ONLINE

Applied Paleoecology and the Crisis on Caribbean Coral Reefs

In a book review published in 1982, the late Peter Williamson characterized paleoecology as "a poorman's applied ecology performed on inadequate data." Whether or not this incendiary remark was justified at the time, there is no disputing that in the years since 1982 paleoecology has provided much insight into the nature of biotic interactions and community structure. As a recent and obvious example, the debate over coordinated stasis has forced us to consider macroecological dynamics at spatial and temporal scales greater than those of the community. Disagreement over these ideas has led to research on how and why fossil assemblages change through time. Paleoecology is clearly thriving as an intellectual pursuit.

The first part of Williamson's remark is the least controversial. Most of us will indeed remain poor in terms of funding for basic research in paleoecology. If taken seriously, however, those stinging words pose an unintentional and ironic challenge: to use paleoecology to solve practical problems. Paleoecologists must direct their efforts to the pressing ecological challenges before humanity, and they must practice applied paleoecology with adequate—that is to say, statistically robust—data. One problem that is clearly important from a practical standpoint is the radically altered composition of reef communities in the Caribbean over the past 25 years.

The regional-scale transition of Caribbean reef communities since the late 1970s from dominance by scleractinian corals to dominance by noncoralline (fleshy and filamentous) macroalgae has provoked strenuous debate about its underlying ecological processes. Is the current situation natural or the product of anthropogenic stresses and disturbances? Knowing whether similar changes occurred in the past is crucial to addressing this question.

By now the wretched state of Caribbean coral reefs should be depressingly familiar. Reef habitats that once supported spectacular coral growth are now covered with brown algae. On the fore reef off the Discovery Bay Marine Laboratory in Jamaica, coral cover at 5–6 m depth dropped from nearly 60% in 1977 to less than 5% in 1992. Macroalgal cover rose from essentially zero to more than 60% during the same period. Likewise, at Carrie Bow Cay, Belize, location of the Smithsonian Institution's field station, coral cover at 12–15 m on the fore reef declined drastically in the 1980s while macroalgal cover jumped from less than 5% to more than 60%. This is great news if you happen to be a phycologist.

The causal connections underlying this change are complex. First, coral mortality from natural and, possibly, human sources has reduced coral cover and opened space on most Caribbean reefs. Second, herbivory has been reduced by the 1983–1984 mass mortality of the sea urchin *Diadema antillarum* and, in at least some places, by overfishing of parrotfish (Scaridae) and surgeonfish (Acanthuridae). Third, the in-

Rich Aronson (right) and Bill Precht grew up not far from each other in Queens, New York. Blissfully unaware of each other's existence, they both visited the Discovery Bay Marine Laboratory in Jamaica as undergraduates in 1978. There they came to love coral reefs just before disaster struck throughout the region. Rich and Bill met at Discovery Bay in 1987, when the reef was already in a sorry state, and they have been working together ever since. Rich is now a Senior Marine Scientist at the Dauphin Island Sea Lab, a consortium of colleges and universities in Alabama dedicated to education and research in the marine sciences. Bill is the Ecological Sciences Program Manager for the international consulting firm PBS&J in Miami.

Rich was trained as a benthic ecologist at Harvard University but went over to the dark side of paleontology when he saw how powerful geological approaches could be in answering ecological questions. Bill was trained as a carbonate sedimentologist at the University of Miami's Rosenstiel School of Marine and Atmospheric Science, but he deeply appreciates the value of understanding short-term ecological fluctuations. Their coring work in Belize was instigated by Jeremy Jackson, the most persuasive advocate of the position that Caribbean reefs have been fundamentally altered in recent times. Bill and Rich, being a couple of smart-asses from Queens, didn't believe it and had to find out for themselves.

This work has been supported on a continuing basis by the Smithsonian Institution's Caribbean Coral Reef Ecosystems Program and the National Geographic Society, and more recently by grants from the National Science Foundation (OCE-9901969 and EAR-9902192).

crease in available space relative to the potential for herbivory has resulted in greatly increased cover and biomass of fleshy and filamentous macroalgae. The increase in macroalgae has limited, in turn, coral recruitment and recovery of coral populations. These dramatic changes have been observed on reefs that run the gamut of anthropogenic perturbation, from areas like Discovery Bay which have been heavily disturbed by fishing for decades, to places such as Carrie Bow Cay, which at least in the 1970s and 1980s was disturbed minimally.

The loss of coral in the Caribbean could slow or halt reef accretion, with the consequence that reefs could drown and coastal erosion could increase, especially since sea-level rise is expected to accelerate in the near future in the face of global warming. If the recent, decadal-scale ecological changes in reef communities are unique on a centennial to millennial scale, then the suspicion that humans are important agents of reef degradation could be well-founded. On the other hand, if changes of this sort occurred in the past, then human interference could be a mere sideshow, a minor factor contributing to the present situation.

The proximal reason that coral cover has declined so precipitously on Caribbean reefs over the last 25 years is that the staghorn coral *Acropora cervicornis* has experienced a Caribbean-wide mass mortality. Other coral species have declined as well, but *Ac. cervicornis* was the dominant space occupant and an important framework builder at intermediate depths (5–15 m) in the fore-reef habitats of windward-facing reefs before 1980. The species ranged into shallower habitats on more protected fore reefs and was also common in back-reef and lagoonal habitats. White-band disease (WBD), a presumed bacterial disease (or group of diseases) that affects only the genus *Acropora*, has been largely responsible for decimating *Ac. cervicornis* on a regional scale. In addition to the WBD pandemic, hurricanes have killed populations of staghorn coral on a local scale. Other sources of local mortality over the past quarter-century have included sediment and nutrient input; predation by corallivorous fish and invertebrates; coral bleaching associated with elevated sea temperatures; and cold water stress in Florida and the Bahamas, which are at the northern limit of the distribution of the species.

Beginning with Ken Mesolella's work in Barbados in the 1960s, paleoecological analyses have revealed that, despite large fluctuations in sea level during the Pleistocene, the composition of Caribbean coral assemblages remained stable and predictable within habitats on a time scale of tens of thousands to hundreds of thousands of years. John Pandolfi and Jeremy Jackson have shown, however, that the composition of Pleistocene coral assemblages was more variable at finer scales. The transition to the present macroalgal-dominated state of Caribbean reefs, observed on a scale of decades, could be an aspect or consequence of this shorter-term variability, as Jeremy Woodley has argued. On the other hand, the recent change could be unprecedented—brought about by an unique conjunction of circumstances. The most direct way to test these alternative hypotheses is to examine the fossil record of reefs during the late Holocene (the last 3,000 yr) on an intermediate temporal scale of hundreds to thousands of years.

We fell into this line of research almost by accident. In 1986, Bill was assisting University of Miami colleague Bob Ginsburg with a training course in Belize for petroleum geologists. The field course included a stop at the Channel Cay reef complex, one of many atoll-like, diamond-shaped shoals in the central sector of the shelf lagoon of the Belizean barrier reef. Because wave energy is attenuated in the lagoon, the Holocene reef sediments on these rhomboid shoals are uncemented, facilitating coring for historical reconstruction. Cores previously extracted from Channel Cay by Gene Shinn and his colleagues at the U.S. Geological Survey and by students at the University of Miami showed that *Ac. cervicornis* had been the dominant coral for at least several thousand years.

As a follow-up to those coring studies, Bill ran some transects up and down the steep outer flanks of the Channel Cay reef, employing the linear point-intercept (LPI) method. The LPI method is a standard visual assessment technique in which a diver lays a fiberglass surveyor's tape on the reef surface and identifies and records the substratum component at regular intervals beneath the tape. It was no surprise that, like the cores, the living community was dominated by *Ac. cervicornis*, to the tune of 70% coral cover; that much was obvious simply from sticking one's face into the water and looking at the reef.

A resurvey in 1990, however, showed that most of the *Ac. cervicornis* was either dying of white-band disease or already dead. In 1993, we surveyed Channel Cay once again. This time the reef flanks were covered by vast fields of staghorn rubble, the result of rapid bioerosion of the dead colonies. Populations of the sea urchin *Echinometra viridis*, a species that is particularly abundant on the rhomboid shoals, swarmed over the dead surfaces, grazing algae. Such intensive grazing promoted the large-scale recruitment of lettuce corals of the family Agariciidae. The most common recruit was a fast-growing species, *Agaricia tenuifolia*. By 1995, *A. tenuifolia* dominated Channel Cay, covering as much as 56% of the available substratum. In fact, *Ag. tenuifolia* replaced *Ac. cervicornis* on all the rhomboid shoals, over an area of at least 375 km^2.

In retrospect, the fact that agariciids took over was not surprising, for that is exactly what one would have predicted from urchin removal experiments that Paul Sammarco did on a patch reef at Discovery Bay in 1974. In Sammarco's small-scale study, grazing by *E. viridis* promoted the growth and survival of *Agaricia* recruits. With so much discussion recently about the problems of scale in ecology and evolution, it is refreshing to see that Sammarco's result scaled up from a patch reef at Discovery Bay to our 375-km^2 study area in the Belizean shelf lagoon. Moreover, scaling up the results of caging experiments by Bob Carpenter, Sara Lewis, and others on Caribbean reefs in the 1970s and 1980s suggested that declining herbivory relative to space available for colonization could promote algal growth on a regional scale, and that is exactly what happened. Nobody could have predicted that diseases would wipe out both *Diadema* and *Acropora* in the 1980s, a point Terry Hughes raised specifically with respect to *Diadema*. Nevertheless, given that those events did transpire, the vast increase in seaweed that followed highlights the value of small-scale ecological experimentation.

Can paleoecological analysis answer the question of prior occurrence? Yes, but testing the hypotheses is no simple matter. It is an unfortunate fact of taphonomy that noncoralline macroalgae do not preserve in the fossil record of coral reefs. Worse still, Ben Greenstein showed that bioturbation rapidly obliterated any signal of the *Diadema* mass mortality from soft sediments in fore-reef habitats in Bonaire and St. Croix. Fortunately, *Ag. tenuifolia* preserves well in lagoonal environments; hence, the rhomboid shoals of Belize provided a way out of this taphonomic quagmire. We were able to assess, albeit indirectly, whether events of the 1980s had a historical precedent.

With our colleague Ian Macintyre of the Smithsonian Institution, we carried out an intensive coring operation on the rhomboid shoals. Instead of rotary drilling or vibracoring, we used a push-coring technique in which scuba divers forced aluminum tubes 4 meters into the uncemented reef framework—and through even the densest coral heads!—by hand. This simple, low-tech method gave us high mobility, allowing us to take a multilevel approach to sampling, with replicate stations and replicate cores within stations. We extracted a grand total of 38 cores from 22 stations spanning our study area, a sampling regime that would not have been feasible with the cumbersome and heavy equipment required for drilling or vibracoring.

The push-cores gave us the high resolution we needed to look at the late Holocene history of the rhomboid shoals. The recent transition to dominance by *Ag. tenuifolia* was preserved as a layer of coral plates at the top of each core. The mass mortality of *Ac. cervicornis*, which provided the opportunity for *Ag. tenuifolia* to take over, appeared just beneath, as a layer of heavily eroded staghorn branches encrusted by recruits of the lettuce coral. Deeper in the cores, which dated to as old as 3,500 uncorrected radiocarbon years, well-preserved branches of *Ac. cervicornis* predominated, suggesting that staghorn coral was the ecological dominant of these rapidly-accreting reefs. Occasionally, we discovered isolated layers of eroded *Ac. cervicornis* branches, evidence that small patches of staghorn coral died occasionally at our coring stations. Some of those eroded branches were encrusted by *Agaricia* recruits. Discrete layers of *Ag. tenuifolia* plates, possibly representing single colonies, also cropped up here and there in space and time. Using probability theory, we were able to falsify the hypothesis that the layers of *Ag. tenuifolia* and eroded *Ac. cervicornis* represented anything more than local phenomena. The punchline is that there was no evidence of a coral mass mortality or large-scale excursion from dominance by *Ac. cervicornis* for at least three millennia before the late 1980s.

Sea level has risen to only a minor degree in Belize over the last 3,500 years; hence, changing sea level could not have been responsible for the observed patterns. The causes were clearly biological, involving the near-extirpation of the incumbent *Ac. cervicornis* by an emergent disease and its replacement by another, opportunistic coral species. If recent events in the Belizean shelf lagoon can be construed as a preservable proxy for what has happened in the rest of the Caribbean, then we are faced with the frightening prospect that the current situation really is different from what has gone before. Dennis Hubbard and co-workers reached a similar conclusion based on cores drilled at Buck Island Reef, St. Croix. We now are coring uncemented reefs in northwestern Panamá, where the living communities are dominated by *Ag. tenuifolia*, as in Belize.

Sadly, the story of the rhomboid shoals has gotten worse. In the summer of 1998, the effects of a high-amplitude El Niño–Southern Oscillation (ENSO) event were enhanced by global warming to produce the highest water temperatures ever recorded in the Belizean shelf lagoon. All the *Ag. tenuifolia* bleached and died as a result. The rapid recovery of any coral species seems unlikely because, although continued grazing by *Echinometra* is keeping the algae in check, cover of the encrusting chicken-liver sponge, *Chondrilla* cf. *nucula*, has increased wildly over the past couple of years.

There is an ancient Chinese curse: "May you live in interesting times." So far, the conclusions that we and other paleoecologists have drawn about Caribbean reefs are fascinating intellectually but almost unbearable from an emotional standpoint. One cause for guarded optimism is increasing public awareness of the ongoing global environmental catastrophe. With any luck, awareness will transform into mild panic and then into political will quickly enough to save reefs from complete destruction. In the meantime, applied paleoecology can answer some of the urgent questions posed by policymakers and environmental managers about coral reefs and other endangered ecosystems.

—RICHARD B. ARONSON AND WILLIAM F. PRECHT