposure Laboratories) and PAR (measured at the study site) for the period December 1999 to December 2005 when overlapping data existed. The two variables were significantly correlated ($r^2 = 0.62$, $n = 73$) indicating that the Allunga radiation data are likely to be reasonably representative of Magnetic Island.

7.2.2 Bleaching Thresholds

Bleaching thresholds were previously constructed for 13 locations on the GBR using in situ water temperature records and concurrent observations of coral bleaching during the anomalously warm summer of 1998 (Berkelmans and Oliver 1999; Berkelmans 2002a). Bleaching thresholds were re-constructed using the methodology outlined in Berkelmans (2002a, b) with a temperature record extended by 7 years and observations of coral bleaching from two more bleaching events, one that was GBR-wide in 2002 (Berkelmans et al. 2004) and another in 2006 that predominantly affected reefs in the southern GBR (GBRMPA 2006). For two of the original 13 locations (Wallace Islet and Norman Reef), there was a gap in the temperature record during the 2002 bleaching event and these sites were omitted from the analysis. Agincourt 3 Reef (~51 km north of Norman Reef) was substituted in place of Norman Reef since its temperature record was complete and, although it suffered no bleaching in 1998, it bleached extensively in 2002. The bleaching period for which time–temperature curves were calculated covered the warmest period during and on the shoulder of each austral summer from 1 November to 30 April.

The accuracy of the bleaching curves was assessed in two ways. First, the performance of the Magnetic Island curve was evaluated in predicting the 2002 bleaching event. Seven visits to Magnetic Island were made during the 2001/02 summer at roughly fortnightly intervals and for each visit a cumulative exposures curve was calculated allowing the onset and development of bleaching and the associated thermal conditions to be assessed in a step-wise fashion. During the field visits, bleaching was assessed by rapid visual surveys with the severity of bleaching estimated as a percentage of coral cover white on upper surfaces in the following bins: 0–1% (no bleaching), 1–10% (mild bleaching), 10–30% (heavy bleaching), 30–60% (very heavy bleaching) and >60% (extreme bleaching). Second, the performance of all original bleaching curves was evaluated in terms of their ability to accurately separate bleaching from non-bleaching years since 1998. Bleaching was assessed either by field or aerial surveys as detailed above and in Berkelmans et al. (2004).

7.2.3 *Mortality Thresholds*

Mortality thresholds were constructed in a similar manner to the bleaching threshold curves. During the 1998, 2002 and 2006 bleaching events, a number of locations suffered high mortality (>50%) of sensitive (and locally dominant) coral taxa. These were mostly members of the pocilloporid and acroporid families. Table 7.1 shows the locations and how much mortality was experienced in each species group. Mortality curves, based on 50% mortality (T_{L50}), were estimated by linear interpolation between the bleaching threshold curve and the time–temperature curve for the summer in which significant mortality took place. For cases with 100% mortality, the T_{L50} curve (for 50% mortality) was assumed to lie half-way between the bleaching threshold (which in theory should result in little or no mortality) and the curve which resulted in 100% mortality. This may overestimate the T_{L50} curve, particularly if the conditions causing 100% mortality were much warmer and sustained much longer than the bleaching threshold. In other words, 100% mortality occurred sooner than the warmest conditions experienced but no direct observations were taken at the time. For cases where 50% mortality resulted, no interpolation was required: the T_{L50} curve was the final time–temperature curve for the summer. For cases with mortality levels between 50% and 100%, the position of the T_{L50} curve was scaled accordingly. As with the bleaching curves, the number of days' exposure does not necessarily represent consecutive days. For the sake of simplicity it was assumed that damage to coral tissue continues from where it left off between one hot period and the next.

7.3 Results

7.3.1 *Is Temperature Appropriate for Modelling Bleaching Thresholds?*

The results of the classification tree show that sea temperature is clearly the most important variable explaining bleaching events. Of the 17 potential variables investigated, only six contributed significantly to the model and, of these, the top three explanatory variables were maximum, average and minimum SST (Fig. 7.1a). Total monthly UV radiation rated less than 18% of the importance of maximum monthly SST to the model and total monthly sun-hours less than 13%. Total global radiation did not contribute significantly to the model. Only one split in the decision tree was required by the final model to accurately predict the seven cases for the onset or continued development of bleaching, being January and February of 1992, January of 1994 and January and February of both 1998 and 2002 (Fig. 7.1b). In all cases this split was on the basis of a maximum monthly temperature >31.46°C. The risk of misclassification, or the probability that these data could be classified by chance alone, was low at 1.3%, as indicated by the cross-validation error (Table 7.2).

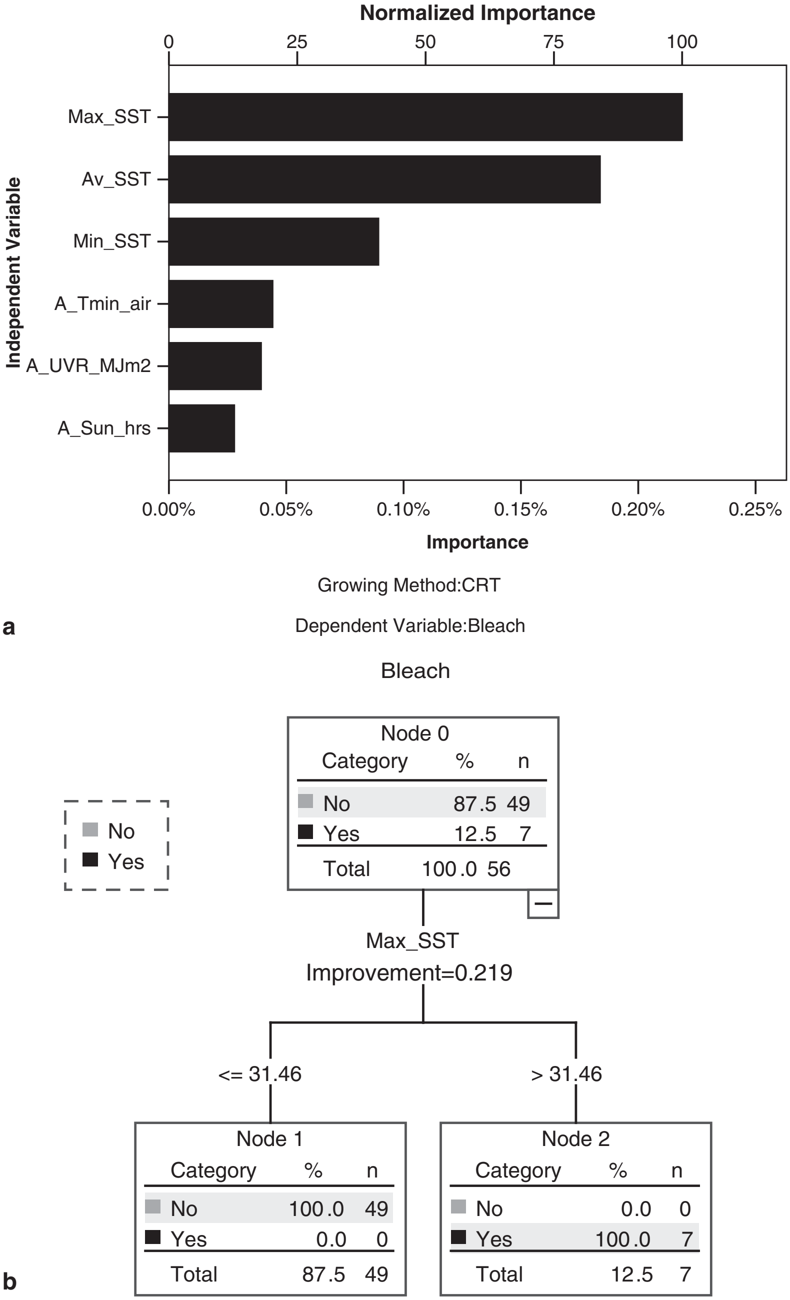

Fig. 7.1 Variables and their relative significance to a classification tree model in: **a** predicting bleaching at Magnetic Island between 1990 and 2004 and **b** the results of the final model classification

Thus, temperature is by far the most important parameter in predicting bleaching events and hence temperature-based models remain an appropriate foundation for a bleaching alert system.

7.3.2 Bleaching Thresholds

A time series evaluation of the bleaching threshold at Magnetic Island first published after the 1998 bleaching event on the GBR (Berkelmans 2002a) clearly shows that it accurately predicted the onset of the 2002 bleaching event (Fig. 7.2). On 21 December 2001, no bleaching was evident, but two weeks later on 7 January the first signs of bleaching were evident with upper surfaces appearing pale to white on staghorn and plating *Acropora* spp. and margins of encrusting *Montipora* colonies. At that time, the time–temperature curve had just exceeded the predicted bleaching curve at temperatures >30.8°C (Fig. 7.2). Over the ensuing weeks the bleaching spread and intensified; and by 8 February ~30% of the hard corals on the reef crest were bleached white with another 50% pale (Berkelmans et al. 2004). By this time the bleaching threshold had been exceeded by a considerable margin. Maximum temperatures and extent and intensity of bleaching were experienced at the time of the visit on 1 March 2002. After this, temperatures declined and early signs of zooxanthella population recovery were evident in individual colonies three weeks later. The Magnetic Island bleaching threshold, therefore, worked well in predicting bleaching at the same site four years after the 1998 bleaching event.

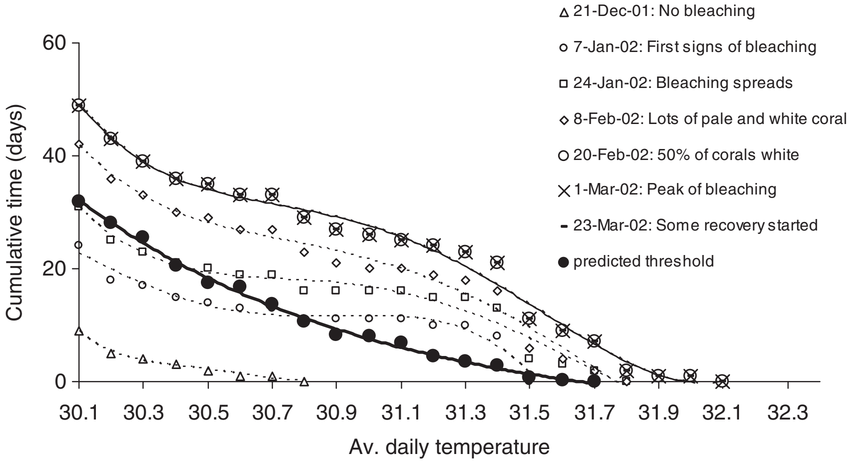

Fig. 7.2 Time-series assessment of the state of bleaching at Magnetic Island during the 2002 bleaching summer with a step-wise view of the time–temperature curve during each visit

A review of the time-integrated bleaching thresholds for 12 of the 13 reefs in Berkelmans (2002a) also shows that, for the majority of these locations, the original bleaching threshold curves still accurately separated the bleaching years from the non-bleaching years (Fig. 7.3). For all but three locations (Daintree coast, Orpheus Island, Magnetic Island) the 2002 curve exceeded the curve of the 1998 bleaching year. Of the three locations that were cooler in 2002 than in 1998, both the Daintree coast and Orpheus Island did not show widespread bleaching (Berkelmans et al. 2004; T. Ayling, personal communication). The 2002 curve for Orpheus Island was below the bleaching threshold as was the Daintree coast at temperatures above 30°C (Fig. 7.3b, f). The 2002 curve at Magnetic Island was below the 1998 curve and the bleaching intensity was also lower (Berkelmans et al. 2004).

The 2006 summer was generally warm for many reefs in the northern and central GBR, but widespread bleaching only occurred in the southern GBR, with inshore reefs most affected, especially in the Keppel Island group (Keppels). Approximately 87% of reef flat and 98% of reef slope coral bleached in this area with 61% and 78% of these habitats (respectively) bleached white (Berkelmans and Jones, in prep.). The 2006 curve for the Keppels clearly shows the intensity of this event, both in terms of the record temperatures experienced and the duration of hot conditions (Fig. 7.3k).

A few locations showed anomalies with time–temperature curves exceeding the bleaching thresholds, but no bleaching reported. For example, conditions at Kelso Reef in 2005 and 2006 greatly exceeded both the predicted bleaching threshold for this location and the 2002 curve (Fig. 7.3a), but no reports of bleaching were received. Access to this location was difficult since a daily tourist operation to this reef stopped. A visit to Kelso Reef in July 2006 showed that >80% of the coral on the reef flat and upper reef slope were dead but since this reef also had an outbreak of crown of thorn starfish over several years, the cause of the mortality may only be in part bleaching-related. Three more sites had their bleaching thresholds adjusted slightly in light of warmer non-bleaching years occurring above the predicted threshold, but still below the coolest bleaching year. These include the Daintree coast, which had its bleaching threshold curve truncated at lower temperatures and slightly raised, as well as Orpheus Island and Halfway Island. At Halfway Island, in particular, the estimated position of the 1998 curve was a long way above the coolest non-bleaching year at that time. The non-bleaching summer of 2004 has since enabled the bleaching threshold to be better estimated. These are considered minor refinements of the estimated position of the bleaching threshold curve in light of more and better data.

More perplexing, however, are four locations where the curve for the 2004 summer exceeded the curves for the known bleaching year of 1998 and yet did not bleach. These locations included Myrmidon Reef, Chicken Reef, Magnetic Island and Daydream Island (Fig. 7.3e, h–j). Possible reasons for this are examined in Sect. 7.4. On balance, the original bleaching curves performed well during the 2002 bleaching event, but subsequent repeated warm summers without bleaching may require a re-interpretation of bleaching thresholds at some sites.

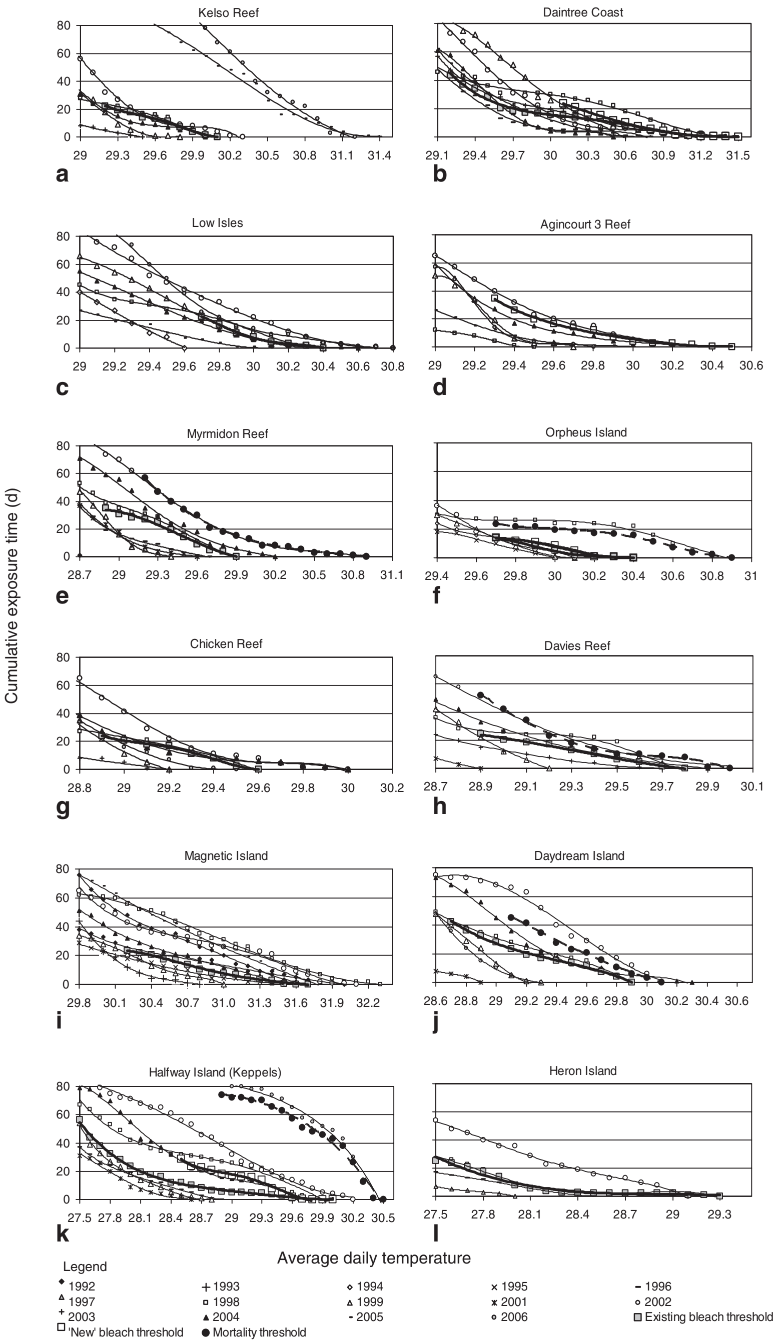

Fig. 7.3 Time–temperature curves for the bleaching summers and three warmest non-bleaching summers for 12 locations on the Great Barrier Reef (**a–l**), including the estimated position of bleaching curves and, where available, mortality curves

7.3.3 Mortality Thresholds

High mortality (>50%) among sensitive hard coral species at six locations in 1998, 2002 and 2006 gives rise to the possibility of estimating a T_{L50} time–temperature curve, effectively a species-specific mortality curve. These locations include Orpheus Island, which suffered high mortality in 1998, Myrmidon Reef, Davies Reef and Stone Island, which suffered high mortality in 2002, and the Keppels, which suffered high mortality in 2006 (Table 7.1). The position of these curves in relation to the warmest year and the bleaching threshold is shown in Fig. 7.3. Re-plotting these curves in relation to their respective bleaching thresholds revealed some interesting patterns. First, when the T_{L50} curves were re-calculated as a time-offset from the bleaching threshold (i.e., days above bleaching threshold), there was no consistent relationship evident (Fig. 7.4a). However, when they were re-calculated as a temperature offset from the bleaching threshold (i.e., °C above bleaching threshold), there was a suggestion of a linear relationship (Fig. 7.4b). With the exception of the Keppels, the T_{L50} curves for the taxa in question were all less than 1°C above the bleaching threshold, many only <0.5°C above the bleaching threshold. The plating *Acropora* species on the reef flat in the Davies Reef lagoon and the pocilloporid, *Seriatopora hystrix*, at Daydream Island in particular had T_{L50} curves

Table 7.1 Locations on the Great Barrier Reef which suffered high (≥50%) mortality as a result of bleaching

Location	Latitude (° S)	Longitude (° E)	Year	Depth range (m)	% mortality	Species group	Reference
Myrmidon Rf	18.3	147.4	2002	0–2	50	Arborescent *Acropora* spp.	GBRMPA 2002
Orpheus Is	18.6	146.5	1998	0–5	70	Staghorn, plate and arborescent *Acropora* spp.	Berkelmans 2001
Orpheus Is	18.6	146.5	1998	0–5	>99	*Millepora tenella* (fire coral) and *A. pulchra*	Shackeroff 1999
Davies Rf	18.8	147.6	2002	0–2	50	Arborescent and plate *Acropora* spp.	Berkelmans, unpublished survey data
Stone Is, Bowen			2002	3–6	80	Staghorn and arborescent *Acropora* spp.	GBRMPA 2002
Stone Is, Bowen			2002	0–4	50	*Millepora tenella* (fire coral)	GBRMPA 2002
Daydream Is	20.3	148.8	2002	8–12	100	*Seriatopora hystrix*	GBRMPA 2002
Halfway Is, Keppels	23.2	151.0	2006	0–2	57	*A. millepora* and staghorn *Acropora* spp.	Berkelmans and Jones, unpublished survey data

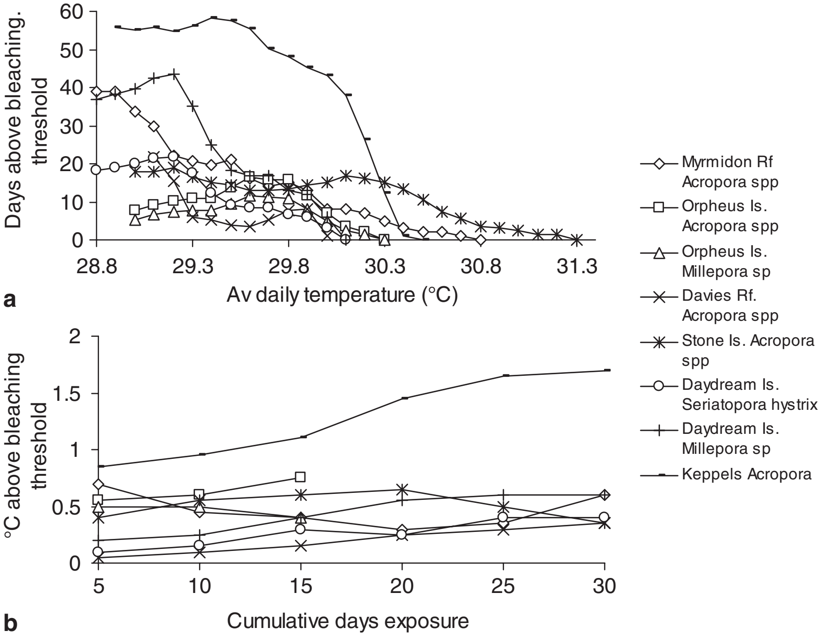

Fig. 7.4 Relationship of mortality curves to: **a** "days above bleaching threshold" and **b** "temperature above bleaching threshold"

just 0.2–0.4°C above their respective bleaching thresholds. In contrast, the corymbose and staghorn *Acropora* species in the Keppels were considerably more resistant to dying after bleaching. Nevertheless, their T_{L50} curve was still <2°C higher than the bleaching threshold (Fig. 7.4b). The mortality curves for these locations and species groups were, therefore, offset from the bleaching threshold curve on the temperature axis, but were still remarkably close to the bleaching thresholds.

7.4 Discussion

Coral reef managers have come to rely on spatially extensive bleaching alert systems such as "HotSpots" (Goreau and Hayes 1994; Gleeson and Strong 1995; Chap. 4) and locally specific systems such as the Coral Reef Early Warning System (Hendee et al. 2001; Berkelmans et al. 2002) and time-integrated bleaching thresholds (Berkelmans 2002a) for valuable information on the build-up of stressful conditions to hard corals, the dominant builders of reefs. Reef managers value such warning systems because they allow them to be the source of timely and credible information about bleaching risk for decision makers, stakeholders and the media (Marshall and Schuttenberg 2006). It also allows for early management responses to be put in place, including the instigation of formal monitoring programs to assess

Table 7.2 Specification criteria and calculated results for a classification trees model which evaluates the contribution of various environmental variables in predicting bleaching at Magnetic Island in 1992, 1994, 1998 and 2002. The summary of the model results shows that only six of the original 17 variables contributed significantly to the model

Model specifications	
Growing method	CRT
Dependent variable	Bleach (yes/no)
Independent variables	BoM_Sun_hrs, Av_SST, Min_SST, Max_SST, Tmax_air, Tmin_air, Dew_9am, Dew_9pm, RHumidity_9am, RHumidity_9pm, Rain, Evaporation, Wet_hrs, A_Sun_hrs, GlobalRad_hor, GlobRad_19deg, UVR
Model results	
Independent variables included in model	Max_SST, Av_SST, Min_SST, UVR, Tmin_air, A_Sun_hrs
Classification error	0.000
Estimated risk (cross-validation error)	0.013
Standard error of risk	0.025

the extent and severity of bleaching and, where appropriate, take local action to ameliorate the risk of further damage to reefs from such activities as dredging, coastal development and point-source pollution. The time-integrated bleaching thresholds have been in use since 2000 as one of the monitoring tools for the Great Barrier Reef Marine Park Authority. The results of this review show they performed well in the time leading up to and including the 2002 bleaching event, but also that there were some inconsistencies in recent years at some sites. The summer of 2004 in particular exceeded the bleaching threshold as well as the 1998 curve at Daydream Island, Myrmidon Reef and Chicken Reef in the central GBR, but, apart from a few pale colonies, no widespread bleaching occurred. Similarly, the 2005 summer at Magnetic Island exceeded the bleaching threshold and the conditions during the 1992 and 1994 bleaching events and was almost equivalent to the 2002 bleaching event, but, apart from pale tops on a few *Porites* bommies, no bleaching was evident. One plausible explanation is that the bleaching curves are too simplistic in modelling the bleaching thresholds because they do not take into consideration any possible recovery by the corals between intra-seasonal heat waves. This is unlikely since temperatures were well above the mean at these sites for almost the entire 2004 summer and the week-to-week fluctuations were smaller than in the 1998 summer and equivalent to the 2002 summer (data not shown). Another plausible explanation is that light levels, UV or other environmental factors were sufficiently lower in the non-bleaching 2004/5 summers compared with the bleaching summers and effectively prevented bleaching. Again, this is unlikely because global radiation near Magnetic Island was higher during the critical 2005 summer months of January/February (total = 1403 MJ/m^2) than the same period during the bleaching summer of 2002 (total = 1301 MJ/m^2) as was total sun hours (546 h vs 533 h, respectively). Total UV-A and B radiation were marginally lower (82.2 MJ/m^2 vs

86.4 MJ/m^2, respectively), but this difference was not statistically significant [$t(2) = 1.12$, $df = 116$, $P = 0.27$]. The results of the statistical analysis at Magnetic Island also show that light, UV and other environmental factors at best only correlate weakly with the bleaching events and were nowhere near as important as temperature in predicting bleaching at this site. A more likely explanation is that corals at Magnetic Island, Daydream Island, Myrmidon and Chicken Reef have undergone some acclimatization after the 2002 bleaching event, possibly through shuffling zooxanthellae types within the coral tissue (Baker et al. 2004; Rowan 2004; Berkelmans and van Oppen 2006) or in part through selection of more thermally-resistant coral and symbiont genotypes among surviving populations.

Since it is likely that a number of reefs have effectively achieved a "step-wise" increase in thermal tolerance since 2002, the next challenge is to adjust the bleaching threshold to a new level. For those sites which survived the extra warm summers without bleaching, this adjustment can be made on the empirical evidence. The question then becomes how far can these thresholds be moved up and how will other locations respond to the next warm summer? If the mechanism of acclimatization is by zooxanthellae shuffling (Baker et al. 2004; Buddemeier et al. 2004), then it is likely that there is a limit of around 1.0–1.5°C by which the bleaching threshold can be increased (Berkelmans and van Oppen 2006). If there is a gradual shifting of community zooxanthella types over multiple bleaching years or warm events, there may need to be an equally gradual increment in the empirical bleaching thresholds. Early warning systems based on these bleaching thresholds may show some false positive warnings as reef communities acclimatize before their increased thermal limits are quantified. This may decrease the reliability of time-integrated bleaching thresholds and other temperature-based early warning systems for some time until any shift can be adequately taken into account in a refined model. These adjustments and improvements in early warning systems are inevitable as our understanding of thermal stress and physiological responses of corals improves and advances in technology allows relevant parameters to be better monitored and interpreted. In the meantime a few false positive warnings may be something that reef managers would rather endure than their counterpart, a false negative.

The results of the classification tree analysis clearly show that temperature is the most important variable in explaining past bleaching events at Magnetic Island and that maximum monthly SST (based on daily averages) was the most important metric. UV (A and B) radiation, sunshine hours and other variables contributed either a small amount or not at all to the final model. This is not to say that UV and light are not important in bleaching, only that the field evidence does not support these factors as explanatory variables for the purpose of bleaching predictions at this site. Unfortunately, lack of global radiation and UVR data preclude similar analyses at other GBR sites. Given the importance of light in the bleaching response of corals as demonstrated experimentally (e.g., Jones et al. 1998) and evidenced in field situations (e.g., Oliver 1985), it is important that more data sets on light regimes influencing coral reefs are collected to better understand the role of light in field conditions and further evaluate its potential in refining early warning systems.

The T_{L50} curves presented here are the first attempt to quantify mortality thresholds for corals under field conditions. A great deal of experimental work has been done to determine the upper thermal limits for a range of corals (e.g., Mayer 1914; Yonge and Nicholls 1931; Coles et al. 1976; Marcus and Thorhaug 1981; Glynn and D'Croz 1990; Berkelmans and Willis 1999; Ulstrup et al. 2006). However, it is extremely difficult to replicate field conditions in controlled laboratory experiments and hence results are hard to apply in early warning systems or scenario modelling. Notwithstanding the fact that there may be some variation in the bleaching thresholds due to acclimatization and, for the same reason, probably also in the mortality thresholds, these T_{L50} curves provide a useful starting point for early warning systems and modelling future effects of climate change on coral reefs (e.g., Wooldridge et al. 2006; Chap. 10). The proximity of the T_{L50} curves to the bleaching threshold curves is clear evidence that there is a fine line between bleached corals recovering or dying in the communities examined here. The fact that all bar one of the mortality thresholds were <1°C and many only <0.5°C above the bleaching threshold illustrates the small quantum of increased temperature required to turn the next big bleaching event into an ecological disaster the scale of which has not been seen on the GBR before, but has already been experienced in the Indian Ocean in 1998 (Wilkinson et al. 1999; Goreau et al. 2000). Keppel Island reefs in the southern GBR were remarkably resilient in comparison with other reefs which suffered high mortality with a mortality threshold 0.9–1.7°C higher than their bleaching threshold. These communities are dominated by the same corymbose and staghorn *Acropora* species which died <0.5°C above their respective bleaching thresholds at Davies Reef and Stone Island in the central GBR. A possible explanation for the variation in mortality thresholds is an increase in resilience by Keppel Island corals through switching to heterotrophic feeding whilst bleached (Grottoli et al. 2006). This notion is supported by long-term chlorophyll monitoring data which shows that chlorophyll *a* in the Keppel Island area is up to 3.5 times higher than in the central offshore GBR (near Davies Reef) and twice the concentration of the central inshore GBR (near Stone Island, Brodie et al. 2007). It should be remembered that these mortality curves only relate to the most sensitive coral species and are not representative of scleractinian corals generally. Nevertheless, the sensitive species including most members of the Acroporidae and Pocilloporidae families (Marshall and Baird 2000; Loya et al. 2001) on Indo Pacific reefs generally also make up the dominant coral cover, contribute most to reef building and provide the three-dimensional complexity on which fish and invertebrates rely for habitat and shelter (e.g., Done 1982; Bell and Galzin 1984). The near-linear relationship of temperature above bleaching threshold with exposure time suggests that the mortality thresholds simply represent a lateral shift in the bleaching thresholds outwards along the temperature axis. This makes mortality thresholds an easy metric to work with and apply in scenario modelling.

In conclusion, time-integrated bleaching thresholds remain an appropriate and useful method for modelling thermal stress in corals. There is a high likelihood that bleaching thresholds have increased at a number of locations on the GBR since the major 2002 bleaching event, potentially as a result of acclimatization. Whilst these increases may be limited in terms of absolute temperature, there is no doubt that they are of great ecological significance. Mortality thresholds developed for a limited number of reefs based on time–temperature curves for 50% mortality of specific taxa indicate a very narrow margin between the bleaching and mortality thresholds for sensitive species.

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Chapter 8
Consequences of Coral Bleaching for Sessile Reef Organisms

T.R. McClanahan, E. Weil, J. Cortés, A.H. Baird, and M. Ateweberhan

8.1 Introduction

Sessile organisms, such as corals and erect algae, provide a complex architecture on coral reefs that is important for capturing light and utilizing dissolved gases and plankton to maintain high primary production (Enriques et al. 2005; Finelli et al. 2006). These sessile organisms also provide refuge and shelter for many mobile animals (Chap. 9). In addition, sessile algae and the coral–algal symbiosis determine carbon fixation and its pathways into organic and inorganic forms. These are the basis for the energy that supports the ecosystem and deposits the calcium carbonate skeletons that create the reef. Bleaching is the loss of the coral symbiont or plant and animal pigments and often leads to a loss of energy or the partial mortality of the affected organism and, when severe, whole-colony mortality. Consequently, the effect of coral bleaching on this group of organisms has major consequences for reef productivity, reef growth, and biodiversity. This chapter reviews studies conducted on coral reefs throughout the world to document the many and varied effects of bleaching on sessile organisms.

Mass mortality events on coral reefs due to large-scale environmental disturbances have been recorded since the 1870s. From 1876 to 1979, 63 mass coral mortalities were reported (Glynn 1993; Chap. 3). During this period, only three minor coral bleaching events were registered. Since 1979, an increasing trend in bleaching has continued and bleaching is now considered among the top three threats to coral reefs by most coral reef biologists (McClanahan et al. 2008b). The ultimate fate of coral reefs remains a contentious and important debate among coral reef scientists (e.g. Buddemeier et al. 2004).

8.2 Affected Taxa

Understanding bleaching and its impact on sessile reef organisms is not an easy task. Bleaching events are highly variable and responses differ greatly among species and even among individuals of the same species (Fig. 8.1; Glynn 1988;

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Fig. 8.1 The 2005 bleaching event in the Caribbean. View of bleached reefs in Puerto Rico (**a**, **b**) and Grenada (**c**, **d**). Acroporids were hit hard in most shallow habitats (**e**) in Puerto Rico. Side-by-side bleached and unbleached colonies of *M. faveolata* raise questions about "resistant" zooxanthellae strains (**f**). Significant numbers of colonies of bleaching-resistant genera such as *Mycetophyllia* were completely white (**g**). Many *Montastraea faveolata* colonies with on-going yellow band disease bleached completely increasing tissue mortality rates (**h**). Other colonies with other diseases such as dark spots in *Stephanocoenia intersepta* (**i**) did not show major changes. Many other zooxanthellated reef organisms like crustose and branching octocorals (**j**, **k**), zoanthids and hydrocorals (**k**) bleached completely. Significant bleaching-associated mortalities were observed in acroporid and agariciid corals (**l**, **m**), crustose octocorals (**j**), zoanthids, and the hydrocoral *Millepora* (**n**)

Lang et al. 1988, 1992; Williams and Bunkley-Williams 1990; Hoegh-Guldberg 1999). Organisms most affected by bleaching include the hydrocorals (e.g. *Millepora* spp.) and scleractinians; however, most cnidarians, including sea anemones, antipatharians, and corallimorpharians, are affected by bleaching. Indeed, most taxa containing symbiotic algae, such as sponges and bivalves, are affected. For example, during the 2005 bleaching event in the Caribbean 60 species of scleractinian corals, 34 octocorals, four hydrocorals, four zoanthids, four anemones, and six sponges bleached (Table 8.1, Fig. 8.1). Even some plants, such as the green alga *Halimeda*, lose pigments in response to thermal stress. Despite the taxonomic extent of bleaching, scleractinian corals have attracted most research attention and are, therefore, the focus of this chapter.

8.3 Immediate Responses

Bleaching causes a reduction in the translocation of photosynthetic products to the host cells and is, therefore, expected to have an immediate impact on individuals, which will cascade to affect populations, communities, and ecosystems (Table 8.2).

Table 8.1 List of scleractinian, hydrozoan, zoanthid, actinarian and corallimorpharian species reported/observed bleached during particular bleaching events in the Caribbean. The susceptibility index is drawn from these reports and personal observations since the 1988 bleaching event. *Susceptibility*: *** highly susceptible, bleaches frequently; ** moderate, bleaches only during significant bleaching events; * resistant, only bleaches during extreme bleaching events. *Mortality*: any reported/observed mortality in any of the past bleaching events (compiled by E. Weil). Sources: Lasker et al. (1984), Williams and Bunkley-Williams (1989, 1990), McField (1999), Weil et al. (2003), Pinzón and Weil (2008)

Species	1983	1987	1993	1995	1998	2003	2005	Susceptibility	Mortality
A. palmata	x	x	x	x	x	x	x	***	x
A. cervicornis	x	x	x	x	x	x	x	***	x
A. prolifera		x		x	x		x	***	x
S. intersepta		x	x		x	x	x	***	x
S. sidereal		x	x	x	x	x	x	***	x
S. radians		x			x		x	**	
S. bournoni		x			x		x		
M. decactis		x					x	*	
M. formosa							x	*	
M. auretenra[a]		x					x	**	x
M. pharensis							x	*	
M. senaria							x	*	
U. agaricities[b]		x		x	x		x	***	x
U. purpurea		x		x	x		x	**	x
U. humilis		x		x	x		x	**	x
U. danae		x		x	x	x	x	***	x
U. carinata		x			x	x	x	***	

(continued)

Table 8.1 (continued)

Species	1983	1987	1993	1995	1998	2003	2005	Susceptibility	Mortality
U. tenuifolia		x			x		x	***	x
A. lamarcki		x			x		x	**	x
A. fragilis		x			x		x	**	
A. pumila		x					x	**	
A. grahamae		x			x		x	*	
A. undata		x					x	*	
H. cucullata		x		x	x	x	x	***	x
M. annularis^{c}		x	x	x	x	x	x	***	x
M. faveolata		x	x	x	x	x	x	***	x
M. franksi		x		x	x	x	x	**	x
M. cavernosa		x		x	x		x	*	X
C. natans^{d}		x		x	x	x	x	**	
*C.amaranthu*s				x			x	**	
D. strigosa		x	x		x	x	x	*	x
D. labyrinthiformis		x	x		x	x	x	*	x
D. clivosa		x			x	x	x	*	x
F. fragum		x	x		x	x	x	**	x
M. aerolata		x			x		x	*	
C. arbuscula					x		x	*	
M. meandrites		x		x	x		x	**	x
M. danae					x		x	*	
Meandrina n.sp.^{e}		x			x		x	**	x
D. stochesii		x					x	**	
D. stellaris							x	*	
D. cylindrus		x		x	x		x	***	x
P. astreoides		x	x	x	x	x	x	***	x
P. colonensis							x	*	
P. branneri		x					x	*	
P. porites		x			x		x	**	x
P. furcata		x					x	**	x
P. divaricata		x		x		x	x	*	
M. angulosa							x	*	x
M. ferox		x			x		x	*	x
M. aliciae		x					x	*	x
M. lamarckiana					x		x	*	x
M. danaana			x		x	x	x	*	x
M. resii			x	x	x	x	x	*	
S. lacera		x					x	*	
S. cubensis		x					x	*	x
I. sinuosa		x			x		x	*	
I. rigida					x		x	*	
E. fastigiata		x			x	x	x	**	x
O. diffusa		x			x		x	**	x
O. varicose							x	**	
O. valeciennesi					x		x	*	
Hydrozoa									

(continued)

Table 8.1 (continued)

Species	1983	1987	1993	1995	1998	2003	2005	Susceptibility	Mortality
M. alcicornis		x	x	x	x	x	x	***	x
M. complanata		x	x	x	x	x	x	***	x
M. squarrosa		x			x		x	**	x
M. striata					x		x	**	?
S. roseous		x			x		x	**	x
Actinaria									
C. gigantea		x			x		x	**	
B. annulata		x			x		x	*	
L. danae		x					x	*	
P. crucifer		x						*	
S. elianthus		x					x	*	
Zoanthids									
P. caribaeorum		x		x	x	x	x	***	x
Z. sociatus		x			x		x	**	
Corallimorpharia									
R. sanctithomas		x						*	
R. floridea		x						*	

[a] *M. aureterna* (Locke et al. 2007) is the former *M. mirabilis*.

[b] *U. agaricites* might include all the taxa in the *U. agaricites* species complex.

[c] *M. annularis* includes the other two species (*M. faveolata* and *M. franksi*) in early reports.

[d] *C. natans* includes *C. breviserialis*.

[e] *Meandrina* n.sp. is a new species formerly confused with *M. meandrites*.

Table 8.2 Potential effects of bleaching

Reduction/interruption of metabolic processes in the host
Significant reduction in translocation of the photosynthetic products
Reduction in growth rates
Reduction in reproductive output – reduction in recruitment/survivorship of larvae
Reduction in mucus production
Reduction in competitive abilities
Reduction in heterotrophic feeding activities
Reduced capacity to regenerate tissue
Increased susceptibility to diseases/stress
Partial/total mortality of the colony
Changes in the structure and functioning of population and reef communities
Reduction in live cover
Reduction/increase in diversity
Phase shifts to different group/species community composition

Zooxanthellae have been estimated to provide 30% of the total nitrogen and 91% of the carbon needs of the coral host (Bythell 1988). Changes in biochemical composition of coral tissue following bleaching include reductions in protein, lipid, mycosporine-like amino acids, and carotenoid concentrations (Michalek-Wagner and Willis 2001a). Bleaching reduces the lipid content of coral tissue, in particular wax esters, and the effect is greater in branching than massive growth forms (Yamashiro et al. 2005). Bleached colonies contain significantly lower lipid and total fatty acid content (as well as lower relative amounts of polyunsaturated fatty acids and higher relative amounts of saturated fatty acids) than healthy and partially bleached corals. This can have consequences for many biological functions (Bachok et al. 2006).

Bleaching and subsequent mortality is also often habitat-specific. For example, mortality is typically lower at greater depth (Brown et al. 1996), in turbid habitats (Marshall and Baird 2000), and in lagoons compared with reef edges (Sheppard 1999). Bleaching and subsequent mortality may also be influenced by the thermal history of sites, which are influenced by habitat (Marshall and Baird 2000; McClanahan et al. 2007a) and a colony's response may be shaped by previous experience of stress (Brown et al. 2000). In general, corals that have survived a previous bleaching event are less prone to subsequent bleaching events for reasons that are not always clear and are still keenly debated (Baker 2003; Baker et al. 2004; Chap. 7).

Bleaching at the assemblage level can vary at many spatial scales. For example, on the Great Barrier Reef (GBR), inshore reefs were more affected than offshore reefs in both the 1998 and 2002 events (Berkelmans et al. 2004), while the opposite was the pattern in the Eastern Pacific (Glynn et al. 2001). Reefs on the GBR also bleached in clusters on a scale of tens of kilometers, which was attributed to local weather patterns, oceanographic conditions, or both (Berkelmans et al. 2004). Spatial variation in assemblage response has also been linked to the taxonomic composition of reef sites, with sites dominated by susceptible species more likely to bleach (Marshall and Baird 2000). Studies of a large-scale bleaching event in the western Indian Ocean in 2005 estimated that half of the bleaching response was attributable to the initial species composition of coral communities (McClanahan et al. 2007a).

Environmental factors that reduce the effects of the stressful conditions or create conditions that promote acclimation to extreme temperatures, irradiation and UV levels are expected to minimize the bleaching impacts. In a recent analysis of SSTs in East Africa, McClanahan et al. (2007a) showed that long-term temperature variability plays a major role in buffering the effects of anomalous increases and thus lowering the heating of the surrounding water. Locations in northern Kenya and southern Somalia that have their temperatures distributed narrowly around the mean have higher degree heating weeks than areas where SSTs had flat distributions (Tanzania, Comoros; Fig. 8.2). Many sites around the central Indian Ocean, such as Lakshadweep, Sri Lanka, Maldives, Chagos, and Seychelles, that suffered higher mortalities in 1998 have their SSTs more narrowly distributed around the mean.

Work in the central Indo-Pacific highlighted important differences in the patterns of mortality among the studied species (Brown 1997; Baird and Marshall 2002). For example, at Orpheus Island, GBR, following the thermal anomaly in 1998 all colonies of *Acropora hyacinthus* and *A. gemmifera* were bleached, with 70–80% whole-colony mortality less than five weeks after the initial bleaching reports. In contrast, no colonies of *Coeloseris mayeri* and *Symphyllia radians* were bleached (Baird and Marshall 1998). These differential susceptibilities are generally consistent among taxa across the Indo-Pacific (McClanahan et al. 2004a). However, it is less clear whether this

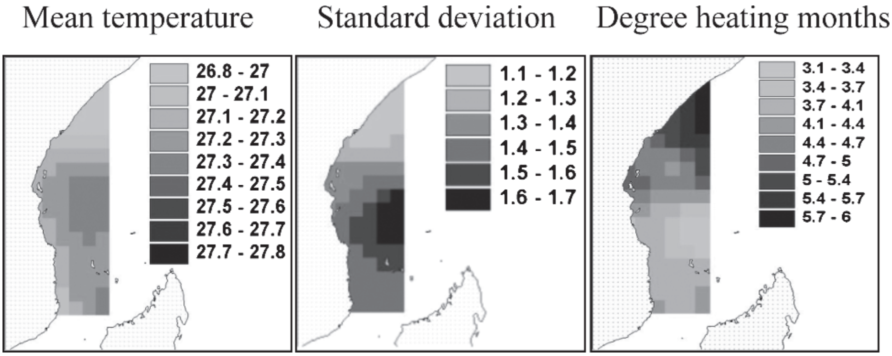

Fig. 8.2 Spatial distribution of the mean, variance (*Standard deviation*), and degree heating months during 1998 along the East African coast, based on Hadley Centre data for 100×100 km grids and based on monthly temperature measurements for the years 1950 to 2002. Degree heating months is the number of months that the temperature is 1°C above the mean for that month

bleaching hierarchy is directly related to rates of mortality (McClanahan 2004) as colonies of some species bleach readily but recover (Baird and Marshall 2002), while other, albeit fewer, species may show no symptoms of stress or obvious loss of pigmentation, but may still suffer mortality (McClanahan 2004).

Other patterns include the observation that branching colonies typically have high rates of whole-colony mortality and little partial mortality. In contrast, rates of whole-colony mortality are low in massive species where the majority of tissue is lost through partial mortality. For example, in a study of individually tagged colonies of four species on the GBR following bleaching, 88% of *Acropora hyacinthus* colonies died, compared with 32% of *A. millepora* and 13% of *Platygyra daedalea* (Baird and Marshall 2002). No whole-colony mortality occurred in *Porites lobata*. However, most surviving *P. daedalea* and *P. lobata* colonies lost some tissue; 88% of *P. daedalea* colonies lost tissue and the mean loss of tissue per colony was 42%. In contrast, partial mortality was rare in the *Acropora* and colonies either survived intact or died. These differences in patterns of mortality have a number of important consequences. Estimates of whole-colony mortality would have vastly underestimated the effect of bleaching on *P. daedalea*. Indeed, the proportion of tissue lost as a result of partial mortality in *P. daedalea* (44%) was greater than the proportion of tissue lost from whole-colony mortality in *A. millepora* (34%; Baird and Marshall 2002). Thus, in terms of tissue loss in the population, *P. daedalea* was more severely affected than *A. millepora*, a result that would not have been predicted from accepted patterns of taxonomic susceptibilities (McClanahan et al. 2004a).

Population-level studies demonstrate that the time taken to respond to warm water varies considerably among species. Massive species take longer to respond to thermal stress, can stay bleached for longer and take longer to die than many branching species, which bleach quickly and either recover, or die, shortly after the temperature stress (Brown and Suharsono 1990; McClanahan et al. 2001; Baird and Marshall 2002). In the GBR, the appearance of bleaching in individually tagged

Acropora colonies changed markedly between censuses only four weeks apart (Baird and Marshall 2002). Consequently, the number of colonies in a particular bleaching state will be the result of three processes: recovery, decline, and stasis. Importantly, even corals that survive a particular bleaching event may nonetheless experience long-term consequences of thermal stress, including reduced reproductive output, reduced growth, and increased susceptibility to other disturbances (Lesser et al. 2007). Consequently, the rank order of species susceptibilities and estimates of the severity of a particular bleaching event depend critically on the time elapsed since the onset of stress.

8.4 Delayed Effects

8.4.1 Reproduction

Studies of organisms with pelagic larval stages suggest that an increase in seawater temperature can potentially increase reproduction and larval production, decrease dispersal distance, and reduce larval mortality (O'Connor et al. 2007). Similarly, an increase in baseline temperature can increase growth rates of corals (Lough and Barnes 2000; Edmunds 2005) and the calcification of coral reefs (Kinsey and Hopley 1991). All of these data and models, however, do not fully consider the possibility of thresholds where effects of increasing temperature may become negative or lethal. Consequently, bleaching represents the threshold where many negative effects arise on what are often the positive effects of increasing water temperature.

Coral reproductive output is affected by bleaching in a number of ways, including: changes in egg size and quality, reduced polyp fecundity, both in the number of polyps with eggs and the number of eggs per polyp, and finally, in the number of whole colonies breeding in a given year. Egg size and number of eggs per polyp were both lower in experimentally bleached colonies than in unbleached colonies of the soft coral *Lobophytum compactum* (Michalek-Wagner and Willis 2001b). Egg quality was also affected, with protein, lipid, mycosporine-like amino acids, and carotenoid concentrations significantly reduced in the eggs of bleached colonies (Michalek-Wagner and Willis 2001a). The effect of bleaching on reproduction is also species-specific. The proportion of colonies of *Acropora hyacinthus* (45%) breeding following the bleaching on the GBR was much lower than that of *A. millepora* (88%; Baird and Marshall 2002).

One of the major consequences of the 2005 bleaching event in the Caribbean was the complete reproductive failure of the *Montastraea* species complex in 2006 (E. Weil, personal observation). This is curious because *A. palmata*, a species that bleached in 2005 and suffered localized significant mortalities in reefs off La Parguera, spawned successfully in reefs off the west coast of Puerto Rico, but not in La Parguera (E. Weil, personal observation). This provides yet another example of the spatial and taxonomic variability in the effect of bleaching on coral reef communities. In the GBR, bleaching caused a substantial decrease in the reproductive output, primarily as a result of a significant decline in colony abundance (Baird and Marshall 2002). For example, the number of gravid *A. hyacinthus* colonies at Pelorus Island in the reproductive season following the 1998 bleaching was only 6% of that in 1997. Similarly, the number of gravid *A. millepora* colonies was 63% of that in 1997.

8.4.2 Size and Growth

Mortality in corals is often size-specific, but the effect of bleaching on the size structure of populations has not been fully resolved. For example, mortality rates following bleaching on the GBR in 1998 were not size-specific; however, only mature colonies were sampled (Baird and Marshall 2002). In contrast, experimental and theoretical work predict that large size may actually be deleterious when corals are exposed to thermal stress (Nakamura and van Woesik 2001) and coral recruits in the field with diameters of <20 mm were unaffected by bleaching (Mumby 1999). Similarly, bleaching can cause partial mortality and a number of studies showed that smaller colonies survive better than larger ones (Loya et al. 2001; Nakamura and van Woesik 2001; Bena and van Woesik 2004; Shenkar et al. 2005). A long-term study of coral size on Kenyan reefs found that bleaching reduced the size of most coral taxa but that the mean size of the taxa was not related to mortality during 1998. This indicates that the size effect is within rather than between taxa (McClanahan et al. 2008a). In contrast, Bak and Meester (1999) proposed that climate change should produce coral populations with fewer small colonies, presumably through poor reproduction and recruitment. Similarly, Edmunds (2005) used a combination of empirically derived temperature growth responses and matrix models to predict that temperature increases of 3°C above current averages would increase the annual growth rates of all three pocilloporid taxa by 24–39%. Ten-year matrix population projections suggested that this sub-lethal increase in temperature would increase the relative abundance of large colonies at the expense of smaller colonies and increase the population size (Edmunds 2005).

There have been few tests of the effect of bleaching on coral growth and the results are ambiguous. Unbleached colonies of *Montastraea annularis* deposited 1.4 mm/year more aragonite than bleached colonies (Porter et al. 1989). Similarly, while moderately affected colonies of *Acropora hyacinthus* and *A. millepora* grew in the six months following bleaching and severely affected colonies did not, the association between bleaching severity and growth was not statistically significant (Baird and Marshall 2002). Post-recruitment mortality is equally unstudied, but evidence from East Africa and the Caribbean suggests that predation can retard the recovery of small corals recovering from bleaching (McClanahan et al. 2005; Rotjan and Lewis 2005). The loss of coral cover in the initial bleaching event may result in more intense predation on those corals that survive.

Other sub-lethal effects of bleaching include a reduction in the antibiotic properties of mucus, making colonies more susceptible to diseases (Ritchie 2006) and abnormal skeletal growth, as observed in massive *Porites* in Kenya (McClanahan et al. 2008c).

8.4.3 Recruitment

The few studies available indicate that coral recruitment is reduced following bleaching. For example, Smith et al. (unpublished data) recorded a 97% reduction in recruitment following a bleaching event that reduced adult coral cover by between 75% and 90%. However, Scott Reef, the site of this study, is a highly isolated reef (Underwood et al. 2008) and it remains unknown whether similar levels of mortality will cause similar reductions in recruitment in highly connected reef systems. Recruitment of corals in the more connected reefs of the Maldives was low after the 1998 bleaching and appeared to decline over time (McClanahan 2000, unpublished data; Loch et al. 2004). Consequently, connected reefs that are badly damaged on a large scale can also exhibit declines in recruitment. However, even when recruitment remains high, recovery of the adult community is not guaranteed. In a study of recovery of reefs after the 1998 event in Palau, sites with the highest coral recruitment had the lowest recovery rates (Golbuu et al. 2007). This suggests that other factors such as habitat, growth, the abundance of remnant colonies, and post-recruitment mortality can frequently have greater effects than early recruitment.

In the Eastern Pacific, while gametes became mature in bleaching years (Glynn et al. 1991, 1996, 2000) subsequent larval recruitment was variable (Guzman and Cortés 2001, 2007). Similarly, while recruitment of *Pavona varians* in Panama was significantly correlated with high seawater temperature, recruitment failed at very high temperatures (Glynn et al. 2000).

8.4.4 Disease

Many investigators have noted coral disease coincident with, or occurring shortly after, bleaching events (Baird 2000; McClanahan et al. 2004b; Willis et al. 2004; Miller et al. 2006; Bruno et al. 2007; Fig. 8.1 h, i). There is a clear synergy between bleaching and disease: changing environmental conditions associated with climate change are expected to increase the virulence of microbes (Rosenberg and Ben-Haim 2002; Lesser et al. 2007); and bleaching compromises the health of corals. Both of these factors should result in a greater incidence of disease (Rosenberg and Ben Haim 2002; Ritchie 2006; Ward et al. 2007). However, given the multiple causes of coral disease, such observations are speculative and require further study.

The Caribbean has seen the greatest proliferation of coral disease (Weil 2004) and many outbreaks are associated with bleaching events. Following bleaching in

2005, many colonies of crustose octocorals, *Briareum asbestinum* and *Erythropodium caribaeorum*, became diseased and died (Fig. 8.1). Other species affected by disease outbreaks, such as white plague and yellow band disease, following the 2005 event included *Montastraea* spp., *Diploria* spp., and *Siderastrea siderea* (Miller et al. 2006; Weil et al. 2006; Fig. 8.1 h).

8.5 Population Dynamics and Community Structure

Due to differential susceptibilities of taxa and populations to thermal stress (Jokiel and Coles 1990; Kayanne et al. 2002), changes in abundance almost always lead to a change in assemblage structure, including reductions in species richness (Loya et al. 2001; McClanahan and Maina 2003), diversity (Warwick et al. 1990), and community composition (McClanahan et al. 2007b). Some of these changes are short-term (Chap. 9; Brown 1997; McClanahan and Maina 2003), while others appear to be very persistent (Chap. 9; Glynn 1994; Berumen and Pratchett 2006; McClanahan et al. 2007b). Population changes have community-level effects, such as temperature-induced change in competitive networks (Alino et al. 1992), that are expected to lead to large-scale changes in assemblage structure in reef communities (Langmead and Sheppard 2004).

Some of the early studies of strong bleaching in the Eastern Pacific during the 1982–1983 El Niño showed large changes in the abundance of many coral populations (Glynn et al. 2001), the local or regional extinction of species (Glynn and Ault 2000; Maté 2003), and the devastation and disappearance of whole reef structures (Eakin 2001). In other cases, large switches in coral dominance are evident; for example, in Cocos Island, Panama, *Pavona clavus* became common after the bleaching. Similarly, *Leptoseris scabra* was not recorded prior to the 2002 event (Guzman and Cortés 2007). These early observations were alarming because they signaled the potential for major changes in reefs. Over the long-term, however, the main reef builders (i.e. poritids, pocilloporids) continue to be the dominant species at these sites (Guzman and Cortés 2001).

Studies in the Indo-Pacific in the 1980s also indicated considerable potential for harm but again the response was variable. For example, on the reef flats of islands in Pulau Seribu, Indonesia, up to 92% of the coral cover and most of the *Acropora* were lost following a 2–3°C rise in temperatures in 1982 (Brown and Suharsono 1990). Similarly, the reefs of Sesoko Island, Japan, experienced a 61% reduction in species richness and an 85% reduction in coral cover following the bleaching in 1998 (Loya et al. 2001). In contrast, recurrent bleaching of corals between 1991 and 1998 on reef flats at Ko Phuket, Thailand, had no discernable effect on coral community measures, such as species richness or diversity. This result is attributed to the domination of these reefs by massive coral species, which are physiologically adapted to intertidal living and display partial rather than whole colony mortality (Brown et al. 2002).

The largest effects of the 1998 event were documented in the western Indian Ocean. In many high coral cover reefs of the Indian Ocean, such as the Maldives, Chagos, and Seychelles that were dominated by *Acropora* and *Montipora* before 1998, cover was reduced to less than 10% after 1998 (McClanahan 2000; Sheppard et al. 2002; Graham et al. 2006). In some of these places, such as the Chagos and Tanzania, recovery of *Acropora* and other branching forms has been rapid (Sheppard et al. 2002; McClanahan, unpublished data). At other locations, the relative dominance of bleaching resistant taxa, such as massive *Porites* or fugitive taxa such as *Pocillopora*, has increased and largely replaced *Acropora* and *Montipora* (McClanahan et al. 2007b). A large-scale survey of the western Indian Ocean found that the relative covers of *Acropora* and *Montipora* were negatively associated with the degree heating weeks in 1998 (McClanahan et al. 2007b). Some areas, such as the granitic islands of the Seychelles and areas in the Maldives, have a low cover of all corals and erect algae now dominate the benthos (Graham et al. 2006; McClanahan, unpublished data).

There was a critical lack of empirical information on coral assemblage structure in the Caribbean during the past decade, which affected our understanding of the effects of bleaching on coral populations. While a massive loss of coral cover was well documented (Gardner et al. 2003), the taxa contributing most to the loss is obscure because most studies lacked sufficient taxonomic resolution. The exception to this pattern is the basin-wide loss of *Acropora* species (Greenstein et al. 1998) and the localized losses of *Agaricia* (Aronson et al. 2002a). Consequently, an assessment of the effect of bleaching relied on data from Pleistocene reefs (Pandolfi and Jackson 2007), which concluded that recent human impacts resulted in changes to coral assemblages without precedent in the last 220 000 years. Shorter-term studies comparing the past few millennia also concluded that most of the change in Caribbean coral assemblages occurred very recently (Aronson et al. 2002b, 2004).

8.6 Ecosystem Processes

Potential effects of coral bleaching on ecosystems include a decrease in net rates of calcium carbonate accretion and possible changes in primary productivity. One study from Ishigaki, Japan, found that during a bleaching year excess organic production was reduced by 75% when compared with a non-bleaching year (Kayanne et al. 2005). Given that coral cover changed little, the study suggested that the change was largely due to reduced productivity of corals, possibly associated with reduced symbiont densities. Corals that die from bleaching can be replaced by more productive algae that could potentially increase organic carbon production, but at the loss of inorganic carbon production. The full consequences of carbon and other nutrient influences associated with bleaching remain key areas for future investigations. The next few decades will be a time of unprecedented change and reorganization of the sessile organisms on coral reefs with likely flow-on effects for the ecosystem, including fisheries (McClanahan 2002; Graham et al. 2007; Chap. 9).

8.7 Interactions with Management

The long-term effects of bleaching on sessile organisms may be influenced by decisions taken by management, in particular by reducing fishing pressure on key functional groups, such as herbivorous fishes, through fishing effects on herbivores and herbivory and coral recruitment (Bellwood et al 2004; Mumby et al. 2006; Hughes et al 2007). No-take areas generally have higher levels of herbivory that can reduce erect algal cover and increase coral recruitment (Mumby et al. 2007). Whether or not this results in higher coral cover and resilience to climatic disturbances is less clear. After the 1998 coral mortality in the western Indian Ocean, many reefs were quickly colonized by rapidly growing turf algae, which was eventually colonized by slower-growing coralline and erect algae (McClanahan et al. 2001; Graham et al. 2006; McClanahan 2008). Corallines were more prevalent in areas with high fish grazing, and while high abundance of corallines should increase coral recruitment, experimental studies also found that coralline algae were associated with a higher loss of coral recruits due to predation; and no differences were detected in the rates of coral recovery between fished and non-fished reefs (Fig. 8.3). Consequently, there is, as yet, little evidence to indicate that either resistance to bleaching or recovery is higher in non-fished reefs (McClanahan et al. 2005, 2006).

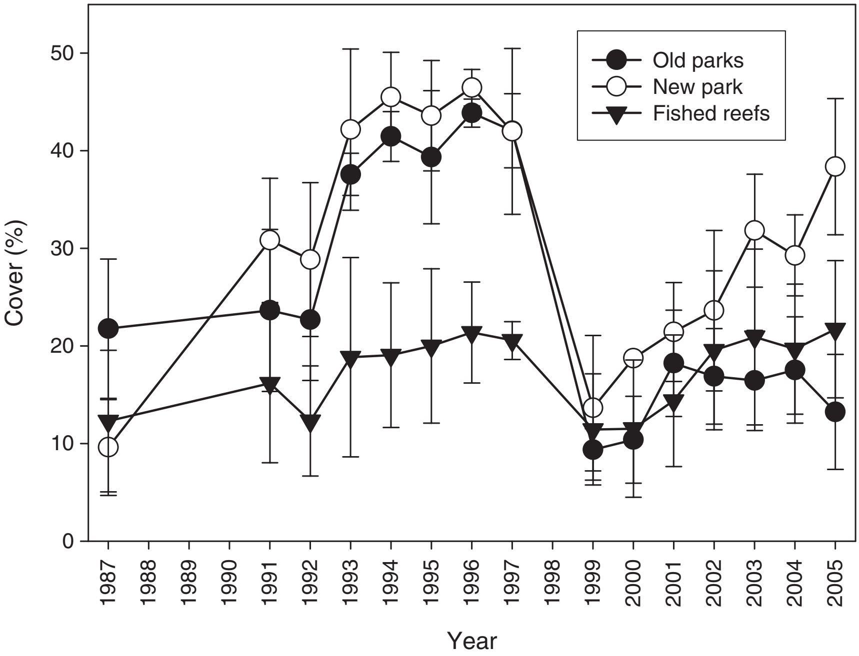

Fig. 8.3 Change in coral cover across the 1998 bleaching event and recovery on Kenyan reefs with different management stages. Four fished reefs, three old parks, and one transitional/new park were monitored. The old parks were closed in 1968 (Malindi), 1972 (Watamu), and Kisite (1973). The new park at Mombasa was closed in 1991

8.8 Conclusions

Reports of coral bleaching have been increasing in the past few decades, overtaking most other human impacts as the most significant threat to reef condition. Reports of bleaching are more frequent following El Niño events (Chaps. 3, 4). Aerosols (Gill et al. 2006), local water quality (Riegl and Piller 2003; McClanahan et al. 2007c), hurricanes (Manzello et al. 2007), and other large-scale oceanographic processes, such as upwelling and oceanographic cycles (McClanahan et al. 2007a, c), can attenuate bleaching events. These factors are all variations on the rising ocean temperature trend that is expected to challenge the adaptive potential of coral reefs in the coming decades (Hoegh-Guldberg 1999; Hughes et al. 2003; Sheppard 2003). Research to date suggests dire consequences to sessile organisms, but the considerable patchiness in responses indicates that refuges from climate change may exist and adaptation to climate change may be possible.

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Chapter 9
Coral Bleaching and Consequences for Motile Reef Organisms: Past, Present and Uncertain Future Effects

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9.1 Introduction

While coral reefs are subject to a wide range of anthropogenic and natural disturbances, sustained and ongoing climate change is rapidly emerging as the single greatest threat to these important ecosystems (Hughes et al. 2003; West and Salm 2003; Munday et al. 2007). The potential effects of climate change on coral reef ecosystems are numerous, but the most devastating effects to date have been large-scale and severe episodes of coral bleaching (Smith and Buddemeier 1992; Goreau et al. 2000; Chap. 3). The global significance of coral bleaching was most evident in 1997–1998, when high sea surface temperatures resulted in severe coral bleaching and high mortality (up to 99% coral mortality) in over 50 countries throughout the world (Chaps. 3, 8). Increasing frequency and severity of mass-bleaching events are clearly linked to climate change (Walther et al. 2002; Hughes et al. 2003) and the longer-term future is potentially catastrophic, not just for corals, but for coral reefs as a whole.

There are no other ecosystems in which the major habitat-forming organisms have been functioning so close to their upper thermal limit. Corals are the fundamental building blocks of coral reefs, providing a spatial diversity of habitats and a three-dimensional structure that supports an exceptional diversity of reef animals. Recent research clearly demonstrates that coral decline has had profound effects on reef fishes and other reef-associated organisms (Sin 1999a; Caley et al. 2001; Jones et al. 2004; Idjadi and Edmunds 2006; Wilson et al. 2006; Munday et al. 2007). Moreover, changes in the composition of coral assemblages, which may occur following severe or recurrent disturbances (Chap. 8), lead to changes in the composition of reef-associated faunas (e.g. Berumen and Pratchett 2006), with potentially major implications for coral reef biodiversity and ecosystem function (Bellwood et al. 2004; Jones et al. 2004).

Studies on the effects of bleaching on motile reef organisms were mostly initiated after the 1997–1998 bleaching event (e.g. Graham et al. 2006; Pratchett et al. 2006), limiting the understanding of long-term impacts (>8 years) of climate-induced coral bleaching. In addition, coral reef environments are commonly exposed to multiple disturbances, making it difficult to identify the role or importance of any one factor (e.g. Jones et al. 2004; Pratchett et al. 2006). Different kinds of disturbances

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(e.g. climate-induced coral bleaching, severe tropical storms, coral disease) may have a range of impacts on coral reefs, but most disturbances are detrimental for corals. Climate change itself will also impact on coral reefs in a multitude of ways. For example, it will cause increasingly frequent and severe episodes of coral bleaching and may also lead to an increasing frequency of severe tropical storms (Webster et al. 2005; Chap. 1). Despite the limitations of short-term studies and the complexities of multiple disturbances, it is important that we assemble the available information on the impacts of coral bleaching, to recognise the future scale of degradation that could occur to coral reefs and develop appropriate responses.

Much of the current knowledge of the indirect effects of coral bleaching relates to changes in the abundance of coral reef fishes immediately following bleaching events (Table 9.1). At least one-quarter of extant fish species are associated with coral reefs (Spalding et al. 2001) and fishes are the most conspicuous, diverse, and well studied group of motile reef organisms. Many coral reef fishes depend on the coral reef habitat for vital resources such as food, shelter, and living space (Jones and Syms 1998). Not surprisingly, many species (up to 75%) exhibit significant declines in abundance following extensive coral depletion (Jones et al. 2004), while a small number of non-coral specialists may actually increase in abundance. The specific effects of coral depletion on coral reef fishes depend on the scale at which fishes interact with benthic habitats, as well as the spatial extent of disturbances. Coral reef fishes are generally resilient to localised disturbances (within or among individual reefs) because depleted populations can be quickly replenished from other unaffected populations (Sale 1991). However, the spatial extent of habitat degradation from climate-induced coral bleaching is immense and may ultimately threaten many species with small geographic ranges (Munday 2004). To fully comprehend the impacts of habitat disturbance on fishes we need to understand both their specific habitat requirements and the ways in which different disturbances affect the biological and physical structure of the substratum.

In this chapter, we review the effects of climate-induced coral bleaching on motile reef organisms, including fishes and motile invertebrates. These effects range from declines in the physiological condition and reproductive output of individuals to declines in biodiversity and the potential for global extinction. Coral-bleaching events represent acute large-scale disturbances, often resulting in extensive coral mortality followed by gradual degradation of the reef framework (Garpe et al. 2006; Graham et al. 2006; Chap. 8). By considering different time-scales, we can distinguish the immediate effects of coral bleaching associated with a reduction or loss of live coral tissue (<3 years) from medium-term changes in the biological and physical structure of reef habitats (3–10 years) and extrapolate these to give a longer-term (>10 year) prognosis for the fate of coral reef ecosystems. The short-term effects of coral mortality (<3 years) are mainly restricted to those species that feed, shelter or recruit on live corals (Wilson et al. 2006). Even so, strongly coral-dependent species may exhibit a range of responses, including altered patterns of resource use, mass migration to coral-rich habitats, recruitment failure and/or localised extinction. These effects may be further magnified following changes in the biological and physical structure of reef habitats, which may occur 3–10 years following extensive coral death (Graham et al. 2006). Most importantly, extensive coral mortality ultimately leads to a decline in structural complexity through the gradual erosion of dead coral skeletons. Structural complexity provided by coral skeletons moderates key biological processes of competition and predation (Beukers and Jones 1997) and exerts a much stronger influence on the abundance and diversity of motile reef organisms than loss of coral cover alone. The few studies which have explored the effects of coral depletion over this time-scale (Jones et al. 2004; Garpe et al. 2006; Graham et al. 2006) clearly demonstrate the far-reaching consequences of coral death and reef degradation on motile reef organisms. It is also

Table 9.1 Published studies on effects of increased temperature and bleaching-induced coral mortality on motile reef organisms. These studies are mostly conducted over very short time-frames (<3 years post-bleaching) and mainly focus on coral reef fishes. *GBR* Great Barrier Reef

Location	No. years post-bleaching	No. species considered (families)	Source
Coral reef fishes			
Cocos Island, Costa Rica	3	1	Guzmán and Cortés 1992
Panama	1	1	Glynn 1985
Eastern Pacific	4	1	Guzmán & Robertson 1989
Moorea, French Polynesia	1	135 (27)	Adjeroud et al. 2002
One Tree Island, GBR, Australia	2	13 (1)	Booth and Beretta 2002
Kimbe Bay, PNG	3	538 (20)	Jones et al. 2004
Kimbe Bay, PNG	5	6 (1)	Munday 2004
Trunk Reef, GBR, Australia	<1	1	Pratchett et al. 2004
Trunk Reef, GBR, Australia	3	15 (1)	Pratchett et al. 2006
Palm Island, GBR, Australia	<1	144 (12)	Thompson and Malcolm 1999
Orpheus Island, GBR, Australia	6	36	Bellwood et al. 2006
Okinawa, Southern Japan	1	1	Kokita and Nakazono 2001
Okinawa, Southern Japan	<1	1	Tsuchiya 1999
Ishigaki Island, Japan	1	110 (19)	Shibuno et al. 1999
Iriomote Island, Japan	2	55	Sano 2004
Chagos	3	203 (29)	Sheppard et al. 2002
Seychelles	7	134 (16)	Graham et al. 2006
Seychelles	1	44 (14)	Spalding and Jarvis 2002
Tanzania	6	91	Garpe et al. 2006
Tutia Reef, Tanzania	<1	84	Lindahl et al. 2001
Kenya	3	(13)	McClanahan et al. 2002a, b
Arabian Gulf, Dubai	3	103	Riegl 2002
Coral reef invertebrates			
Bahia, Brazil	2	24	Attrill et al. 2004
Cocos Island, Costa Rica	3	2 (2)	Guzmán and Cortéz 1992
Panama	1	2 (2)	Glynn 1985
Panama	<1	2 (1)	Glynn et al. 1985
Okinawa, Southern Japan	<1	4 (1)	Tsuchiya et al. 1992
Okinawa, Southern Japan	<1	9 (3)	Tsuchiya 1999
Kenya	3	(2)	McClanahan et al. 2002

likely that extremely severe and/or large-scale bleaching events will have even longer-lasting effects on coral reef ecosystems (over time-frames >10 years), especially given that the frequency and intensity of coral bleaching is expected to increase (Donner et al. 2005; Chap. 10).

9.2 Short-Term Effects (up to 3 Years)

Extensive coral depletion, whether caused by climate-induced coral bleaching or other disturbances, can have pronounced effects on motile reef organisms (e.g. Kaufman 1983; Lassig 1983; Dawson-Shepherd et al. 1992; Jones et al. 2004; Wilson et al. 2006). Most notably, coral depletion is related to rapid and pronounced declines in the abundance of coral reef species that directly depend on scleractinian corals for food (Williams 1986; Kokita and Nakazono 2001; Pratchett et al. 2006), habitat (Tsuchiya et al. 1992; Munday et al. 1997; Munday 2004), and recruitment (Booth and Beretta 2002; Jones et al. 2004; Srinivasan 2007). Effects of coral depletion on strongly coral-dependent species are, nonetheless, highly variable. For example, Munday (2004) found that changes in the abundance of six species of obligate coral-dwelling gobies (*Gobiodon* spp.) following a severe loss of coral habitat ranged from 50% to 100%, depending on their degree of habitat specialisation. Among strongly coral-dependent species, specific responses depend upon: (1) the extent to which populations are limited by the availability of live coral, (2) their versatility in use of alternate resources, and (3) the degree to which sub-lethal responses mitigate or delay declines in abundance (Pratchett et al. 2004; Wilson et al. 2006).

9.2.1 Coral Dependence and Ecological Versatility

There are a diversity of reef-associated species that rely directly on live coral, many of which are very small and often go unnoticed (Munday and Jones 1998; Bellwood et al. 2006). On the Great Barrier Reef (GBR), Jones et al. (2004) and Munday et al. (2007) estimated that 9–10% (107 in ~1220 species) of coral reef fishes specifically rely on live coral for food or shelter and cannot persist on reefs devoid of coral. Similar proportions of motile reef invertebrates are also reliant on corals. For example, 30% of species of decapod crustaceans found on coral reefs often live in or on corals (A. Díaz-Ruíz, personal communication) and 9–10% of these species (mainly *Alpheus* shrimps and xanthid crabs) specifically rely on live corals for food and shelter (Garth 1964; Knudsen 1967; Debelius 2001). Among coral reef fishes, the most diverse and abundant group of fishes that rely on corals are the suite of fishes that live or shelter within branching corals, including damselfishes, gobies, and velvetfishes (Munday et al. 2007). Coral depletion leads to rapid and severe declines in the abundance of these fishes (e.g. Booth and Beretta 2002; Munday 2004), with noticeable effects on biodiversity (Jones et al. 2004; Wilson et al. 2006). In the extreme, reefs comprised entirely of rubble and no live coral have 30–50% less species than reefs with moderate levels of coral cover, due mostly to a lack of coral-dependent species (Sano et al. 1987; Glynn 2006; Graham et al. 2006).

Among motile reef organisms that use corals for food or shelter there is considerable variability in the degree to which they depend on coral; and there are large differences in their responses to coral loss. Coral-feeding butterflyfishes, for example, can be divided into: (1) obligate coral feeders, which feed almost exclusively on live coral, (2) facultative coral feeders, for which corals constitute 20–70% of their diet, and (3) putative non-coral feeders, which are rarely seen to feed on corals (Harmelin-Vivien and Bouchon-Navaro 1983; Pratchett 2005). As would be expected, facultative and non-coral feeders are typically much less affected by declines in live coral, compared with obligate coral-feeding butterflyfishes (Pratchett et al. 2006). However, even among obligate coral-feeding species there are major differences in susceptibility to disturbance, attributable to differences in their degree of dietary specialisation (Pratchett et al. 2006). If species use a wide range of different corals, including some corals that are resistant to disturbance, then they will be relatively unaffected during all but very severe declines in coral cover (Gardiner and Jones 2005). In contrast, highly specialised species that rely on corals highly sensitive to bleaching will be significantly affected. All corals are susceptible to bleaching at some level, but certain genera, such as *Pocillopora*, *Stylophora*, and *Acropora*, are particularly prone to bleaching (Marshall and Baird 2000) and quickly die once bleached (Baird and Marshall 2002; McClanahan et al. 2004). Ironically, it is these corals that are most frequently used by both coral-dwelling and coral-feeding organisms (Munday et al. 1997; Sin 1999b; Vytopil and Willis 2001; Pratchett 2005; Feary et al. 2007; Srinivasan 2007; Fig. 9.1). Some other bleaching-resistant corals, such as branching *Porites* spp., also provide a habitat for fishes and invertebrates, but they tend to be occupied by less-specialised species that use a wide range of different corals (Gardiner and Jones 2005; Hixon and Jones 2005; Brooks et al. 2007).

Overall, there is considerable overlap in the primary coral preferences of coral-dwelling and coral-feeding species, though they do vary in their degree of specialisation (Munday 2004; Gardiner and Jones 2005; Pratchett 2005). For example, in the northern GBR, all species of coral-feeding butterflyfishes have the greatest feeding preference for *Acropora hyacinthus* and/or *Pocillopora damicornis* (Pratchett 2007), but these butterflyfishes consume from 11 to 49 coral taxa (Pratchett 2005). Highly versatile species may escape the full effects of resource depletion by using alternate resources, whereas highly specialised species are severely affected by any reductions in their specific resources, possibly leading to extinction (e.g. Munday 2004). Generalist coral-feeding species may alter their dietary composition in response to changes in prey availability (Pratchett et al. 2004; Berumen et al. 2005) but, even so, these species eventually succumb to extensive coral depletion (Pratchett et al. 2006).

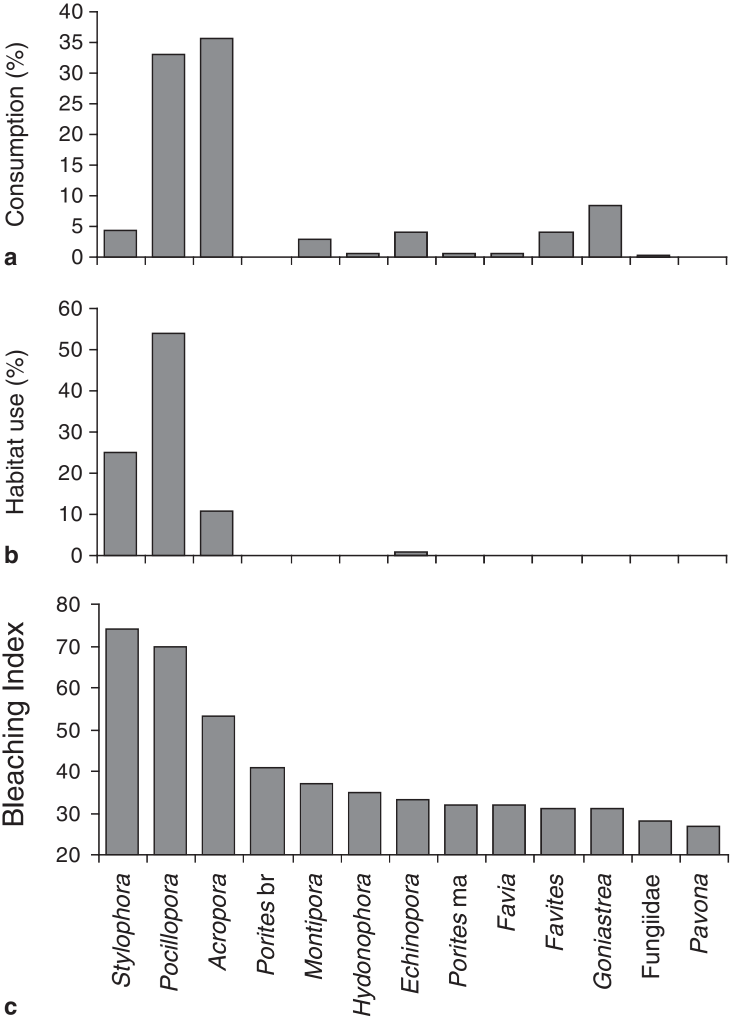

Fig. 9.1 Patterns of percent coral use by: **a** a coral-feeding butterflyfish (*Chaetodon plebius*) and **b** a coral-dwelling damselfish (*Dascyllus aruanus*; Pratchett, unpublished data) compared with: **c** bleaching susceptibility of different coral types (genera plus growth forms: *br* branching, *ma* massive) on the Great Barrier Reef (McClanahan et al. 2004)

9.2.2 Sub-Lethal Effects of Coral Depletion

Even where there is no immediate change in the abundance of motile organisms, coral depletion may still have significant and lasting deleterious effects. For example, reductions in live coral may limit settlement and recruitment for species that are otherwise unaffected by coral depletion (Bouchan-Navaro et al. 1985; Booth and Beretta 2002; Jones et al. 2004; Srinivasan 2007). Pratchett et al. (2004) showed that there was no immediate change in the abundance of *Chaetodon lunulatus* following severe coral bleaching, but this species did exhibit immediate and significant declines in physiological condition. Corallivorous organisms may partially compensate for initial depletion of prey resources by switching prey (Pratchett et al. 2004) or increasing their home ranges (Tricas 1989; Kokita and Nakazano 2001; Samways 2005). These changes in behaviour may allow corallivorous species to persist in the short term, but reduced access to preferred coral prey is likely to reduce energetic intake (Berumen et al. 2005), with implications for growth, reproductive output, and ultimately survivorship (Kokita and Nakazano 2001; Pratchett et al. 2004).

Even species that do not typically feed on scleractinian corals may be adversely affected by declines in coral abundance due to associated reductions in the production of coral propagules. Mass spawning of corals provides a large seasonal pulse of high-energy prey consumed by many different fishes and motile invertebrates, thereby representing a huge injection of energy into coral reef ecosystems (Pratchett et al. 2001; McCormick 2003). Any consumers capable of capturing and digesting coral propagules have been shown to amass considerable lipid stores following coral spawning (Pratchett et al. 2001). This may significantly enhance individual fitness, principally increasing larval quality through maternal effects (McCormick 2003). Further, the timing of mass spawning by corals at some locations (notably the GBR) immediately precedes the major reproductive period for coral reef fishes (Thresher 1984; Claydon 2004). Consequently, widespread reductions in coral cover and associated reductions in the abundance of coral propagules may have small, but potentially significant, effects on the quality and survivorship of larval fishes and the reproductive output of those species that regularly consume coral propagules.

9.3 Medium-Term Effects (3–10 Years)

Although the consequences of bleaching for fishes and motile invertebrate communities in the months and initial years after bleaching events are well documented, there is little information on how bleaching may affect these communities over longer time periods. Following disturbance it can take 5–10 years for coral cover to return to pre-disturbance levels (e.g. Halford et al. 2004; Gardner et al. 2005) or for the reef framework to collapse (e.g. Sheppard et al. 2002). During this period, the reef status lies somewhere between fully recovered, where coral cover has returned to pre-bleaching levels, and a full phase shift, where coral has been replaced by macroalgae and the reef framework may have been seriously eroded. Here we consider the implications of these alternative scenarios for motile fauna.

9.3.1 Recovery Scenario

Recovery of coral communities in the aftermath of severe bleaching is dependent on a number of interacting factors. The severity and spatial extent of the initial coral loss dictates the ability of surviving corals to reproduce and reseed affected areas

(Riegl and Piller 2003; Graham et al. 2006). Isolated reefs are much more sensitive to declines in viability of local populations, whereas well connected reefs, such as those along continental margins or large archipelagos, may have greater scope for sourcing corals from upstream (Ayre and Hughes 2004). If source populations are available to promote recruitment, coral recovery is dependent on the availability of reef substrate suitable for settlement. Here local populations of herbivores play a key role in cropping algae and maintaining the benthos in a suitable state for coral recovery (Bellwood et al. 2004; Mumby et al. 2006; Hughes et al. 2007). In such a scenario, and if other synergistic disturbances do not hinder recovery, coral cover can be regained within 5–10 years (Halford et al. 2004).

Although total coral cover can return to pre-bleaching levels within 10 years, community re-assembly may take much longer; and increased frequency and severity of bleaching is likely to lead to communities dominated by a specific subset of corals that are bleaching-resistant (Arthur et al. 2005). Changes in the relative abundance of different corals then favours different motile reef organisms, leading to changes in the dominance and community structure of these assemblages. For example, Berumen and Pratchett (2006) showed that the relative abundance of different coral-feeding butterflyfishes was altered following a shift in the coral community, instigated by an *Acanthaster* outbreak. When *Acanthaster*-resilient corals proliferated, butterflyfishes that predominantly fed on these corals became the dominant species (Berumen and Pratchett 2006). Similar changes in coral and fish communities will be expected following coral bleaching events, due to marked differences in the susceptibilities of corals to climate-induced coral bleaching. Importantly, the corals that are most susceptible to bleaching (e.g. *Acropora* spp.) are an integral component of reef complexity, their skeletons providing refuge for many species that do not necessarily associate with live coral. If branching corals are replaced by encrusting and massive growth forms, habitat complexity will decline, ultimately reducing the abundance and diversity of fauna reliant on branching corals for shelter.

Disruption of reef-associated communities at the time of bleaching may also change motile species composition, even if the coral communities fully recover. Removal of dominant fish and invertebrate species provides space for new recruits and, as larval supply is stochastic (Doherty 1991), recruitment patterns and subsequent communities will vary. Pre-emption of space by new species might retard the recolonisation of some previous residents, although competitive hierarchies can eventually re-instate species as they gradually recruit back to the reef. This process appears to be particularly important for habitat and feeding specialists (Munday et al. 2001). The re-introduction of specialist species will, however, be dependent on the presence of their preferred coral species.

9.3.2 Reef Collapse

If the coral does not recover, physical and biological forces can lead to erosion of the reef framework and a reduction in structural complexity (Glynn 1997;

Sheppard et al. 2002). Not all reefs are equally susceptible to collapse. In some environments, such as highly exposed reef fronts, corals contribute little to topographic complexity. Also, reefs vary in the amount of time it takes to break down, due to differences in:

- The composition of the initial benthic assemblage, because certain corals (mostly branching), and possibly other reef-building organisms, are much more susceptible to collapse than others (Glynn 1997)
- The degree of exposure to strong wave action, which determines the relative contribution of erect and fragile coral forms to coral composition (Madin and Connolly 2006) and may influence recruitment
- The stability and strength of the underlying ancient reef framework
- The abundance of bioeroders, such as excavating parrotfishes (Bellwood et al. 2003) and urchins (McClanahan and Shafir 1990)
- The successive occurrence of large-scale physical disturbances, such as severe tropical storms

Consequently, different reefs may be in varying degrees of decay from the same disturbance (Graham et al. 2006) and the time-frame to collapse may vary from 3 years to decades (Sheppard et al. 2002; Garpe et al. 2006).

Where the physical structure of benthic reef habitats remains unchanged, but coral cover has not recovered, the species richness, taxonomic breadth, and abundance of the fish community may be largely unchanged (Bellwood et al. 2006; Garpe et al. 2006; Graham et al. 2006). Nonetheless, community composition may have changed markedly, favouring species with generalist life history traits (Bellwood et al. 2006). However, long-term declines in coral cover may result in a loss of fish biodiversity, local extinctions, and dramatic shifts in species composition (Jones et al. 2004; Munday 2004; Berumen and Pratchett 2006; Pratchett et al. 2006). In Kimbe Bay, Papua New Guinea, Jones et al. (2004) estimated that up to 65% of reef fishes require live coral at settlement and the majority of these declined in abundance following a 6-year period of coral decline. Initial declines are expected to be greatest among smaller-bodied species, but smaller size classes within all species may no longer survive to replace adult fishes. Many of these species are long-lived (Choat and Robertson 2002) and thus there may be a lagged response whereby the full effects of bleaching take decades to be realised as adults die and are not replaced (Graham et al. 2007).

Various experimental and correlative studies have highlighted the importance of habitat complexity to diversity, abundance and biomass of motile reef organisms (Luckhurst and Luckhurst 1978; Sano et al. 1987; Grigg 1994; Syms and Jones 2000; Dulvy et al. 2002; Idjadi and Edmunds 2006; Wilson et al. 2007). This suggests that, if the physical matrix of a reef collapses following bleaching, it may result in more substantial impacts than coral loss alone, leading to significant reductions in abundance of many groups, reduced taxonomic distinctness, declines in species richness, and increased community dispersion (Garpe et al. 2006; Graham et al. 2006). Reductions in diversity and abundance may also extend to key functional groups of herbivorous fishes (Graham et al. 2006), directly affecting the recovery potential of the entire ecosystem (Bellwood et al. 2004). Several studies of the short-term impacts of bleaching suggest that herbivores initially increase in abundance (Wilson et al. 2006) and that continued increases, associated with greater algal cover, may be expected to create the space necessary to facilitate coral recovery (Bellwood et al. 2004). However, in extreme cases, a negative feedback may occur, whereby increased herbivory increases bioerosion and, in turn, reduces habitat complexity, resulting in reduced herbivore diversity and abundance (Graham et al. 2006); bioerosion may be especially enhanced in nutrient-enriched coastal environments (Chazottes et al. 2002; Carreiro-Silva et al. 2005). The ecological mechanisms behind negative impacts to fish assemblages when the physical structure of the reef framework collapses are likely linked to the key structuring processes of predation (Hixon 1991), competition (Jones 1991), and recruitment (Doherty 1991).

In terms of recruitment, many reef organisms settle directly among the branches of live corals, presumably because they provide good refuge from predators (Booth and Wellington 1998; Booth and Beretta 2002; Jones et al. 2004). However, the preferred settlement habitat (e.g. among coral species, between living corals vs dead but intact coral skeletons) varies among species (Öhman et al. 1998) and the importance of physical structure in settlement is not yet clear. Where the habitat is complex, the influence of predation may be reduced, increasing the survival of smaller, motile reef organisms (Dulvy et al. 2002; Jones and McCormick 2002; Hixon and Jones 2005; Lee 2006). It is likely, therefore, that competition for refugia could be intense (Hixon and Jones 2005), resulting in less aggressive individuals occupying unfavourable territories and being more susceptible to predation (Holbrook and Schmitt 2002). Reef fishes tend to use refuge holes most appropriate for their body size (Hixon and Beets 1993; Beukers and Jones 1997; Friedlander and Parish 1998). Thus the scale of structural complexity, or the reduction of it, will likely influence the size of fishes that are able to escape predation. Almany (2004) demonstrated that there is a complex interplay between habitat complexity, predation, and competition in determining the early post-settlement survival of common damselfishes, but any decline in structural complexity of reef habitats is likely to be detrimental for the abundance and diversity of motile reef organisms.

9.3.3 Phase-Shifts to Macroalgal-Dominated Systems

Coral mortality following bleaching events provides space on the reef for rapid colonisation by turf-forming algae (Diaz-Pulido and McCook 2002). On reefs where herbivorous fishes and/or urchins are abundant, algal assemblages may remain as cropped turf forms for several years after the bleaching event (Aronson et al. 2002; Arthur et al. 2005). However, if grazing pressure is low, fleshy macroalgae can develop within months of coral depletion (Ostrander et al. 2000; McClanahan et al. 2001; Diaz-Pulido and McCook 2002), limiting the future recovery of coral assemblages (Hughes et al. 2007) and potentially bringing about a phase shift from coral- to macroalgal-dominated reefs. Excess nutrients will further increase the likelihood of habitat degradation by enhancing algal growth, suppressing coral recruitment, and supporting increased densities of bio-eroding organisms (Fabricius 2005).

Shifts from coral- to macroalgal-dominated states will have broad consequences for motile reef fauna. Species that feed, shelter or recruit to live corals will not occur on algal-dominated reefs (Jones et al. 2004). Some species, such as the spiny lobster (*Panulirus argus*) and Nassau grouper (*Epinephalus striatus*), shelter within macroalgal habitats as juveniles (Marx and Herrnkind 1985; Dahlgren and Eggleston 2000) and their abundance may increase when macroalgae proliferate. However, the adult habitat on coral reefs must be preserved if the densities of these animals are to be maintained. Algae also provide a habitat for invertebrate crypto-fauna, with areas of greater algal biomass harbouring a greater abundance of invertebrates (Zeller 1988; Dulvy et al. 2002), which may attract invertebrate predators. Similarly, some fishes, such as *Naso unicornis* and *Kyphosus vaigiensis*, feed primarily on macroalgae (Choat et al. 2002) and may be attracted to reefs where macroalgae are prominent. Macroalgae do not, however, provide structural complexity and reef stability to the same extent as corals and the overall abundance and diversity of motile reef organisms on algal-dominated reefs is much lower, compared with coral-dominated reefs (Sano 2001).

9.4 Long-Term Effects (>10 Years)

Long-term studies (>10 years duration) on the indirect effects of climate-induced coral bleaching have not been conducted due to the relatively recent (mostly since 1998) emergence of bleaching as a global threat to coral reef ecosystems. However, extremely severe and/or large-scale bleaching events will have longer-term effects on coral reef ecosystems (Graham et al. 2007), especially given that the frequency and intensity of coral bleaching are expected to increase (Donner et al. 2005; Chap. 10) and recovery at some locations may be very slow. Changes in ocean chemistry and acidification are also expected to weaken coral skeletons (making them more susceptible to increasingly severe and frequent tropical storms) and reduce reef accretion (Hughes at al. 2003), leading to dramatic changes in the physical and biological structure of coral reef environments. It is inevitable that changes in coral communities and coral reef habitats will have significant impacts on motile reef organisms, including many effects that have not yet been considered. Aside from widespread habitat degradation, increases in temperature will have direct impacts on coral reef organisms because most species are ectotherms, for which cellular and metabolic activities are strongly dependent on ambient temperature. Motile reef organisms are as much dependent on, as they are critical to, the ecosystem function of coral reef environments. Direct or indirect effects of climate change and coral bleaching on motile reef organisms may, therefore, undermine the resilience of coral reef ecosystems, which will have significant ecological and economic ramifications (Bellwood et al. 2004; Worm et al. 2006).

9.4.1 Direct Effects of Climate Change on Motile Reef Organisms

In addition to indirect effects of habitat modification, future increases in ocean temperatures are expected to have direct effects on the whole-organism function, life history, and behaviour of coral reef animals, with concomitant effects on their distribution and abundance (Munday et al. 2007). Geographic range shifts are one of the most frequent and readily observed consequences of climate change for species in a wide range of ecosystems (Walther et al. 2002; Parmesan and Yohe 2003; Perry et al. 2005). As average ocean temperature increases, the geographic ranges of some coral reef animals will shift or expand (Victor et al. 2001), but the ranges of species already living near the present limits of coral reef development will probably contract.

Increasing ocean temperatures are likely to have greatest effects on reproductive output and early life history stages. The reproductive performance of marine ectotherms is strongly influenced by temperature (Van der Kraak and Pankhurst 1997). Although increased temperature may extend the breeding season of some species, it might lead to reduced or bimodal breeding seasons for species already reproducing near their upper thermal limits. The larval stage of marine organisms is also particularly sensitive to ambient temperature. Warmer temperatures can increase growth and development, thereby decreasing larval pelagic duration (Green and Fisher 2003; Bryars and Havenhand 2006), which may lead to higher recruitment (Wilson and Meekan 2002; Meekan et al. 2003) and increased larval survival (Searcy and Sponaugle 2000; Bergenius et al. 2002). However, increased growth and developmental rates will only occur if there is sufficient food and metabolic demands are greater at higher temperatures (Jobling 1997). Ultimately, the number of larvae recruiting to reef populations, and their physiological condition, will depend on complex interactions between temperature, developmental rates, food supply, and ocean currents, all of which are likely to be influenced by global warming.

Acclimatisation to temperature increases occurs in many marine animals (Hawkins 1996), although this capacity is limited for species already living near their thermal limits (Stillman 2003). Local adaptation to increased temperature is also possible, through gene flow from populations already living at higher temperatures and directional selection on existing genetic variability. The rapid generation times of many small fishes and invertebrates (Depzynsky and Bellwood 2005; Hernaman and Munday 2005) could aid local genetic adaptation to increased temperature. However, many other motile reef organisms are very long-lived (e.g. Choat and Robertson 2002) and local adaptation in these species will require much longer time-frames. The consequences of strong genetic selection to increased temperature are unknown, but could include a genetic bottleneck that reduces the capacity of motile reef organisms to adapt to other environmental changes, such as the ongoing degradation of their reef habitat. Direct effects of climate change on coral reef organisms will be more important as ocean temperatures continue to increase, but for now, indirect effects of coral bleaching and habitat degradation are having the greatest impacts on population size and fitness of non-coral organisms.

9.4.2 Impacts on Fisheries and Direct Economic Costs of Coral Bleaching

Climate-induced coral bleaching clearly has significant and far-reaching ecological impacts on coral reef ecosystems, but it also has a significant economic impact. Climate change has had, and will continue to have, profound impacts on the world's fisheries yields (McLean et al. 2001). In the past, the productivity of most fisheries has been strongly linked to major climatic events, such as El Niño and La Niña events, resulting from changes in regional productivity with changing ocean temperature and circulation patterns. On coral reefs, the most pressing and immediate impacts on fisheries yields are likely to arise from flow-on effects of climate-induced coral-bleaching. Independent of existing pressures on fisheries stocks (Worm et al. 2006), declines in productivity and habitat availability from coral loss may lead to declines in the abundance of primary consumers which, in turn, will have impacts extending to higher trophic levels, larger predators, and important fisheries species such as coral trout and snappers (Munday et al. 2007). Currently, there is little evidence that fisheries catches have actually declined after mass coral bleaching, but it is very difficult to detect any short-term changes in fisheries yields in the face of changing fishing pressure (McClanahan et al. 2002; Grandcourt and Cesar 2003). Direct observation of the population structure of fishery target species has, however, revealed marked declines in the abundance of smaller fishes following bleaching (Graham et al. 2007). This suggests that climate-induced coral bleaching has impaired population replenishment, such that some fished populations are destined to decline. Long-term degradation of physical reef structure will inevitably affect abundances, catch rates and compositions of coral reef fishes, with significant implications for human populations and nations that rely on exploitation of these species. Socio-economic consequences of fisheries collapse may be minor where there are alternative (e.g. pelagic) resources or fishing grounds, but in some areas long-term impacts of bleaching on fishers are expected to be substantial (Graham et al. 2007). The state of reef coral and fish communities also affects tourists' perceptions (e.g. Shafer and Inglis 2000; Williams and Polunin 2000), reducing the likelihood of tourists returning to the same location (Uyarra et al. 2005). In many places, especially developed nations, the value of fishes and reefs to tourism is far greater than fishing (Pet-Soede et al. 1999). Climate-induced coral depletion is likely to have significant and possibly irreversible consequences for both tourism and fishing industries (Worm et al. 2006).

9.5 Conclusions

Coral reefs are unique ecosystems in that they harbour an exceptional diversity of motile species. Many of these species have a close association with the coral communities which form the reef framework and contribute to its complex physical structure. While further research on patterns of resource use for coral reef organisms is essential, effects of coral bleaching and associated coral loss clearly extend beyond those species traditionally thought to have specific reliance on corals for food and shelter (e.g. butterflyfishes, damselfishes, gobies). Without corals, tropical reefs will support a very limited diversity of motile reef organisms, mostly highly generalist species that associate with rubble and algal substrates (Jones et al. 2004). Corals and coral reef environments are not expected to disappear completely, but there are likely to be shifts in community structure towards bleaching-resistant species (Hughes et al. 2003; McClanahan et al. 2004), which are less structurally complex and rarely used by coral-dwelling or coral-feeding species (McClanahan et al. 2004). Without intervention and effective management, coral reef habitats may become dominated by highly undesirable yet resilient coral assemblages.

Assemblages of reef-associated animals can recover following disturbances, provided that the benthic communities themselves recover (Halford et al. 2004) which are, in turn, dependent upon an intact fauna of functionally important motile species (Hughes et al. 2007). Resilience and the potential for coral reef ecosystems to recover from past disturbances depends on a range of factors. These include the spatial scale and intensity of disturbances, the temporal pattern of disturbances, whether these disturbances have unique, common, or interacting effects, the availability of reservoir populations for the replenishment of degraded populations, and the functional integrity of the system. By actively reducing or managing these interacting factors we will be best placed to limit, or at least retard, the devastating cumulative impacts of coral bleaching on coral reef communities. This requires an explicit and unequivocal decision to manage reefs to maximise their resilience. Reef stressors that can be directly managed, such as sediment runoff and poor water quality, must be limited or reduced as a matter of urgency (Hughes et al. 2003). Similarly, fishing pressure, especially on important functional groups, must be controlled to maintain functional integrity of reef systems (Bellwood et al. 2004; Marshall and Schuttenberg 2006). In overfished areas it will be necessary introduce measures to restore populations. Marine protected areas are valuable tools because they provide a degree of protection against the impacts of exploitation and a reproductive reservoir for the recovery of impacted populations. We should also encourage the protection of resilient reefs in areas less susceptible to bleaching as a source of population replenishment for nearby reefs that are damaged by bleaching (Salm et al. 2006). This integrated management for reef resilience in conjunction with immediate steps to reduce atmospheric greenhouse gas concentrations is critical for the future of coral reefs.

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Chapter 10
Future Scenarios: a Review of Modelling Efforts to Predict the Future of Coral Reefs in an Era of Climate Change

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10.1 Introduction

Observations of mass coral bleaching over the past 25 years are linked to periods of anomalously warm sea surface temperatures (Glynn 1991; Hoegh-Guldberg 1999; Wellington et al. 2001). This leads to speculation that climate change has increased the frequency and severity of coral bleaching events worldwide (Hoegh-Guldberg 1999). Global climate models predict that the planet's climate could warm by 2–4°C by the year 2100, without substantial effort to reduce greenhouse gas emissions far below current levels (IPCC 2007). This continued climate warming may, therefore, pose a serious threat to the long-term health of coral reef ecosystems (Hughes et al. 2003). At the same time, higher concentrations of atmospheric carbon dioxide are expected to reduce the rates of coral calcification and reef accretion (Kleypas et al. 1999; Guinotte et al. 2003).

This chapter reviews recent efforts to predict the effect of future climate change on coral reefs, focussing on coral bleaching. The chapter includes an introduction to climate modelling, a review of the application of climate models to coral bleaching, a case study on the Great Barrier Reef, and a discussion of future research needs.

10.2 Modelling Future Climates

Global climate models, which can simulate the response of the earth to the emissions of greenhouse gases, provide the basis for predictions of the response of coral reefs to climate change. The earliest climate models were simple representations of radiative properties of the atmosphere and the earth's surface, based on the energy from the sun and the composition of the atmosphere. These simple one-dimensional models evolved into today's complex general circulation models (GCM) that use physical principles to describe the transfer of heat, moisture, and momentum in a three-dimensional grid representing the global climate system.

The current generation of GCMs used in the Intergovernmental Panel on Climate Change (IPCC) assessments link the major components of the climate

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system – atmosphere, ocean, land surface, cryosphere and biosphere – to best capture the range of physical and biological feedbacks associated with climate variability and change. The models are continually updated to improve the representation of important physical processes and are rigorously tested against observed data. One generic metric for contrasting GCMs is their “climate sensitivity”, the predicted level of warming caused by a doubling of atmospheric carbon dioxide (CO_2) concentrations. The GCMs used in the IPCC Fourth Assessment Report (AR4) have climate sensitivities ranging from 2.0°C to 4.5°C, with a long-established mean of 3°C (IPCC 2001, 2007).

Forecasts of sea surface temperatures (SSTs) from GCMs are the most reliable information available for predicting the thermal environment that will influence coral reefs in the future. However, there are several key limitations to the modelled representation of future climates that are particularly relevant to the study of coral reefs. These include: (1) the coarse spatial resolution of GCMs, (2) the representation of natural modes of climate variability, and (3) the uncertainty over future greenhouse gas emissions.

First, the coarse spatial resolution of climate models limits their ability to provide forecasts for coral reefs. For example, the models employed in the IPCC Third Assessment Report and most coral reef studies to date had horizontal resolution of around 250 km and vertical resolution on the order of 100s of metres (i.e., depth of each ocean grid cell). Several of the models used in the AR4 operate at a horizontal resolution of 1° (~100 km) or better in the atmosphere and ocean and at a vertical resolution of 10–100 m in the surface ocean (e.g., Delworth et al. 2006).

Without a representation of the complex bathymetry and hydrodynamics of individual coral reefs, neither of these sets of GCMs can capture processes like the local upwelling of cooler deep waters or heating of shallow waters on the reef flat (Skirving and Guinotte 2001; Wooldridge and Done 2004). The direct GCM output is better suited to represent the mean temperature of an area of ocean containing coral reefs than the temperature surrounding an individual coral reef or an individual coral. Higher resolution regional information can be obtained by downscaling GCM output using dynamical or statistical methods. For example, predictions for an individual reef could be made by forcing a high-resolution hydrodynamic model with the coarser output from a GCM (see Sect. 11.5). Alternatively, statistical relationships between the average temperature for a region and the temperature at specific reef locations could be used to translate GCM output to a higher resolution (Donner et al. 2005).

Second, the ability to project future ocean temperatures for many coral reefs depends on model representation of natural modes of climate variability. Mass coral bleaching events have been linked to large-scale oscillations in the atmosphere–ocean system such as the El Niño–Southern Oscillation (ENSO), the Pacific Decadal Oscillation and possibly the Atlantic Multi-Decadal Oscillation (Wilkinson et al. 1999; Donner et al. 2007; Chap. 4). Therefore, the reliability of future projections for coral reefs will depend on a model’s ability to reliably represent such natural modes of climate variability in the existing climate and the response of those natural modes of variability to human-induced climate warming.

Third, future climate projections depend on assumptions about future changes in climate "forcings", including rates of emission of primary greenhouse gases. The IPCC's Special Report on Emissions Scenarios (SRES) developed 40 different scenarios based on various assumptions about demographic, economic, and technologic change over the twenty-first century (Nakicenovic and Swart 2000). Higher emissions scenarios imagine a future with more reliance on fossil fuel use (e.g., SRES A1f). Middle of the road or "business as usual" scenarios imagine a rough continuation of previous rates of increase in annual greenhouse gas emissions (e.g., IS92A, SRES A1b). The lower, more optimistic emissions scenarios imagine the annual emissions rate increasing slowly over time and eventually decreasing (e.g., SRES B1).

These future scenarios prescribe the emissions, not the atmospheric concentrations, of greenhouse gases and aerosols. The concentration of greenhouse gases in the atmosphere depends both on the emissions and on the response of the planet's ecosystems (e.g., CO_2 uptake) and feedback mechanisms (e.g., melting permafrost, leading to CH_4 release). Since the current rate of CO_2 emissions exceeds the rate of CO_2 uptake by the planet's ecosystems, freezing *emissions* at today's rate will cause a continued increase in atmospheric CO_2 *concentrations*.

"Stabilisation" scenarios are designed to represent the stabilisation of atmospheric greenhouse gas *concentrations* at some point in the future due to emission controls. These scenarios involve large reductions in the rate of emissions. Due to the long residence time of CO_2 and other greenhouse gases in the atmosphere, a certain level of climate warming is expected to occur because of past emissions. As such, GCMs show that, even if the concentration of greenhouse gases were frozen tomorrow, there would still be 0.3–0.9°C of residual or "committed" warming by the end of the twenty-first century (IPCC 2007).

10.3 Predicting Coral Bleaching from Climate Models

The heterogeneity of coral responses to temperature stress poses a central challenge in predicting the impact of climate warming on coral reefs. Hughes et al. (2003) summarised the possible theoretical models describing temperature thresholds for coral reefs under climate change. The simplest model (Hoegh-Guldberg 1999) assumes that mass coral bleaching or mortality will occur when the temperature exceeds some threshold (Fig 10.1a). An alternative model recognises different thresholds based on thermal tolerances (e.g., between coral species or growth forms) or possibly different thresholds for bleaching and mortality (Fig. 10.1b). An adaptive model envisions thresholds that might increase over time due to temperature acclimatisation and/or evolution by corals and their symbionts (Fig. 10.1c). While some of the adaptive model's thresholds change due to acclimatisation in the coral or changes in their endosymbionts (Chap. 7), much of the change would be due to the loss of more temperature-sensitive coral species.

Most studies to date used a single temperature-based threshold of 1–2°C above the usual summer maximum to predict whether mass coral bleaching or coral mortality

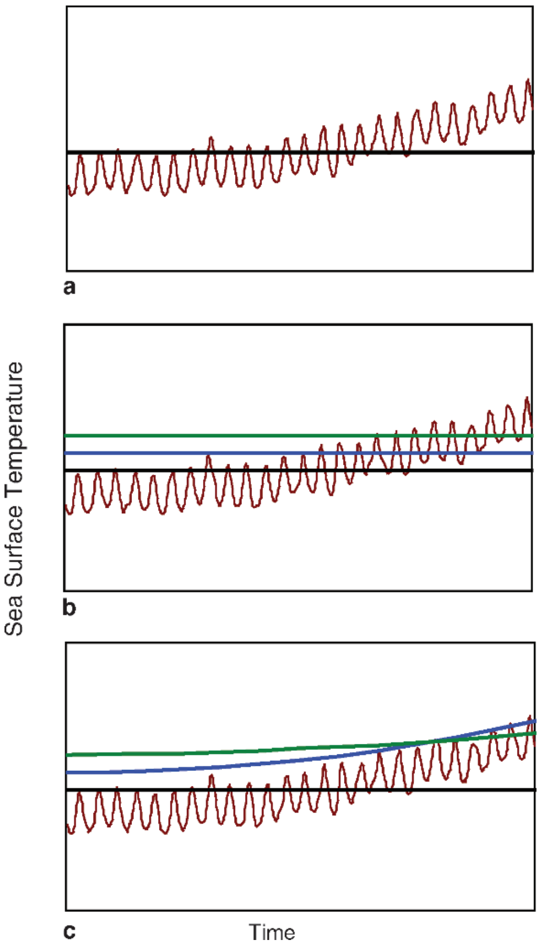

Fig. 10.1 Three models for describing temperature thresholds (*blue* and *green* lines) for predicting coral bleaching: **a** a single constant threshold across all species, **b** multiple constant thresholds, reflecting either differences in bleaching susceptibility (e.g., between species or growth forms) or severity (bleaching vs. mortality) and **c** multiple thresholds that increase in time, due to acclimation and/or evolution by corals and their symbionts (adapted from Hughes et al. 2003). The *red line* represents sea surface temperature, as it increases over time

will occur under future climate scenarios (Hoegh-Guldberg 1999; Sheppard 2003; Donner et al. 2005). Some recent studies also investigated the effect of possible temperature adaptation on the projected frequency of bleaching events, a variant of the approach depicted in Fig. 10.1c (Sheppard 2003; Donner et al. 2005).

The first group of climate change and coral bleaching studies determined temperature thresholds for individual sites from historical observations of coral bleaching or mortality (Hoegh-Guldberg 1999; Sheppard 2003; Jones 2004). Hoegh-Guldberg (1999) was the first major review of the effect of climate change on the occurrence of mass coral bleaching. In that study, the projected future SSTs from three different GCMs (ECHAM4, ECHAM3, CSIRO DAR, see references therein) under a business as usual scenario (IS92a) were used to predict the occurrence of coral bleaching at sites in French Polynesia, Jamaica, Rarotonga, Thailand, and at three sites on the Great Barrier Reef (GBR). For each site, in situ records of monthly SST and observations of mass coral bleaching were used to determine a monthly averaged temperature threshold. That study assumed that if the projected future SST[1] during a given year exceeded the temperature threshold for the site, mass coral bleaching would occur that year. The results suggested that coral bleaching at the level observed during the 1997–1998 mass bleaching event at the seven sites would occur biannually within 20–40 years under business as usual conditions (for further discussion, see Sect. 11.4). The sharp increase in bleaching frequency was predicted to lead to long-term decline of coral cover and ecosystem function.

Sheppard (2003) made future predictions for 33 Indian Ocean coral reefs using temperature thresholds based on observations during the 1998 coral bleaching event. Analysis at the time suggested Indian Ocean coral reefs damaged during 1998 required a minimum of five years for recovery. The study therefore defined the "extinction date" for 33 Indian Ocean reefs as the year in which the probability of SST for the warmest month or the warmest three months surpassing that of 1998 exceeded 20% (once every five years).

A key difference between the Sheppard (2003) analysis and that of Hoegh-Guldberg (1999) is the method of combining historical and modelled future SSTs. Sheppard (2003) blended the historical monthly SSTs from the HadISST 1° × 1° resolution global dataset and simulated future SSTs from the HacCM3 model under a business as usual scenario (IS92a) into one continuous dataset. The projected SSTs for 2000–2100 were estimated by adding the monthly GCM anomalies to the observed climatology and then applying the seasonal amplitude from the historical time series, using statistical fitting between observed and simulated monthly SSTs for the 1950–1999 period. This method accounted for the fact that many GCMs underestimated the seasonal amplitude in SSTs.

The study found the extinction date should occur between 2010 and 2030 for most Indian Ocean coral reefs south of the equator, but not until the latter half of the century for some coral reefs north of the equator (Fig. 10.2). The date for high-latitude reefs in the Arabian Sea may be delayed until the end of the century due to cold water upwelling. At each site, the projected increase in SSTs suggested that adaptation or acclimatisation by corals and their symbionts by 2°C could delay the extinction date beyond the end of this century. Recovery of only 20–30% of the corals in the five years since the 1998 bleaching (Wilkinson 2004) suggests that these extinction dates may be optimistic.

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[1] To eliminate systemic difference between modelled and observed temperatures, the future temperatures are estimated as the sum of model "anomalies" (i.e., modeled January, 2050 SST minus modelled mean January SST for today's climate) and the observations (i.e., January in today's climate).

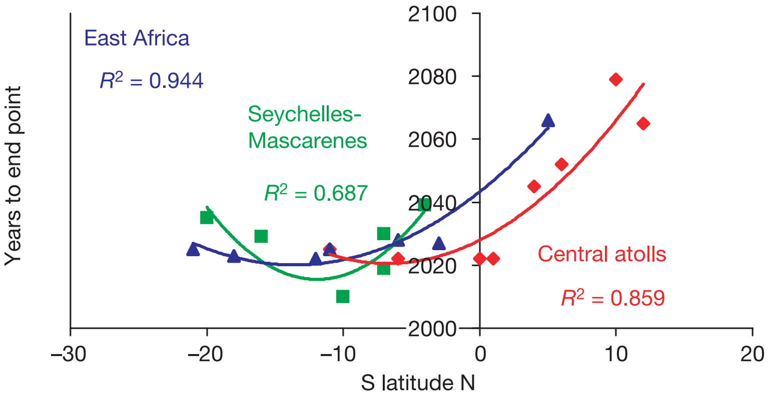

Fig. 10.2 "Extinction dates" for coral reefs across the Indian Ocean. The data points represent the year that the probability of exceeding the SST threshold (the warmest three months of 1998) reaches 0.2, or once every five years, for the individual site. The curves are significant fits for the three main coral reef regions in the eastern Indian Ocean (from Sheppard 2003)

The "blending" of model and instrumental data was also applied to HadCM3 simulated SSTs in the Caribbean Sea (Sheppard and Rioja-Neito 2005). The results demonstrated that the peak temperature observed during 1998, when bleaching occurred in parts of the Caribbean, would be surpassed biannually across most of the Caribbean before the year 2050.

A second approach to modelling coral bleaching uses average maximum temperatures in observed climate data to determine bleaching thresholds (Hoegh-Guldberg 2001, 2005; Donner et al. 2005). The NOAA Coral Reef Watch satellite-based coral bleaching prediction program predicts the onset of bleaching using the degree heating week (DHW), a measure of the accumulated temperatures in excess of the usual summer maximum (Liu et al. 2006; Skirving et al. 2006; Chap. 4). Donner et al. (2005) took advantage of these satellite-derived data products to estimate the frequency of coral bleaching and required rates of temperature adaptation for thousands of locations worldwide for upper and lower business as usual climate scenarios (SRES A2, SRES B2). The historical satellite SST and DHW data provided a reliable way to develop algorithms for predicting the occurrence of thermal stress that can cause bleaching at sites worldwide from GCMs.

Algorithms were developed by transforming the observed 36 × 36 km resolution twice-weekly satellite SST data for 1985–2002 into monthly SSTs at the same satellite resolution and into monthly SSTs at the resolution of the two different GCMs (HadCM3, US National Center for Atmospheric Research's PCM, see references therein). From these a degree heating month (DHM) index was calculated. Historical data analysis showed that DHM > 1°C·month and DHM > 2°C·month were the best proxies for the lower and upper bleaching thresholds, DHW > 4°C·week and DHW > 8°C·week, used by the NOAA Coral Reef Watch program (Liu et al. 2006). A statistical downscaling relationship between the maximum annual SST at the satellite resolution and at the GCM resolution was also developed for each 36 × 36 km grid cell containing a coral reef (3379 cells with HadCM3, 2023 cells with PCM).

The results of Donner et al. (2005) showed the variation in thermal stress and the required temperature adaptation for extended survival of corals under different climate models and emissions scenarios. The accumulation of DHMs exceeds the upper bleaching thresholds across much of the tropics by the 2050s in both models and under either scenario (Fig. 10.3a). Warming is projected to be greatest in the central equatorial Pacific, as both GCMs predict that ENSO-like conditions prevail in a warmer climate. The lower (DHM > 1°C·month) and upper (DHM > 2°C·month) bleaching thresholds are surpassed at the majority of the world's reefs every two years by the 2050s (Fig. 10.3b).

Following a method similar to Sheppard (2003), Donner et al. (2005) estimated the rate of temperature adaptation or acclimatisation required to avoid surpassing the coral bleaching thresholds in future decades. The results indicated the majority of the world's coral reefs would require adaptation of at least 0.2–0.3°C per decade to ensure that low-intensity bleaching events (DHM > 1°C·month) do not occur more than once or twice a decade by the 2030s to 2050s (Table 10.1). The required rates of adaptation vary widely across the tropics, with values of up to 0.5–1.0°C per decade in parts of the central Pacific and Polynesia, even in the GCM with low climate sensitivity.

A third approach to modelling coral bleaching under climate change uses temperatures or thermal stress indices averaged over a large region as representative of the extent of bleaching in the region. McWilliams et al. (2005) contrasted historical SSTs in the Caribbean from the MOHSST6 historical dataset with historical data

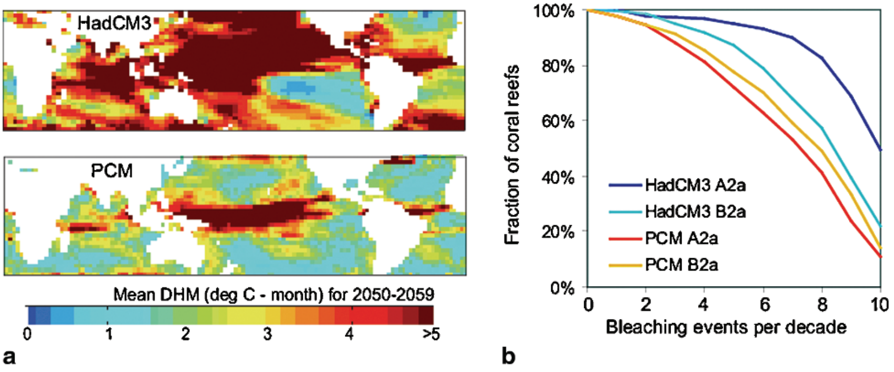

Fig. 10.3 Projected thermal stress measured as degree heating months (*DHM*) for 2050–59 (from Donner et al. 2005): **a** annual mean DHM for 2050–59 according to HadCM3 and PCM in the SRES A2 scenario, **b** number of times per decade that thermal stress exceeds the upper bleaching threshold (DHM > 2°C), expressed as a fraction of world's coral reefs. Significant bleaching is expected at DHM > 1°C·month, mass bleaching and significant mortality are expected at DHM > 2°C·month

Table 10.1 Percentage of reefs requiring thermal adaptation by 2030–2039. Shown is the percent of coral reef grid cells, in the SRES A2 and B2 emissions scenarios that require a 0.5°C or 1.0°C increase in the temperature threshold at which degree heating months begin to accumulate in order to avoid mass bleaching more than once every five years

Ocean region	Coral reefs (%)			
	HadCM3		PCM	
	+0.5°C	+1.0°C	+0.5°C	+1.0°C
Indian Ocean	83–92	46–55	38–57	10–19
SE Asia	58–62	16–17	39–40	6–9
Micronesia	58–79	13–54	58–79	6–7
GBR/Coral Sea	29–67	7–40	17–53	4–6
Polynesia	69–81	24–39	58–82	19–31
Caribbean	75–78	22–30	13–40	0–11

on spatial extent of bleaching determined from the reports to ReefBase (http://www.reefbase.org). Regressions estimated that a 0.1°C increase in Caribbean-average SST would cause a 35% increase in the number of 1° × 1° coral reef cells reporting some bleaching and a 42% increase in the fraction of coral colonies bleached. Although this type of regional bleaching prediction is less meaningful for individual coral reefs, it is well-suited to the application of coarse GCM predictions for the future.

In a recent study of the role of climate change in the 2005 Caribbean bleaching event, Donner et al. (2007) examined the mean thermal stress over the affected region rather than the SSTs at individual sites or individual model grid cells. By focussing on a large region, the study was able to use historical datasets and GCMs (CM2.0, CM2.1, from the US Geophysical Fluid Dynamics Laboratory) to examine the probability of the 2005 bleaching event occurring with and without the effect of past greenhouse gas emissions on the climate. The analysis showed that anthropogenic forcing increased the chance of a coral bleaching event such as that observed in the Caribbean in 2005 by at least an order of magnitude.

The Donner et al. (2007) study also provided further insight into the effect of different emissions scenarios and possible adaptation or acclimatisation by corals and their symbionts on the frequency of mass bleaching events in the future. The GCMs predict that mean DHM over the study region would exceed 2°C·month at least biannually by the 2020s or 2030s under both a business as usual scenario (SRES A1b) and a lower-emissions scenario (SRES B1), in which atmospheric CO_2 concentrations stabilise at double the pre-industrial levels in the year 2100.

However, the results change if corals and their symbionts are able to adapt or acclimatise by 1.0–1.5°C, as observed for some corals (Berkelmans and van Oppen 2006; Chap. 7). In the business as usual scenario, such adaptation would postpone the mass coral bleaching from occurring once every five years until the latter half of the century. In the stabilisation scenario, such adaptation could prevent mass coral bleaching from occurring in the eastern Caribbean more than once a decade throughout this century.

10.4 The Great Barrier Reef: a Case Study

The Great Barrier Reef (GBR) is the world's largest coral reef system, stretching over 2000 km along the northeast coast of Australia at the edge of the Indo-Pacific biodiversity hotspot. It comprises over 3000 individual reefs found inshore, mid-shelf, and up to 200 km offshore. The reefs are subject to a variety of disturbances, including agricultural runoff, riverine flood plumes, crown-of-thorns starfish outbreaks, severe tropical storms, fishing, tourism, and marine shipping. The GBR is also one of the world's most protected reef regions. The Representative Areas Program and the Reef Water Quality Protection Plan have been recently implemented as part of a strategy to maintain biodiversity and support the ecosystem's resilience to aid survival of the reef through climate change (www.gbrmpa.gov.au).

Prior to 1979, no mass bleaching events were reported for the GBR. Since that time, seven mass bleaching events have been recorded: 1980, 1982, 1987, 1992, 1994, 1998, 2002, and most recently in 2006 (Berkelmans and Oliver 1999; Hoegh-Guldberg and Hoegh-Guldberg 2004; Lough et al. 2006). Average SST decreases to the south (poleward) along the GBR and, due to localised adaptation, the threshold temperature at which corals bleach also decreases to the south (Berkelmans 2002). The bleaching events have generally increased in their intensity and extent over time. The 1998 event (40% of reefs bleached) and subsequently the 2002 event (50% of reefs bleached) were each described as the most severe bleaching events recorded on the GBR (Berkelmans and Oliver 1999; Berkelmans et al. 2004).

Using data collected by ships of opportunity, Lough (2001) found that there had been an increase of 0.6°C in the annual average sea surface temperature (SST) for the GBR during the twentieth century. Several studies specifically examined projected increase in SST on the GBR. Lough et al. (2006) extended the Lough (2001) data to 2006 and presented the projected temperature increase on the GBR according to two business as usual climate scenarios (Fig. 10.4). These forecasts suggest that the waters of the GBR will be 1–3°C warmer than at present by the end of this century. The Hoegh-Guldberg (1999) study concluded that temperatures would exceed those observed in 1998 at sites in the northern, central, and southern GBR by the year 2020. Done et al. (2003) found that present-day temperatures in the northernmost tip of the GBR will be experienced at the southern end of the GBR by 2050 in a pessimistic emissions scenario, or by 2100 in an optimistic emissions scenario.

Hoegh-Guldberg (1999) found that the modelled temperature increases are expected to induce annual bleaching events across the GBR by 2050 (Fig. 10.5). The Donner et al. (2005) global assessment generally confirms that result, suggesting that coral bleaching would occur at least once every two years across 83–100% of the GBR by 2050–2059. Done et al. (2003) show that even the most optimistic climate scenario predicts that catastrophic thermal events are possible at mid- and outer-shelf reefs by 2050.

More explicit analysis of predictability of bleaching in the GBR and the impact on community structure was conducted using Bayesian belief networks (BBN; Wooldridge and Done 2004; Wooldridge et al. 2005). BBN link various systemic

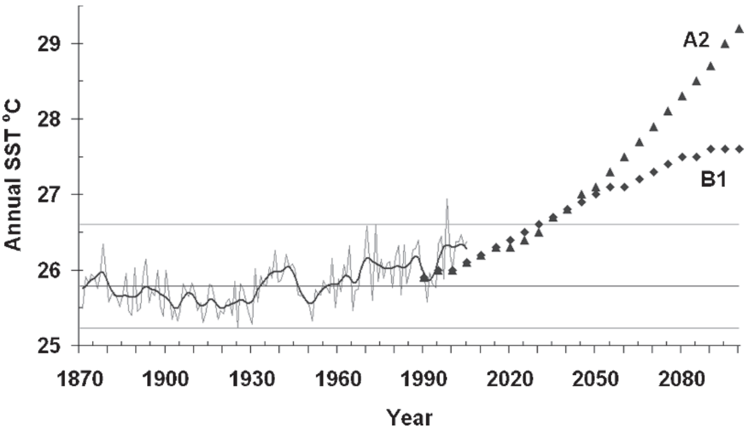

Fig. 10.4 Observed and projected annual mean SST for the Great Barrier Reef. The *thin line* is the annual mean instrumental SST record, 1871–2005 (HadISST and NOAA OI.v2 SST); the *thick black line* is the 10-year Gaussian filter. The *horizontal lines* denote the 1871–1989 mean SST (25.8°C) and the observed range (25.2–26.6°C). Projected SSTs are given for GBR 1990–2100 (ReefClim, Roger Jones, CSIRO) for the B1 (*diamonds*) and A2 (*triangles*) middle of the road climate scenarios. Both scenarios suggest that, by 2035, average GBR SSTs will be outside the range observed in the instrumental record prior to 1990 (adapted from Lough et al. 2006)

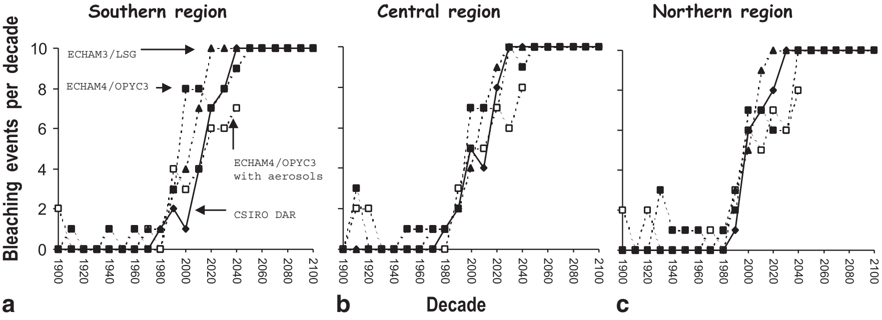

Fig. 10.5 The number of times (per decade) that predicted SSTs will exceed coral bleaching thresholds for: **a** southern (23.5°S, 149.5°E), **b** central (18.0°S, 147.5°E), and **c** northern (11.0°S, 143.0°E) sites on the Great Barrier Reef. The models are ECHAM4/OPYC3 (*black squares*), ECHAM4/OPYC3 with aerosol effect added (*white squares*), ECHAM3/LSG (*black triangles*), and CSIRO DAR GCM (*black dots*; from Hoegh-Guldberg 1999)

variables, their dependencies, and probabilistic outcomes. Wooldridge and Done (2004) described a BBN that linked coral habitat and community type, local SST, climatological SST, and potential for cooling by upwelling of deep water. The BBN successfully predicted the coral mortality category (low, medium, high) for 71% of field observations following the 2002 bleaching on the GBR.

Wooldridge et al. (2005) used another BBN to predict change in the community structure of inshore locations in the central GBR under two climate warming scenarios (1.0–1.5°C or 2.0–2.5°C increase from 1990 to 2050). The BBN determined the probabilistic composition of hard coral, algae, and bare substrate, based on the warming scenario and the mortality and recovery likelihoods of the hard corals. The analysis included two characteristic hard-coral types, predicted SST, varying constraints on algal growth rate, and thermal adaptation of the corals. The study found that natural (i.e., herbivory) or managed constraint of algal growth would be essential to allow recovery of coral populations after bleaching episodes but would not halt long-term climate-related coral reef decline.

The bleaching predictions for the GBR largely assume no temperature adaptation or acclimatisaton by corals over time. Donner et al. (2005) estimates that 17–67% of the coral reefs across the GBR will require at least a 0.5°C increase in their thermal tolerance, while 4–40% will require an increase of 1.0°C, by the year 2030 to avoid frequent harmful bleaching events. Multiple occurrences of bleaching at sites on the GBR are cited as evidence that corals at these sites are not developing greater thermal tolerance (Hoegh-Guldberg 1999). However, recent field and laboratory evidence suggest that the common GBR species *Acropora millepora* can increase its thermal tolerance level by 1.0–1.5°C by shuffling the dominant symbiont in its tissue (Berkelmans and van Oppen 2006; Chap. 7). Such an increase in thermal tolerance might help GBR corals avoid predicted bleaching events in the next several decades, but it is insufficient to meet the larger temperature increase predicted for the latter half of the century (Hoegh-Guldberg 1999; Done et al. 2003; Berkelmans and van Oppen 2006; Lough et al. 2006). An increased understanding of adaptation would aid in determining management strategies for the GBR (Hoegh-Guldberg and Hoegh-Guldberg 2004).

10.5 Future Improvements in Physical Modelling

The general projected increase in thermal stress on coral reefs under future emission scenarios is so rapid and global in scale that it is unlikely to change with future improvement in GCMs (Donner et al. 2005). Future models operating at high horizontal resolution (<1 km) may be instrumental in making specific predictions for individual coral reef complexes. Advances in the application of fluid dynamics theory and computing power are already increasing the resolution of GCMs and hydrodynamic models. For example, the Hybrid Coordinate Ocean Model (HYCOM) can presently operate globally at a horizontal resolution as fine as 1/12° (Metzger et al. 2006) and regionally at horizontal resolution of 1/25° (Kourafalou and Balotro 2006; Prasad and Hogan 2007).

Modelling efforts are being conducted at very high spatial resolutions (<1 km) in and around coral reefs. Skirving et al. (2004) describe a hydrodynamic model of Palau with ~250 m resolution. Mapped ocean currents have been used to determine the vertical mixing of water across the Palau lagoon during periods of low-wind that are characteristic of bleaching events (Skirving and Guinotte 2001). Skirving et al. (2006) describe the reduction in SST due to vertical mixing and link this to the capacity of a water column to absorb solar radiation. Well-mixed regions distribute heat throughout the water column, incurring a small temperature increase throughout the column. In stratified regions, heat is contained near the surface, causing a significant rise in SST. This suggests different temperature climates in which corals exist and, therefore, a different level of acclimatisation to thermal events. The design of protected areas can include the modelled thermal capacitance to provide protection for corals during climate-induced bleaching events (Skirving et al. 2006).

Bode et al. (1997) describe a parameterisation scheme for sub-resolution features, such as those seen in and around coral reefs. This scheme was applied to a tidal model of the southern GBR with a resolution of ~8 km that successfully simulated the tidal amplitude and phase throughout the region. Development of such modelling techniques at various horizontal resolutions will improve the accuracy of forecasts of the effects of climate change and assist design of marine protected areas for coral reef ecosystems.

10.6 Conclusions

Various GCM-based studies present an overall picture of the effect of climate change on the frequency and severity of mass coral bleaching and bleaching-induced mortality around the world. Several studies confirm the original conclusion of Hoegh-Guldberg (1999), that mass coral bleaching could become a biannual event by the 2020s or 2030s at many coral reefs without any thermal adaptations by corals and their symbionts, although important local and regional exceptions have been noted (Sheppard 2003; Donner et al. 2005). Recent work also argues that human-induced warming has already increased the likelihood of mass coral bleaching events in some regions (Donner et al. 2007).

This result is generally robust across different emissions scenarios. Due to time lags in the climate system (between emissions and climate impact) and in the economic system (between a decision to reduce emissions and actual emissions reduction), the simulated climate in different emission scenarios does not diverge until the latter half of the century. There is a greater range in future projections between different GCMs, with different climate sensitivities, than between different emissions scenarios. Nevertheless, even the lowest estimate of business-as-usual projected ocean warming (from the NCAR parallel coupled model) indicates that mass coral bleaching would occur biannually on the majority of coral reefs worldwide by 2050 (Donner et al. 2005).

Corals and their symbionts will have to adapt to rising temperatures to avoid bleaching events that are too frequent to allow the communities to recover. The rate and magnitude at which corals and their symbionts will have to adapt to increasing temperatures appears to vary across the globe (Sheppard 2003; Donner et al. 2005). Climate projections for this century indicate that temperature adaptation might postpone the occurrence of frequent harmful bleaching events and allow corals to survive, provided that policies and technologies alter the path of greenhouse gas emissions and future warming. However, in that case, long-term "committed warming" beyond 2100 could still represent a serious threat to coral reefs (Donner et al. 2007).

An important area for future research is the effect of climate-induced coral bleaching and other disturbances on coral reef community structure. More frequent coral bleaching events, especially when combined with local disturbances such as fishing, pollution or sedimentation, are expected to keep coral and fish species richness low (Wilson et al. 2006; Chap. 10). Ecological models (e.g., Mumby 2006) could be instrumental in describing the effect of higher bleaching frequencies and other disturbances on the extent of coral and macroalgal cover. As more field data become available, models could include multiple coral taxa with different temperature tolerances, growth rates, and reproduction rates (e.g., Wooldridge et al. 2005).

Such combined physical and ecological models will also be critical in estimating the ability of reefs to adapt or acclimatise to warmer ocean temperatures, as well as other local (e.g., fishing pressure) and global (e.g., rising pCO_2) stressors. Models could be used to examine the ecological impact of adaptation by corals and their endosymbionts, such as switching to more temperature-tolerant symbionts (Little et al. 2004; Chap. 7), increased dependence of corals on heterotrophic feeding (Grottoli et al. 2006) or community shifts to more heat-tolerant species (Done 1999). These efforts will help define any management activities that could minimise the effect of the more frequent coral bleaching events expected to occur as the climate continues to warm.

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Chapter 11
Synthesis: Coral Bleaching - Patterns, Processes, Causes and Consequences

M.J.H. van Oppen and J.M. Lough

Global climate is changing as a result of human activities. As we enter a rapidly warming world, "coral bleaching" has entered the lexicon of early climate change impacts. Breakdown, due to thermal stress, of the special relationship between two organisms, coral and algae, has consequences for ongoing maintenance of the structurally complex, biologically diverse, charasmatic and both economically and socially important ecosystems that make up tropical coral reefs. This volume brings together various perspectives on the coral bleaching phenomenon, how it is measured (Chap. 5) and what its consequences are, ranging from deep geological time through to possible future scenarios for tropical coral reef ecosystems.

There is no doubt that sea water temperatures have increased over the past century (Chap. 4) and climate models predict that further temperature rises and greater fluctuations are to be expected (Chap. 10). Many scientific publications state that the frequency and severity of bleaching events have also increased, but a detailed analysis of bleaching reports suggests that there is an insufficient amount of data to support or refute the hypothesis that major bleaching events are increasing in frequency (Chap. 3). The same analysis reports a lack of evidence for an increase in bleaching intensity, despite an increase in thermal stress. One possible explanation is that corals have acclimatised to elevated water temperatures (Chap. 7), through shuffling of their algal symbionts (Chap. 6) or as a result of phenotypic plasticity in other traits. A recent study has shown that algal shuffling can lead to increased thermal tolerance in a natural and non-manipulated coral population (Jones et al. 2008), but it is unlikely that all coral species have this ability to shuffle their symbionts. Alternatively, selection may already have removed the colonies most sensitive to bleaching. The potential for corals to adapt to further increases in sea water temperatures by genetic changes at the level of populations is unknown, but estimates (of heritability) are underway for a range of traits that are relevant to the bleaching tolerance of the coral host and their algal endosymbionts (Csaszar et al., unpublished data).

Modelling efforts show that most corals populations will have to adapt to survive future temperature increases (Chap. 10). If individual coral species are unable to adapt, then large changes in coral community composition (Chap. 8) and loss of diversity (Chap. 2) are likely to result, which will have major down-stream consequences for motile reef organisms (Chap. 9). In the short term, it is important for

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managers to understand which reefs are most resistant to bleaching and how quickly coral reefs can recover from bleaching events, especially those that cause mass coral mortality. The spatial patchiness in thermal stress and responses to thermal stress indicates that “climate change refuges” may exist (Chap. 8). Such refuges are likely to be located either in areas with stable cool water or in those that show historically large fluctuations in sea surface temperatures (McClanahan et al. 2007). Degraded reefs may be reseeded from “climate change refuges” and it is therefore crucial to understand the dispersal potential of corals and other coral reef organisms over ecological time scales (van Oppen and Gates 2006; Hellberg 2007). The direction and distances of recent dispersal events can be measured using genetic approaches (Underwood et al. 2007) or with stable isotope labelling of fish larvae (Almany et al. 2007).

In summary, coral bleaching is a biological response to changes in the physical environment of present-day coral reefs. Several mass coral bleaching events in recent years, most notably 1997–1998, have prompted enhanced research efforts into many aspects of this phenomenon. We now know much more about the causes and consequences of coral bleaching than we did only a decade ago. However, there is still much more to learn and, unfortunately, many of the experiments are happening in real time in the real world. Changes in the physical environment, in particular warming of the tropical oceans, are, without drastic greenhouse gas mitigation strategies, set to continue into the foreseeable future. Continued warming of the tropical oceans, along with other climate change and ocean acidification impacts on coral reefs, is an added human-induced burden on what, in many parts of the world, are already seriously compromised ecosystems due to direct local and regional stresses. In combination, this panoply of human-induced pressures does not bode well for the maintenance of the world’s coral reefs into the future.

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