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Coupling between Physical and Biological Scales [and Discussion]

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Coupling between physical and biological scales

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SUMMARY

Temporal changes in population abundance display a great diversity of patterns. This diversity is acknowledged by reviewers of marine and terrestrial data, but their explanations tend to fall into two categories: internal factors related to population or community structure; and external aspects determined by the environment. The former we associate with terrestrial studies and the latter with marine.

In this paper we shall stress the importance of the characteristic timescales in the dynamics of the populations and their relation to the scales of relevant environmental forces. We shall suggest that the coupling between these different scales, rather than the nature of the internal or external processes themselves, can provide a partial description, if not an explanation, of the diversity of patterns.

1. ECOLOGICAL PATTERNS

Connell & Sousa (1983) stated that, 'long-term studies [of predominantly terrestrial populations] reveal a continuum of temporal variability with no clear demarcation between assemblages that may exist in an equilibrium state and those that do not'. Evidence for multiple steady states was considered inapplicable when 'the physical environment is different in the alternate states'.

Caddy & Gulland (1983), reviewing fish stock variability, said, 'an examination of landing trends reveals four basic patterns: steady, cyclic, irregular and spasmodic. It is not claimed that the boundaries between these groups are exact'. Further, 'the causes of variation fall under two heads; fluctuations in the marine environment and variations in fishing intensity'.

Thus marine and terrestrial systems show a bewildering variety of temporal patterns, but explanations for these patterns are quite different in the two sectors. The marine view would be that relatively large-scale processes, such as El Niño, are the significant factors in population variability (apart from human harvesting). Community dynamics are assumed to smooth out the effects of fluctuations in the environment. Technically, for fish populations, this is done by a formal stock–recruit relation (Rothschild 1986) which assumes density-dependence in the larval or juvenile stages where we usually have negligible data.

Terrestrial concepts normally emphasize the importance of density dependence through detailed consideration of prey–predator or competitive–community interactions. Environmental perturbations will not be 'scrutinized in nearly as much detail as the effects of strictly biological interactions' (Connell & Sousa 1983). The search for explicit evidence for density dependence derives predominantly from the terrestrial literature (e.g. Hassell *et al.* 1989; Den Boer 1991). Theoretically, a great variety of patterns can be obtained from time delay population models of the form

$$N_t = F(N_{t-1},\ N_{t-1},\ \ldots,\ \varepsilon_t),$$

where ε_t is white noise (Turchin & Taylor 1992). These forms include first- and higher-order stochastic equations which are used to simulate ocean processes, and we shall show that the responses are similar.

This brief review indicates that in both sectors, land and sea, the interaction between physical and biological processes is considered. But the comparison also demonstrates that there is a significant difference in emphasis, with a focus on internal mechanisms in terrestrial studies and on external physical forcing for marine populations.

2. TEMPORAL VARIABILITY AS A FUNCTION OF SCALE

These differing explanations can be justified (Steele 1991) by the overlap in the space- and timescales of ocean physics and biology, compared with the separation between these scales in most atmospheric and terrestrial systems (figure 1). The separation between oceanic and atmospheric physics in figure 1 is a consequence of their differing densities and viscosities. The separation in the ecosystem scales may depend in part on these same physical factors; for example, through the effects of gravity. But the different scales of variability of the physical processes in the oceans and the atmosphere can be regarded as the critical factor (Steele 1991). We shall focus on the divergence

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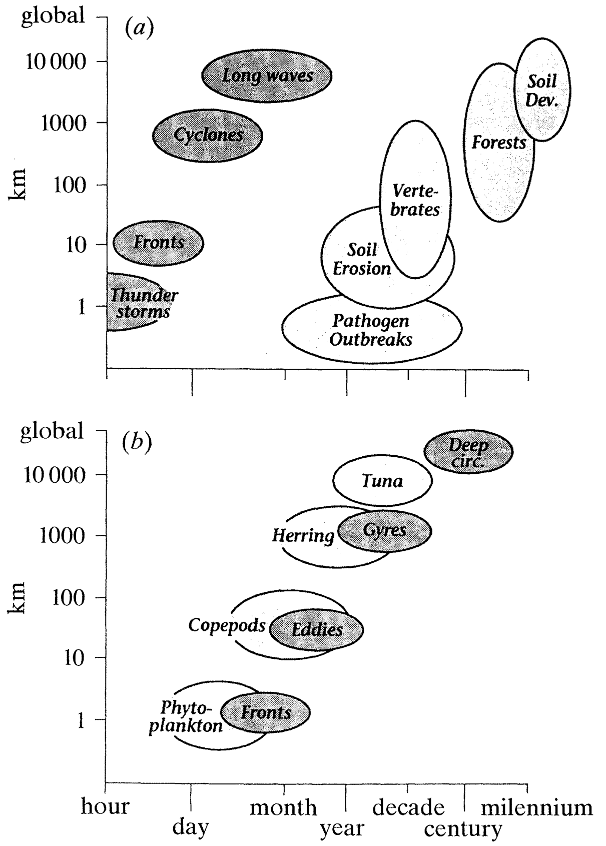

Figure 1. Space- and timescales for (*a*) atmospheric processes and terrestrial groups, demonstrating their marked separation in timescale, and (*b*) similar scales for ocean physics and for major groups in pelagic ecosystems (adapted from Steele 1991).

in the temporal scales and particularly the amplitudes of the variability at different timescales.

The moderating effect of the oceans on climate is obvious and operates through the large capacity of the oceans to store heat. Thus the high frequency variance of the ocean is much less than that of the atmosphere. Conversely, at long timescales the ocean dominates the heat exchanges.

This effect can be simulated by a first-order stochastic equation for upper ocean temperature, T, as a function of time, t (Hasselmann 1976).

$$T_t - T_0 = \alpha[T_{(t-1)} - T_0] + \beta\varepsilon_t, \qquad (1)$$

where T_0 is the initial value, ε_t is white noise with unit variance, $0 < \alpha < 1$, and $\beta > 0$. $\alpha = 0$ gives white noise; $\alpha = 1$ generates an unbounded random walk, i.e. red noise; $0 < \alpha < 1$ has bounded variance as t approaches infinity. This equation has been used by Hasselmann and others to represent the transformation of white noise atmospheric variance to the longer timescales of ocean variability. The parameter

$$\lambda = 1/(1-\alpha),$$

can be regarded as the timescale at which the components of the ocean system go from red to white noise (figure 2) with increasing period (decreasing frequency).

For the upper layers of the ocean (above the seasonal thermocline), $\lambda = 4$ to 6 months (Davis 1976).

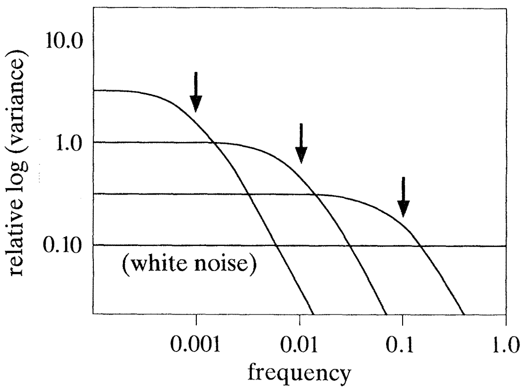

Figure 2. Theoretical power spectra for first order stochastic processes (equation (1) in text) with $\lambda = 0.001$, 0. 01, 0.1 and 1.0 (white noise).

For the non-seasonal component, a value of 4 to 8 years has been used in climate models (Wigley & Raper 1990). The longest timescales, associated with the deep thermohaline circulation, can be of the order of centuries to millenia (Broecker 1991). Beyond these longer scales the land–sea–air becomes a single system with a reddened spectrum (Imbrie 1985). Lemke (1977) proposed that the overall response of the ocean could be represented by a cumulative set of power spectra of the type illustrated in figure 2. The longest available deep ocean temperature record, from the Sargasso Sea, supports this concept to periods over a decade (Wunsch 1981).

Combining the general spectral forms for ocean and atmosphere (excluding the regular, annual, lunar, and diurnal cycles) leads to a schematic joint representation (figure 3). These spectra are derived from temperature data, and temperature is a significant variable for ecological processes. However, it is only one among several physical factors that will affect population or community dynamics. Rainfall and wind are terrestrial examples. In the upper layers of the ocean, where horizontal and vertical water movements may be more important, it is unusual to have long data sets for relevant physical variables that can be used explicitly in ecological contexts. Thus the general nature of the variance relations in figure 3 is used as an index for those physical processes that have an unpredictable, or stochastic, effect on marine or terrestrial populations.

3. A SIMPLE ILLUSTRATION

The essential features in figure 3 are: (i) the plant populations of the open sea (phytoplankton) are the shortest-lived members of their food web, whereas most terrestrial plants (trees and perennial grasses) are the longest-lived components; and (ii) terrestrial populations exist in a white noise atmosphere, whereas marine populations are embedded in a red noise environment.

To illustrate the significance of these interacting scales, a simple prey–predator model is forced by first-order stochastic functions (equation 1) with different response times, λ, but with total variance kept con-

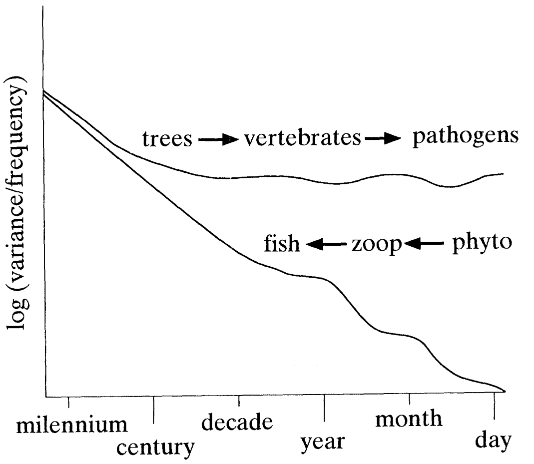

Figure 3. Schematic presentations of the power spectra for atmospheric and oceanic temperature (omitting regular cycles) with examples of timescales of particular food chains.

stant. The model is documented in the Appendix. Its main feature is that it has a Hopf bifurcation giving two stable equilibrium solutions. The parameter values are chosen so that the initial values of prey (X) and predator (Y) lie between the two stable states.

Predator and prey growth rates are taken to be equal and an order of magnitude lower ($a=f=0.1$) than the timescale. This timescale is, for the moment, arbitrary, as the purpose is to look at the effects of different internal and external rates.

The stochastic input is applied to the mortality rate of the predator. The four cases illustrated in figure 4 are for white noise ($\lambda=1$) followed by gradually reddened forcing, $\lambda=0.1$, 0.01, 0.001 (see figure 2). Figure 4*a*, with white noise, shows that a considerable time may elapse before the system ends up in one of the stable equilibria. Thus large changes can occur without contemporaneous forcing. Figure 4*b*, where the forcing has the same timescale as population growth, has the most 'irregular' or 'spasmodic' response. In particular, there are no obvious relations between the prey population and the predators or the forcing function. Figure 4*d* begins to show quasi-cyclic features, and figure 4*c* is intermediate. When external stochastic forcing is applied at the primary trophic level the same general trend in pattern is found: from relatively constant through highly irregular to quasi-cyclic.

The responses to different scales of forcing in figure 4 are qualitatively very different. Thus the same simple ecological model can elicit nearly the whole range of patterns observed in time series such as figure 1; but only when the model is placed in the context of different types and scales of environmental variability.

There is one further inference from this exercise. The simplest responses, relatively constant or quasi-cyclic patterns, occur when there is considerable separation between the growth rates and the variance scales. This corresponds to the mathematical technique of simplifying a system into fast and slow variables, and so the model might be describing the consequences of a mathematical rather than an eco-

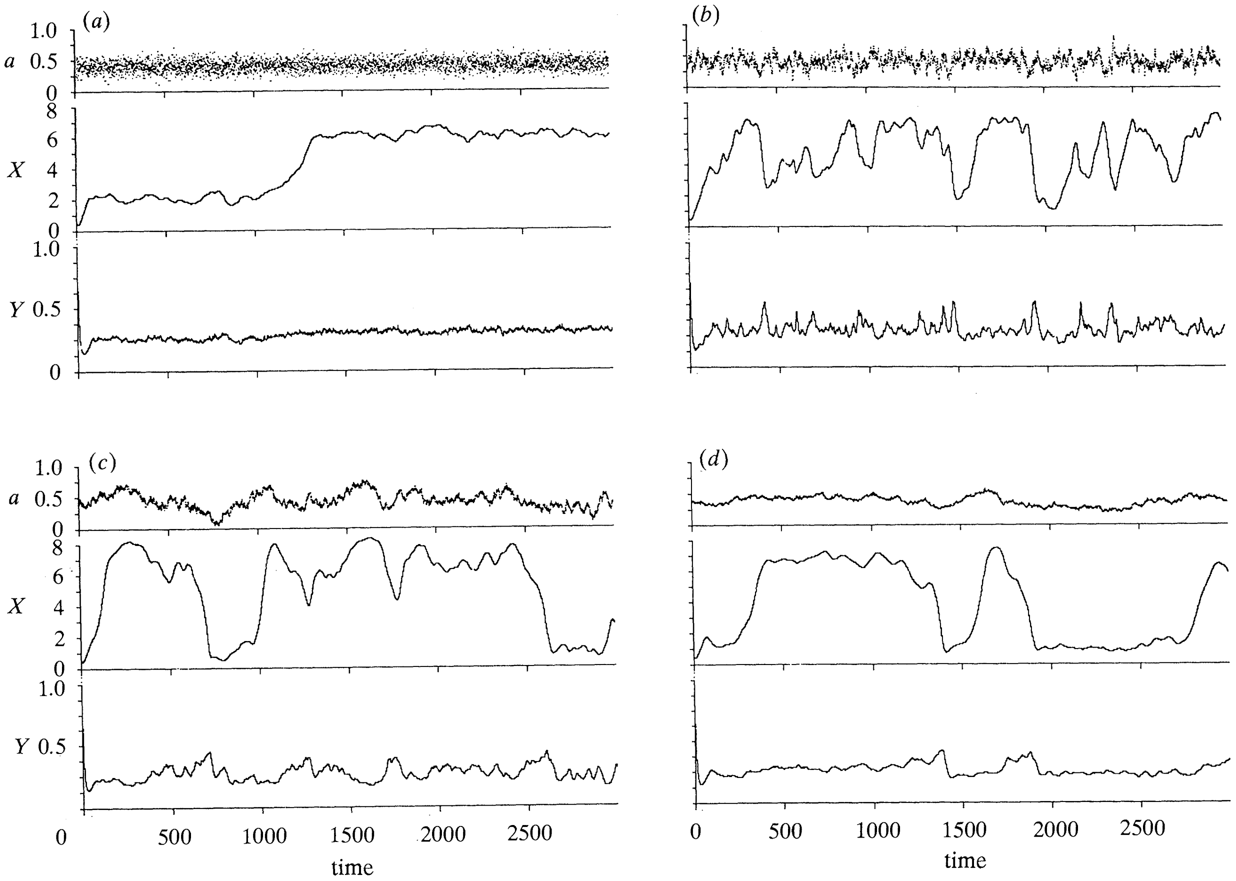

Figure 4. Solutions to a prey (X) and predator (Y) model (see Appendix) When the mortality rate (d) is varied stochastically with timescales of (a) 1.0; (b) 0.1; (c) 0.01; and (d) 0.001.

logical separation of scales. However, this simple example does lend support to the concept that the terrestrial system has evolved a long-lived system of primary production as a response to high frequency variance, whereas the open sea has its longest-lived organisms at the highest trophic levels.

The observed patterns in marine and in terrestrial data (Caddy & Gulland 1983; Connell & Sousa 1983; Turchin & Taylor 1992) do not generally conform to the end points of the white–red illustrations in figure 4. Nor does the real world correspond to a simple model with external forcing of only one parameter. Marine fish populations will respond to physical forcing, but they are also subject to human interventions that certainly are not simply white noise. We are now concerned that climate change can have impacts at scales less than centuries, so that the white noise paradigm for the atmosphere may no longer be useful.

The argument here would be that such external changes will result in qualitative alterations in the patterns of responses rather than just moving the mean values. In particular, changes in the frequency of 'jumps' in abundance may be a characteristic response to changes in forcing (Steele 1985).

4. CONCLUSIONS

A general perception is that a purely inductive approach is not usually a practicable way to get from pattern to process. The alternative is to combine population models with experimental studies of processes at the individual level (e.g. the feeding functions of Holling (1965)). However, there is no necessary one-to-one relation between a modelled process and an observed pattern. The same mathematical formulation can often be derived from different ecological processes, giving an apparent generality to a model such as the one used here.

Previous work assumes that complexity in ecological time series arises from the internal ecological dynamics; either from higher-order community interactions or from time lags in discrete population models (e.g. May 1976; Turchin & Taylor 1992). This conclusion is forced by the premise that variability imposed by the rest of the world, physical or biotic, can be represented as white noise. External forcing of a simple model by first-order stochastic processes can generate the same apparent diversity observed in the data. This diversity is dependent on the relative timescales of forcing and response.

The external forcing is specified only by its location within the model. By implication, forcing applied to the growth rate of the prey or plant, X, on the lower trophic level might be primarily physical. Conversely, stochastic forcing of the mortality rate for the predator, Y, could be considered a closure term representing higher trophic categories. But forcing at either position can be a consequence of either physical or biological variability. Further, both types of forcing can be white or reddened (Williamson 1987; Pimm & Redfearn 1988). In both marine and terrestrial systems, it is the longer timescale changes, or infrequent events, that are considered important. The accepted sources of these random variations have been physical for marine systems and biological for terrestrial ones. This may be appropriate for the intermediate timescales in each system, but it becomes seriously inadequate as we concern ourselves with changes at decadal to century scales, or longer.

The marine focus has been on single populations whose variability is put in a black box labelled 'recruitment dynamics'. This is being replaced by multi-species models in fisheries, where the stock–recruit relation is recognized as a community attribute. Similarly, the terrestrial view was that changes in forest patterns were affected by climate changes on timescales of millenia (Delcourt *et al.* 1983). Now we recognize El Niño as a continental factor and speculate on consequences of climatic change at decadal timescales.

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APPENDIX

A prey–predator, or plant–herbivore, relation can be put in the following form:

$$\mathrm{d}X/\mathrm{d}t = aX(1-X/c) - YX^2/(1+X^2), \quad \text{(A1)}$$

$$\mathrm{d}Y/\mathrm{d}t = fY(X2/(1+X2) - dY/a), \quad \text{(A2)}$$

where the variables X, Y have been normlized to make the two parameters in the last term of (A1) unity. Then: a = maximum growth rate of X; c = carrying capacity of X; f = maximum growth rate of Y.

The term d/a in (A2) plays the role of carrying capacity in the logistic form for Y. The s-shaped form for grazing is used, as this implies the existence of other grazers (Holling 1965). Also, these equations have a Hopf bifurcation for a sufficiently large value of c. The particular form for the parameters was chosen because solutions in the triple valued region are determined solely by choice of d. In the examples in the text (figure 4), $c=10$ and $d=0.4$.

The stochastic forcing is introduced as an additive term on the growth rate, a, and the mortality term, d.

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Discussion

M. Mangel (*Section of Evolution and Ecology, University of California, U.S.A.*). I wish to note a point and then raise a question. In the 1960s and 1970s, a number of applied mathematicians worked on the connection between differential equations driven by white noise and those by coloured noise (e.g. Papanicolaou & Kohler 1974). The general result is that a white noise limit of a red noise equation can be derived, with modification of the deterministic drift terms. There is thus a 'feedback' of the noise into the deterministic part of the system. I wonder if part of the message of Dr Steele's talk is that time series analysis, which is most effective for the study of linear systems, is somewhat limited when considering systems in which state is important, and that we should be focusing on new methods. For example, even the simple nonlinear logistic map $N(t+1)=rN(t)(1-N(t))$, which shows chaotic behaviour in the time series if r is sufficiently large, shows regular behaviour if we plot $N(t)$ versus $N(t-1)$, rather than $N(t)$ versus t.

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J. H. Steele. I would point out that the continuous form of the logistic relation is well behaved. Thus the ecological question is whether a discrete or continuous formulation best represent the biological processes.

C. Clark (*Department of Mathematics, University of British Columbia, Canada*). Dr Steele's marine time-series data consisted entirely of commercial catch data for various fisheries. Yet the only model that he presented for generating simulated time series contained only coupled biological and physical components. Clearly fisheries data involve significant anthropomorphic components, affected by complex economic systems. To what extent does he think that this component can be ignored in attempting to understand the dynamics of marine ecosystems?

J. H. Steele. I agree that human predation is a major factor in fish population dynamics. I would argue that this component could not be considered as 'white noise'. The outcome of the complex economic system that you refer to is likely to contain multi-year trends. Thus the forcing function would be closer to the red noise illustrated in figure 4.