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Population extinction and optimal resource management

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SUMMARY

The optimal exploitation of a population is considered for three stochastic population models; these allow both demographic and environmental variability and the possibility of extinction. The dynamics are linear in the harvest rate; the optimal policy then recommends harvesting at the maximal rate above a critical level (the 'threshold') and at zero rate below. However, in all cases the optimal threshold differs radically according as to whether one maximizes the total return before extinction or the rate of return per unit time over the period before extinction. In the former case the optimal threshold is at the deterministic equilibrium level of the unexploited population, in the latter case it is approximately at the level of maximal sustainable production. Part of the explanation is that maximization of total yield turns out to be almost equivalent to maximization of time to extinction. Both average yield rate and the expected time to extinction vary with the policy, but the second much more powerfully. Both the criteria above are extreme: one obtains a balanced criterion (and an intermediate threshold) if one maximizes rate of return (before extinction) subject to the conservation requirement of a lower bound on the expected time to extinction. In the case when extinction is excluded because of a potential 'rescue effect' one comes to the same view by taking account of the relative time needed to restart an obliterated population. The practical implication is that more attention should be paid to extinction and restart times. For vulnerable populations it is likely that maximal utilization before an inevitable extinction will be achieved at low harvest rates. For large populations or metapopulations, with large times to extinction or quick recovery from a temporary extinction, classical resource models are appropriate.

1. INTRODUCTION

Extinctions, their description and our models for them, reflecting current understanding of these major events, are of public and scientific interest (Chaloner & Hallam 1989; Anon. 1992). Extinctions are well documented over geological time, for example, the dinosaurs, and by recent impacts of Man, for example, the passenger pigeon (*Ectopistes migratorius*) and Steller's sea cow (*Hydrodamalis gigas*). Although presented with understandable caveats, Smith *et al.* (1993) suggest that half the world's species of fish, amphibians, birds, mammals and palm trees may be lost within 1000 years. Knowledge of a species' vulnerability to extinction and capacity for survival are important in understanding the colonization of islands (MacArthur & Wilson 1967). The processes are similar to those associated with the introduction of exotic forms and translocations (Elton 1972), for which scientific support of policy is required. Mathematical models have been developed to explain and predict the dynamics of populations which are subject to stochastic variability and which may be driven to extinction by chance events. The models tend to be of a discrete nature or approximated by diffusion equations; the work is summarized by, for example, Cox & Miller (1965) and Goel & Richter-Dyn (1974), building upon the fundamental studies of Kendall, Feller & Kolmogorov. By these means models have been constructed of colonization (Lande 1987; Williamson 1989) and gene flows (Kimura 1964). The diffusion model also leads (at least in the case of a scalar-state variable) to a ready expression for the steady-state probability distribution of population and harvest; this was applied to marine fisheries by May *et al.* (1978).

The initial models for exploitation of fisheries were deterministic and relatively simple (Graham 1935). Beverton & Holt (1957) used age-structured models; their 'yield-per-recruit' concept has been a basis for fisheries management worldwide. The approach averages out the effect of variable production of young fish (termed 'recruitment'), although Beverton & Holt (1957) and Chapman (1961) developed stochastic models for the case of constant average recruitments. The production of young fish is very variable and apparently random (Cushing 1975) and cannot be neglected in fisheries management. The diffusion formulation allowed May *et al.* (1978) to use complex stock-recruitment (density-development) relations and to introduce the possibility of yield/variance trade-offs. Horwood (1983) used a localized linear-systems theory to develop expressions for variance of population and yield. The models above led to the development of useful principles, based upon a maximization of some suitable quantity such as yield, profit or stability.

Models followed which allowed a stronger form of

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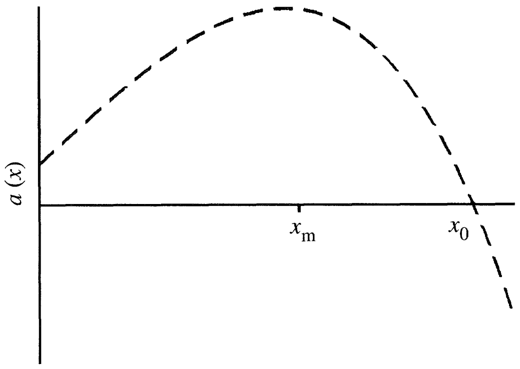

Figure 1. The general production function ($a(x)$) against population size (x), with the points of maximum net productivity (x_{m}) and unexploited equilibrium (x_0); note the general non-zero production at zero population size.

optimization, taking account of transient events. The deterministic models were developed and reviewed by Clark (1976, 1985). Some special cases of stochastic optimal harvesting were formalized (Reed 1984, 1988; Mangel 1985) and local solutions to the more general nonlinear stochastic harvesting and control problem were derived by Horwood & Whittle (1986*a*, *b*). Risk-sensitive versions and large-deviation treatments have also been developed (Horwood 1995). A feature of the stochastic models mentioned is that they recommend an operating point consistent with that which is optimal for a deterministic model. Many authors have emphasized the necessity to allow for uncertainty in resource management, although with differing opinions of the effectiveness of such management; see for example Ludwig *et al.* (1993) and Rosenberg *et al.* (1993).

The simplest deterministic models are expressed in terms of the net reproduction rate $a(x)$ (in terms of biomass) for a population of size (biomass) x. The function $a(x)$ is assumed to have the general character illustrated in figure 1. Significant quantities are the level x_{m} at which the net rate of production of biomass is maximal and the level x_0 at which the population would stabilize in the presence of exploitation.

The impetus for this study comes from the results and conclusions derived by Lande *et al.* (1994, 1995) on the optimal harvesting of populations which have a risk of extinction. They worked with the simple logistic population model which has been extensively used in resource management, and which has served as the basis for important recommendations on management strategy (Schaefer 1954; Clark 1976; Horwood & Whittle 1986*a*). For these simple models the optimal policy has an extreme threshold character: harvesting is carried out at the maximal rate when the population exceeds a critical value (the 'threshold') and at zero rate below it. The population will then stabilize at this threshold value. Previous studies have shown that the threshold value which maximizes rate of return is just x_{m}: the level of maximal net productivity (the maximal sustainable yield or maximal economic yield). If one rather optimizes discounted future return then the threshold falls as the discount rate is increased; ultimately to the value at which the marginal rate of return is zero (or profit is zero, for models linear in harvest rate). The finding by Lande *et al.* was that, if extinction is possible, then the population should be harvested only when it is above its natural, unharvested equilibrium level x_0. They admit the remarkable nature of this result.

It is a disconcerting result. It is unsettling mathematically because the optimal threshold seems to jump discontinuously from the deterministic recommendation x_{m} to the stochastic recommendation x_0, however small the degree of stochasticity. It is even more unsettling to those advising on resource management. The classic deterministic models provide a rationale for the operation of fisheries, whaling, hunting and forestry at the maximal sustainable economic level. The stochastic models which do not envisage extinction imply only slight and understandable deviation from this policy. The results of Lande *et al.* suggest that such advice and management over half a century may have been in error. The fate of populations is extinction, and the deterministic and stochastic models developed for resource management have neglected this aspect.

This paper confirms the fact of the conflicting recommendations for a range of stochastic models, but explains the conflict. It also explains how a proper balance of short- and long-term considerations leads to an intermediate threshold, which reassuringly converges to the classic recommendation x_{m} as the model tends towards determinism. The existence of a physical scale parameter κ which quantifies the closeness of the model to determinism is important in this context.

The paper confirms the apparently conflicting conclusions for three distinct stochastic models: a birth/death model, a diffusion model and a model whose only stochastic element is a random switching between different environmental regimes. The second is an elaboration of the Lande *et al.* analysis. The third differs from the other two in that stochasticity is totally environmental rather than demographic. It does indeed show some difference in conclusions, but the optimality of the two conflicting policies under extinction or non-extinction is again confirmed.

However, in §§5 and 6 we see that, whether extinction is possible or not, the emergence of the two extreme recommendations can in fact be explained. If extinction is possible then one recommendation or the other is optimal according as the criterion is the maximization of the total expected harvest before extinction or of the average expected harvest (i.e. the yield rate) over the time before extinction. The first criterion in particular is extreme because it turns out that maximization of total expected harvest is almost equivalent to maximization of the expected time to extinction, T_{ext}. The value of the yield rate plays almost no role. A balanced criterion would be one which maximized yield rate subject to the conservation condition that T_{ext} should not be smaller than a prescribed value T_{min}. However, T_{ext} increases very rapidly as the stochastic element is weakened: the optimal threshold then drops rapidly to the classical recommendation x_{m}.

If extinction is impossible then an obliterated population must be able to restart by some mechanism; let T_{ext} denote in this case the expected time taken to extinguish the population and T_{res} the expected time needed to restart it. Then the ratio $T_{\text{ext}}/T_{\text{res}}$ is crucial, and the optimal threshold lies near x_m or x_0 according as this ratio is large or small.

2. THE DETERMINISTIC MODEL

The simplest deterministic model has a single scalar variable x, the 'biomass' or stock level, which follows the equation

$$\dot{x} = a(x) - u. \tag{1}$$

Here u is the harvesting rate, which (it is supposed) may be varied as desired. The rate of return is also supposed proportional to u, and normalized to be equal to it. (The model thus neglects two very important elements: the age structure of the stock and the x-dependence of the cost of harvesting at rate u.)

We suppose that the function $a(x)$, the net reproduction rate of the unharvested population, has the concave form illustrated in figure 1. This is the simplest realistic form, but our discussion is easily extended to cover variations from it, such as the presence of an Allee effect. Let x_m and x_0 denote the levels at which $a(x)$ is respectively maximal and zero. An unharvested population would thus reach an equilibrium at $x = x_0$.

It is a relatively direct consequence of the dynamic programming equation for this model that the optimal policy has the threshold form: u is zero for $x \leqslant c$ and takes its maximal value (h, say) for $x > c$. Here c is the threshold, and one seeks now to determine its optimal value. If $a(x) > 0$ for $x \leqslant c$ and $a(x) - h < 0$ for $x > c$ then the harvested population has the equilibrium value c and yields a return at rate $Y = a(c)$. If we do not discount, and so choose a threshold value which maximizes this average return Y, then the optimal threshold is the value x_m which maximizes $a(c)$; (Clark 1976).

A threshold policy will still be optimal for a stochastic model under reasonable assumptions on transition rates. However, there is the effect observed in the introduction: that the optimal threshold seems to lie near x_0 or x_m according as to whether extinction of the population is possible or impossible. This is the effect observed by Lande *et al.* (1994) for a diffusion model, and which we shall now verify for a discrete stochastic model. The explanation and reconciliation will emerge in §6. In §§7 and 8 we shall indicate how these conclusions carry over to the diffusion model and, more interestingly, to a model in which the stochastic variation is environmental rather than demographic. The conclusions extend also to the case of discounted returns, as indicated in §6.

3. A BIRTH/DEATH MODEL WITHOUT EXTINCTION

The first stochastic model we take is a birth/death process. Suppose, for definiteness, that the population being harvested is one of fish; let j be the actual number of fish. We shall set $x = j/\kappa$ where κ is a scaling parameter, presumed large, reflecting the fact that quite usual levels of stock x correspond to large values of j. (We are forced to assume biomass proportional to population size, since we have not allowed for an age structure.) We shall suppose that j follows a continuous-time Markov process on the non-negative integers with possible transitions $j \to j+1$ and $j \to j-1$ at respective probability intensities λ_j and μ_j. These intensities thus correspond to population birth and death rates. The net reproduction rate $\lambda_j - \mu_j$ could be written a_j, and corresponds to $\kappa a(x)$. The scaling parameter κ is important; the model approaches determinism as κ increases.

Necessarily $\mu_0 = 0$, but we shall suppose initially that $\lambda_0 > 0$. That is, that a zero population is replenished (by a trickle of immigration, say), so that extinction is impossible.

Let π_j denote the equilibrium distribution of population size; the probability that the population has size j in the steady state. Then the relation $\pi_j \lambda_j = \pi_{j+1} \mu_{j+1}$ (expressing the balance of probability flux between states j and $j+1$ in equilibrium) implies that $\pi_j \propto \rho_j$, where

$$\rho_j = \frac{(\lambda_0 \lambda_1 \ldots \lambda_{j-1})}{(\mu_1 \mu_2 \ldots \mu_j)}, \quad (j \geqslant 0). \tag{2}$$

(The value of ρ_0 is in fact 1, and we shall take this as being the convention in such cases: that a product has value 1 when the set of labels over which it ranges is empty, see for example expression (9).)

A threshold c for the x-process implies a threshold $d \approx \kappa c$ for the j-process, in that d can be taken as the integer nearest to κc. For simplicity we shall suppose that the harvesting rate h is infinite, although the case of a finite rate can be treated almost as easily. Any excess of population over d is then immediately removed and one effectively has $\lambda_d = 0$ and $\rho_j = 0$ for $j > d$. The population is then confined to the range $0 \leqslant j \leqslant d$ and the average return (i.e. expected rate of return on the original x-scale in the steady state) is then

$$Y = \kappa^{-1} \pi_d \lambda_d = \rho_d \lambda_d / \kappa \sum_0^d \rho_j \tag{3}$$

the term $\pi_d \lambda_d$ representing the expected rate at which excess over c is produced and immediately cropped as harvest.

Suppose now that the ratio $\theta_j = \mu_j / \lambda_{j-1}$ is effectively constant (and less than unity) for j in the neighbourhood of d. The effect of this is that $\rho_{d-j} \sim \rho_d \theta_d^j$ ($j \leqslant d$), so the probability that the population is an amount j below threshold falls away exponentially fast with increasing j. Formula (3) then becomes

$$Y \sim \kappa^{-1} \lambda_d (1 - \theta_d) = \kappa^{-1} (\lambda_d - \mu_d) = a(c). \tag{4}$$

This is just the return rate for the deterministic model, maximized when the threshold c is chosen as the level x_m at which the net reproduction rate is maximal.

This argument can be made precise if we pay attention to the scaling. The nature of the scaling leads one to suppose that the birth and death rates are of the forms

$$\lambda_j = \kappa \lambda(j/\kappa), \; \mu_j = \kappa \mu(j/\kappa) \tag{5}$$

in terms of functions $\lambda(x)$ and $\mu(x)$, corresponding to the deterministic equation $\dot{x} = \lambda(x) - \mu(x) = a(x)$ in the limit of large κ. If $\lambda(x)$ and $\mu(x)$ are continuous then λ_j/μ_j will vary slowly with j if κ is large, with the consequence that the equilibrium distribution of x falls away virtually exponentially as x decreases from $c = d/\kappa$. The probability mass will indeed be concentrated in the region just at and below threshold if κ is large, at least if $\lambda_0 > 0$, because of the assumption implicit in the graph of figure 1, that $a(x) > 0$ for $0 \leqslant x \leqslant x_0$. This implies that μ_j/λ_j is less than unity for $j \leqslant \kappa x_0$ which implies a rapid tailing-off of the distribution as x falls from the threshold value.

Explicitly, it follows from (2) and the hypothesis (5) that we can write

$$\rho_j = e^{\kappa R(x) + o(\kappa)}, \qquad (6)$$

for large κ, where $x = j/\kappa$ and

$$R(x) = \int_0^x \log[\lambda(y)/\mu(y)]dy. \qquad (7)$$

As $R(x)$ is increasing for $x \leqslant x_0$ then it would appear from (6) that the distribution is concentrated where x is largest: at and near threshold. However, we need to refine expression (6) if we are to capture possible anomalies for small x. An appeal to the Euler-MacLaurin formula for numerical integration (see for example Margenau & Murphy (1943) p. 457) gives the refinement of (6)

$$\rho_j/\rho_d = \surd[\lambda(c)\mu(c)/\lambda(x)\mu(x)]\, e^{\kappa[R(x) - R(c)] + o(1)}$$

if the function $\log[\lambda(x)/\mu(x)]$ has a continuous first derivative. Inserting this into expression (3) we find that, for large κ, the dominant contribution to the sum in the denominator is from j near d and we confirm the evaluation

$$Y \sim \lambda(c)\,[1 - e^{-R'(c)}] = \lambda(c)\,[1 - \mu(c)/\lambda(c)] = a(c)$$

consistent with (4).

This calculation fails if $\lambda(x)$ behaves in such a way for small x that extinction is possible. This is the case we consider in the next section.

4. A BIRTH/DEATH MODEL WITH EXTINCTION

Suppose now that $\lambda_0 = 0$, so that extinction is possible (and indeed certain in a finite time if κ is finite and if, as we shall suppose, passage to $j = 0$ is possible from all states and the population is harvested above some finite threshold). Equation (2) then yields simply a distribution concentrated on $j = 0$.

Let F_j be the expected total return before extinction conditional on an initial population of j. (It is understood that the policy is that of harvesting at an infinite rate above the prescribed threshold d.) The dynamic programming equation is then

$$\lambda_j(F_{j+1} - F_j) + \mu_j(F_{j-1} - F_j) = 0, \quad (0 < j < d) \qquad (8)$$

with the effective boundary conditions $F_0 = 0$ and $(F_{d+1} - F_d) = 1$. This last relation follows because any excess over threshold is immediately removed and converted into yield.

Theorem 1. *Assume that passage to* 0 *is possible from all states and that the threshold* d *is finite. Then the relevant solution of* (8) *for is*

$$F_j = \Pi_d\left[\sum_{k=1}^{j} (\mu_1\mu_2\dots\mu_{k-1})/(\lambda_1\lambda_2\dots\lambda_{k-1})\right], \quad (0 \leqslant j \leqslant d). \qquad (9)$$

where

$$\Pi_d = (\lambda_1\lambda_2\dots\lambda_d)/(\mu_1\mu_2\dots\mu_d). \qquad (10)$$

Proof. We can write (8) as $\lambda_j\Delta_{j+1} = \mu_j\Delta_j$ where $\Delta_j = F_j - F_{j-1}$. Using this equation to determine Δ_j in terms of $\Delta_{d+1} = 1$ and then summing to determine F_j, we obtain the solution (9). ∎

Now, the d-dependence of the F_j occurs only through the common factor Π_d, and the optimal threshold will maximize this. The maximizing value will be that at which λ_d/μ_d decreases from a value above unity to one below, so that $a_d = \lambda_d - \mu_d$ decreases through zero. That is, the optimal value of c is x_0, the deterministic equilibrium level of the unharvested population. (The deterministic model has equilibria both at $x = 0$ and $x = x_0$, but only the second of these is stable, under our assumptions.) More exactly, it is less than x_0 by amount not exceeding κ^{-1}.

The two cases thus lead to radically different recommendations, as was observed by Lande *et al.* (1994) for the diffusion model. In the next two sections we explain exactly why this is so and to what alternative view one is led.

5. BEHAVIOUR FOR NEAR-DETERMINISTIC MODELS

To explain the apparent stark contradiction between the two recommended policies we need to obtain a feeling for orders of magnitude of the various quantities occurring as κ becomes large, and so the process approaches determinism.

Consider then the birth/death model with extinction of §4. Because most of the time before extinction will be spent near the threshold value if κ is large (an assertion which we shall shortly justify) we shall consider only F_d, the expected yield before extinction conditional on an initial value d of j.

Let T_j denote the expected time before extinction which is spent in state j (conditional on a start from d). Then, by the same methods which led to the evaluation (9), we find that

$$T_j = \Pi_d\left[\sum_{k=1}^{j} \frac{\mu_1\mu_2\cdots\mu_{k-1}}{\lambda_1\lambda_2\cdots\lambda_{k-1}}\right]\left[\frac{\mu_{j+1}\mu_{j+2}\cdots\mu_d}{\lambda_j\lambda_{j+1}\cdots\lambda_d}\right] \qquad (11)$$

which is consistent with expression (9) for $F_d = \lambda_d T_d$.

When we see the process in terms of the scaled variable $x = j/\kappa$ we shall write $F_j = \kappa F(x)$ and $T_j = T(x)$. We then deduce from expression (9) that

$$F(c) = e^{\kappa R(c) + o(\kappa)} \qquad (12)$$

for large κ, where $R(x)$ is the function defined in (7). We thus see that $F(c)$ grows exponentially fast with κ. Indeed, we see from (11) that the same holds true for the occupation times:

$$T(x) = e^{\kappa R(x) + o(\kappa)} \qquad (13)$$

for any fixed x. Relations (12) and (13) can be refined, but the only more exact relation which we shall need is

$$T_j = (\rho_j/\lambda_0)\left[\sum_{k=1}^{j}(\mu_1\mu_2\dots\mu_{k-1})/(\lambda_1\lambda_2\dots\lambda_{k-1})\right] \approx S\rho_j/\lambda_0, \qquad (14)$$

where

$$S = \sum_{k=1}^{d}(\mu_1\mu_2\dots\mu_{k-1})/(\lambda_1\lambda_2\dots\lambda_{k-1}). \qquad (15)$$

In the next section we shall interpret S/λ_0 as the expected time taken for a population which has been extinguished to be reseeded and to grow to viability. The sum in (14) will differ from S by a term of order at most $\theta^j(1-\theta)^{-1}$, where θ is an upper bound on the ratio μ_j/λ_j in the range $0 < j < d$. The value of j at which this term becomes negligible marks the level at which the population has attained viability.

The scaling argument will again imply that $\theta_j = \mu_j/\lambda_j$ varies only slowly if κ is large, with the implication from (14) that

$$T_{d-j} \sim T_d\,\theta_d^j,$$

for fixed j; an analogue of the corresponding assertion of π_j in §3. If we define $T_{\text{ext}} = \sum_{j=1}^{d} T_j$, the expected time to extinction, then

$$T_d/T_{\text{ext}} \sim 1-\theta_d = 1-\mu(c)/\lambda(c), \qquad (16)$$

so that $1-\theta_d$ is a measure of the proportion of time before extinction which is actually spent at threshold. Moreover, because $\sum_{j\leqslant\kappa x} T_j/T_{\text{ext}}$ decreases to zero with increasing κ we can just as well interpret T_{ext} as the expected time needed to escape permanently from any neighbourhood of d. In other words, the time to extinction is asymptotic (with increasing κ) to the time at which harvesting becomes commercially unprofitable.

Suppose that $\mathscr{Y}$ is the actual total yield (on the x-scale) before extinction and $\mathscr{T}$ the actual time to extinction, so that these are random variables with respective expectations $F(c)$ and T_{ext} (conditional on a start from $x = c$). Then a closer analysis shows that in fact $\mathscr{Y}/F(c)$ and $\mathscr{T}/T_{\text{ext}}$ converge to unity in almost any stochastic sense as $\kappa\rightarrow\infty$. The point is that x recurs to c a great many times before it ultimately drops to zero, and the contributions to $\mathscr{Y}$ or $\mathscr{T}$ from each of these excursions away from c and back are independent and identically distributed random variables. The consequence is that the expectation of the average rate of return before extinction, $\mathscr{Y}/\mathscr{T}$, can be replaced by the ratio of expectations:

$$E(\mathscr{Y}/\mathscr{T}) \approx E(\mathscr{Y})/E(\mathscr{T}) = F(c)/T_{\text{ext}},$$

the relation becoming exact in the limit of large κ. Relation (16) then implies the evaluation

$$\begin{aligned} F(c)/T_{\text{ext}} &= \kappa^{-1}F_d/T_{\text{ext}} \sim \kappa^{-1}\lambda_d(1-\theta_d) \\ &= \kappa^{-1}(\lambda_d-\mu_d) = \lambda(c)-\mu(c) = a(c) \qquad (17) \end{aligned}$$

for the expected average return over the period before extinction.

That is, the expected rate of return over the time before extinction converges to the equilibrium rate of return for the deterministic process as $\kappa\rightarrow\infty$.

6. THE UNDERSTANDING OF THRESHOLD CHOICE

The expression deduced from (9) and (10) for F_d, the expected 'total return' before extinction, is essentially maximal at the value of d which maximizes Π_d, and so for the threshold c near to x_0. Expression (17) for the expected 'rate of return' before extinction (when κ is large) is again maximal for c near to x_{m}. We see then that the discrepancy is not a consequence of differing assumptions, because these two evaluations have been made for the same process; one for which ultimate extinction is certain. It is a consequence of differing criteria. To ask for maximal total return and to ask for maximal average return over the time to extinction (of stock or, almost equivalently, of commercial viability) are two very different things. They differ so because the exponential dependence of T_{ext} upon κ means that T_{ext} varies extremely rapidly with c, whereas the average return (17) varies only moderately. The maximization of expected total return then amounts virtually to the maximization of expected survival time, with the rate of return playing a role which actually becomes ever less significant as κ increases. Indeed, the recommendation is virtually that one should not harvest.

In fact, both criteria are extreme, one taking the yield rate before extinction and the other the time to extinction as virtually the sole consideration. A balanced criterion would be one which chose the threshold c to maximize yield rate $Y = a(c)$ subject to a prescribed lower bound on expected extinction time T_{ext}. Because this last expression depends exponentially upon κ (which is what induces the sensitivity of its dependence upon c) one might consider rather the normalized expression

$$L(c) = \lim_{\kappa\rightarrow\infty}\kappa^{-1}\log T_{\text{ext}}.$$

This has the evaluation

$$L(c) = \begin{cases} R(c), & (c \leqslant x_0) \\ R(x_0) & (c \geqslant x_0) \end{cases} \qquad (18)$$

where R is indeed the function defined in (7).

The two quantities $a(c)$ and $L(c)$ vary jointly with threshold c as indicated in figure 2; $a(c)$ increases with c up to the value x_{m} and declines thereafter; $L(c)$ increases with c up to the value x_0 and is constant thereafter. Thus if one prescribes the value of T_{ext} as at least T_{min}, then $L(c)$ must be at least $\kappa^{-1}\log T_{\text{min}}$. For small enough κ one will thus have to take x_0 as threshold, but as κ increases the recommended threshold will decrease rapidly to the value x_{m}.

Interestingly, one can reach this same view by returning to the model of §3: the birth-death model without extinction. It follows from (14) and (16) that we can write expression (3) for the yield rate in the steady state as

$$Y \cong \frac{\lambda(c)\,T_d}{(S/\lambda_0)+T_{\text{ext}}} \approx a(c)\,[1+(S/\lambda_0\,T_{\text{ext}})]^{-1}, \qquad (19)$$

where the terms neglected are $o(1)$ in κ. Here T_{ext} is now to be interpreted as the time to first extinction for

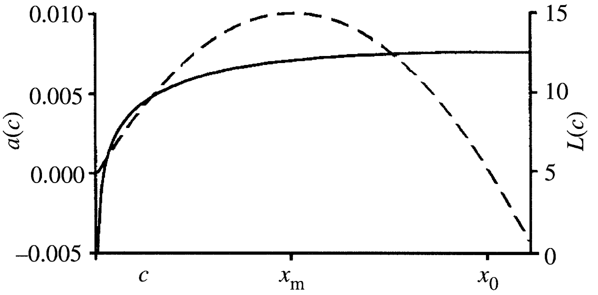

Figure 2. The production function ($a(c)$), denoted by the dashed line; and the normalized logarithm of the time to extinction ($L(c)$) denoted by the solid line. The logistic population model and variance used is that of Lande *et al.* (1994) neglecting the Allee effect.

this immortal population. Now, λ_0 is the rate at which a population which has been reduced to zero is restarted by some external mechanism, so that λ_0^{-1} is the expected 'seeding' time. This seeding does not amount to an effective restart until numbers have been brought up to viability; we can regard (S/λ_0) as the expected time needed for this to occur, the expected restart time. Let us then denote it by T_{res}, so that expression (19) for Y becomes

$$Y \approx a(c)\,[1+(T_{\text{res}}/T_{\text{ext}})]^{-1}. \tag{20}$$

This is then approximately $a(c)$ or $a(c)\,(T_{\text{ext}}/T_{\text{res}})$ according as to whether the restart time is small or large relative to the extinction time. Because T_{res} is effectively independent of c, these two extreme evaluations are equivalent to those obtained for the two extreme criteria in the case when extinction was possible. As one varies the value assumed for T_{res} one moves monotonically between these two extremes, just as one did by varying the prescribed value T_{min} in the constrained optimization of yield rate.

Note that if μ_j/λ_j is slowly varying (and less than unity) for small positive j then $S \approx (1-\mu_1/\lambda_1)^{-1}$, so that

$$T_{\text{res}} \approx \lambda_1/\lambda_0(\lambda_1-\mu_1). \tag{21}$$

The quantity S is then best interpreted as the ratio of individual birth rate to individual net production rate at low population densities.

If we consider discounted criteria then the possibility of extinction is seemingly irrelevant, because any accounting horizon is orders of magnitude smaller than a prudent lower bound for the extinction time, the conservation horizon. As above, then, the constraint of such a lower bound must be imposed explicitly. That is, suppose δ is the discount rate and that $F(c,\delta)$ is the discounted future yield at an operating level (and threshold) of c, calculated on the basis of a deterministic model. Then one should choose c to maximize $F(c,\delta)$, subject again to prescription of a lower bound T_{min} on T_{ext}. As in the undiscounted case above, the effect of this constraint will weaken rapidly as the scale parameter κ increases, and the model approaches determinism.

7. A DIFFUSION MODEL

We shall briefly indicate how the analysis of the last four sections transfers to two other stochastic versions of the model: a diffusion version and an environmental switching version. Some degree of explicit analysis is justified in that the diffusion model was that considered by Lande *et al.* and the switching model brings in a new feature: environmental rather than demographic stochasticity. To repeat the analysis at the level of detail of §§3 and 4 would be tiresome, however: readers who wish for such detail are referred to Whittle (1996). In fact, there will be a single treatment which covers a range of very general versions of the stochastic model, some readers may have recognized the appeal to large deviation theory which is implicit in our κ-scaling arguments. This we hope to give in a later publication.

Suppose the deterministic harvesting equation (1) modified to the stochastic differential equation

$$\dot{x} = a(x) - u + \epsilon, \tag{22}$$

where ϵ is white noise of power $v(x)/\kappa$. We introduce the factor κ so that the model can be made to approach determinism by allowing κ to become larger; a scaling assumption which is in fact consistent with that for the birth/death process.

If the unharvested version of the model (i.e. that for which $u \equiv 0$) has an equilibrium distribution then this has probability density

$$\pi(x) \propto \rho(x) = v(x)^{-1}\mathrm{e}^{-\kappa R(x)}$$

where

$$R(x) = 2\int_0^x a(y)\,v(y)^{-1}\,dy. \tag{23}$$

If harvesting is carried out at an infinite rate for $x > c$ then one finds that the average rate of return is

$$Y = \rho(c)v(c)\bigg/\left[2\int_0^c \rho(x)\,dx\right].$$

Since $R(x)$ increases with x for $x < x_0$ this has the evaluation

$$Y \sim \tfrac{1}{2}v(c)R'(c) = a(c),$$

for large κ; indeed that of the deterministic case, and maximal at x_m.

If extinction is possible, in that the state value $x = 0$ is absorbing for the process (22), then analysis similar to that of §4 shows that $F(x)$, the total expected return before extinction conditional on an initial value x, has the evaluation

$$F(x) = \mathrm{e}^{\kappa R(c)}\left(\int_0^x \mathrm{e}^{-\kappa R(y)}\,dy\right), \quad (0 \leqslant x \leqslant c),$$

in the case of an infinite harvest rate. The value of c maximizing $F(c)$ is essentially the value x_0 which maximizes $\mathrm{e}^{\kappa R(c)}$. In fact, the maximizing value exceeds x_0 by an amount which tends to zero as κ becomes large.

The apparently conflicting conclusions of §§3 and 4 thus hold also for the diffusion model. The reconciliation of §§5 and 6 also holds, with only the modification that $R(x)$ now has the evaluation (23).

8. A MODEL WITH A SWITCHING ENVIRONMENT

Suppose that the model has several environmental regimes, labelled by $i = 1, 2, \ldots$. In regime i the population grows deterministically at net rate $a_i(x)$, but transition can take place to regime j with probability intensity $\kappa\nu_{ij}$. This is then a model in which the stochasticity is of quite a different nature to that of the last two models. It comes from without rather than within, i.e. is environmental rather than demographic. Conclusions could be very different in such a case. Such models are known as 'piecewise deterministic'.

The equivalent deterministic model would be given by equation (1) but with

$$a(x) = \sum_i p_i a_i(x), \tag{24}$$

where p_i is the steady-state probability that the system is in regime i. The model converges to this deterministic version if transitions between regimes take place so rapidly that one is essentially working in an 'average regime'. This occurs in the limit of large κ, so that κ again appears as the natural scaling parameter.

A fixed threshold would certainly not be optimal for such a multi-regime model. It is likely that the optimal policy would be of a threshold nature, but with a different threshold in each regime. In practice, one could not even be sure of what regime one was in, and would have to infer it from imperfect observations. The optimal policy would then necessarily be even more complicated. However, we shall consider only the crude fixed-threshold policy, and shall see how the optimal threshold value compares with that for the equivalent deterministic model.

We shall consider a two-regime case, which is amenable to analysis. A value of x at which $a_1(x)$ and $a_2(x)$ have the same sign cannot have positive probability in equilibrium. Let us suppose then that $a_1(x) = \lambda(x) \geqslant 0$ and $a_2(x) = -\mu(x) \leqslant 0$ over an interval $0 < x < M$ which includes all x-values of interest. We shall set $\nu_{12} = \nu_1$ and $\nu_{21} = \nu_2$.

Suppose initially that extinction is impossible, so that the aim is to maximize the expected rate of return Y in the steady state. We shall suppose that the maximal harvest rate h is infinite. For the deterministic equivalent of the process we have, by (24),

$$a(x) = [\nu_2\lambda(x) - \nu_1\mu(x)]/(\nu_1+\nu_2). \tag{25}$$

We shall suppose that this has the character indicated in figure 1. We also suppose that $\mu(x) = 0$ for $x \leqslant 0$, so that x is indeed confined to $x \geqslant 0$.

The question of extinction or non-extinction is more subtle for this model. Suppose, for example, that $\lambda(0) = 0$ (so that a zero population cannot be replenished) and that $\mu(x)$ is bounded away from zero for positive x. Then extinction would be certain, because there is a non-zero probability that the unfavourable regime 2 can be held long enough that the population is run down to zero. For extinction to be impossible in an isolated population one requires that $\mu(x)$ should tend to zero sufficiently fast as x decreases to zero.

An analysis of the non-extinguishable case shows that the average rate of return under the c-threshold policy is

$$Y = \lambda(c)\Big/\left[1+\kappa\nu_1\int_0^c \exp\left[\kappa R(x)-\kappa R(c)\right]g(x)\,dx\right], \tag{26}$$

where $g(x) = \lambda(x)^{-1}+\mu(x)^{-1}$ and

$$R(x) = \int_0^x [\nu_2\mu(y)^{-1}-\nu_1\lambda(y)^{-1}]\,dy. \tag{27}$$

In the limit of large κ expression (26) indeed reduces to $Y = a(c)$, with $a(x)$ specified by (25).

In the case when extinction is possible one finds that the expected return before extinction is, for any initial state x, proportional to $\lambda(c)e^{\kappa R(c)}$, with R given by (27), and it is this quantity which should be maximized with respect to c. For κ large this amounts to the maximization of $R(c)$, i.e. to the equation $a(c) = 0$, with $a(x)$ having the determination (25). That is, the optimal threshold again approaches the value x_0.

The reconciling analysis of §§5 and 6 again goes through, with $R(x)$ now having the evaluation (27).

9. DISCUSSION

The models presented above are unrealistically simple. Nevertheless, they possess much of the structural form to be found in more realistic and complex models, and their use for optimization purposes has revealed and clarified many of the important features of more complex models (see for example Clark 1976). Furthermore, they reveal the essential effects of stochasticity and scale-dependence which will be seen in more complex models.

For discrete- and continuous-time models, which incorporate demographic stochasticity and for which extinction is not possible through stochastic events, the threshold (and so population level) which maximizes yield rate is close to the point x_m of maximal net productivity (the maximum sustainable yield level, MSYL) as for the equivalent deterministic models (see §§2, 3 and 7).

For these same models, modified so that extinction is possible (and indeed inevitable), the threshold which maximizes expected total future yield is x_0, the point of zero net productivity (see §§4 and 7). These results are consistent with those of Lande *et al.* (1994) and indicate a generally valid conclusion.

The models incorporated a 'demographic' variability which is readily identifiable as such in the birth/death model, but which can be interpreted in different ways for the diffusion model. For example, Lande *et al.* (1994) assumed a noise variance with components of orders x and x^2 in population size x; these can be construed as corresponding to 'demographic' and 'environmental' variability respectively. The character of the variability significantly affects expected times to extinction (Pimm *et al.* 1988).

The switching model of §8 expresses environmental variability in the very explicit form that the 'environmental regime' (and so the nature of the population dynamics) can switch randomly. If we assume a fixed-threshold policy then the threshold which maximizes yield rate is again near the MSYL x_m if extinction is impossible. If extinction is possible then the threshold which maximizes expected total future yield is near, but strictly above, the unexploited equilibrium level x_0. In this case the partially optimized policy exploits the fact that the population will spend periods above x_0.

In §§5 and 6 we resolved the conflict between the two recommendations in a way which is mutually consistent for the two rather different cases: when extinction is possible and when it is not. The analysis required an explicit recognition of the timescale of events, and also of the physical scale of the system itself, which affects the relative scale of stochastic effects. This was to have been anticipated, for, if extinction were to occur over geological timescales, would one not expect to harvest a population robustly? If the model is near-deterministic then, as pointed out by Lande *et al.* (1995), the final run to extinction (from threshold, say) is quick, and the time to extinction is proportionately little more than the time for which the population is near enough to threshold to be commercially viable. This point, discussed briefly and heuristically in §5, is actually the reason why the average yield over the time up to extinction converges to the yield-rate for the deterministic limit model in the limit of large physical scale. In this discussion of timescales it should be emphasized that the introduction of discounting supplies no reconciliation; indeed, it impels one to short-term policies. One must take explicit account of conservation horizons, which are greatly more distant than accounting horizons.

We see from the discussion of §§4 and 5 that the recommendation of the two different thresholds, x_m or x_0, is (in the case when extinction is possible) not a consequence of a difference in models, but of difference in criteria. The total yield before extinction is a product of the average yield-rate and the time to extinction. The average yield rate is a fairly stable quantity, in that it converges to the steady-state value as the process becomes near-deterministic, and varies with threshold in much the same way. However, the time to extinction increases very rapidly as the process approaches determinism. For this reason it shows such a sensitive dependence upon threshold that a choice of threshold to maximize expected yield before extinction effectively maximizes extinction time at the expense of average yield.

An additional insight into this process is given by Reed (1988), who considered the harvest from a population subject to the chance event of collapse from hazards other than harvesting. The extra risk acts in the same way as an increased discount rate, and if the hazard is independent of population density, impels one to harvest harder before Nature strikes. However, if the hazard rate decreases with increasing population size then there is a countervailing effect, inducing one to harvest the population at a higher threshold and so a lower rate.

The objectives of maximizing yield-rate or total yield individually are both extreme. It is natural to consider the balanced policy which optimizes yield rate subject to a lower bound on extinction time which is acceptable on conservation grounds. This is a view propounded by Wissel & Schmitt (1987), and made workable by the $a(c)/L(c)$ evaluations of §6. As variability decreases the optimal threshold under this constraint decreases quite rapidly from the unexploited equilibrium level x_0 to the MSYL x_m.

A similar conclusion holds for models for which extinction is impossible, and so the population is immortal. The yield rate achieved at a given threshold c can be expressed as $Y = a(c)/[1+(T_{res}/T_{ext})]$, where $a(c)$ is the yield rate for the deterministic model at that threshold, T_{ext} is the time to the first extinction (which will not be permanent) and T_{res} is the restart time; the time needed for an extinguished population to be re-seeded and to grow to demographic viability. In maximizing Y with respect to c one effectively maximizes $a(c)$ or T_{ext} according as the ratio T_{ext}/T_{res} is large or small. As physical scale increases then T_{ext} increases very rapidly, and so the optimal threshold falls from x_0 to x_m. An estimate of T_{res} is given in formula (21) under assumptions stated there. If these fail to hold (e.g. if there is an Allee effect) then the expression $T_{res} = S/\lambda_0$ must be approximated in some other way.

Some populations are unique: their extinction is then final. However, most populations are subject to restarts or the so-called ‘rescue effect’. Migration amongst exploited populations of fish, whales and seals is well documented, and captive breeding and release provide another mechanism for restarts. However, the practical determination of models for populations subject to extinctions which may or may not be final demands much of our knowledge. Models of the type we have considered are unlikely to represent the behaviour of populations adequately at low levels. Further, inaccurate modelling of the demographic and environmental stochasticity can be qualitatively misleading (May *et al.* 1978; Shepherd & Horwood 1980). As an example of the quantitative sensitivity of extinction times, if the Allee effect is removed from the population response assumed by Lande *et al.* (1994) then the extinction time is increased by a factor of four, but if the variability is halved then the extinction time is increased by a factor of order 10^5.

Irrespective of model construction, progress has been made in the measurement of quantities such as extinction times, colonization rates and immigration rates (MacArthur & Wilson 1967; Pimm *et al.* 1988; Smith *et al.* 1993) which are useful in the development of conservation plans. However, caution in interpretation is necessary, as one is observing the dynamic process between the conflicting factors of extinction and recolonization (MacArthur & Wilson 1967; Tracy & George 1992) and observations are usually highly selective and over only limited times. It is to be hoped that we do not obtain data on the extinction rates of our great populations of fish and marine mammals, and that such parameters will have to be inferred from other sources of information.

The concept of population extinction has not played an obviously prominent and explicit role in advice on resource management. To some degree this is because extinction time is highly dependent upon the absolute size of populations and many exploited populations are large. However, even large populations will become small. Approaches developed under the Rio Convention on Biological Diversity and the Rio Declaration on Sustainable Development (Anon. 1994*a*, *b*) may bring the issue of extinction into the foreground. Over longer time periods the management objectives considered in this study are naive, for populations subject to extinction. More sophisticated objectives would be required, taking account for example of uncertain future utility of a resource (Reed 1993).

In the meantime, guidance can be given for optimal resource management. If a population has a 'small' expected time to extinction then explicit consideration must be given to the effects of exploitation on the time to extinction in comparison with the benefits from exploitation. 'Small' is obviously a subjective concept in the absence of a detailed understanding, and benefits can be large even from slowly reproducing populations if a surplus is harvested to release capital for alternative investments. However, benefits would have to increase very rapidly with harvest rate to overturn the conclusion that maximal total return would be achieved by a low rate of exploitation. If one specified a minimal acceptable time to extinction which was of the same order as the expected time to extinction in the absence of harvesting then one would reach the same conclusion. If the extinction time is of conservation significance than it follows that benefits should *not* be calculated using economic discount rates, as this feature would quickly dominate results and effectively remove any concern for extinction. If however the natural extinction times, or times to 'first extinction', are 'large'; as they are likely to be for many populations of fish, whales and seals, then a harvest rate close to MEY would be appropriate, and the classical advice on resource management holds.

Finally, in this study we have neglected age-structure, costs and discounting. The appeal to the concept of physical scale (essentially, an application of large-deviation methods) will hold also for the vector case, and it is anticipated that our conclusions will generalize to age-structured population models. If there are costs associated with harvesting then the concept of a 'threshold' becomes more diffuse, but one suspects that the general recommendation of an operating point which drops from the point of zero profit to MEY as the model approaches determinism will hold. As we have already indicated, discounting has the effect of making the contingency of extinction seem so remote as to be irrelevant. Its relevance can be restored only by, again, making the optimization of threshold subject to the conservation constraint of a lower bound on the expected time to extinction.

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