

Chapter 7

Bleaching and Mortality Thresholds: How Much is Too Much?

R. Berkelmans

7.1 Introduction

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

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

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

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

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

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

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

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

7.2 Methods

7.2.1 *Statistical Modelling*

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

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

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

7.2.2 Bleaching Thresholds

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

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

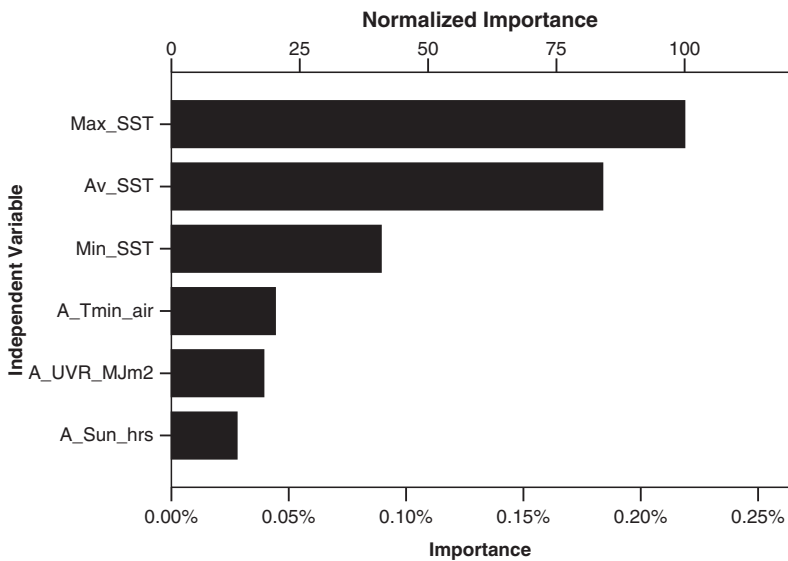
7.2.3 *Mortality Thresholds*

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

7.3 Results

7.3.1 *Is Temperature Appropriate for Modelling Bleaching Thresholds?*

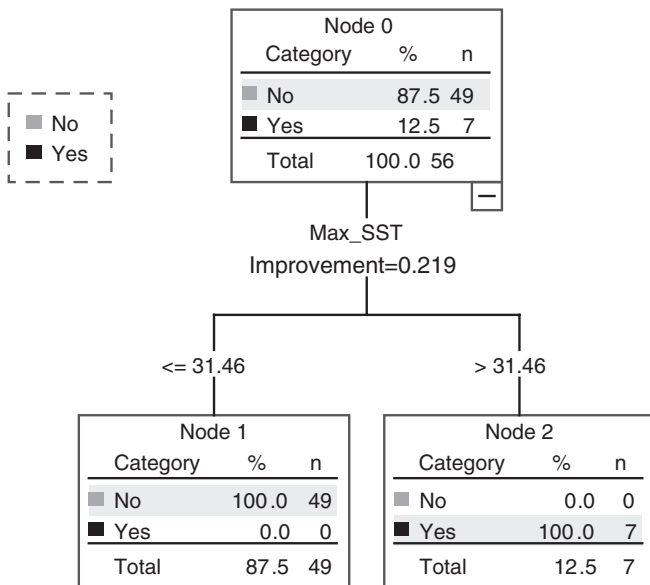
The results of the classification tree show that sea temperature is clearly the most important variable explaining bleaching events. Of the 17 potential variables investigated, only six contributed significantly to the model and, of these, the top three explanatory variables were maximum, average and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



a

Growing Method:CRT
Dependent Variable:Bleach

Bleach



b

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

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

7.3.2 Bleaching Thresholds

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

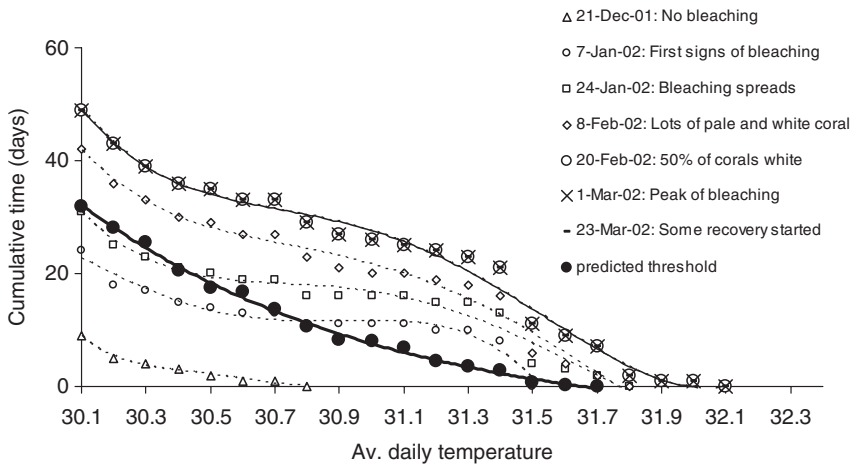


Fig. 7.2 Time-series assessment of the state of bleaching at Magnetic Island during the 2002 bleaching summer with a step-wise view of the time–temperature curve during each visit

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

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

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

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

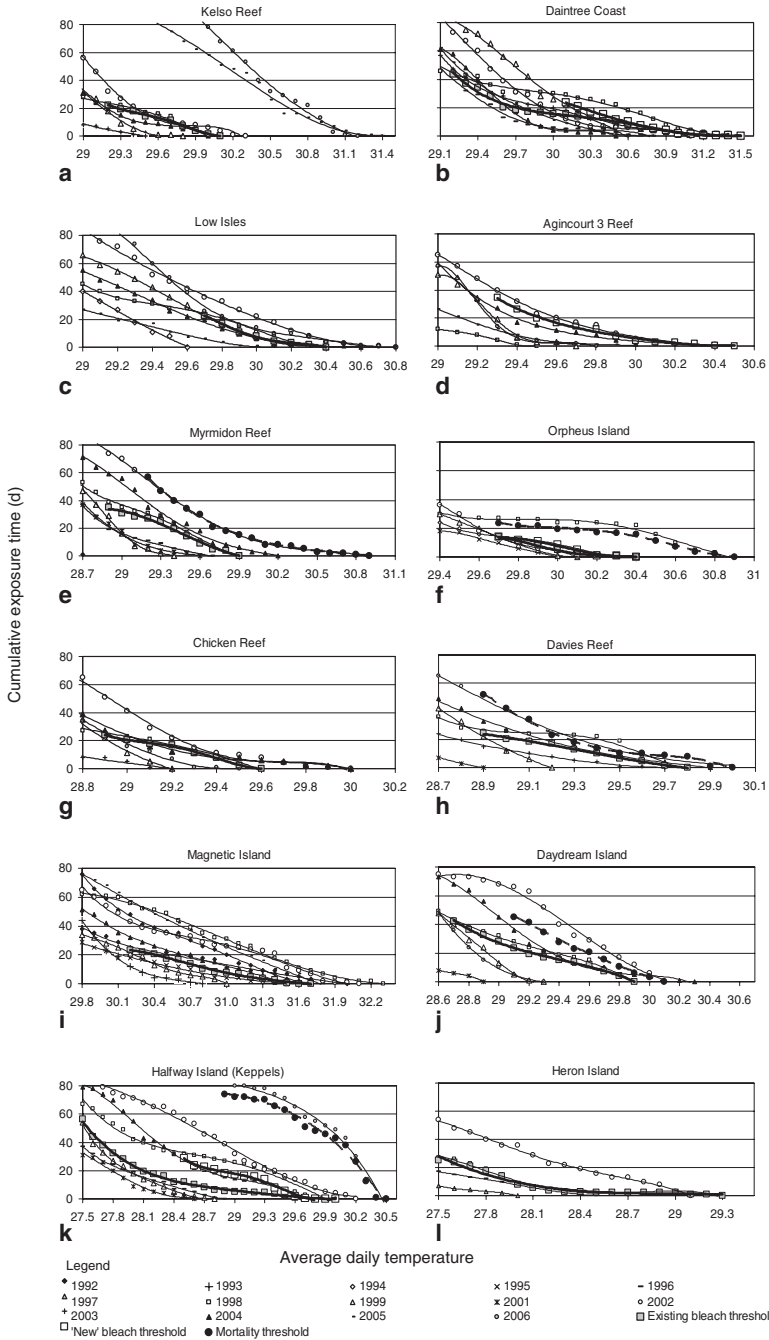


Fig. 7.3 Time–temperature curves for the bleaching summers and three warmest non-bleaching summers for 12 locations on the Great Barrier Reef (a–l), including the estimated position of bleaching curves and, where available, mortality curves

7.3.3 Mortality Thresholds

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

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

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

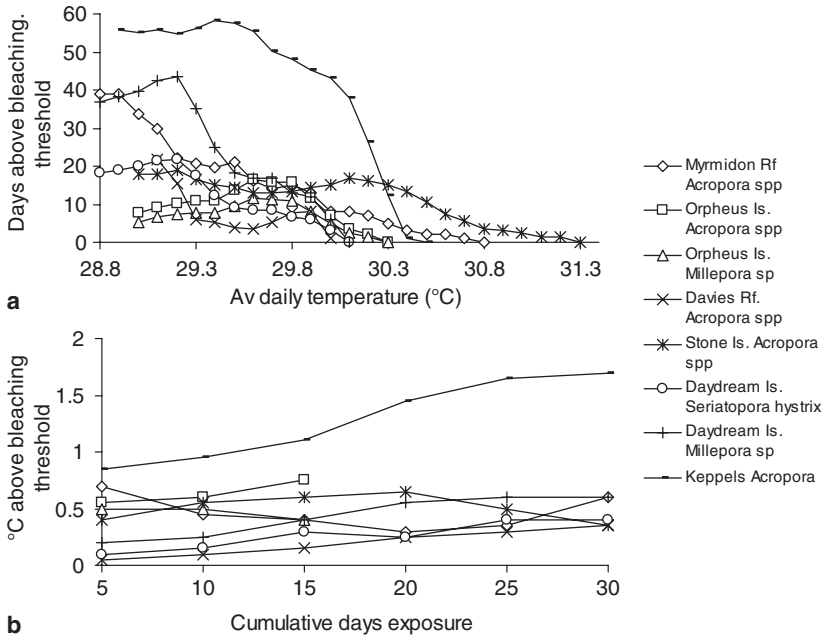


Fig. 7.4 Relationship of mortality curves to: **a** “days above bleaching threshold” and **b** “temperature above bleaching threshold”

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

7.4 Discussion

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

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

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

the extent and severity of bleaching and, where appropriate, take local action to ameliorate the risk of further damage to reefs from such activities as dredging, coastal development and point-source pollution. The time-integrated bleaching thresholds have been in use since 2000 as one of the monitoring tools for the Great Barrier Reef Marine Park Authority. The results of this review show they performed well in the time leading up to and including the 2002 bleaching event, but also that there were some inconsistencies in recent years at some sites. The summer of 2004 in particular exceeded the bleaching threshold as well as the 1998 curve at Daydream Island, Myrmidon Reef and Chicken Reef in the central GBR, but, apart from a few pale colonies, no widespread bleaching occurred. Similarly, the 2005 summer at Magnetic Island exceeded the bleaching threshold and the conditions during the 1992 and 1994 bleaching events and was almost equivalent to the 2002 bleaching event, but, apart from pale tops on a few *Porites* bommies, no bleaching was evident. One plausible explanation is that the bleaching curves are too simplistic in modelling the bleaching thresholds because they do not take into consideration any possible recovery by the corals between intra-seasonal heat waves. This is unlikely since temperatures were well above the mean at these sites for almost the entire 2004 summer and the week-to-week fluctuations were smaller than in the 1998 summer and equivalent to the 2002 summer (data not shown). Another plausible explanation is that light levels, UV or other environmental factors were sufficiently lower in the non-bleaching 2004/5 summers compared with the bleaching summers and effectively prevented bleaching. Again, this is unlikely because global radiation near Magnetic Island was higher during the critical 2005 summer months of January/February (total = 1403 MJ/m²) than the same period during the bleaching summer of 2002 (total = 1301 MJ/m²) as was total sun hours (546h vs 533h, respectively). Total UV-A and B radiation were marginally lower (82.2 MJ/m² vs

86.4 MJ/m², respectively), but this difference was not statistically significant [$t(2) = 1.12$, $df = 116$, $P = 0.27$]. The results of the statistical analysis at Magnetic Island also show that light, UV and other environmental factors at best only correlate weakly with the bleaching events and were nowhere near as important as temperature in predicting bleaching at this site. A more likely explanation is that corals at Magnetic Island, Daydream Island, Myrmidon and Chicken Reef have undergone some acclimatization after the 2002 bleaching event, possibly through shuffling zooxanthellae types within the coral tissue (Baker et al. 2004; Rowan 2004; Berkelmans and van Oppen 2006) or in part through selection of more thermally-resistant coral and symbiont genotypes among surviving populations.

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

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

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

In conclusion, time-integrated bleaching thresholds remain an appropriate and useful method for modelling thermal stress in corals. There is a high likelihood that bleaching thresholds have increased at a number of locations on the GBR since the major 2002 bleaching event, potentially as a result of acclimatization. Whilst these

increases may be limited in terms of absolute temperature, there is no doubt that they are of great ecological significance. Mortality thresholds developed for a limited number of reefs based on time–temperature curves for 50% mortality of specific taxa indicate a very narrow margin between the bleaching and mortality thresholds for sensitive species.

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