CORALS: VICTIMS OF ALGAL OVERGROWTH, BUT CAN THEY FIGHT BACK?

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Coral reefs are threatened in their existence by algal overgrowth and coral disease. In studying the mechanism of coral defense against algal overgrowth, we discovered that algae are transmitting a pathogenic bacterium.

Algal invasions and overgrowth are considered as serious threats to marine ecosystems. Proliferating algae can out-compete other benthic organisms and reduce biodiversity. We used the Caribbean coral reef system to develop vital conceptual understanding of algal-coral habitat interactions. Within 30 years, sudden and large-scale increases in the abundance of macroalgae have led to widespread and dramatic shifts from coral to macroalgal abundance on Caribbean coral reefs. Since increases in macroalgal cover and biomass have generally occurred simultaneously with losses in coral cover, it is widely assumed that there has been a shift in the competitive environment, due to reduced herbivory or increased nutrient availability, so that macroalgae have been overgrowing and killing corals. However, there has been no experimental demonstration that macroalgae could actively overgrow and kill corals and that this process alone could explain coral reef degradation.

We surveyed coral-algal interactions on six reefs in Curaçao (Netherlands Antilles). 30 to 60 % of coral colonies were in contact with, or

Overgrowth of the coral *Meandrina meandrites* by the brown alga *Lobophora variegata*. 20 m depth, Vaersenbaai, Curaçao.

overgrown by macroalgae, demonstrating the importance of coral-algal interactions on reefs. Using a series of experiments involving coral and algal transplantations, we demonstrated that macroalgae in general cannot kill corals through competitive overgrowth. Coral margins onto which the brown alga *Lobophora variegata* was transplanted did not experience greater coral mortality than margins kept free of the alga in 5 out of 6 coral species studied. We showed that most coral species were able to extrude arrow-like killing threads ('mesenterial filaments') over a number of algal species. This extrusion was followed by a persistent discoloration due to the movement of chloroplasts in the green alga *Halimeda opuntia*, providing the first ever-reported coral defensive mechanism against macroalgae. The great abundance and wide distribution of the species of corals and macroalgae used in our study, together with observations of mesenterial filaments in natural interactions, suggest that this mechanism could be commonly involved in interaction between

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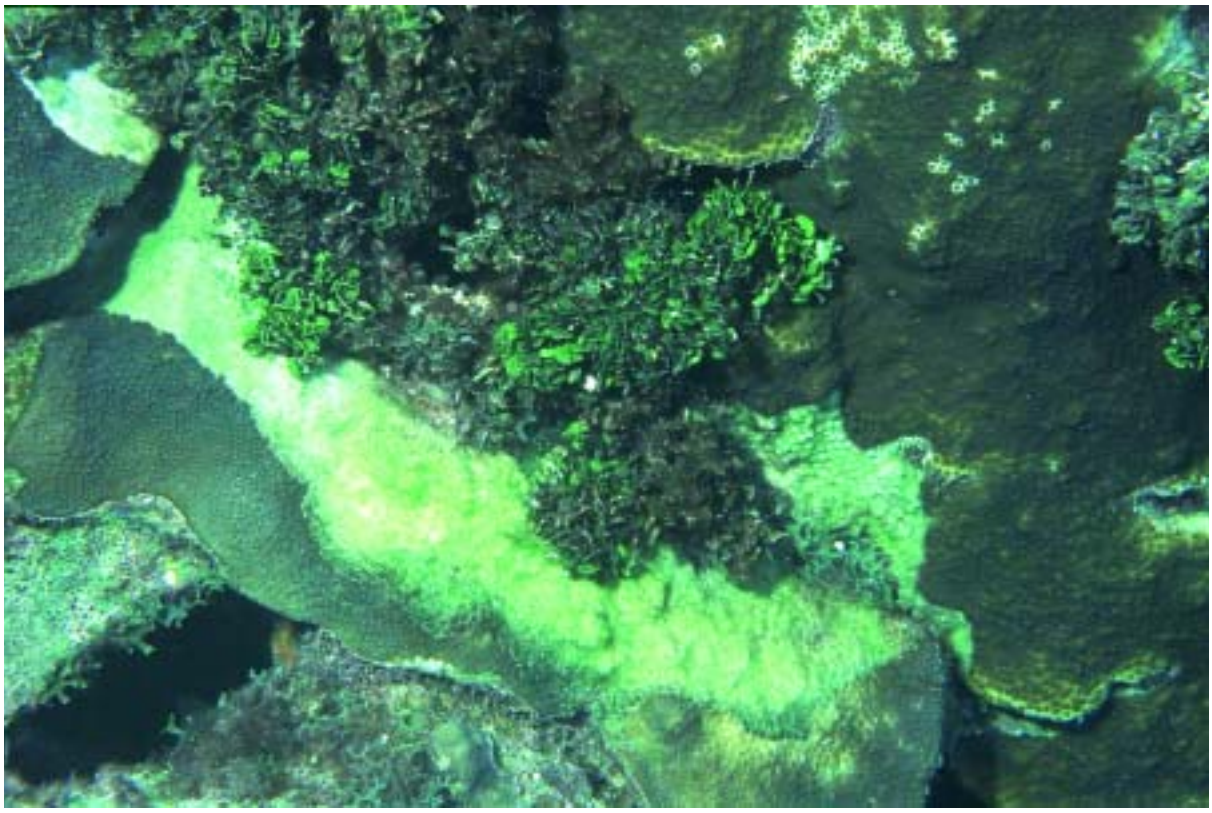

White plague on a colony of the reef-building coral *Montastraea faveolata* with the green alga *Halimeda opuntia* (top) growing at the point of origin of the disease. The bleached area of the colony has been killed by the disease. 8 m depth, Carmabi Buoy Zero, Curaçao.

corals and macroalgae and explain coral resistance against algal overgrowth.

However, we also found that *H. opuntia* was able to spread a virulent coral disease known as white plague that has caused severe and widespread mortality in most Caribbean coral species. Colonies of the dominant coral *Montastraea faveolata* exposed to algal transplants developed the disease whereas unexposed colonies did not. Furthermore, the bacterium *Aurantimonas coralicida*, causative agent of the disease, was present on *H. opuntia* sampled close to, and away from diseased corals, indicating that the alga serves as a carrier for this bacterium.

These results suggest that the spread of macroalgae on coral reefs could account for the elevated incidence of coral diseases over past decades. We propose a new alternative explanation to coral-algal phase shifts in which macroalgae cause coral mortality, not by direct competitive overgrowth, but by promoting mortality from other processes, such as coral disease. In order to save reefs from destructive diseases, it may be necessary to solve the problem of algal overgrowth.