Ecological response in aquatic systems: coping with limits to predictability

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Keywords: ecosystem models, nonlinear dynamics, time series analysis

Abstract

Whether considering climate change, altered nutrient input or environmental flows, there's a growing need to understand and predict ecological responses in aquatic systems: how will the network of interactions between nutrients, primary production and higher trophic levels respond to these changes? What system responses need to be predicted, and what are the limits to predictability? In this paper we argue that for ecological systems a more appropriate and realistic aim may be to focus on system characterisation rather than prediction. We draw on simple, well-studied ecological models to demonstrate why conventional means for assessing predictability fail in such systems, and illustrate an approach that goes some way to addressing these problems.

Introduction

Prediction is an endeavour fraught with danger, and there's a surprisingly wide range in interpretations of what it means to predict. Chaotic systems are widely described as being 'unpredictable' and yet they exhibit regularities or patterns in time that can be characterised and understood very well. Lorenz' famous 'butterfly' attractor is simply a graph that captures such a pattern in the relationship between three varying quantities. Similarly, stochastic systems are unpredictable, and yet again we can characterise their behaviour; we cannot predict the exact time course of heads and tails in a series of coin tosses, but over time we know we'll see roughly equal numbers of each. Appropriate characterisation of the underlying processes gives us our best chance of making appropriate decisions in the face of uncertainty in these systems, and allows us to quantify risk associated with those decisions.

Ecological systems present particular challenges. A fish population can vary in time due to externally-imposed forces (e.g. flow extraction or regulation) and due to internally-generated dynamics (eg. population dynamics emerging from nonlinear interactions between fish and the underlying foodweb). It remains an open debate in ecology whether ecological systems exhibit chaos, although chaotic population dynamics have been observed in laboratory chemostats (Becks *et al*, 2005). When faced with the prospect of managing a complex system, with both internal and external sources of variation in time, it's appropriate to draw on methods established in other disciplines for studying and characterising such systems. In this paper we demonstrate the use of nonlinear time series analysis techniques to characterise and compare behaviour in simple ecological models. These are unashamedly 'toy' models, but they are needed (a) to isolate and demonstrate concisely fundamental problems in predicting ecological response; and (b) to function as a test bed for alternative methods of analysis.

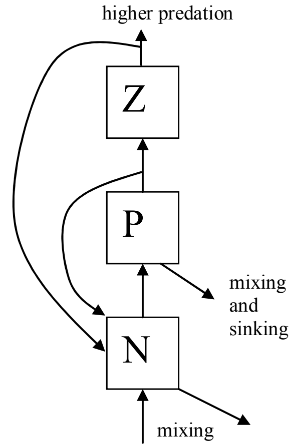
Methods

We employed two models: a simple one-species model that maps population change from one generation to the next, and a three-species food chain.

If population breeding occurs seasonally, with non-overlapping generations, discrete maps can define the relationship between the population in one generation and the next. The simplest such mapping is the well-studied logistic map. The following rule defines the mapping from one point in time, x_n, to the next, x_{n+1}:

$$x_{n+1} = r(1 - x_n)x_n \tag{1}$$

where *r* is a growth rate parameter. The equation can generate a range of behaviour; it can produce the familiar logistic growth curve where x_n grows exponentially from low values and then levels off at a constant value over time, or it can exhibit chaotic fluctuations.



$$\begin{aligned}
\frac{dN}{dt} &= -\frac{N}{e+N}\frac{a}{b+cP}P + rP + \frac{\beta\lambda P^2}{\mu^2+P^2}Z + \gamma q Z + k(N_0 - N) \\
\frac{dP}{dt} &= \frac{N}{e+N}\frac{a}{b+cP}P - rP - \frac{\lambda P^2}{\mu^2+P^2}Z - (s+k)P \\
\frac{dZ}{dt} &= \frac{\alpha\lambda P^2}{\mu^2+P^2}Z - q^n Z
\end{aligned}$$

Figure 1 Diagram and equations for the nutrient-phytoplankton-zooplankton model

Table 1 Default parameter values used by Edwards and Brindley (1999)

Parameter	Symbol	Default value	Reported range
a/b gives maximum *P* growth rate	*a*	0.2 m^{-1} day^{-1}	0.07–0.28
Light attenuation by water	*b*	0.2 m^{-1}	0.04–0.2
P self-shading coefficient	*c*	0.4 m^2 $(g\ C)^{-1}$	0.3–1.2
Half-saturation constant for *N* uptake	*e*	0.03 g C m^{-3}	0.02–0.15
Cross-thermocline exchange rate	*k*	0.05 day^{-1}	0.0008–0.13
Higher predation on *Z*	*q*	0.075 day^{-1}	0.015–0.150 if *n* = 1 0.25 - 2 m^3 g^{-1} day^{-1} if *n* = 2
P respiration rate	*r*	0.15 day^{-1}	0.05–0.15
P sinking loss rate	*s*	0.04 day^{-1}	0.032–0.08
N concentration below mixed layer	N_0	0.6 g C m^{-3}	0.1–2.0
Z growth efficiency	α	0.25	0.2–0.5
Z excretion fraction	β	0.33	0.33–0.8
Regeneration of *Z* predation excretion	γ	0.5	0.5–0.9
Maximum *Z* grazing rate	λ	0.6 day^{-1}	0.6–1.4
Z grazing half-saturation coefficient	μ	0.035 g C m^{-3}	0.02–0.1
Mortality exponent	*n*	1	1 or 2

The second model is a system of three ordinary differential equations representing the population dynamics of a simple nutrient-phytoplankton-zooplankton (NPZ) food chain. Nutrient, phytoplankton and zooplankton ‘stocks’ are linked by flows of carbon between them (Figure 1). Specifically, the NPZ model used by Edwards and Brindley (1997, 1999) is used. The rates of change in N, P and Z are

Rate of change in N = – uptake by P + respiration + Z excretion + Z predation excretion + mixing
Rate of change in P = uptake of N – grazing by Z – sinking – mixing
Rate of change in Z = growth by feeding on P – higher predation

The differential equations are shown in Figure 1. N, P and Z are nutrient, phytoplankton and zooplankton carbon concentrations respectively, with units of g C m^{-3}. Parameter descriptions, units and default values are given in Table 1. The NPZ model is capable of is capable of a range of behaviours, including stable, constant populations in time, oscillating boom-bust cycles and chaos. These have been thoroughly analysed by Edwards and Brindley (1997,1999).

For each model we generated time-series that we refer to as the ‘observed’ time series. The first time series is a chaotic time series from the logistic map, with the growth parameter set to $r = 3.7$. The second time series is a chaotic time series from the NPZ model. In this case $q = 0.1432$, $k = 0.0552$, $N_0 = 1$ and the remaining values were the default values listed in Table 1. The equations were integrated using the *ode15s* integrator in Matlab.

Models for predicting biogeochemical and ecological response in aquatic systems are usually systems of nonlinear differential equations with unknown parameters that need to be fitted. The most common approach to model fitting is to use a sum of squares approach; here the sum of squared difference between the two time series is a ‘distance’ between the two time series, calculated on a point-by-point basis. If the observed measurements are $\{x_{\mathrm{obs}_1}, x_{\mathrm{obs}_2}, \ldots, x_{\mathrm{obs}_n}\}$ and the model points are $\{x_{\mathrm{mod}_1}, x_{\mathrm{mod}_2}, \ldots, x_{\mathrm{mod}_n}\}$ then the sum of squared difference is $E = \sum_{i=1}^{n} \left(x_{\mathrm{mod}_i} - x_{\mathrm{obs}_i}\right)^2$. This conforms to our conventional notion of prediction, and provides a direct measure of how well a model is able to reproduce the exact time course of a series of measurements.

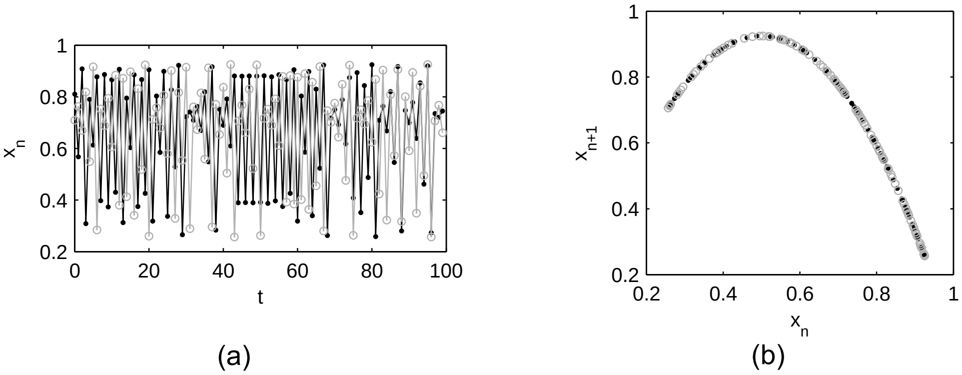
It can be argued, however, that in ecological systems finding a model that captures key dynamical characteristics (eg. boom-bust cycles) is a more realistic aim than expecting to find a model that predicts the exact time course of events. How can these dynamical characteristics be quantified and compared? An approach considered in this paper again relies on the notion of a ‘distance’ between the two time series; however before calculating this distance the time series are transformed so that geometrical patterns in the data (the system attractors) become the objects of comparison.

The key to the transformation is to consider how the observations relate to historical observations; in each case we seek a functional relationship between past and future observations, and use this relationship to construct a measure of comparison.

Results

In the case of the logistic map, we know that there is a very simple function relating past and future values, and the relationship is fully captured by plotting each observation against its predecessor (the return map). The chaotic time series (Figure 2a) when plotted against itself with a time-lag, shows the parabolic function that captures the underlying, deterministic dynamics (Figure 2b).

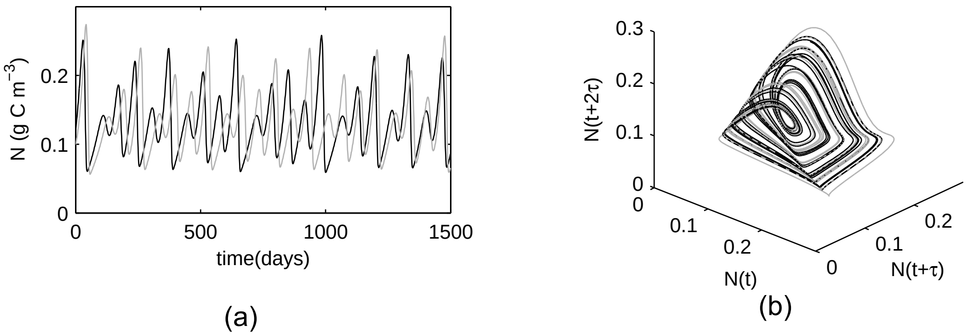
A defining characteristic of chaotic time series is their extreme sensitivity to initial conditions. In the example shown in Figure 2, a mean through the data is a ‘better’ match (in the sum of squares sense) to the time series than a time series generated by exactly the same model with a different initial condition (sum of squares error E = 4.7 vs E = 10.5). Hence the need for an alternative measure of what it means for two time series to ‘match’. In this particular case, it is more appropriate to calculate the ‘distance’ between the geometrical patterns in the return map, than from point-by-point differences in the time domain.



(a) (b)

Figure 2 (a) Two chaotic time series generated from the same logistic map (r = 3.7) (b) the return map for the two time series. Although the time series don't 'match' in the time domain, their return maps do match, demonstrating that they have been generated by the same underlying process.

The logistic map is a trivial example. The NPZ system situation is more complicated; rather than a discrete mapping from past to future, time is continuous and there are now three quantities influencing each other (N, P and Z). Given only nutrient observations (we rarely have measurements of all quantities needed by our models), how do we transform the time series to reveal the deterministic pattern in the nonlinear dynamics? Again, the dynamics are revealed clearly if observations are plotted against past observations, in a procedure called 'time delay embedding' or 'state space reconstruction' (Abarbanel, 1996). This approach is commonly used in other disciplines, but has found little application in ecological systems, mostly likely due to lack of long-term high frequency time series. The method, stripped of its basics, shows the relationship between N(t) and time-lagged versions of the observations, N(t – τ), N(t – 2τ) and so on. Typically the time lag, τ, is chosen by an average mutual information criterion, and the appropriate number of lags is determined by a false nearest neighbour criterion (Abarbanel, 1996). When these steps are followed for chaotic NPZ time series (Figure 3a), the distinctive shape of the attractor is clear (Figure 3b). Thus we can capture the attractor without needing measurements of the other quantities, P and Z, influencing the system dynamics.



(a) (b)

Figure 3 (a) Two chaotic time series generated from the same NPZ model (*q* = 0.1432, *k* = 0.0552, N_0 = 1 and the remaining values were the default values listed in Table 1. Time series temporal resolution is 1 day.) (b) the same time series in reconstructed state space (τ = 16 days). Although the time series don't 'match' in the time domain, their attractors do match, demonstrating that they have been generated by the same underlying process.

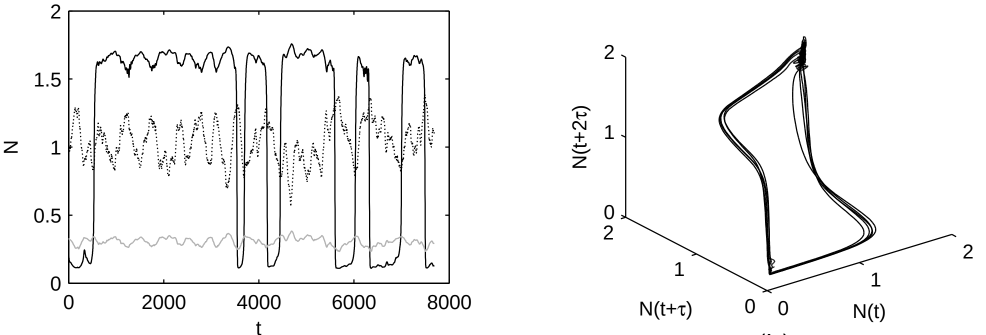
Again, the time series is chaotic and a mean through the data is a 'better' match in the least squares sense than a time series generated from the identical model with a different initial condition (sum of squares error E = 2.9 vs E = 5.7). As before, it is more appropriate to calculate a 'distance' between the attractors than between points in the time-domain. Performing this calculation is non-trivial and there are many possible ways to approach it. We've had some success using cluster-weighted modelling (Gershenfeld, 1999) to represent the reconstructed attractors as probability density distributions, which are then used to calculate joint probabilities as a distance measure.

Discussion and future directions

In advancing our aquatic models from purely physical processes (eg. predicting circulation patterns or density stratification) to include geochemistry (eg. interactions between physical transport and redox conditions) and eventually ecology (eg. effect of altered nutrient delivery on phytoplankton or fish populations), we encounter the very real possibility of oscillatory and chaotic responses due to internal nonlinear dynamics. Nonlinear time-series analysis may provide useful approaches for fitting and validating such models.

In this paper we've demonstrated the point as simply as possible using autonomous models; that is, the dynamics observed in the time series are purely the result of non-linear interactions internal to the system, with no variation 'forced' from outside the system. Real aquatic systems, of course, experience variations due to internal dynamics and external forcing, and this presents an additional set of challenges.

Consider the same NPZ model, now forced with a time-varying stochastic zooplankton mortality parameter, *q* (Figure 4a), as zooplankton specific mortality rates would not be expected to be constant in a real system. Other parameter values are set to the default values in Table 1, with the following exceptions: the quadratic mortality exponent set to *n* = 2 and two different N_0 values were used. In a low-nutrient scenario, N_0 = 0.6 g C m^{-3}, this system simply oscillates about a steady value (Figure 4a), only gently affected by the stochastic variations in *q*. Typically, models are used to test alternative scenarios, often involving increased nutrient delivery to systems. In this case if we consider a high nutrient scenario, N_0 = 2 g C m^{-3}, the system responds very differently (Figure 4a).



(a)

(b)

Figure 4 (a) Time series showing the stochastic *q* forcing (dotted line), the nutrient response at for the low N_0 scenario (grey line) and the nutrient response for the high N_0 scenario (black line); (b) The high N_0 response plotted in reconstructed state space (τ = 16 days).

Note that only the rate at which nutrients are supplied to the system, and nothing else has changed in this model. In particular, the external forcing in *q* remains identical to the low nutrient case, and yet the system now responds in a more extreme manner; it exhibits rapid 'surprise' rapid regime shifts. This type of threshold behaviour has been observed in many ecological systems (Scheffer et al, 2001), and needs to be better understood if we're seeking to manage aquatic systems to be resilient.

Transforming this time series as before, we see that again there is a pattern which captures some of the dynamical behaviour (Figure 4b). Can the nonlinear time series approaches used in this paper can be applied to such forced systems? Experience in other disciplines would suggest that it may be possible (Casdagli, 1992).

Conclusion

The examples presented in this paper clearly demonstrate problems that lie in the way of good analysis of ecological responses. Unfortunately, we are far from having the high-resolution time series and analysis methods to explore these problems in real ecosystems. Even in virtual worlds of numerical simulation, with only moderate increases in model complexity and dimension these methods for characterising system response rapidly become intractable. Nevertheless, these are important concepts and very real problems that need to be tackled. Earth's systems are generally recognised as being in a 'no analogue' state – humans have induced widespread and rapid changes to natural systems that are unprecedented in their magnitude and rate of change – and there's an urgent need to understand how nature will respond (Steffen and Tyson, 2001). Applying the insights gained from simple nonlinear models to real-world problems will be an ongoing challenge. It is certain from these examples that if we are to explore these issues in aquatic systems, we will require high quality, long-term, high frequency measurements in order to unravel the important dynamics underlying observed variations.

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