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Harvesting Strategies for Fluctuating Populations Based on Uncertain Population Estimates

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This paper deals with models for optimal annual harvesting of populations in a fluctuating environment. By adopting threshold harvesting and assuming known population size, the optimal threshold that maximizes the expected cumulative yield before extinction is derived. The optimal threshold is practically independent of the form of density regulation, is smaller than the carrying capacity, and decreases with the environmental variance. We also analyse the effect of uncertainty in the population estimates, defined by a parameter θ_0, which is the coefficient of variation in the population estimate when the population is at the carrying capacity. By adopting threshold harvesting based on the estimated population size, the optimal threshold increases with θ_0. For large uncertainty in the estimates we propose a new harvesting strategy called *proportional threshold harvesting* for which only a given fraction, q, of the difference between the population estimate and the threshold is harvested if the population estimate is larger than the threshold. Numerical calculations show that this method is preferable to pure threshold harvesting when the uncertainty in the estimate exceeds some value depending on the environmental variance. A formula for the optimal threshold for a given q and a small θ_0 is derived. This formula is also independent of the form of density regulation. We also give examples of numerical calculations of the expected time to extinction, mean annual yield and the mean fraction of years the population can be harvested. Finally, we present some simulations demonstrating population fluctuations and harvesting based on uncertain population estimates.

Introduction

Stochastic variation in the environment strongly influences the population dynamics of several species that are or can be subject to harvest (Fogarty *et al.*, 1991; Owen-Smith, 1990; Albon *et al.*, 1987; Sæther *et al.*, 1996a). For populations that are not very large or do not have a very large growth rate, this environmental variability may lead to extinction being of real concern (Lande, 1993). For small populations demographic stochasticity will further increase the probability of extinction. Development of harvesting strategies that takes into account the risk of extinction may therefore be crucial for a proper management of such populations. Previously we have shown (Lande *et al.*, 1995) that when the population size is known and harvesting can be done continuously, threshold harvesting (cf. Getz & Haight, 1989; Quinn *et al.*, 1990; Zheng *et al.*, 1993; Whittle & Horwood, 1995) is the strategy that maximizes the cumulative yield before extinction as well as the sustained annual yield. This means that when the population size is above some threshold c, then harvesting should be carried out with maximum efficiency until the threshold is reached. Below the threshold there should be no harvesting. The value of the threshold depends on the harvesting capacity. A remarkable general result is that the cumulative yield is maximized by choosing the threshold at the carrying capacity, K, if the harvesting capacity is infinite. For limited harvesting capacities the threshold is smaller, and in general the threshold that

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maximizes the expected cumulative yield is larger than the threshold maximizing the average annual yield (Sæther *et al.*, 1996b).

Estimating population sizes in the field is often difficult, resulting in large uncertainties in the estimates (Seber, 1982; Clark & Kirkwood, 1986; Buckland *et al.*, 1994). Obviously, the impact of harvesting on population fluctuations will be strongly affected by these uncertainties. For instance, in a deterministic population model with density-dependence the maximum sustained yield is achieved when the population is kept at the density where its growth is maximum. Small uncertainties in the population estimates can then cause severe rapid reductions in the population size (Ricker 1963). Similarly, in a stochastic model, Beddington & May (1977) show that fluctuations in population size reduce both the maximum mean annual yield and the stability.

In the present paper we examine how harvesting should be performed when the population estimates are uncertain and the risk of extinction is taken into account. Even if threshold harvesting seems to perform quite well with respect to expected yield, it may often lead to very large variances in the annual yield. To cope with this problem we propose a new harvest tactic that we call proportional threshold harvesting. This tactic is also based on a threshold, but one only harvests some fixed proportion of the difference between the population estimate and the threshold each season, which is different from harvesting down towards some threshold at a given rate. The proportional threshold harvesting reduces the expectations slightly, but reduces substantially the annual fluctuations in the yeild. We compare different tactics by computing the mean time to extinction, the expected cumulative yield before extinction, the mean annual yield and the coefficient of variation in the annual yield.

The Population Model

Following Lande *et al.* (1995) we consider models where the annual change in the population size is

$$\Delta N = r(t)N - g(N) - y, \tag{1}$$

where $r(t)$ is the specific growth rate at time t and $g(N)$ is a density regulating term. The quantity y, which may be a stochastic variable, represents annual yields from harvesting. We assume that the specific growth rate $r(t)$ fluctuates stochastically between years with mean $\bar{r}$ and write $\mathrm{Var}[r(t)N|N] = V_r(N)$. Then, if ΔN is not too large relative to N, the process may be approximated by a diffusion (Turelli, 1977; Karlin & Taylor, 1981; Lande *et al.*, 1995) with infinitesimal mean and variance

$$M(N) = E[\Delta N|N] = \bar{r}N - g(N) - M_y(N) = M_r(N) - M_y(N) \tag{2}$$

$$V(N) = \mathrm{Var}[\Delta N|N] = V_r(N) + V_y(N) \tag{3}$$

where $M_y(N)$ and $V_y(N)$ are the expectation and variance in the annual yield y when the population size is N, while $M_r(N)$ and $V_r(N)$ are the infinitesimal mean and variance in the absence of harvesting. The assumption of sufficiently small ΔN is realistic for most species with overlapping generations (Lande *et al.*, 1997). This approach corresponds to applying the Ito calculus to the stochastic differential equation obtained by replacing ΔN and $\Delta t = 1$ in (1) by dN and dt. A simple model incorporating both demographic variance, σ_d^2, and environmental variance, σ_e^2, in $r(t)$ is $V_r(N) = \sigma_d^2 N + \sigma_e^2 N^2$ (Lande *et al.*, 1995; Engen *et al.*, 1996).

The expected cumulative yield before extinction can be expressed by the Green function for the diffusion. Defining the functions

$$s(N) = \exp\left\{-2\int_1^N \frac{M(x)}{V(x)}\mathrm{d}x\right\} \tag{4}$$

$$m(N) = 1/[s(N)V(N)] \tag{5}$$

$$S(N) = \int_1^N s(x)\mathrm{d}x, \tag{6}$$

and noting that $S(\infty) = \infty$ because the boundary at infinity is inaccessable for biologically realistic models, the Green function (Karlin & Taylor, 1981, ch. 15.3) for a process starting at N_0 is

$$G(N,N_0) = \begin{cases} 2m(N)S(N) & \text{for } N < N_0 \\ 2m(N)S(N_0) & \text{for } N > N_0 \end{cases}. \tag{7}$$

With initial population size N_0 the expected time to extinction is given by

$$T(N_0) = \int_1^\infty G(N,N_0)\mathrm{d}N, \tag{8}$$

and the expected cumulative yield before extinction is

$$Y(N_0) = \int_1^\infty M_y(N)G(N,N_0)\mathrm{d}N. \tag{9}$$

Lande *et al.* (1995) have shown that this can be written in the form

$$Y(N_0) = (N_0 - 1) + \int_1^\infty M_r(N)G(N,N_0)\mathrm{d}N. \quad (10)$$

The harvesting strategy that maximizes $Y(N_0)$ also maximizes $Y(1+\delta)$ for $1+\delta < N_0$. This is because the expected yield before extinction is the sum of two parts: the first part is the expected yield until the population first reaches $1+\delta$, and the second part is $Y(1+\delta)$. Sending δ to zero, this implies that the optimal solution is found by maximizing the derivative of $Y(N_0)$ with respect to N_0 at $N_0 = 1$. Taking the derivative of (10) and subtracting the constant 1 this can be written as the integral

$$I = \int_1^\infty M_r(N)m(N)\mathrm{d}N. \quad (11)$$

Hence, the cumulative yield before extinction is maximized by the harvesting tactic that maximizes (11).

Harvesting Strategies

We now assume that estimates $\hat{N}$ of the population size N are available each year. If n individuals are discovered in a proportion α of the population area and p is the probability of discovering each individual in this area, then $\hat{N} = n/(\alpha p)$ is an unbiased estimator of N. If the individuals are randomly distributed, n is binomial with parameters $(N, \alpha p)$ and $\mathrm{Var}(\hat{N}) = N(1-\alpha p)/(\alpha p)$ (Seber, 1982; Buckland *et al.*, 1993). The coefficient of variation of the estimate is $CV(\hat{N}) = \sqrt{(1-\alpha p)/(N\alpha p)}$ and the estimate of this is simply $\widehat{CV}(\hat{N}) \approx \sqrt{(1-\alpha p)/n}$ or just $1/\sqrt{n}$ if αp is small. Patchiness will often make the variances much larger, but still proportional to N. This also applies for line transect sampling, though p in that case must be estimated from the data (Seber 1982). In accordance with these results, it is often a good approximation to assume that the estimators are normally distributed with mean N and variance $\theta^2 N$, where θ is some constant depending on the sampling method, the effort and the degree of patchiness. Harvest quotas are decided once a year at the time when population estimates are available. Considering the general class of strategies $y = y(\hat{N})$, the mean and variance of y conditioned on N are

$$M_y(N) = E[y(\hat{N})|N] = \int y(\hat{N})f(\hat{N}|N)\mathrm{d}\hat{N} \quad (12)$$

$$V_y(N) = \mathrm{Var}[y(\hat{N})|N] = \int y(\hat{N})^2 f(\hat{N}|N)\mathrm{d}\hat{N} - M_y(N)^2 \quad (13)$$

where

$$f(\hat{N}|N) = \frac{1}{\sqrt{2\pi N\theta^2}} \exp\left\{\frac{(\hat{N}-N)^2}{2\theta^2 N}\right\}. \quad (14)$$

Our problem is now to find the harvesting strategies $y(\hat{N})$ that maximize the expected cumulative yield before extinction, which is equivalent to maximizing the integral (11). We have not been able to find the general solution to this problem, but previous results for the case when the population size is known (Lande *et al.*, 1995) indicate that threshold harvesting based on $\hat{N}$ will be a good strategy, at least for small values of θ. We then consider functions of the type

$$y(\hat{N};\, c) = \begin{cases} \hat{N} - c & \text{for } \hat{N} > c \\ 0 & \text{otherwise.} \end{cases} \quad (15)$$

This approach is based on the estimate $\hat{N}$ only. However, since the population model is assumed to be known, we also have some prior information about N that in principle could be used to adjust the estimate. For a given harvesting strategy N will possess some quasi-stationary distribution (Beddington & May, 1977). We could consider N as generated from this distribution, or more realistically, as generated from some prior distribution based on past catches and abundance surveys. A suitable later estimate is then $E(N|\hat{N})$, where the expectation is taken with respect to the posterior distribution conditioned on $\hat{N}$. Using the normal approximation for the bivariate prior distribution of N and $\hat{N}$, the expectation given above is linear in $\hat{N}$, say $q\hat{N} + a$, where $0 \le q \le 1$. This linearity is a general property of the bivariate normal distribution and a good approximation for other bivariate distributions. In general we may consider this as a first order approximation to the function $E(N|\hat{N})$. Applying threshold harvesting based on this improved estimator, we obtain harvesting functions of the form

$$Y(\hat{N};\, q,\, c) = \begin{cases} q(\hat{N} - c) & \text{for } \hat{N} > c \\ 0 & \text{otherwise.} \end{cases} \quad (16)$$

Thus, as in the case of pure threshold harvesting, the population is only harvested when the estimated population size is above some threshold c. However, when $\hat{N} > c$ we only harvest a proportion q of the difference between the estimate $\hat{N}$ and c. This is an alternative to previously proposed harvesting strategies (Getz & Haight, 1989; Quinn *et al.*, 1990; Zheng *et al.*, 1993). We call this strategy of stochastic harvesting with uncertain population estimates *proportional threshold harvesting*. Notice that this tactic is quite different from harvesting $q\hat{N}$ for $\hat{N} > c$ (Getz & Haight, 1989; Quinn *et al.*, 1990; Zheng *et al.*, 1993), which means choosing a constant harvesting rate q for $\hat{N} > c$. The approach defined by eqn (16) implies that the harvest rate increases with $\hat{N}$ for $\hat{N} > c$, being exactly $q(1 - c/\hat{N})$ for $\hat{N} > c$ and otherwise zero. Notice that if we put $c = 0$ (16) is just proportional harvesting as defined by Beddington & May (1977). We anticipate that proportional threshold harvesting should be a better strategy than pure threshold harvesting when the estimated population sizes are very uncertain. In those cases $\hat{N}$ may sometimes be very large compared to N, which will lead to overexploitation and rapid extinction if (15) is applied. By choosing the parameter q smaller than one the harvest is less sensitive to the value of $\hat{N}$, which may be an advantage when $\mathrm{Var}[\hat{N}|N]$ is large.

It is shown in Appendix A that the harvesting strategy given by (16) leads to

$$M_y(N) = q\theta\sqrt{N}[\phi(u) + u\Phi(u)] \qquad (17)$$

where $u = (N - c)/\theta\sqrt{N})$, Φ is the standard normal integral and ϕ is the standard normal density. The infinitesimal variance is given by

$$V_y(N) = q^2\theta^2 N\{(1 + u^2)\Phi(u + u\phi(u) - [\phi(u) + u\Phi(u)]^2\}. \qquad (18)$$

When the population size is known and harvesting can be done continuously in time with unlimited harvesting rate, Lande *et al.* (1995) have shown that the optimal threshold, c, in general is at the carrying capacity K. However, in order to investigate the effect of uncertain population estimates we need to analyse the discrete time model for known population size, which is actually the model obtained by inserting $\theta = 0$ in (12) and (13). In this case $V_y(N) = 0$ since the yield y is constant for given population size N, and

$$M_y(N) = \begin{cases} q(N - c) & \text{for } N > 0 \\ 0 & \text{otherwise.} \end{cases} \qquad (19)$$

It is shown in Appendix B that the value of c maximizing (11) for a given value of q is independent of the model to the first order in the environmental standard deviation σ_e. If we ignore the demographic variance which has practically no effect on the optimal threshold, writing $V_r(N) = \sigma_e^2 N^2$, the threshold is simply

$$c = K\left(1 - \sqrt{\frac{\pi\sigma_e^2}{4q}}\right) + o(\sigma_e^2/q)$$
$$\approx K(1 - 0.8862\sqrt{\sigma_e^2/q}) \qquad (20)$$

where the carrying capacity K is defined by $M_r(K) = 0$ (Appendix B). It has been checked by numerical integrations that this approximation is quite accurate for any realistic value of the environmental variance σ_e^2, provided that q is not too small (say $\sqrt{\sigma_e^2/q} < 0.5$). The derivation of (20) is given in Appendix B.

We see from (20) that the threshold is close to K when q is close to 1, at least if σ_e^2 is small, as for most populations of large-bodied birds and mammals. On the other hand, if we choose a small value of q the value of σ_e^2 may have a large effect on c which decreases when σ_e^2 increases. This effect of the environmental variance on the threshold is confirmed by Sæther *et al.* (1996b) and Lande *et al.* (1997). Sæther and co-workers (1996b) found that the threshold decreased with increasing σ_e^2 for small values of σ_e^2 for quite different types of density-regulation. One may get an intuitive understanding of this effect by writing $\ln(Y)$ as the sum $\ln(Y/T) + \ln(T)$ and considering separately the effect of each term. As σ_e^2 increases the increase in $\ln(Y/T)$ obtained by decreasing the threshold is larger than the decrease in $\ln(T)$ so that the total effect is that the optimal threshold decreases with increasing σ_e^2 [see also Lande *et al.* (1997) for a further discussion of this rather surprising result]. Notice also that, when c is close to K we mainly harvest only individuals generated by the stochastic fluctuations. When σ_e^2 increases we can therefore harvest more, that is, $\ln(Y/T)$ increases, while the effect on $\ln(T)$ may be relatively smaller because the magnitude of the time to extinction mainly is determined by behavior of the process closer to the extinction barrier.

Notice also that as $\sigma_e^2 \to 0$ the solution obtained in the limit is not an appropriate strategy in the deterministic case. Actually, any threshold would give $Y = \infty$ in this case, so it does not make sense to try to maximize Y. Since extinctions cannot occur in the deterministic case one should rather maximize harvest per time unit.

Fluctuations in the Annual Yield

Applying the strategy given by eqn (16), one may be interested in quantities other than the expected total yield before extinction, $Y(N_0)$, and the mean annual yield $Y(N_0)/T(N_0)$. Strategies maximizing either of these functionals may lead to stochastic fluctuations in the annual yield y, which are too large to be acceptable in practice. In order to analyse these stochastic effects we need to consider the so-called quasi-stationary distribution $H(N,N_0) = G(N,N_0)/T(N_0)$ (Karlin & Taylor 1981), which is the distribution of N between time zero and the time of extinction. Then the mean annual yield may be found by taking the double expectation, $E_t y = E_t E[y|N] = E_t M_y(N)$, where E_t represents the expectation through time, or

$$E_t y = \int_1^\infty M_y(N) H(N,N_0)\mathrm{d}N = Y(N_0)/T(N_0). \quad (21)$$

By the same approach we find the variance $\mathrm{Var}[y] = E_t E[y^2|N] - (E_t y)^2$, or

$$\mathrm{Var}[y] = \int_1^\infty [V_y(N) + M_y^2(N)] H(N,N_0)\mathrm{d}N - (E_t y)^2. \quad (22)$$

It may be more informative to use the coefficient of variation, $CV(y) = \sqrt{\mathrm{Var}(y)}/(E_t y)$.

The probability of harvesting with respect to the quasi-stationary distribution is $P(\hat{N} > c) = E_t P(\hat{N} > c|N)$, giving

$$P(y > 0) = \int_1^\infty \left[1 - \Phi\left(\frac{c - N}{\theta\sqrt{N}}\right)\right] H(N,N_0)\mathrm{d}N \quad (23)$$

where $\Phi(\cdot)$ is the standard normal integral.

As an alternative to maximizing the mean annual yield, Quinn *et al.* (1990) and Zheng *et al.* (1993) proposed maximizing the linear expression $(1 - \lambda)Y(N_0)/T(N_0 - \lambda\sqrt{\mathrm{Var}(y)}$ for some λ between zero and one, to avoid large annual variation of the yield.

Results

To illustrate the general theory we use the logistic model of population growth with $M_r(N) = \bar{r}N(1 - N/K)$, where $\bar{r}$ is the mean specific growth rate at small densities and K is the carrying capacity. As in the previous section the demographic variance may be ignored so that $V_r(N) = \sigma_e^2 N^2$. In order to reduce the number of parameters it is important to notice that the model is invariant against scaling. Let Z be a standardized process defined by $E[\Delta Z|Z] = \bar{r}Z(1 - Z)$, $\mathrm{Var}[\hat{Z}|Z] = \theta_0^2 Z$ and $\mathrm{Var}[\Delta Z|Z] = \sigma_e^2 Z^2$ in the absence of harvesting. The process Z and the estimation procedure for Z is then characterized by the parameters ($\bar{r}$, 1, σ_e^2, θ_0^2), where the second parameter is the carrying capacity. Now, defining $N = KZ$, the process N is given by the same model

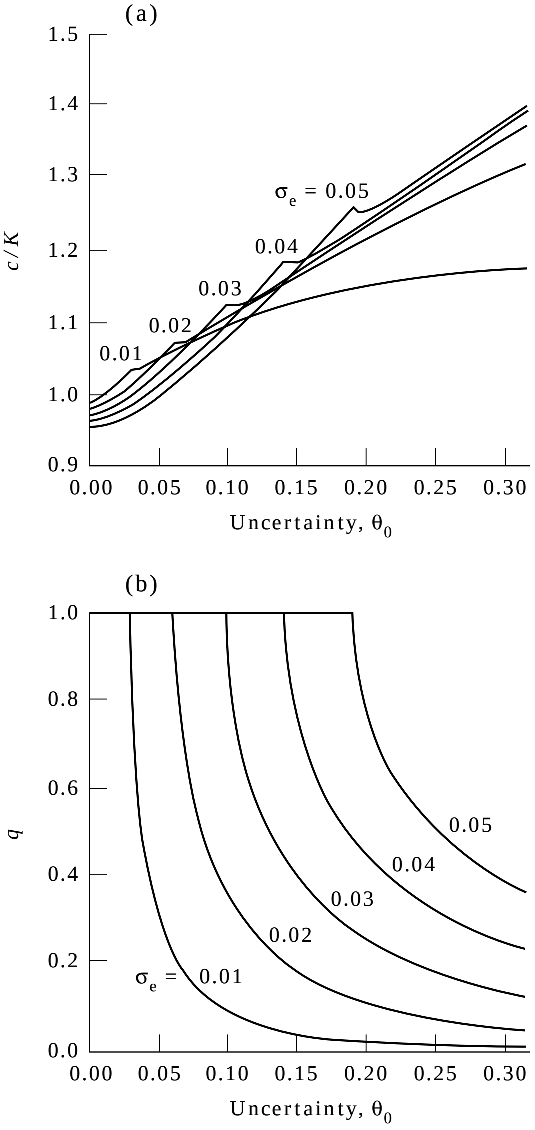

FIG. 1. The relative threshold maximizing the expected cumulative yield before extinction as a function of the uncertainty in estimated population size, θ_0, for different values of the environmental standard deviation σ_e (a). The other parameters are $\sigma_d = 1$, $\bar{r} = 0.1$, and $N_0 = K$. Panel (b) shows the corresponding value of the proportion q of the difference between the estimate and the threshold to be harvested.

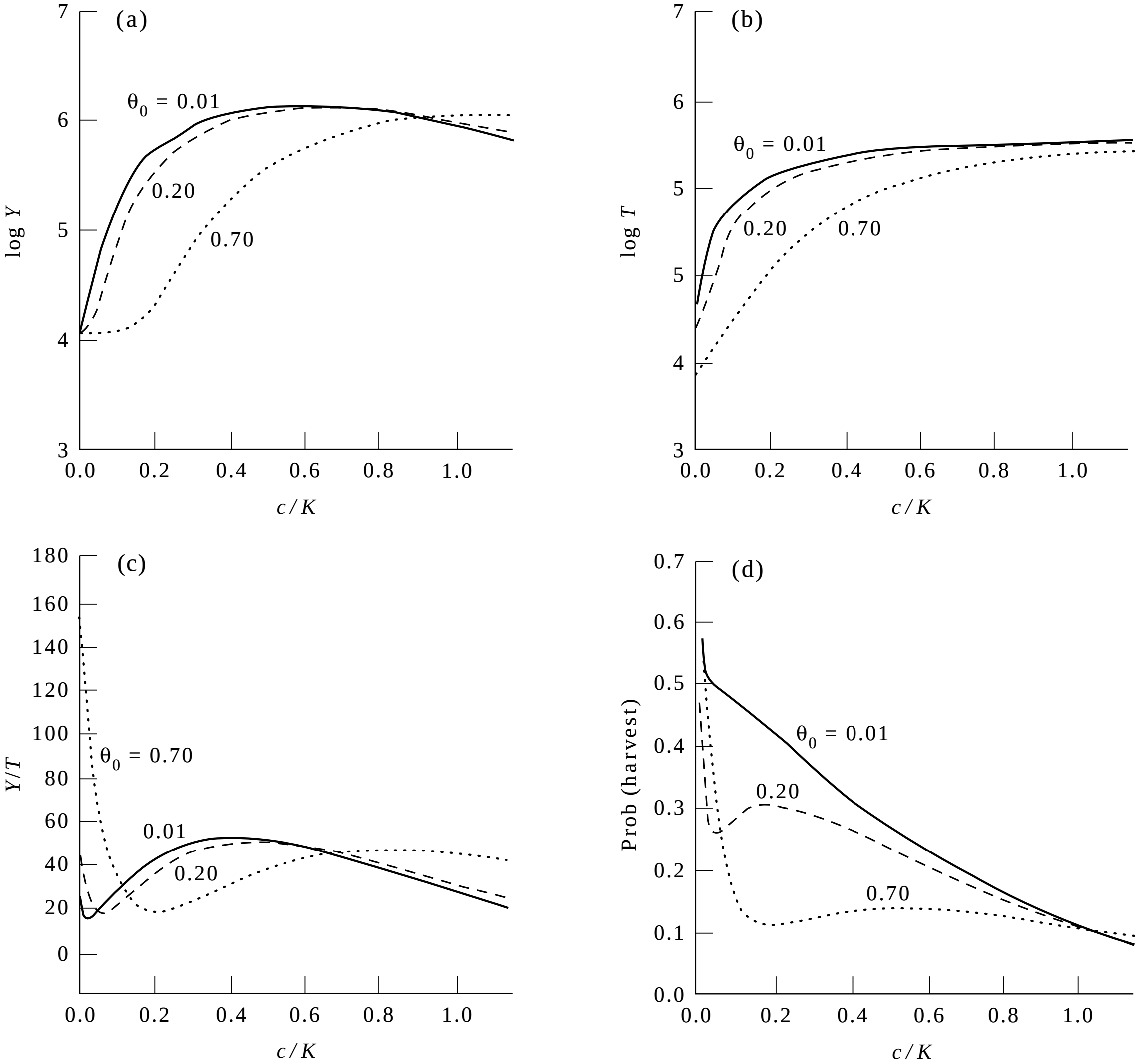

FIG. 2. Logarithm of expected cumulative yield before extinction (a), logarithm of mean time to extinction (b), the ratio of the expected cumulative yield before extinction and the mean time to extinction (c) and the probability of harvesting [eqn. (23)] (d) as functions of the relative threshold. The coefficient of variation of the estimated population size at $N = K$ is $\theta_0 = 0.01$ (solid line), 0.2 (dashed line) and 0.7 (dotted line). The other parameters are $\sigma_e^2 = 0.025$, $\sigma_d^2 = 1$, $\bar{r} = 0.03$, $K = 10\,000$, $N_0 = K$, $q = 0.1$ and the initial population size is at the carrying capacity.

and the same estimation procedure but with parameters ($\bar{r}$, K, σ_e^2, θ^2), where $\theta^2 = K\theta_0^2$, except that extinctions occur at different values. However, the location of the absorbing barrier defining extinction has no impact on the optimal tactic. This is because one will never harvest the population close to this barrier in any case. Notice that if $N = K$, then $CV(\hat{N}) = \theta_0$, so that θ_0 can be interpreted as the coefficient of variation of the estimated population size when the actual population size is at the carrying capacity.

We can see from (20) that the value of $\bar{r}$ has little effect on the optimal threshold. This is consistent with the general result of Lande *et al.* (1995) that the optimal threshold in the continuous case is at K. If we then investigate how the optimal proportional threshold strategy varies with θ_0 and σ_e^2 for the standardized model, the results are immediately applicable for the general model.

The integral (11) is computed numerically as function of the strategy parameters (c,q) and then maximized numerically by the routine AMOEBA (Williams *et al.*, 1988). In order to increase the accuracy in the numerical integration, (11) is first rewritten as indicated in Appendix C. The computations confirm in general that the optimal value of c approaches the value given in eqn (20) when the uncertainty in the estimated population size, θ_0, tends to zero.

For small values of θ_0, that is, small coefficient of variation in the estimator $\hat{N}$, it turns out that the solution is qualitively of the type given by eqn (15), which is pure threshold harvesting. At some value of θ_0 the proportion q suddenly starts to decrease below one, so that the optimal solution is proportional threshold harvesting. This value of θ_0 increases with the environmental variance. In the region when the optimal q is less than one, the optimal threshold, c, typically increases with θ_0. Numerical demonstrations are given for the logistic model in Fig. 1.

The loss in expected cumulative yield because of uncertainty in the population estimate is remarkably small if we choose $q = 0.1$ provided that the threshold c is chosen optimally [Fig. 2(a)]. The threshold for $\theta_0 = 0.01$ is close to the theoretical value for $\theta_0 = 0$ given by eqn (20) which is $c/K = 0.557$. As θ_0 increases, the optimal threshold increases, and there is a substantial loss compared to the optimal solution, about 90%, if we choose $c/K = 0.557$ when $\theta_0 = 0.7$. It is apparent from Fig. 2(b) that this loss is mainly due to a substantial decrease in the expected time to extinction. For $\theta_0 = 0.2$ the corresponding loss is quite small.

The threshold maximizing sustained average annual yield is smaller, about 0.4 for $\theta_0 = 0.01$ [Fig. 2(c)]. Notice that the corresponding loss in average annual yield by choosing a suboptimal strategy is never larger than about 50% when $\theta_0 = 0.7$. This threshold also increases with θ_0.

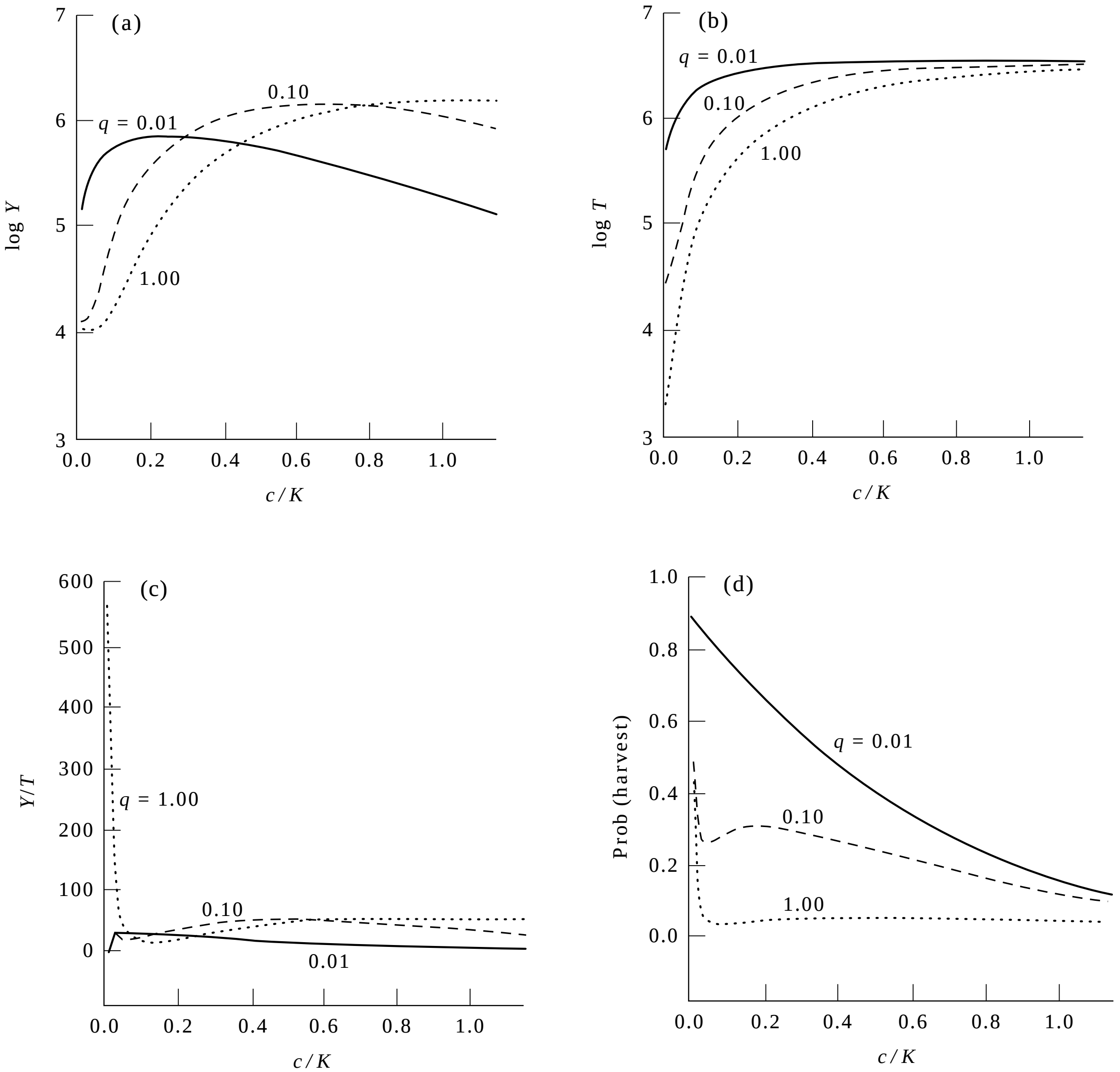

FIG. 3. The same functions as in Fig. 1 with $\sigma_e^2 = 0.025$ and constant coefficient of variation for the estimator, $\theta_0 = 0.2$, and three different values of q, 0.01 (solid line), 0.1 (dashed line), and 1 (dotted line).

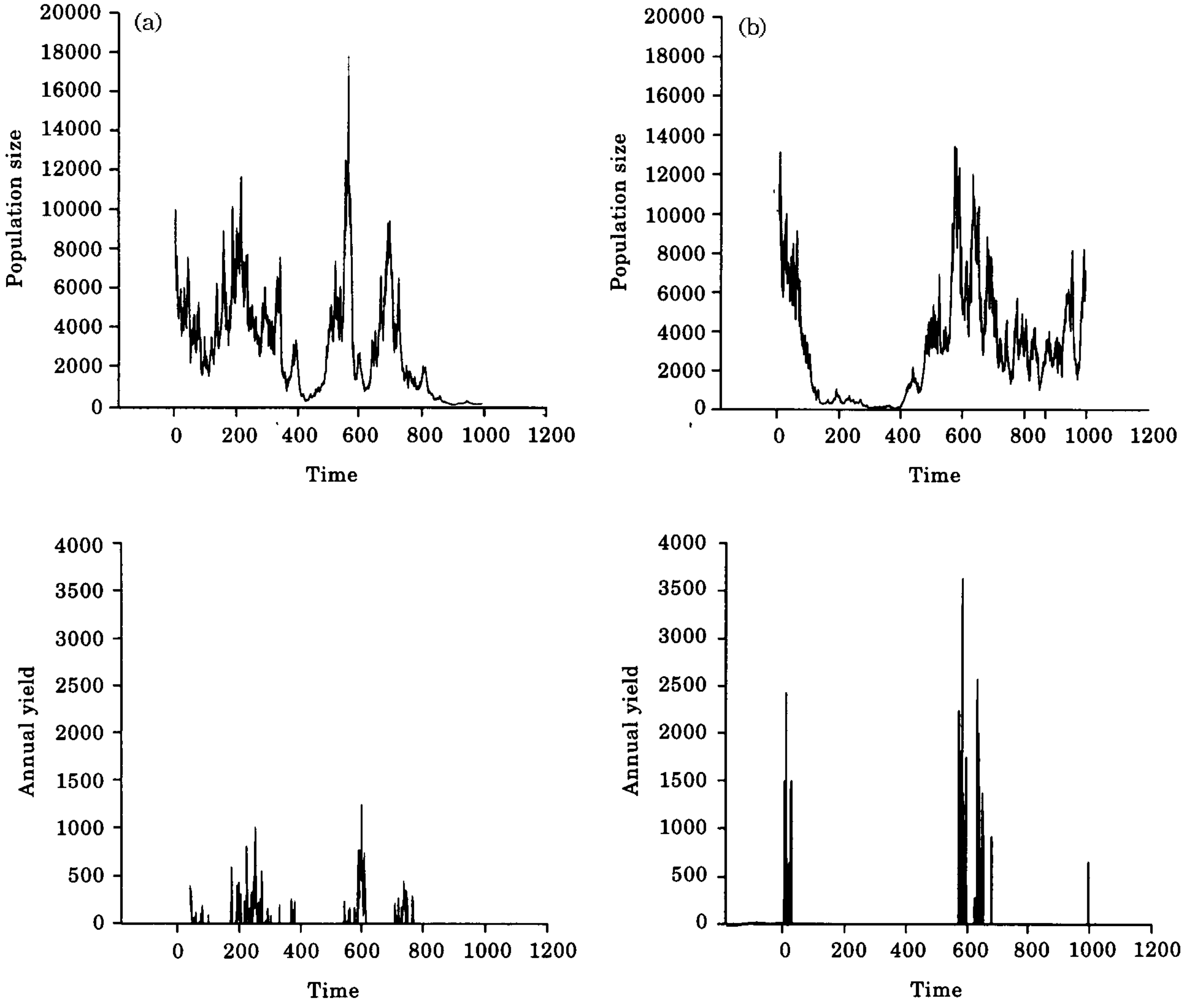

FIG. 4. Simulation of population size and annual yield for two different values of q, $q = 0.1$, $c/K = 0.59$ (a), and $q = 1$, $c/K = 1.04$ (b). In both cases c is chosen so that the expected cumulative yield before extinction is maximized for the given value of q. The coefficient of variation in the estimator when $N = K$ is $\theta_0 = 0.2$, with $\sigma_e^2 = 0.025$, $\sigma_d = 1$, $\bar{r} = 0.01$, and $K = 10000$.

If there is a large uncertainty in the estimator, say $\theta_0 = 0.7$, we can only expect to harvest in about once every 10 years [Fig. 2(d)] if the parameters are as in Fig. 1(a).

The effect of changing q is demonstrated in Fig. 3. The expected cumulative yield changes very little with q provided that the corresponding threshold is chosen optimally [Fig. 3(a)]. Notice that the practical interpretation of choosing $q = 0.01$ is that only 1/100 of the difference between the density estimate and the threshold can be harvested each year. So even if we can harvest almost any year [Fig. 3(d)] the amount harvested is quite small. Rather than being careful in the choice of threshold we now choose to limit the annual harvest.

As an illustration we show simulations of a population with small growth-rate and large environmental variance (Fig. 4). If we choose $q = 1$ the probability of harvesting may be quite small [Fig. 4(b)]. Such populations may have very small abundances for long periods (about 200 years in the example) where harvesting cannot be recommended. However, the population will occasionally be large enough to be harvested. The annual variation in the harvest is shown in the lower panel of Fig. 4. Notice that if we reduce q to 0.1 the annual harvest is somewhat smoothed by reducing the variance in the annual harvest and increasing the probability of harvesting [Fig. 4(a)].

Discussion

It is important to point out that our analysis, although being rather general, is based on some crucial assumptions. Firstly, diffusion approximations to descrete processes has sufficient accuracy only when the relative fluctuations in the population size are not too large. Secondly, our calculations are based on the assumption that the population estimate $\hat{N}$, for a given population size N, is normally distributed. If the estimator has large positive skewness, the solution of (12) and (13) will be different. Quite likely, the effect of uncertainty will increase through an increase in $M_y(N)$ due to the long right-hand tail of the distribution.

Many populations that are subject to harvest are strongly influenced by stochastic variation in the environment. As harvesting tends to reduce the population density, stochastic fluctuations may cause a further reduction in the population size and strongly reduce the expected time to extinction. Harvesting quotas, usually decided once a year, must be determined by considering the dynamics of the population including the effects of fluctuating environment as well as harvesting. Threshold harvesting maximizes the expected cumulative yield before extinction as well as the mean annual yield and the expected cumulative yield among strategies subject to a prescribed risk of extinction (Lande *et al*., 1995; Whittle & Horwood, 1995). If the population size is known exactly, eqn (20), with $q = 1$, is a general formula for the threshold maximizing the expected cumulative yield when harvesting quotas are decided once a year. The threshold is in general smaller than the carrying capacity. If decisions are made continuously in time, the corresponding threshold is exactly at the carrying capacity (Lande *et al*., 1995). Equation (20) also expresses how the threshold decreases when q decreases. This decrease is also demonstrated by Fig. 3(a) in the case of uncertain population estimates.

In practice, quotas must be based on estimated population sizes. For many harvested species population estimates tend to be rather uncertain. Table 1 shows examples of coefficients of variation of estimated population size for some species of fish, birds and large mammals, varying from 0.04 to 0.56, and even values larger than one have been reported (Nichols *et al*., 1981). Fishery management agencies often devote large sums to stock assessments and forecasting, but the coefficient of variation in the population estimates is at best 0.25 as a rule rather than the exception (Clark & Kirkwood, 1986; Overholtz *et al*., 1993; Punt & Butterworth, 1993). When threshold harvesting is performed based on uncertain population estimates, the optimal threshold for the expected cumulative yield before extinction increases [Fig. 1(a)]. This increase in the threshold also causes an increase in the annual variation of the yield, and long periods when harvesting must stop. An alternative strategy, which smooths the annual yield by reducing the variance in annual harvest and increasing the probability of harvesting (Fig. 4), is proportional threshold harvesting, where only a proportion, q, of the difference between the estimate and the threshold is harvested provided that this difference is positive. This approach, which is based on general statistical principles of conditional estimation, implies that the harvest rate increases with the population estimate when this is larger than the threshold, being actually $q(1 - c/\hat{N})$ for $\hat{N} > c$ and otherwise zero. Uncertainty in population estimates tends to increase the optimal threshold which may be substantially larger than K when both stochasticity and uncertainty are large (Fig. 1). Uncertainty in population estimates also increases the optimal threshold for maximizing the mean annual yield (Figs 2 and 3).

TABLE 1

Coefficients of variation of estimates of population size for some species of fish, large mammals and birds

Group	Species	$CV = \theta_0$	Reference
Fish	*Pleurogrammus monopterygius*	0.28	Lowe & Thompson (1993)
	Haddock	0.19–0.26	Smith & Gavaris (1993)
	Various ground fish stocks	0.20–0.50	Overholtz *et al*. (1993)
Large mammals	Moose	0.31–0.56	Crête *et al*. (1986)
	Fin whale	0.16	Buckland *et al*. (1993)
	Spotted dolphin	0.09–0.25	Buckland *et al*. (1993)
	Feral horse	0.04–0.25	Eberhardt (1982)
	Minke whale	0.15	Schweder & Volden (1994)
Birds	Various song birds	0.11–0.27	Buckland *et al*. (1993)

When θ_0 is large, proportional threshold harvesting with $q < 1$ gives a larger expected cumulative yield than pure threshold harvesting (Fig. 1). A similar result was found by Clark & Kirkwood (1986) by maximizing numerically the expected discounted value of future harvest in a stock-recruitment model, without taking into account the probability of extinction. They concluded that pure threshold harvesting was no longer an optimal policy when population estimates were uncertain.

The fact that the threshold optimizing sustained average annual yield increases with θ_0 seems to be in disagreement with the results of Zheng *et al*. (1993). However, they assumed a constant harvesting rate, which is quite different from our proportional threshold harvesting, and performed the joint maximization with respect to threshold and harvesting rate. Then, the threshold as well as the rate decreased with the uncertainty in the estimates. Hence, this may not be inconsistent with our results since in Fig. 2(c) our proportion q is kept constant.

It will be difficult in practice to find the optimal value of q since it depends on the environmental variance, which itself may not be known precisely. However, the expected cumulative yield is not very sensitive to q. A practical recommendation is to choose an intermediate value of q, say $q = 0.1$, and evaluate the optimal threshold given $q = 0.1$. With this threshold only 10% of the difference between the population estimate and the threshold can be harvested per year.

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APPENDIX A

Derivation of Eqns (17) and (18)

Let $Y(\hat{N}, c)$ be as in (15) and let $\hat{N}$ have the normal distribution (14). Then:

$$M_y(N) = \int_c^{\infty} (\hat{N} - c) f(\hat{N}|N)\mathrm{d}\hat{N}. \qquad \text{(A.1)}$$

Defining the variables $x = (\hat{N} - N)/\sigma$ and $u = (N - c)/\sigma$, where $\sigma = \theta\sqrt{N}$ is the standard deviation of $\hat{N}$, gives

$$M_y(N) = \sigma\left[\int_{-u}^{\infty} x\phi(x)\mathrm{d}x + u\int_{-u}^{\infty}\phi(x)\mathrm{d}x\right] \qquad \text{(A.2)}$$

which can be expressed as

$$M_y(N) = \sigma[\phi(u) + \mathrm{u}\Phi(u)]. \qquad \text{(A.3)}$$

The infinitesimal variance is

$$V_y(N) = \int_c^{\infty} (\hat{N} - c)^2 f(\hat{N}|N)\mathrm{d}\hat{N} - M_y(N)^2. \qquad \text{(A.4)}$$

Inserting
$(\hat{N} - c)^2 = (\hat{N} - N)^2 + 2(\hat{N} - N)(N - c) + (N - c)^2$
the first integral may be written

$$\sigma^2\int_{-u}^{\infty}[x^2\phi(x) + 2ux\phi(x) + u^2\phi(x)]\mathrm{d}x$$
$$= \sigma^2[(1 + u^2)\Phi(u) + u\phi(u)], \qquad \text{(A.5)}$$

giving finally

$$V_y(N) = \sigma^2\{(1 + u^2)\Phi(u) + u\phi(u) - [\phi(u) + u\Phi(u)]^2\}. \qquad \text{(A.6)}$$

From these expressions eqns (17) and (18) for the model defined by (16) follows immediately by the laws of expectation and variance of linear functions.

APPENDIX B

Derivation of eqn (20)

Applying the tactic defined by (16) with $\theta = 0$ eqn (11) takes the form

$$I(c) = \int_1^c M_r(N)m_r(N)\mathrm{d}N + \int_c^{\infty} M_r(N)m_r(N)\exp\left\{-2\int_c^N \frac{x - c}{\gamma^2 x^2}\,\mathrm{d}x\right\}\,\mathrm{d}N, \qquad \text{(B.1)}$$

where $m_r(N)$ is $m(N)$ evaluated without harvesting, $\gamma^2 = \sigma_e^2/q$, and the effect of the demographic variance is ignored for densities above the threshold c. Taking the derivative with respect to c we find that the optimal value of c must satisfy the equation

$$\int_c^{\infty} \frac{N - c}{N} M_r(N)m_r(N) \times \exp\left\{-2\int_c^N \frac{x - c}{\gamma^2 x^2}\,\mathrm{d}x\right\}\mathrm{d}N = 0. \qquad \text{(B.2)}$$

As $\gamma \to 0$ the last integral in the expression for $I(c)$ tends to zero. The first integral is maximized for $c = K$, since we assume that $M_r(N) < 0$ for $N > K$. Hence c approaches K as γ tends to zero.

Evaluating the integral in the exponent in (B.2) and introducing the new variable
$u = (N - c)/\gamma$ eqn (B.2) takes the form

$$\int_0^{\infty} M_r(c + u\gamma)m_r(c + u\gamma)\frac{u\gamma^2}{c + u\gamma} \times \exp\left\{-\frac{2}{\gamma^2}\left[\ln\left(1 + \frac{u}{c}\gamma\right) - \frac{u\gamma}{c + u\gamma}\right]\right\}\mathrm{d}u = 0. \qquad \text{(B.3)}$$

Now, $M_r\,(c + u\gamma) \to 0$ as $\gamma \to 0$ since $c \to K$. Hence, to the first order in γ, $M_r(c + u\gamma) \approx M_r'(K)(c + u\gamma - K)$. Sending γ to zero in (B.3) this leads to

$$\int_0^{\infty} u(c - K + u\gamma)\exp\{-\frac{u^2}{c^2}\}\mathrm{d}u + o(\gamma) = 0. \qquad \text{(B.4)}$$

Introducing $v = u/c$ this may be written as

$$K - c = c\gamma\left[\int_0^{\infty} v^2\exp\{-v^2\}\mathrm{d}v\right]\Big/\left[\int_0^{\infty} v\,\exp\{-v^2\}\mathrm{d}v\right] + o(\gamma) \qquad \text{(B.5)}$$

giving finally inserting

$$\int_0^\infty v^2\exp\{-v^2\}\mathrm{d}v = \frac{1}{4}\sqrt{\pi} \text{ and } \int_0^\infty v\ \exp\{-v^2\}\mathrm{d}v = \frac{1}{2},$$

$$c = K(1 - \frac{1}{2}\sqrt{\pi\gamma}) + o(\gamma). \qquad \text{(B.6)}$$

APPENDIX C

Comments on the Numerical Solution of (11)

Splitting up $M(N)$ and $V(N)$ into their components due to population growth and harvesting (10) may be written

$$I = \int_1^\infty \frac{M_r(N)}{V_r(N) + V_y(N)} \times \exp\left\{2\int_1^N \frac{M_r(x) - M_y(x)}{V_r(x) + V_y(x)}\,\mathrm{d}x\right\}\mathrm{d}N. \qquad \text{(C.1)}$$

There is a problem that the integral in the exponent may take rather large values so that even a small relative error gives a significant absolute error, say ε. This creates an error by a factor e^ε in (C.1). To avoid this problem it is preferable to write the integral in the exponent as

$$\int_1^N \frac{M_r(x) - M_y(x)}{v_r(x) + V_y(x)}\,\mathrm{d}x = \int_1^N \frac{M_r(x)}{V_r(x)}\,\mathrm{d}x - \int_1^N \frac{M_r(x)V_y(x) + M_y(x)V_r(x)}{V_r(x)(V_r(x) + V_y(x))}\,\mathrm{d}x. \qquad \text{(C.2)}$$

For the logistic model the first integral can be solved exactly. The second integral, say $I_1(N)$, is practically zero up to about $N = c$ since M_y and V_y are then approximately zero. The integral (11) that we want to maximize with respect to (c,q) is now proportional to

$$I' = \int_1^\infty \frac{1 - N/K}{\sigma_e^2 N^2 + V_y(N)} \exp\left\{\left(\frac{2\bar{r}}{\sigma_e^2} + 1\right)\ln N - \frac{2\bar{r}}{\sigma_e^2 K}N - 2I_1(N)\right\}\mathrm{d}N. \qquad \text{(C3)}$$

This approach significantly increases the accuracy in the integrations.