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Quasiextinction Probabilities as a Measure of Impact on Population Growth

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A probabilistic language based on stochastic models of population growth is proposed for a standard language to be used in environmental assessment. Environmental impact on a population is measured by the probability of quasiextinction. Density-dependent and independent models are discussed. A review of one-dimensional stochastic population growth models, the implications of environmental autocorrelation, finite versus "infinite" time results, age-structured models, and Monte Carlo simulations are included. The finite time probability of quasiextinction is presented for the logistic model. The sensitivity of the result with respect to the mean growth rate and the amplitude of environmental fluctuations are examined. Stochastic models of population growth form a basis for formulating reasonable criteria for environmental impact estimates.

KEY WORDS: environmental assessment; impact; stochastic models; population growth; quasiextinction; environmental fluctuations; first-passage.

1. INTRODUCTION

Those who prepare impact statements are free to use any kind of mathematical model deemed appropriate. However, the model used has a subtle and pervasive effect on the choice of language in which the conclusions are stated. Impact statements are often challenged in courts of law and discussion in such cases often concentrates on the validity of the mathematical models used. Reliability and sufficiency of the data is another often contended problem.

While we do not deny that this is a vital part of every environmental assessment, we would like to concentrate here on a more fundamental problem: the type of the model itself.

Environmental law does not specify what language should be used to characterize the possible "adverse" impact of a particular activity on natural populations. The problem of formulating a unified language in which to express environmental statements is an important social need and a challenge to scientists working in this field. Unfortunately, communication between academic scientists and those working in environmental assessment has been limited. The testimony of distinguished scientists in the courtroom, while valuable, is not a sufficient means of interaction. The formulation of a unified standard language for environmental assessment has not received adequate attention.

If the problem can be at least partly resolved, the form of language can even be incorporated into the requirements set by the relevant laws (e.g., Environmental Protection Act, Endangered Species Act, etc.). This is a very ambitious goal. We wish to contribute a first step towards that goal by suggesting methods of analysis and by proposing a general

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framework for the formulation of a unified language.

We illustrate this paper with a specific case in which we were recently involved: the assessment of the impact of the Indian Point Power Plant on fish populations in the Hudson River, in particular the striped bass. The hearings between utilities and the Environmental Protection Agency (EPA) went on for many years. Thousands of pages of testimony and millions of dollars have been spent. While some of the expert testimony addressed questions of reliability and sufficiency of the data, criticism was also levelled at the model produced by the consultants for the utilities and some witnesses suggested its replacement by a more detailed model incorporating the age structure of the population and ecosystem interactions. However, increased dimensionality will increase the number of parameters and thus aggravate the problems of judging the statistical adequacy of the data. The inconclusive hearings may be related partially to the absence of objective methods for formulating conclusions in an appropriate language.

There is one speakable significant requirement of the language of environmental assessment arising from the wide general public involvement in these problems. We cannot expect from either the general public or from a judge, the technical knowledge of models developed in theoretical biology. Therefore, however technical the ways of obtaining results may be, the final conclusions or recommendations should be made in widely understandable terms. Decision-makers should be able to understand the results, relying on the expert's qualifications only for the ways in which the results were obtained, but not for the interpretation of the meaning of the final statement itself.

2. THEORETICAL BACKGROUND

We will argue in this paper that probabilistic language based on stochastic models of population growth is a good candidate for a standard language to be used in environmental assessment.

There is nothing new in principle in the use of stochastic dynamic models in describing natural processes. It is a reasonably well-developed area of applied mathematics. On the other hand, theoretical problems of stochastic dynamic models are very difficult. Only a very few practically interesting questions in this area have been generally resolved analytically so that every specific set of differential equations designed for modelling particular processes (like population growth, for instance) presents a special problem. While people working in this area are still debating the important "philosophical" question of which calculus, Ito or Stratonovich, to use in population models(1–5) there exists a set of applied problems of immediate concern.

We will characterize the state of understanding the area of stochastic modelling of population growth by discussing several examples.

2.1. Density-Independent Growth

The basic equations of the Malthusian model are either of the discrete-time type,

$$N(t+1) = m(t)N(t), \qquad (2.1)$$

where $N(t)$ is the population size at time t, $m(t)$ is the net growth rate at time t(6), or a continuous-time analog

$$\frac{dN}{dt} = r(t)N(t). \qquad (2.2)$$

This model was studied by Goel and Richter-Dyn(7) Capocelli and Ricciardi,(8) Tuckwell,(9) and Dennis and Patil(10) using the Stratonovich calculus and by Levins,(11) Iosefescu and Tautu,(12) and May.(12) This list is not exhaustive. Leibowitz(14) considered the same model with a special kind of correlated noise. Gleit(15) introduced harvesting into the model. Gopalsamy(16) introduced age-dependence. Lewis(17) considered stochastic time delays caused by random individual maturation time. Gurney and Misbet(18) considered the case of a patchy environment. Polansky(19) studied a two-niche model with migration.

In most of the work which has been done, $r(t)$ has the form

$$r(t) = r + \sigma\varepsilon(t), \qquad (2.3)$$

where r is the mean growth rate, $\varepsilon(t)$ is the standardized white noise, and σ characterizes the amplitude of the fluctuations.

Let us assume that the growth process starts with the population size N_0 and we are interested in the chances of the population size crossing a given preassigned level, $N_c < N_0$, which is meant as a "critical level" corresponding to so-called quasiextinction. The answer is certainly time-dependent. Asymptotically, for infinite time, these chances, P, are given by the simple expression

$$P = \left(\frac{N_c}{N_0}\right)^{2r/\sigma^2} \tag{2.4}$$

for positive r. For negative and zero value of r, the probability is 1. Let us assume now that we want to adopt this probability as the measure of persistence of our population and compare it with the same measure for the population under impact. Assume, for simplicity, that the environmentally induced variance stays the same but impact results in a new and lower value of the mean growth rate, r_{imp}. Let us define as the measure of our impact, I, the relative change in the probability of quasiextinction

$$I = \frac{P_{\text{imp}} - P}{P}. \tag{2.5}$$

We have

$$I = \left(\frac{N_c}{N_0}\right)^{2(r_{\text{imp}} - r)/\sigma^2} - 1. \tag{2.6}$$

Clearly, the greater the reduction in the growth rate, the larger is the value of our index, I. What is more interesting is that if the variance in the growth rate, σ^2, is growing, the index becomes less and less sensitive to the reduction in r. It is, therefore, absolutely insufficient to measure the impact in terms of the reduction of the average growth rate without taking into account the level of variability. What the critical level of quasiextinction, N_c, is, constitutes another problem which should be discussed separately. We wish to show here only the significance of the variance in the growth rate in any reasonable criterion of the impact. In the case of the striped bass in the Hudson River, the survival of the first-year fishes apparently varies 50-fold, depending primarily on the water temperature, thus producing a hugh variance in the year-to-year growth rate. A deterministic model of assessment is, therefore, absolutely misleading as a way of estimating the impact. As it has been shown many times, with different kinds of models, even the mean behavior of the model does not correspond to the behavior of the mean model. This is always the case because the population trajectory is a nonlinear function of demographic parameters.

Another problem appears if we look at finite-time chances as opposed to asymptotic probability of quasiextinction. We have an exact impression for the density function for the first passage time at a prescribed level, N_c(8):

$$g\left(t, \frac{N_c}{N_0}\right) = \frac{\ln\left(\frac{N_c}{N_0}\right)}{\sigma\sqrt{2\pi}\sqrt{t^3}} \exp\left\{-\frac{\left[\ln\left(\frac{N_c}{N_0}\right) - rt\right]^2}{2\sigma^2 t}\right\}. \tag{2.7}$$

This density sums up to the asymptotic probability given by the previous formula, $\int_0^\infty g(t) = P$. We are interested here in the finite integral expressing the chances for the first passage to happen before time T. With this we could make up an index of impact which will be time-dependent and answer the question of what is the measure of the impact for a given length of time. Without calculations it is clear that the result will be strongly time-dependent for a relatively small T, tending to our asymptotic formula with $T \to \infty$. In cases when an impact has a finite duration this could be a reasonable approach to take. We can also calculate the expected time of the first passage through the critical level, its variance, and so on. All of these criteria, which are much harder to calculate than the simple deterministic criteria, seem much more informative than the latter when assessing impact.

2.2. Density-Dependent Growth

A number of people have worked on the logistic equation and its generalization. Levins(11) obtained a steady-state distribution for the population size. Goel and Richter-Dyn(7) and Tuckwell(9) presented the results for the first passage time with implications on the extinction problem. Levikson(20) worked with the near-equilibrium approximation of the model.

The standard form of the logistic equation is

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right), \tag{2.8}$$

where K is the carrying capacity of the environment. In the best understood cases it is assumed that the "noise" is concentrated in r and K is a fixed constant. In this case, the equation can be transformed, by introducing

$$x = \ln \frac{N}{1 - N/K} \tag{2.9}$$

to the simple form

$$\frac{dx}{dt} = r. \tag{2.10}$$

After that, the noise in r is introduced and results are principally similar to the previous exponential growth model. From the point of view of the probability of quasiextinction the results can be obtained by replacing the ratio (N_c/N_0) by another expression involving carrying capacity

$$\frac{N_c\left(1 - \frac{N_0}{K}\right)}{N_0\left(1 - \frac{N_c}{K}\right)}. \tag{2.11}$$

The more difficult case is that of random fluctuations introduced in the carrying capacity, K. Levins(11) first, and then Goel and Richter-Dyn,(7) Feldman and Roughgarden,(2) Levikson,(20) and Turelli(5) considered this problem. Roughgarden(21) used a discrete-time model linearized around equilibrium. This approach enables him to consider even the correlated noise but this advantage is offset by the linearization. It is valid only around the equilibrium.

2.3. Age-Structured Models

The problem of unpredictable variation is quite complex when successive Leslie matrices in the classical demographic model are randomly determined. Following Pollard(22) and Sykes(23) successive Leslie matrices in the demographic equations are either assumed independent or chosen according to a Markov chain. In these papers and in the work of Namkoong(24) the recursion equation for the mean and variance of the age distribution was established. Weissner(25) and Athreya and Karlin(26) studied the conditions for asymptotic extinction. The dynamics of growth rates in stochastically fluctuating environments has been studied numerically by Boyce(27) and analytically by Cohen.(28–31) The most recent results on the distribution of growth rates and extinction are presented in the paper by Tuljapurkar and Orzack.(32)

It is not our intention to discuss all these very interesting works in detail here. We want to underline only that there have been a lot of important things which have been done but it is still a wide open area for research and, in particular, in the direction of estimating quasiextinction probabilities which we connect to the impact measurement. In the next section we will attempt to outline the most important problems which need to be resolved.

3. WHAT SHOULD BE DONE

There are a number of important problems standing in the way of making practical use of theory. We will identify here five of the problems which need to be investigated. All of them can be viewed as "independent axes" in the "space of the problems" we actually encounter. In reality they will appear in combinations.

3.1. Implications of Environmental Autocorrelation

In nearly all the models studied, the environmentally induced fluctuations in the growth parameters are assumed to be of the "white noise" sort, i.e., uncorrelated for any two instants in time. This is a simplifying assumption valuable for the analytical treatment of the problem. Needless to say, in fact, environmental fluctuations are correlated in time. The question is how the typical correlation time compares with both the generation time for a given population and the characteristic time for which the prediction is being made. It is intuitively clear, and can be rigorously shown, that if the time scale of our prediction is much longer than the correlation time, the assumption of white noise is a good approximation. This approximation will not work if the time range under consideration is comparable to the environmental autocorrelation time. For an exponential autocorrelation function and a simple Malthusian growth model the question was considered in Braumann.(33) If we are interested in a short-term prediction, positive autocorrelation will lower the quasiextinction probability (for the fixed variance) compared to the case of white noise. In the long run, however, autocorrelation will not make any difference. The interesting problem is what happens in the case of a not-sign-defined autocorrelation function, when the "typical" sequence of environmental events has a specific temporal structure.

The available record of environmental parameters involving meteorological and geophysical measurements is usually much longer than the time the populations have been observed. At least 50 years of environmental data were available (but not used) in the abovementioned Hudson River case while the fish populations have been monitored only for the last 5–7 years. We should be able to use our understanding of the environmental autocorrelations, which have more sufficient support data to improve our models of population growth if we know how the environment affects population growth.

3.2. Impact in Finite Versus "Infinite" Time

Most of the analytically accessible results relate to the asymptotic properties of a random process describing population growth. The diffusion equation, describing the dynamics of the probability distribution, becomes time-independent in this case and, therefore, easier to deal with. Unfortunately, in many practical cases we need finite-time results. These require the consideration of the full time-dependent diffusion model. Important examples are the cases in which the impact has a finite and predictable duration. The power plants are often planned for a 40–50-year lifetime and, although it could seem like a long time, it is only a few generations for some important species of fish. Individuals of the striped bass live as long as 20 years. The mean generation time is about 9 years. Clearly asymptotic estimates are not acceptable in this case and we need finite time evaluations for all the necessary probabilistic characteristics.

3.3. Nonlinearity and Dimension of the Models

The only models of which we have a reasonably good understanding are quite simple. As in many other cases, we are limited by linearity and low dimension. It is important therefore to consider the most important nonlinear and multiple-dimensional models. One important multidimensional model is a demographic (Leslie) model with age structure and with one random parameter describing survival of the first age class. This has the property that both fertility (number of eggs per female at a given age) and survival parameters for adults do not fluctuate nearly as much as does survival of young. This fluctuation in survival of the young is the single most important source of stochasticity.

In many cases, as with the striped bass, an age-dependent model is a necessity. While the prolonged life span may seem to serve as a buffer against environmental uncertainty, the role of age structure is not clear from the point of view of the extinction probabilities.

The major source of nonlinearity in these models is density-dependence which, to a first approximation, can be concentrated in survival of the first age class, as has been done recently by Levin and Goodyear.(34) They have obtained a number of very interesting results relating to the "chaotic" behavior of the deterministic system.

Surprisingly, in our opinion, the addition of stochasticity to such a system will simplify the behavior as compared to that of the deterministic model. The environmental stochasticity will break down the fine structure of the deterministic behavior and become the leading source of the observed variation.(35, 36) It is not our purpose here to elaborate more on this interesting and important topic. We want only to stress that interaction of stochasticity and nonlinearity, as well as increased dimension, is a promising area which should bring a number of interesting results relevant to applications.

3.4. Monte Carlo Computer Simulations

When problems are not tractable analytically, computer simulations can be used to generate the random processes with given statistical characteristics. Estimation of all the necessary probabilities can then be done numerically. Since we are dealing with estimation of small probabilities, the computations required for carrying out such a program are very extensive. It is important, therefore, to develop methods which would shorten the computations. One approach is to define upper and lower bounds of the desired probabilities based on simpler models. If the nonlinearity, for instance, lies between two linear functions, could we conclude that our quasiextinction probability can be estimated by dealing with two linear models? In general, dealing with the specific type of equations describing population growth, we can hope for an improvement of the Monte Carlo methodology with respect to our particular class of models, thus reducing the amount of necessary calculations.

3.5. Measurement, Parameter Estimation, and Monitoring

With comparatively short, and often marginally sufficient, periods of observation, the problems of what to monitor become very important. The answer clearly depends on the type of model one has in mind while designing a monitoring program. For previously proposed models, the measurement process must be investigated before any practical recommendations can be made.

At first it might seem that stochastic models would require much more data than deterministic models. This question can be answered only in each specific context. Since extinction probabilities are quite resistant to the changes in the statistical characteristics of the process, we will not need very much accuracy in measuring the required characteristics to get a reasonably good qualitative judgment on the desired probabilities. The problem of the sensitivity of the conclusions to the means, variances, and correlation parameters of the growth process is, however, crucial for our ability to apply this methodology to real cases.

4. ILLUSTRATIVE EXAMPLE

Consider the simplest density-dependent growth model, the logistic equation

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right), \tag{4.1}$$

where we assume the carrying capacity, K, to be constant and the mean growth rate, r, subject to environmentally induced fluctuations of the sort described in Sec. 2 of this paper. An analytical expression for the probability P that a population started with initial size N_0 will fall, at least once, below the actual level N_c in a time T is given by the integral

$$P = \int_0^T g(t)\,dt \tag{4.2}$$

where

$$g(t) = \frac{\left|\ln\left(\frac{N_c}{N_0}\frac{(1-N_0/K)}{(1-N_c/K)}\right)\right|}{\sigma\sqrt{2\pi}\sqrt{t^3}} \times \exp\left\{\frac{-\left[\ln\left(\frac{N_c}{N_0}\frac{(1-N_0/K)}{(1-N_c/K)}\right)-rt\right]^2}{2\sigma^2 t}\right\}. \tag{4.3}$$

We have evaluated the integral. The exact result is

$$P(N_c, T|N_0) = \frac{1}{2}\left\{1 + \mathrm{Erf}\left[\frac{\ln\left(\frac{N_c}{N_0}\frac{(1-N_0/K)}{(1-N_c/K)}\right)-rT}{\sigma\sqrt{2T}}\right] + \left[\frac{N_c}{N_0}\frac{(1-N_0/K)}{(1-N_c/K)}\right]^{2r/\sigma^2} \times\left[1+\mathrm{Erf}\left(\frac{\ln\left[\frac{N_c(1-N_c/K)}{N_0(1-N_c/K)}\right]+rT}{\sigma\sqrt{2T}}\right)\right]\right\}, \tag{4.4}$$

where

$$\mathrm{Erf}(z) = \frac{2}{\sqrt{\pi}}\int_0^z \exp(-u^2)\,du. \tag{4.5}$$

Let us examine the probability distribution, P, numerically using the following assumptions:

$$\frac{N_0}{K} = \frac{1}{2},\quad \frac{N_c}{K} = \frac{1}{10}, \tag{4.6}$$

i.e., initially the population is at one-half of the carrying capacity and the critical level is chosen to be at 10% of the carrying capacity. We choose a range of $-0.06 \div 0.06$ (units 1/time) for the mean growth rate, r, and $0.10 \div 0.30$ as the range for variance of the growth rate, σ. Five periods of time, $T = 10, 50, 100, 10{,}000, \infty$ are examined so that the time effect on the probability can be seen (Figs. 1–4).

As would be expected, the probability, P, of passing once below the critical level, N_c, increases with time for each fixed r and σ. The higher the variance, the less sensitive the probability, P, to a reduction in r, so that in 10 years (Fig. 1) the effect could be insignificant. The longer the time, T, the more influential is the effect of a given reduction in r.

For r negative we can observe a seemingly counterintuitive effect of the probability reduction with

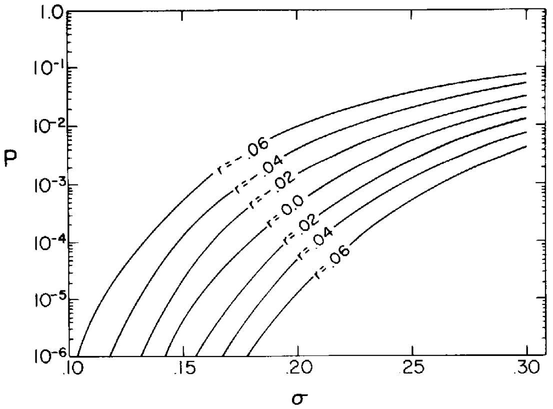

Fig. 1. The probability, P, of passing below the critical level, N_c, after 10 years.

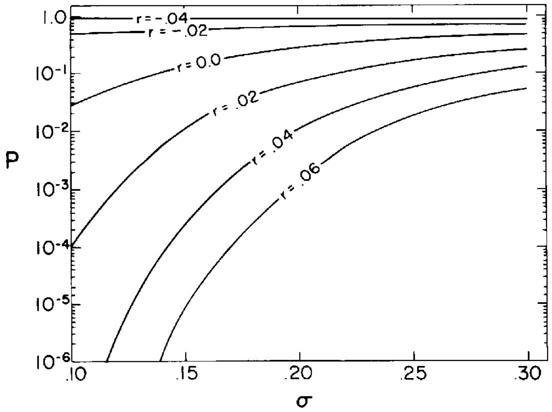

Fig. 3. The probability, P, of passing below the critical level, N_c, after 100 years.

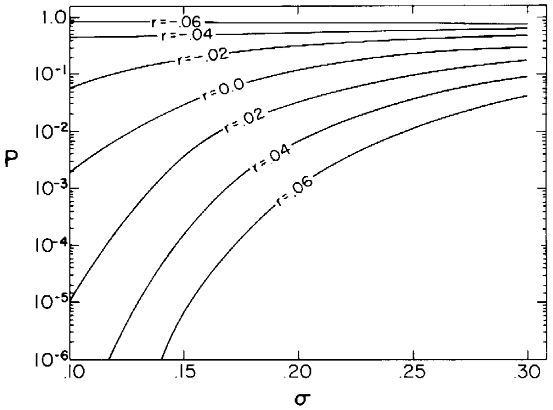

Fig. 2. The probability, P, of passing below the critical level, N_c, after 50 years.

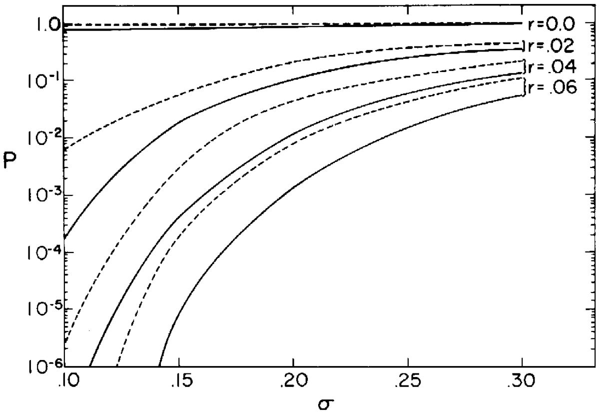

Fig. 4. The probability, P, of passing below the critical level, N_c, for 10,000 years (solid line) and the asymptotic probability (of ever passing the critical level, $T = \infty$ (broken line).

Table I.

	T_L	T_U
$\sigma = 0.1$	73	3 million
$\sigma = 0.2$	18	3/4 million
$\sigma = 0.3$	8	1/3 million

growing environmental variance. In reality, with negative r a population will certainly fall below the critical level, given enough time. Stochasticity increases the chances of staying above the critical level. This effect is seen only for large enough time, T, and strongly negative values of r. See Fig. 2 with $r = -0.06$ for a demonstration of this effect.

For the stable population when the growth rate, r, is zero except for very large fluctuations the probability of quasiextinction is generally low. For this population we present estimates (Table I) of when asymptotic values may be used for the probability, P, and when we must go to the exact solution. There are two times of interest: an upper bound beyond which the $T = \infty$ asymptotic value may be used and a lower bound, below which the $T = 0$ asymptotic may be used. These we will denote by T_U and T_L, respectively.

Thus, for example, for $\sigma = 0.1$ the lower bound time, T_L, is 73. For all times before this, we may with absolute error of no more than 10^{-2} use the time equals zero asymptotic value, $P = 0$. Similarly, the upper bound time, T_U, is three million. For all times greater than this, to within an error of 10^{-2} we may use the time equals infinity asymptotic value, $P = 1$.

For all intermediate times between T_L and T_U the exact formula must be used. The above time ranges show that asymptotic values are typically of no use in environmental assessment. For the striped bass case discussed earlier the generation time is about nine years. We see that when the variance is high the probability of quasiextinction is substantially above the short time asymptotic value of zero, but below the long time value of 1. We therefore must use the exact equation to calculate P.

Consider now the dependence of the chances of quasiextinction on the level N_c. Clearly, the question of how to define the level, N_c, is a biological one and no a priori mathematical argument will lead to a solution. We can however ask the meaningful question of how sensitive are the chances of quasiextinction to this level N_c. In Fig. 5 we have plotted the quasiextinction probability, P, against the N_c/K with all other parameters fixed. It is clear that for each of the variances, the probability, P, decreases very rapidly with decrease in N_c/K, and hence is very sensitive to how the level N_c/K is defined.

Although we do not pretend that the analysis of this admittedly simple model can be directly applied to a particular population, it demonstrates the importance of taking into account environmentally induced stochasticity in estimating an impact. It stresses the relative importance of the different parameters characterizing population growth and the value of an "impact time," T, for which the impact is estimated.

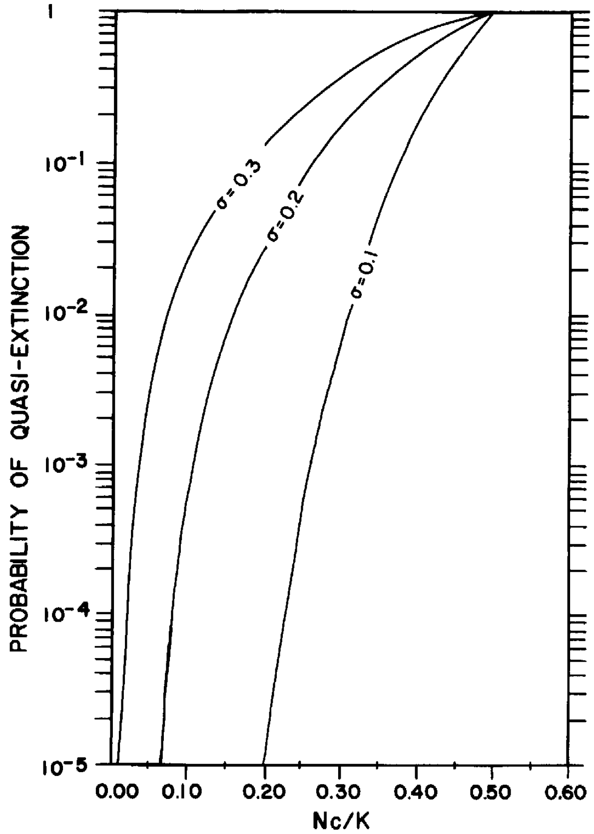

Fig. 5. The probability, P, of passing below the critical level, N_c. The critical level divided by carrying capacity at time $T = 10$ for a stable $r = 0$ population.

5. CONCLUSIONS

Decision-makers should be presented with an adequate description of risks involved in accepting one or another of the alternative solutions of the environmental problems. In our opinion, presenting the probabilities of certain "adverse" events to happen under different managerial policies is the reasonable and objective way to describe the limited state of our present knowledge about the natural populations in question. It seems likely that in many cases, clear valid probability statements can be made even though we may not be in a position to build an explicit model to describe the precise path that a population will follow. This would permit an estimation of impact in a form that may under some circumstances be of greater managerial value than tracking the population from year to year. For example, predicting next year's population may be critical for fishery management, while estimation of the probability of eliminating a population in the next 50 years may be critical for assessing the danger of having an irreversible impact on an ecosystem. The existing theoretical basis developed for the population growth models suggests that the methodology for such an impact estimation can be developed and successfully applied to the analysis of real environmental problems.

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University of New York at Stony Brook. The conclusions represent the views of the authors and do not necessarily reflect opinions, policies, or recommendations of the Environmental Protection Agency.

APPENDIX A

We summarize here the fundamental equations of exponential growth in a random environment. As was remarked in Sec. 2, the exponential growth model with noise in r is principally similar to the logistic model, with noise in r and the carrying capacity constant. This allows us to solve the simpler exponential model and then transform the results to yield a solution for the logistic model.

Consider the deterministic exponential growth equation[8]

$$\frac{dN}{dt} = rN(t)$$
$$N(0) = N_0, \tag{A.1}$$

where $N(t)$ is the site of the population at time t and r a parameter representing growth rate. N_0 is the initial population site.

Now we claim that the population interacts with the environment stochastically through the parameter r as follows: replace r with $r(t)$ where

$$r(t) = r + \varepsilon(t), \tag{A.2}$$

r is constant and $\varepsilon(t)$, for any fixed t, is a random variable normally distributed such that

$$\langle \varepsilon(t) \rangle_{\text{ave}} = 0 \tag{A.3a}$$
$$\langle \varepsilon(t_1)\varepsilon(t_2) \rangle_{\text{ave}} = \sigma^2 \delta(t_2 - t_1), \tag{A.3b}$$

where the brackets denote ensemble averages. In other words, $\varepsilon(t)$ is a zero average delta-correlated Gaussian process (white noise) having spectral density σ^2.

We thus have the fluctuation equation[37]

$$\frac{dN}{dt} - rN = N\varepsilon(t). \tag{A.4}$$

With the assumptions on $\varepsilon(t)$ (A.3) it can be shown the growth of the population is described by a Markov process $N(t)$ whose transitions pdf $f(N,t|N_0)$ satisfies the forward diffusion (or Fokker–Planck) equation:

$$\frac{\partial f}{\partial t} = -\left(r + \frac{\sigma^2}{2}\right)\frac{\partial}{\partial N}(Nf) + \frac{\sigma^2}{2}\frac{\partial^2}{\partial N^2}(N^2 f)$$
$$0 < N < \infty. \tag{A.5}$$

The drift $A(N)$ and infinitesimal variance $B(N)$ of the process are

$$A(N) = \left(r + \frac{\sigma^2}{2}\right)N$$
$$B(N) = \sigma^2 N^2. \tag{A.6}$$

Also as is shown in Capocelli and Ricciardi[8] by means of the substitutions

$$\Phi(N,t|N_0) = N(N_0/N)^{2r/\sigma^2} \times \exp\left\{\frac{r^2 t}{2\sigma^2}\right\} f(N,t|N_0) \tag{A.7a}$$
$$y = y_0 + \ln(N/N_0) \tag{A.7b}$$

the diffusion equation (A.5) is transformed to

$$\frac{\partial \Phi}{\partial t} = \frac{\sigma^2}{2}\frac{\partial^2 \Phi}{\partial y^2} \qquad -\infty < y < \infty \tag{A.8}$$

with initial condition

$$\Phi(y,0|y_0) = \delta(y - y_0). \tag{A.9}$$

This can be solved, and then upon transformation back to the population site, N, we obtain for $f(N,t|N_0)$

$$f(N,t|N_0) = \frac{1}{\sigma\sqrt{2\pi t}}\frac{1}{N}\exp\left[-\frac{\left(\ln(N/N_0) - \sigma t\right)^2}{2\sigma^2 t}\right]. \tag{A.10}$$

The above equations, with more detail may be found in the interesting paper by Capocelli and Ricciardi.[8]

APPENDIX B. QUASIEXTINCTION PROBABILITIES

The problem of quasiextinction is equivalent to the mathematical problem of first-passage time. The following simple argument[37] demonstrates that the first-passage time problem associated with a certain diffusion process is solvable by adding to the initial condition (A.9) the following boundary condition:

$$f(N_c, t|N_0) = 0, \quad \text{all } t. \tag{B.1}$$

Define t_{fp} to be the time to first reach the boundary N_c. This first-passage takes place at times which vary from realization to realization, so that the first-passage time

$$T_{fp} = t_{fp} - t_0 \tag{B.2}$$

is a random variable.

Let the region under consideration be the interval

$$N_c \le N < \infty,$$

where $N(t)$ is a Markov process with initial distribution

$$f(N, t_0|N_0) = \delta(N - N_0). \tag{B.3}$$

To calculate $\langle T_{fp} \rangle_{\text{ave}}$ we exclude any realization of the random process $N(t)$ as soon as it takes the boundary value N_c for the first time. We describe the remaining realizations by a probability density $f(N, t|N_0)$ such that

$$\Delta W = f(N, t|N_0)\,dN + O\left[(\Delta N)^2\right] \tag{B.4}$$

is the probability that at time t, the process $N(t)$ takes a value in the interval $[t_0, t]$. Then the integral

$$W(t) = \int_s^\infty f(N, t|N_0)\,dN \tag{B.5}$$

gives the probability that $N(t)$ never reaches the boundary during the time interval $[t_0, t]$.

Initially we have

$$W(t_0) = 1 \tag{B.6}$$

since no realization could have reached the boundary, N_c, in the first instant the process begins.

Within the interval $[N_c, \infty]$ the probability density, $f(N, t|N_0)$, is governed by the Fokker–Planck equation (A.5) described in Appendix A, since no trajectories terminate, and, hence, be excluded inside $[N_c, \infty]$. Near the quasiextinction level, N_c, however, practically all trajectories reach N_c and must be excluded. Hence, the probability density $f(N, t|N_0)$ vanishes on the boundary

$$f(N_c, t|N_0) = 0. \tag{B.7}$$

Let $P(t)$ be the probability that the quasiextinction level is first reached during the time interval $[t_0, T]$. Then we have

$$P(t) = W(t_0) - W(T) \tag{B.8}$$

or

$$P(t) = 1 - \int_{N_c}^\infty f(N, t|N_0)\,dN. \tag{B.9}$$

Upon substitution of $f(N, t|N_0)$ for the exponential model (Appendix A) with the additional boundary condition (B.1) we obtain for the chances of quasiextinction:

$$P(T) = \frac{1}{2}\left[1 + \text{Erf}\left[\frac{\ln(N_c/N_0) - rT}{\sigma\sqrt{2T}}\right] + \left(\frac{N_c}{N_0}\right)^{2r/\sigma^2}\left[1 + \text{Erf}\left[\frac{\ln(N_c/N_0) + rT}{\sigma\sqrt{2T}}\right]\right]\right] \tag{B.10}$$

where

$$\text{Erf}(z) = \frac{2}{\sqrt{\pi}}\int_0^z \exp(-u^2)\,du.$$

The asymptotic values when $T \to \infty$ are:

$$\lim_{T \to \infty} P(T) = \begin{cases} 1 & r \le 0 \\ (N_c/N_0)^{2r/\sigma^2} & r > 0 \end{cases}. \tag{B.11}$$

Note that we are considering the case $N_c < N_0$, i.e., quasiextinction.

Now the transformation to the logistic model is made by the substitution in all of the results

$$\frac{N_c}{N_0} \to \frac{N_c}{N_0}\frac{(1 - N_0/K)}{(1 - N_c/K)}.$$

The above transformation is proper only for N_c and N_0 less than K.

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