

REPLY COMMENT

Refining coral bleaching experiments and models through reiterative field studies

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Knowledge in science develops through interactions between observation, description, measurement, experiment, modeling, and prediction. Controlled experiments that confirm model predictions can be intuitive and persuasive, but they are just 2 steps in an iterative process that ultimately requires returning to the field and testing results against field observations. Our article on coral bleaching in Mauritius (McClanahan et al. 2005) was one of the first attempts to use field data to test the seminal experiments on water flow and bleaching by Nakamura & van Woesik (2001) and Nakamura et al. (2003, 2005), as well as Sheppard's (2003) important model of coral extinction in the western Indian Ocean. Our findings did not support the straightforward predictions of either the laboratory experiment or the model, and motivated van Woesik et al. (2005, this volume) to question the validity of our field data. However, an equally valuable approach is to reevaluate the original experiments and models and attempt to identify elements that refine our predictions in the future.

Laboratory vs. field experiments. Experiments suffer a number of problems that are associated with isolation in time and space, as well as unanticipated interactions between species. These problems are often most acute in laboratory settings, which can create initial conditions that can be critical to the outcome of experiments. Consequently, interpretations of experimental results need to carefully consider these problems. Species choice and source environments can greatly influence experimental outcomes, because organisms have the potential to acclimatize and adapt

over different time scales. Although physical models such as that proposed by Nakamura & van Woesik (2001) can be useful in elucidating processes, organismal complexity limits the ability of these models to predict response entirely; as van Woesik et al. (2005) point out, corals possess some physiological mechanisms that can allow rapid acclimatization. However, there are also slower processes that can determine the limits to this rapid acclimatization potential. These slower processes include changes in algal symbiont communities within coral hosts (Baker 2003), particularly in response to the environment perceived during early ontogeny (Little et al. 2004) that can affect production processes and tolerance to stressful warm water (Castillo & Helmuth 2005). The coral host also has a significant role to play in determining bleaching response (Bhagooli & Hidaka 2004, McClanahan et al. 2004, Ralph et al. 2005), and may acclimatize more slowly than its algal partners; understanding how hosts and symbionts respond differently would be useful in resolving conflicting patterns.

We argue that, while higher flow rate may indeed mitigate bleaching and enhance recovery in situations where the environment is relatively constant, in cases where the environment is highly variable, low flow can produce corals adapted to stressful temperature (Castillo & Helmuth 2005). This is particularly true in field situations, where enclosed lagoons with slow water flow can be subject to environmental variation far exceeding that found on open forereefs with rapid flow. Consequently, corals in areas of natural low flow might be naturally more resilient to environmental

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extremes, because of their experience living with high environmental variability (McClanahan & Maina 2003, Castillo & Helmuth 2005).

The next generation of experiments might investigate the effects of water flow on bleaching at locations where organisms originate from different environments and might include reciprocal transplantation of colonies. We predict that experimental outcomes will be site-, species-, and genotype-dependent and that the time scale of physiological changes will also depend on these factors. It would be unwise to conclude that the responses seen in short-term acclimation experiments in the laboratory equivalently represent the outcomes of long-term acclimatization in the field, particularly when these long-term experiments have never been undertaken.

Methodology. While our field methods are simple and inexpensive, we believe that more sophisticated methods are unlikely to yield different results. The clod card method, although imperfect, nevertheless represents an elegant way of integrating water flow over many tidal cycles for relatively reliable field comparisons. Hand-held Doppler meters give accurate short-term measurements and are excellent choices for tanks with constant water flow; however, in field conditions where tides and wind-driven currents influence flow, the accuracy, utility, and practicality of this method is reduced. The problem noted with clods by van Woesik et al. (2005) is quite small, as measured by Porter et al. (2000), and occurs largely under special conditions of oscillatory flow. Van Woesik's student Anzai (2001) found that the adjusted r^2 between clod weight loss and controlled water flow in a flume was 0.962 and, given that the water temperatures were similar at all of our study sites, the temperature effect is unlikely to be significant. For short-term field studies of bleaching where there is a need to quickly compare mean flow rates, the clod card method remains the best choice.

Our own criticism of the clod method was that we did not have historical water flow measurements for our study sites in Mauritius. Consequently, because our results were provocative, we measured bleaching during the 2005 bleaching event in East Africa at sites where there was greater historical dataset on water flow. We again found a positive relationship between water flow and bleaching, but with an r^2 of 0.86 (T. R. McClanahan, unpubl. data), higher than the 0.56 value we found in Mauritius. Consequently, incorporating more measurements that include site history improved rather than disproved the relationship.

Community structure of Mauritian lagoons is quite uniform, as shown by the high amount of variation predicted by the first 2 PCA axes. This allows us to use bleaching indices for each site, because these values

were not greatly influenced by taxonomic composition. Although the east side of Mauritius has large colonies of *Acropora* and other taxa, the actual *Acropora* cover is similar on both sides of the island. We found that *Acropora* cover was slightly higher, but not significantly different ($F = 0.74$) on the low-bleaching west side of the island compared to the high-bleaching east side ($34 \pm 10\%$ vs. $25 \pm 20\%$), indicating that a site's bleaching index is not greatly influenced by *Acropora* dominance. The bleaching index uses density, or numbers of individual colonies per sample, of the taxa studied, so colony size and cover are not part of the site calculation. This may under-represent bleaching when cover is considered an important measure of the site's response, but would bias away from dominance effects by any specific taxa. We found that some coral taxa with small colony sizes, such as *Alveopora* and *Seriato-pora*, had higher bleaching indices than the large colonies of *Acropora* and *Montipora*, which indicates that large colonies are not always more susceptible to bleaching than small colonies. This further indicates that taxa and associated genetics, rather than colony size, are stronger factors influencing bleaching, and that the mass transfer theory is a less useful predictor of community-level bleaching response.

Modeling of coral bleaching. We believe that the failure of the model by Sheppard (2003) to accurately predict bleaching response in Mauritius reflects assumptions that equate 1998 conditions with 'extinction'. The largest problem is that temperature anomalies are often highly variable at small spatial scales, as shown by satellite imagery (Wooldridge & Done 2004) and bleaching response can often be very site-specific, as exemplified in our Mauritian study. The model does not capture this harlequin pattern, where structure is observed with longitude as well as latitude, and island and lagoon effects are also consistent and deterministic. Consequently, the model's latitudinal predictive scale is too coarse to make reliable predictions in areas such as the central Indian Ocean atolls, East Africa, and the Seychelles-Mascarene Islands. Within each of these regions there are large differences in temperature history that involve both stochastic and deterministic processes. A 50 yr temperature time series dataset collected from East Africa (Hadley Center Data, <http://www.cru.uea.ac.uk/cru/info/modelcc>) indicates the presence of a substantial temperature gradient not only from south to north but also from east to west, making it difficult to rely on specific predictions based on latitude alone. Island effects around the Seychelles, Mauritius, and Madagascar are also likely to be strong.

We agree that it is probably too early to use single anecdotal comparisons of the model to prove or disprove predictions, but there are fundamental issues that need to be reconsidered. For example, differences

in temperature history result in non-uniform acclimatization conditions for corals and, until our understanding of the relationship between temperature history and acclimatization is improved, it will be difficult to predict future mortality patterns. Finally, the model also faces difficulties projecting the conditions of 1998 into the future. Sites that were relatively unaffected in 1998 may remain relatively unaffected in the future if some underlying deterministic process is operating that mitigates bleaching and mortality. Difficulties with the model are also highlighted by its use in the Caribbean, where conditions for 'extinction' have already been reached for the southern Caribbean (Sheppard & Rioja-Nieto 2005). Recent field data indicate that these areas were in fact the least affected by previous bleaching (Gardner et al. 2003, Kramer 2003), indicating that a temperature threshold and the 1998 baseline alone will not determine bleaching and mortality response of coral reefs to thermal stress.

Historical temperature regimes, past bleaching episodes, and genetic variation and/or change within and between different species of coral host and/or their algal symbionts will all contribute significantly to bleaching variability and response (Baker et al. 2004). Rather than looking at time to extinction, we should study and predict changes in community structure due to successive bleaching events, and focus on their variability over local scales and responses at specific sites where coral response to warming is variable or anomalous and where corals are likely to acclimatize and persist. Our study highlights how local variability can be more important than general trends from large-scale model predictions, and reveals elements where the model might be improved through finer resolution. We suggest that, given the high site variability and genetic variation observed during bleaching events, the 'extinction' of coral reefs, as measured by a 0.2 probability of the return of the 1998 conditions, is unlikely. Instead, patchy reorganization of coral communities and associated detrimental impacts on reef ecosystem function and diversity are more probable outcomes. Local studies such as ours, which identify anomalous responses or fail to meet predictions, are of particular utility in testing this assertion and improving our predictive capability in the future.

LITERATURE CITED

- Anzai R (2001) The effects of coral morphology and water flow rates on coral growth and passive diffusion. MS thesis, University of Ryukyus, Okinawa
- Baker AC (2003) Flexibility and specificity in coral-algal symbiosis: diversity, ecology and biogeography of *Symbiodinium*. *Annu Rev Ecol Evol Syst* 34:661–689
- Baker AC, Starger CJ, McClanahan TR, Glynn PW (2004) Corals' adaptive response to climate change. *Nature* 430:741
- Bhagooli R, Hidaka M (2004) Release of zooxanthellae with intact photosynthetic activity by the coral *Galaxea fascicularis* in response to high temperature stress. *Mar Biol* 145:329–337
- Castillo KD, Helmuth BST (2005) Influence of thermal history on the response of *Montastrea annularis* to short-term temperature exposure. *Mar Biol* DOI: 10.1007/s00227-0046-x
- Gardner TA, Cote IM, Gill JA, Grant A, Watkinson AR (2003) Long-term region-wide declines in Caribbean corals. *Science* 301:958–960
- Kramer PA (2003) Synthesis of coral reef health indicators for the western Atlantic: results of the AGGRA program (1997–2000). *Atoll Res Bull* 496:1–58
- Little AF, Van Oppen MJH, Willis BL (2004) Flexibility in algal endosymbioses shapes growth in reef corals. *Science* 304:1492–1494
- McClanahan TR, Maina J (2003) Response of coral assemblages to the interaction between natural temperature variation and rare warm-water events. *Ecosystems* 6: 551–563
- McClanahan TR, Baird AH, Marshall PA, Toscano MA (2004) Comparing bleaching and mortality responses of hard corals between southern Kenya and the Great Barrier Reef, Australia. *Mar Pollut Bull* 48:327–335
- McClanahan TM, Maina J, Moothien-Pillay R, Baker AC (2005) Effects of geography, taxa, water flow, and temperature variation on coral bleaching intensity in Mauritius. *Mar Ecol Prog Ser* 298:131–142
- Nakamura T, van Woesik R (2001) Water-flow rates and passive diffusion partially explain differential survival of corals during the 1998 bleaching event. *Mar Ecol Prog Ser* 212:301–304
- Nakamura T, Yamasaki H, van Woesik R (2003) Water flow facilitates recovery from bleaching in the coral *Stylophora pistillata*. *Mar Ecol Prog Ser* 256:287–291
- Nakamura T, van Woesik R, Yamasaki H (2005) Photoinhibition of photosynthesis is reduced by water flow in the reef-building coral *Acropora digitifera*. *Mar Ecol Prog Ser* 301: 109–111
- Porter ET, Sanford LP, Suttles SE (2000) Gypsum dissolution is not a universal integrator of 'water motion'. *Limnol Oceanogr* 45:145–158
- Ralph PJ, Larkum AWD, Kuhl M (2005) Temporal patterns in effective quantum yield of individual zooxanthellae expelled during bleaching. *J Exp Mar Biol* 316:17–28
- Sheppard CRC (2003) Predicted recurrences of mass coral mortality in the Indian Ocean. *Nature* 425:294–297
- Sheppard C, Rioja-Nieto R (2005) Sea surface temperature 1871–2099 in 38 cells in the Caribbean region. *Mar Environ Res* 60:389–396
- Van Woesik R, Nakamura T, Yamasaki H, Sheppard C (2005) Comment on 'Effects of geography, taxa, water flow, and temperature variation on coral bleaching intensity in Mauritius' (McClanahan et al. 2005). *Mar Ecol Prog Ser* 305:301–303 (this issue)
- Wooldridge S, Done T (2004) Learning to predict large-scale coral bleaching from past events: a Bayesian approach using remotely sensed data, *in-situ* data, and environmental proxies. *Coral Reefs* 23:96–108