

CORAL REEF RESPONSES TO TEMPERATURE STRESS: THERMAL ADAPTATION



CO₂SCIENCE & SPPI ORIGINAL PAPER ♦ December 23, 2014

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Citation: Center for the Study of Carbon Dioxide and Global Change. "Coral Reef Response to Temperature Stress: Thermal Adaptation." Last modified December 23, 2014. <http://www.co2science.org/subject/c/summaries/bleachresptemp.php>.

As living entities, corals are not only acted upon by the various elements of their environment, they also *react* or *respond* to them. And when changes in environmental factors pose a challenge to their continued existence, they sometimes take major defensive or adaptive actions to insure their survival. A simple but pertinent example of one form of this phenomenon is *thermal adaptation*, which feature has been observed by several researchers to operate in corals in response to the stress of high temperature. This summary presents a review of such scientists' work, demonstrating that predictions of vast coral demise due to global warming are unlikely to occur.

[Fang et al. \(1997\)](#)¹ experimented with samples of *Acropora grandis* taken from the hot water outlet of a nuclear power plant near Nanwan Bay, Taiwan. In 1988, the year the power plant began full operation, the coral samples were completely bleached within two days of exposure to a temperature of 33°C. Two years later, however, "samples taken from the same area did not even start bleaching until six days after exposure to 33°C temperatures," thus illustrating their ability to thermally adapt.

[Middlebrook et al. \(2008\)](#)² reported similar findings. They collected multiple upward-growing branch tips of the reef-building coral *Acropora aspera* from three large colonies at the southern end of Australia's Great Barrier Reef and placed them on racks immersed in running seawater within four 750-liter tanks maintained at the mean local ambient temperature (27°C) and exposed to natural reef-flat summer daily light levels. Then, two weeks before a simulated bleaching event—where water temperature was raised to a value of 34°C for six days—they boosted the water temperature in one of the tanks to 31°C for 48 hours, and in another tank they boosted it to 31°C for 48 hours one week before the simulated bleaching event. In the third tank they had no pre-heating treatment, and in the fourth tank they used no pre-heating nor any simulated bleaching event. And at different points throughout the study, they measured photosystem II efficiency, xanthophyll and chlorophyll *a* concentrations, and *Symbiodinium* densities.

Results indicated the symbionts of the corals exposed to the 48-hour pre-bleaching thermal stress "were found to have more effective photoprotective mechanisms," including "changes in non-photochemical quenching and xanthophyll cycling." They further determined "these differences in photoprotection were correlated with decreased loss of symbionts, with those corals that were not pre-stressed performing significantly worse, losing over 40% of their

¹ <http://www.co2science.org/articles/V2/N7/C4.php>.

² <http://www.co2science.org/articles/V11/N24/C2.php>.

symbionts and having a greater reduction in photosynthetic efficiency,” whereas “pre-stressed coral symbiont densities were unchanged at the end of the bleaching.” In light of these findings, Middlebrook *et al.* say their study “conclusively demonstrates that thermal stress events two weeks and one week prior to a bleaching event provide significantly increased thermal tolerance to the coral holobiont, suggesting that short time-scale thermal adaptation can have profound effects on coral bleaching.”

In another laboratory-based study, [Bellantuono *et al.* \(2012\)](#)³ “tested the response of *Acropora millepora* to thermal preconditioning by exposing coral nubbins to 28°C (3°C below bleaching threshold) for 10 days, prior to challenging them with water temperatures of 31°C for 8 days,” while “in another treatment (non-preconditioned), corals were exposed to 31°C without prior exposure to the 28°C treatment.” They conducted all of these procedures in a set of “transparent tanks plumbed into flowing sea water, with four replicate tanks for each treatment.”

The three researchers discovered short-term preconditioning to higher-than-ambient temperatures (but still 3°C below the experimentally determined bleaching threshold) for ten days provided thermal tolerance for the scleractinian coral and its symbionts. And based on various genotypic analyses they conducted, they determined “the acclimatization of this coral species to thermal stress does not come down to simple changes in *Symbiodinium* symbiont shuffling and/or the bacterial communities that associate with reef-building corals bacterial shuffling.” These findings, Bellantuono *et al.* write, suggest “the physiological plasticity of the host and/or symbiotic components appears to play an important role in responding to ocean warming.” They then describe some real-world examples of this phenomenon possibly playing a crucial role in preserving corals exposed to extreme warm temperatures in the past (Fang *et al.*, 1997; Middlebrook *et al.*, 2008; Maynard *et al.*, 2008b).

South of Malta in the Mediterranean Sea, [Naumann *et al.* \(2013\)](#)⁴ collected live specimens of two scleractinian cold-water coral (CWCs) species, *Dendrophyllia cornigera* and *D. dianthus*. They transferred the specimens into two identically equipped and darkened 100-L flow-through aquaria through which Mediterranean subsurface seawater was continuously pumped from a 50-meter depth and supplied to the tanks at a rate of about one liter per minute. They maintained this water at a temperature of 12.5 ± 0.1°C for approximately 30 months before initiating the primary phase of their experiment, which was to increase the temperature of one of the aquariums by 0.5°C per day up to 17.5 ± 0.1°C, thereafter maintaining it for a further 87 days, while conducting “daily visual assessments of coral health (i.e. tentacle protrusion, suspension feeding and mortality/survival) and monthly growth measurements by the buoyant weight technique (Davies, 1989),” ultimately translating the latter into coral dry weight data.

The three researchers write, “over the entire experimental period, both CWC species showed neither differences in tentacle protrusion and suspension feeding nor mortality at ambient (12.5°C) or elevated (17.5°C) seawater temperatures.” They also state, “*D. cornigera* specimens developed a non-quantified number of new polyps at both temperatures suggesting efficient

³ <http://www.co2science.org/articles/V15/N28/C3.php>.

⁴ <http://www.co2science.org/articles/V16/N49/B1.php>.

thermal acclimatization.” In addition, they report “*D. dianthus* exhibited growth rates for ambient and elevated temperatures of $0.23 \pm 0.08\%$ per day and $0.19 \pm 0.06\%$ per day, whereas *D. cornigera* grew at $0.05 \pm 0.01\%$ per day under ambient and $0.14\% \pm 0.07\%$ per day under elevated temperature conditions.” Their findings “suggest that *D. dianthus* and *D. cornigera* may be capable of surviving in warmer environments than previously reported, and thus challenge temperature as the paramount limiting environmental factor for the occurrence of some CWC species.”

Outside the laboratory and in the real world of nature, multiple researchers have confirmed the phenomenon of thermal adaptation in corals in response to temperature-related stresses.

[Brown et al. \(2002\)](#)⁵ conducted a 17-year study of coral reef flats at Ko Phuket, Thailand, assessing coral reef changes in response to elevated sea temperatures in 1991, 1995, 1997, and 1998. Although the authors state many corals bleached “during elevated sea temperatures in May 1991 and 1995,” they report “no bleaching was recorded in 1997.” In addition, they write, “in May 1998 very limited bleaching occurred although sea temperatures were higher than previous events in 1991 and 1995 (Dunne and Brown, 2001).” When bleaching did take place, they note, “it led only to partial mortality in coral colonies, with most corals recovering their color within 3–5 months of initial paling.”

[Riegl \(2003\)](#)⁶ reviewed what was known at the time about the responses of coral reefs to high-temperature-induced bleaching, focusing primarily on the Arabian Gulf, which they note “has recently experienced high-frequency recurrences of temperature-related bleaching (1996, 1998, 2002).” Riegl reports in each of the three high-temperature years, sea surface temperature (SST) anomalies of 2 to 2.5°C above average *in situ* measured summer maximum SSTs persisted from April to September, and local maxima of *in situ* measured SSTs were 35.5°C in 1996 and 37°C in 2002. In response to these high-temperature events, *Acropora*, which during the 1996 and 1998 events always bleached first and suffered heaviest mortality, bleached less than all other corals in 2002 at Sir Abu Nuair (an offshore island of the United Arab Emirates) and actually recovered along the coast of Dubai between Jebel Ali and Ras Hasyan. Thus Riegl states, “the unexpected resistance of Sir Abu Nuair *Acropora* to bleaching in 2002 might indicate support for the hypothesis of Baker (2001) and Baker *et al.* (2002) that the symbiont communities on recovering reefs of the future might indeed be more resistant to subsequent bleaching,” and “the Arabian Gulf perhaps provides us with some aspects which might be described as a ‘glimpse into the future,’ with ... hopes for at least some level of coral/zooxanthellae adaptation.”

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⁵ <http://www.co2science.org/articles/V6/N53/C2.php>.

⁶ <http://www.co2science.org/articles/V9/N12/B1.php>.

[Jimenez and Cortes \(2003a\)](#)⁷ documented coral cover variability in the Pacific between 1992 and 2001, when the El Niño warming events of 1991–1992 (weak) and 1997–1998 (“the strongest in recorded history”) affected coral communities along the Costa Rican central Pacific coast, after which they reported their observations, as well as those of other scientists pertaining to these and earlier warming events caused by the El Niños of 1982–1983 (very strong) and 1986–1987 (moderate). The authors report there was a “paucity of bleaching and mortality in the study area in 1987 despite sea temperature anomalies similar to or higher than in other years in which bleaching and mortality occurred,” and this situation “may have been the result of the higher cloud cover and runoff which, in combination, decreased solar radiation stress.” Likewise, they suggest “similar atmospheric conditions during 1998 may explain the considerably small number of corals that bleached that year in the upwelling area of [Costa Rica’s] Golfo de Papagayo,” where they report “few corals bleached, even though sea temperature anomalies were higher than in autumn 1997.”

As to the 1997–1998 El Niño, considered to be “the strongest event on record (McPhaden, 1999; Enfield, 2001),” the authors report “mortality of entire colonies associated with this event was remarkably low in Costa Rica, less than 6% (Jimenez *et al.*, 2001),” and “only one coral species, *Psammocora stellata*, disappeared at one locality (Cambutal) after the 1997–1998 warming event.” In addition, this disappearance “did not have an effect on the percent of total cover, which was not significantly dissimilar to previous years.” They further report “this species was not affected in Mexico by the 1997–1998 warming episode (Carriquiry *et al.*, 2001).”

As for other potential explanations for these observations, Jimenez and Cortes note conspecific corals “have shown differences in susceptibility to bleach, mortality rates and recovery capabilities (Brown, 1997; Hoegh-Guldberg, 1999; Marshall and Baird, 2000; Fitt *et al.*, 2001; Glynn *et al.*, 2001),” which may “reflect corals’ adaptation to local conditions, different warming intensities at each locality, thermal acclimation, and presence of several clades of symbionts.” In fact, they state moderate warming events “may positively affect coral reef communities,” noting “increases in growth rates, reproductive activity and recruitment pulses have been observed after some El Niño episodes (Glynn *et al.*, 1991, 1994; Feingold, 1995; Guzman and Cortes, 2001; Vargas-Angel *et al.*, 2001; Jimenez and Cortes, 2003b).”

[Guzman and Cortes \(2007\)](#)⁸ note coral reefs of the eastern Pacific Ocean “suffered unprecedented mass mortality at a regional scale as a consequence of the anomalous sea warming during the 1982–1983 El Niño.” At Cocos Island (5°32’N, 87°04’W), in particular, where they conducted a survey of three representative reefs in 1987, they found remaining live coral cover was only 3 percent of what it had been before the great El Niño four years earlier (Guzman and Cortes, 1992). Based on this finding and the similar observations of other scientists at other reefs, they predicted “the recovery of the reefs’ framework would take centuries, and recovery of live coral cover, decades.” In 2002, therefore, nearly 20 years after the disastrous coral-killing warming, they returned to see how correct they were after their initial assessment of the El Niño damage, quantifying “the live coral cover and species composition of five reefs, including the three previously assessed in 1987.”

⁷ <http://www.co2science.org/articles/V7/N3/C3.php>.

⁸ <http://www.co2science.org/articles/V10/N32/EDIT.php>.

Regarding thermal tolerance, the most interesting aspect of their study was the occurrence of a second major El Niño between the two assessment periods. In fact, Guzman and Cortes state “the 1997–1998 warming event around Cocos Island was more intense than all previous El Niño events,” noting temperature anomalies “above 2°C lasted 4 months in 1997–1998 compared to 1 month in 1982–83.” Nevertheless, they report, “the coral communities suffered a lower and more selective mortality in 1997–1998, as was also observed in other areas of the eastern Pacific (Glynn *et al.*, 2001; Cortes and Jimenez, 2003; Zapata and Vargas-Angel, 2003),” which indicates some type of thermal adaptation occurred after the 1982–83 El Niño.

In an article published in the scientific journal *Coral Reefs*, [Maynard *et al.* \(2008a\)](#)⁹ question the wisdom of “popularizing predictions based on essentially untested assumptions,” among which they list the IPCC-held claims, “all corals live close to their thermal limits” and “corals cannot adapt/acclimatize to rapid rates of change.”

In discussing the first of these “untested assumptions,” the three Australian researchers say “predictions that reefs will disappear as a result of global warming are based, at least in part, on the assumption corals are living close to their maximum thermal limits.” However, they note, “the severity of bleaching responses varies dramatically within and among taxa,” citing McClanahan *et al.* (2009), and “such variable bleaching susceptibility implies that there is a considerable variation in the extent to which coral species are adapted to local environmental conditions.”

The three scientists further report little is known about the sensitivity of coral population response to climate-induced changes in vital rates; but they state a large body of evidence “supports temperature tolerance varying among species, populations, communities, and reef regions (Marshall and Baird, 2000; Coles and Brown, 2003).” Hence, they conclude, “even in the absence of an adaptive response, a change in the relative abundance of species is a far more likely outcome of climate change than the disappearance of reef corals,” citing Loya *et al.* (2001), McClanahan (2002), and Hughes *et al.* (2003).

The three researchers, moreover, clearly accept there is “an adaptive response,” in contradiction of the second untested assumption Maynard *et al.* (2008a) discuss, stating “a number of studies suggest that bleaching mortality rates have declined and thermal tolerance has increased in some regions.” They report, for example, “mortality rates in the Eastern Pacific were significantly lower in 1998 when compared with 1982 and 1983 (Glynn *et al.*, 2001),” and “Maynard *et al.* (2008b) found thermal tolerance of three common coral genera on the Great Barrier Reef to be greater in 2002 than that expected from the relationship between temperature stress and bleaching severity observed in 1998.”

Such variable bleaching susceptibility implies that there is a considerable variation in the extent to which coral species are adapted to local environmental conditions.

⁹ <http://www.co2science.org/articles/V12/N3/EDIT.php>.

As to how this adaptation is accomplished, the Australian scientists say there is “circumstantial evidence for ongoing evolution of temperature tolerance between both species and reefs,” citing Coles and Brown (2003). In addition, they suggest “symbiont shuffling from less to more stress-resistant clades is another mechanism by which corals may increase the thermal tolerance of the holobiont.” And they declare “there is growing evidence that such shuffling can increase thermal tolerance, at least in the short term (Berkelmans and van Oppen, 2006).” Thus Maynard *et al.* (2008a) conclude, “it is premature to suggest that widespread reef collapse is a certain consequence of ongoing bleaching, or that this will inevitably lead to fisheries collapses.”

Focusing on coral reefs of the Tiahura outer reef sector at the western end of the north shore of Moorea, French Polynesia, a region which “is largely free of direct anthropogenic disturbances,” [Adjeroūd *et al.* \(2009\)](#)¹⁰ describe the results of detailed observations made there periodically since the early 1970s and annually since 1991. This history, they write, “constitutes one of the longest records of coral reef dynamics.” Concentrating on the period of detailed annual observations (1991 and onward), the ten researchers documented a significant decline in coral cover followed the two disturbances of 1991 (a major bleaching event and a cyclone), when “coral cover (pooled among genera) declined from 51.0 ± 9.5% in early 1991 to 24.2 ± 14.4% in 1992, and 22.5 ± 9.3% in 1993.”

This decline, they write, was “among the most rapid of this magnitude recorded following natural disturbances.” In contrast, however, they found “the bleaching events of 1994, 2002 and 2003 had no detectable effects on coral cover, even though the thermal anomalies causing these events and their short-term impacts in terms of bleaching prevalence were similar to the 1991 bleaching event.”

Adjeroūd *et al.* say their results reveal “corals can recover rapidly following a dramatic decline,” and they note similar recoveries of coral cover have been documented at several other locations, citing Connell (1997), Halford *et al.* (2004), Emslie *et al.* (2008), and Sheppard *et al.* (2008). In addition, they state their work “supports the hypothesis that some reefs will undergo gradual changes in structure of their coral communities in response to major stress rather than collapse abruptly,” citing Loya *et al.* (2001), Hughes *et al.* (2003), and Wakeford *et al.* (2008).

[Maynard *et al.* \(2008b\)](#)¹¹ analyzed the bleaching severity of three genera of corals (*Acropora*, *Pocillopora*, and *Porites*) along five sites in the central section of Australia’s Great Barrier Reef in late February and March of 1998 and 2002. Regarding the influence of temperature, the four

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¹⁰ <http://www.co2science.org/articles/V12/N47/B1.php>.

¹¹ <http://www.co2science.org/articles/V11/N39/EDIT.php>.

researchers report “the amount of accumulated thermal stress (as degree heating days) in 2002 was more than double that in 1998 at four of the five sites,” and “average surface irradiance during the 2002 thermal anomaly was 15.6–18.9% higher than during the 1998 anomaly.” Nevertheless, they found “in 2002, bleaching severity was 30–100% lower than predicted from the relationship between severity and thermal stress in 1998, despite higher solar irradiances during the 2002 thermal event.” In addition, “coral genera most susceptible to thermal stress (*Pocillopora* and *Acropora*) showed the greatest increase in tolerance.”

Maynard *et al.* state their findings are “consistent with previous studies documenting an increase in thermal tolerance between bleaching events (1982–1983 vs. 1997–1998) in the Galapagos Islands (Podesta and Glynn, 2001), the Gulf of Chiriqui, the Gulf of Panama (Glynn *et al.*, 2001), and on Costa Rican reefs (Jimenez *et al.*, 2001).” They also note “Dunne and Brown (2001) found similar results to [theirs] in the Andaman Sea, in that bleaching severity was far reduced in 1998 compared to 1995 despite sea-temperature and light conditions being more conducive to widespread bleaching in 1998.”

The Australian scientists say “the range in bleaching tolerances among corals inhabiting different thermal realms suggests that at least some coral symbioses have the ability to adapt to much higher temperatures than they currently experience in the central Great Barrier Reef,” citing Coles and Brown (2003) and Riegl (1999, 2002). In addition, they note, “even within reefs there is a significant variability in bleaching susceptibility for many species (Edmunds, 1994; Marshall and Baird, 2000), suggesting some potential for a shift in thermal tolerance based on selective mortality (Glynn *et al.*, 2001; Jimenez *et al.*, 2001) and local population growth alone.” In addition, they say their results suggest “a capacity for acclimatization or adaptation.” In conclusion, Maynard *et al.* (2008b) say “there is emerging evidence of high genetic structure within coral species (Ayre and Hughes, 2004),” suggesting “the capacity for adaptation could be greater than is currently recognized.” Indeed, as Skelly *et al.* (2007) state, “on the basis of the present knowledge of genetic variation in performance traits and species’ capacity for evolutionary response, it can be concluded that evolutionary change will often occur concomitantly with changes in climate as well as other environmental changes.”

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Focusing more on such evolutionary possibilities, [Meyer et al. \(2009\)](http://www.co2science.org/articles/V13/N7/C1.php)¹² “performed controlled crosses between three genetically distinct colonies of the branching coral *Acropora millepora*,” and then “compared the families of larvae (which in this species naturally lack symbionts) for several physiological traits.” They conducted this work at two different water temperatures—the standard culturing temperature of 28°C and an elevated temperature of 32°C—as well as an even higher temperature of 34°C they maintained for two full days.

¹² <http://www.co2science.org/articles/V13/N7/C1.php>.

Results of the U.S., Canadian, and Australian researchers' analysis confirmed the existence of phenotypic variance for several pertinent thermal and dispersive factors among the families of coral they studied. This finding, they write, "suggests the existence of considerable heritable variation in natural coral populations," and this in turn supports "the possibility of effective adaptive responses to climate change." In addition, they report other analyses of the species they studied have found "high levels of genetic diversity both within and between reefs (Smith-Keune and van Oppen, 2006)," and "studies in other coral species have also uncovered substantial genetic diversity within populations (Ayre and Hughes, 2000; Underwood, 2009; Wang *et al.*, 2009)." Myer *et al.* thus conclude "additive genetic variance exists within coral populations for several traits that might reasonably be expected to have fitness consequences during global climate change," which "supports the possibility of effective adaptive responses to climate change."

Writing as background for their work, [Grimsditch *et al.* \(2010\)](#)¹³ say "it has been shown that it is possible for colonies to acclimatize to increased temperatures and high irradiance levels so that they are able to resist bleaching events when they occur." They note, in this regard, "threshold temperatures that induce coral bleaching-related mortality vary worldwide—from 27°C in Easter Island (Wellington *et al.*, 2001) to 36°C in the Arabian Gulf (Riegl, 1999)—according to the maximum water temperatures that are normal in the area, implying a capacity of corals and/or zooxanthellae to acclimatize to high temperatures depending on their environment."

In a further exploration of this phenomenon, Grimsditch *et al.* examined "bleaching responses of corals at four sites (Nyali, Mombasa Marine Park, Kanamai and Vipingo) representing two distinct lagoon habitats on the Kenyan coast (deeper and shallower lagoons)." This was done for the coral community as a whole, and zooxanthellae densities and chlorophyll levels were monitored for three target species (*Pocillopora damicornis*, *Porites lutea*, and *Porites cylindrica*) during a non-bleaching year (2006) and a mild bleaching year (2007). Results indicated "during the 2007 bleaching season, corals in the shallow lagoons of Kanamai and Vipingo were more resistant to bleaching stress than corals in the deeper lagoons of Mombasa Marine Park and Nyali." This result suggests, they write, "corals in the shallower lagoons have acclimatized and/or adapted to the fluctuating environmental conditions they endure on a daily basis and have become more resistant to bleaching stress."

[Osborne *et al.* \(2011\)](#)¹⁴ note "coral decline is frequently described as ongoing with the integrity and persistence of the reef system threatened by a number of different stressors," citing Bellwood *et al.* (2004), and "climate change is widely regarded as the single greatest threat to coral reef ecosystems." Therefore, and further noting "the scale and extent of bleaching on the GBR [Great Barrier Reef] since 1998 is unprecedented (Oliver *et al.*, 2009)," and "coral disease is an emerging stressor that was first recorded on the GBR in the early 1990s (Willis *et al.*, 2004; Lough, 2007)," as well as the fact that various harmful environmental disturbances "appear to be increasing in frequency and severity," they decided to quantify the trend in live coral cover of the GBR over the critical temporal interval of 1995–2009, which the IPCC contends was the warmest decade and a half experienced by the planet in the past millennium.

¹³ <http://www.co2science.org/articles/V13/N52/B2.php>.

¹⁴ <http://www.co2science.org/articles/V14/N26/B1.php>.

The scientists surveyed coral communities annually between 1995 and 2009 on 47 reefs in six latitudinal sectors across 1300 km of the GBR, surveying between two and five reefs in each sub-region. They did so at three sites on the northeast flank of each reef, with each site consisting of five 50-m transects marked by steel rods at depths between six and nine meters, and “percent cover of live hard coral was estimated from a randomly selected sequence of images taken along the transects using a point-sampling technique in a quincunx pattern (Adbo *et al.*, 2004).”

Results indicated “coral cover increased in six sub-regions and decreased in seven sub-regions,” with some of the changes “being very dynamic and others changing little.” But with respect to the entire reef system, they report “overall regional coral cover was stable (averaging 29% and ranging from 23% to 33% across years) with no net decline between 1995 and 2009.” And to emphasize this fact, they forthrightly state they found “no evidence of consistent, system-wide decline in coral cover since 1995.” Thus, in spite of all of the purportedly unprecedented negative influences arrayed against them over the past decade and a half, GBR corals appear to have held their own, adapting to the purported onslaught of stresses and maintaining a stable presence over the totality of their 1300 km linear expanse.

According to [Oliver and Palumbi \(2011\)](#)¹⁵, “the vast majority of studies that investigate the effects of fluctuating thermal regimes on thermal tolerance have examined daily thermal cycles in which the hottest temperatures lasted on the timescale of hours,” and in eight of ten such studies—performed on taxa as diverse as corals, crustaceans, fish, and amphibians—“organisms that were acclimated to a daily fluctuating thermal regime showed thermal tolerance or tolerance-relevant gene expression (e.g., heat shock proteins) that was equal to, or greater than, that of organisms acclimated to a thermal regime held constant at the maximum temperature of the fluctuating regime,” citing Hutchison and Ferrance (1970), Otto (1974), Sastry (1979), Thorp and Wineriter (1981), Threader and Houston (1983), Podrabsky and Somero (2004), Schaefer and Ryan (2006), and Putnam *et al.* (2010).

Working among back-reef pools in American Samoa that differ in diurnal thermal variation, Oliver and Palumbi experimentally heat-stressed *Acropora hyacinthus* corals from a thermally moderate lagoon pool and a more thermally variable pool that naturally experienced two- to three-hour high temperature events during summer low tides, after which they compared coral mortality and photosystem II photochemical efficiency of colony fragments they collected from each of these lagoons that they exposed to either ambient (28.0°C) or elevated (31.5°C) water temperatures. The two researchers report in the heated treatment, “moderate pool corals showed nearly 50% mortality whether they hosted heat-sensitive or heat-resistant symbionts,” whereas “variable pool corals, all of which hosted heat-resistant symbionts, survived well, showing low mortalities statistically indistinguishable from controls held at ambient temperatures.” Also in the heated treatment, they state, “moderate pool corals hosting heat-sensitive algae showed rapid rates of decline in algal photosystem II photochemical efficiency,” whereas those “hosting heat-resistant algae showed intermediate levels of decline.” And as might have been expected, they found “variable pool corals hosting heat-resistant algae showed the least decline.”

¹⁵ <http://www.co2science.org/articles/V14/N29/C3.php>.

Oliver and Palumbi say their results suggest “previous exposure to an environmentally variable microhabitat adds substantially to coral-algal thermal tolerance, beyond that provided by heat-resistant symbionts alone,” indicating a latent potential of Earth’s corals to adapt to warmer temperatures than scientists believed possible in the past, should they gradually begin to experience recurring daily episodes of greater warmth in a gradually warming world.

In a study designed to investigate how coral assemblages in the Persian Gulf might cope with global warming via reproductive biology, [Bauman et al. \(2011\)](#)¹⁶ examined six locally common coral species on two shallow reef sites in Dubai, United Arab Emirates, in 2008 and 2009, to investigate their patterns of reproduction, focusing primarily on the timing and synchrony of spawning. Results indicated the reproductive biology of the six coral species in the southern Persian Gulf “appears to be well adapted to extreme annual environmental fluctuations” and is “remarkably similar to conspecifics elsewhere in the Indo-Pacific (Baird et al., 2009a,b).” They also found “the adaptive capacity of corals in the Persian Gulf is likely facilitated by a combination of short-term acclimation in individuals during acute environmental conditions (e.g., recurrent bleaching events) and long-term adaptation among coral populations to chronic environmental conditions (e.g., extreme temperatures).”

Bauman et al. state their work “confirms that corals are capable of reproductive activities under extreme environmental conditions,” as Coles and Fadlallah (1991) and Coles and Brown (2003) also found. Hence, they state, “coral populations can survive and proliferate in extreme conditions that are projected to occur in many other regions of the world by the end of this century,” noting, “the recovery of these coral assemblages following mortality induced by a number of recent temperature-related bleaching events (1996, 1998 and 2002) suggests these assemblages are also resilient to extreme fluctuations in water temperature,” citing in this regard Riegl (1999, 2003) and Burt et al. (2008).

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[Serrano et al. \(2013\)](#)¹⁷ investigated the adaptation of corals to temperature-related stresses through range expansion or migration. In prefacing their work, the team of researchers state, “despite the evidence that some coral species appear to be responding to climatic warming by expanding their distributions toward the poles (Wooddroffe, 2011), it has been argued that latitudinal migration is unlikely to occur rapidly enough to respond to the current projected temperature change (3–6°C over the next 100 years (IPCC, 2007)) due to the significant distance involved (i.e., the latitudinal temperature gradient is ~1.5°C/1000 km), the effects of temperature on reproduction, and the decrease in carbonate ion concentrations at high

¹⁶ <http://www.co2science.org/articles/V14/N28/C3.php>.

¹⁷ <http://www.co2science.org/articles/V16/N29/B2.php>.

latitudes.” To test this contention, Serrano *et al.* analyzed a long-term, large-scale observational dataset to characterize the dynamics of a hermatypic coral (*Oculina patagonica*) in regard to its “recent northward range shift along the coast of Catalonia,” while examining “the main factors that could have influenced this spread,” which they did “by monitoring 223 locations including natural and artificial habitats along >400 km of coastline over the last 19 years (1992–2010).”

The six Spanish scientists report *Oculina patagonica* “increased from being present in one location in 1992 to occur on 19% of the locations in 2010, and exhibited an acceleration of its spreading over time driven by the joint action of neighborhood and long-distance dispersal.” They further note the “northward expansion has occurred at the fastest rate (22 km per year) reported for a coral species thus far.” Regarding the significance of these findings, Serrano *et al.* write, “a coral species with particular biological characteristics that allow it to withstand the temperature challenge that accompanies northward migration as well as the natural and anthropogenic side effects that this type of migration involves (i.e., competition with macroalgae, high sediment loads, turbidity, water chemistry) has accomplished a successful northward expansion and may be able to keep pace with the global warming prediction of ~3°C over the next 100 years.”

[Yamano *et al.* \(2011\)](#)¹⁸ report “although most studies of climate change effects on corals have focused on temperature-induced coral bleaching in tropical areas, poleward range shifts and/or expansions may also occur in temperate areas, as suggested by geological records and present-day eyewitnesses in several localities,” citing Greenstein and Pandolfi (2008) and Precht and Aronson (2004). To explore this subject further, Yamano *et al.* collected records of coral species occurrence from eight temperate regions of Japan along a latitudinal gradient,” where they obtained what they describe as “the first large-scale evidence of the poleward range expansion of modern corals, based on 80 years of national records ... where century-long measurements of *in situ* sea-surface temperatures have shown statistically significant rises.”

Results indicated “four major coral species categories, including two key species for reef formation in tropical areas, showed poleward range expansions since the 1930s, whereas no species demonstrated southward range shrinkage or local extinction,” adding “the speed of these expansions reached up to 14 km per year,” which they say “is far greater than that for other species.” They further note, “in regions with poleward current flows (east coast of the United States [Precht and Aronson, 2004], east coast of South America, east coast of Africa and east coast of Australia [Figueira and Booth, 2010]) the speed would be much greater.”

The Japanese scientists conclude their results, “in combination with recent findings suggesting range expansions of tropical coral-reef associated organisms, strongly suggest that rapid, fundamental modifications of temperate coastal ecosystems could be in progress.” In light of these facts, they suggest, “temperate areas may serve as refugia for tropical corals in an era of global warming.”

¹⁸ <http://www.co2science.org/articles/V14/N24/B2.php>.

[Van Woosik et al. \(2012\)](#)¹⁹ examined the response of more than 30,000 coral colonies at 80 sites in Palau during a regional thermal-stress event in 2010, to determine “whether any habitats were comparatively resistant to thermal stress.” The six scientists discovered (1) “bleaching was most severe in the northwestern lagoon, in accordance with satellite-derived maximum temperatures and anomalous temperatures above the long-term averages,” (2) corals there “suffered the most extensive bleaching and the highest mortality,” but (3) “in the bays where temperatures were higher than elsewhere, bleaching and mortality were low.” As for why this was so, they suggest “constant exposure to high temperatures, and high vertical attenuation of light caused by naturally high suspended particulate matter buffered the corals in bays from the 2010 regional thermal-stress event.” In concluding their paper, van Woosik *et al.* say their study shows “reefs around bays were more resistant to regional thermal stress than patch and outer reefs,” and “nearshore reefs in the bays are therefore valuable refuges to buffer coral-reef ecosystems against climate change-induced disturbances,” and they thus “should be given high conservation status because they provide refugia for coral populations as the oceans continue to warm.”

[Carilli et al. \(2012\)](#)²⁰ note “observations indicating that mass bleaching events have recently become more common, combined with projected increases in heat stress, have prompted dire predictions for the future of coral reefs under unabated greenhouse gas emissions scenarios,” citing Hoegh-Guldberg (1999) and Donner *et al.* (2005). However, they write, “there is evidence that corals may adapt to better withstand heat stress via a number of mechanisms,” as “corals might acquire more thermally-resistant symbionts (Buddemeier and Fautin, 1993; Rowan, 2004), or might increase their own physiological mechanisms to reduce bleaching susceptibility by producing oxidative enzymes (Coles and Brown, 2003) or photoprotective compounds (Salih *et al.*, 2000).” They emphasize there is evidence suggesting the susceptibility of a given coral or reef to bleaching depends on the thermal history of that coral or reef (Thompson and Van Woosik, 2009; Donner, 2011; Brown *et al.*, 2002). They thus explored that phenomenon in their study.

Carilli *et al.* “collected cores from massive *Porites sp.* corals in the Gilbert Islands of Kiribati to determine how corals along a natural gradient in temperature variability responded to recent

Reefs around bays were more resistant to regional thermal stress than patch and outer reefs. Near shore reefs in the bays are therefore valuable refuges to buffer coral-reef ecosystems against climate change-induced disturbances, and thus should be given high conservation status because they provide refugia for coral populations as the oceans continue to warm.

¹⁹ <http://www.co2science.org/articles/V16/N26/C3.php>.

²⁰ <http://www.co2science.org/articles/V15/N49/B2.php>.

heat stress events,” and “examined changes in coral skeletal growth rates and partial mortality scars (Carilli *et al.*, 2010) to investigate the impact of the bleaching event in 2004 (Donner, 2011) on corals from different temperature variability regimes.”

The three researchers—from Australia, Canada, and the United States—discovered the spatial patterns in skeletal growth rates and partial mortality scars found in corals from the central and northern islands suggest “corals subject to larger year-to-year fluctuations in maximum ocean temperature were more resistant to a 2004 warm-water event,” and “a subsequent 2009 warm event had a disproportionately larger impact on those corals from the island with lower historical heat stress.” Thus in the concluding sentence of their paper’s abstract, Carilli *et al.* say their study indicates “coral reefs in locations with more frequent warm events may be more resilient to future warming.”

[Penin *et al.* \(2013\)](#)²¹ “compared variations in spatial and taxonomic patterns between two bleaching events at the scale of an island (Moorea Island, French Polynesia),” where “nine stations involving three locations (Haapiti, Tiahura, and Viapahu) and three depths (6, 12, and 18 m) have been routinely surveyed for various scientific purposes since 2001,” as described by Penin *et al.* (2007a, 2010). They measured bleaching intensity “two weeks following the first signs of bleaching (Penin *et al.*, 2007b)” for six coral genera (*Acropora*, *Montipora*, *Montastrea*, *Pavona*, *Pocillopora*, and *Porites*) at each of the nine stations in 2002 and 2007. The six coral genera accounted for 88% of the total coral assemblage.

Their measurements showed the “thermal stress was similar between the two years studied.” However, they note, “the bleaching intensity was lower in 2007 (25–49%) than in 2002 (39–72%),” and “the response to elevated temperature was delayed in the latter year.” In addition, “the outer slopes at Moorea Island are located in an oligotrophic oceanic environment and are not under terrestrial influence, which makes it unlikely that there was any effect of nutrients on the response of the corals, as has been proposed for other reef ecosystems (Wooldridge and Done, 2009).” The three researchers conclude “it is likely that the observed decrease in stress response was the result of acclimatization of the coral/algal holobionts (Berkelmans *et al.*, 2004; Maynard *et al.*, 2008) or an influx of thermo-tolerant colonies between 2002 and 2007.” Providing further support for their conclusions, they note several “similar decreases in susceptibility to thermal stress have been documented between successive bleaching events, including between 1991 and 1994 at Moorea Island (Adjeroud *et al.*, 2002), between 1998 and 2002 on the Great Barrier Reef in Australia (Maynard *et al.*, 2008b), and between 1982–83 and 1997–98 in Panama (Glynn *et al.*, 2001), Costa Rica (Jimenez *et al.*, 2001), and at the Galapagos Islands (Podesta and Glynn, 2001).”

As background for their work, [Mayfield *et al.* \(2013\)](#)²² write, “recent work has found that pocilloporid corals from regions characterized by unstable temperatures, such as those exposed to periodic upwelling, display a remarkable degree of phenotypic plasticity,” and “some recent works have shown that not all corals bleach, or even manifest signs of stress, at elevated temperatures predicted to characterize reefs in the coming decades (Barshis *et al.*, 2013).” They

²¹ <http://www.co2science.org/articles/V16/N37/C3.php>.

²² <http://www.co2science.org/articles/V17/N8/B2.php>.

also note “corals from highly variable temperature environments of both American Samoa (Oliver and Palumbi, 2011) and southern Taiwan (Mayfield *et al.*, 2011, 2013) have previously been shown to withstand exposure to temperatures (e.g., 30–31°C) that induce bleaching or even mortality in conspecifics from other regions (Jokiel and Coles, 1990; Brown, 1997).”

To “uncover the long-term impacts of elevated temperature exposure to corals from reefs that experience episodic upwelling,” Mayfield *et al.* conducted a mesocosm-based experiment in which *P. damicornis* specimens collected from an upwelling coral reef on Houbihu (a small embayment within Nanwan Bay, southern Taiwan) were exposed for nine months to nearly 30°C, a temperature that the corals normally encounter in situ for just a few hours per year (Mayfield *et al.*, 2012). The three researchers write, “upon nine months of exposure to nearly 30°C, all colony (mortality and surface area), polyp (*Symbiodinium* density and chlorophyll *a* content), tissue (total thickness), and molecular (gene expression and molecular composition)-level parameters were documented at similar levels between experimental corals and controls incubated at 26.5°C, suggesting that this species can readily acclimate to elevated temperatures that cause significant degrees of stress, or even bleaching and mortality, in conspecifics of other regions of the Indo-Pacific.”

As more and more research is conducted it is becoming more and more apparent that the doom and gloom predictions of widespread coral decline due to global warming are unlikely to occur.

In light of their findings and those of other scientists studying the subject, Mayfield *et al.* state, “there is now a growing body of evidence to support the notion that corals inhabiting more thermally unstable habitats outperform conspecifics from reefs characterized by more stable temperatures when exposed to elevated temperatures,” citing Coles (1975), Castillo and Helmuth (2005), and Oliver and Palumbi (2011). They report also report, “in other systems, provocative gene expression changes, such as the constitutive up-regulation of genes involved in thermotolerance (e.g., *hsps*; Heath *et al.*, 1993; Feder, 1996), underlie the capacity for organisms to inhabit high and/or variable temperature environments,” as Barshis *et al.* (2013) also documented in corals.

Indeed. As more and more research is conducted it is becoming more and more apparent that the doom and gloom predictions of widespread coral decline due to global warming are unlikely to occur.

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