

NEWS AND VIEWS

PERSPECTIVE

The susceptibility and resilience of corals to thermal stress: adaptation, acclimatization or both?

VIRGINIA M. WEIS

Department of Zoology, Oregon State University, Corvallis, OR 97331, USA

Coral reefs are threatened with worldwide decline from multiple factors, chief among them climate change (Hughes *et al.* 2003; Hoegh-Guldberg *et al.* 2007). The foundation of coral reefs is an endosymbiosis between coral hosts and their resident photosynthetic dinoflagellates (genus *Symbiodinium*) and this partnership (or holobiont) is exquisitely sensitive to temperature stress. The primary response to hyperthermic stress is coral bleaching, which is the loss of symbionts from coral tissues—the collapse of the symbiosis (Weis 2008). Bleaching can result in increased coral mortality which can ultimately lead to severely compromised reef health (Hoegh-Guldberg *et al.* 2007). Despite this grim picture of coral bleaching and reef degradation, coral susceptibility to stress and bleaching is highly variable (Coles & Brown 2003). There is enormous interest in discovering the factors that determine susceptibility in order to help us predict if and how corals will survive a period of rapid global warming. In this issue, Barshis *et al.* (2010) examine the ecophysiological and genetic basis for differential responses to stress in *Porites lobata* in American Samoa. They combine a reciprocal transplant experimental design between two neighbouring, but very different reef environments with state-of-the-art physiological biomarkers and molecular genetic markers for both partners to tease apart the contribution of environmental and fixed influences on stress susceptibility. Their results suggest the presence of a fixed, rather than environmental effect on expression of ubiquitin conjugates, one key marker for physiological stress response. In addition, the authors show genetic differentiation in host populations between the two sites suggesting strong selection for physiological adaptation to differing environments across small geographic distances. These conclusions point the study of coral resilience and susceptibility in a new direction.

Received 11 December 2009; revision received 22 January 2010; accepted 25 January 2010

Correspondence: Virginia M. Weis,
E-mail: weisv@science.oregonstate.edu

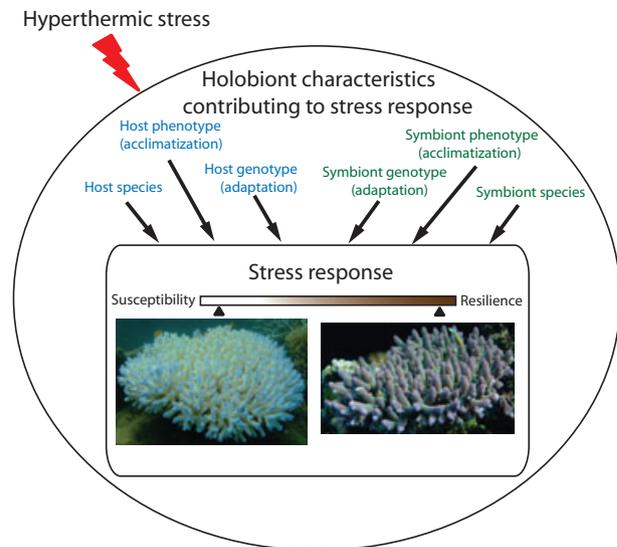


Fig. 1 Characteristics of the coral holobiont that could contribute to a stress response. These characteristics, acting alone or in combination result in a response that falls along a continuum from susceptibility to resilience. Highly susceptible corals often bleach whereas resilient corals keep their symbionts. Bleached colony: *Acropora nasuata*, healthy colony: *A. spatulata*, both from South West Pelorous Island on the inshore Great Barrier Reef. Photographs courtesy of Madeleine van Oppen, Australian Institute of Marine Science.

The list of holobiont characteristics contributing alone or in combination to a coral stress response (Fig. 1) is doubled by the nature of the coral–dinoflagellate symbiosis itself. Indeed, even this is a gross oversimplification because it ignores the diverse and complex microbiota resident on and in corals (Rohwer *et al.* 2002) that are also critical players in coral health (Rosenberg *et al.* 2007). It is not surprising, therefore, that there is no unified view held by coral ecologists as to the dominant or primary factors that determine where a coral holobiont falls on the susceptibility–resilience continuum and whether its position could change or shift with climate change.

The most obvious holobiont characteristics potentially contributing to a stress response are the host and symbiont species partnership combinations. Many studies have examined the dynamics and differential performance of the symbiont clades and subclades in corals before, during and after stress. There is clear evidence that some symbionts are more stress tolerant than others (Rowan 2004; Robison & Warner 2006; Loram *et al.* 2007). Much interest has been focused on clade D symbionts in the IndoPacific as being more stress tolerant than the dominant clade C types

(Baker *et al.* 2004; Rowan 2004; Abrego *et al.* 2008; Oliver & Palumbi 2009). These studies set up the question of whether an increase in the prevalence of D-containing hosts after bleaching events is a result of differential survival of these D-containing hosts or of shuffling or switching of symbionts types within the host after bleaching (Baker *et al.* 2004; Berkelmans & van Oppen 2006; Sampayo *et al.* 2008). Host species also vary in their ability to withstand the effects of bleaching. Differential production of mitigative antioxidants (Richier *et al.* 2005) and varying abilities to acquire nutrition heterotrophically by feeding when bleached (Grottoli *et al.* 2006) are two examples in hosts described to date.

There is ample evidence that corals can be tolerant of and even thrive in temperature extremes (Coles & Brown 2003). In addition, there are plenty of examples of physiological response variation in corals, such as differing levels of fluorescent proteins, mycosporine-like amino acids and a diversity of antioxidant enzymes (Baird *et al.* 2009). However, the big question remains: what are the mechanisms that result in differences in thermal tolerance and physiological response? Are they due to genotypic adaptation—where selection drives differences in susceptibility over evolutionary times scales or rather are they due to phenotypic acclimatization—where organisms respond to extremes using their existing genomic repertoire within the lifetime of an individual? There is evidence of genotypic adaptation of several host species to different thermal environments across broad latitudinal gradients on the Great Barrier Reef (Smith-Keune & van Oppen 2006; Ulstrup *et al.* 2006). In addition, phenotypic plasticity of both host- and symbiont-specific characters in response thermal stress has been documented. The coral *Goniastrea aspera* was found to be resistant to hyperthermic-stress-induced bleaching when colonies had previously experienced stress and bleaching (Brown *et al.* 2002). Likewise, symbionts photoacclimated to high light levels were found to be tolerant of a hyperthermic stress compared with nonacclimated controls (Robison & Warner 2006). It is these questions of adaptation and acclimatization that lie at the very centre of Barshis and coworkers' study.

The authors performed a reciprocal transplant study of corals between a fore reef and back reef site in American Samoa within 5 km of one another with very different thermal characteristics. The fore reef site was a more stenothermal environment with very low daily fluctuations in temperature. In contrast, the back reef site was a eurythermal environment with daily temperature fluctuations of up to 6 °C. Colonies of *P. lobata* were transplanted and then sampled, over a period of several days, for genetic identity of both symbiont and host and for a suite of physiological biomarkers for stress in host tissues: heat shock protein 70, manganese superoxide dismutase and ubiquitin-conjugated and 4-hydroxynonenal-conjugated proteins. The investigators found significant fixed and environmental effects on biomarkers response but with high variability on both temporal and treatment scales. This points to the great difficulty in using high-resolution diagnostic tools, that limit

sample size because of their labour- and cost-intensive nature, on highly variable field samples (van Oppen & Gates 2006). However, the response of ubiquitin conjugates was one stunning exception: all samples originating from the fore reef stenothermal site, regardless of transplant destination or time of sampling, had very low levels of ubiquitin conjugates compared to back reef samples. These results indicated the presence of a fixed, or genotypic, rather than a plastic, phenotypic, effect on this physiological response.

The real surprise to me came with the analysis of the genetic makeup of hosts and symbionts between the two sites. Whereas the symbionts were found to be a homogeneous population across the sites, the authors found significant genetic differentiation in host populations between the two sites. Such subdivision across such a small distance, <5 km, suggests strong selection for physiological adaptations to these differing temperature regimes.

These results expand our thinking about how corals might respond to rapid climate change. *P. lobata* from the stable fore reef did not upregulate ubiquitin conjugates when placed in the fluctuating back reef. This could indicate that genotype constrains or limits the capacity of corals to respond to thermal changes. Furthermore, the absence of symbiont population subdivision or cladal differences between sites, unlike findings in some other studies (e.g. Oliver & Palumbi 2009) suggests that dynamic changes in symbiont make up with stress may not always occur, further limiting the capacity to adjust to temperature increases. This study therefore expands the possibilities of dynamic contributions and interplay between holobiont characteristics that determine a stress response. Discerning and predicting patterns among these characteristics might ultimately help managers in decisions about which corals or areas of reef to protect as the planet warms.

References

- Abrego D, Ulstrup KE, Willis BL, van Oppen MJH (2008) Species-specific interactions between algal endosymbionts and coral hosts define their bleaching response to heat and light stress. *Proceedings of the Royal Society B-Biological Sciences*, **275**, 2273–2282.
- Baird AH, Bhagooli R, Ralph PJ, Takahashi S (2009) Coral bleaching: the role of the host. *Trends in Ecology and Evolution*, **24**, 16–20.
- Baker AC, Starger CJ, McClanahan TR, Glynn PW (2004) Coral reefs: Corals' adaptive response to climate change. *Nature*, **430**, 741.
- Barshis DJ, Stillman JH, Gates RD, Toonen RJ, Smith LW, Birkelands C (2010) Protein expression and genetic structure of the coral *Porites lobata* in an environmentally extreme Samoan back reef: does host genotype limit phenotypic plasticity? *Molecular Ecology*, **19**, 1705–1720.
- Berkelmans R, van Oppen MJH (2006) The role of zooxanthellae in the thermal tolerance of corals: a 'nugget of hope' for coral reefs in an era of climate change. *Proceedings of the Royal Society of London Series B*, **273**, 2305–2312.
- Brown BE, Downs CA, Dunne RP, Gibb SW (2002) Exploring the basis of thermotolerance in the reef coral *Goniastrea aspera*. *Marine Ecology Progress Series*, **242**, 119–129.
- Coles SL, Brown BE (2003) Coral bleaching - capacity for acclimatization and adaptation. *Advances in Marine Biology*, **46**, 183–223.

- Grottoli AaG, Rodrigues LJ, Palardy JE (2006) Heterotrophic plasticity and resilience in bleached corals. *Nature*, **440**, 1186.
- Hoegh-Guldberg O, Mumby PJ, Hooten AJ *et al.* (2007) Coral reefs under rapid climate change and ocean acidification. *Science*, **318**, 1737–1742.
- Hughes TP, Baird AH, Bellwood DR *et al.* (2003) Climate change, human impacts, and the resilience of coral reefs. *Science*, **301**, 929–933.
- Loram JE, G. Trapido-Rosenthal H, Douglas AE (2007) Functional significance of genetically different symbiotic algae *Symbiodinium* in a coral reef symbiosis. *Molecular Ecology*, **16**, 4849–4857.
- Oliver T, Palumbi S (2009) Distributions of stress-resistant coral symbionts match environmental patterns at local but not regional scales. *Marine Ecology Progress Series*, **378**, 93–103.
- van Oppen M, Gates RD (2006) Conservation genetics and the resilience of reef-building corals. *Molecular Ecology*, **15**, 3863–3883.
- Richier S, Furla P, Plantivaux A, Merle P-L, Allemand D (2005) Symbiosis-induced adaptation to oxidative stress. *Journal of Experimental Biology*, **208**, 277–285.
- Robison JD, Warner ME (2006) Differential impacts of photoacclimation and thermal stress on the photobiology of four different phylogenetic types of *Symbiodinium* (Pyrrophyta). *Journal of Phycology*, **42**, 568–579.
- Rohwer F, Seguritan V, Azam F, Knowlton N (2002) Diversity and distribution of coral-associated bacteria. *Marine Ecology Progress Series*, **243**, 1–10.
- Rosenberg E, Koren O, Reshef L, Efrony R, Zilber-Rosenberg I (2007) The role of microorganisms in coral health, disease and evolution. *Nature Reviews Microbiology*, **5**, 355–362.
- Rowan R (2004) Coral bleaching - Thermal adaptation in reef coral symbionts. *Nature*, **430**, 742.
- Sampayo EM, Ridgway T, Bongaerts P, Hoegh-Guldberg O (2008) Bleaching susceptibility and mortality of corals are determined by fine-scale differences in symbiont type. *Proceedings of the National Academy of Sciences, USA*, **105**, 10444–10449.
- Smith-Keune C, van Oppen M (2006) Genetic structure of a reef-building coral from thermally distinct environments on the Great Barrier Reef. *Coral Reefs*, **25**, 493–502.
- Ulstrup KE, Berkelmans R, Ralph PJ, van Oppen M (2006) Variation in bleaching sensitivity of two coral species across a latitudinal gradient on the Great Barrier Reef: the role of zooxanthellae. *Marine Ecology Progress Series*, **314**, 135–148.
- Weis VM (2008) Cellular mechanisms of Cnidarian bleaching: stress causes the collapse of symbiosis. *Journal of Experimental Biology*, **211**, 3059–3066.

V.M.W. examines the cellular and molecular mechanisms underlying coral-dinoflagellate symbioses. Her lab group is interested in the cellular processes and pathways that regulate the initial establishment and ongoing maintenance of a healthy partnership as well as those involved in the dysfunction and collapse of the symbiosis during coral bleaching.

doi: 10.1111/j.1365-294X.2010.04575.x