PREDICTING THE FUTURE IN A NONLINEAR WORLD

HAO YE, ETHAN DEYLE, GEORGE SUGIHARA
UCSD, Scripps Institution of Oceanography

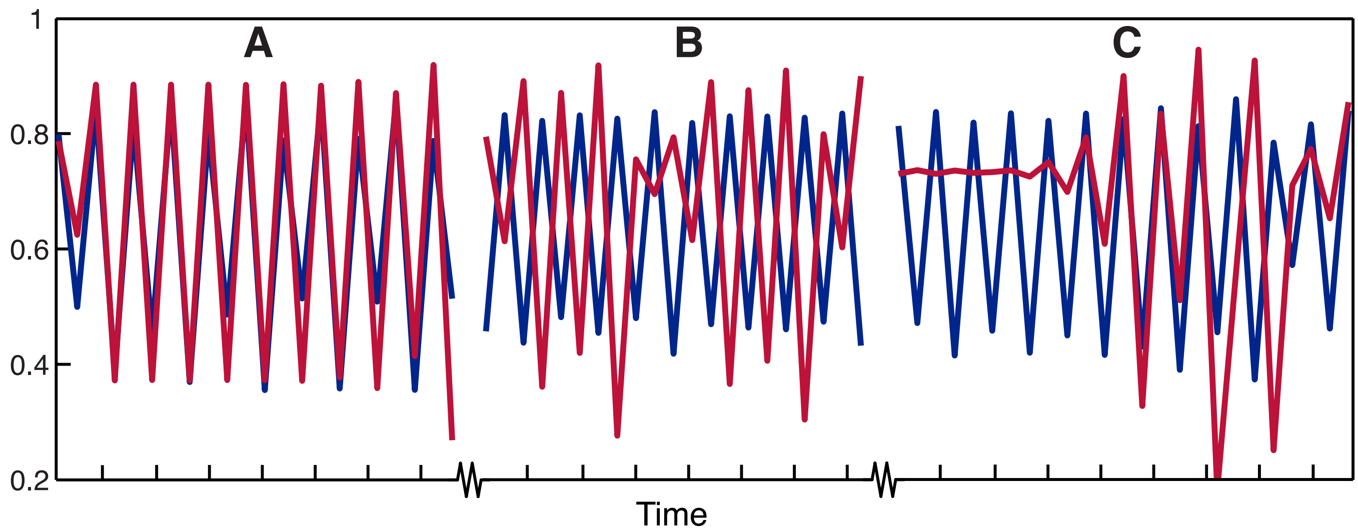

Figure 1. (From Sugihara et al. 2012). Correlations between variables (red and blue) can be ephemeral in nonlinear systems. In panel A, the two variables appear correlated, but in panel b, the variables appear anti-correlated. In panel c, and over longer time periods, there is no correlation, even though the system is dynamically coupled. See Sugihara et al. 2012 for model details and parameters.

Complex nonlinear dynamics are a general characteristic of ecosystems and a challenge for scientists who seek to understand, model, and manage them. These complex dynamics can result from the interaction between endogenous feedbacks, external forcing, and noise (i.e., stochasticity) and can lead to gradual shifts, switching between alternative stable states, deterministic chaos, mirage correlations, and critical transitions. Although the presence of nonlinear, state-dependent behavior means that it may not be possible able to predict the exact state of ecosystems 10–50 years from now, there remains a need for analytical tools that can address the nonlinear behaviors of real ecosystems. Such tools are important to produce accurate forecasts in the short-term, to understand key ecological mechanisms, and to enable adaptive management strategies that remain robust in response to such phenomena as climate change and invasive species.

A fundamental problem with traditional modeling approaches is that they are based on parametric equations, which represent very specific hypotheses about system behavior that can be difficult to justify (Wood and Thomas 1999). Moreover, these models often make simplifying assumptions (e.g., that systems are at equilibrium, different interactions are linearly separable) that do not line up with the known nonlinear reality. Consequently, these models can lack the flexibility to predict future behavior even when they are able to fit the observed data. For example, in nonlinear systems, correlations between variables may not be detectable even if they are dynamically coupled (fig. 1). Thus, variables can appear correlated for the duration of a research study, but this correlation may vanish even though the dynamics have not changed.

One alternative to conventional parametric models is the framework of Empirical Dynamic Modeling (EDM), which does not assume any particular set of equations for the relationships between variables, but instead reconstructs behavior directly from time series data. EDM is based on Takens' Theorem (Takens 1981) and the method of time delay embedding (Packard et al. 1980), which enables it to describe dynamical relationships that are too complex or subtle to capture in a simple set of equations. A brief description of the methods can be found in this short animation: http://simplex.ucsd.edu/EDM_101_RMM.mov.

In addition to the basic methodology of EDM, different techniques have been developed that extend the approach for specific applications: testing for the influence of exogenous factors (Dixon et al. 1999; Deyle et al. 2013), identifying causal interactions (Sugihara et al. 2012; Clark et al. 2015), and even leveraging data from ecological or spatial replicates (Hsieh et al. 2008; Clark et al. 2015). Here, we describe the usage of EDM in two real-world examples of ecological forecasting: (1) identification of a causal linkage between sea surface temperature and Pacific sardine populations in the California Current system and (2) an investigation into the influence of environmental variability on Fraser River sockeye salmon recruitment.

Sea Surface Temperature and Pacific Sardine in the California Current Ecosystem

There has been a long-standing question about whether fluctuations in forage fish abundance are environmentally driven. A well-known example is found in the case of Pacific sardine (*Sardinops sagax*) in the California Current Ecosystem. In California, the Pacific sardine fishery was a rare example of management that explicitly considers environmental conditions. The rationale for this policy was based on work by Jacobson and MacCall (1995), which reported a significant relationship between sea surface temperatures (SST) and recruitment. However, several more recent studies that reanalyze the relationship using newer data have brought the correlation between SST and recruitment into question. The conclusions depend on both the temperature measures examined and the fitting methodology employed (McClatchie et al. 2010; Lindegren and Checkley 2013; Jacobson and McClatchie 2013).

This conundrum can be resolved by using EDM. From a nonlinear perspective, the lack of a significant correlation does not necessarily indicate a lack of causality. Indeed, an analysis of this system using the method of convergent cross mapping (CCM) revealed that information about sea surface temperature (SST) was encoded in sardine time series, suggesting an effect of SST on sardine populations (Sugihara et al. 2012). However, a bottom-line test of whether temperature should be considered for management purposes is if temperature measurements can actually improve forecasts of sardine abundance.

Using EDM models with different environmental measures included as additional coordinates, we found that several temperature variables (SIO pier temperature and the Pacific Decadal Oscillation) did significantly improve forecasts (Deyle et al. 2013). These results provide confirmation that environmental factors do contain information (beyond that of the biological time series) useful for prediction, but to different degrees depending on the variable. Thus, for management purposes, it makes sense to include as robust a measure as possible of the relevant ecosystem affecting Pacific sardines. Indeed, the latest revision to management, by the Pacific Fishery Management Council, establishes harvest control guidelines that respond to a temperature index derived from CalCOFI data, thought to be a better indicator of whether conditions are beneficial or detrimental for recruitment.

Environmental Influences on Fraser River Sockeye Salmon

A similar question of environmental drivers involves sockeye salmon from the Fraser River system in British Columbia, Canada. Early work on this system found that the productivity of these salmon was related to ocean regimes (Beamish et al. 1997) and recent studies suggested that anomalous oceanic conditions experienced by juvenile salmon were responsible for extreme recruitment in 2009 and 2010 (Thomson et al. 2012). However, explicit incorporation of environmental factors into extensions of the standard Ricker model have, to date, produced no significant improvement in actual forecasts (MacDonald and Grant 2012).

Using time series of salmon abundance and the same environmental variables tested in official forecast models, we applied the equation-free framework of EDM, and found that forecasts were significantly improved by the inclusion of environmental factors for the 9 historically most abundant stocks (Ye et al. 2015). In conjunction with the lack of improvement in conventional fisheries models, these results suggest that the interaction between environment and Fraser River sockeye salmon is state-dependent, and therefore not readily encapsulated in simple mechanistic equations (i.e., the extended Ricker stock-recruitment model).

More generally, we note that, although simple parametric models may work over short time periods, such models need to be constantly refit (e.g., an analysis by Beamish et al. 2004 showing better fits of the simple Ricker model when data are partitioned by climate and ocean regimes, a Kalman-filter based approach from Peterman et al. 2000 wherein the Ricker model parameters undergo random drift). Consequently, when the system enters a new state where relationships change, the models will lack predictive power. Moreover, such models are unsatisfactory from a scientific perspective, because they do not explain actual ecological mechanisms—instead the models track the nonlinear behavior of the system phenomenologically as if it were random and therefore do not predict.

CONCLUSIONS

These examples demonstrate the utility of EDM as a data-driven approach for understanding and predicting the future in a nonlinear world. As a general framework, current methods (e.g., CCM, simplex projection) only address certain basic applications, but further developments will continue to bridge the gap between theory and practical usage. As a result, there is a huge potential for increasing use of the EDM framework in situations where parametric models are currently the norm. In addition to the situations described above, where the advantages of EDM for understanding nonlinear behavior are clear, we also note that the ability of EDM models to evolve with new data means that it is inherently more flexible than fixed model structures. Consequently, it is an ideal tool for adaptive prediction in systems changing due to climate change, human impacts, or other unknown factors.

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Part III

SCIENTIFIC CONTRIBUTIONS