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Visibility of the environmental noise modulating population dynamics

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Characterizing population fluctuations and their causes is a major theme in population ecology. The debate is on the relative merits of density-dependent and density-independent effects. One paradigm (revived by the research on global warming and its relation to long-term population data) states that fluctuations in population densities can often be accounted for by external noise. Several empirical models have been suggested to support this view. We followed this by assuming a given population skeleton dynamics (Ricker dynamics and second-order autoregressive dynamics) topped off with noise composed of low- and high-frequency components. Our aim was to determine to what extent the modulated population dynamics correlate with the noise signal. High correlations (with time-lag −1) were observed with both model categories in the region of stable dynamics, but not in the region of periodic or complex dynamics. This finding is not very sensitive to low-frequency noise. High correlations throughout the entire range of dynamics are only achievable when the impact of the noise is very high. Fitted parameter values of skeleton dynamics modulated with noise are prone to err substantially. This casts doubt as to what degree the underlying dynamics are any more recognizable after being modulated by the external noise.

Keywords: noise; population dynamics; Ricker model; AR(2) model; external disturbance

1. INTRODUCTION

The core of population ecology is in gaining an understanding of the factors causing fluctuations in population density. Since Andrewartha & Birch (1954) there have existed various views on the relative merits of density-dependent and -independent processes in being responsible for population fluctuations (Murray 1993; Turchin 1995, 1999). For example, research on game animal dynamics abounds with suggestions that short-term population fluctuations to a degree find their explanation in weather and climate factors (Siivonen 1956, 1957; Arditi 1979; Slagsvold & Grasaas 1979; Schröder *et al.* 1982; Eiberle & Matter 1984, 1985*a*,*b*; Steen *et al.* 1988; Swensson *et al.* 1994). This in fact dates back to the speculated causes of the dynamics of the snowshoe hare and the Canada lynx (Elton 1924; Sinclair *et al.* 1993).

The rationale in this study was to hunt for weather and climate variables that correlate with long-term data on population dynamics. This is because of a temptation to find biologically rational explanations for the effect of almost any weather-derived variable on population fluctuations via mortality and reproduction, the key elements of population persistence. The origin of the idea is in the climatic control theory (Bodeheimer 1938; Andrewartha & Birch 1954), which states that populations are strongly influenced by weather and are thus regulated by these factors.

Despite repeatedly articulated caveats (Royama 1977, 1992; see Lindström (1998) for a detailed review of the topic), now and then the climatic control paradigm arises. Recent concern about global warming of the climate (Ropelewski & Jones 1987; Hurrell 1995; Trenberth & Hoar 1996; Dai *et al.* 1998) has revived the approach of correlating observed ecological time-series with climate indices such as the North Atlantic Oscillation (NAO), North Pacific Index (NP), El Niño Southern Oscillation (ENSO) or Palmer Drought Severity Indices (SOI). The aim is to correlate, with or without time-lags, one of the global climate indices, e.g. annual mean, winter season, moving monthly average or monthly values, with extant long-term population data. Most often this has been done with the NAO and, for a great variety of taxa, statistically significant correlations (or closely so) have been reported. These mostly deal with aquatic organisms, e.g. North Atlantic phytoplankton density (Reid 1978), toxic plankton algae on the Swedish west coast (Belgrano *et al.* 1999), the dynamics of two calanoid copepod species in the North-East Atlantic (Fromentin & Planque 1996), oceanic macrobenthos (Kröncke *et al.* 1998; Tunberg & Nelson 1998), annual landing statistics of the European herring and sardines (Alheit & Hagen 1997) and extent of the geographical range of distribution of the North American Atlantic salmon during the sea phase (Friedland *et al.* 1993). There are also some examples from terrestrial ecosystems: flowering phenology and reproductive traits in some plant species (Schmitt 1983; Galen & Stanton 1991), the population dynamics of moose and white-tailed deer (Post & Stenseth 1999) and red deer (Forchhammer *et al.* 1998), breeding biology of migratory birds in the UK (Forchhammer *et al.* 1998) and sexual dimorphism in red deer (Post *et al.* 1999).

Our above list of references is by no means exhaustive; it is just to indicate that the hunt for statistical associations between population data and climatic fluctuations is intensive. Contrary to the empirical search for statistical

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signs of association between population data and external fluctuations we will tread a different path. We have selected an approach whereby both the dynamics of the focal population as well as the external modulating signal are known. The task is straightforward. Using basic time-series tools we will seek to determine whether the modulated population data and the modulating signal are associated in any way. In order to accomplish this, we shall make use of a variety of renewal models accounting for the skeleton of the long-term dynamics of populations. The external process modulating the dynamics was split into low-frequency (occurring at irregular intervals) and high-frequency components (occurring annually). These two components together comprise the noise modulating the skeleton dynamics of populations.

2. POPULATION RENEWAL AND ENVIRONMENTAL FORCING

In our approach, we obtain the skeleton of the population dynamics, which the noise modulates. In order to achieve this, we denote the population size (X_{t+1}) at time $t+1$ as a function of its former size, which is affected by the high-frequency (H) and low-frequency (L) components of the noise:

$$X_{t+1} = f(X_t, \ldots H_t, \ldots L_t, \ldots). \tag{1}$$

The notation ... refers to the possible existence of longer than first-order time-lags. For practical convenience we let the modulating noise be $M_t = H_t L_t$. Thus, we are seeking $\rho(X_{t+1}, M_{t,\ldots})$ by using the cross-correlation technique with various time-lags (e.g. Box *et al.* 1994).

In order to obtain the low-frequency component of the noise we need two parameters, i.e. the probability of occurrence (p), which is drawn from uniform random numbers ($0 < p = 1$), and its intensity μ_t; thus, we have (e.g. Ranta *et al.* 1997)

$$\mu_t = \begin{cases} \hat{\mu} \text{ if } p(t) < \bar{p}, & 0 \leqslant \bar{p} \leqslant 1 \\ 1 \text{ otherwise} \end{cases}. \tag{2}$$

Here, $\hat{\mu}$ is drawn from uniform random numbers ranging from $1 - w_G$ to $1 + w_G$, where $0 < w < 1$. The high-frequency component is likewise drawn from uniform random numbers ranging from $1 - w_L$ to $1 + w_L$; here also $0 < w < 1$. Thus, $\bar{L} = 1$, $\bar{H} = 1$ and $\bar{M} = 1$. With high-frequency noise $\bar{p}_H$ was always unity, whereas with low-frequency noise $\bar{p}_L$ varied (below).

In order to implement the population renewal process into equation (1) we decided to use two different models. This was to ensure that the results obtained were general enough and not just anomalies of any particular class of population models. We selected the Ricker model as it yields dynamics characterized by the single parameter r, the population growth rate. In addition, the behaviour of Ricker dynamics is well understood (May 1981). As a second model for a surrogate of population dynamics we used second-order autoregressive processes [AR(2)]. It is known that AR(2) models display a rich ensemble of dynamic behaviour, from stable dynamics via cyclic dynamics to more complex dynamics (Royama 1992; Box *et al.* 1994). Thus, for the $f(X_{t,\ldots})$ term we have the following two equations for Ricker and AR(2) dynamics, respectively:

$$X_{t+1} = X_t \exp[r(1 - X_t)], \tag{3}$$

and

$$X_{t+1} = \varphi_1 X_t + \varphi_2 X_{t-1} + \delta + \varepsilon_t. \tag{4}$$

The parameter r in equation (3) is the growth rate (here $1 \leqslant r \leqslant 3.5$) (figure 1*a*) and the two autoregressive parameters in equation (4) were taken to be $-2 < \varphi_1 < 2$ and $-1 < \varphi_2 < 1$. The term ε is normally distributed with mean 0 and variance 1. For the AR(2) process to hold, the following two additional conditions have to be met (e.g. Box *et al.* 1994): $\varphi_2 + \varphi_1 < 1$ and $\varphi_2 - \varphi_1 < 1$. In order to implement the noise M and modulate the dynamics of the populations we write equations (3) and (4) as

$$X_{t+1} = f(X_t, X_{t-1}) \times M_t, \tag{5}$$

(the delayed density dependence on X_{t-1} is for the AR(2) process only). The long-term mean of the noise is 1.0, while its range greatly depends on the w_L and w_H parameters of the low- and high-frequency components.

We used the growth rate r as the bifurcation parameter for the Ricker model and applied all feasible combinations of φ_1 and φ_2 for the AR(2) model. The simulations were initiated by drawing a random number from a uniform distribution between 0.1 and 0.5 for $X(1)$ and, in the case of the AR(2) model, for $X(2)$ as well. Altogether 100 time-units were allowed to elapse in order to remove the transient phase. The next 500 time-units were used to score $\rho(X_t, M_{t-1})$ using the cross-correlation coefficient. We shall report the results of 100 replicated runs for each parameter combination.

There is obviously an unlimited choice of values of $\bar{p}_L$, $\bar{p}_H$, w_L and w_H for the noise M. We decided upon the following. We set $\bar{p}_L = 0.2$, $w_L = 0.5$ and $w_H = 0.2$ for the basic explorations. Based on the results obtained we selected a few examples of differing population dynamics and made a more thorough search while allowing $\bar{p}_L$ to assume values of 0.5 and 0.1 while both w_L and w_H ranged from 0.05 to 0.9. For this exercise we set r to 1.85, 2.6 and 3.0 for the Ricker equation, while the AR(2) coefficients φ_1 and φ_2 were taken to be (i) 0 and 0.25, (ii) -1.25 and -0.75, and (iii) 1.25 and -0.75.

Finally, we took the noise-modulated population data and estimated the model parameter values for the Ricker dynamics, which were generated using $r = 1.85$, 2.6 and 3.0. We decided to restrict ourselves to the Ricker dynamics as the growth rate had such readily interpretable implications (figure 1*a*). Again, in order to reduce the number of combinations $\bar{p}_L$ was set to 0.5, while the amplitudes for both the low- and high-frequency disturbances were drawn from a uniform distribution ranging from 0.05 to 0.9. Here, we let the length of the sampled time-series vary from 20 to 500 time-units. We found a reason for this final task as little is known about the characters of the modulating external noise affecting natural populations. In addition, the extant time-series from real populations are frequently rather short.

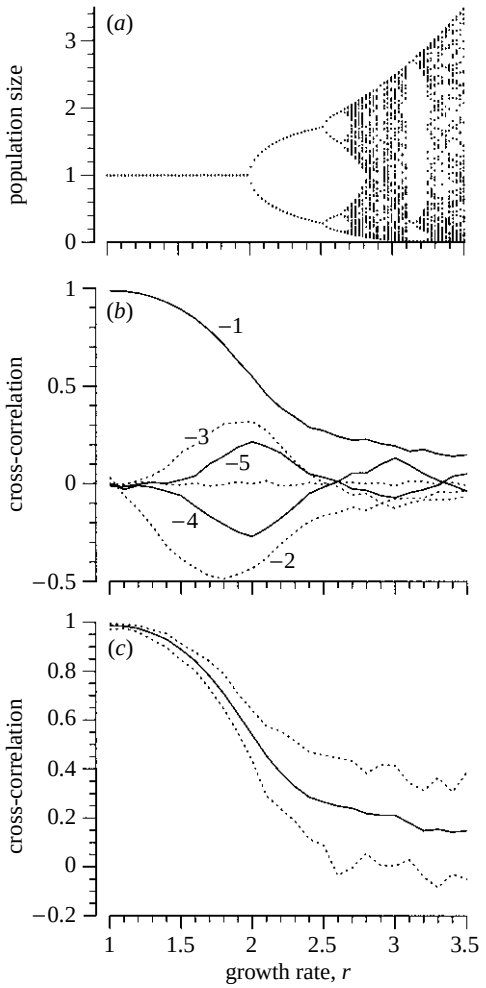

Figure 1. (*a*) Bifurcation diagram for the Ricker dynamics. (*b*) Cross-correlation (means of 100 replicated runs) with the Ricker dynamics and the noise; lags from 0 to −5 time-steps are shown separately. (*c*) Cross-correlations with lag −1 for the Ricker dynamics and the external noise. The solid line indicates the average over 100 replicated runs and the dotted lines include 95% of all observed correlation coefficients. The *x*-axis in all panels is the growth rate (*r*) of the Ricker equation.

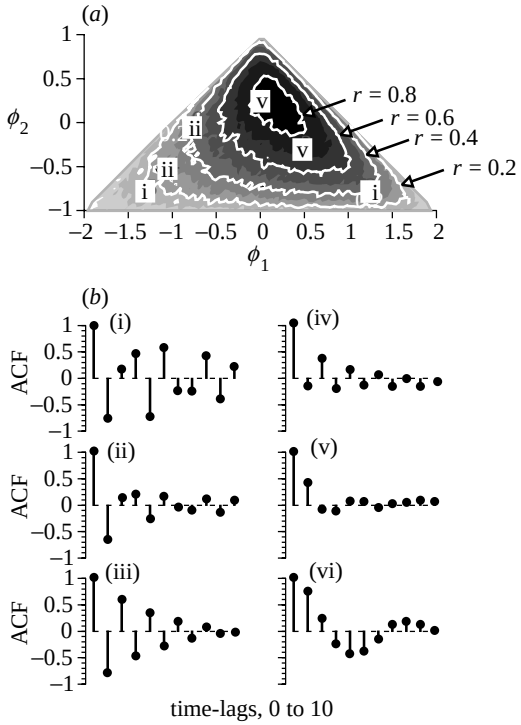

Figure 2. (*a*) Cross-correlations (with lag −1) for the AR(2) dynamics graphed against the feasible values of the parameters φ_1 and φ_2. The darker the shading the higher the cross-correlation coefficient between the dynamics and the modulating noise (means of 100 replicated runs). The white contours indicate cross-correlations of $r_{-1}=0.2$, 0.4, 0.6 and 0.8. The numbers (i)–(vi) indicate selected dynamics with φ_1 and φ_2 values. (*b*) Graphed corresponding autocorrelation functions with time-lags from 0 to 10. The parameter values used for φ_1 and φ_2 are (i) −1.25 and −0.75, (ii) −1 and −0.5, (iii) −0.75 and 0, (iv) 0 and 0.25, (v) 0.5 and −0.25 and (vi) 1.25 and −0.75.

3. RESULTS

Our results appear rather straightforward. In our exploration, we first set the probability of occurrence of the low-frequency noise to $\bar{p}_L=0.2$ and the two amplitude parameters to $w_L=0.5$ and $w_H=0.2$. With the Ricker dynamics, the highest correlations between the modulated dynamics and the noise modulating the population dynamics are, understandably, achieved with a lag of −1. With increasing lag the cross-correlation coefficients decay rapidly (figure 1*b*); this finding is also true for the AR(2) dynamics. However, a far more interesting observation is that the highest correlations are associated with stable dynamics. Once the Ricker dynamics approach two-point periodicity the correlation rapidly goes down (figure 1). Low correlation coefficients are found between the modulated population dynamics and the noise in the region of complex dynamics, while rather high correlations of up to *ca.* $r_{-1}=0.4$ can occasionally be encountered in this region of the Ricker dynamics. However, small negative correlations are also just as likely (figure 1*c*).

The analysis of the AR(2) dynamics echoed the main result of the Ricker dynamics. High correlations were achievable in the region of simple dynamics (labelled (iv) and (v) in figure 2*a*), but, contrary to this, with φ_1 and φ_2 from the region of the parameter space yielding more complex dynamics, the maximum achievable cross-correlations were low, much less than 0.4 (figure 2).

The exploration with the Ricker and AR(2) dynamics with the parameter values selected (figure 3) and more versatile noise characterization confirmed what we found with the limited exploration. High correlations with the modulated population dynamics and modulating noise are only found when the dynamics are stable or nearly stable (figure 3*a*,*d*). Once the dynamics become periodic or more complex, high cross-correlations disappear (figure 3*b*,*c*,*e*,*f*). The probability ($\bar{p}_L$) of the occurrence of the low-frequency noise appears not to play such an important role in the emerging pattern of cross-correlations provided it is high enough (figure 3). However, once the low-frequency component is present (we experimented with $\bar{p}_L$ ranging from 0.5 to 0.05) slightly higher cross-correlations are usually obtained, particularly in the low-range values of the parameters w_L and w_H. In fact, analyses of the extant time-series of the NAO and ENSO have revealed the presence of low-frequency components in the noise signal (e.g. Hurrell 1995; Trenberth & Hoar 1996).

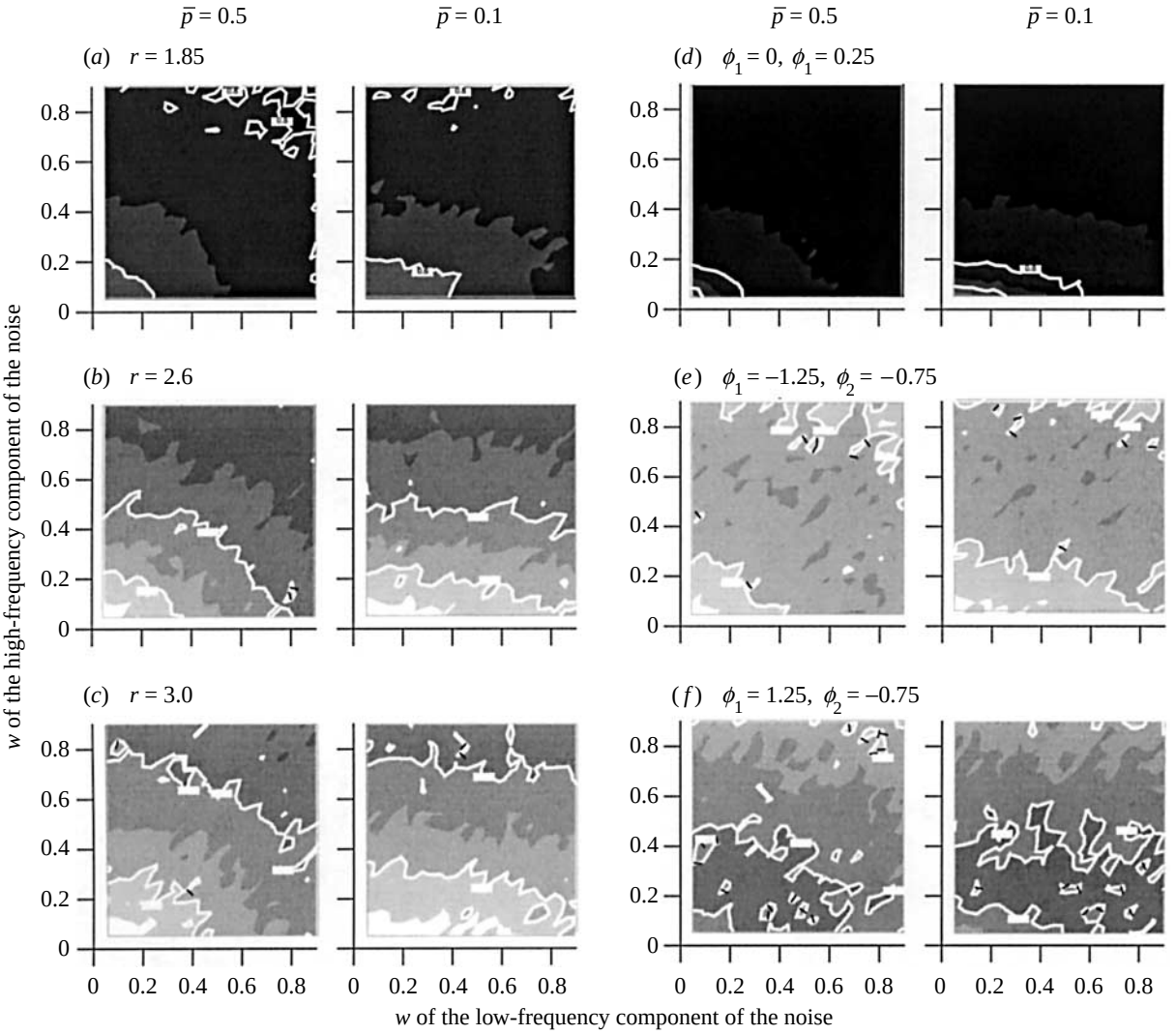

Figure 3. Cross-correlation (lag −1) contour graphs (with the population dynamics and the noise) for (*a–c*) the Ricker dynamics and (*d*,*e*) the AR(2) dynamics against the amplitude component (*w*) of the low- (*x*-axis) and high-frequency (*y*-axis) components of the noise. The parameter values used are indicated. The darker the shading, the higher the cross-correlation (means of 100 replicated runs). The white isoclines are drawn at 0.2 intervals, e.g. in (*a*) the lower one near the origin is the 0.6 correlation and the islets of the upper corner indicate correlations of 0.8 or higher.

The conclusions of our explorations are unambiguous. Noise-disturbed population dynamics and the disturbing noise correlate with a lag of −1, but the correlation wanes once the population dynamics become periodic or more complex. In this region high cross-correlations are occasionally achievable but only when the noise impact is strong. However, with heavy noise reconstructing the skeleton of the population dynamics becomes more difficult. This was exemplified by our attempt to reconstruct the value of parameter *r* in the Ricker dynamics. With noise modulating the dynamics the fitted parameter tends to err. Not surprisingly, the shorter the available time-series, the larger the error range (figure 4). For example, when initially $r = 2.6$ (four-point periodicity) the fitted values based on the noisy dynamics can range from stable dynamics to chaotic dynamics (figure 4*b*). Alternatively, $r = 1.85$ (stable dynamics) can yield an impression of periodic dynamics when modulated with the external noise or, when $r = 3.0$ (complex dynamics), the parameter fitting can result in either periodic or complex dynamics (figure 4*c*).

4. DISCUSSION

We studied whether data on variable population dynamics can be correlated to environmental time-series, which were interpreted here as external noise signals affecting the quality of population dynamics. While acknowledging the number of studies attempting to correlate population dynamics to environmental changes, the current null expectation seems to be that the environment acts as a driving force in population dynamics, even such that its qualitative properties are qualitatively transported to these dynamics. According to our major findings, a correlation with a time-lag of −1 may be observed between noise-disturbed population dynamics and the disturbing noise when the population growth rate is low. However, the correlation disappears rapidly with increasing growth rate, indicating that complex dynamics tend to mask the effects of environmental noise on population dynamics.

Our results appear to be highly relevant when assessing the strength of climatic forces in population dynamics

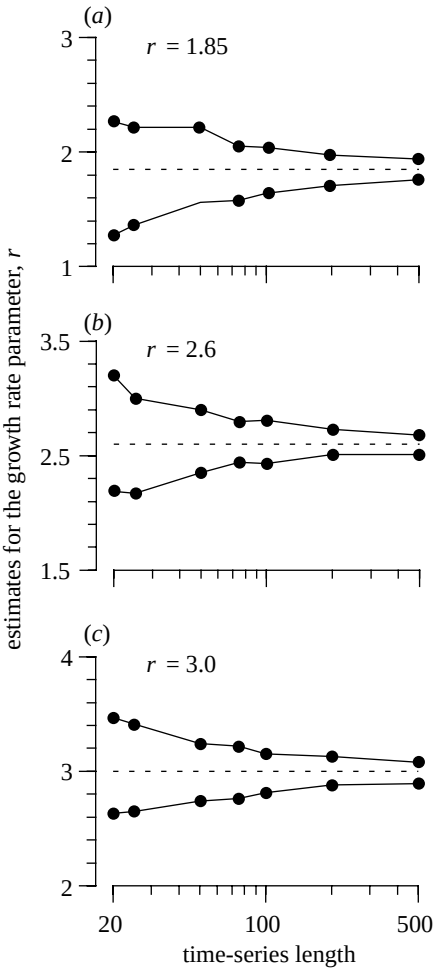

Figure 4. Parameter fit for the skeleton of the Ricker dynamics in a noisy world graphed against the length of the sampled time-series. For implementing of the noise, see the text. The range limited by the solid lines with dots includes 95% of all fitted values. For this kind of dynamics these values result in the Ricker dynamics referred to in figure 1*a*. The expected parameter value is inserted and indicated with the broken line.

because species differ widely in their growth rates. Consequently, we may suggest that slowly growing species such as mammals (Leirs *et al.* 1997; Post *et al.* 1997; Grenfell *et al.* 1998; Lima *et al.* 1999), fish (Friedland *et al.* 1993; Dippner 1997) and birds (Forchhammer *et al.* 1998) are likely to respond to climatic variability in a straightforward way, whereas rapidly multiplying organisms, usually small-bodied invertebrates and micro-organisms, should predominantly show weaker correlations with environmental forces (but see Fromentin & Planque 1996; Kröncke *et al.* 1998; Reid *et al.* 1998; Tunberg & Nelson 1998; Belgrano *et al.* 1999). However, it is possible that many rapidly multiplying organisms may have a relatively weak ability for buffering environmental changes due to, for example, a shorter life span, smaller body size and limited control of movement. Moreover, indirect climatic forces mediated by other species in the food web can also blur the effect of the growth rate (Ives & Jansen 1998; Ripa *et al.* 1998).

A further finding is that increasing the strength of the noise signal strengthens the correlation between population dynamics and noise. However, once external noise and population dynamics appear to correlate well due to the strong amplitude of external forces, the underlying dynamics are modulated by the noise such that the skeleton of the population dynamics is weakly recognizable. Consequently, the intrinsic growth rate and the level of external noise control the driving forces jointly in population dynamics. Thus, we suggest that studies may result in biased conclusions about the relative roles of the density-dependent and -independent causes of population fluctuations, even when a correct model is used in analysing the data.

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