PROJECTING VIABILITY OF *TOTOABA MACDONALDI,* A POPULATION WITH UNKNOWN AGE-DEPENDENT VARIABILITY

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Abstract. For the endangered fish totoaba (*Totoaba macdonaldi*), as for other endangered species, the relative amount of environmental variability in demographic rates at various life stages is uncertain. Because of the ontogenetic migratory pattern of this species, four life history stages, (a) prerecruits, (b) juveniles, (c) pre-adults, and (d) adults, experience different environmental conditions. We used a diffusion equation approximation of random Leslie matrices to explore the effects on extinction risk of environmental variability in each of these life stages and correlation between stages. Variability in pre-adults and adults had a greater effect on the probability of extinction than did variability in prerecruits and juveniles. In general, correlation between stages increases the rate of increase of the variance of the logarithm of abundance and, hence, the probability of extinction. For example, when all life stages vary coherently, the rate of increase of the variance is the square of a weighted sum of elasticities, while when all stages vary independently, the rate of increase is the same weighted sum of the squared elasticities. The maximum extinction rate occurs when all life history rates in a Leslie matrix vary coherently. Specifically, when the coefficient of variation is the same in each parameter, the rate of increase of the standard deviation of the logarithm of abundance equals the coefficient of variation of the environmental variability. We also evaluated the accuracy of the diffusion equation approximation by comparing predicted extinction rates with those from Monte Carlo simulations of totoaba with variability in each of the four stages. The diffusion equation approximation accurately predicted probabilities of extinction in all cases except one, random variability in recruitment, where it underestimated simulation results substantially. This is apparently due to the large random jumps in abundance in this case. The diffusion equation approximation accurately predicted quasi-extinction of the adult portion of the population.

Key words: age structure; extinction; population viability; random environment; totoaba.

INTRODUCTION

Totoaba (*Totoaba macdonaldi*) is a long-lived sciaenid fish endemic to the Gulf of California. The totoaba population has been brought to its current endangered status by a variety of anthropogenic factors (see Cisneros-Mata et al. 1995). Adults were heavily fished for over 50 yr until 1975, when the fishery was banned, and poaching persisted through at least the early 1990s. Juveniles (called ''machorros'') are common in the by-catch of the shrimp fishery. Pre-adults are affected by a sport fishery in the northern Gulf of California (Fig. 1). The spawning and nursery grounds of totoaba have been altered by control of the Colorado River flow and agricultural waste, which is thought to have had a negative impact on the survival of very early life stages of totoaba.

Strategic planning for protection and recovery of this endangered fish requires estimation of the effects of various anthropogenic influences on the risk of extinc-

tion. Estimation of these risks requires knowledge of the way in which the random environment influences this population. While there is enough information to estimate average rates of survival and reproduction, and the population seems to have been roughly constant in recent years, we do not know how the random environment influences various stages in the life cycle of totoaba. The nature of this random influence, i.e., the relative magnitude of environmental variability on life history parameters at different points in the life cycle, has both a critical effect on probability of extinction and a potential influence on the response of the population to proposed improvements in habitat and exploitation. We need to know, for example, whether random variability in early life history stages is more important than random variability in later life history stages, as regards probability of extinction. This knowledge will help set priorities for future research aimed at determining the actual levels of variability in sensitive stages.

Most previous approaches to population viability of other age- or stage-structured species have focussed on the behavior of deterministic population models. These
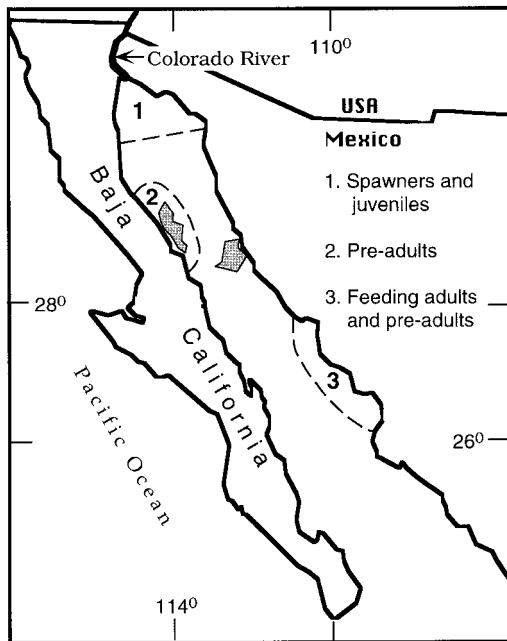
FIG. 1. Various habitats of different life stages of totoaba in the Gulf of California, Mexico. Adults (7–25 yr old) spawn near the Colorado River (1); juveniles remain there during their first 2 yr; adults and pre-adults (3–6 yr old) concentrate south of the spawning/nursery grounds (2); in winter, pre-adults and adults migrate farther south (3).

typically have involved computation of sensitivities or elasticities of the rate of growth of deterministic age- or stage-structured models. For example, Crouse et al. (1987) numerically explored the effects of variation in life history parameters on the rate of increase of a stage-structured model of loggerhead sea turtles, then compared results to analytical computations of sensitivity. In another example, Doak et al. (1994) compared elasticities of various parameters of a stage-structured model of desert tortoise to numerical computation of the effects of realistic (not infinitesimal) changes in parameter values on the rate of increase. Moloney et al. (1994) computed the actual dependence of the change in the rate of population increase on the magnitude of change in various parameter values using a matrix model of a Wandering Albatross population.

These deterministic approaches to population viability analysis will not necessarily accurately describe the effects of life history on the probability of extinction. In fact, they may not even accurately describe their effects on population growth rate. Stochastic models are required to accurately predict rates of increase and probabilities of extinction. For example, Tuljapurkar's (1990) "crossover effect" implies that as increasing amounts of random variability are added to two deterministic populations with different population growth rates, the relative order of their growth rates can be reversed.

In addition to their work on the deterministic model

Doak et al. (1994) evaluated stochastic effects of variability in life history parameters through simulation, and addressed the effects of correlation among these parameters. In particular, they examined the impact of correlated random variability in life history parameters on random growth rate of the population by viewing the population abundances that resulted from Monte Carlo simulations as estimates and by computing their 95% confidence limits. Their analysis showed that correlation among parameters in their example increased the distance between confidence limits, but their characterization of results in terms of confidence limits does not directly reflect their effects on the probability of extinction. Confidence intervals express the probability of being below a certain abundance at a time t, but do not include the possibility of having gone below that level before time t, and returned to above that level before time t. Here we use an expression for first passage time, which more accurately reflects the risk of extinction.

These studies have not fully evaluated the general, practical consequences of age- or stage-specific patterns of random environmental influence because the sensitivity of the deterministic growth rate to changes in life history parameters does not predict the changes in growth rate nor probability of extinction. To manage populations to reduce the probability of extinction, we need to use realistic stochastic models. Furthermore, because there is often uncertainty as to the age or stage at which the random environment influences populations, a comprehensive understanding of the consequences of randomness in various stages is needed for (1) making robust decisions regarding corrective actions to reduce the risk of extinction and (2) directing future research to areas with greatest potential impact. In addition, studies such as that of Doak et al. (1994) point out that we need to know how correlation between parameters affects the probability of extinction.

One could approach this need for a general understanding of the effects on extinction probabilities of randomness in various life history stages using either an analytical or a numerical approach. The above analyses of specific practical situations were based primarily on numerical simulation, and some population biologists favor that approach because of its almost unlimited flexibility. However, numerical analyses yield results only for the specific situations simulated, while analytical approaches are inherently more general. Examination of analytical expressions can tell how results will vary with different parameter values and functional forms, yielding interpretations that stretch beyond the specific situation and species of interest. Also, with accuracy depending roughly on the square root of the number of trials times the probability being investigated, many simulations are required for each case to determine low probabilities of extinction (Harris et al. 1987). There seems, therefore, as much reason to include analytical solutions in the set of tools

used by biologists dealing with population viability as there is in other applied fields (e.g, fisheries, pest management), where their value has been amply demonstrated.

An analytical framework exists for examining the effects of variability on the risk of extinction, although it has not been applied much to practical problems (but see examples in Dennis et al. 1991). Tuljapurkar and Orzack (1980) showed that the logarithm of total abundance of an age-structured population affected by a serially independent random environment will be asymptotically normal, and Tuljapurkar (1982, 1989, 1990) provided methods for computing the mean and variance of this distribution in terms of covariances of environmental variability in various life history parameters and sensitivities of the population growth rate λ. These results have been applied to the problem of the evolution of life histories (Orzack and Tuljapurkar 1989, Tuljapurkar 1990). Lande and Orzack (1988) modelled these results in terms of a diffusion process, and gave expressions for probabilities of extinction. Dennis et al. (1991) also described this model and used it to develop a method for estimating population growth rates and variability from time series of abundance of endangered populations.

Here we describe how we have applied this theory of random matrix models of age-structured populations to the practical question of determining how environmental variability in various life history stages influences the probability of extinction of totoaba. We first use this analytical approach to derive a simple, graphical method of determining the impact of variability in each life history parameter on the risk of extinction. We then test this analytical method by comparing expected risks of extinction computed from the analytical method with those from numerical simulations. There are reasons to test analytical results in practical applications. Derivation of the analytical method involves several assumptions of small random noise, hence at some level of variability it may no longer be valid (cf. numerical tests of deterministic sensitivity by Lande and Orzack [1988], Doak et al. [1994], Moloney et al. [1994]). The results we obtained for totoaba provide a case study applicable to other kinds of populations.

In the following, we first give a brief description of the life cycle of totoaba and how we estimated vital rates for the age-based projection matrix. We then proceed to the derivation of a simple, general expression for the rate of increase in the variance in abundance, which we use to estimate extinction risks under various scenarios. Finally, we compare analytical and numerical results and discuss sources of discrepancies and how they can be reconciled.

Life History and Analysis

Totoaba

Different ontogenetic stages of totoaba occupy different habitats (Fig. 1). Prerecruits (<1 yr old) and juveniles (1 and 2 yr old) inhabit the shallow upper Gulf of California and the Colorado River delta, both of which are characterized by extremely variable temperatures, salinities, and perhaps pollutant loads. Preadults (3–5 yr olds) and postspawning adults (6–25 yr old) are thought to concentrate farther south in more benign subsurface waters with less-variable environmental conditions (Barrera-Guevara 1990, Cisneros-Mata et al. 1995). This ontogenetic spatial pattern is likely to produce different levels of natural variability of each of the four life stages. Knowledge of the relative impact on extinction risk of variability in each of the four stages is needed to assess research priorities and to formulate management strategies that will be robust to uncertainty in the ontogenetic pattern of environmental variability.

To estimate probabilities of extinction, we require age-specific reproductive and mortality rates as well as knowledge of variability in these rates. For totoaba, we have estimated the age-specific pattern of reproduction, and computed a crude estimate of adult and juvenile mortality (M. A. Cisneros-Mata et al., *unpublished manuscript*). Important uncertainties include such fundamental characteristics as the rate of increase of the population, and the life history stages at which the random environment affects vital rates. To evaluate the latter, we explore here the effects of random variability at four different points in the life history of totoaba: prerecruits, juveniles, pre-adults, and adults. With regard to uncertainty in the current rate of increase, recent observations indicate that the population is no longer declining (Cisneros-Mata et al. 1995). We therefore explored the various aspects of viability assuming that the totoaba population was at a constant level (i.e., growth rate of the average population, λ, equal to 1.0). In general, we expect that populations of concern in viability analysis will typically have values of λ near 1.0 because if λ is < 1.0 extinction is certain while if λ is much greater than 1.0 the population is likely to be increasing. Neither of these cases would be likely to require refined estimates of population risk.

Values of life history parameters were previously estimated from information on age structure, spawning, and indices of abundance (M. A. Cisneros-Mata et al., *unpublished manuscript*). An average annual survival rate of 0.798 for pre-adult and adult females was estimated from analysis of the age structure from 1955 to 1990. An annual survival of 0.01 for juveniles (1 and 2 yr old) was obtained using catch-per-unit-effort data as an index of abundance. We expressed age-specific reproductive rates in terms of the number of female juveniles per adult female of a given age that survive to enter the population each year at 1 yr of age, and refer to this as per capita recruitment. These were based on estimates of fecundity at each age scaled to yield a population growth rate $\lambda = 1.0$. We used the resulting recruitment schedule and age-specific survival probabilities in our analyses of extinction risks here
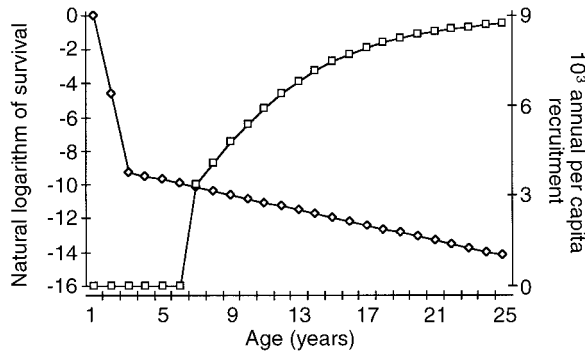
FIG. 2. Average annual per capita recruitment and survival of totoaba. Recruitment (□) is expressed as females of 1 yr of age per adult female, for a stable population having 100 females of 25 yr of age. Survival (◇) represents numbers surviving at a given age, relative to numbers in the youngest age class (i.e., 1 yr).

(Fig. 2). The qualitative consequences of results obtained with these parameter values will hold for a range of values near $\lambda = 1.0$.

Analysis of extinction rates

In a randomly varying, uncorrelated environment, the long-run natural logarithm of population abundance of a population represented by a Leslie matrix will be approximately normally distributed with mean $\ln N_0 + \mu t$ and variance $\sigma^2 t$, where t is the time since initial abundance N_0, μ is the growth rate of the mean, and σ^2 is the growth rate of the variance (Tuljapurkar and Orzack 1980, Tuljapurkar 1982, 1989, 1990). The growth rates of the mean and the variance of log abundance are given by:

$$\mu = \ln \lambda - \sigma^2/2 \tag{1a}$$

and

$$\sigma^2 = (1/\lambda^2)\delta^T C \delta \tag{1b}$$

where λ is the dominant eigenvalue of the average Leslie matrix L, δ is the vector (and δ^T its transpose) of sensitivity coefficients (i.e., partial derivatives of λ with respect to entry c_{ij} of the matrix), and C is the variance–covariance matrix of variability in the elements of L. The sensitivities of λ to variability in an element c_{ij} of the Leslie matrix can be computed from (Caswell 1989):

$$\frac{\partial \lambda}{\partial c_{ij}} = \frac{v_i w_j}{\langle W, V \rangle} \tag{2}$$

where w_j is the jth element of the right eigenvector (i.e., the stable age distribution), v_i is the ith element of the left eigenvector (i.e., Fisher's reproductive value), and $\langle W, V \rangle$ is the scalar product of the right and left eigenvectors. Elements of the right and left eigenvectors are (Caswell 1989):

Right

$$w_1 = 1$$

$$w_j = p_1 p_2 \cdots p_{j-1} \lambda^{-j+1} \quad \text{for } j > 1$$

Left

$$v_1 = 1$$

$$v_i = b_i \lambda^{-1} + p_i v_{i+1} \quad \text{for } i > 1$$

where p_i = survival probability at age i and b_i = per capita recruitment for adult females of age i.

Using a diffusion equation approximation, Lande and Orzack (1988) expressed the cumulative probability that the population declines below a threshold size N before time t given an initial size N_0 as:

$$p_t[N|N_0] = \Phi\left[\frac{\ln(N/N_0) - \mu t}{\sigma\sqrt{t}}\right]$$
$$+ e^{[2\mu \ln(N/N_0)]/\sigma^2}\Phi\left[\frac{\ln(N/N_0) + \mu t}{\sigma\sqrt{t}}\right] \tag{3}$$

where $\Phi(z)$ is the area under the standard normal probability distribution up to z (cf. Dennis et al. 1991). Rather than true extinction, this expression describes the probability that the population will drop below a specified threshold abundance considered dangerous and undesirable, an approach termed quasi-extinction analysis (e.g., Ginzburg et al. 1982, Dennis et al. 1991). Lower levels of abundance may be undesirable for a variety of reasons, such as decreasing probability of finding mates or increasing demographic stochasticity.

Because variability in parameter values is typically expressed in relative terms (e.g., as a percentage of the mean) rather than as absolute variability, we expressed Eq. 1b in terms of relative variability, using the coefficient of variation CV = (standard deviation)/mean. For each parameter of the Leslie matrix we have, for example, $\text{CV}_b = S_b/\bar{b}$ for per capita recruitment, where S_b = standard deviation and $\bar{b}$ = mean per capita recruitment. Substituting this into Eq. 1b yields

$$\sigma^2 = e^T D e, \tag{4}$$

where e is a column vector of elasticities of λ with respect to the elements c_{ij} of the Leslie matrix, which is defined in terms of the mean value of the element as (cf. Caswell 1989):

$$e_{ij} = \frac{1}{\lambda}\frac{\partial \lambda}{\partial c_{ij}}\bar{c} \tag{5}$$

where $\bar{c}$ is the mean value of the age-specific parameter c_{ij}, and D is a symmetric matrix with elements

$$D_{ik} = \text{CV}_i \text{CV}_k r_{ik} \tag{6}$$

with CV_i and CV_k being coefficients of variation of the age-specific rates i and k, and r_{ik} the correlation coefficient between those rates. The indices i and k refer to the way in which the parameters are ordered in the

sensitivity and elasticity vectors. For the totoaba population, for which we assumed an age of first reproduction of 7 yr and a maximum life-span of 25 yr (Cisneros-Mata et al. 1995), we expressed the (transposed) vector of sensitivities as:

$$\delta^{\mathrm{T}} = \left[\frac{\partial\lambda}{\partial b_7} \cdots \frac{\partial\lambda}{\partial b_{25}} \frac{\partial\lambda}{\partial p_1} \cdots \frac{\partial\lambda}{\partial p_{24}}\right]. \quad (7)$$

Elements of the elasticity vector are written in the same order.

Formulation of Eq. 4 allows a simple result for a specific case. If all parameters in the totoaba population vary by the same relative amount and are completely correlated, then σ^2, the growth rate of the variance, will equal the square of the coefficient of variation CV, or

$$\sigma^2 = \mathrm{CV}^2 \text{ for } \mathrm{CV}_i = \mathrm{CV}_k = \ldots = \mathrm{CV}, \text{ and } r_{ik} = 1. \quad (8)$$

This follows from the fact that the sum of all elasticities equals 1.0 (de Kroon et al. 1986, Mesterton-Gibbons 1993). This result provides a benchmark for values of the growth rate of the variance under other conditions. CV^2 is the maximum value of σ^2 under all possible combinations of correlation between randomly varying parameters.

Next we explored the relative influence on the rate of increase of the variance of different levels of variability in different stages, and correlation between stages. We divided the totoaba life cycle into the four distinct stages that reside in different habitats: prerecruits, juveniles, pre-adults, and adults. We considered different scenarios regarding the point and nature of variability due to environmental effects experienced by the rates of each stage. We assumed that age-specific rates within stages varied each year in a coherent fashion with a given coefficient of variation. From Eq. 1b we have that:

$$\begin{aligned}
\sigma^2 = &[(\mathrm{CV}_b X + r_{bj}\mathrm{CV}_j Y + r_{bp}\mathrm{CV}_p Z \\
&+ r_{ba}\mathrm{CV}_a Q)\mathrm{CV}_b X \\
&+ (r_{bj}\mathrm{CV}_b X + \mathrm{CV}_j Y + r_{pj}\mathrm{CV}_p Z \\
&+ r_{ja}\mathrm{CV}_a Q)\mathrm{CV}_j Y \\
&+ (r_{bp}\mathrm{CV}_b X + r_{pj}\mathrm{CV}_j Y + \mathrm{CV}_p Z \\
&+ r_{pa}\mathrm{CV}_a Q)\mathrm{CV}_p Z \\
&+ (r_{ba}\mathrm{CV}_b X + r_{ja}\mathrm{CV}_j Y + r_{pa}\mathrm{CV}_p Z \\
&+ \mathrm{CV}_a Q)\mathrm{CV}_a Q] \quad (9)
\end{aligned}$$

where CV_x is the coefficient of variation of rate x, and r_{xy} is the correlation coefficient between pairs of rates x and y (x, y defined as: b = recruitment, j = juvenile survival, p = pre-adult survival, and a = adult survival). The coefficients X, Y, Z, and Q are the sums of elasticities related to variability of rates within each stage:

$$X = \frac{1}{\lambda}\sum_{i=7}^{25}\frac{\partial\lambda}{\partial b_i}\bar{b}, \qquad Y = \frac{1}{\lambda}\sum_{i=1}^{2}\frac{\partial\lambda}{\partial p_i}\bar{p}_j,$$

$$Z = \frac{1}{\lambda}\sum_{i=3}^{6}\frac{\partial\lambda}{\partial p_i}\bar{p}_p, \quad \text{and} \quad Q = \frac{1}{\lambda}\sum_{i=7}^{24}\frac{\partial\lambda}{\partial p_i}\bar{p}_a.$$

We now can rewrite Eq. 1b in terms of a four-dimensional matrix expression:

$$\sigma^2 = \boldsymbol{\alpha}^{\mathrm{T}}\boldsymbol{\beta}\boldsymbol{\alpha} \quad (10)$$

where $\boldsymbol{\alpha}^{\mathrm{T}} = [XYZQ]$ is a (transposed) column vector of elasticities, and

$$\boldsymbol{\beta} = \begin{bmatrix}
\mathrm{CV}_b{}^2 & \mathrm{CV}_b\mathrm{CV}_j r_{bj} & \mathrm{CV}_b\mathrm{CV}_p r_{bp} & \mathrm{CV}_b\mathrm{CV}_a r_{ba} \\
\mathrm{CV}_j\mathrm{CV}_b r_{jb} & \mathrm{CV}_j{}^2 & \mathrm{CV}_j\mathrm{CV}_p r_{jp} & \mathrm{CV}_j\mathrm{CV}_a r_{ja} \\
\mathrm{CV}_p\mathrm{CV}_b r_{pb} & \mathrm{CV}_p\mathrm{CV}_j r_{pj} & \mathrm{CV}_p{}^2 & \mathrm{CV}_p\mathrm{CV}_a r_{pa} \\
\mathrm{CV}_a\mathrm{CV}_b r_{ab} & \mathrm{CV}_a\mathrm{CV}_j r_{aj} & \mathrm{CV}_a\mathrm{CV}_p r_{ap} & \mathrm{CV}_a{}^2
\end{bmatrix}$$

$$(11)$$

is a (symmetric) matrix of variability containing all coefficients specifying the nature of variation of rates within stages (given by their CVs) and between pairs of stages (given by r_{xy}).

Eq. 10 is a general expression for the growth rate of the variance that can be used to compute quasiextinction probabilities ($p_t[N \mid N_0]$) for populations under various situations. For example, when all rates vary in a coherent fashion ($r_{xy} = 1$, all x, all y), the rate of increase in the variance is:

$$\begin{aligned}
\sigma^2 = &\left[\frac{\mathrm{CV}_b}{\lambda}\sum_{i=7}^{25}\frac{\partial\lambda}{\partial b_i}\bar{b} + \frac{\mathrm{CV}_j}{\lambda}\sum_{i=1}^{2}\frac{\partial\lambda}{\partial p_i}\bar{p}_j + \frac{\mathrm{CV}_p}{\lambda}\sum_{i=3}^{6}\frac{\partial\lambda}{\partial p_i}\bar{p}_p\right. \\
&\left.+ \frac{\mathrm{CV}_a}{\lambda}\sum_{i=7}^{24}\frac{\partial\lambda}{\partial p_i}\bar{p}_a\right]^2. \quad (12)
\end{aligned}$$

The growth rate of the variance is the square of the sum of elasticities over each stage, weighted by the coefficient of variation of the stage. Note that, as pointed out above, if all rates vary with the same coefficient of variation CV, then σ^2 is equal to the coefficient of variation squared (CV^2) because the sum of all elasticities equals 1.

In this case, variability within each stage contributes to the total variability in direct proportion to its elasticities. This result has a useful graphical interpretation. If one plots cumulative elasticities of λ with respect to age-specific per capita recruitment and survival (Fig. 3), the variance due to variability in a specific stage (i.e., within a range of parameters on the ordinate) can be easily determined by reading its relative contribution to cumulative elasticity on the abscissa. Thus for totoaba, random variability in survival through the first 6 yr of age accounts for $\approx 60\%$ (i.e., [70% $-$ 10%] on Fig. 3) of the total possible σ, whereas variability in per capita recruitment over all ages accounts for $\approx 10\%$.

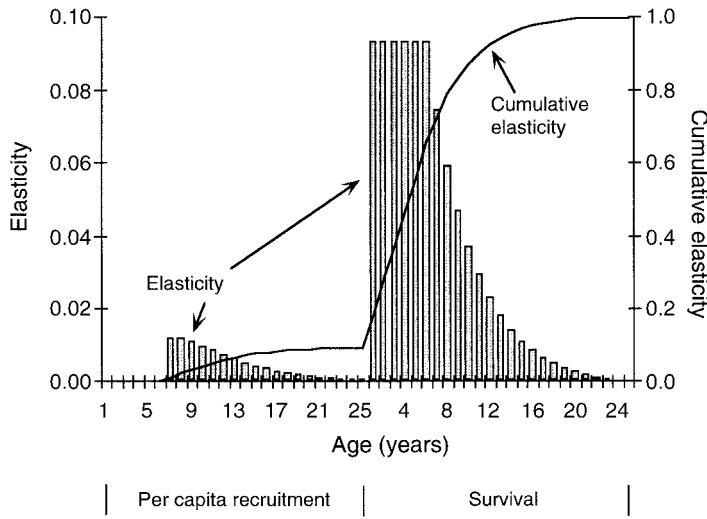A second case of interest is when the environment randomly affects rates within any stage independently

FIG. 3. Elasticity and cumulative elasticity of the average population growth rate of totoaba to changes in survival and per capita recruitment. Cumulative elasticity was computed as the cumulative sum of elasticities to age-specific changes in both survival and per capita recruitment. The value of a given age-specific elasticity represents its relative contribution to σ^2, the rate at which the variance of the logarithm of abundance increases. The values of σ^2 for coherent variability in several parameters are the sums of their elasticities.

(i.e., $r_{xy} = 0$, all x, all y) of rates within other stages. In this case,

$$\sigma^2 = \left(\frac{\mathrm{CV}_b}{\lambda} \sum_{i=7}^{25} \frac{\partial\lambda}{\partial b_i} \bar{b}\right)^2 + \left(\frac{\mathrm{CV}_j}{\lambda} \sum_{i=1}^{2} \frac{\partial\lambda}{\partial p_i} \bar{p}_j\right)^2$$
$$+ \left(\frac{\mathrm{CV}_p}{\lambda} \sum_{i=3}^{6} \frac{\partial\lambda}{\partial p_i} \bar{p}_p\right)^2 + \left(\frac{\mathrm{CV}_a}{\lambda} \sum_{i=7}^{24} \frac{\partial\lambda}{\partial p_i} \bar{p}_a\right)^2. \quad (13)$$

The growth rate of the variance is the squared weighted sum of elasticities of λ to changes in stage-specific rates, weighted by the coefficient of variation. If all rates vary with the same coefficient of variation CV,
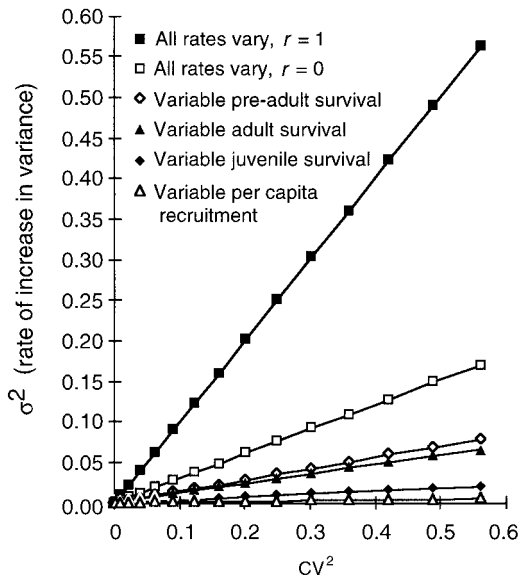

FIG. 4. Relationship between σ^2, the rate of increase of the variance of the logarithm of abundance, and the amount of variability in the life history parameters (square of the coefficient of variation, CV^2) using the analytical solution in a variety of situations regarding life stage and intensity of variability.

then σ^2 is proportional to the sum of within-stage elasticities squared, rather than the squared sum of all elasticities involved, as in the first scenario. Thus, Fig. 3 could still be used in this case, but the sums over elasticities would be squared before combining them. This result, compared to Eq. 12 immediately shows that σ^2 will always be less when rates vary independently than when they vary in a correlated fashion.

Eqs. 12 and 13 imply an ordering of the rate of increase in the variance for cases with equal coefficients of variation CV in each stage. The variance will increase faster when all stages vary coherently ($r_{xy} = 1$), less when all stages vary independently ($r_{xy} = 0$), and still less for variability restricted to any single stage (Fig. 4). Also, for a given coefficient of variation, the sum of the terms in σ^2 corresponding to each single varying rate is equal to the variance when all rates are uncorrelated with the same coefficient of variation, an additivity property of the growth rate of the variance. For example, in Fig. 4 we see that for the case when only pre-adult survival varies, σ^2 is 0.065; for the case in which only adult survival varies, σ^2 is 0.055; for the case in which only juvenile survival varies, σ^2 is 0.025; and for the case in which only per capita recruitment varies, σ^2 is 0.005. The sum of these four rates of increase in the variance is 0.15, which is the value corresponding to the rate of increase in the situation when all four rates vary in an uncorrelated fashion. This is less than the maximum possible value, $\mathrm{CV}^2 = 0.48$, the squared coefficient of variation, which is the rate of increase in the variance with perfect correlation among stages.

Thus far we have established how the rate of increase in the variance of the logarithm of abundance depends on the nature of environmental variability and the age or stage where variability is experienced by the population. We next determine the way in which this translates into the probability of quasi-extinction. This prob-
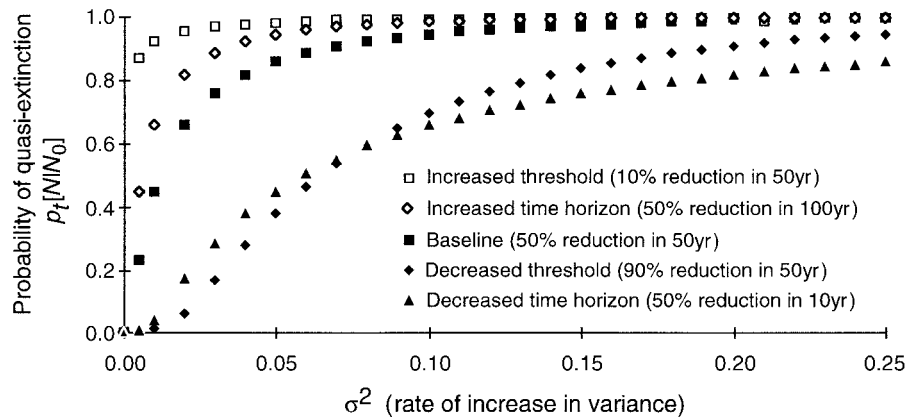
FIG. 5. Dependence of the probability of quasi-extinction ($p_t[N \mid N_0]$) on σ^2, the rate of increase of the variance of the logarithm of abundance for various values of threshold and time horizon, using the analytical solution.

ability will vary depending on how we specify threshold population sizes and time horizons. To describe this dependence, we examined the relationship between the σ^2 and the probability of quasi-extinction $p_t[N \mid N_0]$ for several variations about a baseline situation of a threshold at 50% of the original totoaba population size and a time horizon of 50 yr. We analyzed the sensitivity of the baseline $p_t[N \mid N_0]$ to thresholds of 10% and 90% of initial population abundance and time horizons of 100 and 10 yr, respectively. Increasing threshold or time horizon with respect to the baseline situation increases the probability of quasi-extinction (Fig. 5). For the three highest thresholds and time spans we considered (including those of the baseline), the calculated risks were more sensitive to changes in σ^2 than for lower thresholds and time spans, especially at low values of σ^2, the growth rate of the variance. This indicates that even modest environmentally driven variability will yield high risks when either small reductions in population size or moderate reductions over a long time period are detrimental.

A pair of examples demonstrates how the results of these analyses can be used to compare the effects of variability in different stages. If the random environment influences only recruitment of totoaba, as is assumed in fishery analyses for most other species, and there is 20% variability (cv = 0.2), from Fig. 3 the variance will grow at a rate of $\approx$10% of cv^2, or $\sigma^2 =$ 0.004. From Fig. 5, the probability of a population decline of 50% in 50 yr is near 0.4. If, on the other hand, that same level of variability were present in the juvenile and pre-adult stage (the first 6 yr of life), σ^2 would be $\approx$60% of cv^2, or 0.024, leading to a probability near 0.7 of a decline by 50% in 50 yr.

Numerical tests of analytical results

We have shown how the calculated risk of extinction depends on underlying assumptions based on an analytical model. These results are useful only insofar as the analytical method accurately predicts extinction

rates. We therefore tested performance of the analytical solutions under various scenarios. We compared analytical results to Monte Carlo simulations with a stochastic Leslie matrix. For each scenario 2000 trials were performed, recording the year in which the stock fell below a specified threshold (first passage time). One event in this number of trials would correspond to a probability of 0.0005. The lowest probability of quasi-extinction $p_t[N \mid N_0]$ given here is 0.015, so that at least 30 threshold crossings in 2000 trials were represented. From the binomial probability distribution, this lower limit yields a standard error in $p_t[N \mid N_0]$ of $\approx$0.003 (cf. Harris et al. 1987).

To generate random variability in life history parameters, random numbers were drawn from normal distributions with means given by average survival of juveniles, pre-adults, and adults, and per capita recruitment, and with standard deviations corresponding to the desired coefficient of variation. The random numbers were constrained to lie between 0 and 1 when survival was varied and to be $>$0 when recruitment was varied; if a number fell outside the limits it was discarded and another was chosen. We then computed probabilities of quasi-extinction for the same set of passage times and thresholds described in the previous section. There are, of course, other approaches to generation of biologically realistic distributions of vital rates (e.g., use of distributions that are between 0 and 1 or greater than 0 by definition). We chose this one to determine how a simple, ad hoc approach would work, and to determine the effects of the truncation involved. We computed probabilities of extinction for the analytical method using both the specified mean and variance in parameter values and the mean and variance actually realized following truncation.

We first analyzed performance of the analytical solution for situations where a random environment affected vital rates of different stages individually (i.e., varying one rate while the rest were fixed). The four cases considered were: variable per capita recruitment
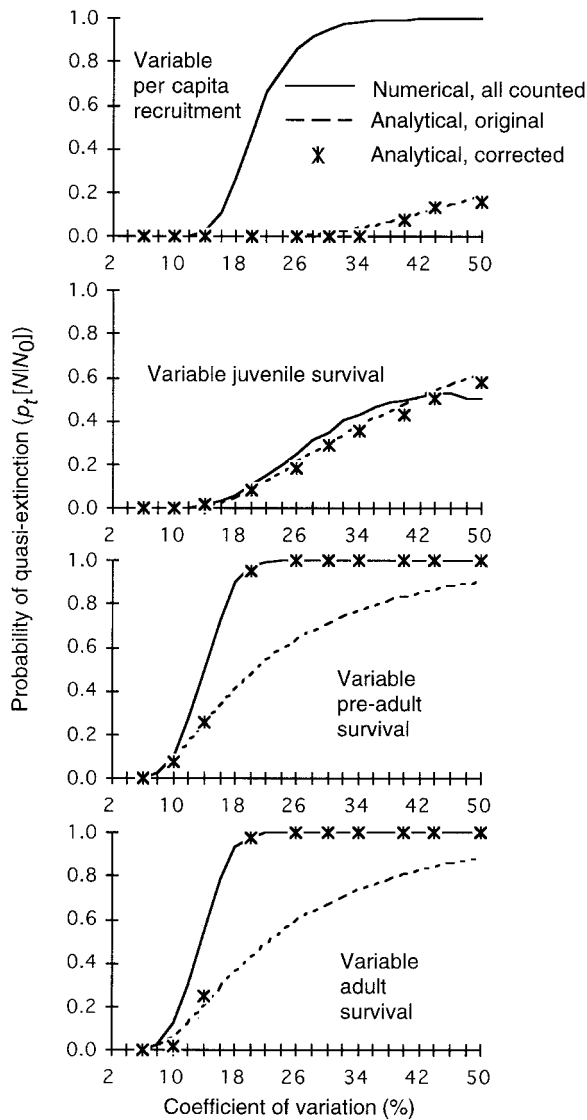
FIG. 6. Comparison of numerical and analytical results for the risk of quasi-extinction ($p_t[N \mid N_0]$) of the abundance of totoaba as a function of increased random variability in life history parameters, expressed in terms of the coefficient of variation (CV) of interannual per capita recruitment and survival of juveniles, pre-adults, and adults. Analytical results are given both uncorrected for truncation errors and corrected. The time horizon was 100 yr, the quasi-extinction threshold was 50% of original population size, and $\lambda = 1.0$. In each case 2000 simulations were performed.

and variable survival of juveniles, pre-adults, and adults. The risks of extinction computed analytically reflected the sum of elasticities over each age. These sums were 0.09, 0.19, 0.37, and 0.35 for variable per capita recruitment, survival of juveniles, pre-adults, and adults, respectively (see Fig. 3). That is, the estimated risk using the analytical solution was lower when recruitment varied alone, intermediate when only juvenile survival varied, and greater and virtually the

same when either pre-adult or adult survival varied (Fig. 6).

Numerical solutions diverged from analytical solutions as the coefficient of variability increased in three of the four cases: per capita recruitment, pre-adult survival, and adult survival (Fig. 6). In two of these cases, the disagreement between numerical and analytical solutions is entirely due to truncation of the distributions of random values in the simulations, in particular the effect of truncation on the mean. Because specified mean survival of pre-adult and adults (0.798) was near the upper bound (1.0), discarding random numbers >1.0 affected the right-hand side of the distribution, decreasing the mean, and consequently increasing the probability of extinction (Fig. 7). Note that truncation has little impact on the mean and coefficient of variation in the case in which per capita recruitment varies, hence accounting for this small effect does not yield analytical probabilites of extinction that match the simulated results.

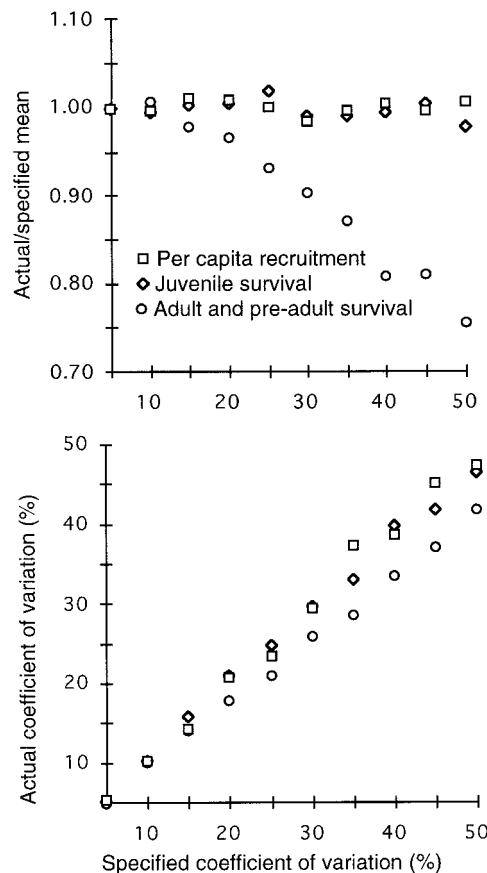Next we examined behavior of models in which all

FIG. 7. Variation of actual means and coefficients of variation (CV) of 500 random numbers generated from normal distributions with specified means and increasing CVs. Random numbers were constrained to lie between 0 and 1 for survival, and to be >0 for recruitment. The differences between specified and actual values result from elimination of numbers falling outside the limits.
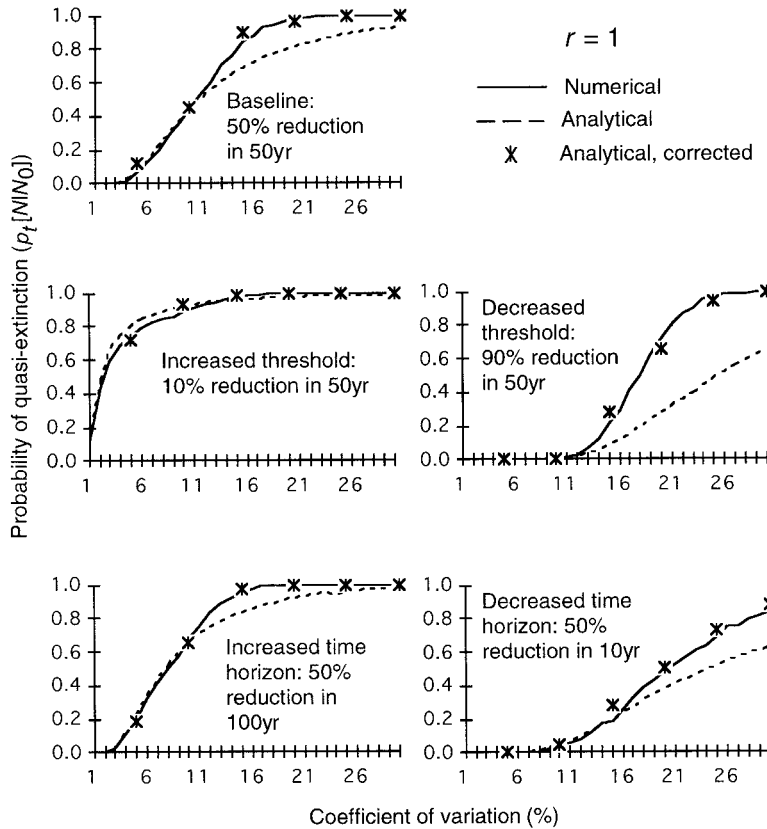
FIG. 8.   Comparison of numerical and analytical results for the risk of quasi-extinction ($p_t[N\,|\,N_0]$) with increasing variability (CV), when all parameters of the Leslie matrix vary randomly in complete synchrony ($r = 1$). Analytical results are given both uncorrected for truncation errors and corrected. The sensitivity of ($p_t[N\,|\,N_0]$) to variable threshold population size and time horizon was investigated. Baseline represents risk of a 50% reduction of initial total population size in 50 yr. Threshold and time horizon were increased and decreased relative to the baseline case, with 2000 simulations performed for the numerical solution. Original population growth rate (λ) was 1.

four stages were influenced by a random environment with the same coefficient of variation. We compared the completely correlated case with the uncorrelated case, and for each we examined the effects of time periods and threshold levels in the definition of extinction. For the cases in which variability is completely correlated, projections of the analytical method using the realized variances matched the simulated results well (Fig. 8). For cases in which variability in the various stages were uncorrelated, probabilities were generally less than the corresponding cases in which they were correlated, as would be expected from the effects of correlation on the growth rate of the variance (Fig. 9). In these cases, the analytical projections fell slightly below the simulated results, even when the former use the realized means and variances.

We also tested the diffusion equation approximation for the case in which the definition of quasi-extinction involved only adults. The threshold assumed in the definition of quasi-extinction is often chosen to reflect the abundance below which dynamics change, i.e., the presence of an Allee effect. A common Allee effect is the nonlinear decline in the probability of finding a mate as abundance declines to low levels. Other effects of low population numbers such as inbreeding and skewed sex ratios, also involve only adults. For these mechanisms the number of subadults is not relevant, hence we tested a definition of extinction in terms of adults only. A second reason for testing this definition is the failure of the diffusion equation approximation to accurately predict extinction risk in the case in which recruitment varies (Fig. 6). Diffusion equation approximations have been known to fail when random changes are large. Because of the low juvenile survival rate, the variable recruitment case is the case with the largest relative annual random change in abundance. This gives reason to suspect that failure of the diffusion approximation is the cause of the disparity (see *Discussion*). We therefore wanted to test whether counting only adults, thereby reducing the relative annual change in abundance while keeping the dynamics the same, solved this problem. The results were essentially identical to the case in which total abundance was counted, except that the diffusion equation approximation accurately predicted the numerical result in this case (Fig. 10).
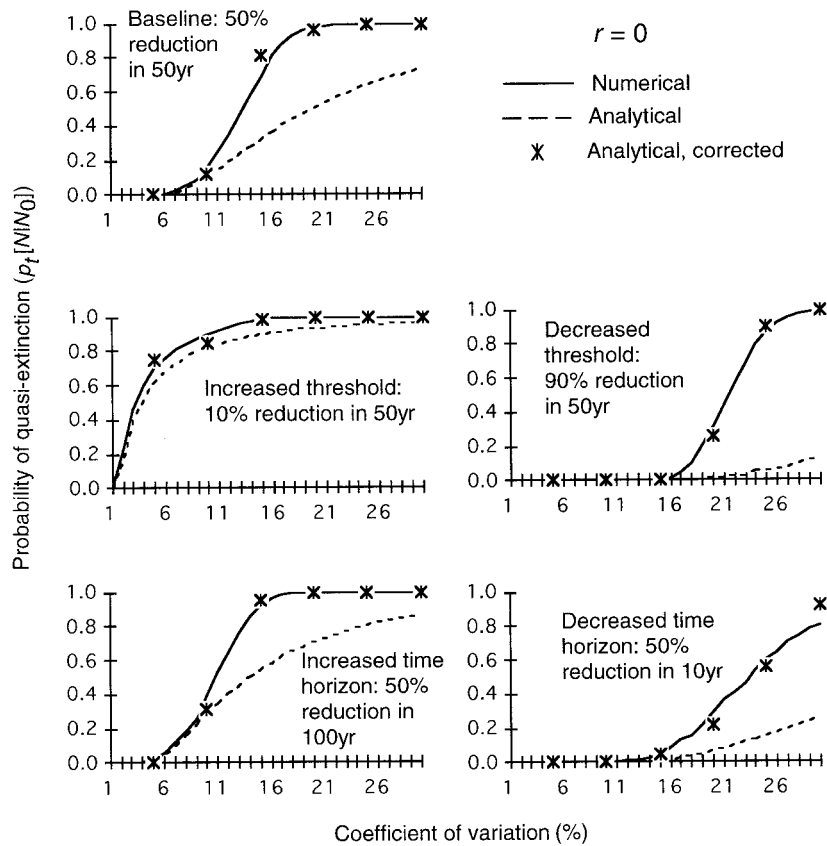
FIG. 9. Same as Fig. 8, except that parameters of the Leslie matrix were uncorrelated ($r = 0$).

DISCUSSION

The totoaba population appears to be more sensitive to environmental variability affecting older stages than that affecting younger stages. This suggests to managers that if the potential impact of the random environment on older stages is not accounted for in population viability analyses, they may seriously underestimate probabilities of extinction. Analyses of the impacts of variability in fish populations often assume that most of the variability is in recruitment, primarily because recruitment is more easily estimated than natural adult mortality. For this same reason, it is doubtful that the expense of an estimate of random variability in adult survivals will be seen as worthwhile. Rather, the results obtained here suggest that in the development of recovery or protective strategies, we must demonstrate that they are robust to variability in adult survival (see M. A. Cisneros-Mata et al., *unpublished manuscript*).

This result assumes variability in each of the four life history stages of totoaba is independent of the other stages. If variability is correlated, it could have a much greater effect on the probability of extinction, and the relative importance of stages could change. The spatial separation of habitats (Fig. 1) argues for variability in the different life history stages of totoaba being rela-

tively independent. However, there is some evidence that the Gulf as a whole is subject to large-scale forcing associated with El Nino events.

Our test of the validity of the analytical method due to Lande and Orzack (1988) showed that it underestimates the probability of extinction in the case in which variability is in recruitment only. Lande and Orzack (1988) investigated the accuracy of their analytical approximation to find that except for a slight overestimation by the analytical solution with respect to simulations (due to the simulation being in discrete time), the methods showed good agreement. The two cases presented were a population without age structure and random growth rate, and a population with two age classes and random fertility and fixed survival. We have considered here a population with more age structure, i.e., with 25 age classes and with entries of the matrix varying coherently or independently among stages, and individually. Because (1) other similar diffusion approximations fail when the jumps in the state variable or the rate of drift are large (e.g., Ludwig 1976, *in press*, Ewens 1964, Grasman and Ludwig 1983), and (2) the variation in total abundance due to variation in each of the four stages is greatest for the recruitment case, we expect this problem is due in part to violation of the assumption of small changes in the state variable
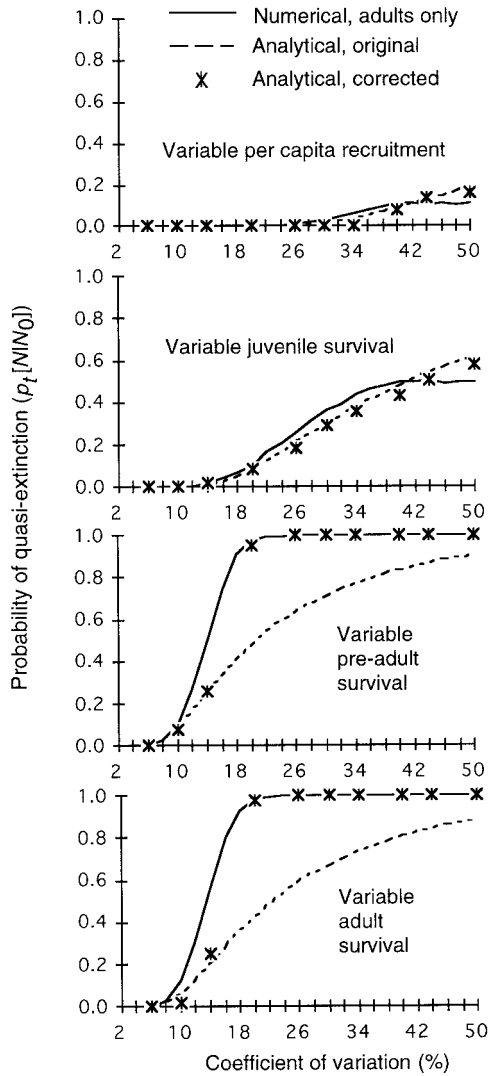
FIG. 10. Comparison of numerical and analytical results for the risk of quasi-extinction ($p_t[N \mid N_0]$) of totoaba as a function of increased random variability in life history parameters, expressed in terms of the coefficient of variation (CV) of interannual per capita recruitment and survival of juveniles, pre-adults, and adults. In this case quasi-extinction was defined to be the decline of adult abundance (rather than total abundance) to less than a specified level. Analytical results are given both uncorrected for truncation errors and corrected. The time horizon was 100 yr, the quasi-extinction threshold was 50% of original population size, and $\lambda = 1.0$. In each case 2000 simulations were performed.

involved in the use of the diffusion equation approximation. It could also be due to violation of a similar assumption in the derivation of Eqs. 1a and b. Note that the variation in total abundance is highest for the recruitment case because the first age class is so much larger than the others (due to the low early survival). As a consequence, when the Allee effect implied in the definition of quasi-extinction involved only spawners (i.e., Fig. 10), not juveniles (Fig. 6), this effect was not present.

The question of how correlation between stages affects probability of extinction was posed earlier in a numerical example (Doak et al. 1994), but the general nature of the influence was not explored. Here we have shown that, in general, correlation between demographic rates at different ages increases the probability of extinction. Furthermore, we have shown that the difference between correlated variability and uncorrelated variability is esentially the difference between summing variability terms squared vs. summing variability terms, then squaring the sum.

The approach taken here expresses the probability of extinction from a stochastic matrix model more accurately than the confidence interval approach taken by Doak et al. (1994). Expressing results in terms of confidence limits expresses only abundance at the current time, not the proportion of random population trajectories that have gone extinct up to that time. As an example of how large the difference between the two approaches can be, if the stochastic rate of increase μ is zero, from Eq. 3 we see that the probability of extinction up to time t is twice the probability of being below the extinction level at time t.

The approach taken here may be useful for other species. Applied population biologists are attempting to assess population viability and formulate strategies for recovery of many other populations that have been reduced to low abundance through human activities (e.g., Boyce 1992, Burgman et al. 1993, Caughley 1994, Caughley and Gunn 1996). Such efforts are typically limited by a paucity of the information on life histories needed to estimate extinction risks. Although there is usually enough information available to estimate average reproductive and mortality rates, the relative impact of the random environment on them is typically uncertain. Because the pattern of random influences is poorly known, there is a need for better understanding of how variability at different points in a life history affects extinction risk (Boyce 1992, Schemske et al. 1994). A graph such as Fig. 3 provides a method of simply and graphically combining elasticities to determine how variability in different life history parameters influences probability of extinction. Although the results incorporate elasticity and are related to sensitivity of λ to parameter values, the dependence of extinction rates on values of life history parameters are not as simple as might be expected from earlier deterministic studies. The relative contribution of variability in each parameter values depends not just on its elasticity, but also on the amount of variability and its correlation with variability in other life history parameters. Use of a plot such as Fig. 3 for the case in which variability is in recruitment is limited to definitions of quasi-extinction in which only adult abundance is counted. After obtaining σ^2, one could use the general relationship depicted in Fig. 5 to estimate the probability of quasi-extinction for one of the given pairs of thresholds and time horizons.

In such evaluations of the impact of age-specific patterns of variability on the probability of extinction, some of the results obtained here could provide useful guidelines. For example, one would know that if all rates varied in a correlated fashion ($r = 1$), σ^2 would be exactly CV^2, the squared coefficient of variation. While this situation may be rare, occurring, for example, when all life stages were relatively evenly sensitive to the same limiting factors, such as temperature or food production, it is useful to be able to calculate a maximal probability of extinction for any definition of quasi-extinction and relative level of environmental variability. It is also useful to know that for a given threshold and time horizon the risk of extinction will increase with increasing correlation. This can intuitively be interpreted as a consequence of the law of large numbers. Interannual variability of population numbers is lower when rates vary independently because random environmental effects average out, decreasing σ^2 (and $p_t[N \mid N_0]$). Another potentially useful aspect is the additivity property of the growth rate of the variance σ^2: for a given amount of variation the sum of the values of σ^2 for single varying rates amounts to the value of σ^2 when all rates vary with $r = 0$ (Fig. 4).

The success of our simple description of the distribution of variability in life history parameters also has useful implications for other efforts. The simple approach to simulation of truncating Gaussian variability in life history parameters when it falls outside the feasible range gave the same result as the analytical method when the true resulting means and variances were used. Thus the analytical method gives accurate extinction probabilities, even when the parameter distributions are skewed. Slade and Levenson (1984) pointed out the substantial effect that skewness in the distribution of vital rates could have on the distribution of population abundance. The skewed distribution in their single example was more extreme than the distributions produced here, having low-probability, high survivals outside the range of the symmetrical distribution to which they were comparing it.

A caveat concerning the models we discussed here is that they are based on random Leslie matrices, and thus any form of density dependence is neglected. Lande and Orzack (1988) suggest their analytical solution will be valid for short time horizons provided that the difference between initial and modal population size is large and initial growth is not limited. The linear model will yield more reliable results when populations are at very low levels, e.g., after an introduction or when harvested to very low numbers. The latter is probably a common situation in the case of threatened or endangered species if their habitat and carrying capacity in general have not been severely reduced. If density-dependent effects are present, for fish they would most likely be in the relationship between stock and recruitment. The stock-recruitment relationship could be simply asymptotic, indicating a fixed carrying capacity of the larval or juvenile environment (i.e., a Beverton-Holt type; Beverton and Holt 1957), or it could be over-compensatory (i.e., a Ricker type; Ricker 1954). Since totoaba has been reduced to its current level by harvest, it is likely that the population is below densities at which density dependence would be present. However, it is also possible that reductions in flow to the nursery grounds near the mouth of the Colorado River have contributed to the decline. Since the totoaba population does not display the dramatic fluctuations associated with over-compensatory, Ricker-type models, it is likely that their stock-recruitment relationship is asymptotic. In that case reduced flows would merely reduce the carrying capacity. Results obtained by Ginzburg et al. (1990) indicate that a model without density dependence, as used here, yields conservative probabilities of extinction when the true stock-recruitment relationship is asymptotic.

The urgency brought on by increased awareness of declining populations worldwide has prompted analysts to use simple models in short-term efforts towards the conservation of biological populations (e.g., Soulé 1987, Boyce 1992, Burgman et al. 1993, Caughley 1994, Caughley and Gunn 1996). It is, however, to be expected that these efforts will need to use increasingly realistic, stochastic age-structured models, in spite of the continuing problem of scarcity of ecological data. Consequently, future use of extinction models for the management and conservation of populations will require continuing improvements in our understanding of the way in which environmental variability and life history parameters interact to create various levels of extinction risk.

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