Fluctuations
Variability
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Amplification of environmental fluctuations by marine ecosystems

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ABSTRACT

Environmental variability is an important cause of fluctuations in marine ecosystems. In order to assess the contribution of a particular environmental signal we need to know not only how strongly it is coupled to the biological components, but also how responsive the ecosystem is to fluctuations on that time scale. Some ecosystems appear to have characteristic resonant frequencies, and even a weak environmental signal at one of these frequencies can cause large changes in population sizes. It is already known that some commercial fish stocks undergo abundance cycles which can be explained in this way, since models of their population dynamics exhibit resonances at or near the appropriate frequencies, and in this paper it is shown that resonance is found in Lotka-Volterra models of predator-prey systems. Thus resonance appears to be a likely cause of many of the fluctuations found in marine ecosystems.

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RÉSUMÉ

L'amplification de fluctuations de l'environnement dans les écosystèmes marins

La variabilité de l'environnement est une cause importante de fluctuations dans les écosystèmes marins. Pour mieux comprendre l'importance d'un facteur particulier de l'environnement, il faut connaître non seulement son importance par rapport aux composants biologiques, mais aussi la vitesse avec laquelle l'écosystème réagit. Quelques écosystèmes semblent avoir des fréquences de résonance caractéristiques, et même une légère perturbation de l'environnement à l'une de ces fréquences peut causer d'importants changements dans le développement des populations. On sait que quelques stocks de poissons commercialisables changent périodiquement, ce qui peut être expliqué par cette hypothèse, puisque les modèles de leur dynamique de populations montrent des résonances aux périodes voisines. Ce travail montre qu'il existe une résonance dans les modèles de Lotka-Volterra des systèmes prédateur-proie. Ainsi la résonance semble être une cause probable de beaucoup de fluctuations dans les écosystèmes marins.

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INTRODUCTION

There are many possible ways in which fluctuations can arise in ecosystems. They may be intrinsic in the dynamics of the populations, as in the case of systems which behave like Lotka-Volterra predator-prey models. Alternatively they may be induced by external factors such as changes in temperature. In many cases it appears that the best explanation is a combination of the two; external factors drive the fluctuations, but their magnitude is determined by the ability of the system to respond to oscillations of different frequency. The analysis of

such cases depends on how sensitive the magnitude of the fluctuation is to frequency; if the frequency dependence is weak, then the externally driven nature of the fluctuations can be identified by relatively straightforward statistical methods, such as lagged correlation analysis. However, if the response of the system is strongly frequency-dependent then a driving force at the appropriate frequency may have a much larger effect than equally strong forcing effects at other frequencies. This can occur if the system has one or more resonant frequencies, but it is difficult to identify resonant behaviour from a limited set of data without a good understanding of the dynamics of the system. Since not all kinds of ecosystem models lead to resonant behaviour, this paper deals with understanding the situations under which resonances can occur and identifying cases in which they are likely to be an important factor in the fluctuations of marine ecosystems.

CONDITIONS FOR RESONANCE

Resonance is a familiar phenomenon in physics and engineering, where it is associated with second-order differential equations such as that for the damped driven harmonic oscillator

$$mX'' = -kX - qX' + f(t), \qquad (1)$$

where X'' and X' refer to the second and first time derivatives of X and f(t) is a forcing function (m, k, and q are constants). For small values of q this system has a pronounced resonance in the vicinity of $2\pi(k/m)^{1/2}$, and for periodic forcing functions with frequencies close to this value the system variable X oscillates at the same frequency with a large amplitude. Since the system is linear, the effects of different periodic components of the forcing function are additive and thus the system is effectively capable of picking out those frequency components which are close to resonance and responding only to those. This is the way a radio receiver works; from the entire frequency spectrum of electromagnetic waves it selects and amplifies only those frequencies to which it is tuned. The larger the value of q, the wider the range of frequencies to which the system responds and the less pronounced the response.

A single first-order differential equation like those widely used in population biology does not exhibit resonance and the amplitude of the response decreases continuously as the frequency is increased. This is probably why the possibility of resonance has generally been ignored by population biologists and ecologists. However, once one has a system of two or more first-order differential equations it becomes possible to generate resonant behaviour. The reasons for this are fairly mathematical but can be illustrated by reference to equation (1); define $V = X'$ and replace X'' by V' so that the single second-order equation can be rewritten as two completely equivalent first-order equations

$$V' = -kX - qV + f(t) \qquad (2\,a)$$

and

$$X' = V, \qquad (2\,b)$$

which exhibit the same resonant behaviour. Thus the equation for the damped harmonic oscillator is mathematically equivalent to a model of a type common in ecology, and I will show in a following section that equations (2) correspond to the usual Lotka-Volterra model for a predator-prey system.

In general one can find resonant behaviour in any system of two or more first-order differential equations, although it may not always be present or, if present, may be too heavily damped to be observed. Since it does not occur with single equations, it should be viewed as a systemic property of communities arising out of their mutual interactions. It can also occur in age-structured population models when coupling exists between different age classes (*e.g.*, cannibalism).

A similar situation holds for discrete models. First-order finite difference equations, such as the stock-recruitment models widely used in fisheries, do not exhibit resonance. However, systems of coupled difference equations (community models) can often lead to resonance, as can higher-order models such as

$$x_{t+1} = ax_t + R(x_{t-N}), \qquad (3)$$

which describes a stock with survivors from the previous season plus recruits from N seasons earlier (Silvert, Smith, 1981).

RECOGNIZING RESONANCE IN ECOSYSTEM MODELS

The theory of resonance is basically a linear theory, while most ecosystem models are nonlinear. This means that while we can use linearized theories to study the occurence of resonance, prediction of the magnitude of resonant effects requires that we go back to the original nonlinear theory. Actually, the same situation is found in physics. Most mechanical oscillators, such as water waves and pendula and springs, are nonlinear. The theory of the linear harmonic oscillator has proved quite useful in predicting the frequencies at which large oscillations are likely to occur, but it is absolutely useless when it comes to calculating when a wave or a spring will break, when a pendulum will swing full circle, or when a bridge will fall down. Thus in dealing with linearized models of ecosystems it is important to realize that the resulting models can help identify frequencies at which large fluctuations are likely to be found, but that these models are unlikely to provide adequate quantitative descriptions of these fluctuations.

The mathematical methods required for a complete study of resonance in ecosystems are quite complex; since they have been discussed in detail elsewhere (Silvert, Smith, 1981), only a brief summary will be given here. For brevity I shall focus on continuous models (systems of differential equations) and omit discussion of discrete models (finite-difference equations).

Let x be a vector describing the state of an ecosystem, typically the vector of population sizes. Given a model

of the form

$$x' = f(x), \tag{4}$$

with equilibrium solution x_0 such that $f(x_0) = 0$, let $X = x - x_0$ measure the displacement of the system from equilibrium; the linearized form of the model is then

$$X' = AX, \tag{5}$$

where A is the community matrix $A = \partial f/\partial x$. To see how this linearized model responds to a periodic disturbance of frequency $2\pi w$ we look at steady-state solutions of

$$X' - AX = B \cos wt = \mathrm{Re}\{ B e^{iwt} \}, \tag{6}$$

where Re { . } refers to the real part of the complex exponential — this is a mathematical device to simplify the notation (which may also make it more obscure). The solutions are of the form

$$X = \mathrm{Re}\{ R(w) B e^{iwt} \} \tag{7}$$

where

$$R(w) = (iwI - A)^{-1} \tag{8}$$

is the « response function » and I is the unit matrix. The frequencies for which perturbations of a given magnitude generate the largest population fluctuations are those for which $R(w)$ has the largest components, which are values for which the determinant of the matrix $(iwI - A)$ is small. These are values for which iw is close to an eigenvalue of A, and thus the closer these eigenvalues are to the imaginary axis, the stronger and more sharply defined are the resonances.

This analysis shows why resonances are not found in single-population models, since the community matrix reduces to a single real number which is its own eigenvalue, so the resonant frequency (the imaginary part of the eigenvalue) is zero. The only time we find resonances is when the community matrix has complex eigenvalues.

By comparing the above analysis with the usual treatment of ecosystem stability (May 1974) we see that whereas an ecosystem model is formally stable if the eigenvalues all have negative real parts, it can still exhibit a strong resonant response if one of the eigenvalues is complex and lies near the imaginary axis.

RESONANCE IN THE LOTKA-VOLTERRA-VERHULST MODEL

The traditional Lotka-Volterra predator-prey model with a Verhulst density-dependent term and a variable growth rate is

$$p' = (a + g(t) - qp - kz) p \tag{9 a}$$

$$z' = (kp - b) z, \tag{9 b}$$

where p is the prey population (say phytoplankton) and z the predator (zooplankton). The equilibrium levels are $p_0 = b/k$ and $z_0 = a/k - qb/k^2$. The equations for the displacements from equilibrium $P = p - p_0$ and $Z = z - z_0$ are (to lowest order)

$$P' = -(qb/k) P - bZ + (qb/k) g(t) \tag{10 a}$$

$$Z' = (a - qb/k) P, \tag{10 b}$$

which are the same as equations (2) for the damped harmonic oscillator with suitable redefinition of the variables (Z and P instead of X and V) and of the constants. Thus the Lotka-Volterra-Verhulst model should have resonance properties similar to those found in mechanical and electrical systems. In the weakly damped case (q small) the resonant frequency is close to $2\pi(ab)^{1/2}$ which is the characteristic frequency of the Lotka-Volterra neutrally stable limit cycle; in this case the eigenvalues of the community matrix are pure imaginary (May 1974). The stronger the density-dependence of the phytoplankton population, the greater the damping and the weaker the resonance.

This example shows that the conditions for resonance can be found in commonly used models of marine ecosystems. Predator-prey relationships, cannibalism by adults, and other types of interaction which give rise to lagged negative feedback are likely to cause resonance. The effects of resonance are likely to be reduced by instantaneous self-regulatory processes such as density-dependent growth.

CONCLUSIONS

Resonance is certainly possible in marine ecosystems, as the Lotka-Volterra-Verhulst model shows, and it poses a difficult challenge for both the theorist and the experimentalist. From a theoretical point of view the prediction of resonance is difficult because the frequency and breadth of a resonance are sensitive to interaction parameters which are usually more difficult to estimate than are parameters describing single populations. Furthermore, previous work on difference-equation models of commercial fish populations has shown that these resonant frequencies may be quite different from those corresponding to biological time scales like age at first maturity (Silvert, Smith, 1981). From an experimental point of view it is difficult to identify resonant responses from the limited data sets generally available to marine scientists, especially when there are large theoretical uncertainties in the predicted resonant frequencies. The best methods to use appear to be those of time series analysis, since comparison of the fluctuation spectra of marine populations with the spectrum of a possible environmental forcing function gives the frequency-dependent response function; however, this approach must be used with caution since the methodology of spectral analysis cannot deal adequately with nonlinear effects. Ironically this means that the largest and presumably most significant fluctuations in the system are likely to be the most difficult ones to analyze.

The significance of these difficulties is that they show that fluctuations in marine ecosystems may not be easy to identify as arising either from the internal

dynamics of the biological populations or from external forcing functions. It may be the interaction of both causes through the mechanism of resonance which causes fluctuations of unexpected frequency and amplitude.

The methodology of response theory and the study of resonance come from the physical sciences, and the difficulties described above are well known to physical scientists and engineers. Unexpected resonances in bridges and other structures are known to occur and have on occasion led to spectacular and catastrophic failures. Most of us are familiar with the sudden onset of resonance which often occurs when an automobile reaches critical speed on a dirt road. In these cases the mechanism of resonance is clearly seen, and yet it is extremely difficult to predict. We may have to face this situation in ecology as well ; we may find that many of the fluctuations in marine ecosystems are associated with resonant behaviour, and even with this understanding we may not be able to develop a predictive capacity.

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