The hologenome theory disregards the coral holobiont: reply from Rosenberg *et al.*

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The major criticisms of Leggat and colleagues[1] are: first, "bleaching is a broad stress response in corals, which has been observed even in the absence of the proposed bacterial causal agents" and second, "there is no experimental evidence to support a role for bacteria in the mass coral-bleaching events that occur over large geographical scales." Regarding the first major criticism, it cannot be concluded that bleaching occurs even in the absence of the proposed bacterial causal agents, because there are no microorganism-free corals (or for that matter, any microorganism-free animals in nature). In fact, there are two well-documented examples of coral bleaching (all Koch's postulates were satisfied) where the causative agent was a specific *Vibrio* strain[2,3]. In both cases, an increase in temperature was the stress factor that upregulated the expression of virulence genes encoded by bacterial pathogens. Thus, bleaching could be the result of chemical or physical stress — for example, temperature — which could affect the activities of one or more of the numerous microbial species that are already associated with the coral (as suggested by Rohwer and colleagues[4]). This could occur through infection by an external primary pathogen or by some direct effect on the coral holobiont. Regarding the second major criticism, we did not claim in the Review that bacterial infection is responsible for mass coral bleaching. To the best of our knowledge, no microbiological study has yet been performed during a mass bleaching event. Consequently, the question remains unresolved.

An additional criticism was that we ignored the literature that links mass bleaching with the anomalous temperatures that disrupt photosynthesis. The subject of the Review is specifically coral microbiology. As such, we did not review the data for and against the hypothesis that coral bleaching is the direct result of increased temperature, which disrupts photosynthesis in the endosymbiotic zooxanthellae. However, the Review does contain a section dealing with the three major stress factors that contribute to coral disease — climate change, water pollution and over fishing These factors are known to alter the bacterial communities that are associated with corals[5–10] and, consequently, might contribute to the bleaching disease.

The hologenome theory of evolution originally emanated from an attempt to understand a few bleaching experiments. However, as outlined in the Review, the theory is based on information that was taken from a wide range of interactions between microorganisms and eukaryotes. We are currently examining the theory both theoretically and experimentally and plan to present a more complete version in the near future. Interestingly, the paper of Rohwer and colleagues[11] (also referred to in the correspondence by Leggat and colleagues[1]), which reports the distribution of bacteria in corals and their possible role in coral health, not only does not contradict the hologenome theory but provided some of the information on which the theory was developed.

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