

these possible functions, ciliopathies may turn out to involve alterations in signals transmitted from cilia, not just in signals they receive.

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Coral Reefs: Building a Better Crystal Ball

Reef corals are ancient taxa, yet they are highly sensitive to environmental change. Recent research indicates that unless global CO₂ emissions are dramatically reduced, we are just decades away from the collapse of coral reef ecosystems.

John F. Bruno

“Predictive ecology threatens the ivory towers of academic ecology and may force ecologists to compete with engineers and other scientists on the unforgiving ground of real life rather than in the meadows of arcane theory.” – R.H. Peters, “A Critique for Ecology” [1]

Ecologists are understandably leery of prediction. In any given ecological system, there are millions of interacting parts that are constantly moving and evolving. There are nested feedbacks, multiple scales of interaction and unpredictable perturbations.

Forecasting the result of tweaking such biological complexity is daunting. Yet, society needs ecologists to do exactly that: namely, to predict the ecological outcomes of policy decisions on everything from genetically modified

crops to exotic species introductions. For example, we know that greenhouse gas emissions are having large and growing ecological impacts. But where are the tipping points? How much and how quickly do we need to reduce emissions to avoid catastrophic and irreversible ecological change? And how much, if at all, can local management increase system ‘resilience’ to climate change? A paper by Emma Kennedy, Peter Mumby and colleagues [2] in a recent issue of *Current Biology* tackles this challenge head on by modeling the fate of coral reefs under different emissions and management scenarios.

Coral reefs are being degraded by overfishing, disease and predator outbreaks, as well as various forms of pollution [3]. On top of this, CO₂ emissions are warming the ocean and also making it more acidic because the

extra CO₂ reacts with seawater to form carbonic acid [4]. Scleractinian corals are the ‘foundation species’ [5] of tropical coral reefs. They secrete calcium carbonate skeletons that, over time, create vast structures that form the basis of complex ecosystems with thousands of species (Figure 1) [6]. Ocean warming is already killing corals [7] and laboratory experiments suggest that ‘ocean acidification’ will reduce the growth of coral colonies (and presumably whole-reef calcification) by roughly 25% by the end of this century. In combination, all of these stressors are thinning coral populations and reducing the structural complexity of the habitat corals create [8,9]. This has knock-on effects on fishes, invertebrates, and other reef inhabitants [10]. Additionally, reefs with little living coral quickly stop accreting vertically and begin to erode due to the actions of animals such as worms and sea urchins, called ‘bioeroders’, that burrow into and scrape away coral skeletons.

Disassembly Rules for Coral Reefs
Kennedy et al. [2] forecast the structural decay of Caribbean reefs based on emission scenarios from the new ‘representative concentration



Figure 1. Complex coral.

A healthy Caribbean coral reef featuring the staghorn coral, *Acropora cervicornis*. The complex structure of this reef provides habitat for the richest marine biodiversity on Earth. Maintaining such complexity is possible but requires the combined approach of reducing greenhouse gas emissions and careful management of fishing and pollution impacts. (Photo: George Stoyle.)

pathways' (RCPs) developed for the Intergovernmental Panel on Climate Change (IPCC) AR5 report, scheduled to be published in 2014. Unlike the scenarios they replace (A1, B1, A1F1, etc.), the RCPs are not based on social, technological, and economic storylines. Instead, they are simply plausible trends in atmospheric CO₂ concentration and are named for the corresponding additional heat retained by 2100 in W m⁻² [11]. Kennedy *et al.* [2] extracted trends in ocean warming from the newest global climate models for RCP 2.6 and 8.6, the minimum and maximum emissions scenarios, respectively. RCP 2.6 is considered quite optimistic as it assumes that

emissions peak roughly ten years from now and drop to zero about 50 years after that.

These projections were then linked to whole-reef carbonate budgets and a virtual scaffolding of ecology with a whopping 115 parameters, defined primarily from the published literature. Parameters included the coverage, morphology and relative calcification rates of key coral species, and the density of bioeroders and herbivores. The simulation was then used to project reef-wide carbonate budgets, i.e. whether reefs were accreting or eroding, under RCP 2.6 and 8.6, on initially healthy or unhealthy reefs, and with or without local management. In

this model, a healthy reef is covered by 25% living coral. Higher coral cover generally means more habitat and greater accretion.

The findings of Kennedy *et al.* [2] are sobering. Even under RCP 2.6, only reefs that are still healthy and well managed are predicted to continue accreting through 2100. It is difficult to express how unlikely this trifecta would be. Just a third of Caribbean reefs are still healthy under the models definition [12] or are in a marine protected area, a place where fishing is managed [13]. Furthermore, many MPAs fail to restore fish and coral populations [13]. Thus, even if something close to RCP 2.6 were achieved, few reefs would benefit because healthy reefs and effective reef management are uncommon in the Caribbean.

Many of my colleagues in the coral reef ecology and conservation community argue that local management can make reef ecosystems resilient to climate change by protecting fishes that eat algae and perform other functions. Kennedy *et al.* [2] found that effective management could buy a reef roughly ten years before it began to erode. Some will view this as proof of success. But I don't consider prolonging the existence of a small fraction of an ancient ecosystem by just a decade a success worth celebrating. Local management may be necessary but it is not sufficient: it is crucial that it be combined with "vastly reduced CO₂ emissions" [2], i.e. RCP 2.6. It is also crucial that it is effective. Declaring a reef a marine protected area and then failing to enforce fisheries restrictions or implement watershed management will not help.

Beyond its scope and complexity, several other aspects of this mechanistic simulation model are relatively novel. For example, Kennedy *et al.* [2] clearly defined their parameters and assumptions, which is not always the case with ecological models, and performed extensive sensitivity analysis. Additionally, most related models predict changes in the abundance or distribution of a population and only make qualitative inferences about the implications for people. This model zeroes in on a key ecosystem function. Maintaining calcification and reef accretion is essential given rapid sea level rise to maintain the protection by reefs of coastal villages from storms.

Known Unknowns

Follow-up work that builds on Kennedy *et al.* [2] and other related models will have to incorporate more of the noise that makes community ecology so interesting to achieve more nuanced and realistic scenarios. For example, the ocean isn't warming uniformly. The warming of tropical oceans so far has been manifested as warm patches that last for days to weeks and are generally less than 100 m² large [14]. The future scale, return time and spatial dynamics of such warm anomalies will fundamentally determine how warming affects reef communities. Additionally, we are only just beginning to measure natural fluctuations in seawater pH on reefs [15] and we really have very little idea how these patterns will be affected by CO₂ emissions and acidification.

Probably the biggest challenge is developing and incorporating realistic responses of individuals, populations and communities to rapid and widespread environmental change. First, we need a better understanding of how much long-lived individuals, such as massive corals, can acclimatize to changing temperature and pH. Second; what is the scope of natural selection to facilitate increased tolerance to new conditions? We certainly know corals can adapt. But we also know there are limits to adaptation, evidenced by the fact that 99.9% of the metazoan species that have ever existed on the earth are now extinct. After all, organisms are not optimized; their physiology, morphology and life history are the outcome of endless trade-offs and compromises. And given the dependence of enzyme kinetics on temperature, thermal stress seems to be especially vexing to adapt to. Third, there is also community-level selection for species tolerant of thermal stress to consider. Such compositional changes appear to be altering the response of coral communities to warming and other perturbations [16].

There are certainly other aspects of the model that could be modified as our understanding of climate change and coral reefs increases. But we clearly know enough to act. When considered alongside earlier simulations [17,18], and the wealth of field observations [19,20] and experiments that demonstrate the sensitivity of reefs to ocean warming, the findings of Kennedy *et al.* [2] paint a bleak picture. Finally, this paper really drives home

the value of basic science. The simulation model is built on generations of ecology, the applied value of which could not have been foreseen. Basic ecological information about seemingly mundane variables, such as species-specific growth rates, has become invaluable in a rapidly changing world.

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Genetics: Swinging Ciliates' Seven Sexes

Ciliates are well known for their unusual tricks of nuclear remodeling. A roulette-like method for mating type choice in *Tetrahymena* adds an interesting new twist to their repertoire.

James G. Umen

“How do I love thee, let me count the ways ...” If you are a ciliate of the species *Tetrahymena thermophila* you can count to seven — one for each of your possible mating types. Though a bit less poetic than Elizabeth Barrett

Browning's famous sonnet, a recently published paper by Cervantes *et al.* [1] on the *Tetrahymena* mating locus does an elegant job of explaining the genetic basis for *Tetrahymena*'s seven sexes, and likely explains the basis for multiple sexes in other ciliates.