REPORT

William K. Fitt · Barbara E. Brown
Mark E. Warner · Richard P. Dunne

Coral bleaching: interpretation of thermal tolerance limits and thermal thresholds in tropical corals

Abstract 'It should be clear that the upper temperature limit for life cannot be accurately defined' (Schmidt-Nielsen 1996). The thermal physiology of zooxanthellate reef corals is reviewed in this paper in the context of organismal and biochemical responses occurring during coral bleaching, with emphasis on methods of detection and interpretation of animal and algal symbiont stress. Coral bleaching, as presently defined in the literature, is a highly subjective term used to describe a variety of conditions pertaining to low symbiont densities in the coral–algal complex, including response to thermal stress. Three general types of high-temperature bleaching are defined: physiological bleaching, which may or may not include higher-than-normal temperature responses; algal-stress bleaching, involving dysfunction of symbiotic algae at high light and/or high temperatures; and animal-stress bleaching, where coral cells containing symbiotic algae are shed from the gastrodermal layer of cells. Since none of these methods of bleaching is mutually exclusive, a combination of intrusive and non-intrusive techniques is necessary to determine which mechanisms of symbiont loss are occurring. While quantification of symbiont densities, algal pigments, and coral tissue biomass provide unambiguous evidence of bleaching severity, measurements of physiological and biochemical degradation offer additional correlative evidence of temperature stress. Pulse-amplitude-modulated (PAM) fluorometry has emerged as an easy and relatively inexpensive non-invasive technique for monitoring symbiotic algal function both in situ and in the laboratory, when proper assumptions and interpretations are made. The roles of global warming, water quality, acclimation/adaptation processes, and relation to coral disease and reef heterogeneity are also discussed. A thorough understanding of the organismal responses occurring during bleaching will help explain changes in coral populations and in the coral reef community, and perhaps assist in predicting the future of reef corals and coral reefs during the next century of global climate change.

Keywords Coral · Bleaching · Zooxanthellae · Chlorophyll fluorescence · PAM fluorometry · Temperature threshold

W.K. Fitt (✉) · M.E. Warner
Institute of Ecology, University of Georgia,
Athens, Georgia 30602, USA
E-mail: fitt@sparrow.ecology.uga.edu
Tel.: +1-706-5423328
Fax: +1-706-5423344

M.E. Warner
Department of Botany, University of Georgia,
Athens, Georgia 30602, USA

B.E. Brown · R.P. Dunne
Department of Marine Sciences and Coastal Management,
University of Newcastle upon Tyne, NE1 7RU, UK

Introduction and terminology

Bleaching, defined as the loss of algal symbionts and/or their pigments, is a classic response of tropical symbiotic corals and related cnidarians and mollusks to a variety of environmental stresses. These stresses include, but are not limited to, decreased salinity (reviewed in Coles and Jokiel 1992); increased temperature (reviewed in Jokiel and Coles 1990); low temperature (Steen and Muscatine 1987; Gates et al 1992); exposure at low tide (Vaughan 1914; Yonge and Nicholls 1931a); sedimentation (Bak 1978; Dollar and Grigg 1981); darkness (Yonge and Nicholls 1931a); solar radiation (Brown et al. 1994); or a combination of these factors.

Over the last 17 years, recurrent local, regional, and global bleaching events have occurred, many of which have resulted in significant coral mortality (Jokiel and Coles 1990; Glynn 1993; Brown 1997a). The most widespread and severe bleaching occurred during 1997–1998 when reefs in over 42 countries were affected, with massive coral mortality being noted in southern Japan (Loya, personal communication) and Sri Lanka, the Maldives, India, Kenya, Tanzania, the Seychelles, and

other sites in the IndoPacific (Wilkinson et al. 1999). Recent interest in establishing thermal tolerances of corals has grown out of scientific concern for the future of coral reefs following the 1998 bleaching events. These widespread occurrences are typically linked to thermal stress, with the most severe symptoms seen at the end of the warmest season.

The concept of identifying thermal thresholds comes from the notion that knowing the thermal limits of a species of coral will somehow assist us in understanding the bleaching phenomenon and perhaps help in predicting the frequency and intensity of bleaching events. In fact, 'hot-spots' detailing temperature anomalies globally, together with 'Degree Heating Weeks' indices (which relate duration and magnitude of 'hot spots' to timing of bleaching) are now routinely used to sound bleaching alarms (Goreau and Hayes 1994; Goreau et al. 1997). While such information is extremely useful in making scientists, environmentalists, and the public more aware of the global crisis occurring on coral reefs, the information conveyed cannot accurately predict bleaching, is open to misinterpretation, and may lead to potentially erroneous statements concerning the physiological fate of the corals involved.

For example, the main environmental triggers of the bleaching response involve both elevated sea temperature and solar radiation (Coles and Jokiel 1978; Fitt and Warner 1995; Brown 1997a; Hoegh-Guldberg 1999). The interaction between the two factors is seen in a hypothetical model (Fig. 1) based on existing bleaching information from the field and laboratory. From this figure it is clear that bleaching can theoretically result from either high sea temperatures and low irradiance (Marcus and Thorhaug 1981), 'normal' sea temperatures and high irradiance (Brown et al. 1994), and/or a com-
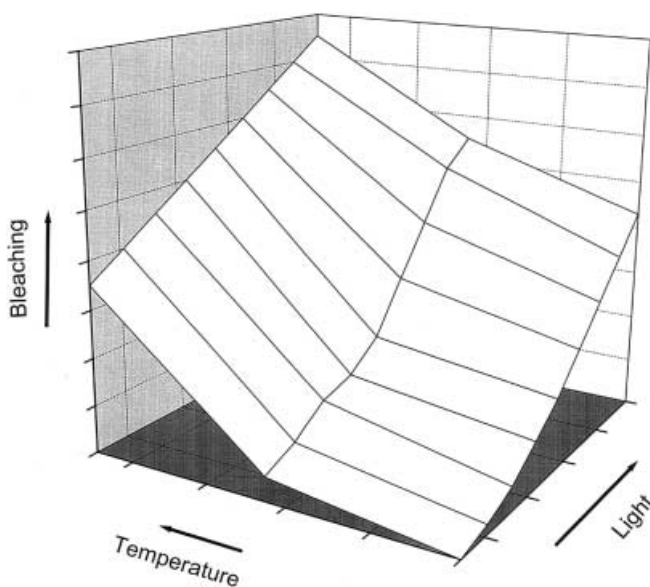
bination of these factors (Glynn and D'Croz 1990). Quantifying actual sea temperatures and irradiance values where bleaching can be expected to occur is complicated and will depend on other variables, such as the status of the symbiosis and the time of year when the experiment is carried out (Stimson 1997; Brown et al. 1999a; Fagoonee et al. 1999; Fitt et al. 2000). Complicating all of this is the actual length of exposure time to both variables. The link between sea temperature and irradiance in inducing bleaching was recognized over two decades ago when Jokiel and Coles (1977) and Coles and Jokiel (1978) reported that 'coral tissues can better withstand temperature extremes at reduced light intensities.' Despite this knowledge, authors have continued to discuss thermal thresholds and upper thermal tolerance limits of corals in terms of one variable only, namely temperature (Marcus and Thorhaug 1981; Neudecker 1981; Berkelmans and Willis 1999; Hoegh-Guldberg 1999). Furthermore, while earlier papers discussed upper thermal limits in the context of upper lethal limits (Mayer 1914; Jokiel and Coles 1977; Glynn and D'Croz 1990), more recent publications have used coral bleaching susceptibility as a 'proxy' for thermal thresholds and upper thermal limits (Goreau and Hayes 1994; Berkelmans and Willis 1999; Hoegh-Guldberg 1999). The links between bleaching and subsequent recovery or death of corals, however, are poorly defined, with virtually no literature available on critical densities of symbiotic algae that are needed to maintain a viable coral colony.

It is therefore timely to re-evaluate the thermal physiology of reef corals and their symbiotic algae. The aim of this mini-review is to lay out a framework for interpretation of thermal tolerance and thresholds of corals while at the same time indicating how sublethal responses to temperature (i.e. bleaching; impairment of photosynthesis) may be related to other variables in setting the physiological limits of corals. In so doing, the paper will focus on elevated sea temperature bleaching that is most evident during periods of annual maximum sea temperature in tropical and subtropical seas. In this review we have concentrated on the physiological, biochemical, and molecular basis of bleaching with regard to responses on the organismal scale, and have not attempted to review the exhaustive literature on population and reef community responses of bleaching and recovery.

Fig. 1 Hypothetical model relating various combinations of natural light intensity and high and 'normal' temperatures to bleaching of reef corals

Thermal tolerance in relation to reef corals

Heat stress in animals and plants involves breakdown of enzymatic pathways, resulting in biochemical and metabolic dysfunction (Cossins and Bowler 1987). The level of stress depends on the absolute temperature, length of exposure, and presence of other environmental factors (i.e. light, salinity, water motion). Ultimately, death may result, with a variety of damaging sublethal effects occurring during shorter exposures to lethal temperatures or during longer exposure to sublethal temperatures.
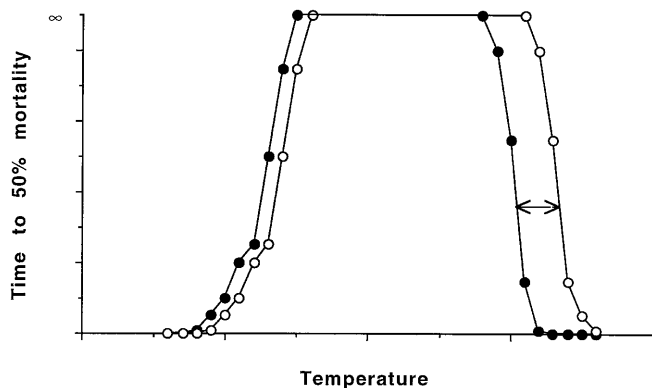
The damaging effects of high temperature are thus time dependent and it is important to note that it is not possible to cite a single lethal temperature without specifying the exposure period (Cossins and Bowler 1987). Figure 2 shows the general relationship between absolute temperature and exposure time (defined as the time at which 50% of the organisms die and 50% survive), clearly illustrating that there are numerous combinations of temperature and exposure time that lead to mortality (Schmidt-Nielsen 1996). A brief history of thermal research on corals follows.

Some of the earliest experimental work on reef corals was designed to test temperature tolerances of reef corals in laboratory experiments (Mayer 1914; Edmondson 1928). The detailed protocol of these early experiments involved an assessment of thermal limits of corals for given exposure times. Temperatures were recorded when feeding reactions and normal metabolic processes were inhibited, as well as at the death point (Mayer 1914). Results clearly showed that some species died at lower temperature maxima than other species, and although the exposure times ranged from only minutes to hours, species susceptibility to elevated temperature (e.g. *Siderastrea radians* vs. *Montastraea annularis*) was very similar to that recorded in recent Caribbean bleaching experiments (Warner et al. 1996). Most importantly, Mayer (1914, 1918) recognized that both exposure time and the rate of increase of seawater temperature surrounding corals were critical to the results of the experiment.

In 1929 Yonge and Nicholls (1931a, 1931b) observed bleaching (loss of symbionts) in corals living in intertidal pools on the Great Barrier Reef. They suspected that elevated sea temperatures, at low tide, played a role in this response and so followed up their observations with a series of experiments where corals were exposed to an elevated temperature in natural light at 36 °C for various exposure times between 0.5 and 4 h before being returned to ambient temperature for recovery. Yonge

and Nicholls (1931a, 1931b) concluded that elevated temperature was a prime factor in eliciting the bleaching response. They also noted that corals would die if exposed to high temperatures for long periods, but that they could survive moderately high temperatures if only exposed to them for short periods.

Following these studies conducted in the early part of the twentieth century, Jokiel and Coles (1974, 1977) and Coles and Jokiel (1977, 1978) built up a substantial literature on the effects of thermal discharges on corals living next to a power-generating station in Hawaii. This body of work was the first to quantify coral bleaching in response to elevated temperatures and to demonstrate seasonal differences in thermal tolerance of corals, as well as highlighting again the importance of length of exposure time on upper lethal temperatures. Other important findings include the fact that some subtropical corals appeared to have an upper lethal limit that was 2 °C lower than their tropical counterparts (Coles et al. 1976), and that corals were able to show limited acclimation to elevated sea temperatures (reviewed in Brown 1997b).

More recently, Glynn and D'Croz (1990) conducted high temperature tolerance experiments on the Pacific coral *Pocillopora damicornis* in order to explain bleaching observations in the eastern Pacific associated with the 1982–1983 El Niño southern oscillation (ENSO). Corals were exposed to 28, 30, or 32 °C for up to 10 weeks in outdoor tanks while monitoring algal symbiont density, coral tissue protein and algal chlorophyll *a* concentrations, and histological abnormalities. The rate of decrease over time for all parameters was greater with increasing temperature.

The extensive ENSO-associated coral bleaching in the Indo-Pacific in 1983, as well as in the Caribbean in 1987, prompted much concern among scientists who began to focus their research on the bleaching mechanism and the environmental triggers that elicit bleaching (see Brown 1997a and Hoegh-Guldberg 1999 for reviews). In the 1990s ecological surveys of natural bleaching events dominated the literature (see Glynn 1993 and 1996 for reviews), with a prolific number of papers appearing after the 1997–1998 bleaching (Berkelmans and Oliver 1999; Mumby 1999; Sheppard 1999; Wilkinson et al. 1999; Goreau et al. 2000).

Experimental work in recent years on thermal tolerances of corals, however, has been limited to a single study by Berkelmans and Willis (1999), while the mechanisms of temperature-mediated bleaching in corals and their symbiotic algae have been addressed by Fitt and Warner (1995); Iglesias-Prieto et al. (1992); Iglesias-Prieto and Trench (1997); Jones et al. (1998); Lesser (1996); and Warner et al. (1996, 1999). While Berkelmans and Willis (1999) claimed to define the upper thermal limits for two corals from the Great Barrier Reef, their study actually determined bleaching thresholds rather than lethal temperatures. The authors argued that the bleaching signal was a reliable indicator of subsequent mortality in *Pocillopora damicornis*; however,

Fig. 2 Tolerance of organisms to temperature extremes: effect of exposure time (time to 50% mortality) decreases with extreme high or low temperatures. *Arrow* denotes theoretical differences between either seasonal acclimation (e.g. *filled symbols* winter, *open symbols* summer) or two different species (*filled symbols* species #1, *open symbols* species #2)

the largely qualitative assessment of bleaching status and the lack of mention of the fate of controls in recovery trials leave this aspect of the study open to question.

Extrapolating thermal tolerance limits (i.e. death) from sublethal loss of symbiotic algae in reef corals (i.e. bleaching) requires more information than a simple temperature measurement. In the case of reef corals experiencing seasonal maximum temperatures, the exposure time, absolute temperature, diel variation, and irradiance would be useful in relating to the physiological response of both animals and their algal symbionts. Precedents for this type of approach already exist in the field of thermal biology. They include multidimensional representations of the boundaries for median lethality for temperature and other variables for marine invertebrates (McLeese 1956) and the construction of response surfaces for the interaction of two environmental parameters upon mortality (Alderdice 1972; Cossins and Bowler 1987). Such a format allows an easy and more precise assessment of the likely consequences of a given combination of factors, which in the case of corals might be sea temperature and irradiance. Parameters measured in corals could include mortality, changes in algal density, altered photosynthesis, or any other appropriate sublethal response. Recent work on the effects of multiple stressors (i.e. elevated temperature and elevated salinity) on the coral *Montastraea annularis* allowed the construction of a physiological response surface with the combined effects of single and multiple stressors displayed in one plot (Porter et al. 1999). In this example the authors measured responses to stressors in terms of net photosynthesis. The application of such techniques to the combined effects of sea temperature and irradiance would mark a major step forward, not only in the understanding of thermal tolerances of corals, but also in the relationship between sublethal responses and the death point.

Definitions of bleaching

There are at least three general kinds of coral bleaching described in the literature, defined here for the sake of simplicity as 'physiological bleaching,' 'algal-stress bleaching,' and 'animal-stress bleaching.' All result in live corals that look pale or white, as skeletal color is reflected through the coral tissue, compared to the normal dark brown coloration of symbiotic corals. It is important to note here that none of these forms of bleaching is mutually exclusive, making interpretation of the underlying mechanisms of bleaching from a ' bleached' coral a challenging endeavor!

'Physiological bleaching'

Two sets of facts (or in some cases assumptions) are necessary in order to understand physiological bleaching. First, coral tissue can only hold so many symbiotic dinoflagellates, implying that there are physiological constraints placed on the size of the population of symbionts living in their host cells. This phenomenon was first described in symbiotic green hydra some years ago (e.g. McAuley 1994), and has been confirmed or presumed to be true in virtually all cnidarian–algal symbioses (Jones and Yellowlees 1997; Fitt 2000; Fitt and Cook 2001). Therefore the density of symbionts is directly correlated with the amount of host tissue; obviously each host may harbor different densities, and changes in these 'steady-state' densities may occur in relation to changes in environmental variables (e.g. temperature, solar radiation, nutrients).

Second, seasonal changes in solar radiation and sea temperature are characteristic of virtually all reef environments, including those near the equator, and result in predictable seasonal changes in coral tissue parameters. While this may seem obvious, only recently have data been published detailing seasonal changes in coral tissues and their zooxanthellae (Stimson 1997; Brown et al 1999a; Fagoonee et al. 1999; Fitt et al. 2000). Seasonal maximum density of symbiotic dinoflagellates and their pigmentation typically occurs during the coolest season with the lowest solar radiation (winter–spring, or often the rainy wet season near the equator), while the lowest densities are usually documented at the end of the warmest season occurring together with the highest intensities of solar radiation. Decreasing densities of symbionts between the cool and warm season are directly correlated with similar decreases in host tissue biomass, while increasing symbiont densities typically precede and are thought to drive increases in host tissue biomass (Fitt et al. 2000). A possible explanation for the seasonal changes is that the combined effects of elevated seawater temperature and irradiance result in higher respiration rates of both coral tissues and symbionts during the warm season. For instance, increases in temperature potentially lower net photosynthesis, P:R ratios, and translocation rates – all related to higher energy demand at higher temperatures. Higher light in the form of photosynthetically active radiation (PAR = 400–700 nm), and perhaps the longer wavelengths of the ultraviolet radiation (UVR) range (UV-A 320–400 nm), are thought to exacerbate the effects of higher temperature and are described below.

'Algal-stress bleaching'

The concept of physiological stress and dysfunction of symbiotic algae has its basis in the definitions of photoinhibition (Osmond 1994). 'Chronic photoinhibition' is the term for *non-reversible* photodamage, usually involving malfunction of one or more biochemical pathways involved in synthesis or turnover of components of the photosystems. Chronic photoinhibition is thought to result in the death of individual symbiotic dinoflagellates, and eventual release of damaged symbionts from the host by exocytosis or host cell detachment (Gates

55

et al. 1992). Some forms of chronic photoinhibition can be monitored with pulse amplitude modulated (PAM) fluorometry, providing that readings are made before damaged symbionts leave the host and, more importantly, that other parameters are used in conjunction with the fluorometry readings in order to distinguish between other types of photoinhibition.

'Dynamic photoinhibition' is the term for *reversible* photostress response by algae. In the language of PAM fluorometry, dynamic photoinhibition falls under the category of non-photochemical quenching, i.e. photon energy that is directed away from photosynthesis via one of several possible pathways. Reversible dynamic photoinhibition includes the midday shunting of extra photons away from photosystem II via the xanthophyll cycle in symbiotic dinoflagellates living in shallow water corals – presumably in order to keep excess light energy from damaging components of the photosynthetic pathway (Ambarsari et al. 1997; Brown et al. 1999b). Dynamic photoinhibition can also be measured by PAM fluorometry, and sometimes occurs as a precursor to chronic photoinhibition, as algae attempt to protect themselves from short-lived midday elevated solar radiation conditions.

Whether dynamic photoinhibition and chronic photoinhibition occur simultaneously depends on the solar radiation level and temperature tolerance of particular symbiotic dinoflagellates (see Warner et al. 1996), as well as the exposure time to particularly high light and temperature regimes. Furthermore, different types of non-photochemical quenching may exist simultaneously, making it difficult to fully identify their biochemical and molecular origins.

'Animal stress bleaching'

Gates et al. (1992) proposed that the symbiont plays a more passive role in bleaching, remaining in host digestive cells that are shed from the gastrodermal layer of cells. However, bleaching is the result of relative tolerances of the algal versus the animal components of the symbiosis. Laboratory studies have confirmed that symbiotic dinoflagellates are usually less heat tolerant than their host, and that different symbiotic associations show different levels of stress tolerance (Clark and Jensen 1982; Jokiel and Coles 1990; Iglesias-Prieto et al. 1992; Fitt et al. 1993; Fitt and Warner 1995; Warner et al. 1996; Iglesias-Prieto and Trench 1997). Indeed, when one of the most sensitive biochemical assays of heat stress, namely heat shock protein (hsp) production, is measured in corals exposed to a series of elevated temperatures, hsp production in the coral host is not elicited until after a 2-h heat shock at 33 °C, whereas significant algal loss has already taken place within a 2-h exposure at a lower temperature of 30 °C (Sharp et al. 1997). Such a result is supportive of the view that the algae are more susceptible to thermal stress than their coral hosts.

While shedding of host cells containing symbiotic algae may not be prevalent in the field at current sea surface temperature (SST), experimental laboratory protocols involving rapid and large changes in temperature may in fact induce this type of bleaching (e.g. Steen and Muscatine 1987; Gates et al. 1992). It is possible that localized hydrographic conditions may exist on a reef that would involve animal stress in a fashion that would include release of animals cells containing symbiotic algae; however, it seems unlikely that such a mechanism would act on regional or even reefal scales.

How to determine which type of bleaching is occurring

Intrusive techniques

Intrusive techniques of monitoring bleaching usually involve collecting a piece of coral and removing coral tissue in order to retrieve the symbiotic dinoflagellates. Physiological measurements of intact corals, such as photosynthesis and respiration determinations, may precede tissue removal, but ultimately these measurements must be standardized to coral surface area, algal density, or some component of tissue biomass such as protein or ash-free weight (i.e. Porter et al. 1989). Symbiont densities and their pigment content comprise the most reliable and replicable data providing unambiguous quantification of bleaching and recovery processes. Such data have been used to describe bleaching severity (Porter et al. 1989; Glynn and D'Croz 1990; Szmant and Gassman 1990; Hoegh-Guldberg and Salvat 1995; Le Tissier and Brown 1996; Ambarsari et al. 1997; Brown et al. 2000a), document recovery processes distinct from bleaching (Fitt et al. 1993), and correlate with biochemical and physiological measurements (Warner et al. 1996, 1999). Note that symbiont density (per unit surface area or tissue biomass such as protein) needs to be compared with chlorophyll content in order to eliminate the rare bleaching phenomenon involving only loss of pigmentation (e.g. Hoegh-Guldberg and Smith 1989).

Little work has been done on sensitive indicators of temperature stress in corals and/or their symbiotic algae, such as the induction of heat shock proteins (Sharp et al. 1994; Black et al. 1995; Hayes and King 1995; Fang et al. 1997; Downs et al. 2000). Such 'stress proteins' are believed to confer an ability upon cells to survive previously lethal temperatures, and their induction has been observed on exposure of corals to elevated temperatures in the Caribbean genus *Montastraea* (Black et al. 1995; Downs et al. 2000) and the Indo-Pacific coral *Goniopora djiboutiensis* (Sharp et al. 1994, 1997). Transplantation of the latter, from a subtidal habitat to a shallow reef flat for 32 days, resulted in an elevation in constitutive levels of heat shock protein (hsp 70) compared with controls. A quantitative relationship between the concentration of some hsp and levels of thermal tolerance has been suggested by Landry et al. (1987), with other studies

showing that intracellular levels of hsp 70 may indicate the presence of retained thermal tolerance (Li and Werb 1992; Anderson et al. 1993). Such findings suggest that this assay may have some use in probing the thermal limits of reef corals. Other small molecular weight stress proteins such as hsp 22 and hsp 25 in chloroplasts may also prove to be useful biomarkers, with hsp 22 playing an important role in protection of photosystem II (PS II) during thermal stress (Heckathorn et al. 1999; Downs et al. 2000).

Other critical proteins, whose presence and/or turn-over rates can also be easily assessed, offer additional evidence of temperature stress. For instance, rates of degradation of the thermally sensitive PS II protein D1 were greater than its resynthesis at high temperature in some types of symbiotic dinoflagellates from Caribbean corals, correlated with low fluorescence ratios (see below) and reduced densities of symbionts as well as the timing of seasonally higher-than-normal temperatures on the reef (Warner et al. 1999). Other components of photosynthesis are also temperature dependent, including enzymes associated with PS I and carbon fixation, such as Rubisco (Jones and Hoegh-Guldberg 1999). The sequence of biochemical events, or in this case the breakdown of biochemical components, occurring during algal-stress coral bleaching in nature is not well understood, and is currently being investigated.

Oxidative stress related to oxygen radical formation has been demonstrated in some symbiotic associations under 'normal' homeostasis (Dykens et al. 1992), as well as during periods of light and temperature stress (Lesser et al. 1990; Lesser 1997). Oxygen radicals such as superoxide and hydrogen peroxide have typically been measured indirectly by quantifying the enzymes responsible for their removal, such as superoxide dismutase, catalase, and ascorbate peroxidase. Choloroplast membranes contain a high proportion of galactolipids with highly unsaturated fatty acids, and are therefore extremely susceptible to damage via active forms of oxygen under conditions of high light and temperature (Tardy and Havaux 1997; Asada 1999). Such oxidative stress can be measured as an increase in lipid peroxidation (e.g. Downs et al. 2000), leading to a loss in the structural integrity of the cellular membrane. While there is evidence of reactive oxygen production during thermal stress in symbiotic dinoflagellates (Lesser 1996) or exclusively in the host (Nii and Muscatine 1997), the precise biochemical targets of such oxygen radicals remain an area of intense research.

The main drawback of intrusive techniques is obviously their destructive nature, and therefore scientists and reef managers alike strive to keep these important methods of sampling to a minimum by collecting very small coral pieces or cores. Modern molecular techniques, coupled with powerful, new, non-intrusive monitoring methods detailed below, may soon allow thumbnail-sized flecks of live tissue to identify the mechanisms and severity of thermal stress with little or no impact on the reef.

Non-intrusive techniques

Coloration

The lack of normal brown coloration has led to the 'bleached coral' terminology that has been prevalent in the literature for years (see Yonge and Nicholls 1931a). It is easy to understand why most descriptions of bleaching events have inevitably relied on subjective visual assessment of coral color. While these descriptions have served the useful purpose of 'sounding the alarm' and recording severe events, they do little to identify the nature or cause of bleaching (loss of symbionts or their pigment or both), and even less in relating severity and quantifiable differences between species, reefs, sites, seasons, years, etc. Yet the literature continues to be filled with such descriptions (e.g. Ostrander et al. 2000), requiring that scientists and managers alike be aware of the limitations of such colorimetric interpretations.

A few studies have attempted to correlate symbiont density with quantifiable color, and have established for particular events, reef sites, and species significant regressions that can be used in limited subsequent sampling (Berkelmans and Willis 1999). However, because of seasonal differences in pigmentation and our limited understanding of animal pigmentation, this method requires such constant recalibration of color-regressions, that it seems more efficient to always determine symbiont density and pigment content.

Fluorometry

Chlorophyll fluorescence measurement is a very powerful and useful tool for monitoring the physiology of symbiotic dinoflagellates within scleractinians. The two techniques currently available for measuring changes in chlorophyll fluorescence under dark- and light-acclimated conditions are pulse amplitude modulation (PAM) fluorometry and fast repetition rate (FRR) fluorometry (Warner et al. 1996; Gorbunov et al. 2000; Lombardi et al. 2000). For this discussion, we will focus primarily on PAM fluorometry, since it represents instrumentation which is more readily available to most laboratories.

PAM fluorometry has become both an efficient and relatively inexpensive method of collecting data in situ with the advent of submersible instrumentation, allowing for complete non-invasive measurements to be made (Beer 1998; Beer and Ilan 1998; Ralph et al. 1999). While previous work has shown that PAM fluorometry may yield a wealth of information about the photosynthetic state of symbiotic algae, these techniques are not without limitations. Likewise, care must be taken when interpreting fluorescence data, as there are numerous biochemical explanations for the fluorescence patterns recorded, many of which are not easily discernible from one another by fluorescence analysis alone.

The true beauty of the fluorescence technique lies in the simple fact that light energy reaching a photosynthetic organism can follow only three pathways (Krause and Weis 1991). First, light energy may be used in photosynthesis via photochemical reactions in the reaction center of photosystem II (PS II), i.e. 'photochemical quenching.' Second, and in competition with this process, is the dissipation of light energy away from the PS II reaction center in the form of minute quantities of heat, known as 'non-photochemical quenching.' Third is radiative decay of the energy via fluorescence, which is the pathway of light energy that is measured directly in fluorometry. By measuring the emitted fluorescence, it is possible to determine the amount of light energy used in photochemical as well as non-photochemical processes, which typically function simultaneously (Schreiber and Bilger 1993).

If the coral/algae are held in the dark for a sufficient time, the capacity of the photochemical pathways to absorb light energy is maximized (the PS II reaction centers are said to be in a fully open state). In such a state the very small amount of light energy in the measuring pulse of the PAM fluorometer will almost entirely be absorbed by the PS II reaction centers and the fluorescence will be minimal (F_o). A brief application of a very intense light can then be applied, causing the reaction centers to saturate and the fluorescence signal then rises to a maximum level (F_m). The measurement of F_o and F_m allows for the calculation of the F_v/F_m ratio, where the 'variable fluorescence,' F_v, equals F_m-F_o. This ratio, known as fluorescence yield, is one of the parameters most frequently recorded with the PAM technique. It is indicative of the potential photochemical capacity of PS II within the algae. When photosynthesis is working at peak efficiency, F_v/F_m values as measured by PAM fluorometry are typically in the range of 0.50–0.70, depending on the species of coral and its depth location (Warner et al. 1996; Jones et al. 1998). Fluorescence yield values measured by the fast repetition rate (FRR) technique are usually lower (0.45–0.35) than PAM measurements (Gorbunov et al. 2000), due primarily to the fact that the FRR technique measures the F_m after a single turnover saturating flash (Kolber and Falkowski 1998), while the PAM technique utilizes a multiple-turnover protocol. There is currently considerable debate concerning the potential for overestimating the 'quantum yield' by PAM fluorometry (Kolber and Falkowski 1998), or underestimating yield by single-turnover methods such as FRR (Schreiber et al. 1995); however, examination of the theoretical and biochemical aspects of measuring chlorophyll fluorescence by these methods is beyond the scope of this review.

The two different sets of quenching reactions, photochemical and non-photochemical, may simultaneously affect the fluorescence yield (F_v/F_m). Determining which reactions are changing when the fluorescence yield changes is the challenge. There are a number of critical assumptions that must be addressed when interpreting F_v/F_m ratios:

1. Dark acclimation must precede measurement of F_o and F_m and must be long enough to ensure that the PS II reaction centers are fully open and competing non-photochemical events are removed. The length of dark acclimation is especially important for accurate F_v/F_m determination. One specific time period (e.g. 15 min in the dark) is not necessarily long enough for algal symbionts in all species of corals, or even the same species of coral over the course of the day. For example, the IndoPacific coral *Goniastrea aspera* is subject to very high levels of early afternoon solar radiation during spring tides, especially when exposed to air intertidally (Brown et al. 1994). F_v/F_m values for these corals were in the normal range for healthy zooxanthellae before and shortly following sunrise, and a dark acclimation period of 20 min was adequate to record maximal quantum yield. However, measurements of the same corals following a 20-min dark adaptation at midday showed significantly lower F_v/F_m values. Such a marked decrease in F_v/F_m could be misinterpreted as long-term damage originating strictly from chronic photoinhibition. However, a 60-min dark adaptation period during midday measurements yielded significantly higher F_v/F_m ratios compared to those taken after 20 min, thus indicating that multiple photoprotective processes were occurring in the light-harvesting complex and the PS II reaction centers of zooxanthellae. This phenomenon indicates that dissipation of non-photochemical quenching of chlorophyll fluorescence can vary over the course of the day, and may also vary with coral species and collection site.

2. Previous PAM fluorometry work with terrestrial plants, and several species of algae, has provided a good model for interpreting fluorescence patterns in relation to the biochemical phenomena that are responsible for them. However, one must never assume that such interpretations will be equally applicable when working with all forms of plants and algae, given the large differences in the photosynthetic pigments and structure of the light-harvesting proteins between the different groups of algae. This is especially true for interpretation of F_o and F_m. For example, previous work with higher plants has shown that elevated temperature may lead to the detachment of the light-harvesting complex from the PS II reaction center, resulting in a rapid rise in the F_o value (Schreiber and Berry 1977; Mishra and Singhal 1990). However, PS II reaction center damage in symbiotic dinoflagellates, either by elevated temperature (between 30 and 32 °C) or by exposure to chloroplast protein synthesis inhibitors, does not result in the classic rise in the F_o value seen in other photosynthetic organisms (Warner, unpublished data).

Conversely, other changes in F_o fluorescence in symbiotic dinoflagellates closely match results recorded from terrestrial plants and chlorophytes (Brown et al. 1999b). For example, diel decreases in F_o can correlate

well with the de-epoxidation of the xanthophyll diadinoxanthin to diatoxanthin within the light-harvesting complex of zooxanthellae. The peak conversion of these xanthophyll pigments occurs around midday during periods of high irradiance. The end result of the xanthophyll cycle is that large amounts of photon energy are diverted away from the reaction centers of PS II, thereby increasing the non-photochemical quenching of chlorophyll fluorescence. This pathway provides a mechanism for photoprotection from the potentially damaging excess irradiance that all shallow-water reef corals are exposed to over the course of the day. Lower F_v/F_m ratios measured in corals at midday are often due to such protective pathways, rather than indicative of permanent damage in PS II (Brown et al. 1999b; Hoegh-Guldberg and Jones 1999). These results corroborate with the presence of the xanthophyll cycle in other dinoflagellates as well as higher plants (Demmig-Adams and Adams 1992; Olaizola et al. 1994; Frank et al. 1996).

The assumptions presented above also apply to measurements of chlorophyll fluorescence in the field, especially when interpreting what is happening before, during, and after bleaching events. Fluorometry provides a snapshot of photosystem II, hopefully improving the identification of biochemical damage responsible for bleaching. While many bleaching studies have relied on the assessment of bleaching by the color of the coral alone, fluorescence analysis shows that the long-term physiological 'outlook' of the symbiotic algae should never be based on this qualitative indicator. A good example is shown in the illustrations of bleached corals (Fig. 3). Figure 3a shows a bleached coral collected during a 6-week period in summer 1997 when seawater temperatures in the Florida Keys were 31 °C, while Fig. 3b shows a bleached coral from the Bahamas that was collected several weeks following the summer temperature maximum in 1999. While both corals appear to be severely bleached, the F_v/F_m values over the bleached sections of each colony indicate that the symbionts in each are functioning quite differently. Symbiotic dinoflagellates in the Florida coral (Fig. 3a) exhibit signs of true chronic photoinhibition, while those in the Bahamas coral (Fig. 3b) appear healthy and clearly in a recovery phase, as the quantum yields of these algae match those recorded for non-photoinhibited unbleached corals.

Knowledge of previous environmental parameters, such as temperature, light, and tidal exposure history of a specific coral and site, is essential when interpreting chlorophyll fluorometry in field specimens. Since photosynthetic efficiency of corals varies significantly over multiple time scales (from time of day to seasons), care must be taken in interpreting data from bleaching events. For example, a decline in the mean F_v/F_m value from 0.65–0.58 may be statistically significant, yet may simply reflect seasonal or daily variation of the normal photosynthetic efficiency of the corals rather than algal stress or dysfunction. Indeed, changes in fluorescence patterns should be used cautiously when extrapolating to biochemical or molecular physiological patterns; other physiological and biochemical data are often mandatory in order to assure accurate interpretations of fluorometry data.

Special considerations

Global warming

Evidence of sea-surface temperature warming has been found throughout much of the tropics, especially in the northern hemisphere (Strong et al. 2000), and is correlated to increasing concentrations of carbon dioxide and other greenhouse gases in the earth's atmosphere. Highly significant increases in sea temperature in the world's tropical oceans have been noted in the past century, with rates of increase ranging from 0.07–0.5 °C per decade (Table 1). While decadal increases in temperature of this magnitude may seem small at first glance, such increases become very significant for corals living close to their thermal limits in oceans where the background temperatures are steadily rising over time. The hypothesis that corals and other reef organisms might be the first to show adverse effects of global warming has been widely stated (Goreau 1990; Jokiel and Coles 1990; Glynn 1991; Goreau and Hayes 1994) and relates to the concept that even slight increases may push an organism over its physiological limits (Jokiel and Coles 1990).

In the Caribbean-wide bleaching event of 1987, however, water temperatures did <u>not</u> exceed normal

Fig. 3 A Bleached coral (*Montastraea* sp.) collected from the Florida Keys during a bleaching event in summer 1997. **B** Bleached coral (*Montastrea* sp.) collected from the Bahamas several weeks following a bleaching event in 1999. Note that while the coloration is similar for both pieces of coral, F_v/F_m values indicate very different photosynthetic capacities
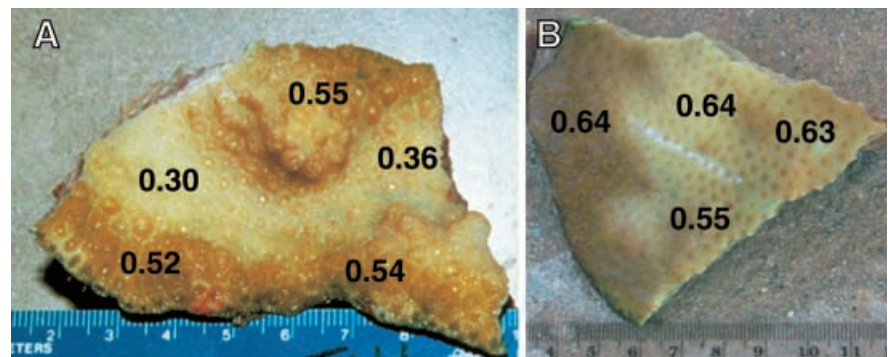
Table 1 Rates of sea temperature increase (°C per decade) based on 'in situ' sea temperature measurements made at La Parguera Marine Station, Puerto Rico, the Comprehensive Atmosphere Ocean-Atmosphere Data Set (COADS) and the Integrated Global Ocean Services System blended data (IGOSS), and the Meteorological Office Historical Sea Surface Temperature data set (MOHSST) for a selection of tropical locations. Use of long-term sea temperature data sets (MOHSST or COADS) prior to 1941 introduces known errors for which a step-correction has had to be applied. Refinements of this correction are still being made. Use of pre-1941 long-term data therefore still involves extra degrees of uncertainty compared to post-World-War-II data sets (Foland and Parker 1995)

Locality	Period examined	Rate of increase	Authority
Puerto Rico[a]	1966–1995	0.25	Winter et al. (1998)
Jamaica[b]	1903–1999	0.125	Hoegh-Guldberg (1999)
Phuket, Thailand[b]	1904–1999	0.154	Hoegh-Guldberg (1999)
Phuket, Thailand[c]	1945–1995	0.126	Brown et al. (1996)
Tahiti[b]	1926–1999	0.069	Hoegh-Guldberg (1999)
Tahiti[c]	1956–1995	0.08	Brown (1997a)
Milne Bay, PNG[c]	1956–1996	0.09	Davies et al. (1997)
GBR, Australia[b]	1902–1999	0.125–0.168 (depends on latitude)	Hoegh-Guldberg (1999)
Tropical oceans	1982–1996	0.001–0.053 (depends on latitude)	Strong et al. (2000)

[a] La Parguera Marine Station
[b] COADS and IGOSS
[c] MOHSST

temperature maxima (Attwood et al. 1992), but the duration of maximum temperature was much longer than normal. These observations suggested that 'physiological bleaching' rather than 'algal-stress bleaching' played the major role in 1987 in reducing tissue biomass and therefore density of symbiotic dinoflagellates (see Porter et al. 1989; Szmant and Gassman 1990; Fitt et al. 1993). Repercussions of global warming may manifest themselves not only in terms of higher-than-normal temperatures, but also in longer-than-normal duration of seasonal high temperatures.

Depressed sea levels, resulting from El Niño events (Wyrtki 1985) and other coupled ocean–atmosphere phenomena (Chambers et al. 1999; Webster et al. 1999) linked to climate variability, may also contribute to coral bleaching. For instance, coral reefs in the eastern Indian Ocean experienced sea levels 30–40 cm lower than normal for a period of 9 months in 1997–1998 (Chambers et al. 1999; Webster et al. 1999). This resulted in a form of 'algal stress bleaching' in shallow reef flat corals in west Thailand between late 1997 and early 1998 termed 'solar bleaching,' because it is primarily triggered by exposure to high solar radiation (Brown et al. 2000a) and not to elevated sea temperature.

Relation to coral disease

Climate and environmentally mediated physiological stresses may compromise host resistance and increase frequency of opportunistic diseases (Harvell et al. 1999). The increase in numbers and severity of coral diseases (Cervino et al. 1998; Richardson 1998) suggests that reef corals, especially in the Caribbean, may be more physiologically stressed now than they have been in the past 5,000 years or more (Aronson and Precht 1997; Greenstein et al. 1998). Many coral diseases peak in severity and incidence at the end of the warmest season (Edmunds 1991; Kuta and Richardson 1996; Richardson et al. 1998), corresponding with the time when coral tissues are thinnest and symbiont densities lowest (Fitt et al. 2000).

In the Mediterranean the incidence of bleaching in the coral *Oculina patogonica* also increases at the end of the warmest period of the year. It has been suggested that bacterial virulence of the bacterium *Vibrio* AK-1, associated with elevated water temperature, leads first to bleaching and then death of the coral (Kushmaro et al. 1998). Subsequent work on the mechanisms involved revealed that bacterial adhesion to the coral was greatly increased at higher temperatures (when the bacterium was grown at 25 °C), with no adhesion evident at the lower temperature of 16 °C (Toren et al. 1998). The authors suggest that elevated sea temperatures might cause bleaching in *Oculina* by allowing the expression of adhesion genes in *Vibrio* AK-1. Once established in the coral tissues, the coral pathogen apparently produces an array of extracellular materials that inhibit photosynthesis and lead to loss of algal pigments and subsequent algal lysis (Ben Haim et al. 1999).

Solar radiation interactions

Solar radiation plays a fundamental role in influencing thermal tolerance and thresholds in corals by both thermal heating of seawater and helping to disrupt biochemical pathways within the symbiotic dinoflagellates. First, solar radiation is the 'heat engine' that directly drives the heating/cooling cycle of the ocean. The sea absorbs about 96% of all solar energy falling on it (Gregg and Carder 1990) and in the process is warmed. This is seen on daily as well as seasonal time scales. The daily range of temperatures in tropical seawater varies widely with habitat. For instance, Fig. 4 shows that while daily temperature fluctuations on a forereef slope
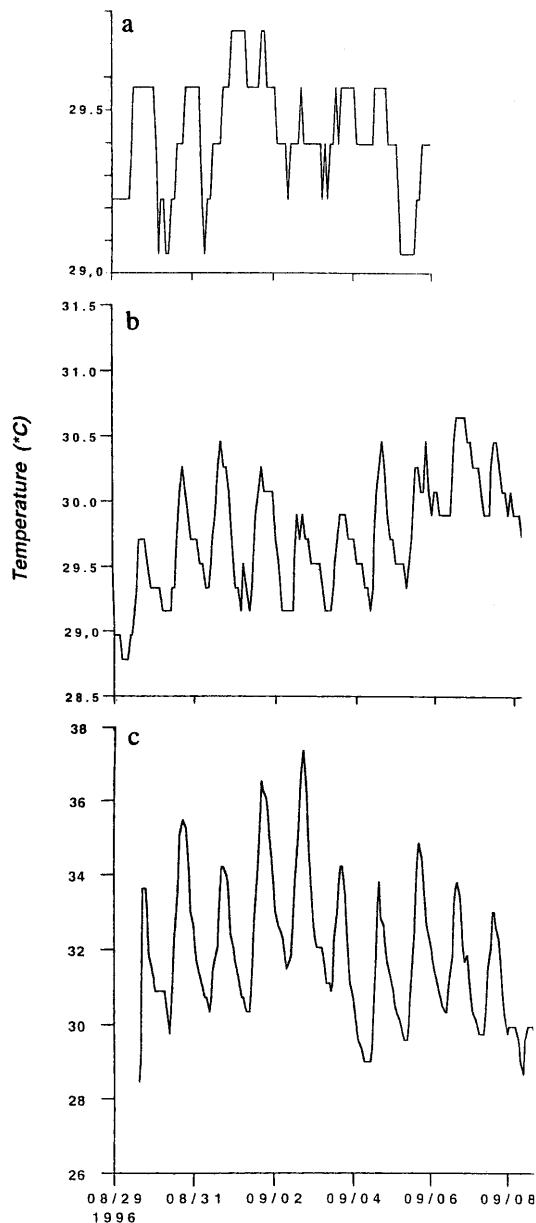
Fig. 4 Daily variation in temperature recorded from **a** the fore reef, **b** patch reef in the back reef, and **c** shallow seagrasses adjacent to mangrove in the Florida Keys during August 1996. *Step-like 'curves'* reflect longer intervals between data points

are typically ≤ 0.5 °C, those on the backreef are greater, and within shallow seagrass and mangrove habitats and tidepools may exceed 5 °C. Daily peaks in temperature generally occur near the end of the light period, and shallower sites tend to experience greater fluctuations than deeper sites. Seasonal temperature variation is generally greater than 3 °C, and may exceed 15 °C depending on the geographical location of the reef (i.e. Fitt et al. 2000). The net result of the two cycles is that corals experience a low-frequency (12-month wavelength) sinusoidal sea temperature variation whose amplitude may be considerable, superimposed with generally smaller-amplitude high-frequency diel fluctu-

ations (see review by Brown 1997b). The possibility of daily, solar-driven dynamic photoinhibition, linked to a combination of light and temperature stress, is a likely scenario for most corals during summer or dry season conditions.

The second aspect of solar radiation that plays an important role in coral bleaching involves photosynthetically active radiation (PAR) and ultraviolet (UV) radiation at the scale of the photochemistry and in conjunction with heat stress within symbiotic dinoflagellates. Coles and Jokiel (1978) first reported experiments where coral tissues withstood temperature extremes better at reduced light intensities. It is the excess of the quantum or photon energy needed for efficient photosynthesis in any given physiological state that can lead to disruption and damage of the photosynthetic apparatus. Any abnormal stress such as high temperature will lower photosynthetic efficiency and thus leave more excess photon energy available to disrupt algal physiology. The shorter the wavelength of the radiation, the more energy is contained in each photon, with greater potential for direct molecular damage. For instance, the effects of high-energy UVR on chemical bonds within DNA, RNA, and protein are well known (Jagger 1985; Häder 1997), as are photoprotective mechanisms such as chemical sunscreens in corals called mycrosporine-like amino acids (MAA) (Shick et al. 1996). Coral fluorescent pigments may also act to protect coral and their algal symbionts from harmful wavelengths of light (Kluter and Hoegh-Guldberg 2000). However, the combination of high PAR with high temperature in corals has received little experimental attention. Fitt and Warner (1995), testing various wavelengths of light on intact corals immersed in 32 °C seawater, found that photosynthetic efficiency decreased fastest with the shorter compared to longer wavelengths of PAR. Interestingly, the UV-B (280–320 nm) component of natural sunlight did little to change fluorescent patterns of symbiotic dinoflagellates, possibly indicating that protection mechanisms such as MAA were effective in blocking these wavelengths, or alternatively that effective molecular repair mechanisms exist. However, UV-A (320–400 nm) and short blue wavelengths (400–495 nm) were responsible for the most drastic reductions in photosynthetic efficiency of coral symbionts at 32 °C (Fitt and Warner 1995).

Solar radiation is, therefore, both an indirect (by driving the seawater warming cycle) and direct (through photochemical damage) contributor to coral bleaching. If the bleaching response is to be used as a basis for determining thermal tolerance limits and thermal thresholds, the contributing direct role of solar radiation must also be determined. Photosystems that are already damaged by thermal stress will be susceptible to photoinhibition at lower solar irradiance and dose compared to those operating normally, and conversely higher solar radiation stress will be tolerated by algae that are operating at the lower end of their temperature range.

Water clarity

Bleached corals show decreased host tissue biomass and zooxanthellae densities (Porter et al. 1989; Szmant and Gassman 1990; Fitt et al. 1993). In addition, most reef corals appear to have the least tissue biomass with lowest densities of algal symbionts at the end of their hottest season (Brown et al. 1999a; Fitt et al. 2000). Similarly, many corals of the same species living deeper on the reef show decreased densities of symbionts and tissue biomass, as do some corals living in shallow water but shaded due to high sedimentation or algal blooms (see references in Fitt and Cook 2001). In all of these instances there appears to be a link between the algal symbionts and the host tissue biomass, such that anything that reduces photosynthesis will influence symbiont density and ultimately host tissue biomass. In this regard, factors leading to reduced 'water clarity' achieve the same result as 'physiological bleaching' and 'algal-stress bleaching:' reduced photosynthesis, loss of animal biomass, and lower densities of symbiotic dinoflagellates. Therefore it would be difficult to look at a coral exhibiting decreased densities of zooxanthellae and host tissues and know how they got that way, unless other data are available (e.g. temperature records, depth of coral, time of day/year, and location collected, fluorescence and pigmentation data, history of local environmental perturbations, etc.).

Previous history, adaptation, and acclimatization

Recovery from normal seasonal reductions in host tissue biomass and symbiont densities usually occurs over the coolest season (winter, wet season) and into the slow temperature buildup of the next warm season (spring and into the dry season) (Fitt et al. 1993, 2000; Brown et al. 1999a). If the next season's decline in algal density and host tissue biomass begins before full recovery from the last warm season, the possibility of a downward trend in these parameters, leading to a physiologically weaker coral or eventual death, exists. Several reef-building corals in the Caribbean appear to be showing such a trend (Fitt, Warner, Chilcoat, unpublished data). Whether corals slowly starve to death during such 're-petitive bleaching' or become infected with a disease organism while in a weakened physiological state is a moot point.

At the other end of the scale, corals may achieve an improved tolerance to high temperature through experimental or seasonal acclimatization (e.g. Fig. 2; Coles et al. 1976; Jokiel and Coles 1977; Coles and Jokiel 1978), where mechanisms of enzyme replacement (isozymes) or protection enable normal physiological function during different seasons. Notable examples of more drastic modification of physiology and biochemistry include those corals that have apparently managed to adapt and function normally with symbiotic dinoflagellates in extreme temperature and salinity conditions in parts of the Arabian Sea in the northern Indian Ocean (Kinsman 1964; Coles 1997) and the Gulf of Carpentaria in northern Australia. Additional research is needed in describing acclimation and adaptation of the coral–algal complex to seasonal and longer-term changes in environmental variables such as temperature and light.

There is also evidence that some corals may utilize pre-exposure to particular environmental conditions to acclimatize to otherwise stressful conditions. For instance, exposure to high solar radiation prior to maximum seasonal seawater temperature may limit bleaching due to anomalous sea temperature/irradiance effects (Brown et al. 2000a). This phenomenon is probably due to early activation of photoprotective mechanisms present in some corals, such as behavioral retraction and greater efficiency and presence of the xanthophyll cycle (Ambarsari et al. 1997; Brown et al. 1999b). It is possible that small-molecular-weight stress proteins in the algal chloroplasts, which improve thermal tolerance and are elicited by exposure to high solar radiation and other stresses, are also involved (Heckathorn et al. 1999).

Reef heterogeneity

The highly variable reef environment is a major influence on coral bleaching patterns at all scales ranging from macro- to micro-climate (see Brown 1997b). The widely reported bleaching patterns of corals subject to elevated sea temperature, where apical surfaces of the colony bleach but the sides do not (Williams and Bunkley-Williams 1990), suggest that irradiance may strongly influence bleaching responses within a single colony. Equally, bleaching patterns in single coral colonies may be interpreted in terms of niche partitioning of different types of zooxanthellae, where colonies host algae of different haplotypes (Rowan et al. 1997). The latter study hypothesized that patterns of bleaching in *Montastraea annularis* might be explained by the preferential elimination of a symbiont associated with low irradiance from the brightest parts of its distribution, thus highlighting the importance of coral microhabitat.

Few studies, however, have focused on describing the microclimate of corals with respect to bleaching (Brown et al. 1994; Brown et al. 2000a, 2000b), though several have shown the importance of microclimate on irradiance reaching corals (Roos 1967; Jaubert and Vasseur 1974; Brakel 1979; Sheppard 1981; Ohlhorst and Liddell 1988; Helmuth et al. 1997). Recent work in Belize (Mumby 1999) suggests that the incidence of bleaching in juvenile corals was less than that of adults, possibly the result of reduced irradiance encountered by juveniles in their cryptic habitats, though no quantitative measurements were made. The fine-scale spatial variability of coral bleaching responses to local conditions imposes a serious limitation on upscaling from individual colonies or species to entire reefs of reef provinces.

Conclusions

'Coral bleaching' is a term referring to reduction of densities of symbiotic dinoflagellates and inevitable decreased host tissue biomass: physiological conditions that may arise from one or more environmental stresses. It is not possible to measure only one parameter of a coral and relate it to one parameter of the environment (i.e. temperature) and draw any reliable conclusions as to causes or severity of stresses impinging on corals or coral reefs. It is possible, however, to measure a variety of environmental factors (e.g. temperature and duration, light intensity and wavelengths) and relate those to non-intrusive fluorometric measurements, as well as destructive sampling of biochemical and molecular markers from small samples of coral, in order to infer causes of coral stress and the fate of stressed corals. The interpretation of such measurements must take into account diel and seasonal fluxes as well as local environmental history.

Using visible bleaching as an indicator of upper thermal limit might be a convenient marker for a researcher, but it bears little relationship to physiological processes occurring in corals and their symbionts. What we call 'bleaching' is an arbitrary and artificial physiological concept in the life of a coral. Many (if not most) corals have already lost half or more of their complement of symbionts by the time a human is capable of detecting lighter coral color, even in so-called 'non-bleaching years' (i.e. seasonality). In other words, all corals appear to experience the physiological stress of reduced tissue biomass and concomitant loss of algal symbionts weeks to months before the human eye detects any signal. Even when visible bleaching is categorized as being severe (with colonies often described as white or almost white) the coral may still retain as much as 20–50% of the original algal population, with many of the remaining symbionts possibly in 'good health' (Porter et al. 1989 ; Brown et al. 1995). Therefore, the concept of a 'bleaching threshold temperature' is not very meaningful to either corals or humans.

If bleaching is to be used as a 'proxy' for death in future studies of thermal tolerance limits of corals, it will be imperative to be able to unequivocally link the sublethal bleaching response (from which many corals do recover in the field) to the death point of corals. Critical densities of symbiotic algae that are needed to maintain a viable colony need to be established. Additionally, it is necessary to specify not only exposure times, but also what irradiances were used in temperature experiments. Indeed, if experiments in the laboratory are to have any relevance to the natural world, multifactorial studies of responses to physical stressors are required where absolute temperature, irradiance, and exposure time are minimum variables.

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