Reconstructibility of Density Dependence and the Conservative Assessment of Extinction Risks

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Abstract: *The probability of extinction is sensitive to the presence and character of density dependence controlling the dynamics of a population. This means that our capacity to estimate a population's risks of extinction under varying environmental conditions or competing management regimes is linked to our ability to reconstruct from data the density-dependence relationships governing the natural dynamics, especially when data do not reveal a trend of population growth or decline. In an example using* Gadus morhua, *we show that even 10- or 20-year data sets are too short to make precise estimates of these risks. We also observe, however, that under moderate or weak density dependence, the computed risks are lower than when density dependence is not included in the model. We propose, therefore, that when available data sets are insufficient for reconstructing reliable measurements of density dependence, conservative estimates of extinction probabilities can be made from models that simply omit density dependence.*

Resumen: *La probabilidad de extinción es sensible a la presencia y al carácter de la dependencia de densidad que controla la dinámica de una población. Esto significa que nuestra capacidad para estimar los riesgos de extinción de una población bajo condiciones ambientales cambiantes, o diferentes régimenes de manejo, está relacionada a nuestra capacidad de reconstruir, en base a datos, las relaciones de dependencia de densidad que gobiernan la dinámica natural de poblaciones, especialmente cuando no se dispone de información que revele tendencias de crecimiento o declinación de poblaciones. En un ejemplo, utilizando* Gadus morhua, *demostramos que aún los datos sobre un período de 10 ó 20 años son insuficientes para hacer estimaciones precisas sobre estos riesgos. Sin embargo, observamos que incluso en una situación de dependencia de densidad moderada o débil, los riesgos calculados son más bajos que cuando la dependencia de densidad no es incluída en el modelo. Por ello proponemos, que, cuando no se dispone de datos suficientes para reconstruir estimados confiables de dependencia de densidad, se pueden hacer estimaciones conservadoras de probabilidades de extinción a partir de modelos que simplemente omiten los aspectos de dependencia de densidad.*

Introduction

The dynamics of population growth together with fluctuations in environmental conditions result in stochastic variation in the abundance of any natural population of organisms. Biological management often seeks to minimize or limit this variability for economically or aesthetically valuable species, and uses ecological risk analysis to estimate the probability that a population will suffer extinction or fall below some specified level of abundance, a fate that can be termed "quasiextinction" (Ginzburg et al. 1982). We use this term inclusively for population declines and extinctions.

Quasiextinction risks can be estimated for population dynamic models, either by analytical solution or with computer simulations. Simulations are usually required when the models include much of the complexity of natural systems, such as age structure or density dependence (Ferson et al. 1989). In either case, the estimations that are possible depend of course on the parameters and vital rates used in the model of population dynamics, which are themselves estimated with error. Theoretical considerations and our experience (Saila et al. 1990) with computer simulations in estimating quasiextinction risks suggested that risks can be quite sensitive to the form and strength of density dependence in the population model. This is a serious problem because density dependence is often difficult to measure from limited population census data (see, for example, Gaston & Lawton 1987; Pollard et al. 1987). This paper explores the sensitivity of quasiextinction risk estimations to ignorance about density dependence.

Density Dependence

Density dependence is the phenomenon by which the effective value of a vital rate such as survivorship or fecundity per individual depends on the absolute density of the population. By this we mean that an individual's average fecundity, reproductive success or the chance that it dies is not constant or even statistically stationary, but rather, will change as a function of the density of the population. The significance of this phenomenon in natural populations has been debated in ecology for decades (see Hassell 1986; Strong 1986). Although density dependence is any nonconstant relationship of a vital rate to the current population size, it has often been viewed as a mechanism regulating natural population size toward its equilibrium (known as the carrying capacity). For example, when a population is overcrowded, production or survival of offspring is often depressed, due to competition among the offspring for finite resources or perhaps to changes in parental behavior. When the population is undercrowded relative to the equilibrium population size, these effects are lessened so that production and survivorship increase. Insofar as density dependence manifests itself in this

pattern, it will be a "restoring force" that tends to draw the population size over time to the carrying capacity. Despite widespread acceptance of this idea, it has been subject to vocal criticism, and identifying the precise mechanisms of density dependence and evaluating its real intensity in natural systems have proved to be difficult problems.

The influence of density dependence on a population model can be controlling in several ways. For instance, it is well known that a Leslie matrix usually has three possible behaviors: exponential growth, exponential decline, and, under very delicately adjusted parameters, equilibrial balance. When density dependence is added to a Leslie matrix model, the parameter range under which equilibrium occurs can expand infinitely. In general, the trajectories from population models can depend quite sensitively, especially in terms of asymptotic behavior, on how density dependence is represented in the model and on the strength of density dependence that the parameter values imply. Of course, it follows that the probabilities of extinction and quasiextinction computed from the models can be dramatically influenced by errors in representing density dependence.

The empirical data necessary to calibrate a model of density dependence include abundance measurements, sometimes of inconspicuous classes such as the youngest individuals, collected over several years. Therefore the requisite data are usually expensive to gather or are simply not available. Since density dependence can be difficult to estimate, it is importrant to explore how our ability to make correct measurements of density dependence will affect our estimations of quasiextinction probabilities. To this end, we did a sensitivity study of quasiextinction risk as a function of the strength of density dependence for a species for which reasonably detailed life history information is available. To determine the level of imprecision likely to accompany our estimating density dependence from data, we conducted a reconstruction experiment in which we generated and statistically analyzed hypothetical population trajectories and then compared the computed density dependence parameters to the "true" parameters used to construct the data. Together, these studies allow us to see what error we could make in estimating risk of quasiextinction when density dependence is known only imprecisely.

Saila et al. (1990) suggested a potentially very useful finding about how the ecological risks one can compute from a model of population dynamics may depend on whether the model incorporates density dependence. If density dependence generally acts as a restoring force, it seems reasonable that, in many if not most cases, models that include density dependence would exhibit less fluctuation than models that don't include it, because density-dependent trajectories experience a pull toward their equilibrium. Since quasiextinction probabilities

are determined by the size of fluctuation in population size, models without density dependence (which are of course comparatively easy to construct) could in general be conservative estimators of extinction risks. If, then, the simple model shows an acceptably small chance of loss of the population, one might reasonably expect that a more complex and realistic model incorporating density dependence would show such a chance to be as small or smaller. In this study we tried to quantify the level of conservativism that could be expected from a model that omits density dependence.

We used a model of one species as an example with which to show the relationship between density dependence and extinction risks. The resulting details thus depend on the particularities of this species, but the general findings illustrate the potential complexity that can arise in a variety of species.

Methods

The Model and Parameters

We modeled the demography of *Gadus morhua* (cod), an iteroparous fish that can live up to 20 or more years. We used RAMAS (Ferson et al. 1988), an age-structured population model incorporating environmental stochasticity and density dependence, to simulate population trajectories and estimate the risk of quasiextinction.

In general, there are many ways to incorporate density dependence into a population model. For fish, a common assumption is that density dependence operates primarily on early life stages, usually within the first year after hatching. Since cod evidently eat large numbers of their own young (Ponomarenko 1968), we assumed the Ricker function (Ricker 1975, p. 282) would be a suitable model of density dependence in the species. This function is

$$R = \alpha'P \exp(-\beta'P)$$

where P is population size of parents and R is recruitment into the population. This function nonlinearly relates total reproductive effort (i.e., P) to reproductive success such that, after a peak of success, additional effort is actually counterproductive and results in a decrease in reproductive success. Ricker himself (1975, p. 286) reported estimates of α' and β' for cod that were computed from Garrod's (1967) data. Since the Ricker function is a simple stock-recruitment model, the parameter estimates were expressed in units of parents and recruits. But our age-structured approach is considerably more detailed because it recognizes that fecundity varies with the age of individuals. Thus, we needed to generalize the Ricker function for an age-structured model and re-express the parameter estimates in compatible units. To do this we chose, in our implementation, to measure reproductive effort by the total number

of eggs produced in a given year and to measure reproductive success by the number of recruits that actually enter the population. We converted the parameters to these units with the equations

$$\alpha = \frac{\alpha'}{rF}$$

$$\beta = \frac{\beta'}{rF}$$

where r is sex ratio as the fraction females, and F is the average weighted fecundity over all age groups for the equilibrial abundance distribution. This conversion is simple but it must be solved iteratively since the average weighted fecundity depends on the Ricker parameters. After this conversion, the transformed parameters are used throughout the simulations.

In our generalization, α would ideally be estimated with a nonlinear regression of the number of zero-year-olds on the number of eggs estimated by, for instance, belly counts of fecund females. For many species, however, counting the number of zero-year-olds is virtually impossible. When, as is often the case, the number of zero-year-olds cannot be assessed, it may only be possible to estimate the product of α and the survivorship of zero-year-olds into an older age class. For cod, we in fact assumed that the stock-recruitment relationship was between parental stock of year t and one-year-olds at year $t + 1$. Therefore the relationship includes the transition from eggs to zero-year-olds (Ricker curve) and from zero-year-olds to one-year-olds (p_0). Therefore the relationship estimated is

$$N_1(t + 1) = p_0 \, \alpha \, E(t) \exp(-\beta \, E(t))$$

where E is the parental investment measured in number of eggs.

In our RAMAS model with Ricker density dependence, the next generation is computed from the current one under the rules

$$E(t) = \sum f_i N_i(t) r$$
$$N_0(t) = \alpha E(t) \exp(-\beta \, E(t))$$
$$N_{i+1}(t + 1) = p_i N_i(t) \quad \text{for } i \geq 0$$

where t represents time and i indexes age; N_i, f_i, and p_i are age-structured vectors of abundance, fecundity, and survivorship; α and β are the parameters of the Ricker model, and E is the potential reproduction from a single year. The fecundity and survivorships are random variates drawn from a distribution described statistically.

We used estimates for the vital rates including survival and fecundity as well as their variances from Saila et al. (1990), which were specifically derived for RAMAS. The values are expressed in terms of numbers of individuals (as opposed to biomass units). The rates

p_i and f_i were lognormally distributed with means and coefficients of variation as listed in Table 1. The vital rates were simulated without cross-correlations. The sex ratio in cod is approximately 50:50, so r is 0.5.

Since we do not have separate estimates for α and p_0, but an estimate of their product $\alpha\, p_0$, we used this estimate as p_0 in RAMAS and set $\alpha = 1$. The only reason for this (as opposed to using the estimate as α and setting $p_0 = 1$, or arbitrarily dividing the estimate between α and p_0) is that RAMAS represents environmental stochasticity by varying survivorships but not the density dependence parameters. Therefore our scheme allows us to mimic the variability in recruitment that is apparent in Garrod's data.

In all simulations, we used the equilibrium distribution for the initial population sizes $N_i(0)$ which started the simulations. For every set of input parameters we had to find the equilibrium distribution. To do this we first set the abundances to an arbitrary vector and generated 250 replicate trajectories over an initial equilibration period. We then used the mean vector after 50 years as the starting distribution of abundances. Fifty years appeared to be long enough for transient effects to die down. We ran the simulations for 40 years (which is nearly twice the duration of sampling available for cod).

Sensitivity Analysis

For the sensitivity study, we varied the strength of density dependence over a range around the estimate derived from Ricker (1975). To do this, we first chose a value for β and then found the value of α that yielded the same mean adult population size at equilibrium.

Table 1. Parameters of the model.

Means

Age	Survival $\bar{p}_i$	Fecundity $\bar{f}_i$
0	α	0
1	0.78	0
2	0.78	0
3	0.61	361,100
4	0.61	565,900
5	0.61	801,900
6	0.61	885,700
7	0.61	1,100,000
8	0.61	1,195,000
9	0.61	1,641,000
10	0.61	2,475,000
11	0.61	2,484,000
12	0.61	3,900,000
13	0.61	3,933,000
14	0.61	3,757,000
15	0.61	4,460,000
16	0.61	6,200,000
17	0.61	5,423,000

CVs

Age	Survival	Fecundity
0	0.20	—
>0	0.10	1.85

"Adult" means all age classes greater than zero years old; we used adults rather than the total of all classes because the stochastic variation in abundance of zero-year-olds often obscures the more significant variation in the older age classes. RAMAS similarly uses adult abundance as the variable with which to express quasiextinction risks. Figure 1 shows the resulting Ricker functions used in the simulations as well as the actual parameter values they represent. The functions do not all intersect at one point because we calibrated with adults rather than number of eggs. Each of the several density dependence models were equilibrated separately to yield different initial abundance distributions. Using these five sets of parameters RAMAS generated a series of population trajectories. For each of the models, we made 250 replicate simulations that differed only in the strength of density dependence. The outputs from these simulations were the quasiextinction risk curves as functions of several threshold values.

Reconstruction

To assess the reconstructibility of density dependence, we collected as output from RAMAS the number of eggs at each year t and the number of one-year-old individuals at the next year $t + 1$. We simulated population growth over forty years from which we selected 10, 20, 30, and then all 40 years of output to analyze. All trajectories were replicated 50 times. We used the nonlinear regression analysis NLIN (SAS 1985) on these num-
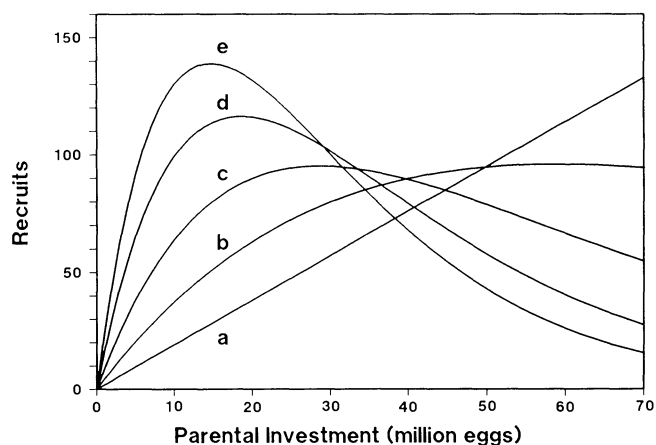

Figure 1. Ricker curves representing different levels of density dependence. These functions yield the same number of total adults in an age-structured model.

Legend	Density dependence	$\alpha\ (\times 10^{-6})$	$\beta (\times 10^{-8})$
(a)	None	1.9	0.0
(b)	Very weak	4.4	1.7
(c)	Weak	9.0	3.5
(d)	Best estimate	17	5.4
(e)	Strong	26	6.8

bers to reconstruct the β parameter of the Ricker function. The reconstructed values were divided by the true value and plotted as distributions for each of the four sample sizes. This reconstruction is the best that could be hoped for with real data since our variables were "collected" without any measurement error and since we knew by construction which model of density dependence to fit in the regression. This analysis therefore estimates an upper bound on the reliability of reconstructing density dependence from real data. Authentic reconstructions will probably have less reliability and greater errors than we observed.

Results

Sensitivity Analysis

Figure 2 summarizes the influence of density dependence on quasiextinction risk for cod. It shows superimposed quasiextinction curves for five different levels of density dependence. Each quasiextinction curve shows the probability of the population size falling below certain threshold values (x axis) at least once during the 40 years simulated. Thus, whatever density dependence really is, there is very little chance that the population will fall below 40 individuals any time in the next four decades, and it is virtually certain that the population will go below 265 which, by design, is the carrying capacity. Assuming that our best estimate of density dependence is correct, there is nearly a 50-50 chance that the population will fall below 150 individuals, which represents a considerable amount of fluctuation from carrying capacity in the population's abundance over time.

Perhaps surprisingly, the influence of density dependence on this risk is not a monotonic function of its

strength as measured by β. When density dependence is zero, i.e., when there is no tendency for the population to remain at the abundance at which it started, the quasiextinction risks are rather high. When very weak density dependence is introduced into the model, the risks are radically reduced as the trajectories are strongly tethered to their carrying capacity. As the strength of density dependence is increased, the intensity of the restoring force is greater, but the consequence is higher rather than lower quasiextinction risks. This occurs because strong density dependence in the Ricker model causes the population trajectories to experience damped cycles, from which stochasticity allows them to reach even lower levels. Under stronger density dependence, this function could generate cycles with greater amplitudes and even deterministic chaos (May & Oster 1976; Guckenheimer et al. 1977) in the population trajectories (Ginzburg & Ferson 1990). We observe that the influence of density dependence on the magnitude of quasiextinction risk can be quite large. If our best estimate is correct, there is about a 50% chance that the population will fall below 150. However, as can be seen in Figure 2, if the estimates for density dependence are substantially in error, the chance could range between negligibility and 0.85, a rather high risk. Even curves that look quite close could result in very different risk estimates since the vertical difference is the quantity of interest. Since quasiextinction risk is quite sensitive to the strength of density dependence, it is prudent to ask what measurement error there could be in density dependence estimated from field data, and what miscalculation it might precipitate in our estimate of quasiextinction risk.

Reconstructibility

Figure 3 shows the output from 10 years of a single, randomly selected trajectory simulated using the best estimate (derived from Ricker 1975) for density dependence, which is represented as a dotted line on the graph. Also shown is the estimated density dependence fitted to these 10 points by a nonlinear regression. Although there was no noise added to density dependence itself in the model, stochastic variation representing the natural levels of variability in other demographic parameters induces the scatter off the dotted line. Reconstructibility depends on the discrepancy between the strength of density dependence used to create the trajectory and that which can be computed by regression from the result. Figure 4 shows 200 such reconstructions over several sample sizes. Plotted are the estimated values of the β parameters divided by the true value of the parameter used in the simulation. Each point represents the parameter estimated from a single population trajectory and the vertical bars represent plus or minus two standard deviations of these 50 esti-
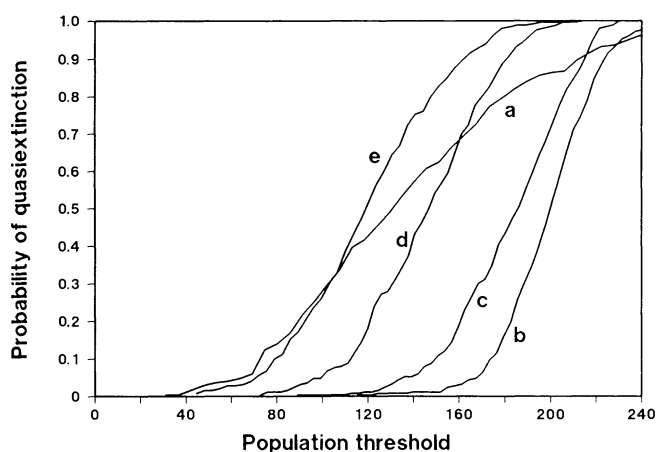

Figure 2. Quasiextinction probabilities under different assumptions of density dependence for a 40-year time horizon. Density dependence: (a) none; (b) very weak; (c) weak; (d) best estimate; (e) strong.
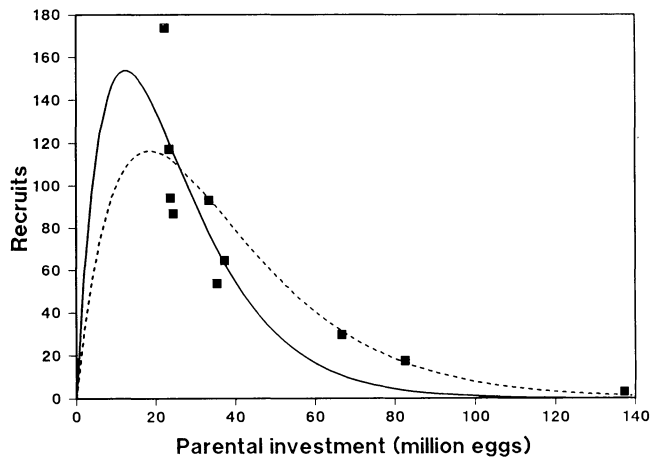
Figure 3. Example of the reconstruction of density dependence with a small sample size. The number of eggs produced over 10 years is plotted against the number of resulting one-year-olds a year later. The dotted line is the density dependence function used to create the simulation, and the solid line is the fitted regression line for the 10 points.

mates. The parameter estimates are more precise when more years are included in fitting the curve. This simple consequence of sample size actually has profound implications since real data sets with more than a dozen years of data are extremely rare.

Among three species of fish we considered in equivalent simulations (not described in this paper), cod shows the best reconstructibility for the value of β. This
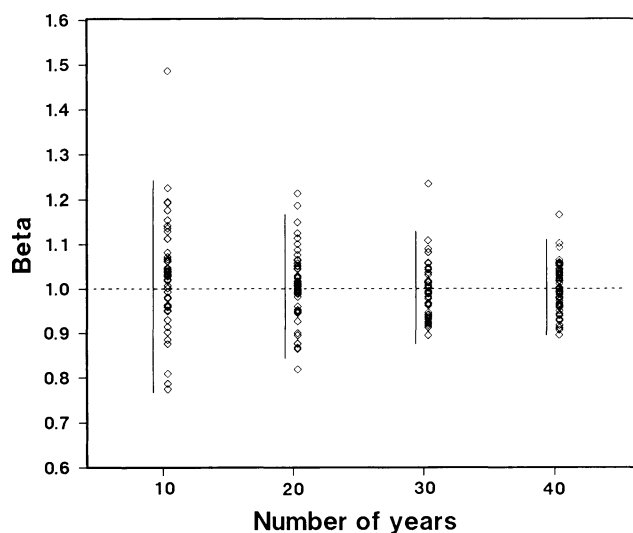
is apparently due to its high coefficient of variation for fecundity, which causes the trajectories to explore a larger range of the fecundities and thus yield better regressions. This, together with our simulations' advantages over authentic estimations of density dependence from field data, suggests that the scatters in the figure are as small as or smaller than one could expect to achieve using real-world data. Thus, it seems probable that the uncertainties implied by scatter of these magnitudes are the minimal consequences of errors in reconstruction of density dependence; the errors we can expect from most other real data will only be larger.

Figure 5 expresses the sensitivity of quasiextinction risk to the strength of density dependence in a different way. On this graph we can estimate the magnitude of the mistake in the predicted risk that would be the result of measurement error in β. If we assume that an estimate of density dependence could be off by as much as two standard deviations from its true value, such a discrepancy would translate into as much as a fivefold error in the risk estimation. The impact depends somewhat on which threshold abundance we focus on. Does such an extreme effect of measurement error suggest that quasiextinction is too unstable an index to be useful in monitoring natural populations? This might be the case if there were not an interesting feature of these graphs (described in the next section).

Conservative Risk Estimation

The quasiextinction risks computed for a model without density dependence are quite high. In fact, for all thresh-

Figure 4. Reconstructed β values for 50 simulations using 10, 20, 30, and 40 years' worth of data. The values are divided by the true value. The vertical bars to the left of data points show plus and minus two standard deviations.
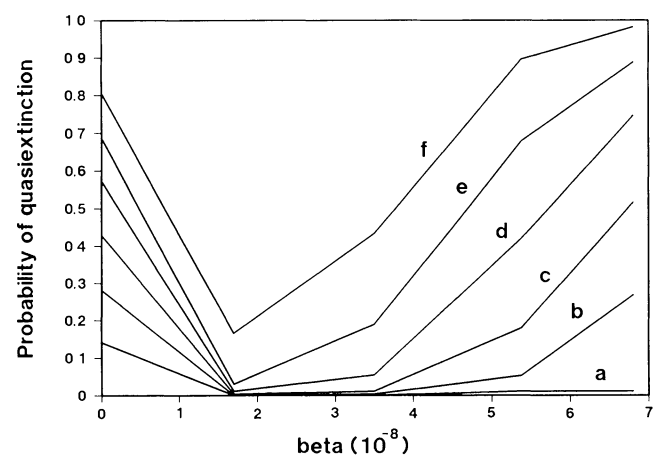

Figure 5. Quasiextinction probabilities at six different thresholds as functions of the strength of density dependence. The thresholds are (a) 30%, (b) 38%, (c) 45%, (d) 52%, (e) 60%, and (f) 68% of the equilibrated level of 265 individuals. Our best estimate of the true density dependence is β = 5.4 × 10^{-8}

olds lower than two-thirds of the carrying capacity, they are higher than those from the model using our best estimate of density dependence. In general, compared to models with plausible estimates of density dependence, the density-independent simulation gives conservative estimates of risk, for most low thresholds. The degree of conservativism depends on the true level of density dependence, but the effect is especially strong for low thresholds, which are, of course, the most relevant ones in conservation matters. Density dependence stronger than the range in the first figure entrains the population dynamics in limit cycles and then in deterministic chaos. This can result in very high quasiextinction risks that easily exceed the putatively conservative risks. In fact, by choosing the model of density dependence carefully, one can achieve any quasiextinction risk desired. Whether we believe we have found a way to conservatively estimate these risks depends on whether we believe density dependence is actually so extreme in natural settings. That the species persist in evolutionary time is an argument that it is not, but contrary evidence may exist (Schaffer & Kot 1986). The possibility that density dependence usually only lessens the risks of quasiextinction is very important since, if true, one can estimate upper bounds on the risks, which may be sufficient for the purposes at hand.

It is the strong nonlinear character of the Ricker function that results in the breakdown of this conservativism at very high levels of density dependence. Had we used the Beverton-Holt function (Ricker 1975) or any of a host of other monotonic relationships instead of the Ricker function to describe density dependence, we would have seen an asymptotic approach to carrying capacity since these functions do not allow the trajectories to overshoot their carrying capacity (Ginzburg & Ferson 1990). Whenever density dependence has this character, conservativism will hold over all strengths of density dependence.

The quasiextinction risk curves in Figure 2 are the cumulative frequency distributions of trajectory minima. In models without density dependence, the trajectories form a loose bouquet emanating from the starting point, the initial population size at time zero. When density dependence acts as a restoring force to draw the trajectories toward the carrying capacity, this bouquet gets tighter with increasingly strong density dependence. But, as evidenced by the crossing of the risk curves at high thresholds, the constricting of the trajectory minima is an uneven one. The very low minima are squeezed more toward the center of the distribution than the central ones are to the carrying capacity. This nonlinear bunching of the trajectory minima implies that the risk curves from models with density dependence will be steeper than that from the density-independent model. In the extreme case of perfect cy-

cles, the risk curve would be a step function with the step at the minimum the trajectories reach. This means that it is only for low population thresholds that conservativism seems to hold.

Although it clearly requires further study, the finding of conservativism may mitigate in very large part the conclusions about sample sizes implied by the results from this paper. For species with reasonably detailed information available, from which good estimates of the strength of density dependence can be made, quasiextinction risks can be computed with fair accuracy. For species on which there is little life history and demographic data, a model without density dependence may allow at least a conservative estimate of those probabilities. As more data over longer periods of time become available for the species, the estimations can be improved. In intermediate cases, perhaps sensitivity studies such as the one described here can be used to find upper and lower bounds on the quasiextinction risks by exploring the range of plausible density dependence strengths.

Conclusions

Politically minded scientists and managers appreciate an important feature of the probabilistic estimates of extinction: they explicitly avoid concrete predictions. This is both the good and the bad thing about these kinds of estimates. It's good because it admits the native stochasticity that is inherent in ecological processes. It's bad because it is hard to falsify a probabilistic prediction. Shrugging with the immunity of a weather forecaster, we can always claim we never said the population wouldn't go extinct; we just said it had low probability of going extinct. In fact, validating probabilistic models requires extremely large data sets that include information not only on means but on the statistical distributions of the phenomena modeled. For most systems with any level of complexity, this virtually assures that no relevant and complete data set will soon be collected. A practical response to the two-edged sword of probabilistic prediction is of course to scrupulously evaluate the assumptions of the models used to make the estimations. Another is to assure that where uncertainty persists in the modeling process we make conservative assumptions. That is, when we are concerned with the risk of an undesirable event such as a population's reduction or extinction, we evaluate upper bounds on the probability that it will occur. This uncertainty ranges from imprecision in the value of a vital rate that is hard to measure, to tentativeness in decisions about the model's structure itself.

When a population is decreasing, or even increasing, RAMAS (or a comparable method) should be used to

estimate the extinction risks for future population fluctuation. When no trend toward growth or decline can be discerned in a noisy population trajectory, the approach using an equilibrated population model in RAMAS that we describe in this paper can be used. Using the demography of the cod as an illustration, we explored the question of whether the life history data that are typically available for species of concern are sufficient to make reasonably reliable estimates of the character of density dependence that would be useful in assessing quasiextinction risks. We see from the example that, for some species of concern, one cannot expect, given the data available, to be able to estimate density dependence relationships very well. The error in the reconstruction of density dependence can translate into a considerable error in estimation of extinction risk. The duration of time series data from which density dependence is computed is probably insufficiently long to make reliable estimations of the functional parameters for many species of interest. Since the probability of quasiextinction depends rather sensitively on the density dependence relationship used in the population model, this is a serious impediment to the timely calculation of these risks. The possibility that density dependence generally or usually only lessens the risks of quasiextinction is very important since, if true, one can make at least conservative estimates of the risks, which may be enough. Whether this is true for many other species remains an empirical question deserving further study.

Acknowledgments

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