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THE SENSITIVITY OF EXPLOITED POPULATIONS TO ENVIRONMENTAL "NOISE", AND THE IMPLICATIONS FOR MANAGEMENT

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INTRODUCTION

Natural populations experience fluctuations in many aspects of their environment, such as temperature or food availability, which may affect their mortality or their reproductive success. Such fluctuations - environmental "noise" - are therefore normally reflected in fluctuations of population size. Some populations do not fluctuate much, even as a result of large environmental fluctuations, and are presumably fairly well stabilized against such perturbations. Others, on the other hand, seem to be very sensitive to environmental noise. Clearly, a population which is in a precarious state is more likely to be driven to extinction if it is highly sensitive to noise than if it is fairly well stabilized. Exploitation of a species can modify both mortality and reproductive rates, and may therefore modify the sensitivity to noise, and hence affect the likelihood of extinction.

These considerations suggest that, when assessing the effect of exploitation on natural populations, we should consider not only the effect on overall population size, but also the effect on the sensitivity of population size to environmental noise. This aspect has recently been studied in the context of whale populations by Beddington and May (1977). They concluded that sensitivity to noise increased under exploitation, and would become infinite for a population exploited at MSY. It has recently been observed (Horwood and Shepherd, 1977; Shepherd, 1977) that this conclusion depends on the details of the population model used and the form of environmental noise assumed, and is only valid for the rather special (and in practice rather unlikely) conditions specified by Beddington and May.

The purpose of this paper is therefore to point out that the analysis of sensitivity to environmental noise is not at all easy, and requires detailed knowledge of the mechanisms of population size regulation and of the environmental factors responsible for population size fluctuations. It is in fact more difficult, and requires more information, than the prediction of population size changes under exploitation - which is itself quite difficult enough. For management purposes any results concerning the sensitivity of populations to environmental noise therefore need to be treated with extreme caution.

THE RETURN TIME

An attractive measure of sensitivity to environmental noise is the variance of population numbers generated by a given variance in some environmental variable, such as temperature, or carrying capacity. We may illustrate the method of analysis conveniently using a simple bulked-population first-order differential equation model for a population, where N is population size and

$$\frac{dN}{dt} = NG(N) \qquad (1)$$

G (N) is the density-dependent net reproduction rate, including mortality from both natural causes and exploitation, ie

$$G(N) = R(N) - M(N) - F(N) \qquad (2)$$

The analysis may be extended with various degrees of difficulty to handle multiple-age, finite difference and time-lagged models, but the basic method remains similar.

We assume that the population is fluctuating around some fairly well-defined mean level, N^*, given by

$$G(N^*) = R(N^*) - M(N^*) - F(N^*) = 0 \qquad (3)$$

and examine the size of fluctuations around N^*. Writing $n = N - N^*$ and retaining only first-order terms we obtain

$$\frac{dn}{dt} + \frac{n}{\tau} = 0 \qquad (4)$$

τ is the return time, given by

$$\tau = -1/(N^* G'(N^*)) \qquad (5)$$

If the fluctuations are sufficiently small, this linear approximation about equilibrium will be adequate, and even if the fluctuations are large it may tell us much of interest. Nevertheless, one should recognize that:

(a) the return time is only a complete description of transient behaviour about equilibrium for the simple system we have chosen. More complicated models lead to much more diverse behaviour which cannot be so simply described, although it is still possible to arrive at a definition of return time which retains much the same information (see eg May 1973);

(b) the treatment is only valid if there is indeed an equilibrium population size, determined by density-dependent effects, about which the population fluctuates in a fairly well-behaved manner. It is not obvious that this is always so, but such an assumption is almost essential in order to make any progress, and is commonly also made in assessments of population size.

THE DEPENDENCE OF RETURN TIME ON THE LEVEL OF EXPLOITATION

So far, therefore, we recognize that the treatment is only approximate, but have no serious reservations about its general validity. The next step is to assess the dependence of return time on the level of exploitation, F, which of course influences the equilibrium population size N^* and hence τ via equation (5).

This is carried out by analysis of the detailed form of G (N). Beddington and May (1977) studied the usual logistic equation, for which

$$R(N) - M(N) = r(1-N/K) \quad (6)$$

where r is the intrinsic rate of increase and K is the carrying capacity. They showed that, for constant F (ie for constant fishing mortality),

$$\tau = 1/(r - F) \quad (7)$$

In this case therefore the return time increases as exploitation increases, and in fact becomes infinite if F = r (when, however, the population size is of course reduced to zero anyway). However, Beddington and May also pointed out that if the population is exploited at constant yield (ie so that Y = NF is constant), then

$$\tau = 1/(r\sqrt{1-Y/Y_{max}}) \quad (8)$$

where Y_{max} is the maximum sustainable yield (MSY), equal to rK/4.

In this case, therefore, although the return time still increases as exploitation increases, the behaviour is more extreme, since it goes infinite if the population is exploited at its MSY. We remark below that this behaviour depends on the details of the model used, and point out here only that, even when this particular model is used, it occurs ONLY for exploitation at constant yield. That is to say, for exploitation where a quota is set, always EXACTLY taken, and never revised, regardless of the state of the stock. It is not likely (nor perhaps even feasible) that such a management scheme would ever be used, and one should therefore regard an infinite return time as an extreme case which would never occur in practice. Furthermore, Horwood and Shepherd (1977) have shown that for equally plausible population models (eg incorporating the Beverton and Holt stock/recruitment relationship), exactly the opposite behaviour of return time on exploitation is indicated, so that it is reduced by increasing exploitation.

Thus we find that the behaviour of return time as a function of exploitation depends crucially on the nature of the population model used. At present we are too ignorant to predict reliably even the direction in which it should change, and any conclusions reached via assessments of its behaviour should be treated with great circumspection.

THE INFLUENCE OF RETURN TIME ON SENSITIVITY TO NOISE

The final stage of the method is to assess the way in which variations of return time influence sensitivity to noise. It is not fruitless to pursue the analysis further, even in view of what has been said above, since it may be that something may be discovered about return times other than by analysis of population models: perhaps by spectral analysis of population fluctuations. If this should prove to be so, it might indeed provide a most valuable tool with which to test population models.

Beddington and May (1977) concluded that an increase of return time would lead to an increased sensitivity to noise - hence their concern about the possibility of return time becoming infinite. However, Shepherd (1977) has shown that the behaviour depends on the form of noise assumed. The increased sensitivity noted by Beddington and May occurs only when the noise perturbs the reproductive rate directly: the opposite effect occurs if the noise only perturbs reproductive rates indirectly (via a perturbation of carrying capacity, for example). Thus it is not possible to say whether an increased return time should lead to an increased or reduced sensitivity to noise, unless one knows the source of the fluctuations, and can introduce them into the model equations accurately. This is not normally so.

CONCLUSIONS

It is possible to estimate the sensitivity of populations to environmental noise, and how this is influenced by exploitation, by examining the transient response of models of the population dynamics, and in particular by studying the characteristic time for the population to return to equilibrium after perturbation (the return time).

It transpires that whether the return time increases or decreases as a result of exploitation depends on the detailed form of density-dependence in reproductive and mortality rates, and no generally valid conclusion can yet be stated.

It also transpires that whether the sensitivity to noise is increased or decreased by an increase of return time depends on the nature of the environmental noise, and whether it perturbs reproductive rates directly, or only indirectly via the carrying capacity, for example.

Our present understanding of the nature of regulation and the source of fluctuations in the numbers of most populations is thus clearly insufficient for any firm conclusions to be stated concerning the effect of exploitation on the sensitivity of populations to environmental noise. It is however clear that the possible pathological sensitivity to noise of populations under pure "quota" management suggested by Beddington and May (1977) occurs only under very extreme and rather unlikely conditions. It should not therefore be a major factor influencing the decisions of those responsible for managing exploited natural populations, nor should it be allowed to discredit the concept of MSY as the focus for (but not necessarily the target of) deliberations on management procedures.

Nevertheless, management bodies should be aware that the sensitivity of a population to environmental noise may be affected by the degree of exploitation, and should be alert to the possibility that increased sensitivity may develop in some populations. Should this occur it should be regarded as a serious matter, and management objectives would need to be modified accordingly.

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