

GLOBAL WARMING, CORAL REEFS, AND SYMBIONT SHUFFLING

Climate alarmists typically decry the bleaching of corals that often follows periods of anomalous warmth at various places around the globe. In doing so, however, they malign the very phenomenon that enables corals to "reinvent" themselves and adapt to global warming.



SPPI & CO₂SCIENCE ORIGINAL PAPER ♦ March 21, 2012

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Citation: Center for the Study of Carbon Dioxide and Global Change. "Global Warming, Coral Reefs, and Symbiont Shuffling." Last modified March 21, 2012. <http://www.co2science.org/subject/c/summaries/bleachrespsymb.php>.

Although once considered to be members of the single species *Symbiodinium microadriaticum*, the zooxanthellae that reside within membrane-bound vacuoles in the cells of host corals are highly diverse, comprising perhaps hundreds of species, of which several are typically found in each species of coral (Trench, 1979; Rowan and Powers, 1991; Rowan *et al.*, 1997); and as a result of this fact, a particularly ingenious way by which almost any adaptive response to any type of environmental stress may be enhanced in the face of the occurrence of that stress would be to replace the zooxanthellae expelled by the coral host during a stress-induced bleaching episode by varieties of zooxanthellae that are more tolerant of the stress that caused the bleaching.

[Rowan *et al.* \(1997\)](#)¹ have suggested that this phenomenon occurs in many of the most successful Caribbean corals that act as hosts to dynamic multi-species communities of symbionts, and that "coral communities may adjust to climate change by recombining their existing host and symbiont genetic diversities," thereby reducing the amount of damage that might subsequently be expected from another occurrence of anomalously high temperatures. In fact, Buddemeier and Fautin (1993) have suggested that coral bleaching is actually an adaptive strategy for "shuffling" symbiont genotypes to create associations better adapted to new environmental conditions that challenge the *status quo* of reef communities. Saying essentially the same thing in yet another way, [Kinzie \(1999\)](#)² suggested that coral bleaching "might not be simply a breakdown of a stable relationship that serves as a symptom of degenerating environmental conditions," but that it "may be part of a mutualistic relationship on a larger temporal scale, wherein the identity of algal symbionts changes in response to a changing environment."

Coral communities may adjust to climate change by recombining their existing host and symbiont genetic diversities, thereby reducing the amount of damage that might subsequently be expected from another occurrence of anomalously high temperatures.

This process of replacing less-stress-tolerant symbionts by more-stress-tolerant symbionts is also supported by the investigations of [Rowan and Knowlton \(1995\)](#)³ and Gates and Edmunds

¹ <http://www.co2science.org/articles/V2/N9/C5.php>.

² <http://www.co2science.org/articles/V2/N15/C6.php>.

³ <http://www.co2science.org/articles/V2/N9/C6.php>.

(1999); and the strategy seems to be working, for as Glynn (1996) has observed, “despite recent incidences of severe coral reef bleaching and mortality, no species extinctions have yet been documented.”

These observations accord well with the experimental findings of Fagoonee *et al.* (1999), who suggest that coral bleaching events “may be frequent and part of the expected cycle.” [Gates and Edmunds \(1999\)](#)⁴ additionally report that “several of the prerequisites required to support this hypothesis have now been met,” and after describing them in some detail, they conclude “there is no doubt that the existence of multiple *Symbiodinium* clades, each potentially exhibiting a different physiological optima, provide corals with the opportunity to attain an expanded range of physiological flexibility which will ultimately be reflected in their response to environmental challenge.” In fact, this phenomenon may provide the explanation for the paradox posed by Pandolfi (1999), i.e., that “a large percentage of living coral reefs have been degraded, yet there are no known extinctions of any modern coral reef species.” Surely, this result is exactly what would be expected if periods of stress lead to the acquisition of more-stress-resistant zooxanthellae by coral hosts.

In spite of this early raft of compelling evidence for the phenomenon, Hoegh-Guldberg (1999) challenged the symbiont shuffling hypothesis on the basis that the stress-induced replacement of less-stress-tolerant varieties of zooxanthellae by more-stress-tolerant varieties “has never been observed.” Although true at the time it was written, a subsequent series of studies has produced the long-sought proof that transforms the hypothesis into fact.

Coral bleaching can promote rapid response to environmental change by facilitating compensatory change in algal symbiont communities.

[Baker \(2001\)](#)⁵ conducted an experiment in which he transplanted corals of different combinations of host and algal symbiont from shallow (2-4 m) to deep (20-23 m) depths and vice versa. After 8 weeks nearly half of the corals transplanted from deep to shallow depths had experienced partial or severe bleaching, whereas none of the corals transplanted from shallow to deep depths bleached. After one year, however, and despite even more bleaching at shallow depths, upward transplants showed no mortality, but nearly 20 percent of *downward* transplants had died. Why?

The symbiont shuffling hypothesis explains it this way. The corals that were transplanted upwards were presumed to have adjusted their algal symbiont distributions, via bleaching, to favor more tolerant species, whereas the corals transplanted downward were assumed to not have done so, since they did not bleach. Baker suggested that these findings “support the view that coral bleaching can promote rapid response to environmental change by facilitating compensatory change in algal symbiont communities.” Without bleaching, as he continued, “suboptimal host-

⁴ <http://www.co2science.org/articles/V2/N15/C1.php>.

⁵ <http://www.co2science.org/articles/V4/N29/C3.php>.

symbiont combinations persist, leading eventually to significant host mortality.” Consequently, Baker proposed that coral bleaching may “ultimately help reef corals to survive.” And it may also explain why reefs, though depicted by climate alarmists as environmentally fragile, have survived the large environmental changes experienced throughout geologic time.

One year later [Adjeroud et al. \(2002\)](http://www.co2science.org/articles/V6/N52/C3.php)⁶ provided additional evidence for the veracity of the symbiont shuffling hypothesis as a result of their assessment of the interannual variability of coral cover on the outer slope of the Tiahura sector of Moorea Island, French Polynesia, between 1991 and 1997, which focused on the impacts of bleaching events caused by thermal stress when sea surface temperatures rose above 29.2°C. Soon after the start of their study, they observed a severe decline in coral cover following a bleaching event that began in March 1991, which was followed by another bleaching event in March 1994. However, they report that the latter bleaching event “did not have an important impact on coral cover,” even though “the proportion of bleached colonies ... and the order of susceptibility of coral genera were similar in 1991 and 1994 (Gleason, 1993; Hoegh-Guldberg and Salvat, 1995).” In fact, they report that between 1991 and 1992 total coral cover dropped from 51.0% to 24.2%, but that “coral cover did not decrease between 1994 and 1995.”

In discussing these observations, Adjeroud *et al.* write that a “possible explanation of the low mortality following the bleaching event in 1994 is that most of the colonies in place in 1994 were those that survived the 1991 event or were young recruits derived from those colonies,” noting that “one may assume that these coral colonies and/or their endosymbiotic zooxanthellae were phenotypically and possibly genotypically resistant to bleaching events,” which is exactly what the symbiont shuffling hypothesis would predict. Hence, they further state that “this result demonstrates the importance of understanding the ecological history of reefs (i.e., the chronology of disturbances) in interpreting the specific impacts of a particular disturbance.”

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In the same year, [Brown et al. \(2002\)](http://www.co2science.org/articles/V6/N53/C2.php)⁷ published the results of an even longer 17-year study of coral reef flats at Ko Phuket, Thailand, in which they assessed coral reef changes in response to elevated water temperatures in 1991, 1995, 1997 and 1998. As they describe it, “many corals bleached during elevated sea temperatures in May 1991 and 1995, but no bleaching was recorded in 1997.” In addition, they report that “in May 1998 very limited bleaching occurred although sea temperatures were higher than previous events in 1991 and 1995 (Dunne and Brown, 2001).” What is more, when bleaching did take place, they say “it led only to partial mortality in coral colonies, with most corals recovering

⁶ <http://www.co2science.org/articles/V6/N52/C3.php>.

⁷ <http://www.co2science.org/articles/V6/N53/C2.php>.

their color within 3-5 months of initial paling,” once again providing real-world evidence for what is predicted by the symbiont shuffling hypothesis.

The following year, [Riegl \(2003\)](#)⁸ reviewed what is known about the responses of real-world coral reefs to high-temperature-induced bleaching, focusing primarily on the Arabian Gulf, which experienced high-frequency recurrences of temperature-related bleaching in 1996, 1998, and 2002. In response to these high-temperature events, Riegl notes that *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. As a result, Riegl states that “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 that “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.”

In a contemporaneous paper, [Kumaraguru et al. \(2003\)](#)⁹ reported the results of a study wherein they assessed the degree of damage inflicted upon a number of coral reefs within Palk Bay (located on the southeast coast of India just north of the Gulf of Mannar) by a major warming event that produced monthly mean sea surface temperatures of 29.8 to 32.1°C from April through June of 2002, after which they assessed the degree of recovery of the reefs. They

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determined that “a minimum of at least 50% and a maximum of 60% bleaching were noticed among the six different sites monitored.” However, as they continue, “the corals started to recover quickly in August 2002 and as much as 52% recovery could be noticed.” By comparison, they note that “recovery of corals after the 1998 bleaching phenomenon in the Gulf of Mannar was very slow, taking as much as one year to achieve similar recovery,” i.e., to achieve what was experienced in one *month* in 2002. Consequently, in words descriptive of the concept of symbiont shuffling, the Indian scientists say “the process of natural selection is in operation, with the growth of new coral colonies, and any disturbance in the system is only temporary.” Consequently, as they conclude in the final sentence of their paper, “the corals will resurge under the sea.”

Although these several 2001-2003 findings were very significant, a quartet of papers published in 2004 - two in [Nature](#)¹⁰ and two in [Science](#)¹¹ - finally “sealed the deal” with respect to establishing the symbiont shuffling hypothesis as a fact of life, and an ubiquitous one at that.

⁸ <http://www.co2science.org/articles/V9/N12/B1.php>.

⁹ <http://www.co2science.org/articles/V7/N39/B1.php>.

¹⁰ <http://www.co2science.org/articles/V7/N33/EDIT.php>.

Writing in *Nature*, Rowan (2004) described how he measured the photosynthetic responses of two zooxanthellae genotypes or clades -- *Symbiodinium C* and *Symbiodinium D* -- to increasing water temperature, finding that the photosynthetic prowess of the former decreased at higher temperatures while that of the latter increased. He then noted that “adaptation to higher temperature in *Symbiodinium D* can explain why *Pocillopora* spp. hosting them resist warm-water bleaching whereas corals hosting *Symbiodinium C* do not,” and that “it can also explain why *Pocillopora* spp. living in frequently warm habitats host only *Symbiodinium D*, and, perhaps, why those living in cooler habitats predominantly host *Symbiodinium C*,” concluding that these observations “indicate that symbiosis recombination may be one mechanism by which corals adapt, in part, to global warming.”

Clinching the concept, was the study of Baker *et al.* (2004), who “undertook molecular surveys of *Symbiodinium* in shallow scleractinian corals from five locations in the Indo-Pacific that had been differently affected by the 1997-98 El Niño-Southern Oscillation (ENSO) bleaching event.” Along the coasts of Panama, they surveyed ecologically dominant corals in the genus *Pocillopora* before, during and after ENSO bleaching, finding that “colonies containing *Symbiodinium* in clade D were already common (43%) in 1995 and were unaffected by bleaching in 1997, while colonies containing clade C bleached severely.” Even more importantly, they found that “by 2001, colonies containing clade D had become dominant (63%) on these reefs.”

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After describing similar observations in the Persian (Arabian) Gulf and the western Indian Ocean along the coast of Kenya, Baker *et al.* summarized their results by stating they indicate that “corals containing thermally tolerant *Symbiodinium* in clade D are more abundant on reefs after episodes of severe bleaching and mortality, and that surviving coral symbioses on these reefs more closely resemble those found in high-temperature environments,” where clade D predominates. Hence, they concluded their landmark paper by noting that the symbiont changes they observed “are a common feature of severe bleaching and mortality events,” and by predicting that “these adaptive shifts will increase the resistance of these recovering reefs to future bleaching.”

Meanwhile, over in *Science*, Lewis and Coffroth (2004) described a controlled experiment in which they induced bleaching in a Caribbean octocoral (*Briareum* sp.) and then exposed it to exogenous *Symbiodinium* sp. containing rare variants of the chloroplast 23S ribosomal DNA (rDNA) domain V region (cp23S-genotype), after which they documented the symbionts’ repopulation of the coral, whose symbiont density had been reduced to less than 1% of its original level by the bleaching. Also, in a somewhat analogous study, Little *et al.* (2004)

¹¹ <http://www.co2science.org/articles/V7/N29/B2.php>.

described how they investigated the acquisition of symbionts by juvenile *Acropora tenuis* corals growing on tiles they attached to different portions of reef at Nelly Bay, Magnetic Island (an inshore reef in the central section of Australia's Great Barrier Reef).

Lewis and Coffroth wrote that the results of their study show that "the repopulation of the symbiont community involved residual populations within *Briareum* sp., as well as symbionts from the surrounding water," noting that "recovery of coral-algal symbioses after a bleaching event is not solely dependent on the *Symbiodinium* complement initially acquired early in the host's ontogeny," and that "these symbioses also have the flexibility to establish new

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associations with symbionts from an environmental pool." Similarly, Little *et al.* reported that "initial uptake of zooxanthellae by juvenile corals during natural infection is nonspecific (a potentially adaptive trait)," and that "the association is flexible and characterized by a change in (dominant) zooxanthella strains over time."

Lewis and Coffroth thus concluded that "the ability of octocorals to reestablish symbiont populations from multiple sources provides a mechanism for resilience in the face of environmental change," while Little *et al.* concluded that the "symbiont shuffling" observed by both groups "represents a mechanism for rapid acclimatization of the holobiont to environmental change." Hence, the results of both studies

demonstrate the reality of a phenomenon whereby corals may indeed "grasp victory from the jaws of death" in the aftermath of a severe bleaching episode, which is also implied by the *fact* - cited by Lewis and Coffroth - that "corals have survived global changes since the first scleractinian coral-algal symbioses appeared during the Triassic, 225 million years ago."

By the end of 2004, more and more researchers had begun to recognize the reality and strength of the symbiont shuffling hypothesis as an adaptive means for corals to cope with environmental change, especially as it pertains to rising water temperatures. In a review paper published at the end of the year, for example, [Fautin and Buddemeier \(2004\)](#)¹² enunciated five fundamental assumptions that underlie the *adaptive bleaching hypothesis* (ABH), as they termed it, reviewing the scientific literature as it pertained to each of them. According to the two scientists, the symbiont shuffling hypothesis "has the potential to enhance long-term survival of the hosts, helping to reconcile the long-recognized paradox that coral reefs seem sensitive to environmental perturbation in the short term, but robust over geological time." And with respect to the five fundamental assumptions underlying the hypothesis, they further note that "virtually all evidence adduced thus far is consistent with, much supportive of, and none fatal to, the ABH." Indeed, they write that "there seems to be a virtually continual opportunity for creation of new holobionts upon which selection can act and thus provide prompt, dynamic response of the symbioses to changing environmental conditions," noting

¹² <http://www.co2science.org/articles/V8/N17/EDIT.php>.

that “it now appears that adaptive change in the dominant symbiont can occur over the entire range from normal background fluctuations in algal populations to acute bleaching events.”

With respect to the latter phenomenon of severe bleaching -- which can indeed be induced by rising temperatures, especially within the context of reduced reef vitality owing to the many *local* assaults of humanity upon the watery environment in which corals live -- Fautin and Buddemeier report that bleaching may “(1) accelerate the process of change, and/or (2) change the set of possible trajectories for how these communities might recover by dramatically changing the starting abundance of each symbiont type and thereby shifting the system out of a region of local stability (where symbiont community structure tends to return to the same equilibrium after minor disturbance) into a region of relative instability (where many more recovery outcomes are possible).” And in closing, the two marine biologists cite the conclusion of Baker (2002) that “the real question is not whether coral-algal associations can adapt by recombining, but rather how, and over what timescales, they do so.”

In the years that have followed since 2004, many more studies have further elevated the symbiont shuffling hypothesis into its rightful place as a full-fledged *theory*.

Writing in the journal *Marine Ecology Progress Series*, [Chen et al. \(2005\)](#)¹³ studied the seasonal dynamics of *Symbiodinium* algal phylotypes via bimonthly sampling over an 18-month period of *Acropora palifera* coral on a reef flat at Tantzal Bay, Kenting National Park, southern Taiwan, in an attempt to detect real-world symbiont shuffling. Results of the analysis revealed two levels of symbiont shuffling in host corals: (1) between *Symbiodinium* phylotypes C and D, and (2) among different variants within each phylotype. Furthermore, the most significant changes in symbiont composition occurred at times of significant increases in seawater temperature during late spring/early summer, perhaps as a consequence of enhanced stress experienced at that time, leading Chen *et al.* to state that their work revealed “the first evidence that the symbiont community within coral colonies is dynamic ... involving changes in *Symbiodinium* phylotypes.”

Also in 2005, [van Oppen et al.](#)¹⁴ sampled zooxanthellae from three common species of scleractinian corals at 17 sites along a latitudinal and cross-shelf gradient in the central and southern sections of the Great Barrier Reef some four to five months after the major bleaching

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¹³ <http://www.co2science.org/articles/V8/N48/B1.php>.

¹⁴ <http://www.co2science.org/articles/V9/N19/B1.php>.

event of 2002, recording the health status of each colony at the time of its collection and identifying its zooxanthella genotypes, of which there are eight distinct clades (A-H) with clade D being the most heat-tolerant. Results of the analysis revealed that “there were no simple correlations between symbiont types and either the level of bleaching of individual colonies or indicators of heat stress at individual sites.” However, they say “there was a very high post-bleaching abundance of the heat tolerant symbiont type D in one coral population at the most heat-stressed site.”

With respect to the post-bleaching abundance of clade D zooxanthellae at the high heat-stress site, the Australian researchers say they suspect it was due to “a proliferation in the absolute abundance of clade D within existing colonies that were previously dominated by clade C zooxanthellae,” and that in the four to five months before sampling them, “mixed C-D colonies that had bleached but survived may have shifted (shuffling) from C-dominance to D-dominance, and/or C-dominated colonies may have suffered higher mortality during the 2002 bleaching event” and subsequently been repopulated by a predominance of clade D genotypes.

Adult corals are capable of acquiring increased thermal tolerance and the increased tolerance is a direct result of a change in the symbiont type dominating their tissues from Symbiodinium type C to D.

In 2006, working within Australia’s Great Barrier Reef system, [Berkelmans and van Oppen](#)¹⁵ investigated the thermal acclimatization potential of *Acropora millepora* corals to rising temperatures through transplantation and experimental manipulation, finding that the adult corals “are capable of acquiring increased thermal tolerance and that the increased tolerance is a direct result of a change in the symbiont type dominating their tissues from *Symbiodinium* type C to D.” Two years later, working with an expanded group of authors ([Jones et al., 2008](#)¹⁶), the same two researchers reported similar findings following the occurrence of a natural bleaching event.

Prior to the bleaching event, Jones et al. report that “*A. millepora* at Miall reef associated predominantly with *Symbiodinium* type C2 (93.5%) and to a much lesser extent with *Symbiodinium* clade D (3.5%) or mixtures of C2 and D (3.0%).” During the bleaching event, they further report that “the relative difference in bleaching susceptibility between corals predominated by C2 and D was clearly evident, with the former bleaching white and the latter normally pigmented,” while corals harboring a mix of *Symbiodinium* C2 and D were “mostly pale in appearance.” Then, three months after the bleaching event, they observed “a major shift to thermally tolerant type D and C1 symbiont communities ... in the surviving colonies,” the latter of which types had not been detected in any of the corals prior to bleaching; and they report that “this shift resulted partly from a change of symbionts within coral colonies that survived the bleaching event (42%) and partly

¹⁵ <http://www.co2science.org/articles/V10/N3/B1.php>.

¹⁶ <http://www.co2science.org/articles/V11/N28/B1.php>.

from selective mortality of the more bleaching-sensitive C2-predominant colonies (37%).” In addition, they report that all of the colonies that harbored low levels of D-type symbionts prior to the bleaching event survived and changed from clade C2 to D predominance.

In conclusion, Jones *et al.* say that “as a direct result of the shift in symbiont community, the Miall Island *A. millepora* population is likely to have become more thermo-tolerant,” as they note that “a shift from bleaching-sensitive type C2 to clade D increased the thermal tolerance of this species by 1-1.5°C.” As a result, they say their results “strongly support the reinterpreted adaptive bleaching hypothesis of Buddemeier *et al.* (2004), which postulates that a continuum of changing environmental states stimulates the loss of bleaching-sensitive symbionts in favor of symbionts that make the new holobiont more thermally tolerant.” In fact, they state that their observations “provide the first extensive colony-specific documentation and quantification of temporal symbiont community change in the field in response to temperature stress, suggesting a population-wide acclimatization to increased water temperature,” a finding that bodes especially well for earth’s corals in a warming climate.

In a much larger geographical study, [Lien *et al.* \(2007\)](#)¹⁷ examined the symbiont diversity in a scleractinian coral, *Oulastrea crispata*, throughout its entire latitudinal distribution range in the West Pacific, i.e., from tropical peninsular Thailand (<10°N) to high-latitudinal outlying coral communities in Japan (>35°N), convincingly demonstrating in the words of the six scientists who conducted the study, “that phylotype D is the dominant *Symbiodinium* in scleractinian corals throughout tropical reefs and marginal outlying non-reefal coral communities.” In addition, they learned that this particular symbiont clade “favors ‘marginal habitats’ where other symbionts are poorly suited to the stresses, such as irradiance, temperature fluctuations, sedimentation, etc.” Being a major component of the symbiont repertoire of most scleractinian corals in most places, the apparent near-universal presence of *Symbiodinium* phylotype D thus provides, according to Lien *et al.*, “a flexible means for corals to *routinely cope* [italics added] with environmental heterogeneities and survive the consequences (e.g., recover from coral bleaching).”

The clade D symbiont backgrounds detected in their study can potentially act as safety-parachutes, allowing corals to become more thermo-tolerant through symbiont shuffling as seawater temperatures rise due to global warming.

Also in 2007, [Mieog *et al.*](#)¹⁸ utilized a newly developed real-time *polymerase chain reaction* assay, which they say “is able to detect *Symbiodinium* clades C and D with >100-fold higher sensitivity compared to conventional techniques,” to test 82 colonies of four common

¹⁷ <http://www.co2science.org/articles/V10/N37/B1.php>.

¹⁸ <http://www.co2science.org/articles/V11/N3/B2.php>.

scleractinian corals (*Acropora millepora*, *Acropora tenuis*, *Stylophora pistillata* and *Turbinaria reniformis*) from eleven different locations on Australia’s Great Barrier Reef for evidence of the presence of background *Symbiodinium* clades. Results of the analysis showed that “ninety-three percent of the colonies tested were dominated by clade C and 76% of these had a D background,” the latter of which symbionts, in their words, “are amongst the most thermo-tolerant types known to date,” being found “on reefs that chronically experience unusually high temperatures or that have recently been impacted by bleaching events, suggesting that temperature stress can favor clade D.” Consequently, Mieog *et al.* concluded that the clade D symbiont backgrounds detected in their study can potentially act as *safety-parachutes*, “allowing corals to become more thermo-tolerant through symbiont shuffling as seawater temperatures rise due to global warming.” As a result, they suggest that symbiont shuffling is likely to play a role in the way “corals cope with global warming conditions,” leading to new competitive hierarchies and, ultimately, “the coral community assemblages of the future.”

In another study, [Loram et al. \(2007\)](#)¹⁹ examined the giant sea anemone *Condylactis gigantea* that occurs on the Bermuda platform. Results indicated that “the *C. gigantea* symbiosis with clade B is bleaching susceptible, responding to elevated temperature by massive algal expulsion.” Following bleaching, however, recovery of the corals, in the words of the authors, “can involve the replacement of the resident alga by bleaching-resistant *Symbiodinium* of a different clade,” and that “this shift can be adaptive for the host through enhanced resistance to subsequent bleaching stress,” so that symbioses comprised of mixed algal symbionts may “be at an advantage in times of rapid global climate change,” the potential for which adaptive survival strategy was clearly indicated by the results of their detailed experiments.

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.

One year later [Maynard et al. \(2008a\)](#)²⁰ reported that “a number of studies suggest that bleaching mortality rates have declined and thermal tolerance has increased in some regions.” As one example, they write that “mortality rates in the Eastern Pacific were significantly lower in 1998 when compared with 1982 and 1983 (Glynn *et al.*, 2001),” while as another example they say that “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.” With respect 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 the review of Coles and Brown (2003). In addition, they suggest that “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

¹⁹ <http://www.co2science.org/articles/V11/N3/B3.php>.

²⁰ <http://www.co2science.org/articles/V12/N3/EDIT.php>.

growing evidence that such shuffling can increase thermal tolerance, at least in the short term (Berkelmans and van Oppen, 2006).” As a result, Maynard *et al.* (2008a) conclude that “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 a bit more on the details of symbiont shuffling, [Zurel *et al.* \(2008\)](#)²¹ introduce their study of the subject by stating that one of the means by which a coral host may survive periodic high temperature extremes is “by replacing its dominant symbionts with others that are more suitable for the new conditions.” In this regard, they say that there are “two modes of acquisition of the symbiotic algae by the sexually-produced offspring of host species: either by direct transmission to the egg or the brooded larvae [as in a *vertical* or “closed” system], or from the ambient environment [a *horizontal* or “open” system] by the post-larval stages.” However, there has been a long-standing question about the ability of cnidarian hosts and their symbionts that operate in a *closed* mode to vary from that mode and become an *open* system when certain conditions might warrant it. Against this backdrop the four Israeli researchers examined the possible entry of stained heterologous clade C zooxanthellae obtained from polyps of the soft coral *Heteroxenia fuscescens* into primary polyps of the soft coral *Litophyton crosslandi*, which is known to host clade A symbionts and is believed to be a vertically-transmitting-only cnidarian.

Results of their experiment led Zurel *et al.* to report that “primary polyps of *L. crosslandi* allowed the entry of DAPI-stained heterologous motile clade C zooxanthellae into their tissues, a finding that contradicts the previously held notion about the closed nature of this symbiotic system.” Such findings, in the words of the Israeli biologists, demonstrate that “cnidarian hosts previously considered as true closed system symbioses, may in fact possess the ability for entry and possible residence of heterologous symbionts also from the environment,” and that it further supports “earlier findings by van Oppen (2004), suggesting a certain degree of flexibility in the closed system symbiosis,” which flexibility, in their words, “may be beneficial to these hosts under stressful conditions, including bleaching events.”

More real-world evidence for symbiont shuffling came in 2009, when a UK researcher ([Crabbe, 2009](#)²²) employed a number of demographic tools to analyze the resilience of the fringing reefs around Discovery Bay, Jamaica, by documenting the responses of their populations “to a number of environmental stressors, in particular hurricanes and the mass bleaching event of 2005,” which the researcher described as “by far the major acute influence on the reef sites.” In doing so the author reports “there was a reduction in numbers of colonies in the smallest size class for all the species at all the sites in 2006, after the mass bleaching of 2005, with subsequent increases for all species at all sites in 2007 and 2008.” And as a result of this observation the UK researcher concluded that his results “indicate good levels of coral resilience on the fringing reefs around Discovery Bay in Jamaica.” Also in regard to this noteworthy feat, he states that together with a colleague he “found a variety of clades of zooxanthellae, including clade C,” among the corals at Dairy Bull Reef (Crabbe and Carlin, 2007),” and he says that “the potential for symbiont shuffling, as we have found in 111 colonies

²¹ <http://www.co2science.org/articles/V11/N40/B1.php>.

²² <http://www.co2science.org/articles/V12/N37/C1.php>.

of *Acropora* species from the Ningaloo Reef, Australia (Crabbe and Carlin, 2009), may be a factor in their recovery,” citing the further work of Stat *et al.* (2008).

In spite of the hope symbiont shuffling provides -- that the world’s corals will indeed be able to successfully cope with the possibility of future global warming, be it anthropogenic-induced or natural -- some researchers have claimed that few coral symbioses host more than one type of symbiont, which has led alarmists to argue that symbiont shuffling is not an option for most coral species to survive the coming thermal onslaught of global warming. But is this claim correct? Not according to the results of [Apprill and Gates \(2007\)](#)²³.

Working with samples of the widely distributed massive corals *Porites lobata* and *Porites lutea* - which they collected from Kaneohe Bay, Hawaii - Apprill and Gates compared the identity and diversity of *Symbiodinium* symbiont types obtained using cloning and sequencing of *internal transcribed spacer region 2* (ITS2) with that obtained using the more commonly applied downstream analytical techniques of *denaturing gradient gel electrophoresis* (DGGE).

Results of this analysis revealed “a total of 11 ITS2 types in *Porites lobata* and 17 in *Porites lutea* with individual colonies hosting from one to six and three to eight ITS2 types for *P. lobata* and *P. lutea*, respectively.” In addition, the two authors report that “of the clones examined, 93% of the *P. lobata* and 83% of the *P. lutea* sequences are not listed in GenBank,” noting that they resolved “sixfold to eightfold greater diversity per coral species than previously reported.”

In a “perspective” that accompanied Apprill and Gates’ important paper, van Oppen (2007) wrote that “the current perception of coral-inhabiting symbiont diversity at nuclear ribosomal DNA is shown [by Apprill and Gates] to be a significant underestimate of the wide diversity that in fact exists.” These findings, in her words, “have potentially far-reaching consequences in terms of our understanding of *Symbiodinium* diversity, host-symbiont specificity and the potential of corals to acclimatize to environmental perturbations through changes in the composition of their algal endosymbiont community,” which assessment, it is almost unnecessary to say, suggests a far greater-than-previously-believed ability to do just that in response to any further global warming that might occur.

In a contemporaneous study, [Baird *et al.* \(2007\)](#)²⁴ also discount the argument that symbiont shuffling is not an option for most coral species,

How many coral species can host more than one sub-clade? The answer, of course, is that most if not all of them likely do; for biogeographical data suggest that when species need to respond to novel environments, they have the flexibility to do so.

²³ <http://www.co2science.org/articles/V10/N28/B1.php>.

²⁴ <http://www.co2science.org/articles/V11/N3/EDIT.php>.

because, as they see it, it is the *sub*-clade that must be considered within this context, citing studies that indicate “there are both heat tolerant and heat susceptible sub-clades within both clades C and D *Symbiodinium*.” Hence, the more relevant question becomes: How many coral species can host more than one *sub*-clade? The answer, of course, is that most if not all of them likely do; for they note that “biogeographical data suggest that when species need to respond to novel environments, they have the flexibility to do so.”

So how and when might such sub-clade changes occur? Although most prior research in this area has been on adult colonies switching symbionts in response to warming-induced bleaching episodes, Baird *et al.* suggest that “change is more likely to occur between generations,” for initial coral infection typically occurs in larvae or early juveniles, which are much more flexible than adults. In this regard, for example, they note that “juveniles of *Acropora tenuis* regularly harbor mixed assemblages of symbionts, whereas adults of the species almost invariably host a single clade,” and they indicate that larvae of *Fungia scutaria* ingest symbionts from multiple hosts, although they generally harbor but one symbiont as adults.

Because of these facts, the Australian researchers say there is no need for an acute disturbance, such as bleaching, to induce clade or sub-clade change. Instead, if ocean temperatures rise to new heights in the future, they foresee juveniles naturally hosting more heat-tolerant sub-clades and maintaining them into adulthood.

In a further assessment of the size of the symbiont diversity reservoir, especially among juvenile coral species, [Pochon *et al.* \(2007\)](#)²⁵ collected more than 1,000 soritid specimens over a depth of 40 meters on a single reef at Gun Beach on the island of Guam, Micronesia, throughout the course of an entire year, which they then studied by means of molecular techniques to identify unique *internal transcribed spacer-2* (ITS-2) types of *ribosomal* DNA (rDNA), in a project self-described as “the most targeted and exhaustive sampling effort ever undertaken for any group of *Symbiodinium*-bearing hosts.”

Throughout the course of their analysis, Pochon *et al.* identified 61 unique symbiont types in only three soritid host genera, making the Guam *Symbiodinium* assemblage the most diverse derived to date from a single reef. In addition, they report that “the majority of mixed genotypes observed during this survey were usually harbored by the smallest hosts.” As a result, the authors speculate that “juvenile foraminifera may be better able to switch or shuffle heterogeneous symbiont communities than adults,” so that as juveniles grow, “their symbiont communities become ‘optimized’ for the prevailing environmental conditions,” suggesting that this phenomenon “may be a key element in the continued evolutionary success of these protests in coral reef ecosystems worldwide.”

In support of the above statement, [Mumby \(1999\)](#)²⁶ analyzed the population dynamics of juvenile corals in Belize, both prior to, and after, a massive coral bleaching event in 1998. Although 70 to 90% of adult coral colonies were severely bleached during the event, only 25% of coral *recruits* exhibited signs of bleaching. What is more, one month after the event, it was

²⁵ <http://www.co2science.org/articles/V11/N17/B3.php>.

²⁶ <http://www.co2science.org/articles/V3/N21/C2.php>.

concluded that “net bleaching-induced mortality of coral recruits ... was insignificant,” demonstrating the ability of juvenile corals to successfully weather such bleaching events.

In another study demonstrating the important role of juvenile corals, [Cantin et al. \(2009\)](#)²⁷ examined the amount of photosynthetic “rent” paid by two different clades of *Symbiodinium* (C1 and D) to their coral hosts (juvenile *Acropora millepora*) for the privilege of living within the latter’s calcareous “houses.” This was done by measuring the “financial transfer” to nine-month-old corals that had been developed “from crosses involving the same parent corals,” which “planned parenthood” minimized any host genetic differences that might otherwise have influenced the physiology of the host-symbiont “lease agreement.”

Results indicated that “*Symbiodinium* C1 exhibited a 121% greater capacity for translocation of photosynthate to *A. millepora* juveniles along with 87% greater relative electron transport through photosystem II under identical environmental conditions.” In addition, they note that “*A. tenuis* and *A. millepora* juveniles in a previous study exhibited 2 to 3 times faster growth rates when associated with *Symbiodinium* C1 compared to those associated with *Symbiodinium* D (Little et al., 2004) at the same field site where juveniles were reared in the present study.” Given such findings, Cantin et al. concluded that “the differences in carbon-based energy transfer between symbiont types may provide a competitive advantage to corals associating with *Symbiodinium* C1, particularly during their early life histories, when greater energy

Corals may be even more adept at successfully coping with rising temperatures than has previously been believed.

investment into rapid tissue and skeletal growth can prevent overgrowth of juveniles by competitors and mortality from grazers.” Likewise, they opine that “as the community structure of coral reefs shifts in response to global climate change and water quality impacts, opportunistic corals harboring symbionts that enable maximum rates of growth may similarly gain a competitive advantage.”

In one further study, [Fitt et al. \(2009\)](#)²⁸ write that the various *Symbiodinium* clades that comprise the algal symbiont found in their coral host had been thought for some time “to exert a major influence on the ability of reef-building corals to survive high-temperature stress,” which is indeed correct; but they add that if the host itself plays a role in this process, “the hypothesis that corals simply shuffle or swap their *Symbiodinium* for clades that are more thermally tolerant does not tell the whole story.” In fact, it

suggests that corals may be even *more* adept at successfully coping with rising temperatures than has previously been believed.

To explore this possibility, Fitt et al. studied a number of coral host and *Symbiodinium* properties and processes in two ubiquitous Indo-Pacific reef corals that are known to be either

²⁷ <http://www.co2science.org/articles/V12/N35/C1.php>.

²⁸ <http://www.co2science.org/articles/V12/N37/C2.php>.

very susceptible (*Stylophora pistillata*) or resistant (*Porites cylindrica*) to heat stress, while exposing them to seawater temperatures of either 28°C (normal ambient) or 32°C (elevated) for five days before returning them to the normal ambient temperature. In doing so, the group of sixteen scientists report finding “both physiological and biochemical differences of both symbiont and host origin in the response to high-temperature stress.” Consequently, they say that “hypotheses that talk only in terms of the thermal characteristics of the symbiont may miss critical information concerning questions surrounding the thermal tolerance of corals in the coming century.” In this regard, they additionally note “there are dynamic photoprotective mechanisms in both the host and zooxanthellae that include ultraviolet radiation absorbing mycosporine-like amino acids (Shick and Dunlap, 2002; Lesser, 2004), excess excitation energy dissipation in photosystem II via the xanthophyll cycle (Brown *et al.* 1999; Gorbunov *et al.*, 2001), the expression of heat-shock proteins and other stress markers (Black *et al.*, 1995; Downs *et al.*, 2000; Lesser and Farrell, 2004), the up-regulation of antioxidant enzymes (Lesser, 1996; Lesser and Farrell, 2004; Lesser, 2006), host energy reserve utilization (Porter *et al.*, 1989; Grotoli *et al.*, 2004, 2006), and heterotrophic plasticity (Grotoli *et al.*, 2006),” all of which phenomena, in their words, “presumably have underlying influences on any response to thermal stress, and hence, contribute to the overall differences within and between species in regard to their bleaching sensitivity.”

Corals have survived such warmth -- and worse -- many times in the past, and there is no reason to believe they cannot do it again, if the need arises.

In conclusion, and in light of the many observations discussed above, the prospect of earth’s corals being able to successfully cope with the possibility of further increases in water temperatures, be they anthropogenic-induced or natural, appears more than likely, if not altogether certain. Corals have survived such warmth -- *and worse* -- many times in the past, including the Medieval Warm Period, Roman Warm Period, Holocene Optimum, as well as throughout numerous similar periods during a number of prior interglacial periods; and there is no reason to believe they cannot do it again, if the need arises.

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