

# The Potential for Temperature Acclimatisation of Reef Corals in the Face of Climate Change

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Coral bleaching has taken centre-stage in the debate over the likely biological effects of global environmental change. Central to any judgements on this issue is the ability of corals to display increased tolerance of debilitating or lethal conditions through phenotypic adaptations, such as heat-hardening, longer-term acclimatisation responses or even trans-generational epigenetic effects. But the key question is whether the magnitude of such responses can match the predicted increases in sea temperatures over the period of global warming. In the recent literature, much has been said about the potential for acclimatisation in tropical reef corals and how it may, or may not, be significant in the context of the world's changing climate (Hughes et al. 2003; Hoegh-Guldberg 2004; Donner et al. 2007; Hoegh-Guldberg et al. 2007; Maynard et al. 2008a; Donner 2009). In fact, we know remarkably little about the potential for and extent of acclimatisation in corals, and the complex physiology and behaviour underlying the phenomenon (Edmunds and Gates 2008; Maynard et al. 2008a). It is important at this stage to define the terms used in this chapter following Bligh and Johnson (1973) since there has been, and continues to be, considerable confusion in their use in the literature together with established concepts in thermal biology (see Box 1).

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## Box 1 – Terms and Concepts Used in Considering Resistance Adaptations of Corals

### Terminology

Genotypic adaptation is a process whereby natural selection adjusts the frequency of genes that code for traits affecting fitness (Cossins and Bowler 1987; Willmer et al. 2004) and which typically occurs over many generations. In contrast, phenotypic adaptation refers to adaptive changes made by an organism within its lifetime. These phenotypic responses are usually short-medium term (minutes or hours for diurnal responses, or days and weeks for seasonal responses) and reversible, but are limited in extent by the organism's genotype (Coles and Brown 2003). They can also occur during development to generate altered morphologies usually with irreversible consequences. Acclimatisation refers to phenotypic adaptations in response to fluctuations in natural conditions, whilst acclimation is reserved for adaptations generated under controlled laboratory experiments when the effects of the factor of interest can be isolated. Since there is no useful adjective to be derived from acclimatisation, 'acclimatory' is frequently used in the literature to describe responses of organisms in their natural environment (Willmer et al. 2004).

### Resistance Adaptations

Phenotypic responses manifest themselves either as responses induced over the 'normal' range of

(continued)

**Box 1** (continued)

temperatures that affect the rates of living ('capacity' adaptations, see Precht et al. (1973)) or as responses that enhance survival of extreme conditions ('resistance' adaptations). The latter are usually induced by prior short- or long-term exposure to mildly stressful conditions and they generally comprise rapidly occurring but transient increases in resistance to lethal stress ('hardening' responses), or to more slowly developing and more long-lasting resistance (as with seasonal resistance acclimatisation). Damage, debilitation and death are heavily dependent on the length and frequency of exposure to extreme environmental conditions since thermal damage is progressive and cumulative over time. The rate by which damage occurs is also very highly dependent on lethal temperature (i.e. the  $Q_{10}$  temperature coefficient is very high, see appendix in Schmidt-Nielsen (1997)), such that a small increase in exposure temperature (i.e. 0.1°C) can induce a disproportionately large increase in the rates of damaging processes. However, thermal damage can be mitigated by repair using a suite of mechanisms of which the best known are heat shock (stress) proteins and those which repair oxidative damage. Tolerance and resistance are often linked to the status of these mechanisms. All of these considerations relate directly to the concept of 'phenotypic plasticity', in which single genotypes can generate different phenotypes in response to exposure to different environmental conditions (Pigliucci et al. 2006). Some, but not all, phenotypic plasticity is adaptive.

### Measuring Thermal Resistance

A widely used and more ecologically meaningful approach to the determination of thermal tolerance properties is the critical thermal maximum (CTM) in which animals are warmed or cooled at a constant rate (e.g. 1°C/h) and the temperature at which a loss of a critical locomotory, postural or behavioural attribute is observed (i.e. loss of righting response, or of orientation). However, CTM is negatively related to heating rate, and is generally affected by the prior thermal conditioning of the animals, and ecologically relevant experimental conditions need to be chosen (Terblanche et al. 2007).

Underlying our attempts to predict the status of corals in future years are two important considerations – first, to what extent can they acclimatise to changing environmental conditions, and second, how close are these organisms to their thermal limits? As highlighted by Edmunds and Gates (2008), it is not a case of whether corals can or cannot acclimatise to changing environmental conditions but rather to what degree they are able to acclimatise. According to Donner et al. (2005), who combined NOAA bleaching predictions with atmosphere-ocean general circulation models, the thermal tolerance of corals must increase by 0.2–1.0°C per decade over the next 30–50 years if bleaching is not to become an annual or biannual event on the world's coral reefs. The arguments highlighted by Hoegh-Guldberg (1999, 2004), Donner et al. (2005) and Hoegh-Guldberg et al. (2007) suggest that corals will be unable to physiologically adjust in the time frame required to match this rate of warming.

Closely related to the above are two claims that have become engrained in the recent coral literature. They are that corals are living close to their upper lethal temperatures (Mayer 1914; Edmondson 1928; Coles et al. 1976) and, second, that coral bleaching, in response to steadily rising sea temperatures, has increased in frequency and intensity in recent years (Hoegh-Guldberg 1999, 2004; Hughes et al. 2003; Donner et al. 2005; Hoegh-Guldberg et al. 2007) implying that thermal thresholds have changed little during the last 2 decades (Kleypas et al. 2008). Coral bleaching (i.e. the loss of zooxanthellae and/or their pigments) in response to stresses such as elevated temperature are discussed in detail in Chapter 23 Coral Bleaching: Causes and Mechanisms and the bleaching response, while not precisely defining the thermal limits of the coral, has regularly been used as a sensitive indicator of thermal sensitivity of the holobiont (see reviews by Jokiel and Coles 1990; Glynn 1993; Hoegh-Guldberg 1999).

In this Chapter we shall revisit the above claims in the context of evidence provided from other poikilotherms (organisms with a variable body temperature) on the possible limitations of living at temperatures close to lethal limits. We shall also review recent evidence for acclimatisation of corals to elevated temperature and solar radiation while briefly exploring the new and emerging science of epigenetics (the study of heritable changes in gene expression and function that cannot be explained by changes in DNA sequence) and the implications that this may have for a more thorough understanding of the acclimatisation potential of reef corals in future decades. Defining the magnitude of resistance adaptations is complicated by several factors, notably (i) complications arising from the symbiotic engagement of host and zooxanthellae, since they may have different individual sensitivities as well as possessing interacting effects on thermal sensitivity, (ii) the existence of stressors in addition to damaging high temperature, including solar radiation and desiccation, and (ii) the sheer complexity of the natural environment with the interplay of tidal, diurnal and other multiannual cycles.

## 1 Historical Perspectives on Coral Acclimatisation and Acclimation

Interestingly, physiological adjustments to environmental factors such as temperature and salinity were discussed by some of the earliest scientists working on corals (Mayer 1914; Edmondson 1928) while Yonge (1940) attributed much of the success of the stony corals to their considerable powers of 'adaptation'. In this context Yonge was using the term in a broad context to incorporate both long-term genotypic adaptation (as defined above) and short-term phenotypic acclimatisation. His views were strongly influenced by his field and experimental observations of corals living on shallow, inter-tidal reef flats during the 1928–1929 Great Barrier Reef Expedition. Although unsuccessful, because of methodological constraints, he was the first to attempt measurement of coral acclimatisation responses through the assessment of monthly zooxanthellae densities in reef corals (British Natural History Museum Archives 1928). Indeed, it was over 50 years later before we appreciated the significance of seasonal adjustments in the depths of coral tissue and zooxanthellae densities in response to increased temperature and solar radiation (Stimson 1997; Brown et al. 1999; Fagoonee et al. 1999; Fitt et al. 2000).

Subsequently, studies of the temperature physiology of corals and their powers of acclimation were carried out by Coles and Jokiel (1978) in their evaluation of the effects of a thermal effluent from a power-generating station in Hawaii. Their experiments not only established that *Montipora verrucosa* was capable of acclimation to temperatures of 1–2°C above the summer maximum temperature but that this species was able to tolerate a fluctuating temperature regime. Furthermore, they established that sub-tropical coral species appeared to have an upper lethal limit that was 2°C lower than their tropical counterparts (Coles et al. 1976). These studies and others are discussed in detail in Brown (1997) and Coles and Brown (2003) in their reviews of the acclimatisation potential of corals to rising sea temperatures.

By the late 1990s concern about the effects of climate change on coral reefs prompted renewed interest in acclimatory responses of corals with Berkelmans and Willis (1999) demonstrating that the winter bleaching threshold of *Pocillopora damicornis* on the Great Barrier Reef was 1°C lower than the summer threshold for this species. In addition, Berkelmans (2002) concluded that thermal adaptation occurred on scales of 10–100 km on the Great Barrier Reef with cross-shelf and latitudinal differences in bleaching thresholds corresponding to specific temperature regimes on mid and outer-shelf reefs.

Clearly, early workers were intrigued by the environmental rigours experienced particularly by inter-tidal corals and their ability to endure hours of aerial exposure, high

temperatures and solar radiation. As coral reef science developed in the early 1970s, thermal thresholds of corals were a focus for those evaluating the effects of potentially polluting discharges. By the 1990s, questions over the extent of thermal acclimatisation by corals and the rate at which physiological adjustments could be made were frequently voiced. These questions continue to be asked as projections are attempted of coral reef status by the middle of the twenty-first century (Berkelmans et al. 2004; Donner et al. 2005; Hoegh-Guldberg et al. 2007; Baker et al. 2008; Donner 2009).

Before looking at the recent evidence for acclimatisation in reef corals it is valuable to review the latest thinking of thermal physiologists working on similar problems with other phyla and the idea that species living in tropical climates are likely to suffer disproportionately from small temperature increments.

## 2 Organisms Living Close to their Lethal Limits are more Vulnerable to the Effects of Climate Change

Janzen (1967) has argued that because tropical ectotherms had evolved in relatively benign aseasonal environments, they should be thermal specialists with a limited ability to acclimate compared with higher latitude, more generalist species. More recent work (Tewksbury et al. 2008) notes that while these conclusions are broadly supported by several studies on terrestrial ectotherms they do not necessarily hold in the marine environment where thermal specialists are found at both high and low latitudes with thermal generalists being common in the mid-latitudes. According to Tewksbury and his colleagues, such a pattern mirrors the seasonality of ocean temperatures leading to the conclusion that both tropical and high-latitude organisms live at near-stressful temperatures, which could make them particularly susceptible to global warming.

An elegant study by Stillman (2002) on the thermal tolerance limits of the porcelain crab across both latitudinal boundaries and vertical gradients in the inter-tidal/sub-tidal zone has shown that the upper thermal tolerance limits of a number of crab species mirrors their microhabitat conditions with a strong positive correlation between lethal temperatures and maximal habitat temperature. Interestingly, a porcelain crab species from the upper inter-tidal habitat, which had evolved the greatest tolerance to damaging high temperatures, appeared to have much reduced acclimation capacity when thermally conditioned to 8°C and 18°C, compared with lower inter-tidal and sub-tidal species. These results led Stillman (2003) to conclude that the upper inter-tidal species would be the most susceptible to the smallest increases in microhabitat temperatures

and hence most vulnerable to climate warming. He argued that intertidal species might be living closer to their thermal maxima and may have reduced their abilities to increase their upper thermal tolerance limits when compared with sub-tidal species. Similar results were obtained for turban snails of the genus *Tegula*, which inhabit the intertidal and subtidal zone (Hellberg 1998) with thermal limits of protein synthesis reflecting their vertical distribution on the shore while inter-tidal species displayed reduced acclimation abilities compared to those in the sub-tidal zone. In reviewing this work Somero (2005) concluded that ‘warm adapted intertidal species face current – and most likely, future-threats from high temperatures than less heat-tolerant, subtidal congeners’.

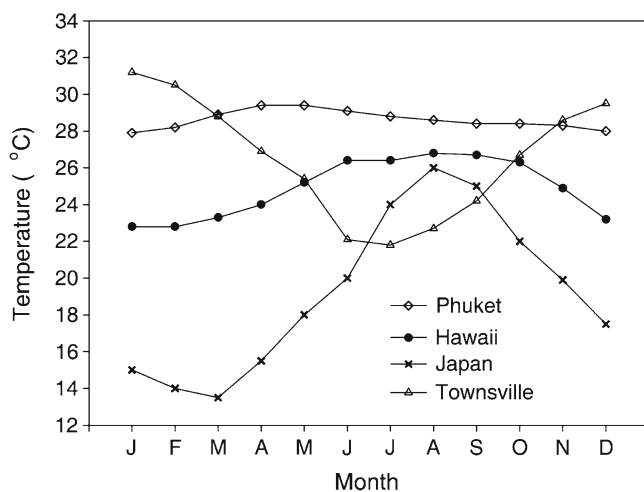
But how relevant are these conclusions to reef corals? Certainly it would appear from the existing literature that the thermal limits of corals are dictated, at least in part, by their thermal environment both on a latitudinal (Coles et al. 1976) and a seasonal basis (Berkelmans and Willis 1999). However, the temperature environment encountered by corals worldwide is very variable as shown in Fig. 1 with corals in low latitudes living at high temperatures with relatively little seasonal variation (~2–3°C) while those at high latitudes, such as in the Iki Islands of Japan, experience annual lows of 14°C and annual highs of 27.5°C (Nomura 2004). Considerable seasonal temperature ranges are also recorded for corals living in the Arabian region (Sheppard et al. 2002). Marked fluctuations (>6°C) in daily temperatures have been noted for corals living in the vicinity of upwelling areas in Oman (Coles 1997), as well in the Andaman Sea (Phongsuwan personal communication) and Chagos archipelago where reefs are subject to the effects of internal waves (Sheppard 2009). Such fluctuations are likely to have significant bearing on overall thermal sensitivity as suggested in field studies of thermally induced coral

bleaching (McClanahan and Maina 2004; McClanahan et al. 2007). Furthermore, some of the most temperature-susceptible branching corals known, i.e. corals of the genus *Acropora* and genus *Pocillopora*, have been found in the vicinity of geothermal vents in the Banda Sea, Indonesia where temperatures of 34°C were recorded (Tomascik et al. 1997).

Clearly corals have adapted over time to a wide range of temperature scenarios but it seems likely that annual and daily variations in temperature might also play a role, alongside maximal habitat temperatures, in defining thermal tolerances. This is particularly likely for high latitude sites where corals experience low winter temperatures that lead to declines in photochemical efficiency (Suwa et al. 2008) or even bleaching (Nomura 2004; Hoegh-Guldberg and Fine 2005), factors which could have profound implications for the energy budgets of corals as they approach maximal summer temperatures later in the year. Indeed, it might be argued that temperature increases associated with climate change might provide some benefit to the corals of high latitude reefs since the negative effects of winter low temperatures might be eliminated and the physiological status of the coral improved to face the rigours of an increased summer maximum.

Unlike the porcelain crabs and turban snails described earlier, the thermal tolerances of corals are defined not only by their maximum temperature exposure but also by their experience of solar radiation (Fitt et al. 2001; Lesser and Farrell 2004; Brown and Dunne 2008) since the latter plays a key role in the bleaching process (see Chapter 23) as temperature rises. Because light is so central in either reducing or improving bleaching tolerance at elevated sea temperatures (Brown and Dunne 2008), the thermal limits of corals must be influenced by the combination of both the thermal and light regimes of their microhabitat.

Corals typically undergo thermal damage and bleaching at temperatures above 32°C, yet many other species, both vertebrate and invertebrate, including those inhabiting higher latitudes, can withstand much higher temperatures. For example, (i) goldfish can be conditioned indefinitely at temperatures up to 38°C and can display complex trained behaviours even above 40°C (Hoyland et al. 1979); (ii) some tropical marine fish species in Indonesia display upper critical thermal maxima of 40°C or above (Eme and Bennett 2009) (ii) European diving beetles of the genus *Agabus* display a mean upper lethal limit of 43–46°C (Calosi et al. 2008), (iii) the tropical prawn *Macrobrachium acanthurus* can be acclimated to 32°C and displays a CTM of 39.8°C (Diaz et al. 2002), and (iv) tropical bivalves typically display upper thermal limits at approx 36–40°C (Compton et al. 2007). Indeed, the upper tolerances of tropical corals are closer to that of freshwater crayfish inhabiting the cool temperate rivers of northern Europe (Cossins and Bowler 1976). Thus, it seems clear that corals are not as thermally resistant as might be



**Fig. 1** Average monthly sea temperatures over the year for four different reef locations: Phuket, Thailand (After Brown et al. 1996); Hawaii (After Jokiel and Brown 2004); Iki Islands, Japan (After Nomura 2004) and Townsville, Australia (After Kenny 1974)

expected from their tropical distribution, which is perhaps surprising given their sessile nature as adults and their inability to avoid stress by moving in a thermal gradient.

This sensitivity might have two explanations. First, it might well be that the apparently high thermal sensitivity of corals is due to some fundamental physiological limitation which is not evident in other taxa. Corals certainly possess conventional heat shock proteins (HSP) responses (Sharp et al. 1997) and the cnidarian genome (see Section 5 [Genomics Approaches to Stress Responses in Corals](#)) certainly contains a broad range of stress-response genes. But they might lack some other critical protective response that is expressed in more complex organisms. Alternatively, their sensitivity might be linked to some property of the symbiotic relationship between zooxanthellae and host. Second, it may be that the microclimatic conditions experienced by corals occupies a lower range of temperatures than is currently appreciated, and that their tolerance states relate to this rather than the temperatures indicated by large geographic-scale models or remote sea-surface measurements. In any case, the thermal microenvironment of intertidal and sub-tidal zones is a complex mosaic over space and time due to the powerful influences of solar and tidal cycles, and the experiences of animals within that niche cannot be simply characterised by a single temperature. This applies particularly to the sea-surface temperatures generated by satellite imaging, which by estimating surface skin of the ocean does not reflect the degree of variability with depth, the occurrence of cold upwelling or other micro-environmental features. This mosaic presents opportunities for survival even in a globally warmed world, i.e. thermal refugia. A similar situation was recorded by Huey et al. (2009) who found that tropical species of forest lizard were active over a lower temperature range and displayed lower thermal tolerance limits than lizard species inhabiting more open, lowland tropical sites, and this was found to match the lower temperatures beneath the forest canopy. Thus, the thermal properties of forest and savannah lizards were linked to the microclimatic properties of their respective environments. Similarly, it may be that the corals inhabit waters with temperatures well below those causing damage and have evolved a resistance appropriate to the temperature variations more frequently experienced than for the occasional thermal bleaching event.

### 3 Has Coral Bleaching Increased in Intensity and Frequency in Recent Years?

One of the earliest attempts to collate the incidence of bleaching events over time was that of Glynn (1993) who showed that major bleaching had only been documented since the 1980s with very few records prior to this date. One explanation that

Glynn suggested might account for this pattern was the lack of interest and accessibility to reefs prior to 1970 though he noted that in the 1960s and 1970s there were few bleaching reports despite an active and expanding reef research base.

However, one of the earliest documented examples of coral bleaching was made by Yonge on the Great Barrier Reef Expedition of 1928–1929 (Yonge and Nicholls 1931). In March 1929 Yonge and his colleagues noted extensive bleaching and mortality of reef flat corals at Low Isles (Fig. 2) during a period of calm conditions when seawater temperatures reached at least 35°C. Although these observations led Yonge to experimentally investigate the loss of zooxanthellae at elevated temperatures he never published photographs of the bleached reef in the extensively illustrated scientific reports of the expedition. Having witnessed recovery of many of the bleached corals within 3 months in the field (Yonge and Nicholls 1931), one can only assume that Yonge thought that there was nothing extraordinary about this bleaching episode and that it was a phenomenon that might be witnessed regularly by corals living on the shallow reef flat.

One of the first references to the fact that bleaching events were occurring more and more frequently was that of Hoegh-Guldberg (1999), though no quantitative evidence was provided in this paper. An earlier publication (Brown et al. 1996) documenting the steadily rising sea temperatures over a 50-year period in the eastern Indian Ocean certainly predicted an increased frequency of bleaching in this region but it was not until Oliver et al. (2009) analysed the comprehensive



**Fig. 2** Coral bleaching at Low Isles, Great Barrier Reef on March 21st 1929 (Photograph from C.M. Yonge collection held at the British Museum of Natural History and reproduced with the permission of the latter)

ReefBase bleaching database that any attempt was made to quantify the incidence of bleaching events over recent time. These authors concluded that their data did not allow them to differentiate between true increases in bleaching frequency and increases in reporting effort. They did, however, identify four major bleaching peaks on a global level in the previous 20 years, but stressed that this number was too small quantitatively to establish that the frequency of severe events was increasing. Similarly, their data did not indicate any increases in the intensity of bleaching over this time. This result was in stark contrast to the findings of Eakin et al. (2009) who demonstrated clear increases in both the frequency and intensity of bleaching-level temperature stresses derived from instrumental observations of global SST and modern near real-time satellite data. Oliver et al. (2009) explained this mismatch by considering coral colonies that survived severe bleaching, such as that in 1998, as being more capable of surviving subsequent thermal stress. In other words, they suggested that corals have accommodated to the steadily rising sea temperatures over recent years. This explanation is also one of a number used by Berkelmans (2009) to account for the fact that bleaching did not occur at four sites on the Great Barrier Reef in 2004 despite the bleaching threshold temperatures far exceeding those eliciting bleaching in 1998. Other explanations invoked the modulating effects of light and the selection of more thermally resistant holobiont genotypes among surviving populations.

Reduced susceptibility to bleaching was also observed at sites around Phuket, Thailand, in 1997 and 1998 when environmental stresses (both temperature and solar radiation) were much higher than in 1991 and 1995 when extensive bleaching was witnessed (Dunne and Brown 2001). In this case, experience of unusually high solar radiation in the months preceding the seasonal maximum temperature, which leads to improved thermal tolerance (Brown et al. 2002a), was suggested as the explanation for reduced bleaching in 1997–1998. Interestingly, despite steadily rising sea temperatures over the last 60 years at this location, which is in the Indian Ocean warm pool, there have been no major bleaching events in recent years on the scale of those witnessed in 1991 and 1995. A more recent example of possible acclimatisation involves that of increased thermal tolerance of three major coral genera, namely *Acropora*, *Pocillopora* and *Porites*, on the Great Barrier Reef in 2002 following earlier thermal stress in 1998 when bleaching was extensive (Maynard et al. 2008b). In this example, bleaching was 30–100% lower in 2002 than that predicted from the relationship between bleaching severity and thermal stress in 1998, in spite of much higher solar irradiances in 2002. Prior experience of high solar radiation before the 2002 event and selective mortality of less tolerant genotypes, as a result of the 1998 bleaching, were not considered to be significant in explaining the observed increase in thermal tolerance of corals. However, symbiont shuffling,

trophic plasticity and/or access to heterotrophic feeding and physiological acclimatisation were highlighted as possible mechanisms accounting for the improved coral tolerances observed in 2002.

We therefore conclude that despite the popular notion that global bleaching events are increasing in intensity and frequency there is at present no rigorous evidence to support such a statement and furthermore some suggestion that the thermal tolerances of corals in different parts of the world are adjusting to warmer scenarios. In the following section, we examine the existing evidence for resistance acclimatisation in reef corals.

#### 4 Recent Work on Phenotypic Resistance Adaptations to Thermal/Irradiance Stresses in Reef Corals

The recent literature on responses of reef corals to thermal and irradiance stresses can be broadly divided into two categories. First, acclimatisation studies on the effects of experimentally elevated temperature and/or solar radiation on corals which have acclimatised to particular conditions (i.e. high or low sea temperatures and/or irradiance) in their natural environment (Brown et al. 2002a, b; Anthony and Hoegh-Guldberg 2003; D’Croz and Mate 2004; Castillo and Helmuth 2005; Berkelmans and van Oppen 2006; Dove et al. 2006; Griffin et al. 2006; Brown and Dunne 2008) and second, a number of acclimation studies where corals were experimentally pre-exposed to high temperatures and high or low solar radiation before subsequent evaluation of their physiology at a later date under stressful temperature conditions (Visram and Douglas 2007; Yakovleva and Hidaka 2004; Castillo and Helmuth 2005; Middlebrook et al. 2008).

Where acclimatisation had been demonstrated then it appears to involve several different processes – these include changes in physiological/biochemical traits of both the coral host and/or its zooxanthellae (Brown et al. 2000, 2002a,b; Brown and Dunne 2008); the replacement of bleaching susceptible zooxanthellae by genetically distinct, bleaching-resistant zooxanthellae (Rowan 2004; Baker et al. 2004) or by shifts in the dominant members of zooxanthellae populations in corals, which host multiple clades or types of algae (Berkelmans and van Oppen 2006).

As far as physiological traits are concerned, then the field experience of high irradiance on the western surfaces of *Goniastrea aspera* colonies from Phuket, Thailand was shown to confer subsequent temperature tolerance mediated, at least in part, by high levels of stress proteins and antioxidants in the coral host and improved xanthophyll cycling in the zooxanthellae (Brown et al. 2000, 2002b). Stress proteins have also been shown to be critical in seasonal

acclimatisation of other marine invertebrates (Hoffman and Somero 1995; Roberts et al. 1997) with increased stress protein and antioxidant enzyme activity being noted in several studies on thermally stressed corals (Downs et al. 2000, 2002; DeSalvo et al. 2008). The overall thermal tolerance of corals is affected by both coral host and zooxanthellae (Baird et al. 2009) with publications highlighting properties of the host (Salih et al. 2000; Brown et al. 2002b; Bhagooli and Hidaka 2004; Dove 2004; Grottoli et al. 2006; Ainsworth et al. 2008) and the zooxanthellae (Baker et al. 2004; Rowan 2004; Tchernov et al. 2004; Berkelmans and van Oppen 2006) in influencing bleaching susceptibility at elevated temperatures.

The background thermal tolerance of *G. aspera*, discussed above, will be affected by the fact that it hosts Clade D zooxanthellae, which are recognised as being the most thermally tolerant zooxanthellae known to date (Rowan 2004; see also Chapter 23). More specifically, these corals harbour symbionts identified as type D1a (Pettay and LaJeunesse 2009) on both east and west surfaces of the colony though the zooxanthellae on the western surfaces appear to have improved photoacclimatory abilities compared with those on the east (Brown and Dunne 2008).

A clear example of corals, with mixed symbiont populations, acquiring improved thermal tolerance through changing the dominant symbiont type is that documented by Berkelmans and van Oppen (2006). These authors investigated the potential for acclimatisation of the branching coral *Acropora millepora*, which hosts both Clade C and Clade D zooxanthellae. Corals were able to gain an increased thermal tolerance in the order of 1–1.15°C by switching their dominant symbiont Clade to Clade D. The authors argue that although this capability is significant in the context of global climate change, in the absence of other mechanisms of thermal acclimatisation it would not be sufficient to meet the required tolerance increases of 0.2–1.0°C per decade demanded by some models (Donner et al. 2005).

It is thus clear that corals have a number of mechanisms by which they can respond to changes in their thermal and irradiance environments and that these can be effected within a relatively short time period (~9 months in the case of symbiont shuffling as described by Berkelmans and van Oppen (2006)). The timescale of acquisition of thermal tolerance in *G. aspera* is also relatively short being in the order of 1–3 years as inferred from bleaching patterns in corals of different heights in the field. Many of the corals displaying non-bleached western surfaces during bleaching events were 4–6 years old (Brown et al. 2000) and these colonies would not have been exposed to differential irradiance regimes on east and west faces until they were ~1–2 years of age. How long the irradiance ‘memory’, and the thermotolerance it confers, is retained in the absence of the environmental signal that first induced the tolerance is unknown though preliminary observations suggest that the ‘memory’ might be retained for

several years (see Section 6 [Epigenetics and Its Significance for Coral Acclimatisation to Elevated Temperature](#)).

It is important to point out that not all corals have the ability to improve their thermal tolerance by shuffling their symbionts, with *A. millepora* from some sites on the Great Barrier Reef retaining their native dominant clade and showing greater bleaching susceptibility when manipulated in the same way as their congeners from other reefs (Berkelmans and van Oppen 2006). Similarly, while some laboratory studies show temperature acclimation of corals after pre-exposure to elevated seawater temperatures (Yakovleva and Hidaka 2004; Middlebrook et al. 2008), others do not (Visram and Douglas 2007) though as the latter authors point out it is often extremely difficult to mimic environmental conditions on the reef in laboratory manipulations. Nevertheless, it appears that there is overwhelming evidence for acclimatory ability in different coral species to increased sea temperatures and that this could very well account for the apparent increase in thermal tolerance of three major genera on the Great Barrier Reef between 1998 and 2002 (Maynard et al. 2008b).

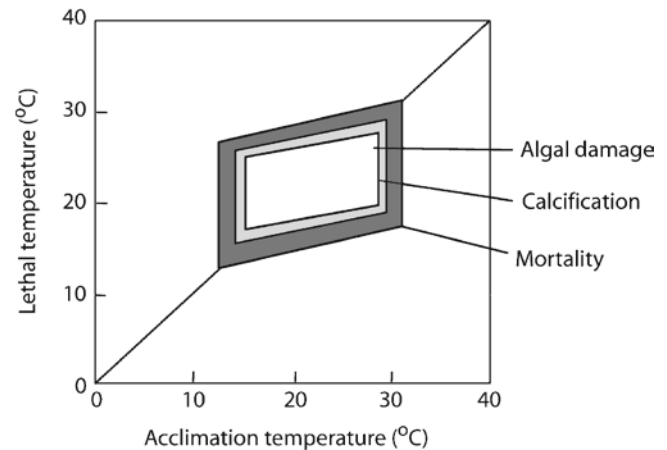
Hoegh-Guldberg (2009) has recently dismissed phenotypic acquired tolerance responses as having any bearing on the ability of corals to tolerate future warmer climates, justifying this by pointing to the small scale of protective responses in relation to the challenges of the projected increase in environmental temperature. Hoegh-Guldberg et al. (2007) went further in suggesting that evidence of coral phenotypic resistance adaptation to bleaching is equivocal or nonexistent, the implication being that there was sufficient experimental exploration of the issue to make a proper judgement. Obura (2005) recognised that thermal tolerance properties of corals are particularly complex and argues for a more explicit definition of terms. This would permit the separation of adaptive responses so that the underpinning tolerance traits can be more properly quantified, and the status of coral reefs can be more precisely defined over time. The current literature is very limited in quantifying acquired tolerance responses in corals, including both rapid heat hardening and longer-term acclimation responses. Indeed, Hoegh-Guldberg and colleagues (Middlebrook et al. 2008) recognise this point, in stating that only a single study has examined thermal acclimation experimentally. Good examples of the systematic approaches required (conditioning and exposure regimes, CTM’s, tolerance polygons, etc.) are those described by Cossins and Bowler (1987) and put into effect in respect of reef fish by Eme and Bennett (2009). It is therefore premature to reject a meaningful role for acquired tolerance adaptations in mitigating the effects of global warming. But being colonial corals are especially tractable and interesting for this kind of analysis since it is possible to replicate the analysis of single genotypes, and they can potentially display differentiated adaptive states across the colony.

An important issue in defining the survivable thermal limits of corals, and their ability to display resistance acclimation

responses, is to establish an ecologically meaningful criterion of thermally induced debilitation or death. Conventional methods of quantifying tolerance properties for other organisms (see Cossins and Bowler 1987) involves exposing a sample of animals from a single population to a range of lethal temperatures over time and recording the time or temperature causing 50% mortality ( $LT_{50}$ ). In order to determine the extent to which  $LT_{50}$  can be modified by prior thermal experience some batches of animals need to be pre-conditioned for at least 3 weeks to a range of temperatures over the normal, non-stressful range of temperatures. Their  $LT_{50}$  can then be determined as before. The resulting data can be used to construct a 'tolerance polygon', which defines the tolerable thermal niche of that population of animals (Fig. 3). At present a range of different measures of thermal debilitation have been used for corals by different investigators (see Table 1), which are mainly focused on the viability and performance of the photosynthetic apparatus and bleaching of zooxanthellae rather than mortality of the holobiont itself. But Obura (2005) argues that bleaching does not inevitably lead to the coral mortality and shows examples from the coast of Kenya of an inverse relationship in the branching coral *Pocillopora damicornis*. Moreover, measures of thermal injury and death vary considerably depending on the methods used, and this directly affects any conclusions drawn regarding the effects of global warming. Thus, to develop a more meaningful prediction of global effects on coral viability it is important first to identify the critical lesions of thermal damage leading not just to loss of photosynthetic performance but also to long-term viability of the holobiont. In addition to the existing ideas of bleaching susceptibility and photosystem damage, this could be related to other possible lesions of the host tissue, such as loss of energy supply due to debilitation of oxidative phosphorylation (El-Wadawi and Bowler 1995), or collapse of ion gradients across cellular plasma membranes

(Gladwell 1975; Cossins and Bowler 1976), both of which have been documented in other taxa.

Of course, phenotypic resistance adaptations have their limits, particularly at the high end of the spectrum of predicted temperatures and when faced by a 6°C warmed planet. But there is good reason to expect that phenotypic resistance



**Fig. 3** Hypothetical tolerance polygons constructed for a coral holobiont. The polygons represent the effect of acclimation temperature upon the upper and lower thermal limits of a coral for three different measures of effect, namely holobiont mortality, inhibition of coral calcification and onset of algal damage. The upper line of each polygon is based on data for 50% debilitating effects of high temperature and the lower line for low temperatures, and the polygon is constructed for each with vertical construction lines. The polygons thus contains the combination of acclimation and lethal temperatures within which median effects are evident. Similar lines can be constructed for any other level of effect as a series of 'onion skins' around the median limits; thus the algal damage polygon lies within that for other measurements indicating that it has greater thermal constraints. The slope of the graphs indicating upper and lower thermal limits reflects the effect of prior thermal history upon the thermal tolerance; animals displaying large such responses typically have a slope of 0.3. The diagonal line indicates where lethal temperature equals the acclimation temperature

**Table 1** Examples from the recent literature of parameters measured during experimental exposure of corals to elevated temperatures where P/R=photosynthesis/respiration measurements and calcif.=coral calcification

Authors	Coral			Symbiont			
	Mortality	Calcif.	HSPs/anti-oxidants	Algal density	Algal pigments	Fv/Fm	P/R
Downs et al. (2000)			X				
Downs et al. (2002)					X		
Brown et al. (2002b)			X	X	X	X	
Reynaud et al. (2003)		X		X			X
Bhagooli and Hidaka (2004)	X					X	
Yakovleva and Hidaka (2004)				X	X	X	
Lesser and Farrell (2004)			X		X	X	
Griffin et al. (2006)			X				
Grottoli et al. (2006)					X		X
Visram and Douglas (2007)					X		
Middlebrook et al. (2008)				X	X	X	
Anthony et al. (2008)		X		X <sup>a</sup>	X <sup>a</sup>		X

<sup>a</sup>Bleaching metric derived colorimetrically from digital photography as luminance reduction relative to maximal algal densities/chlorophyll concentration



adaptations can indeed provide meaningful protection, thereby enhancing survival. First, stress exposures in the field are highly variable both in space and time and whilst some corals will be damaged and may die, others will have time to mount protective responses. This variability means that a fraction of any population will survive based on resistance enhancements perhaps in thermal refugia. Second, the processes leading to thermal damage, and thus the extent of damage caused by a specified period of exposure, is very heavily dependent on temperature.  $Q_{10}$ s for damaging processes can exceed 50 (Cossins and Bowler 1987) rather than two to three for most biological processes, so that an increase of just 0.1°C in lethal limits can have a disproportionately large effect in slowing the rate of damage accumulation, mitigating damage for a given exposure, and this can make the difference between survival and death. Third, as already described, stress genes are as inducible in corals as in other taxa.

## 5 Genomics Approaches to Stress Responses in Corals

The recent publication of a draft genome sequence of the first cnidarian, the starlet sea anemone, *Nematostella vectensis* (Putnam et al. 2009), has demonstrated that the cnidarian genome possesses a surprising degree of conservation of gene content and even gene synteny with vertebrate animals. This represents the oldest conserved synteny in the eukaryotes and suggests that cnidarians are better models for understanding the vertebrate genome than the more widely used invertebrate model species, such as *Drosophila* and *Caenorhabditis*. This includes an almost complete list of genes known to be part of developmental signalling pathways including those involved in signal transduction, cell communication and adhesion pathways, as well as genes responding to environmental disturbance, such as heat shock proteins and molecular chaperones, superoxide dismutases, etc. Thus, there is no reason to expect that cnidarians lack any molecular apparatus involved in stress responses. The ability to identify coral genes using conventional homology-based methods favours the direct application of contemporary post-genomic technologies to the problem of acquired thermotolerance mechanisms in corals.

Recent years have seen the increasing application of transcript screening technologies in stress tolerance studies of corals (Forêt et al. 2007). All studies to date have generated cloned cDNA libraries whose PCR amplification generated hybridisation probes are arrayed on the surface of glass microscope slides. The number of genes represented on arrays is rapidly increasing as cDNA libraries expand; thus, Edge et al. (2005) created a microarray containing just 32 cDNA gene probes from *Acropora cervicornis* and *Montastraea faveolata*

to test the effects of elevated temperature, salinity and UV light; DeSalvo et al. (2008) generated 1310 cDNA probes from the latter species and most recently Bay et al. (2009) have constructed microarray for *Acropora millepora* composed of a 18,000 cDNA probes. However, the need for sequence data for emerging model species will be more easily met by the combination of new, very high throughput sequencing technologies. Thus, Meyer et al. (2009) have recently generated 600,000 sequence reads for *A. millepora* in just one run of the Roche 454 instrument, which on assembly generated a comprehensive list of 11,000 genes. This in combination with in situ synthesis of microarrays from *in silico* sequence data (e.g. Agilent) offers a rapid and low-cost route to microarray generation.

Given that to date most published studies have been constrained by lack of sequence data and microarray probes, what has been achieved so far in understanding thermal responses of corals? DeSalvo et al. (2008) have compared *M. faveolata* exposed to thermal stress and bleaching with non-stressed controls to find 392 differentially expressed genes. Of these, only 68 were identified by homology-searching, revealing roles in a range of stress-related processes such as those involved in HSP expression and oxidative stress. They also completed a simple time-course experiment thereby classifying genes into different groups or clusters according to speed and direction of response. Bay et al. (2009) have explored array differences in *A. millepora* from two locations in the Great Barrier Reef varying in turbidity, and responses to relocation to clean water conditions. Again, small proportions of genes displayed differential expression between sites but these differences were lost on transfer of specimens from both sites to common garden conditions for 10 days. The small array developed by Edge et al. (2005) revealed gene responses to increased temperature including carbonic anhydrase, thioredoxin, a urokinase plasminogen activator receptor (uPAR) and three ribosomal genes. Richier et al. (2008) employed microarrays containing 10 K anonymous (unsequenced or unidentified) probes predominantly from host tissues of the temperate sea anemone *Anthopleura elegantissima* to assess thermal responses. Of these 2.7% or 284 genes were differentially expressed due to thermal or UV treatment, and of these only a fraction of these probes possessed an identity by homology alignment when sequenced. Nevertheless, certain gene responses were discovered including a 18-fold up-regulation of ferritin, a protein involved in cytoprotection and immunity.

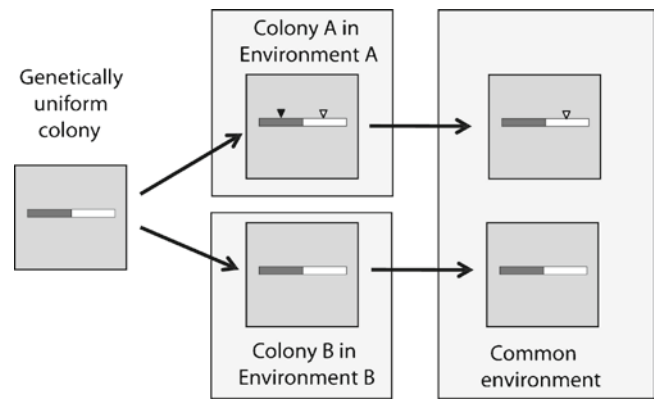
Whilst it is still early in the application of these advanced technologies, and gene coverage is incomplete, these papers show clear promise in defining in much greater detail the responses of corals to environmental stress. The technical approach has strong comparative properties allowing correlation of responses to acquired

tolerance and thermal sensitivity between species, populations and sites, and comparing specimens exposed to experimental stress treatments. Knowledge of gene identity and function is obviously crucial for relating responses to biological processes and pathways, but arrays offer strong phenotyping or classification capability, which allows discrimination between specimens in relation to prior experience or genotype, etc.

## 6 Epigenetics and Its Significance for Coral Acclimatisation to Elevated Temperature

Being colonial and possessing indeterminate growth properties, corals may grow over time into sufficiently large structures such that different regions of the colony might be exposed to quite divergent kinds and amounts of stress. This includes the east- and west-facing surfaces or upper and lower parts of inter-tidal corals and light and shade adapted parts of sub-tidal coral colonies. These regions might well develop into quite different phenotypic forms, some of which might endow stress-adaptive properties in some parts of the colony relative to others. However, there is some anecdotal evidence that differentiated parts of a single colony, which possess a common genetic constitution, might retain divergent properties even when subsequently exposed to common garden conditions. Thus, the normally high-light-adjusted, west-facing sides of *Goniastrea aspera*, when subjected to shade conditions for 4 years, still appeared to retain a greater temperature tolerance when subjected to elevated temperatures compared to the east-facing sides (Brown, personal communication).

Seasonal and short-term acclimatisation are generally reversible, so these long lasting effects appear to result from mechanisms other than the conventional. This might relate to earlier concepts of genetic assimilation when inducible phenotypes become fixed at least for a period of time, or when developmental experiences have lifelong and even trans-generational effects, as with 'canalisation' (Pigliucci et al. 2006), genomic imprinting, gene silencing etc. Based largely on advances in genome science, these so-called epigenetic mechanisms have moved from vague ideas to suggest a range of specific mechanisms (Pal and Hurst 2004; Suzuki and Bird 2007) by which long-lasting, even multi-generational, resistance adaptations might become fixed. The ecological significance of long-lasting epigenetic influences is now becoming rather well established including the vernalisation response in plants, effects of carcinogens and teratogens and trans-generational effects of starvation and dietary effects on the *agouti* gene (Pal and Hurst 2004; Suzuki and Bird 2007; Bosssdorf et al. 2008).



**Fig. 4** Hypothetical involvement of acclimatisation and epigenetic modification in generating tolerant phenotypes in corals. A single coral (indicated by the box with a bar containing two genes) grows and splits into two parts one of which by virtue of its orientation to the sun is exposed to much more intense solar radiation (Environment A) than the other (Environment B) over several growing seasons. Both colonies possess exactly the same genotype. The two new corals develop divergent thermal phenotypes, linked to some modification in the expression of the two genes in Colony A relative to Colony B, as indicated by the arrowheads. Conventional phenotypic adaptation results in restoration of one gene to its pre-existing state when the colony is returned to its previous (common) environment with the loss of the black arrowhead; that is, the phenotypic change is fully reversible. However, the persistence of the white arrowhead in colony A under the same conditions is *prima facie* evidence of an epigenetic effect (Modified after Bosssdorf et al. 2008)

Epigenetic changes can be induced by interaction of small non-coding RNA products with gene promoters or enzymatic modification of histones, but the most exciting mechanism, and which is currently the subject of intense interest in a variety of cancer, plant and animal model systems (Pal and Hurst 2004; Suzuki and Bird 2007; Bosssdorf et al. 2008; Kronforst et al. 2008), is the stable modification of chromosomal regions by DNA methylation. The latter can be readily fingerprinted by modifying a standard AFLP protocol (Vos et al. 1995) with methylation-sensitive endonucleases (methylation-sensitive AFLP) (Xu et al. 2000). Restriction fragments that correlate with distinct phenotypes can be cloned subsequently and used as probes enabling a microarray-based approach to genome-wide identification of responding genes (Yamamoto and Yamamoto 2004). The power of this approach lies in the ability to compare phenotypically different forms of the same genomic DNA sequence, generated over the same time period and in the ability to explore multiple specimens from each of several different genotypes. Divergent patterns between corals or parts of corals subjected to different experiences would thus point directly at an adaptive role for DNA methylation and open up a new direction for future research in this model system (Fig. 4). If shown to exist in corals this would have a considerable impact on our understanding of how corals can maximise their survival in a globally warmed climate.

## 7 Summary and Conclusions

1. The potential for corals to display phenotypic resistance adaptations to the damaging or lethal environmental conditions in an era of warming climate should not be dismissed, particularly on the basis of a currently inadequate understanding of the primary lesions of thermal damage, and of coral resistance acclimatisation.
2. Prior experience of high solar radiation levels or elevated temperatures has been shown to increase the thermal tolerance of corals both in the field and in the laboratory. Also, there is now limited evidence from work in the field that some corals have increased their temperature tolerances and reduced their bleaching susceptibility in recent bleaching events where temperature elevations and solar radiation levels were comparable with earlier bleaching episodes. Coral mortality was low in earlier events and was not considered significant as an explanation of reduced bleaching susceptibility, which was attributed to acclimatisation and/or adaptation.
3. Mechanisms implicated in increasing thermal tolerance involve algal clade shuffling and switching, improved photoprotective defences by symbiotic algae and up-regulated stress protein and antioxidant enzyme responses in both symbiotic algae and coral host.
4. The role of epigenetics mechanisms in acclimatisation to warming sea temperatures is currently unexplored in corals, but is suggested by observations of the divergent long-term thermally tolerant phenotypes of split coral colonies. This offers an additional potential mechanism that might significantly contribute to the prolonged survival of corals in a warming climate.

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