23 Temperature Stress and Coral Bleaching

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23.1
Introduction

23.1.1
The Bleaching Phenomenon

Reef corals are symbioses that consist of an animal partner and dinoflagellate algae commonly known as zooxanthellae. This delicate association functions only within a very narrow range of environmental conditions in shallow tropical seas (Wells 1957). The symbiosis is thought to have developed as a means of coping with very low concentrations of nutrients in tropical marine waters (Muscatine and Porter 1977). This association provides benefits to both partners. The zooxanthellae are primary producers and supply their coral hosts with photosynthetic products vital to meeting their energetic requirements. In return, the zooxanthellae receive living space and nutrients in the form of waste metabolic products from the host. The tight cycling within the symbioses facilitates the high productivity and calcification rates observed in corals (Falkowski et al. 1984).

"Coral bleaching" occurs when environmental conditions disrupt the symbiosis, leading the degeneration and/or expulsion of zooxanthellae from the coral host. As a result of photosynthetic pigment loss, the white skeleton becomes visible through the transparent coral tissue, giving the organism a "bleached" white appearance. Bleaching is fatal to the coral unless the symbiotic relationship can be quickly re-established. Reef corals play a central role in coral reef communities, so their continued health is of critical importance.

Since the 1980s, spectacular regional bleaching events have occurred on coral reef areas throughout the world with increasing frequency and increasing geographic extent. These mass bleaching events correlate with elevated sea surface temperatures (SST). The mass bleaching phenomenon is believed to be associated with global warming due to anthropomorphic release of carbon dioxide and other gasses (reviewed by Jokiel and Coles 1990; Williams and Bunkley-Williams 1990; Glynn 1991, 1993; Goreau 1992; Pittock 1999; Fitt et al. 2001). The issue of global warming and mass coral bleaching will undoubtedly continue to be a major concern in the field of coral reef ecology.

23.1.2
Bleaching as a Disease Symptom

Coral bleaching is a condition that fits all the definitions of disease (Chap. 25, Rosenberg, this Vol.). The term bleaching describes a symptom that is produced by a variety of adverse physical, chemical and biological conditions in the environment. The term bleaching is quite subjective and has been applied to corals showing various degrees and patterns of pigment loss.

Bleaching can be caused by changes in numerous environmental parameters acting alone or in combination. These include increased sea surface temperatures (Jokiel and Coles 1990), low temperature (Steen and Muscatine 1987; Gates et al. 1992), increased irradiance (Lesser et al. 1990), decreased irradiance (Yonge and Nicholls 1931b; Franzisket 1970), altered spectral quality in the visible range (Kinzie et al. 1984), altered spectral quality in the ultraviolet radiation (UVR) range (Gleason and Wellington 1993), low salinity (Goreau 1964; Coles and Jokiel 1978), sedimentation (Meehan and Ostrander 1997; Philipp and Fabricius 2003), infectious disease (Kushmaro et al. 1996, 1998; Ben-Haim and Rosenberg 2002), exposure at low tide (Vaughan 1914; Yonge and Nicholls 1931b), oil contamination (Guzman et al. 1991) and exposure to toxic materials (Jones 1997; Jones and Steven 1997). Bleaching represents a single symptom that can be caused by a wide range of environmental stresses acting alone or in concert. Therefore, bleaching alone tells us little about the cause of the disease.

23.1.3
Coral Bleaching as an Environmental Indicator

Even the casual observer can easily recognize highly bleached corals. Thus, bleached corals have some value as an indicator of environmental stress. For example, documentation of severe bleaching events of 1998 depended on reports from untrained as well as trained observers on many remote reefs (Wilkinson et al. 1999). Establishing cause and effect of bleaching is a great challenge, because the term is highly subjective, imprecise and has many causes (Fitt et al. 2001). Conflicting reports arise because the "cause" has already passed before the conspicuous bleaching "effect" is noted. The damage has been done to the coral before bleaching becomes apparent. Observers generally are forced to conduct retrospective analysis based on limited environmental data. Measurements of the critically important environmental and physiological factors involved are usually not available. Thus, differences in the interpretation of causality arise.

23.1.4
Phenomenology Versus Mechanisms

The issue of coral bleaching will be discussed in two broad areas: (1) the phenomenology of bleaching and (2) the mechanisms involved in bleaching. The

first category is descriptive and relatively straightforward. Coral bleaching events have happened, continue to occur with increasing frequency, and have been documented. Locations, species involved and environmental conditions that lead to bleaching have been described. The second category of mechanisms is far more uncertain and speculative and subject to extensive revision as new information is produced (see Chap. 25, Rosenberg, this Vol.). Interpretation of possible mechanisms might change, but the observed phenomena will remain. One of the main reasons for describing mechanisms is to provide predictive information on the possible future impact of continued global warming and the ability of reef corals to adjust to the increasing temperatures. For the purposes of this discussion, several terms will be defined. **Acclimation** refers to short-term physiological changes that lead to increased tolerance. In general, this term is applied in a situation where an organism is exposed to changes in a single parameter, generally under laboratory conditions. **Acclimatization** refers to longer-term phenotypic changes in response to changes in the natural environment. Such phenotypic responses are usually reversible. The process is limited by genotype, which determines the ultimate ability of a coral to tolerate stress in the environment. **Adaptation** is a long-term selective process that influences the genotype and thereby the ability of a coral to function in its environment and acclimatize to changes. It is useful to begin this discussion by describing what is known of the phenomenology of bleaching, because any proposed mechanisms must account for and be consistent with these observations.

23.2
Phenomenology Overview

Reef corals symbioses constantly adjust the population of zooxanthellae and/or the concentration of photosynthetic pigment per cell to meet changing environmental conditions. Under normal circumstances degraded zooxanthella cells are continually moved and released into the coelenteron (Boschma 1925, 1926; Yonge and Nicholls 1931a, b; Gates et al. 1992; Brown 1997; Stimson et al. 2002). Under severe environmental conditions most symbionts will be expelled, resulting in a bleached colony. Death results in reef corals if the association is not quickly re-established.

23.2.1
Bleaching and Coral Function

23.2.1.1
Photosynthesis and Respiration Phenomena

Photosynthesis (P) to respiration (R) ratio in corals decreases with increasing temperature above normal summer ambient temperature (Coles and Jokiel 1977). Tropical corals from Enewetak showed a higher P:R ratio at high tem-

perature compared to subtropical varieties of the same species from Hawaii. Coles and Jokiel (1978) conducted controlled experiments involving corals acclimated for 2 months at different temperatures. Carbon fixation was subsequently measured in the corals held at those temperatures and showed that mean carbon fixation was substantially lower in the highest temperature treatment (28 °C) compared to the treatment approximating summer ambient (26 °C).

23.2.1.2
Growth and Regeneration Phenomena

Corals show optimum growth near the local summer temperature maxima (Jones and Randall 1973; Houck et al. 1977; Jokiel and Coles 1977; Coles and Jokiel 1978). A small prolonged increase of only 1–2 °C above this value will reduce skeletal growth (Jokiel and Coles 1977; Coles and Jokiel 1978). Short-term measurements of calcification rate in the coral *Pocillopora damicornis* show two calcification peaks, one at approximately 27 °C and a second at approximately 31 °C (Clausen and Roth 1975). The 27 °C peak is more prominent in subtropical Hawaiian corals and the 31 °C peak predominates in the more tropical Enewetak corals. Reduction of skeletal growth in corals at higher than normal summer temperatures has been shown in field experiments by Hudson (1981). During the 1987–1988 coral bleaching event in Jamaica, bleached colonies stopped growing during the bleaching period while unbleached corals grew at normal rates (Goreau and MacFarlane 1990). Tissue regeneration rates are lower when comparing bleached versus unbleached colonies (Meesters and Bak 1993).

23.2.1.3
Reproduction

Szmant and Gassman (1990) found that bleached corals are unable to complete gametogenesis, even in corals that have regained pigmentation. Highly bleached soft corals showed a significant reduction in reproductive output for two seasons after the corals regained full pigmentation (Michaelek-Wagner and Willis 2001a). Temperatures above normal summer maximum slow or prevent the development of gonads in corals (Hoegh-Guldberg 1999). Coral larvae exposed to 33 °C for 24 h (Edmunds et al. 2001) showed increased mortality, and reduced metamorphosis time compared to exposures at ambient temperatures (28 °C). Larval P:R ratios decreased with short-term exposures to elevated temperatures in these experiments, so presumably their longevity and competence are reduced. Settlement of *Pocillopora damicornis* coral larvae can be induced by brief exposure to high temperature (Edmondson 1946; Coles 1985). However, successful coral recruitment and growth rate of newly settled corals decreases dramatically at higher temperature, with tenfold reductions at 1 °C above the annual temperature maximum (Jokiel and Guinther 1978).

23.2.2
General Principles of Bleaching Phenomena

Complex ecological factors are involved in the bleaching phenomenon, but some generalizations are possible.

23.2.2.1
Regional Differences and Universal Response

Coles et al. (1976) concluded that corals throughout the world are living within 1–2 °C of their upper limit during the summer months in both tropical and sub-tropical environments. This statement has been substantiated by numerous other studies (Table 23.1). The 1–2 °C threshold has been observed universally, even though maximum seasonal temperature varies by 9 °C or more over the geographic range of these corals. Consequently, "bleaching hotspots" (reefs

Table 23.1. Estimated bleaching thresholds in relation to long-term mean summer maximum SST at various geographic locations

Location	Mean summer max. (°C)	Bleaching threshold (°C)	Increase above summer max. (°C)	Reference
Easter Island	25	27	2.0	Wellington et al. (2001)
Sodwana Bay, South Africa	26.5–27.0	27.5–28.8	1.0–1.8	Celliers and Schleyer (2002)
Hawaii	27–28	29–30	1.0–2.0	Jokiel and Coles (1990)
Gulf of Panama	28	–	–	Glynn (1977)
Gulf of Panama	–	30	2.0	Glynn and D'Croz (1990)
Gulf of Chiriqui	28	–	–	Glynn (1977)
Gulf of Chiriqui	–	30	2.0	Glynn and D'Croz (1990)
Bermuda	28	30	2.0	Cook et al. (1990)
Tahiti	28.2	29.5	1.3	Brown (1997)
Johnston Atoll	28.4	–	-	US Dept Commerce (1970)
Johnston Atoll	–	30.0	1.6	Cohen et al. (1997)
Puerto Rico	29	30	1.0	Goenaga and Canals (1990)
Enewetak	29–30	31–32	1.0–2.0	Coles et al. (1976)
Lizard Island, Australia	29	30	1.0	Hoegh-Guldberg and Smith (1989)
Papua, New Guinea	29	30.3	1.3	Davies et al. (1997)
Phuket, Thailand	29.5	30.1	0.7	Brown et al. (1996)
Belize	29.5	30.0–30.5	1.0–1.5	Aronson et al. (2000)
Palau	29.7–30	31	1.0–1.3	Bruno et al. (2001)
Maldives	30.3	31.4	1.1	Edwards et al. (2001)
Arabian Gulf	34	–	–	Coles (1988)
Arabian Gulf	–	35–36	1.0–2.0	Wilkinson et al. (1999)

likely to suffer from mass bleaching) have been defined as positive SST anomalies that exceed long-term mean maximum summer SST by 1–2 °C (Strong et al. 1997). The use of temperature increase above mean maximum summer SST rather than temperature yields a more predictive estimate. However, the satellite-derived temperature anomalies are based on offshore SST, which are generally 1–2 °C cooler than inshore waters during the summer months. Additional inshore heating of shallow restricted water masses by high solar irradiance during periods of low wind is needed to achieve bleaching temperatures.

The 1–2 °C margin of safety for reef corals identified by Coles et al. (1976) has already been eroded by global trends in warming on coral reefs. Corals are now living closer to their limit during summer months, and thus we are observing more frequent and more intense bleaching episodes. Since 1996, coral reefs throughout the world have been warming at a rate of approximately 0.01–0.02 °C per year or approximately 0.3–0.6 °C during that time interval (e.g., Brown et al. 1996; Hoegh-Guldberg 1999; Fitt et al. 2001; Winter et al. 2001). Climatic evidence suggests that the thermal tolerance thresholds of corals throughout the world will be exceeded every summer by the year 2030 (Hoegh-Guldberg 1999).

23.2.2.2
Temperature–Irradiance

A great deal of evidence indicates that the two primary factors involved in mass bleaching events are temperature and irradiance (reviewed in Fitt et al. 2001). High levels of solar irradiance interact with high temperature to produce coral bleaching (Jokiel and Coles 1977; Coles and Jokiel 1978; Hoegh-Guldberg and Smith 1989; Goenaga and Canals 1990; Fitt and Warner 1995; Brown et al. 1999a). A synergistic interaction occurs between temperature and irradiance (Coles and Jokiel 1978) that leads to chlorophyll reduction and lower rates of carbon fixation at temperatures above normal summer ambient. Individual corals usually show more pronounced bleaching and mortality on upper surfaces of the colony exposed to higher irradiance. Corals at shallow depths are exposed to high irradiance and are generally more prone to bleach at a given temperature than those at greater depths (Fisk and Done 1985; Oliver 1985; Lang et al. 1988; Wilkinson et al. 1999; Marshall and Baird 2000). Corals living at the same temperature and depth in turbid areas suffer less from bleaching than adjacent areas with higher turbidity (Phongsuwan 1998). High-temperature anomalies in the Society Islands during 1998 did not result in a bleaching episode, apparently because high cloud reduced solar radiation (Mumby et al. 2001).

High temperature and high irradiance are correlated. Obviously, this is because high temperature occurs during the summer season when irradiance is at its maximum. Further, high solar input combined with low wind conditions is the direct cause of high temperature anomalies. Two components of the solar spectrum are frequently implicated in bleaching. High photosynthetically active radiation (PAR) in conjunction with heat stress reduces the photosyn-

thetic rate of the zooxanthellae (Coles and Jokiel 1977, 1978; Lesser et al. 1990). Ultraviolet radiation (UVR) may also be a detrimental factor that aggravates bleaching in corals (Jokiel 1980; Lesser et al. 1990; Gleason and Wellington 1993). Total solar energy, PAR and UVR are highly correlated (Jokiel et al. 1997). PAR and UVB are simply portions of the solar spectrum that are dependent variables on total solar radiation. PAR and UVR reaching the corals are further elevated during bleaching episodes because water transparency generally increases during the warming period due to low wind speed (Goenaga and Canals 1990; Rowan et al. 1997). The sudden and prolonged changes in water column clarity that occur during calm periods result in increased irradiance at all depths and may contribute substantially to coral bleaching (Gleason and Wellington 1993). Elevated levels of solar irradiance prior to the onset of high temperature may protect corals from subsequent bleaching (Dunne and Brown 2001).

23.2.2.3
Temperature–Irradiance–Duration

Duration of exposure to both temperature and irradiance is the third major factor controlling bleaching (Coles et al. 1976; Coles and Jokiel 1978). Prolonged exposure to temperatures slightly higher than the summer maximum can eventually produce bleaching in corals (Jokiel and Coles 1977). There is a strong relationship between severe bleaching and cumulative heat stress under conditions that exceed the normal summer maximum of 29 °C in Puerto Rico (Winter et al. 2001). Thus, the "hot spot" model (Strong et al. 1997) has recently been upgraded to include duration as well as intensity of heating. Bleaching thresholds are defined in degree heating weeks (DHWs), which are not allowed to accumulate unless the sea surface temperature is at least 1 °C above the maximum expected summertime temperature (Liu et al. 2003). One DHW is equivalent to 1 week of sea surface temperature at 1 °C above the expected summertime maximum. Two DHWs represent either 1 week at 2 °C above the expected summertime maximum or 2 weeks at 1 °C above the expected summertime maximum. Severe bleaching generally accompanies DHWs in excess of ten (http://www.osdpd.noaa.gov/PSB/EPS/method.html). The "hot spot model" does not include the effect of irradiance.

A conceptual model relating solar irradiance, heating above summer maximum, length of exposure and bleaching is presented as Fig. 23.1. The general model is based on published reports and 30 years of personal observation under experimental and field conditions. Extremely low irradiance situations are omitted for purposes of simplicity because darkness will inevitably lead to bleaching (Yonge and Nicholls 1931b; Franzisket 1970). The three-dimensional surface represents a bleaching tolerance "roof". Corals living at temperature-irradiance-duration conditions under the roof will not bleach. Those living under conditions at or slightly above the roof will bleach. Rapid mortality results from conditions higher above the roof. Note that at low irradiance, cor-
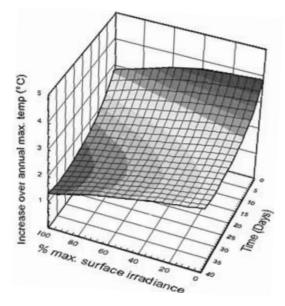
■ Fig. 23.1. The bleaching threshold for corals can be represented by a three-dimensional surface that is determined by a temperature increase above mean annual summer maximum, percent of peak annual surface irradiance (figure excludes very low levels of irradiance) and exposure time. Bleaching and eventual death occur under conditions at or above the ceiling

als can withstand exposure to high temperatures (3–4 °C over long-term mean summer maxima) for short time periods. At high irradiance, this capacity is reduced. In all cases, resistance to bleaching diminishes over time. At full solar irradiance, corals bleach at 1–2 °C above the mean annual maximum temperature within 2–4 weeks (Table 23.1). Shaded portions of colonies, colonies growing in deeper water, or corals under cloud cover at the same temperature will bleach at a slower rate. This is a generalized relative model assuming a more or less constant diurnal cycle of temperature and irradiance. The model describes conditions that on average lead to mass bleaching. Various species show higher or lower tolerance (e.g., Marshall and Baird 2000; Bruno et al. 2001). Another important point is that bleaching thresholds are defined in terms of mean temperature. Corals can tolerate considerable fluctuations (up to several degrees for limited periods) on reefs that can occur at low tide (e.g., Jokiel and Coles 1974; Craig et al. 2001), but the mean temperature ultimately determines the threshold.

This model assumes a relatively constant diurnal cycle of irradiance. Rapid increases in irradiance can occur in reef areas subjected to high terrigenous sedimentation. Prolonged periods of high wind create wave action that keeps fine sediments in suspension and greatly reduce irradiance penetration. In response, the corals photoacclimatize to the low light conditions. Onset of calm conditions under clear skies allows the sediments to settle with a consequent
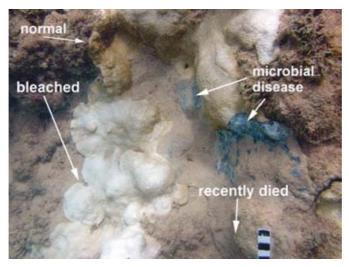
■ **Fig. 23.2.** Coral *Montipora capitata* growing on vertical wall was bleached by high turbidity and irradiance stress at Pilaa, Kauai. Microbial disease has invaded the bleached tissue. Unbleached tissues remain in area partially shaded by reef overhang. Scale in cm

rapid increase in irradiance reaching the corals. Such sudden increases in irradiance can result in bleaching (Fig. 23.2) at normal temperatures (Hoegh-Guldberg and Smith 1989).

23.2.2.4
Interactions Between Temperature–Irradiance and Other Ecological Factors

Water Motion. The relationship between duration, temperature and irradiance is further modified by water motion. Vigorous water motion has long been known to favor reef coral development. Water motion in the form of currents removes sediment and waste products and moderates factors such as temperature, salinity and oxygen concentration on the reef. Water motion influences growth, mortality and reproduction rate, and appears to influence corals by controlling the rate of material exchange across the interface between the seawater and the coral tissue (Jokiel 1978). *Acropora digitata* colonies held at 30 °C under low water-flow conditions suffered high bleaching mortality while colonies at the same temperature under high-flow conditions showed no bleaching effects (Nakamura and van Woesik 2001). Low wind conditions with resulting low water motion frequently occur during bleaching events, exacerbating the temperature–irradiance-induced stress (Goenaga and Canals 1990; Gleason and Wellington 1993).

Sedimentation/Turbidity. Turbid environments reduce high solar irradiance during periods of thermal stress and, consequently, can protect them from

bleaching (Phongsuwan 1998). On the other hand, turbid environments can be the cause of bleaching, even at normal temperatures. For example, Fig. 23.2 shows a coral bleached at normal temperature in a high sediment environment off Pilaa, Kauai. Light intensity was greatly reduced in the inshore waters by high turbidity produced by massive mudflows from a grading project. Prolonged NE trade wind conditions produced onshore waves that kept the sediment in suspension. The corals became photoacclimatized to a very low irradiance. When the winds ceased, the sediment settled and the water became highly transparent. The corals were suddenly exposed to high irradiance, which caused them to bleach as described by Hoegh-Guldberg and Smith (1989). This type of bleaching has been observed in localized high sediment environments on the islands of Molokai, Kahoolawe, Lanai and Kauai (Jokiel, unpubl. observ.). Acevedo and Goenaga (1986) noted bleaching in south-western Puerto Rico that resulted from a turbidity plume that persisted for over 45 days.

Infectious Disease. Bleaching as a result of infectious disease agents is an emerging area of coral reef research (see Chap. 25, Rosenberg, this Vol.). Coral bleaching of the introduced Mediterranean coral *Oculina patagonica* has been linked to the infection and growth of the bacterium *Vibrio shiloi* at elevated temperature. These pathogens have been isolated and inoculated into unaffected coral colonies to cause bleaching of coral host tissues. Infection and bleaching are temperature-dependent. Most of the *O. patagonia* colonies bleach annually during the summer months as temperatures reach a maximum of 30–31 °C (Kushmaro et al. 1996, 1998). The corals recover during the winter months when SST falls to a minimum of 16 °C. The bacterium dies and lyses at the low temperature and cannot be detected in corals during the winter months. A similar bleaching relationship between the ubiquitous Pacific coral *Pocillipora damicornis* and the bacterium *Vibrio coralyticus* have also been demonstrated (Ben-Haim and Rosenberg 2002). It remains to be seen if such bacterial processes are involved in regional mass bleaching events (see Chap. 25, Rosenberg, this Vol.).

In some cases, increased disease caused by infectious agents may be the result of coral bleaching rather than the cause. In Hawaii, corals bleached by high sediment conditions on Molokai, Lanai, Kahoolawe and Oahu have shown evidence of microbial infections (Fig. 23.2). Coral bleaching could be a contributing factor in the outbreaks of various coral diseases that have occurred in Florida and Caribbean waters during the last decade (Cervino et al. 1998; Richardson et al. 1998).

Reduced Salinity. Even short-term exposure to salinity below 30 parts per thousand reduces the tolerance of coral to increased temperature, and these detrimental effects are further aggravated by exposure to high light intensities (Coles and Jokiel 1978). Salinity reductions from Hurricane Flora in 1963 resulted in bleaching of all reef corals to a depth of 3 m in the Port Royal area of Jamaica (Goreau 1964). On the other hand, a major reef kill in Kaneohe Bay, Oahu resulted in death without bleaching of corals to depths of 3 m (Jokiel et al. 1993).

23.2.3
Evidence for Acclimatization

Reef corals show a remarkable ability to acclimatize to changes in solar irradiance (e.g., Falkowski et al. 1990; Anthony and Hoegh-Guldberg 2003; see Chap. 9, Stambler and Dubinsky, this Vol.), but show little ability to acclimatize to elevated temperatures beyond their normal living range. Coles and Jokiel (1978) held corals under controlled laboratory conditions for 56 days at 28, 26, 24 and 20 °C and then exposed them to high temperature (31.5 °C). Mortality was inversely related to acclimation temperature. The increase in survival between the +2 °C temperature acclimation group (28 °C) and the summer ambient group (26 °C) was only 13%, so the effect was not substantial.

Marshall and Baird (2000) noted differences in the bleaching rate on different reefs and concluded that acclimatization due to previous thermal history was involved. Meesters and Bak (1993) concluded that acclimatization had occurred in corals growing in a thermal power plant plume during the 1990 bleaching event in Curaçao. Bleached corals from the heated plume showed higher rates of regeneration and regained their pigment at a higher temperature compared to bleached corals from outside the thermal plume. Berkelmans and Willis (1999) noted a difference in upper thermal limits of coral on a seasonal basis. Glynn and D'Croz (1990) found corals from an upwelling area in the Gulf of Panama to undergo greater bleaching at 30 °C in controlled experiments than the same species from the nonupwelling Gulf of Chiriqui, where ambient temperatures are higher and more stable.

Evidence of acclimatization to increased temperature in all of the above field studies is suspect, as many important environmental variables could not be controlled in the field observations. Differences in irradiance and water motion rather than temperature could easily account for the observed differences in bleaching tolerance. Acclimatization to higher temperature must be demonstrated under conditions with all other factors being held the same in the comparison.

23.2.4
Evidence for Adaptation

From the point of view of observed phenomena, the only evidence for genetic adaptation is the biogeographic observation that reef corals and/or their zooxanthellae show quite different bleaching thresholds that are related to maximum summer temperature regimes within their region. On a global scale, reported coral bleaching thresholds span a range of 9 °C or more (Table 23.1). On a local scale, different species and even different clones of the same species show differences in thermal tolerance (Marshall and Baird 2000; Stimson et al. 2002). During bleaching events, some colonies remain pigmented while adjacent colonies of the same species undergo bleaching, suggesting normal biological variation and genetic plasticity in response to high temperature.

23.3
Mechanisms Involved in Bleaching, Acclimatization and Adaptation

23.3.1
Primary Mechanisms of Cause

There is a widespread acceptance of the view that photoinhibition and damage to the photosynthetic apparatus of the zooxanthellae is a primary causal mechanism for bleaching (Chap. 9, Stambler and Zubinsky, this Vol.). However, this view is being challenged by the infectious disease hypothesis as discussed elsewhere in this volume (see Chap. 25, Rosenberg, this Vol.). According to the photoinhibition hypothesis, the early effects of heat stress on the photosynthesis of the zooxanthellae begin with strong nonphotochemical quenching of chlorophyll fluorescence, marked decrease in photosynthetic oxygen evolution and decreases in optimal quantum yield of photosystem II (PSII) and lead to damage of PSII and photoinhibition (e.g., Jones et al. 1998; Warner et al. 1999). In culture, photosynthesis in the zooxanthellae is impaired at temperatures above 30 °C and ceases completely at 34–36 °C (Iglesias-Prieto et al. 1992). Thus, any mechanism that prevents or reduces irradiance damage to photosystems of the zooxanthellae at high temperature will enhance the ability of the reef coral to resist bleaching.

Thus, one can argue that bleaching results from disruption of the delicate plant-animal association due to a breakdown of photosynthesis in the zooxanthellae, rather than a direct lethal effect on either partner. On an individual basis, the plant or animal components of the symbiosis appear to have slightly higher thermal limits and each can live independently at temperatures above the bleaching threshold. Once they have lost their symbionts, many corals will continue to live for a limited period of time under the same conditions of high temperature that led to their bleaching. Zooxanthellae isolated from the coral *Montipora verrucosa*, will grow well in culture at 31 °C (Kinzie et al. 2001), a temperature that will lead to rapid bleaching in the symbiosis (Jokiel and Coles 1977). Presumably, there is a mechanism in the coral that recognizes "healthy" zooxanthellae that are contributing fixed carbon to the animal host. Perhaps once a zooxanthella is metabolically unable to "pay the rent", it is recognized as dysfunctional by cellular processes and is evicted. Bhagooki and Hidaka (2002) exposed polyps of the coral *Galaea fasicularis* to temperatures of 24, 28 and 30 °C for 7 days. The corals held at 24 or 28 °C released low levels of degraded zooxanthellae particles. The temperature-stressed coral exposed to 30 °C released large numbers of healthy looking zooxanthellae, suggesting that high temperature caused a physiological dysfunction that lead to bleaching.

Bleached corals have lost most of their photosynthetic capacity and must depend on heterotrophic feeding and stored lipids to meet their energy needs. This is not possible, given the reliance of corals on photosynthesis (Mucatine 1990). Thus, depletion of energy reserves has been proposed as a mechanism

to account for the failure of corals to complete gametogenesis even after re-
gaining pigmentation (Szmant and Gassman 1990). Reduced survival, devel-
opment, dispersal and recruitment of coral planula larvae at high temperature
have been attributed to lower energy availability (Edmunds et al. 2001). Lipid
and protein content remained lower in bleached colonies of the soft coral
Lobophytum compactum and eggs produced by these colonies for at least
8 months following bleaching (Michalek-Wagner and Willis 2001b). Prolonged
and repeated bleaching reduces energy reserves of the coral and may reduce
the ability of coral to resist disease (Fig. 23.2).

23.3.2
Acclimatization Mechanisms

23.3.2.1
Production and Modification of Proteins and Enzyme Systems
Involved in Metabolic Processes

The primary physiological challenge of increased temperature to reef corals
and all other organisms is centered on the effect of temperature on enzyme re-
action rates. The well-known concept of Q_{10} is defined as the ratio of enzyme
reaction velocities at different temperatures and approximately doubles over a
10 °C range. Under conditions in their normal living range, organisms can ac-
climatize in order to offset the effects of temperature increases through quan-
titative changes in enzyme concentrations and/or by changing to variants with
different kinetic properties (Hochachka and Somero 1984). As temperature in-
creases, the coral symbiosis acclimatizes by modifying enzyme systems and
other biochemical components in order to maintain homeostasis. The geno-
type of the coral and the genotype of the symbiotic algae set the ultimate limit
on temperature acclimatization, because both the plant and the animal com-
ponents of the symbiosis must act in unison to maintain the fragile nature of
the relationship. Coral bleaching is a clear sign that the limits of coral acclima-
tization have been exceeded.

   Heat shock proteins involved in acclimatization to temperature are found in
reef corals (reviewed by Gates and Edmunds 1999). These serve to lessen the
negative impact of higher temperature by reducing aggregation of structurally
nonnative proteins, refolding reversibly heat-damaged proteins and aiding in
the insertion of proteins into organelles. Both host and symbiotic algae produce
heat shock proteins in response to elevated temperature (Brown et al. 2002b).

23.3.2.2
Mechanisms That Reduce Photoinhibition

Photoinhibition due to high temperature combined with high solar radiation
is a primary factor influencing mass coral bleaching and is discussed in detail
by Stambler and Dubinsky (Chap. 9, Stambler and Dubinsky, this Vol.). Coral

bleaching starts with damage to the photosynthetic apparatus before there is a loss of zooxanthellae. Under normal conditions of temperature and irradiance, photosynthesis proceeds with uptake of dissolved carbon dioxide and water and transfer of protons through the photochemical systems of the light reaction. This is followed by release of oxygen and fixation of organic carbon in the dark reaction (reviewed by Fitt et al.2001; Chap. 9, Stambler and Dubinsky, this Vol.). At higher temperature and high irradiance, the rates of these processes can be increased to a level where more protons are produced in the light reaction than can be utilized to form organic carbon in the dark reaction (Brown 1997). A number of mechanisms serve to reduce such photosynthetic impairment.

Protective Enzymes. The production of oxygen free radicals or other toxic forms of oxygen in both the algal symbiont and coral host tissues increases at high temperature and high irradiance and can cause cellular damage, expulsion of symbionts and accelerate bleaching (Lesser et al. 1990; Lesser 1997). The enzymes superoxide dismutase, catalase and ascorbatae peroxidase act to detoxify active forms of oxygen. These enzymes inactivate harmful oxygen radicals and thereby prevent cellular damage. Activity and concentration of these protective enzymes increase in response to elevated temperature.

Production of Accessory Pigments. Ambarsari et al. (1997) and Brown et al. (1999b) have described the xanthophyll cycle in corals, which ameliorate the damaging effects of light at high levels of irradiance. Corals with a high capacity for dissipating excess excitation energy through this cycle appear to be less prone to temperature bleaching (Warner et al. 1996).

Production of Screening Pigments. Corals contain a group of UVR-absorbing compounds known as micosporine-like amino acids commonly known as MMAs (Dunlap et al. 1986) that show a maximum concentration in shallow water where high levels of UVR are present. MAAs increase bleaching resistance (Lesser et al. 1990) and counteract the effects of harmful UVR (Dunlap and Shick 1998). MAAs show high scavenging activities of the singlet oxygen and superoxide radical with very strong antioxidant activity on lipid peroxidation. Soft corals suffering MAA reduction caused by a previous bleaching event still amplified these compounds twofold in eggs, demonstrating the importance of MAAs in survival of the larvae (Michaek-Wagner and Willis 2001b). Coral larvae increase MAA in high UVR environments (Kuffner 2001). Reef corals often are not able to increase MAAs at a rate sufficient to counter the rapid UVR increases resulting from sudden increases in water clarity and can bleach as a result (Gleason and Wellington 1993). Corals growing in high water motion environments maintain high concentration of MAA protective compounds irrespective of irradiance (Jokiel et al. 1997). Thus, reef corals growing under conditions of high water motion are essentially pre-adapted to tolerate sudden increases in high solar radiation that accompany the onset of clear sky conditions associated with regional SST increases. Therefore, water motion can be an important environmental factor in bleaching resistance.

Corals contain other pigments that reduce irradiance reaching the zooxanthellae through reflection, absorption, fluorescence and/or scattering of excess or potentially damaging energy at different wavelengths. Green fluorescent pigment-like (GFP-like) proteins that fluoresce under UVR and/or visible light appear to play a role in protecting the photosynthetic machinery of the symbiotic dinoflagellates from the adverse effects of high irradiance (Dove et al. 2001; Labas et al. 2002). These pigments fluoresce the potentially damaging short wavelength radiation to longer green wavelengths. In the process they serve to reflect and scatter the energy away from the zooxanthellae. Corals containing GFP-like pigments are less prone to bleaching than nonfluorescent colonies of the same species (Salih et al. 2000). Nonfluorescent purple-blue pigments commonly found in corals may serve to reflect short wavelength radiation away from the zooxanthellae.

23.3.3
Behavioral Protective Mechanisms

Corals display limited behavioral responses at all life stages that may allow them to avoid bleaching and damage due to high temperature and high irradiance. Behavior related to reproduction, dispersal and settlement of larvae is largely directed at avoidance of unfavorable environmental conditions and unfavorable habitats that can lead to bleaching. Corals of the species *Pocillopora damicornis* extrude their brooded planula larvae into the water column when subjected to abnormally high temperature (Edmondson 1946). Presumably, this behavior reduces the metabolic demand on the coral polyps and allows the larvae to escape localized conditions of high temperature and high irradiance. Most broadcast spawning corals produce buoyant eggs and sperm bundles that rise to the surface layer of the ocean (Harrison et al. 1984). This mechanism serves to concentrate the gametes and insures higher rates of fertilization. During the day, however, the surface layer receives very high levels of irradiance and can be heated to temperatures 1–2 °C warmer than deeper water. Corals spawn in the evening, so the gametes and developing larvae are not subjected to the high damaging irradiance and higher surface temperatures during fertilization and early development of the planula larvae. Coral larvae will move vertically in the water column and appear to select depth of optimal light intensity (Kawaguti 1941; Raimondi and Morse 2000). Larvae will delay settling under conditions of high UVR (Kuffner 2001). Coral larvae actively select suitable settlement sites (Edmondson 1946; Harrigan 1972). After initial attachment to a substrate, the planula larvae will detach if conditions are unfavorable and presumably find another more suitable location (Harrigan 1972). In some cases, newly settled polyps will detach and undergo reverse metamorphosis even after initiating skeletal formation (Richmond 1985). Coral larvae of different species will select different light regimes of intensity and spectral quality before settling (Mundy and Babcock 1998). The larvae of many species tend to settle in shaded cryptic areas away from high light intensity (Morse et

al. 1988; Raimondi and Morse 2000). Such behavior may allow them to avoid bleaching due to high irradiance as well as avoiding competition from macro-algae and providing protection from predation by grazers. Some species of coral selectively settle on specific crustose coralline algae, perhaps because these algae are indicators of a temperature-irradiance environment that is favorable to juvenile coral over the long run. In some cases, juvenile corals show less bleaching compared to adult colonies on the reef (Mumby 1999). A possible explanation is that the juveniles live in a micro-habitat with lower irradiance. However, mortality of juvenile corals during a bleaching event can be much higher than the mortality rate of mature colonies (Harriott 1985).

Polyp behavior among adult colonies may play a role in alleviating bleaching. Expansion of polyps can increase surface area to facilitate exchange of harmful metabolic products at high temperature (Abe 1939). Contraction of polyps into their calyces can reduce irradiance impact and reduce bleaching (Brown et al. 1994).

23.4
Adaptation Mechanisms

The primary mechanism controlling adaptation to higher temperature is natural selection (Darwin 1859). Variation in bleaching response within various species is known to occur. Genetic adaptation occurs when the less resistant members of a population are eliminated by the ecological conditions, leaving organisms with higher fitness to reproduce and recruit to an available habitat. To date, bleaching events have not resulted in complete mortality of any coral population, so the surviving genotypes presumably have high-temperature tolerance that will be imparted to their offspring. The process of natural selection for bleaching-tolerance at higher levels of temperature and irradiance is already underway. The time required for such genetic adaptation in reef corals is unknown, but presumably would take many coral generations and hundreds to thousands of years.

The time needed for adaptation could be decreased substantially if corals are able to substitute thermally resistant zooxanthellae for less resistant types as proposed by the "adaptive bleaching hypothesis" (Buddemeier and Fautin 1993; also Chap. 24, Buddemeier et al., this Vol.). Adaptation of reef corals to higher temperature by this mechanism remains to be demonstrated. Numerous species and types of zooxanthellae are now recognized (see Chap. 8, Baker, this Vol.), and their response to temperature and irradiance probably varies. For example, Jokiel and York (1982) showed the existence of sun-loving and shade-loving varieties of zooxanthellae. Differences in bleaching resistance that corresponded to zooxanthellae symbiont genotypes in the ubiquitous Pacific reef coral *Pocillopora damicornis* have been reported (Glynn et al. 2001). Further, some coral species have colonies that contain several types of zooxanthellae, which can undergo selective loss of the most sensitive type during thermal stress (Rowan et al. 1997). Reciprocal transplant experiments over a

range of depths disrupted coral symbioses and showed that bleaching may provide an opportunity for replacement of the expelled zooxanthellae by other types of symbionts (Baker 2001). However, there may be costs involved, as shown by higher mortality in species that vary their algae with depth as compared to species that retain a single type of algae. Bleached anemones infected with a variety of zooxanthellae from other hosts often did not grow as well as anemones re-infected with their normal type of zooxanthellae (Kinzie and Chee 1979). Thus, new combinations of symbiont and host will be subject to the same process of natural selection as the other corals on the reef and may succeed or may be eliminated from the population.

23.5
Climate Change, Bleaching and the Future of Coral Reefs

The pattern of bleaching events that has increased in frequency and extent over the past 20 years will continue with increased severity in the future. Hoegh-Guldberg (1999) points out that reef corals have shown little ability to acclimatize or adapt to increasing global SST. Repeated bleaching has occurred at various locations over the past 20 years without any apparent increase in ability of the corals to acclimatize or adapt to higher temperature. The weight of available evidence is that coral reefs will be subjected to major environmental changes in future decades (Pittock 1999). Reef corals are already living at their thermal limit, and undergoing unprecedented mass bleaching due to higher summer temperatures (Wilkinson et al. 1999; Chap. 26, Hoegh-Guldberg, this Vol.). For example, the 1998 bleaching event in Belize central shelf lagoon areas produced catastrophic mortality (Aronson et al. 2002). Based on an analysis of reef cores, this was the first bleaching-induced mass mortality in at least the last 3000 years. Corals have continued to flourish despite major environmental and sea level fluctuations in the past (Buddemeier and Smith 1999). However, the ability of coral reefs to cope with such disturbances in the past is no guarantee of continued resilience in the face of unprecedented and much more rapid anthropogenic stresses (Hughes 1994). For example, in Jamaica, the effects of overfishing, hurricane damage and disease combined to destroy most corals. A dramatic phase shift has occurred, producing a system dominated by fleshy macroalgae (Hughes 1994). A study in the Bahamas from 1994 to 1998 documented the impact of a massive bleaching event that resulted in a significant decline in coral abundance and a rapid transition to an alga-dominated community (Ostrander et al. 2002). In future scenarios of projected climate change, it is likely that coral community decline will be influenced as much by increases in the frequency and intensity of extreme events as well as being impacted by increases in means of environmental parameters of temperature, atmospheric CO_2 and sea level (Done 1999).

Do reef corals possess mechanisms that may allow them to rapidly adjust to changing global conditions? Information on this question has been compiled by Buddemeier and Fautin (1993), Buddemeier and Smith (1999), Coles and

Brown (2003) and Buddemeier et al. (Chap. 24, this Vol.). Reef corals have the ability to acclimatize (modify phenotype) in response to the wide range of conditions normally encountered in their natural environment. For example, Hawaiian reef corals adjust readily to their normal seasonal temperature ranging from 21 to 28 °C without difficulty. However, prolonged exposure to temperatures of 29–30 °C at high irradiance typically exceeds the tolerance limits set by their genotype, and further acclimatization does not occur. The corals bleach. The ability of corals to acclimatize over a wide range of normal temperatures does not translate into an ability to acclimatize or adapt to higher than normal temperatures. The acclimatization limits are fixed by genotype and can only be increased through adaptation. The process of adaptation requires natural selection over many generations and could take hundreds to thousands of years in long-lived organisms such as corals. Conservationists and others concerned with the preservation of coral reefs have proposed a broad pragmatic approach to the bleaching problem that circumvents the need to understand mechanisms. The focus is on the identification and protection of those reef areas with the highest probability of enduring global changes (Salm and Coles 2001). These areas are to be integrated into a global network of coral reefs that would maintain high diversity and biomass and replenish the more impacted reef areas. Certain environmental factors favor survival or recovery of corals and other affected organisms during mass bleaching events. There are strong between-species and between-genera differences in susceptibility of corals to bleaching and mortality (Berkelmans and Willis 1999). Done (1999) used the term "tolerance" to describe intrinsic ability of species or colonies to withstand stressful events. West and Salm (2003) use the term "resistance" to expand the term "tolerance" to include extrinsic local environmental factors (upwelling, turbidity, strong currents, high cloud cover, topography, etc.) that allow coral reef communities to remain healthy during regional bleaching events. They also propose the term "resilience" to describe the ability of reef areas to recover after bleaching events. Some reefs have been observed to recover very quickly after an acute event (Coles and Brown, 2003) and would be said to have high resilience. Others recover slowly or not at all and would be said to have low resilience. The resilience of a reef is a function of abiotic as well as biotic factors. Coral reefs showing high resistance and high resilience would be set aside and protected from stresses such as sedimentation, fishing and eutrophication. Presumably, such protection would thereby reduce the anthropogenic stress load from fishing, pollution, sedimentation, etc. and increase the ability of these reefs to cope with global warming. These protected areas would represent a reservoir of reef corals that could repopulate impacted areas and thereby reduce, but not prevent, global reef decline. The proposed reserve system is contingent on the uncertain political willingness and economic ability of the international community to set aside and protect large reef areas.

23.6
Unresolved Questions and Future Research

The phenomenon of bleaching has now been well documented, yet the capacity of coral populations to adjust to global warming remains unknown. Further, the mechanisms involved are not fully understood and may even involve infectious agents (see Chap. 25, Rosenberg, this Vol.). On the level of phenomenology, coral bleaching has provided a clear early warning signal of future climatic change and more widespread impacts on coral reefs. There are considerable uncertainties in predictions of future rates of global change as well as uncertainties in biological response (e.g., bleaching) to such change. Humanity is rapidly moving forward with an unwitting experiment that involves massive anthropomorphic change to our planet. Perhaps the only way to answer questions on the fate of reefs will be to document the success or failure of these reefs to adapt to change over the next century. There will be increasing research opportunities to study the causes and consequences of coral bleaching and reef response, and to further document the decline of reef systems. In the future, descriptions of the causes of coral bleaching must be based on measurement of a wide range of interacting environmental factors, including the primary factors of temperature duration, solar irradiance intensity, spectral quality and water motion. Additional stresses that can result from global climate change include higher and more variable temperature, more frequent storms, changes in ocean currents, decreased salinity due to increased precipitation, and sea level rise. Global changes in ocean carbonate chemistry due to increased anthropogenic CO_2 will probably lead to reduced calcification rates in corals (Kleypas et al. 1999). Other anthropogenic stressors include nutrification, overfishing, increased sedimentation, increased levels of pollutants (pesticides, heavy metals, chlorinated hydrocarbons, etc.), shoreline construction and other factors. The impact of biological factors such as increased rate of disease, increased dominance of reefs by macroalgae, and impact of introduced species are unknowns that will contribute to the complexity of the problem. The bleaching response of corals to temperature varies with changes in other environmental parameters. These interactions are most important near the limits of tolerance for a given parameter (Coles and Jokiel 1978). Thus, synergistic effects due to a combination of the above climatic, oceanic, biological and anthropogenic factors are likely to have the greatest effect on coral reef ecosystems (Pittock 1999), and need to be described and understood in more detail.

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