PROCEEDINGS OF THE ROYAL SOCIETY B

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Proc. R. Soc. B
doi:10.1098/rspb.2008.0606
Published online

*Comment*

# Coral bleaching and disease should not be underestimated as causes of Caribbean coral reef decline

In his recent paper 'A clear human footprint in the coral reefs of the Caribbean', Mora (2008) identifies the drivers of change in Caribbean coral reef communities based on the results of comprehensive analysis. Caution is warranted in accepting some of his major conclusions because, as he himself states, the analysis is a 'snapshot of the potential drivers of coral reef change' and because some of the methods that were used and assumptions that were made seem questionable. In fact, the analysis is a snapshot that looks not at trends, change over time or actual causes of decline but at static measures, and the end result is a misleading picture. Mora concludes 'human activities related to agricultural land use, coastal development, overfishing and climate change had created independent and overwhelming responses in fishes, corals and macroalgae.' In contrast, his analysis indicates that 'thermal stress' and coral diseases have played a minor role in causing reef degradation in the Caribbean. In fact, disease and bleaching have been underestimated as causes of coral reef decline in the Caribbean.

All of the biological data used in the analysis are from one-time surveys conducted between 1999 and 2001 under the auspices of the Atlantic and Gulf Rapid Reef Assessment Project (AGRRA). It is important to note that the factor used in the analysis was not changes in living coral cover over time but rather recent coral mortality. Furthermore, recent coral mortality was calculated as 'the fraction of coral colonies in a transect with 100% of their outward-facing surfaces recently dead'. This approach, which is inconsistent with AGGRA methods, could greatly underestimate mortality by ignoring colonies that are partially dead (even in planar view). Large patches of *Montastraea annularis*, the most abundant species on some Caribbean reefs, are not accounted for accurately when numbers of colonies are counted because they cannot be differentiated into separate colonies. Recent coral mortality exhibits effects of stressors within the last few weeks and would not be expected to reflect possible damage from hurricanes over a 40-year span (as suggested in this paper). This problem with the use of different temporal scales occurs with the treatment of other factors as well.

It is not clear how much of a role Mora attributes to, or at least estimates for, humans in influencing climate change. Coral bleaching associated with elevated seawater temperatures is considered a major indicator of climate change. There is no mention of bleaching at any of the surveyed reef sites, but it is not evident if bleaching was not present at the sites from 1999 to 2001 or if it was intentionally omitted from the analysis. Thermal stress is not defined in the paper or supplementary material, although there is the statement that 'reef sites in warmer environments indeed have had higher coral mortality'. Perhaps thermal stress was calculated as the 'frequency of pentads (i.e. five day periods) in which temperature was 1°C above typical summer temperature'. What is typical? Thermal stress and average temperature are treated distinctly in figure 2 but lumped together in figure 3 (Mora 2008).

Mora also states 'While the effective implementation of marine protected areas (MPAs) increased the biomass of fish populations, coral reef builders and macroalgae followed patterns of change independent of MPAs'. Because this analysis is based on a snapshot that does not reflect changes over time after the establishment of MPAs, particularly marine reserves, it is not valid to use it to support conclusions regarding the effectiveness of MPAs.

In addition, the suggestion that increasing abundance of *Diadema* will help reefs recover is logical, but it is more applicable to shallow depths. All data for the analysis are apparently from fore-reef zones, although the depths are not provided. Note also that herbivory is a rate, and not identical with herbivore biomass.

It would be interesting to see the results of a similar analysis focused on *Acropora palmata* zones. This species, now listed as threatened under the US Endangered Species Act, does not seem to have been included.

Obviously, it is challenging to determine the causes of major changes in complex coral reef ecosystems. The different stressors and their effects vary greatly, and differ in different locations. It is easier to quantify physical damage from a vessel grounding than the effects of overfishing and sedimentation. The characteristics of the major groups of organisms vary widely also. For example, although the analysis in this paper and in many others use single values of macroalgae, macroalgal abundance can vary widely over the course of a year, while coral cover and fish biomass will usually change more slowly. Because of slow coral growth rates, coral cover cannot possibly rebound as quickly as fish biomass.

In this paper, generalizing and extrapolating from the results of one-time surveys carried out over just a few years has created an incorrect and misleading perspective. Although it is irrefutable that human activities have played a major role in causing reef degradation in the Caribbean, it is important to focus not only on better management of more tractable activities such as fishing and anchoring but

The accompanying reply can be viewed at http://dx.doi.org/doi:10.1098/rspb.2008.0984.

*Received* 26 June 2008
*Accepted* 16 July 2008

also on support for more research on coral diseases, the links between human activities and diseases, and the synergy between bleaching and (other) diseases (e.g., Muller *et al*. 2008). Losses of over 50–60 per cent of the living coral cover from reefs in the United States Virgin Islands were observed following massive bleaching in 2005 and a subsequent severe outbreak of disease (Miller *et al*. 2006; Rogers *et al*. 2008; Wilkinson & Souter 2008), and similar losses were seen in Puerto Rico (E. Weil 2008, personal communication). None of the factors Mora identified as drivers of Caribbean reef decline has caused such large losses over the course of a single year.

Caroline Rogers
*US Geological Survey,*
*Caribbean Field Station,*
*1300 Cruz Bay Creek,*
*St. John, VI 00830*
*E-mail address:* caroline_rogers@usgs.gov

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PROCEEDINGS OF THE ROYAL SOCIETY B

Proc. R. Soc. B
doi:10.1098/rspb.2008.1289
Published online

*Invited reply*

# Degradation of Caribbean coral reefs: focusing on proximal rather than ultimate drivers. Reply to Rogers

In recent decades, coral reefs worldwide have been declining at the same time that ocean temperature, fishing and coastal development (and associated pollution and loss of habitat) have increased. Unfortunately, the causality and strength of possible relationships remains a matter of debate (e.g. Aronson *et al.* 2004; Grigg *et al.* 2005; Mora *et al.* 2007). Using region-wide biological, environmental and anthropogenic databases, in combination with statistical methods to control for spatial autocorrelation and collinearity among predictors, I (Mora 2008) demonstrated that humans, through mechanisms associated with agricultural land use, coastal development, fishing and increases in ocean temperature have been responsible for various overwhelming conditions in coral reefs throughout the Caribbean. Rogers (in press) claims that this region-scale analysis underestimated the roles of bleaching and infectious diseases, therefore creating an incorrect and misleading perspective. It should be noted that my paper (Mora 2008) was intended to address the root causes of coral reef degradation (see §1 in Mora 2008). By narrowing the scope of the problem of coral reef degradation, Rogers (in press) failed to realize that bleaching and outbreaks of infectious diseases are *proximal* drivers caused by upper-level or *ultimate* stressors, which were the main aim of my paper (Mora 2008). Although all drivers are worth scientific interest, from the ecological and conservation point of view, it is the identification and resolution of *ultimate* drivers that should be a priority for the conservation of coral reefs.

Outbreaks of infectious diseases in corals, for instance, have been associated with increases in ocean temperature (here, corals become vulnerable to opportunistic pathogens due to bleaching, starvation and/or thermal stress itself; Harvell *et al.* 1999; Bruno *et al.* 2007) and increases in nutrients and terrestrial run-offs (here, the stressors favour the growth of pathogens and/or decrease the resistance to infectious diseases; Bruno *et al.* 2003; Kuntz *et al.* 2005; Kline *et al.* 2006). Regardless of the mechanism, it is clear that outbreaks of infectious diseases often result from corals' exposure to certain anthropogenic stressors. I concur with the statement by Lesser *et al.* (2007) that 'environmental insults are the cause of the physiological stress that subsequently leads to coral mortality and morbidity by many mechanisms including overwhelming infections by opportunistic pathogens', and the statement by Bruno *et al.* (2003) that 'human activities have impaired host resistance and/or have increased pathogen virulence'. Similarly, bleaching or the loss of symbiotic zooxanthellae is well known to be driven by the exposure of corals to different stressors, most commonly ocean warming. Although infectious diseases and bleaching are part of the mechanism leading to coral reef degradation, being the last and perhaps most evident responses, it is clear that they are transitional stages in a chain of actions and reactions triggered by upper-level human stressors, of which the most important were analysed through different proxies in my paper (Mora 2008).

Rogers (in press) criticizes other aspects of the paper that deserve specific responses:

(i) Rogers argues that I underestimate coral mortality by failing to account for corals that were partially alive. I did indeed use only total colony mortality as the response variable for corals; the reason being that partially alive corals can regrow and therefore including them may lead to a rather unstable response variable; the same argument applies to the use of beaching as a response variable, given that corals can recover from it. Once a coral dies, it will remain stably dead.

(ii) Rogers claims that the conclusions on marine protected areas (MPAs) are 'not well founded' given that they are based on a 'snapshot' of the status of coral reefs. The paper clearly stated that the analysis represented a snapshot, which incurs obvious limitations such as the fact that one cannot assess temporal patterns or levels of recovery after stressors. However, I did not make any statement about temporal trends or rates of recovery inside MPAs. In fact, the analysis was constrained to test the hypothesis of whether coral reefs vary in health among MPAs with different effectiveness, which could be tested given spatial gradients in both variables (see Mora *et al.* 2006; Mora 2008). At least two papers, in different parts of the world and using detailed temporal data, support the conclusion that MPAs help fishes but have done little for corals (Jones *et al.* 2004; McClanahan 2008).

(iii) Finally, Rogers wonders about the tests regarding climate change in the my paper (Mora 2008). It is important to clarify that by climate change I referred to temperature, given that other environmental variables were analysed independently and referred more specifically (e.g. hurricanes). For the climate variable I used two proxies, described in

The accompanying comment can be viewed at http://dx.doi.org/doi:10.1098/rspb.2008.0606.

*Received* 9 September 2008
*Accepted* 22 September 2008

detail in the electronic supplementary material of Mora (2008), which were analysed independently using regression methods (fig. 2 in Mora 2008) but concatenated in a latent variable defined as climate in the structural equation model (fig. 3 in Mora 2008), which provides a more robust variable in the face of collinearity or complementarity.

I agree with Rogers (in press) that disentangling the drivers of coral reef degradation is 'challenging', but I think that it is not impossible. Analysing existing data (in many cases, collected locally and systematically over broad spatial scales and freely available) with modern and robust statistical approaches should advance knowledge from subjective opinions to empirically corroborated conclusions and provide better recommendations for the ultimate conservation of coral reefs. The conclusion that humans have created a clear footprint on Caribbean coral reefs still stands; in Rogers' own words 'it is irrefutable that human activities have played a major role in causing reef degradation in the Caribbean'.

Camilo Mora[1,2,*]
[1]*Scripps Institution of Oceanography, University of California, San Diego, CA 92093, USA*
[2]*Department of Biological Sciences, Dalhousie University, Halifax, Nova Scotia, Canada B3H 4J1*
*Author and address for correspondence: Scripps Institution of Oceanography, University of California, San Diego, CA 92093, USA (moracamilo@hotmail.com).

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