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 (2009) 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 (2009) 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 (2009) 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

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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 (2009) 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’.

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