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A Theory of Stochastic Harvesting in Stochastic Environments

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ABSTRACT: We investigate how model populations respond to stochastic harvesting in a stochastic environment. In particular, we show that the effects of variable harvesting on the variance in population density and yield depend critically on the autocorrelation of environmental noise and on whether the endogenous dynamics of the population display over- or undercompensation to density. These factors interact in complicated ways; harvesting shifts the slope of the renewal function, and the net effect of this shift will depend on the sign and magnitude of the other influences. For example, when environmental noise exhibits a positive autocorrelation, the relative importance of a variable harvest to the variance in density increases with overcompensation but decreases with undercompensation. For a fixed harvesting level, an increasing level of autocorrelation in environmental noise will decrease the relative variation in population density when overcompensation would otherwise occur. These and other intricate interactions have important ramifications for the interpretation of time series data when no prior knowledge of demographic or environmental details exists. These effects are important whenever the harvesting rate is sufficiently high or variable, conditions likely to occur in many systems, whether the harvesting is caused by commercial exploitation or by any other strong agent of density-independent mortality.

Keywords: population dynamics, environmental stochasticity, colored noise, harvesting.

The temporal fluctuation of natural populations is one of the most well-studied problems in population ecology. The underlying processes causing the observed patterns have been attributed to both intrinsic demographic (density-dependent) mechanisms and to stochastic or more regular variations in the environment (Higgins et al. 1997; Leirs et al. 1997; Forchhammer et al. 1998; Grenfell et al. 1998;

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Myers et al. 1998; Bjørnstad et al. 1999; Stenseth 1999; Stenseth et al. 1999*a*, 1999*b*). A major challenge has been, and still is, to disentangle the relative contribution of endogenous and exogenous factors determining changes in abundance in time. It is generally agreed that observed patterns necessarily are a combination of them both (e.g., Turchin 1999; Lundberg et al. 2000; Fromentin et al. 2001).

In this article, we show how a stochastic population theory can be used to partition different sources of variation in population density. The basic components of this theory apply to any population that can be reasonably well described and analyzed by a nonstructured single-population model in a nonspatial context.

Although the variance partitioning is general, we choose as a model system a population that is harvested. A considerable part of our current understanding of population dynamics is based on data collected or motivated by harvesting (Kendall et al. 1998), for example, the famous fur trade records of the Canada lynx (*Lynx canadensis*) collected by the Hudson Bay Company and Statistics Canada (Stenseth et al. 1999*a*). Also, exploited populations are very clearly affected by two major processes determining their dynamics: recruitment and harvesting. One could equally well view the problem as one of a population in a seasonal environment where reproduction (or, rather, recruitment) is the major source of density dependence, whereas there is strong, but density-independent, mortality during the nonbreeding season. Taking the harvesting example, we add two important aspects to the existing harvesting theory: stochastic harvesting and temporally autocorrelated environmental noise.

Harvesting is often considered to be nothing but an extra source of mortality, decreasing average population density unless completely compensated for (Kokko and Lindström 1998; Boyce et al. 1999; Jonzén and Lundberg 1999). Independent of whether a constant effort or a density-dependent harvesting strategy (e.g., a threshold or fixed-stock policy) is implemented, the fraction annually removed from a population is best described as a stochastic process (Lauck et al. 1998; Patterson 1999; Mangel 2000). In this article, the annual harvest fraction is a stochastic variable independent of density, and we note that possible mechanisms of a time-variant harvest fraction are obser-

vation error on which the target is based as well as imperfect control.

Contemporary harvesting theory (e.g., May et al. 1978; Shepherd and Horwood 1979; Horwood and Shepherd 1981; Getz and Haight 1989; Lande et al. 1995, 1997) is built on the assumption of uncorrelated environmental stochasticity, so-called white noise. There are, however, good reasons to believe that positively autocorrelated noise is a better null model for environmental variability (Steele 1985; Pimm and Redfearn 1988; Halley 1996). Recent work has shown that autocorrelation per se influences population models in terms of expected extinction risk (Ripa and Lundberg 1996; Petchey et al. 1997; Morales 1999; Heino et al. 2000) and also that it may be significant in determining how exploited populations should be managed (Koslow 1989; Spencer 1993; Walters and Parma 1996).

Using an exploited population as a model system does not imply that we are interested here in the management problem per se but, rather, in how two important stochastic processes work in concert to produce observed population dynamics. Then, of course, understanding to what extent population variance can be explained by different processes does have both a general theoretical interest as well as potential far-reaching implications for population management and conservation.

Model

Consider a general population model where harvesting (or, strictly speaking, any density-independent mortality factor) takes place after reproduction such that

$$\tilde{N}_t = f(N_t, u_t), \quad \text{(reproduction)} \tag{1a}$$

$$Y_t = H(\tilde{N}_t, w_t), \quad \text{(harvest)} \tag{1b}$$

$$N_{t+1} = \tilde{N}_t - Y_t, \tag{1c}$$

where $\tilde{N}_t$ and N_t are the population densities before and after harvesting, respectively, and Y_t is the yield. We let the renewal function, $f(N_t, u_t)$, be nonlinear with respect to N_t, but there is no need here to specify the exact form. The yield function is dependent on the population density before harvesting takes place as well as on some yet unspecified stochastic element. Stochasticity enters the model in two ways, both as environmental variation (u_t) and in the harvesting process (w_t). We define the environmental noise (u_t) as a first-order autoregressive process, AR(1):

$$u_t = \alpha u_{t-1} + \sigma_u \varepsilon_t, \tag{2}$$

where α is the autocorrelation coefficient, ϵ_t is a series of

normal random deviates with mean 0 and unit variance, and σ_u determines the amplitude of the fluctuations. Hence, if $\alpha > 0$, u_t is positively autocorrelated, and we get so-called red noise (Steele 1985). Setting $\alpha = 0$, reduces u_t to "white" noise with standard deviation σ_u. There may be several reasons for variation in the yield process (Mangel 2000), and we let w_t be i.i.d. with mean 0 and a given standard deviation.

Equations (1) describe a nonlinear stochastic model, and nonlinearities are often complicated to deal with. Fortunately, stochastic linear models often serve as good approximations of their nonlinear counterparts and work as powerful theoretical tools to disclose ecological relationships (Roughgarden 1975; Nisbet et al. 1977; Horwood 1983; Taylor 1992; Ives 1995; Ripa and Heino 1999; Ripa 2000). We will therefore approximate the nonlinear model with a linear one. As a linearization point, we choose the (deterministic) stable equilibrium value of the population, N^*, evaluated at the expected value of the noise ($E(u_t) = u^* = 0$; $E(w_t) = w^* = 0$):

$$\tilde{N}^* = f(N^*, u^*), \tag{3a}$$

$$Y^* = H(\tilde{N}^*, w^*), \tag{3b}$$

$$N^* = \tilde{N}^* - Y^*. \tag{3c}$$

By substituting equations (1a) and (1b) into equation (1c) and linearizing at N^*, we get

$$x_t = a(1 - c)x_{t-1} + b(1 - c)u_{t-1} - dw_{t-1}, \tag{4a}$$

where $x_t = N_t - N^*$. In a similar way, we obtain

$$\tilde{x}_t = a(1 - c)\tilde{x}_{t-1} + bu_{t-1} - adw_{t-1}, \tag{4b}$$

$$y_t = c\tilde{x}_t + dw_t, \tag{4c}$$

where $\tilde{x}_t = \tilde{N}_t - \tilde{N}^*$ and $y_t = Y_t - Y^*$. The symbols *a–d* in equations (4) denote the partial derivatives

$$a = \frac{\partial f(N^*, u^*)}{\partial N}, \tag{5a}$$

$$b = \frac{\partial f(N^*, u^*)}{\partial u}, \tag{5b}$$

$$c = \frac{\partial H(\tilde{N}^*, w^*)}{\partial \tilde{N}}, \tag{5c}$$

$$d = \frac{\partial H(\tilde{N}^*, w^*)}{\partial w}. \tag{5d}$$

It is important to understand the meaning of the partial

derivatives since they describe how the population responds to changes in population density and the stochastic elements. A key parameter is *a*, the slope of the renewal function at equilibrium, which determines the endogenous population dynamics. Depending on whether $a > 0$ or $a < 0$, the endogenous dynamics are under- or overcompensatory, respectively (Ripa and Heino 1999). The sensitivity of the population renewal to environmental noise is determined by *b*. Finally, *c* and *d* describe the sensitivity of the yield to population density (before harvesting) and to the variability in harvesting (w_t), respectively.

To facilitate the interpretation of *b*, *c*, and *d*, it is possible to make further assumptions about the model structure without losing generality in the population dynamics. We therefore let

$$f(N_t, u_t) = f_N(N_t)e^{u_t}, \qquad (6a)$$

$$H(\tilde{N}_t, w_t) = h\tilde{N}_t(1 + w_t). \qquad (6b)$$

Equation (6a) represents the assumption that environmental variability affects the population growth in a multiplicative manner, a common assumption (Hilborn and Mangel 1997). In equation (6b), we assume a stochastic harvest but with a constant mean fraction *h*. This relationship could arise, for instance, if the harvest target is set as a constant fraction of a population-density estimate with measurement error, in which case the standard deviation of w_t, $\mathrm{SD}(w_t)$, corresponds to the coefficient of variation of the population-density estimate.

Substituting equations (6) into equations (3b) and (3c) and equations (5b)–(5d) yields

$$Y^* = h\tilde{N}^*, \qquad (7a)$$

$$N^* = (1 - h)\tilde{N}^*, \qquad (7b)$$

$$b = f_N(N^*) = \tilde{N}^*, \qquad (7c)$$

$$c = h, \qquad (7d)$$

$$d = h\tilde{N}^*. \qquad (7e)$$

Equations (7c)–(7e) give direct density and harvest-level interpretations of the derivatives *b*, *c*, and *d*, which we will use later to interpret our result.

We are now interested in deriving expressions of the variance of the processes described by equations (4). To achieve this, we *z*-transform the equations and rearrange them to standardized autoregressive, AR(*p*), format (Box and Jenkins 1976). As a result, the calculation of the variance of the population density, before and after harvesting, and the yield is straightforward (app. A). We will use this general model to investigate the role of variable har-

vesting and environmental stochasticity in generating variation in population density and yield.

The qualitative behavior of the general model is important to understand broad patterns. However, we should also try to quantify the relative importance of the various model parameters and make sure that we are using parameter values that are relevant to real systems. As an example, we will therefore analyze the model

$$N_t = N_{t-1} \exp{(r - \beta N_{t-1} + u_t)}[1 - h(1 + w_t)], \qquad (8)$$

where *r* is the maximum per capita growth rate, β measures the strength of direct density dependence, and u_t and w_t are again the stochasticity in the recruitment and harvesting process, respectively. Equation (8) can now be linearized, and the equilibrium densities and the partial derivatives are given in appendix B.

We are interested in the proportion of the total variance due to harvesting. This proportion is referred to as "the relative impact of variable harvest" and is denoted q_i, where *i* refers to x, $\tilde{x}$, or y, depending on whether we are analyzing the variance in population density after harvest x, before harvest $\tilde{x}$, or in yield y. We can get the answer from the variance expressions given in appendix A (eqq. [A6]–[A8]). The right-hand side of each variance expression is the sum of two stochastic processes due to recruitment and harvesting, respectively. By our definition, q_i is the ratio of the expression to the right of the plus sign and the total variance. Two other important properties are the coefficient of variation (CV) of the yield and the population density. We will use the linearized version of equation (8) in all figures showing how CV and the relative importance of harvesting vary with mean harvest fraction, variation in harvest, and temporal autocorrelation in the environment. To make sure that the linear approximation is reasonable, we will also simulate the nonlinear model (eq. [8]) 10,000 generations and calculate CV for comparison with the linear model. To avoid the possibility of occasional negative harvest fractions, we truncated w_t at ± 1.

Results

Following the procedures outlined in appendix A, we arrive at analytical expressions of the variance of population density before and after harvesting as well as at those of the yield. Let us first make the common assumption of uncorrelated environmental noise ($\alpha = 0$). Then equations (A6)–(A8) simplify to

$$V(x_t) = \frac{b^2(1-c)^2 V(u_t) + d^2 V(w_t)}{1 - a^2(1-c)^2}$$

$$= N^{*2} \frac{V(u_t) + [h^2/(1-h)^2]V(w_t)}{1 - a^2(1-h)^2}, \quad (9a)$$

$$V(\tilde{x}_t) = \frac{b^2 V(u_t) + a^2 d^2 V(w_t)}{1 - a^2(1-c)^2}$$

$$= \tilde{N}^{*2} \frac{V(u_t) + a^2 h^2 V(w_t)}{1 - a^2(1-h^2)}, \quad (9b)$$

$$V(y_t) = \frac{b^2 c^2 V(u_t) + d^2[1 - a^2(1-2c)]V(w_t)}{1 - a^2(1-c)^2}$$

$$= Y^{*2} \frac{V(u_t) + [1 - a^2(1-2h)]V(w_t)}{1 - a^2(1-h)^2}. \quad (9c)$$

These are the variance expressions of population density after (x_t) and before harvesting ($\tilde{x}_t$) and of the yield (y_t), assuming uncorrelated environmental stochasticity. In the lower expressions, we have made use of the results in equations (7) based on the assumptions of a multiplicative environmental stochasticity and a constant fraction harvest (eqq. [6a] and [6b]). We notice that q_i (the relative impact of variable harvest) is an increasing function of c, the partial derivative of the yield with respect to population density, which, for some models, can be interpreted as the fraction harvested, that is, h in equation (6b). Furthermore, all variances are independent of the sign of a, that is, of whether the endogenous dynamics is under- or overcompensatory. The magnitude of a is, however, still important. Interestingly, variable harvesting makes no contribution to $V(\tilde{x}_t)$ when $a = 0$ (perfect compensation).

An important feature of the environmental noise is the autocorrelation. We can study the effect of autocorrelated noise by letting α in equation (2) take on values different from 0. Hence, the full equations including α but assuming equations (6a) and (6b) become

$$V(x_t) = N^{*2} \frac{\gamma V(u_t) + [h^2/(1-h)^2]V(w_t)}{1 - a^2(1-h)^2}, \quad (10a)$$

$$V(\tilde{x}_t) = \tilde{N}^{*2} \frac{\gamma V(u_t) + a^2 h^2 V(w_t)}{1 - a^2(1-h)^2}, \quad (10b)$$

$$V(y_t) = Y^{*2} \frac{\gamma V(u_t) + [1 - a^2(1-2h)]V(w_t)}{1 - a^2(1-h)^2}, \quad (10c)$$

where $\gamma = [1 + \alpha a(1-h)]/[1 - \alpha a(1-h)]$ is a term capturing the influence of environmental variability due to environmental autocorrelation; γ is high when α and a are of the same sign (cf. Roughgarden 1975; Ripa and Heino 1999). Thus, the variance of a population with un-

dercompensating dynamics will increase as the autocorrelation of the environment increases. At the same time, the relative importance of variable harvest will decrease. A population with overcompensating dynamics, however, will be relatively more affected by a variable harvest in a positively autocorrelated environment than in an uncorrelated environment.

So far, all conclusions are based on the qualitative behavior of the general model. The question is, however, to what extent variable harvesting contributes to the variance in density and yield for parameter values that seem plausible in natural systems? In figure 1, we plot the relative importance of variable harvesting (q_i) as a function of mean harvest fraction h and the standard deviation of the variation in harvest, SD(w_t). Remember that SD(w_t) can be interpreted as the coefficient of variation of the population-density estimate if the population is observed with an error.

In figure 2, we demonstrate how the relative importance of variable harvesting depends on α, h, and the intrinsic growth rate r. In general, the importance of harvest variability increases with increasing h, with the exception of perfect compensation pointed out above. The effect of increasing the environmental autocorrelation (α) is, however, different for the yield and the population density. It also depends on whether we measure the population density before or after harvesting as well as the value of r. Finally, figure 3 demonstrates how the CV of population density (before and after harvesting) as well as the yield vary with autocorrelation of the environmental variability (α) and the expected harvest fraction (h). Increasing the environmental autocorrelation for a fixed h results in increasing or decreasing CV depending on whether the endogenous dynamics are under- (low r) or overcompensatory (high r). When α is fixed and we instead increase h, CV of the yield always increases independent of the endogenous dynamics. The CV of the population, however, increases with increasing h for undercompensatory dynamics but reaches a minimum at intermediate h when the endogenous dynamics without harvesting are overcompensatory. The reason behind this seemingly ambiguous effect of h on the CV of the population is that harvesting has a dampening effect, shifting the slope of the renewal function at the equilibrium.

Discussion

We have shown that the relation between population dynamics and two different sources of stochasticity, recruitment, and density-independent mortality (e.g., harvesting), may be rather complicated and also contingent on population demography as illustrated by the intrinsic growth rate. Previous studies on variability in exploited
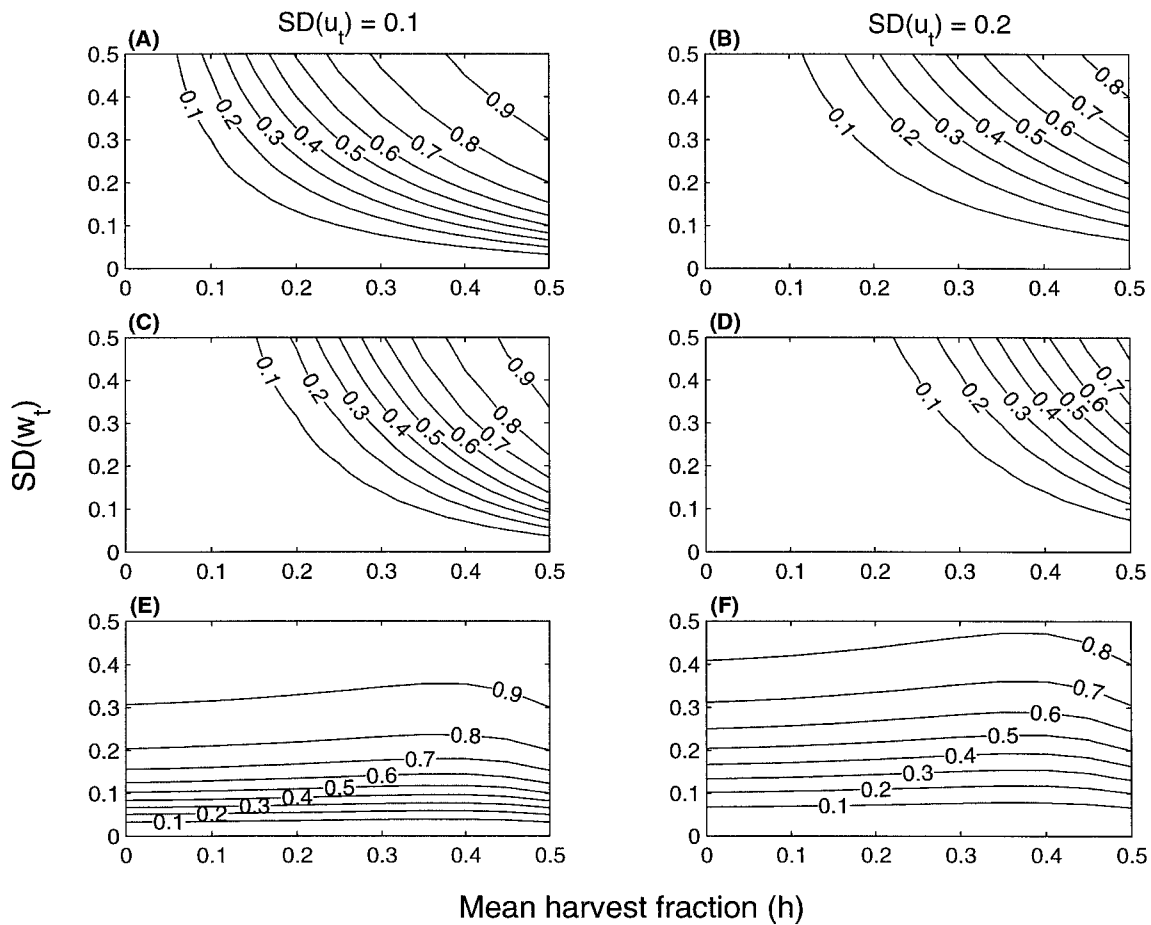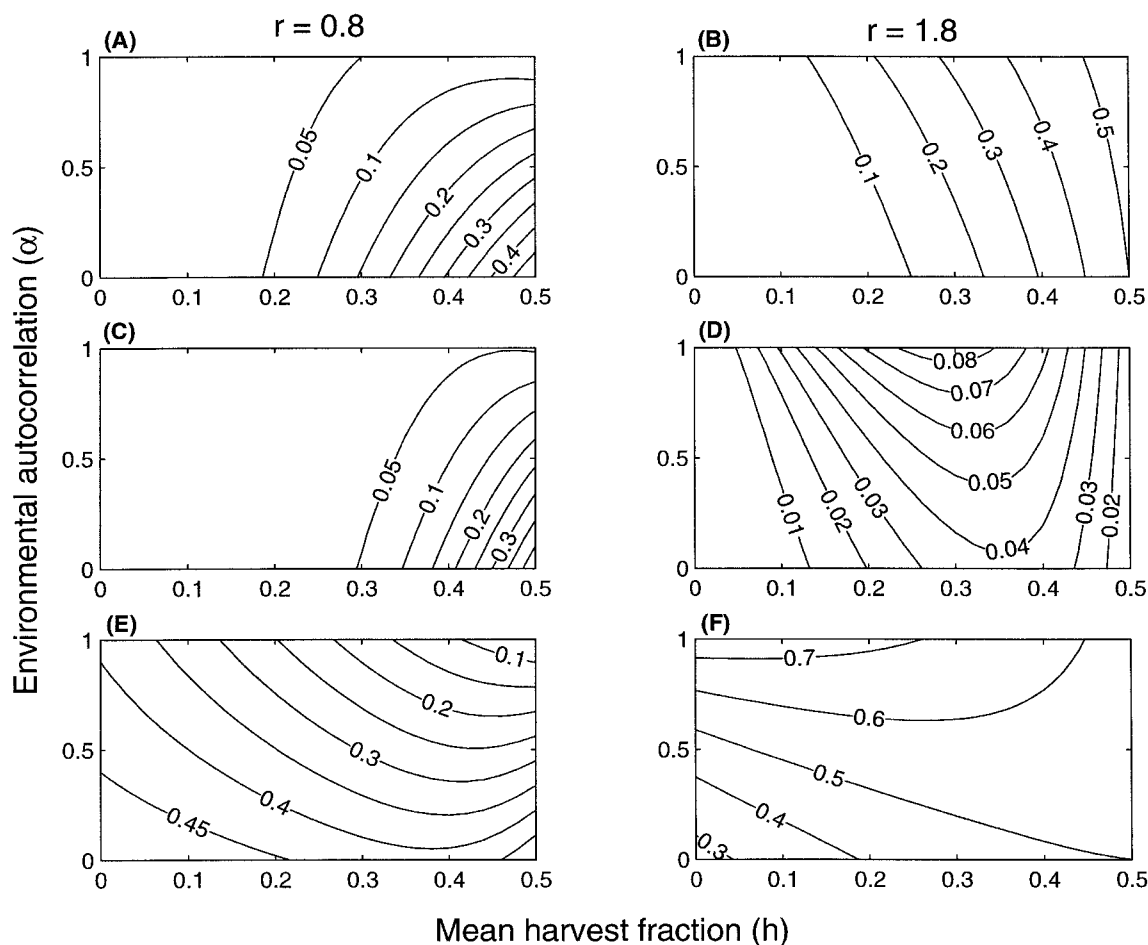
Figure 1: The proportion of the variance in population density after harvesting (*A* and *B*), before harvesting (*C* and *D*), and the yield (*E* and *F*) due to the mean harvest fraction (*h*) and standard deviation in the harvesting process, SD(w_t). The other parameter values are $\beta = 0.01$, $r = 0.8$, and the standard deviation of the environmental noise, SD(u_t) = 0.1 (*left column*) or 0.2 (*right column*).

marine populations (reviewed by Fogarty et al. 1991) have emphasized the inherent variability related to the recruitment process. However, for many commercially exploited populations, the most important part of the environment is not abiotic but, rather, the harvesting mortality (e.g., Jonzén et al. 2001). We have clearly shown that for realistic values of variance in harvest rate and environmental noise, harvesting may explain a considerable proportion of the variance in yield and population density. The exact proportion is very much dependent on the relative magnitude of $V(w_t)$ and $V(u_t)$. One may argue that environmental stochasticity should be far more important than harvesting in explaining the population variance in many fish populations due to the extremely variable recruitment (Fogarty et al. 1991). However, there are two reasons why harvesting may be an equally important source of variation also in exploited fish populations. First, the mean harvest fraction

is often very high in commercial marine fisheries. Second, it is extremely difficult to sample marine fish populations, and this difficulty results in observation error (e.g., Hilborn and Walters 1992). In a recent study, SD(w_t) was found to be as high as 0.3–0.5 (Fromentin et al. 2001). If decisions about annual harvest quotas are based on such rough estimates of density, the implemented harvest fraction will be time variant. Imperfect control or a strategy varying the annual harvest fraction on purpose may further reinforce the variation in harvest fraction. Hence, one should not rule out harvesting as a major source of population variability simply because the variation in recruitment is striking. One should remember, however, that harvesting to some extent can be controlled, but recruitment is always an uncontrollable source of uncertainty that population management has to deal with.

The fact that stochastic harvesting translates into pop-

Figure 2: The proportion of the variance in population density after harvesting (*A* and *B*), before harvesting (*C* and *D*), and the yield (*E* and *F*) due to harvesting as a function of environmental autocorrelation (α) and the mean harvest fraction (*h*). The other parameter values are $\beta = 0.01$, $SD(u_t) = SD(w_t) = 0.1$, and $r = 0.8$ (*left column*) or 1.8 (*right column*).

ulation variability has a very important implication when we analyze time series data on abundance from exploited populations. Recently, Becerra-Muñuz et al. (1999) found that ARIMA models, a family of linear time series models, were less capable of explaining data from exploited populations than from unexploited ones. Our results are in line with that empirical finding, indicating that models not including harvesting may be less capable of explaining the population dynamics of exploited populations. The effect of harvesting is most pronounced if the population is sampled after harvesting but before the recruitment. Hence, if autoregressive (AR) models are fitted to such data, as is often done, one should also include data on yield in the estimation to avoid bias due to harvesting. This is always done in fishery and hunting studies but rarely in mainstream ecology. Failing to do so may lead to erroneous

conclusions about the population demography when one interprets the AR coefficients as density dependence.

In population ecology as well as wildlife and fisheries management, the data at hand are often time series of abundance or an index of abundance. The task is then to figure out the underlying processes giving rise to the observed pattern (i.e., the population dynamics). The standard procedure is to fit models incorporating details of demography, for example, structure and magnitude of density dependence, to data. The residuals of the model fit (not explained by measurement error) are often interpreted as environmental stochasticity or process error. The environmental stochasticity, therefore, becomes model dependent and a time series of abundance may be consistent with different assumptions about demography (the model structure) and environmental stochasticity (the residuals;
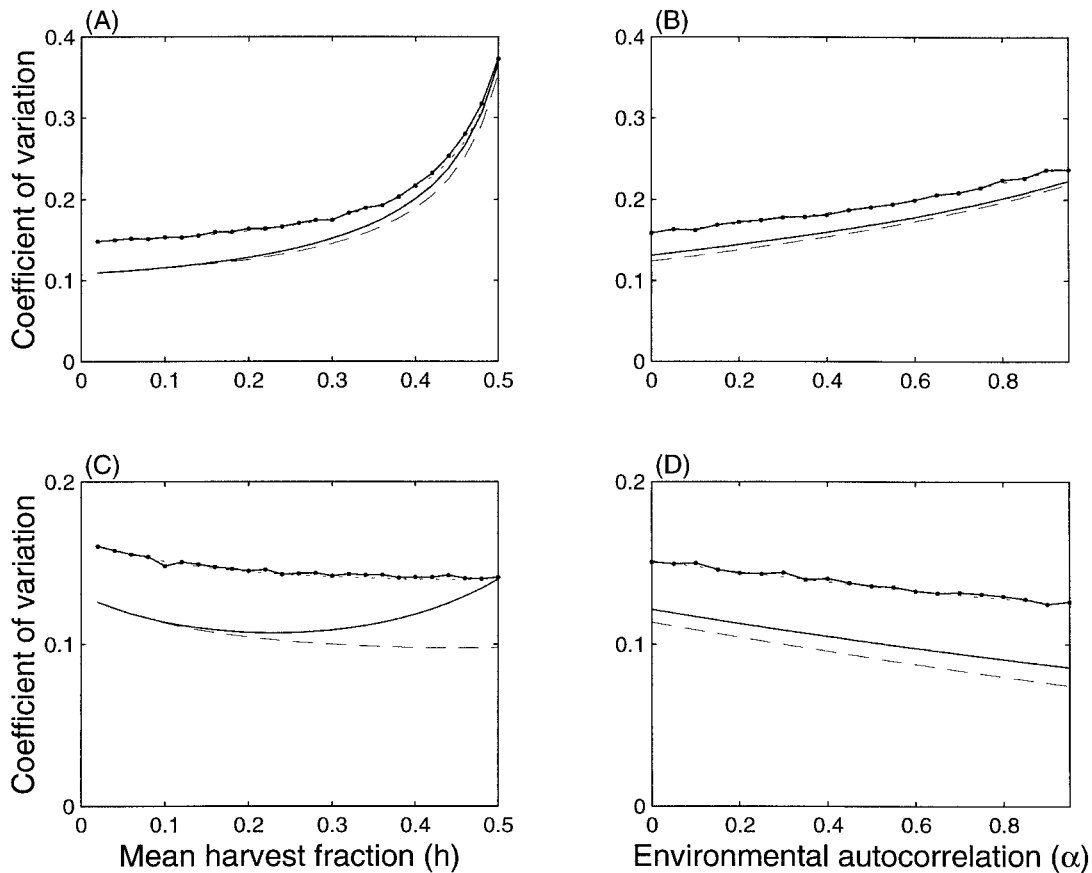
Figure 3: Coefficient of variation of population density before (*dashed line*) and after harvesting (*solid line*) and the yield (*dotted line*) as a function of environmental autocorrelation (α) and the mean harvest fraction (h). In *A* and *B*, $r = 0.8$; and in *C* and *D*, $r = 1.8$. Furthermore, $\alpha = 0.3$ in *A* and *C*, and $h = 0.3$ in *B* and *D*. The other parameter values are $\beta = 0.01$ and $SD(u_t) = SD(w_t) = 0.1$. To illustrate the accuracy of the linear approximation, we have inserted a line (*solid with filled circles*) for the coefficient of variation of the yield when one simulates the nonlinear model (eq. [8]) 10,000 generations. As with the linear approximation, we corrected for the dependence of $SD(u_t)$ on the autocorrelation coefficient (α) to keep $SD(u_t)$ constant (see Ripa and Lundberg 1996).

Roughgarden 1975; Royama 1981; Williams and Liebhold 1995, 1997). By combining stochastic and autocorrelated recruitment with stochastic mortality, we have shown how these processes are necessarily intertwined with the demography in terms of the AR(1) coefficient (see app. A). We suggest that any attempt to fit AR models to time series of abundance, aiming at identifying and interpreting the AR coefficients as demographic parameters, should include important autocorrelated environmental factors as covariates in the models. This is, of course, not a technical requirement in time series analysis, but failing to do so can potentially mislead ecologists to erroneous conclusions about the relative importance of endogenous and exogenous factors (Jonzén et al. 2002). Hence, we suggest that the environment should become an integral part of the models (see also Lundberg et al. 2000).

Recognizing the need to incorporate environmental sto-

chasticity in population models raises the question of how this should be done. One could think about a density-dependent effect of environmental noise such that the magnitude of the environmental variability changes with population density (Horwood and Shepherd 1981), a problem we have not addressed in this article. We do believe, however, that our general conclusions would still hold under alternative formulations. There are certainly other general features, for example, space and trophic interactions, that we have not dealt with either, and we welcome future studies investigating under what circumstances our general results would change considerably.

The approach taken in this article is based on linear approximation of a nonlinear stochastic model. The linear approximation is likely to apply for "small" perturbations from a dynamic equilibrium, where the meaning of "small" depends on the linearity of the model. Because the equi-

librium is a function of harvesting and we evaluate the variation around equilibrium, this approach is perfectly valid for investigating the dynamics of exploited populations that are fluctuating far from the density they would have in the absence of harvesting. The simulation of the nonlinear model further demonstrates that the linear model is a good approximation of the nonlinear counterpart. However, some nonlinear models have multiple equilibria, and deviations from one equilibrium point may push the population to a new stable state (Holling 1973). Such a situation is not described by the linear analysis performed here.

We have demonstrated how two stochastic processes, recruitment and mortality exemplified by harvesting, interact with population demography to produce observable population dynamics. The patterns presented here show how populations should respond to exploitation depending on demography (over- or undercompensatory dynamics) as well as temporal autocorrelation in the environmental noise modulating recruitment. Furthermore, we have shown that stochastic harvesting may explain a con-siderable proportion of the variance in population density and yield if the mean harvest rate is high and the magnitude of $V(w_t)$ is comparable to or larger than $V(u_t)$. That calls for a reconsideration of the role of harvesting as a stochastic process and potential source of population variability.

APPENDIX A

Derivation of the Variance Expressions

If $x_t(t = 0, 1, 2, \ldots, k - 1)$ is a discrete time series, its z-transform (Jordan and Smith 1999) is

$$X(z) = \sum_{t=0}^{k-1} z^{-t} x_t. \tag{A1}$$

The z-transforms of equations (2) and (4a) are

$$U = z^{-1}\alpha U + E \Rightarrow U = \frac{E}{1 - z^{-1}\alpha}, \tag{A2}$$

$$X = a(1 - c)z^{-1}X + b(1 - c)U - dW, \tag{A3}$$

where X, U, E, and W are the z-transforms of x_t, u_t, ϵ_t, and w_t, respectively. Actually, one has to use the periodic expansion of x_t, that is, assume $x_{t \pm k} = x_t$ for all t, to arrive exactly at equations (A2) and (A3). This has no importance for long time series. Inserting equation (A2) into equations (A3) and solving for X gives

$$X = \frac{b(1 - c)}{[1 - a(1 - c)z^{-1}](1 - \alpha z^{-1})} E - \frac{d}{[1 - a(1 - c)z^{-1}]} W. \tag{A4}$$

Matching terms in powers of z^{-1} to the general formulas of an AR(p) process, we find that the first term of equation (A4) corresponds to an AR(2) process with the first and second AR coefficients equal to $\phi_1 = a(1 - c) + \alpha$ and $\phi_2 = -a\alpha(1 - c)$, respectively. The second term of equation (A4) describes an AR(1) process. Hence, X is the sum of two independent stochastic processes: a second-order autoregressive process (due to environmental variation) and a first-order autoregressive process (due to variable harvesting).

In the same way, we find the z-transform of the population density before harvesting (eq. [4b]). The harvesting process (eq. [4c]) is simply a function of equations (4a) and (4b), and the variance can be calculated from the two

former processes. The variance of a second-order autoregressive process, AR(2), is given by (Box and Jenkins 1976)

$$V(x_t) = \frac{\sigma_\varepsilon^2(1 - \phi_2)}{(1 + \phi_2)[(1 - \phi_2)^2 - \phi_1^2]}, \tag{A5}$$

where ϕ_1 and ϕ_2 are the first and second AR coefficients, respectively, and σ_ε determines the magnitude of the fluctuations (see eq. [2] for the structure of an AR process). We can now calculate the variance of the population density after (x_t) and before ($\tilde{x}_t$) harvesting as well as that of the yield (y_t):

$$V(x_t) = \frac{b^2(1 - c)^2[1 + \alpha\, a(1 - c)]}{[1 - a^2(1 - c)^2][1 - \alpha\, a(1 - c)]} V(u_t) + \frac{d^2}{1 - a^2(1 - c)^2} V(w_t), \tag{A6}$$

$$V(\tilde{x}_t) = \frac{b^2[1 + \alpha\, a(1 - c)]}{[1 - a^2(1 - c)^2][1 - \alpha\, a(1 - c)]} V(u_t) + \frac{a^2 d^2}{1 - a^2(1 - c)^2} V(w_t), \tag{A7}$$

$$V(y_t) = c^2 V(\tilde{x}_t) + d^2 V(w_t). \tag{A8}$$

Finally, the variance of the environmental variation, $V(u_t)$, is given by

$$V(u_t) = \frac{\sigma_u^2}{1 - \alpha^2}. \tag{A9}$$

Because $V(u_t)$ increases with increasing α, we let $V(u_t)$ be fixed when we study the effect of autocorrelation per se.

APPENDIX B

Equilibrium Densities and Partial Derivatives

The equilibrium population density after and before harvesting are

$$N^* = \frac{r + \ln(1 - h)}{\beta},$$

$$\tilde{N}^* = \frac{r + \ln(1 - h)}{\beta(1 - h)}. \tag{B1}$$

Taking the partial derivatives according to equations (5), we get

$$a = \frac{\partial f(N^*, u^*)}{\partial N} = \frac{1 - r - \ln(1 - h)}{1 - h},$$

$$b = \frac{\partial f(N^*, u^*)}{\partial u} = \frac{r + \ln(1 - h)}{\beta(1 - h)},$$

$$c = \frac{\partial H(\tilde{N}^*, w^*)}{\partial \tilde{N}} = h, \tag{B2}$$

$$d = \frac{\partial H(\tilde{N}^*, w^*)}{\partial w} = h\tilde{N}^*.$$

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