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USING KNOWLEDGE OF RECRUITMENT TO MANAGE HARVESTING

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Abstract. Numerous field studies show that changing environmental conditions and ecological interactions within complex food webs can influence the dynamics of populations. Nonetheless, the potential benefit of understanding and predicting this variation to manage harvesting rarely has been considered. Here we develop analytic approximations to explore the relationship between the proportion of variation in annual recruitment that can be predicted and the expected annual harvest yield arising from fixed escapement harvesting methods. Simulations suggest that these approximations are reliable, provided that the unpredicted variance in recruitment is not large and the escapement threshold is set below carrying capacity. As an example of how these approximations may be applied, we use demographic and environmental data from a trapped population of martens (*Martes americana*) in Ontario to evaluate the effect on harvest yield of improvements in prediction of recruitment based on fluctuations in its prey base. We conclude that realistic improvements in forecasting of recruitment lead to only a modest increase in the average annual harvest and increase the variation in realized harvests, but could substantially reduce the risk of over-harvesting when escapement levels are set low.

Key words: *carnivore; conservation; food web; harvesting; marten; Martes americana; resource management; stochasticity.*

INTRODUCTION

Our ability to sustain harvested populations of renewable natural resources is often inadequate due to limitations in our understanding of critical biological processes, sketchy demographic data for even well-studied systems, poor frameworks for decision-making, and faulty policy formulation (Clark 1976, Ludwig et al. 1993, Lande et al. 1994, Hilborn et al. 1995, Jonzen et al. 2002). All of these problems are exaggerated by our ignorance of the underlying sources of variability that influence all natural populations. Assuming a constant environment, it is not difficult in principle to identify optimal policies for resource extraction, given prevailing ecological, social, and economic constraints. However, variability considerably complicates the assessment of management options.

Fluctuations in population sizes originate from many sources, including environmental variability, and inter- and intraspecific interactions. Harvesting represents an additional perturbation. There are many possible harvest strategies. Managers may prefer removal of a fixed proportion of the population, a fixed number of indi-

viduals regardless of population size, or all or a fixed proportion of the population that exceeds a threshold population size. All of these perturbations feed back into the population dynamics. Here we focus on harvesting strategies conducted to maintain a constant population size. The harvesting objective is simply to remove the equivalent of the annual net recruitment. This form of harvesting is known as fixed escapement harvesting, and the resulting population dynamics obviously will be greatly simplified.

The extent to which escapement will remain fixed and population size constant depends on how accurately preharvest population size can be ascertained. Usually the most detailed information regarding population size comes from analysis of the preceding harvest, so predicting preharvest population levels in essence requires accurate prediction of yearly recruitment. Recruitment rates will depend on the reproductive biology of the species, and how biotic and abiotic factors impact reproductive rates and juvenile survival. Our ability to predict recruitment rates should increase with our understanding of the population biology of particular harvested populations. But how will this increased knowledge affect the efficiency with which populations can be harvested? Here we develop a model framework with which we can examine these issues.

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Specifically, we ask how an improvement in our ability to predict recruitment rates will affect the expected harvest over the long term for a fixed escapement harvesting strategy, the variability of the realized harvest, and the persistence time of the exploited population.

THE MODEL

Consider a population of size N at time t , denoted N_t , that recruits annually at a per capita rate governed by the density-dependent function $g(N_{t-1}, Z_t, \varepsilon_t)$. Here, Z_t represents a time-varying density-independent biotic or abiotic feature of the environment that is measurable, and ε_t represents the net effect of other time-varying features that are unpredictable, either because they were not measured or are not measurable. Variation in this recruitment function can be attributed to a density-dependent component, density-independent components, or left as unexplained and therefore unpredicted variation.

A simple iterative equation for the dynamics of this unharvested population may be written as

$$N_t = g(N_{t-1}, Z_t, \varepsilon_t)N_{t-1}. \quad (1)$$

If the population is to be harvested with a fixed escapement strategy whose objective is to maintain the population at size \tilde{N} , then the harvest at each time interval (henceforth assumed to be yearly), is required to be $g(N_{t-1}, Z_t, \varepsilon_t)N_{t-1} - \tilde{N}$. Assume that estimates of population size are available each year based on analysis of the harvest in the preceding year. Assume that an explicit functional form for $g(N_{t-1}, Z_t, 0)$ exists, from which, based on analysis of the residuals from the fit of this function to recruitment data, a direct estimate of the variance of ε is available and denoted σ_ε^2 . We further assume that ε_t are centered and independently and identically distributed. The best available prediction of the required harvest is $g(N_{t-1}, Z_t, 0)N_{t-1} - \tilde{N}$, which when subtracted from Eq. 1 gives the following dynamics for the harvested system:

$$N_t = g(N_{t-1}, Z_t, \varepsilon_t)N_{t-1} - [g(N_{t-1}, Z_t, 0)N_{t-1} - \tilde{N}]. \quad (2)$$

If errors in the estimated recruitment each year are independent of each other, and the average population is stationary, sequential values of N_t will be independently and identically distributed. We use the Delta method for deriving approximations to the means and variances of functions of random variables (see for example Walsh and Lynch 1995). Because this method is based on Taylor-series expansions, the approximations will become less accurate as the coefficients of variation of the random variables become large. Using this method, which makes no other assumptions about the distribution of underlying random variables, approximate expressions for the mean (μ_N), and variance (σ_N^2) of the harvested population size, N_t , are as follows:

$$\mu_N \approx \tilde{N} \left(1 + \frac{\sigma_\varepsilon^2}{2} \frac{\partial^2 g}{\partial \varepsilon^2} \right) \quad (3a)$$

$$\sigma_N^2 \approx \mu_N^2 \sigma_\varepsilon^2 \left(\frac{\partial g}{\partial \varepsilon} \right)^2. \quad (3b)$$

If Z_t is independently and identically distributed, with mean μ_Z and variance σ_Z^2 , the mean of the recruitment function is approximated by

$$\mu_g \approx g(\mu_N, \mu_Z, \mu_\varepsilon) + \frac{\sigma_N^2}{2} \frac{\partial^2 g}{\partial N^2} + \frac{\sigma_Z^2}{2} \frac{\partial^2 g}{\partial Z^2} + \frac{\sigma_\varepsilon^2}{2} \frac{\partial^2 g}{\partial \varepsilon^2}. \quad (4)$$

These and all subsequent partial derivatives are evaluated at the mean value of parameters contained within them. The average annual harvest (μ_H) is given by

$$\mu_H = E[g(N_{t-1}, Z_t, 0)N_{t-1} - \tilde{N}]. \quad (5)$$

Noting that $E[g(N_{t-1}, Z_t, 0)N_{t-1}] = \mu_g \mu_N + \text{cov}[g(N_{t-1}, Z_t, 0), N_{t-1}] \approx \mu_g \mu_N + \sigma_N^2 (\partial g / \partial N)$, and assuming that $\mu_N \sim \tilde{N}$, we can substitute Expressions 3b and 4 into the following expression:

$$\mu_H \approx \mu_g \mu_N + \text{cov}[g(N_{t-1}, Z_t, 0), N_{t-1}] - \tilde{N} \quad (6)$$

and after some simple rearrangement, we obtain

$$\mu_H \approx \tilde{N} \left[g(\mu_N, \mu_Z, \mu_\varepsilon) + \frac{\sigma_Z^2}{2} \frac{\partial^2 g}{\partial Z^2} + \frac{\sigma_\varepsilon^2}{2} \frac{\partial^2 g}{\partial \varepsilon^2} - 1 \right] + \frac{\sigma_\varepsilon^2 \tilde{N}^3}{2} \left(\frac{\partial g}{\partial \varepsilon} \right)^2 \frac{\partial^2 g}{\partial N^2} + \sigma_\varepsilon^2 \tilde{N}^2 \left(\frac{\partial g}{\partial \varepsilon} \right)^2 \frac{\partial g}{\partial N}. \quad (7)$$

If the total variance in recruitment attributable to density-independent sources remains constant (i.e., $\sigma_Z^2 + \sigma_\varepsilon^2$ is constant), then we can evaluate how μ_H changes as the proportion of explained density-independent variance increases and the proportion of unexplained density-independent variance decreases. If the recruitment function is such that $\partial^2 g / \partial Z^2 = \partial^2 g / \partial \varepsilon^2$, then the first part of Expression 7 ($\approx \tilde{N}(\dots)$) is invariant to increases in σ_Z^2 that are balanced by decreases in σ_ε^2 (i.e., assuming $\sigma_Z^2 + \sigma_\varepsilon^2$ to be constant).

The second part of Expression 7 can be rearranged to give $\tilde{N}^2 (\partial g / \partial \varepsilon)^2 [(\tilde{N}/2)(\partial^2 g / \partial N^2) + \partial g / \partial N] \sigma_\varepsilon^2$. Defining

$$\theta = \tilde{N}^2 \left(\frac{\partial g}{\partial \varepsilon} \right)^2 \left(\frac{\tilde{N}}{2} \frac{\partial^2 g}{\partial N^2} + \frac{\partial g}{\partial N} \right) \quad (8)$$

Expression 7 can be rewritten as

$$\mu_H \approx \tilde{N} \left[g(\mu_N, \mu_Z, \mu_\varepsilon) + \frac{\sigma_Z^2}{2} \frac{\partial^2 g}{\partial Z^2} + \frac{\sigma_\varepsilon^2}{2} \frac{\partial^2 g}{\partial \varepsilon^2} - 1 \right] + \theta \sigma_\varepsilon^2 \quad (9)$$

and we can see that since the first term is invariant given that $\sigma_Z^2 + \sigma_\varepsilon^2$ is constant, a change in σ_ε^2 of $\Delta \sigma_\varepsilon^2$ will result in a change in μ_H of about $\theta \Delta \sigma_\varepsilon^2$. This method of approximating the effects of improved recruitment prediction on harvest yield should work well except when μ_g is very close to 1. When μ_g is close to 1, the population remains close to carrying capacity, recruitment is minimal, average harvests are very low, and the relative accuracy of the approximation is impaired.

If the errors in estimates of annual recruitment, ε_t , are independent of each other (i.e., they show no temporal autocorrelation), then sequential values of the population size following harvest, N_t , will be independently and identically distributed. If recruitment is overestimated by more than the escapement (i.e., $g(N_{t-1}, Z_t, 0)N_{t-1} - g(N_{t-1}, Z_t, \varepsilon_t)N_{t-1} > \tilde{N}$) then the projected harvest exceeds the escapement, and attempting to collect this harvest will result in the population being driven downwards toward extinction. In principle the probability of this occurring can be estimated directly from the fraction of the distribution of N_t that corresponds to values of projected population sizes ≤ 0 . Unfortunately an explicit expression for this distribution is not simple, and would be sensitive to the distribution of Z_t . In practice persistence times will be obtained best by simulation.

AN EXAMPLE

We demonstrate the use of this analytic framework by applying it to a possible harvest scheme for martens (*Martes americana*). Trapping of martens is an important economic activity in the northern forests of Canada and the United States (Strickland and Douglas 1987). In Ontario, martens are harvested via trapping conducted during the late autumn and early winter. Marten harvests are currently managed in Ontario through the setting of trapline quotas, which vary considerably from year to year (Fryxell et al. 2001). Wildlife managers in Ontario adjust quotas in response to changes in the ratio of young vs. old animals and trapping success relative to the previous year's quota (Fryxell et al. 2001). Hence, symptoms of population decline such as declining trapping success tend to trigger compensatory harvesting responses by regional managers. We suggest that, with slight modification, this kind of dynamic regulatory system could be used to approximate a constant escapement harvesting system, with past information on trapping success being used to maintain population levels at roughly constant levels. According to this scenario, past trapping success would be used to assess postharvest population abundance, with this information used in turn to predict potential recruitment of individuals into the population over the coming year and trapline quotas appropriate to this projected recruitment. Note that there is no necessity for assessment of marten abundance beyond the information obtainable from past harvest statistics, in keeping with the information constraints typically facing most wildlife managers.

Like many other terrestrial carnivores (Bulmer 1975, Tapper 1979, Peterson 1999), Ontario marten populations fluctuate in conjunction with their primary prey (Thompson and Colgan 1987, Fryxell et al. 1999, 2001). Monitoring of prey populations should accordingly improve forecasts of annual changes in marten recruitment, allowing managers to anticipate population response to environmental variation. Earlier work

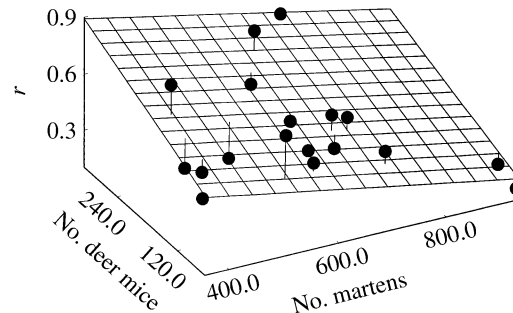


FIG. 1. Instantaneous rate of population growth by martens ($r_t = \ln[N_t/N_{t-1}]$) in the Bracebridge district of Ontario, in relation to marten abundance the previous year (N_{t-1}) and deer mouse abundance (catch per 1000 trap-nights) during the current summer (Z_t). Annual harvests have been added back into the populations to recover the estimated growth rate in the absence of harvesting. The multiple regression model that best fits these points is depicted by the surface, and deviations of observations from predictions are indicated by vertical spikes. An additional assumption of this analysis is that biases caused by the presence of N_{t-1} on both sides of the regression model will be inconsequential.

has shown that abundance estimates of three small-mammal species (*Peromyscus maniculatus*, *Tamiasciurus hudsonicus*, and *Glaucomys sabrinus*) are correlated with changes in marten abundance in the Bracebridge District of Ontario (Fryxell et al. 1999). Of these three species, *P. maniculatus* (the deer mouse) is an order of magnitude more numerous than the other two species (Fryxell et al. 1998), and its abundance is also the most strongly correlated with rates of change in the marten population (Fryxell et al. 1999).

In the absence of knowledge of the marten's prey base, recruitment is hypothesized to be purely density dependent. Regulation arises from territorial conflicts, either through energy expended in aggression or through direct reduction in survival (Fryxell et al. 1999). Using the demographic data reported in Fryxell et al. (2001), the instantaneous rate of increase of martens was first calculated by $r_t = \ln(N_t/N_{t-1})$, with N_t referring to preharvest marten abundance in the 6500-km² Bracebridge District, and N_{t-1} referring to postharvest abundance the previous year, to remove the impact of harvesting from the marten time series. Akaike's information criterion for small samples (AIC_c) was then used to evaluate the utility of alternate demographic models (specifically density-dependent models vs. prey- and density-dependent models) for predicting the instantaneous rate of increase by martens (Burnham and Anderson 1998:51). For the density-dependent model, the rate of increase is predicted by

$$r_t = a_1 + a_2 N_{t-1} + \varepsilon_t \quad (10)$$

($a_1 = 0.81$, $a_2 = -0.00051$, $R^2 = 0.25$, $\sigma_\varepsilon^2 = 0.0229$). However, if deer mouse density in the current year (Z_t) is also used to predict the rate of increase (Fig. 1),

$$r_t = a_1 + a_2 N_{t-1} + a_3 Z_t + \varepsilon_t \quad (11)$$

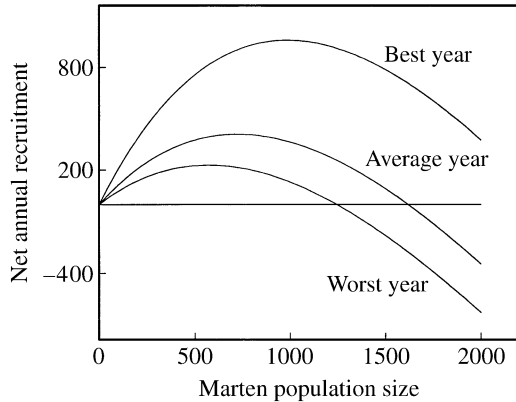


FIG. 2. Net annual recruitment to the marten population in the 6500-km² Bracebridge district of Ontario as a function of marten population size (N) in years of average, maximum, and minimum prey density (Z), modeled using a rearrangement of Eq. 11: net annual recruitment = $N(e^{a_1+a_2N+a_3Z} - 1)$.

($a_1 = 0.57$, $a_2 = -0.0005$, $a_3 = 0.0016$, $R^2 = 0.64$, $\sigma_\varepsilon^2 = 0.0122$), then the explanatory power of the density- and prey-dependent regression model is significantly greater ($AIC_c = -20.513$) than that of the density-dependent model ($AIC_c = -14.886$). Since no significant autocorrelation is present in the residuals, the ε_t are considered to be independently and identically distributed. One useful way to visualize the effect of this variability in recruitment is to calculate the net change in population abundance corresponding to extreme levels of prey abundance (Fig. 2). When deer mouse abundance is at its maximum observed value, the carrying capacity (i.e., the population size at which $r_t = 0$) of martens in the Bracebridge administrative district is ~ 2400 animals. In an average year, the carrying capacity is 1600 individuals, dropping to 1300 individuals in years when deer mouse density falls to the lowest observed value. Net recruitment of martens varies considerably as a function of prey availability and is maximized at intermediate levels of marten abundance, typically 500–1000 individuals (Fig. 2). By monitoring the deer mouse density, the level of uncertainty in the predicted recruitment can be approximately halved. We proceed by evaluating how reductions in σ_ε^2 affect the expected harvest level, the variation in harvest, and population persistence time of a closed marten population if harvest was managed with a fixed escapement strategy.

Available data from a time series of 46 years of deer mouse trapping (Fryxell et al. 1998) indicates that the average density of deer mice is 145 mice captured per 1000 trap nights, with a variance = 4080.7. For simplicity, however, we subsume a_3 (estimated to be 0.0016) into the mean and variance to obtain $\mu_Z = 0.0016 \times 145 = 0.232$ and $\sigma_Z^2 = 0.0016^2 \times 4080.7 = 0.0104$, so we can write the recruitment function as $g(N_{t-1}, Z_t, \varepsilon_t) = \exp(a_1 + a_2 N_{t-1} + Z_t + \varepsilon_t)$. Note that $\partial^2 g / \partial Z^2 = \partial^2 g / \partial \varepsilon^2$ and that $(\sigma_\varepsilon^2 / 2)(\partial^2 g / \partial \varepsilon^2)$ is small, so

that $\mu_N \approx \tilde{N}$ as required. By monitoring the deer mouse population, the unanticipated variation in recruitment can be reduced (variation is essentially removed from an unpredictable source, ε , and attributed to a predictable source, Z) and improvements in harvests can be estimated from Expression 7 for any selected value of escapement. For example, if $\tilde{N} = 500$, $\sigma_\varepsilon^2 = 0.0229$, $\sigma_Z^2 = 0$, the expected harvest, μ_H , from Expression 7 is ~ 365 individuals. With knowledge of deer mouse densities σ_ε^2 is reduced from 0.0229 to 0.0122; thus $\Delta\sigma_\varepsilon^2 = -0.0107$, $\sigma_Z^2 = 0.0104$, and $\theta = -573$, and a modest increase in μ_H of $\theta \Delta\sigma_\varepsilon^2 = 6$ individuals (or 1.6%) is expected to result.

Fig. 3A shows the predicted analytic effects of reducing the unpredicted density-independent variation in marten recruitment on harvest levels, as a function of escapement. Average harvest yields are, as expected, greatest at intermediate escapement levels, but the effects of unpredicted variation in recruitment are almost imperceptible. Numerical simulations show almost identical effects. There are higher proportionate benefits of more information when escapement is left very high (Fig. 4). For example, when escapement is set to 1400, perfect prediction of density-independent variation in recruitment would lead to a 40% increase in harvest, but the numerical increase in harvest at this high escapement level would still be small in absolute terms. In contrast, perfect prediction of recruitment variation at an escapement of 400 individuals would produce only a 2% improvement in yield relative to that achievable in the absence of knowledge about prey density.

Fig. 5 shows the effect of reducing the unpredicted density-independent variation in recruitment on the constancy of harvest levels (as measured by the coefficient of variation), as a function of escapement. Harvest variation is much more pronounced at escapements approaching the ecological carrying capacity than when escapement is low. Improved understanding of recruitment variation reduces the variability of harvests at low escapements, but has the opposite effect at high escapements.

Fig. 6A shows simulated distributions of N_t for the fully stochastic situation (no knowledge of prey fluctuation; $\sigma_\varepsilon^2 = 0.0229$, $\sigma_Z^2 = 0$), and for when prey fluctuations are incorporated in the recruitment prediction ($\sigma_\varepsilon^2 = 0.0122$, $\sigma_Z^2 = 0.0107$), assuming escapement to be 200. In the former case the accuracy of recruitment prediction is reduced, harvests can then exceed population size, and increased levels of extinction can result (with probability 0.032). Fig. 6B shows how expected population persistence time, T_E changes as a function of the balance of σ_ε^2 and σ_Z^2 . The decrease in T_E is almost loglinear with increasing σ_ε^2 , and T_E is substantially overestimated by assuming N_t to be normally distributed, as a result of the kurtosis in the distributions of N_t .

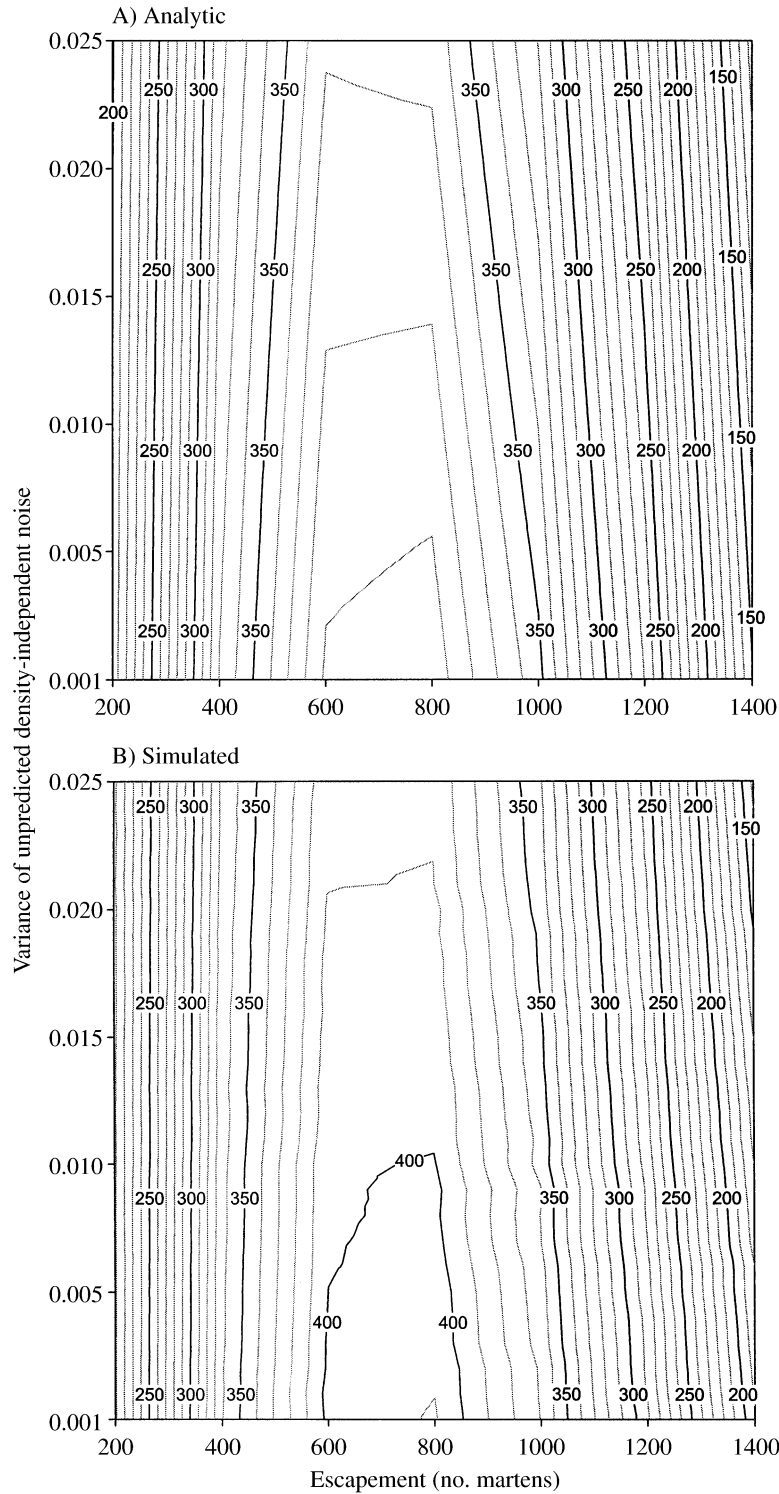


FIG. 3. The effect of unpredicted variation in recruitment on harvest levels of martens is shown, as a function of escapement. Numbers within the graph represent numbers of martens harvested. Overall variation in recruitment is held constant ($\sigma_z^2 + \sigma_\varepsilon^2 = 0.025$), but the fraction of this total that is represented by σ_ε^2 is varied from 0% to 100%. (A) The graph shows the analytic approximation using Expression 7. (B) Simulation results are based on 10^5 years of harvesting using Eq. 2 with identical parameters. Both Z and ε are modeled as independently and identically distributed Gaussian random variables (the time-series of deer mouse densities exhibited no significant autocorrelation), negative harvests are defined as zero yield, and the population is reset to the escapement level if extinction occurs.

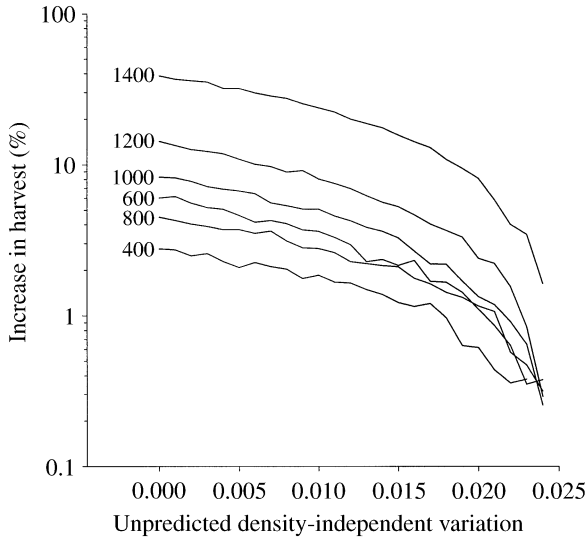


FIG. 4. Simulation results (100 000 harvests) are shown for the improvement in harvest yield, expressed as the average percentage increase over that obtained at maximum unpredictability ($\sigma_e^2 = 0.025, \sigma_z^2 = 0$), as the unpredictability in recruitment is reduced (finally to $\sigma_e^2 = 0, \sigma_z^2 = 0.025$). Overall variance in recruitment is held constant (so that $\sigma_e^2 + \sigma_z^2 = 0.025$). Different escapement levels are indicated on the graph. Note the log scale on the y-axis; parameters are as for Fig. 3.

DISCUSSION

Anticipating recruitment fluctuations likely will have only a modest effect on absolute yield from fixed-escapement harvesting strategies. The biological explanation for these results is straightforward. Average recruitment can be predicted with only limited accuracy, so actual escapement will be distributed above and below the target escapement in some distribution, only equaling it on average. The more accurately recruitment can be predicted, the closer will be the match between realized and target escapement. However, improvements in recruitment prediction will result only in changes to expected harvest if the costs, measured in units of future recruitment, of over-harvesting are not exactly balanced by the benefits of under-harvesting. For example, if the reduction in recruitment that might follow as a consequence of escapement exceeding the target by 10% is matched by the increase in recruitment arising from escapement falling 10% below target, there is, on average, no cost to inaccurate recruitment prediction. If on the other hand, the reduction in recruitment resulting from a 10% over-harvest, is greater than the increase resulting from a 10% under-harvest (i.e., $\partial^2 g / \partial N^2 < 0$), then average harvest levels could increase with greater predictive accuracy of recruitment.

Improved forecasting of recruitment can lead to a substantial decrease in the risk of over-harvesting, par-

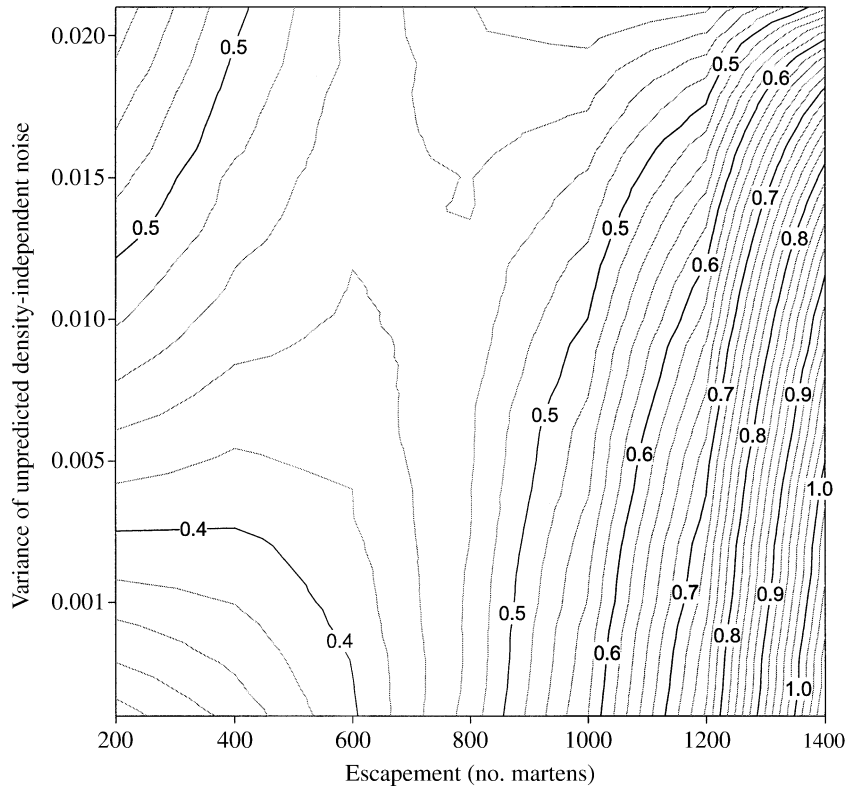


FIG. 5. The coefficient of variation of annual harvest as a function of σ_e^2 and escapement. Total variation is again maintained constant at 0.025, with recruitment parameters as for Fig. 3.

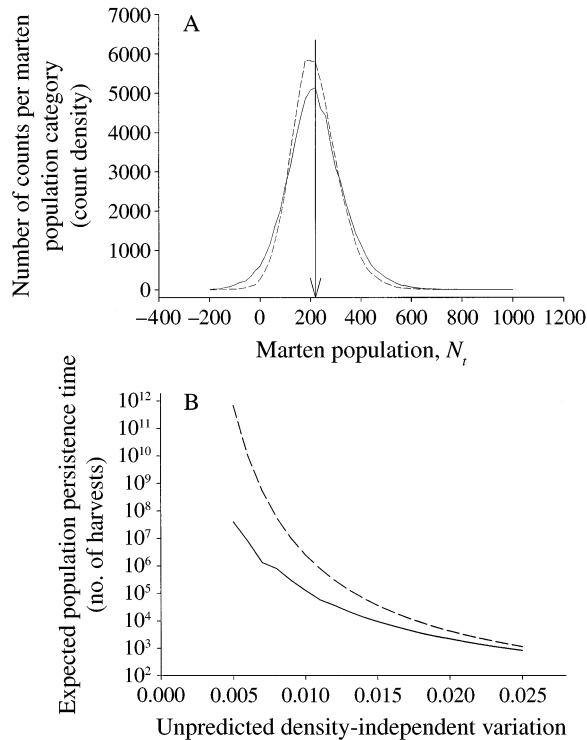


FIG. 6. (A) The distribution of N_t deduced from 60 000 iterations of Eq. 2. Escapement is set at 200. The solid line is the distribution of N_t when only 25% of variation in recruitment is explained and all density-independent variation is unpredicted ($\mu_N = 208$, $\sigma_N = 115.5$, skewness = 0.25, kurtosis = 0.71). The probability that projected harvest exceeds actual population size and extinction occurs is estimated to be 0.032. The dashed line is the distribution of N_t when 64% of variation in recruitment is explained and density-independent variation attributable to the prey base is incorporated ($\mu_N = 208$, $\sigma_N = 94.9$, skewness = 0.39, kurtosis = 0.7). In this case the probability that projected harvest exceeds actual population size is estimated to be <0.009 . (B) Solid line: population persistence time estimated by direct simulation of 40×10^6 iterations of Eq. 2, with escapement set at 200, as a function of σ_e^2 ($\sigma_e^2 + \sigma_N^2 = 0.025$). The upper dashed line shows the population persistence time, estimated as $1/\int_{-\infty}^1 \mathcal{N}(\mu_N, \sigma_N^2) dx$.

ticularly in intensely exploited stocks. When coupled with an aggressive (low escapement) harvesting policy, a sequence of years with below-average recruitment could result in local extinction of the stock. Anticipation of annual variation in recruitment via monitoring of prey abundance can provide vital early warning that over-harvesting is imminent. Additional knowledge about food web dynamics can help avert this disaster. Although locally over-harvested populations might be rescued by occasional colonists arriving from nearby source populations, such as nature reserves (Quinn et al. 1993, Hastings and Botsford 1999, Lundberg and Jonzen 1999), presumably population managers rarely would want to take that risk.

Our results support the conclusions of Walters (1989) that there is little hope of substantially improving yield

by more accurate forecasting of recruitment. On the other hand, Spencer (1997) showed that time-varying harvest policies could improve average yields as much as twofold higher in multiequilibrium systems with temporally autocorrelated environmental stochasticity. Analysis of fixed escapement harvest strategies are much more tractable than other strategies such as fixed proportion harvesting, because within an estimable error, population size is returned to a fixed level after each harvest. Since the projected harvests are re-estimated each year, errors do not propagate in the system over a time period of more than one year (as they would do in a fixed proportion harvesting strategy; see for example, Jonzen et al. 2002). Therefore the results of this analysis are likely to apply even when errors in projected recruitment are correlated through time (e.g., as might occur in periodic environments or environment that vary cyclically due to interspecific interactions). Clearly, further work is needed to verify the truth of this conjecture.

Although we have illustrated our model using a terrestrial fur-bearer species, the American marten, the phenomenon we describe is quite general and our theoretical conclusions potentially applicable to a broad range of exploitation systems. Research programs are underway in a variety of species ranging from Atlantic cod (*Gadus morhua*) to Canvasback Ducks (*Aythya valisineria*) to better understand sources of recruitment variation. No doubt some of this research interest stems from long-term interest in improving the prediction of demographic rates, in anticipation of improved harvest management. For example, waterfowl managers have made impressive strides over the past several decades in identifying key environmental parameters, such as pond abundance across the prairies, that influence the recruitment of young birds to waterfowl populations (Nichols et al. 1995). Annual data on habitat variables and population abundance are used by regulatory agencies to adjust a complex set of harvest regulations for waterfowl populations in the United States and Canada. Our results suggest that combining habitat assessment with waterfowl abundance to dynamically adjust waterfowl harvests may be unlikely to produce substantial improvement in average annual yield. On the other hand, such an approach may be very useful in preventing accidental over-harvesting of waterfowl populations to unacceptably low levels, perhaps a more important conservation objective in the long term.

Because extinction risk is inversely related to escapement in stochastic environments, escapement close to the ecological carrying capacity may be more defensible from a conservation point of view than escapement that maximizes mean yield (Lande et al. 1994, 1997, Roughgarden and Smith 1996). If managers follow a conservative strategy of harvesting only when the population is near its carrying capacity, then our results imply at best a modest proportionate increase in the average annual yield obtained by im-

proved forecasting of recruitment. More aggressive exploitation policies are unlikely to realize sizeable improvement in average yields resulting from greater accuracy in recruitment forecasting. On the other hand, improved recruitment forecasting can reduce substantially the risk of over-harvesting under intense exploitation pressure.

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