Coral reefs as chaos: an assumption-free, system-state approach to causality, dynamics and predictions

SUMMARY

Although there is a high risk of continued reef loss on a global scale, responses to widespread stressors at local and regional scales indicate that resilience to chronic stress is possible and highly variable. Coral reefs are complex systems that exhibit nonlinear behavior, including chaos, feedbacks, multistabilities, cascading effects, adaptation and emergent phenomena. Using traditional models to resolve dynamical processes that control resilience is problematic, due to error from excluded variables, incorrectly identifying mirage correlations as system drivers, and untestable assumptions about relationships between variables. Alternatively, a changing coral reef can be considered a nonlinear dynamical system, whose trajectory through different states over time depends on previous states, and is determined by a set of rules.

I present a promising new technique for understanding and forecasting ecosystems that is adapted from single-species Empirical Dynamic Modeling (EDM), using time series data to reconstruct nonlinear state-space. This reconstruction preserves the topology of the system's attractor manifold, which represents the trajectory of linked variables through state-space. This allows us to correctly discern shared causal drivers from interactions, as well as predict the data values and timing of major systemic change. Without the need for error-inducing model assumptions, this approach has outperformed other forecasting models in multispecies assemblages in other systems. Extending the techniques of nonlinear dynamics to the ecosystem scale and coral reefs will both improve our knowledge of previously intractable coral reef dynamics, as well as improve the predictability of complex ecological systems. This research will establish tools that directly inform ecosystem-based management in a changing world. Furthermore, these approaches are likely to be interchangeably useful with any complex nonlinear system, thereby magnifying the impact of the results.

RATIONALE

There is widespread consensus that management efforts would benefit from adopting an ecosystem-based approach. This would allow us to be explicit about the trade-offs between disparate system uses that are generated by interspecies interactions and their shared responses to abiotic drivers. Coral reefs are complex systems that vary in structure, species diversity, and ecological processes across space and time (Hatcher, 1997). Globally, coral reef survival is increasingly tenuous: many coral reefs are declining in coral cover (Gardner et al, 2003; Bruno and Selig, 2007), have reduced function and resilience (Nystrom et al, 2000), and individual coral colonies have degraded health where intensive human influence is present (Richardson, 1998; Hughes et al, 2003). Yet, ecosystem approaches to understanding coral reefs remain insoluble. The majority of management in the US is based on a small number of species assessments with limited understanding of how each contributes to system-scale dynamics. These traditional models, which do not explicitly include observations of multiple scales and dynamics over time, by definition overlook critical facets of coral reef dynamical systems that are likely important to explaining long-term system behavior and health.

Despite abundant empirical evidence that the many biotic and abiotic functional processes on which reefs depend interact nonlinearly (Hughes et al, 2005, Mumby et al, 2007), these multi-species assessment data are modeled mechanistically using a small number of parameters that rely heavily on ecological assumptions. These assumptions range from constant natural mortality and diet preferences to a lack of variation among individuals and the absence of contemporary evolution. In nonlinear systems, the relatively small errors from those model assumptions propagate unpredictably into large differences in model predictions, and the management advice they generate. Outside of a handful of well-studied systems (e.g. rocky intertidal communities, small lakes), it is impossible to test these assumptions by direct observation or experimental manipulation. **Figure 1.** is a food web of a relatively low-diversity Jamaican coral reef (Roopnarine and Hertog, 2012), without microbial, physical or chemical interactions. This overwhelming tangle highlights the practical impossibility of correctly specifying a parameterized model for systems like it. Regardless of how many species they represent, all of the tools currently available to reef management are based on the implicit assumption that we know how the system works (or that there are only a few candidate models to choose from), which of course, we do not. State-space EDM approaches provide an alternative to these models that does not rely on ecological assumptions.

Coral reefs exhibit chaotic behavior that is locally unstable but globally stable (e.g. Huppert and Stone, 1998). A nonlinear system can be simplified into a trajectory through state-space where each point in the trajectory contains the state dynamics of the system and forms an attractor manifold. Using EDM, we can reconstruct the chaotic attractor manifold of the system using its historical data (see **Figure 2.**), which shows where the system has been and where the system will go in terms of its globally stable dynamics, and regardless of its local instabilities.

It was recently shown that nonparametric methods based on EDM outperform mechanistic models in both forecasting (Perretti et al, 2013; Perretti et al, 2013a) and management (Boettiger et al, 2015; Munch et al. *in review*) for population data generated with a variety of simulation models. Although these methods were originally derived for deterministic systems (Takens, 1981), they have since been generalized to stochastic systems (Starke et al, 1997; Ragwitz and Kantz, 2002), nonstationary systems (Munch et al, 2016; Hegger et al, 2000), short time series (Hsieh, 1998), and systems with substantial observation noise (Casdagli, 1991).

SCIENTIFIC OBJECTIVES

This work targets information gaps of direct relevance to managing coral reef ecosystems with the following scientific objectives:

1. Identify causal drivers of coral reef ecosystem decline
2. Identify mechanisms and timing of regime shifts in coral reef ecosystems
3. Predict near-term future of reef system structure and function
4. Provide dynamically-explicit management recommendations to prevent collapse and enhance resilience of reef systems

These objectives will be achieved by:

1. Developing a causal network of interactions for a reef system
2. Discerning bifurcation topology of regime shifts
3. Forecasting the future of populations, multi-species assemblages, reef systems and human-ecosystem coupled systems
4. Using increased understanding of causality, dynamics and forecasting to work with local

experts in order to strategically optimize coral reef conservation and management efforts

METHODS

The intent of the proposed work is to use techniques of nonlinear dynamics and forecasting, namely empirical dynamical modeling (Ye et al, 2015), convergent cross-mapping (Sugihara et al, 2012), and bifurcation theory (Kuznetsov, 2013), to develop ecosystem-implicit models that inform management actions. These approaches treat an observable as a trajectory through state-space, and if we can reconstruct the attractor manifold that describes that system's trajectory, we can recreate its dynamics and make predictions about its trajectory into the near future. To test these approaches empirically, we will use existing long-term time series from the Florida Keys reef region that has extensive data resources originating from academic institutions, citizen science monitoring programs (e.g. the REEF database), Florida Keys National Marine Sanctuary Research and Monitoring Program (e.g. Keller, 2001), and South Florida National Coral Reef Monitoring Program (via https://grunt.sefsc.noaa.gov/rvc_analysis20/).

Background

Takens' (1981) theorem states that for any dynamical system, we can recover exact system dynamics from a time series of a single observable, using time lags as surrogate dimensions of the attractor. Thus, given a time series from a single species, Takens provides a rigorous justification for modeling the next state n_t, in terms of past states, as

$$n_t = f(n_{t-1}, n_{t-2}, \ldots n_{t-E}) + \epsilon_t$$

where f is a function that converts the history of values into the next estimate for that variable. Although data for only one species is being used, Takens' theorem guarantees that, as long as there are enough time lags, the estimated f implicitly incorporates the dynamics of all other species. Therefore, we can use lags to reconstruct the chaotic attractor, which inherently contains the dynamics of the system (**Figure 3.**) This has been extended to multiple observables (Deyle and Sugihara, 2011).

1. Identifying causal drivers/Developing causal network

Ecosystems are characterized by weak coupling among species and external forcing from abiotic factors (Grenfell et al, 1998) that apply to multiple species simultaneously, thereby creating 'mirage correlations' between species (Sugihara et al, 2012). Convergent cross-mapping (CCM) allows us to distinguish between coupled species and those that share a common driver by determining if the state of one attractor manifold can reliably estimate states of the others (Sugihara et al, 2012, **Figure 4.**)

To adapt the single-species method of empirical dynamical modeling to ecosystems, we will first define an ecosystem value for each reef as an index of known indicators of function (e.g. coral recruitment, algae community structure) adapted from the IUCN Coral Health Index (Kaufman et al, 2011), producing a single 'ecosystem value' for each time observation. We can then use CCM of the ecosystem value manifold and various population demographics (e.g. coral mortality, crustose coralline algae abundance) to identify causal drivers of ecosystem change as either bidirectionally causal due to coupling, unidirectionally causal, or transitively causal, which implies interactions with an indirect factor (Sugihara et al, 2012). Using this set of interactive and causal variables that were not used to produce the ecosystem value, we can produce a causal network of dynamical interactions between these variables (see **Figure 5.**). This will thereby tease apart the dynamics that lead to ecosystem change, with an ideal ecosystem value defined *a priori.* CCM will be performed with a suite of available biotic, abiotic and human economic factors (from sources described above) to develop the causal network for a single reef and a reef region.

2. Identifying mechanisms and timing of regime shifts/discerning bifurcation topology
Bifurcation occurs when a small change in a system's state parameters produces a topological change in the behavior of the system (Kuznetsov, 2013). Stable states in ecology are similarly vulnerable to changes that lead to catastrophic phase shifts between alternative stable states, and this is a well-documented source of coral reef ecosystem loss that is often 'permanent' on observable time-scales (Hughes et al, 2003). For example, if there were a pencil balancing on top of a desk, movement and position would be its state parameters. A small change in either, or a small interaction between the two, could cause the pencil to leave its balanced state and topple over, creating a system bifurcation from the balanced to the toppled system state. In an ecosystem, these state or control parameters are likely to be causal drivers of change when derived from the methods above (1.) and can be tested as mechanisms using methods in bifurcation theory. Bifurcation theory analyzes the movement of these control parameters near fixed points, or points of stability, in their state-space topology. When applied to an ecosystem, this reveals patterns of dynamical behavior in each stable state, and as one state approaches the critical threshold to another. If the existence and behavior of control parameters are known, we can predict what values of these variables will lead to a bifurcation, as well as its timing.

The literature on early critical threshold detection focuses on methods appropriate for systems with a stable fixed point approaching a fold catastrophe, in which critical slowing down is expected as the dominant eigenvalue of the system approaches zero (Sheffer et al, 2009). While the hosts of indicators that have been developed recently seem to work reasonably well in some cases (e.g. Karr et al, 2015), they fail when time series are short and noisy (Perretti and Munch, 2012). Moreover, there are many other types of bifurcations that might be ecologically relevant (Boettiger and Hastings, 2013). Using methods analogous to those in (Deyle et al, 2015), we should be able to estimate the dominant eigenvalue of the discrete time Jacobian, giving an estimate of the local Lyapunov exponent (Brown et al, 1991). This can be used to measure divergence of nearby trajectories, and provide a robust indicator of an impending regime shift that works for a wider range of bifurcations than the indicators based on critical slowing down.

3. Forecasting the future of reef systems
Populations and ecosystems are notoriously difficult to predict because of their nonlinearity and complexity. We will use EDM to reconstruct the chaotic attractor manifolds of individual species abundance, as well as the index of ecosystem value described in (1.) EDM approaches are based on locally-weighted regressions in which the distance between points in state-space determines the weights, which allows a near-term forecast into the future of the system's trajectory. We will investigate the predictive power of using EDM to make population predictions for individual reef species, multi-species assemblages, and system health at individual and regional reef scales. The ecosystem value described above will be used as a proxy for health at the system and regional scales. Multidimensional embedding will be used to make predictions about coupled human-ecosystem forecasts, using the Halpern Index adapted for this system (Halpern et al, 2012).

4. Management recommendations
These studies will produce a suite of the following actionable results and tools with direct management value. *Objective 1.* will yield two products, a list of causal drivers and their relative strengths for a given reef region, and a causal network for a given reef region. The causal network will be delivered both graphically for that region and as a model that can be used to create causal networks for other systems. *Objective 2.* will result in a document with a graphical depiction of a phase portrait for a given reef, and an explanation of the mechanisms and timing of potential regime shifts in that system under different scenarios. *Objective 3*. will produce a set of near-term forecasts for individual populations, multi-species assemblages, an individual reef, a reef region and a coupled human-reef system that can be used to test EDM methods and make recommendations. A small working group of local ecologists, managers and stakeholders from the reef region, and the investigators of this project, will be created with the objective of converting the results into policies. The outcome of this working group will be a document with specific and actionable monitoring, management and policy recommendations for their locale.

RELEVANCE OF RESULTS
Despite enormous effort, our knowledge of marine systems is relatively poor, in part due to their overwhelmingly complexity, as well as the difficulty of observation. Given these data limitations, we are fortunate to be able to develop tools for which comparatively little data are needed, which also explicitly account for the dynamical nonlinearity of interactions in these systems. The proposed work will develop tools to facilitate robust management of marine systems that allow us to address the complexity of biotic and abiotic interactions on coral reefs, without making untestable assumptions, introducing error from excluded variables, or incorrectly identifying mirage correlations as system drivers.

The contribution of causality identification and a causal network of interactions will deepen our understanding of the interdependent dynamics among factors in a complex system, allowing us to target particularly influential components for efficient management. The application of bifurcation theory to ecological regime shifts has been underemployed in the literature, and its development will becoming increasingly valuable as more systems move towards their ‘tipping points’ with increased anthropogenic influence. Coral reefs offer an ideal model system for developing the theory and practical utility of ecosystem stabilities.

EDM forecasting on a suite of indicators is both inherently valuable for predicting how those variables will dynamically respond to change, as well as improving our understanding and application of EDM. Developing these methods for use at a range of scales will be indispensable to future ecosystem managers of all complex systems, but particularly those that are vulnerable and in need of intervention in the near-term.

The proposed work is essential to understanding coral reef dynamics, while also expanding the application of nonlinear dynamics to more and larger marine systems. This research will advance evidence-based coral reef conservation and directly inform management action and management performance assessment. Therefore, this project aligns closely with both NOAA’s and my own missions to improve our knowledge and ability to predict complex ocean ecosystem dynamics, and to use it to conserve our valuable resources.

Figure 1. Food web of Jamaican coral reef (Roopnarine and Hertog, 2012)

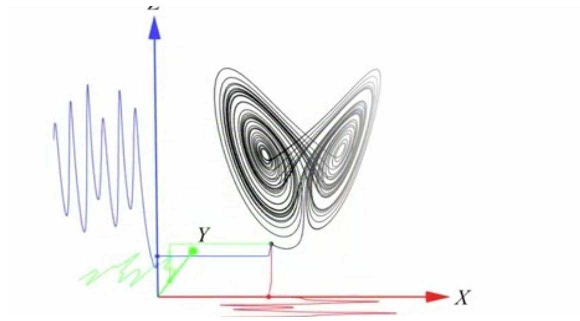

Figure 2. A graphical representation of a chaotic attractor constructed from three time series variables (Ye, 2015)

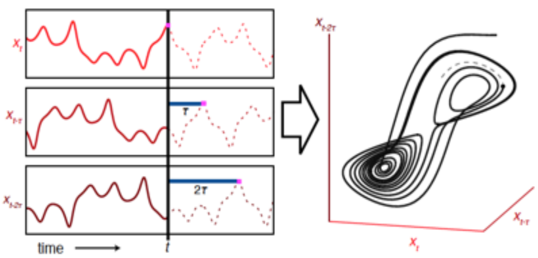

Figure 3. A graphical representation of how a chaotic attractor can be reconstructed from three lags in a time series (Ye, 2015)

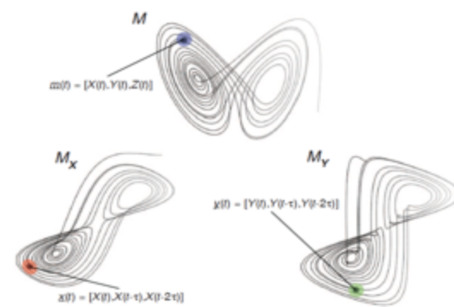

Figure 4. Graphical representation of convergent cross-mapping (Sugihara et al, 2012)

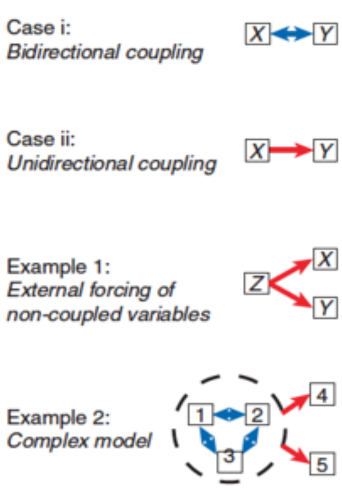

Figure 5. Conceptual cases of coupling and example causal networks that can be derived (Sugihara et al, 2012)

References

Boettiger, Carl, Marc Mangel, and Stephan Munch. "Avoiding tipping points in fisheries management through Gaussian process dynamic programming." *Proceedings of the Royal Society of London B: Biological Sciences* 282.1801 (2015): 20141631.

Boettiger, Carl, and Alan Hastings. "Tipping points: From patterns to predictions." *Nature* 493.7431 (2013): 157-158.

Brown, Reggie, Paul Bryant, and Henry DI Abarbanel. "Computing the Lyapunov spectrum of a dynamical system from an observed time series." *Physical Review A* 43.6 (1991): 2787.

Bruno, J. F., and E. R. Selig. "Regional decline of coral cover in the Indo-Pacific: timing, extent, and subregional comparisons." *PLoS One* 2.8 (2007): e711.

Casdagli, Martin, et al. "State space reconstruction in the presence of noise." *Physica D: Nonlinear Phenomena* 51.1-3 (1991): 52-98.

Deyle, Ethan R., et al. "Tracking and forecasting ecosystem interactions in real time." *Proc. R. Soc. B*. Vol. 283. No. 1822. The Royal Society, 2016.

Deyle, Ethan R., and George Sugihara. "Generalized theorems for nonlinear state space reconstruction." *PLoS One* 6.3 (2011): e18295.

Gardner, T. A., et al. "Long-term region-wide declines in Caribbean corals." *Science* 301.5635 (2003): 958-960.

Grenfell, B. T., et al. "Noise and determinism in synchronized sheep dynamics." *Nature* 394.6694 (1998): 674-677.

Halpern, Benjamin S., et al. "An index to assess the health and benefits of the global ocean." *Nature* 488.7413 (2012): 615-620.

Hatcher, B. G. "Coral reef ecosystems: how much greater is the whole than the sum of the parts?" *Coral Reefs* 16.1 (1997): S77-S91.

Hegger, Rainer, et al. "Coping with nonstationarity by overembedding." *Physical review letters* 84.18 (2000): 4092.

Hsieh, Chih-hao, Christian Anderson, and George Sugihara. "Extending nonlinear analysis to short ecological time series." *The American Naturalist* 171.1 (2007): 71-80.

Hughes, T. P., et al. "Climate change, human impacts, and the resilience of coral reefs." *Science* 301.5635 (2003): 929-933.

Hughes, T. P., et al. "New paradigms for supporting the resilience of marine ecosystems." *Trends in Ecology & Evolution* 20.7 (2005): 380-386.

Huppert, Amit, and Lewi Stone. "Chaos in the Pacific's coral reef bleaching cycle." *The American Naturalist* 152.3 (1998): 447-459.

Karr, Kendra A., et al. "Thresholds in Caribbean coral reefs: implications for ecosystem‐based fishery management." *Journal of Applied Ecology* 52.2 (2015): 402-412.

Kaufman L., et al. "Coral Health Index (CHI): measuring coral community health. (2011) Science and Knowledge Division, Conservation International, Arlington, VA, USA

Keller, B. D., editor. Sanctuary Monitoring Report 2000. (2001) U.S. Environmental Protection Agency, Florida

Kuznetsov, Yuri A. *Elements of applied bifurcation theory*. Vol. 112. Springer Science & Business Media (2013).

Mumby, P. J., et al. "Thresholds and the resilience of Caribbean coral reefs." *Nature* 450.7166 (2007): 98-101.

Munch S.B., et al. "Empirical dynamic programming for model-free ecosystem based management." *In review*

Munch, Stephan B., Valerie Poynor, and Juan Lopez Arriaza. "Circumventing structural uncertainty: A Bayesian perspective on nonlinear forecasting for ecology." *Ecological Complexity* (2016).

Nyström, M., et al. "Coral reef disturbance and resilience in ahuman-dominated environment." *Trends in Ecology & Evolution* 15.10 (2000): 413-417.

Perretti, Charles T., Stephan B. Munch, and George Sugihara. "Model-free forecasting outperforms the correct mechanistic model for simulated and experimental data." *Proceedings of the National Academy of Sciences* 110.13 (2013): 5253-5257.

Perretti, Charles T., George Sugihara, and Stephan B. Munch. "Nonparametric forecasting outperforms parametric methods for a simulated multispecies system." *Ecology* 94.4 (2013a): 794-800.

Perretti, Charles T., and Stephan B. Munch. "Regime shift indicators fail under noise levels commonly observed in ecological systems." *Ecological Applications* 22.6 (2012): 1772-1779.

Ragwitz, Mario, and Holger Kantz. "Markov models from data by simple nonlinear time series predictors in delay embedding spaces." *Physical Review E* 65.5 (2002): 056201.

Richardson, L. L. "Coral diseases: what is really known?" *Trends in Ecology & Evolution* 13.11 (1998): 438-443.

Roopnarine, Peter D., and Rachel Hertog. "Detailed food web networks of three Greater Antillean coral Reef systems: the Cayman Islands, Cuba, and Jamaica." *Dataset Papers in Science* 2013 (2012).

Scheffer, Marten, et al. "Early-warning signals for critical transitions." *Nature* 461.7260 (2009): 53-59.

South Florida National Coral Reef Monitoring Program Data Portal. (Accessed 2018) https://grunt.sefsc.noaa.gov/rvc_analysis20/

Stark, J., et al. "Takens embedding theorems for forced and stochastic systems." *Nonlinear Analysis: Theory, Methods & Applications* 30.8 (1997): 5303-5314.

Sugihara, George, et al. "Detecting causality in complex ecosystems." *Science* 338.6106 (2012): 496-500.

Takens, Floris. "Detecting strange attractors in turbulence." *Dynamical systems and turbulence, Warwick 1980*. Springer Berlin Heidelberg, 1981. 366-381.

Ye. (2015) Nonlinear Tools for a Nonlinear World: Applications of Empirical Dynamic Modeling to Marine Ecosystems. PhD Thesis, UC San Diego.

Ye, Hao, et al. "Equation-free mechanistic ecosystem forecasting using empirical dynamic modeling." *Proceedings of the National Academy of Sciences* 112.13 (2015): E1569-E1576.