EXTINCTION-EFFECTIVE POPULATION INDEX: INCORPORATING LIFE-HISTORY VARIATIONS IN POPULATION VIABILITY ANALYSIS

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Abstract. Viability status of populations is a commonly used measure for decision-making in the management of populations. One of the challenges faced by managers is the need to consistently allocate management effort among populations. This allocation should in part be based on comparison of extinction risks among populations. Unfortunately, common criteria that use minimum viable population size or count-based population viability analysis (PVA) often do not provide results that are comparable among populations, primarily because they lack consistency in determining population size measures and threshold levels of population size (e.g., minimum viable population size and quasi-extinction threshold). Here I introduce a new index called the "extinction-effective population index," which accounts for differential effects of demographic stochasticity among organisms with different life-history strategies and among individuals in different life stages. This index is expected to become a new way of determining minimum viable population size criteria and also complement the count-based PVA. The index accounts for the difference in life-history strategies of organisms, which are modeled using matrix population models. The extinction-effective population index, sensitivity, and elasticity are demonstrated in three species of Pacific salmonids. The interpretation of the index is also provided by comparing them with existing demographic indices. Finally, a measure of life-history-specific effect of demographic stochasticity is derived.

Key words: branching process models; demographic stochasticity; effective population size; lineage extinction probability; matrix population model; Pacific salmonids; population viability analysis (PVA); stage-structured model.

INTRODUCTION

Determining viability status of populations is an important task in management of depleted populations (Boyce 1992, Beissinger 2002). For example, the International Union for the Conservation of Nature and Natural Resources Red List (IUCN 2001) categorizes populations based on their estimated viability status. Furthermore, both the Marine Mammal Protection Act of 1972 and the Endangered Species Act of 1973 in the United States mandate a consideration of extinction risk in population management. However, currently the application of population viability analysis (PVA) suffers from a serious limitation in lack of standardization in population size measures and associated population threshold levels. Here, I present a new population index that overcomes this limitation when evaluating potential population extinction from demographic stochasticity, which is one of the most important factors determining the extinction of depleted populations.

Currently, two general approaches exist for determining the viability status of populations. In one approach,

threshold population sizes are determined and populations are categorized into different viability statuses based on whether their population sizes are above or below the thresholds. These thresholds are often determined from various genetic, demographic, and spatial considerations (De Master et al. 2004); however, there is no consensus on the manner in which the threshold should be determined. In another approach, estimated probability of extinction is used as a measure of extinction risk. In the most common method, a population under the threat of extinction is thought to fluctuate around a monotonic trend and the fluctuation (variance) and trend (mean) in the change in population size are used to determine the probability of population extinction. This idea is translated into a mathematical equation in the form of a diffusion model (see Tuljapurkar and Orzack 1980, Lande and Orzack 1988, Dennis et al. 1991, Holmes 2001, Morris and Doak 2002). The latter approach is called a count-based population viability analysis (Morris and Doak 2002).

One of the most desired properties of PVA is the comparability of its results for assessing the status of different populations. However, the current PVA are deficient in this property. For example, the count-based PVA calculates the probability that the estimated population size reaches a predetermined threshold number within a specified time. Below this threshold

level, which is often called the quasi-extinction threshold, the population is considered effectively extinct. Thus, this probability is regarded as the risk associated with population extinction. However, the calculated probability and the actual extinction risk often do not have a clear relationship because both the quasi-extinction threshold and the measure of population size are not consistent among studies.

Measures of population size are often arbitrary. In some studies, population size may be defined as the sum of all individuals in a population, and in other studies, it may be defined as the sum of all individuals in a broad life stage category such as "mature" (e.g., IUCN 2001, McClure et al. 2003). These assumptions inherently define individuals in different stages as contributing equally to the population. This is clearly not the case (Lande and Orzack 1988, Morris and Doak 2002). For example, individuals that are about to reproduce and those that are mature but must wait until the following year for reproduction represent different levels of contribution to the population. Similarly, juveniles and mature individuals contribute differently. Thus, how we observe a population can strongly affect our estimate of its extinction probability unless life stage differences are accounted for.

Confounded with the arbitrary measures of the population size is a general lack of agreement on the threshold number; some studies have used a quasi-extinction threshold ranging from 1 to 100 individuals (e.g., Armbuster and Lande 1993, Maschinski et al. 1997, Morris and Doak 2002), while others have used some percentage of the initial population size (McClure et al. 2003), despite the fact that estimated population extinction probability is very sensitive to the quasi-extinction threshold (Ginzburg et al. 1982). This arbitrariness is also true with other types of threshold values used in population viability analysis. Although the threshold values are often accompanied by biological or mathematical justifications, the use of different values across studies originates from a lack of consensus in determining quasi-extinction thresholds. One of the common arguments in determining the threshold value is that it should be the level above which demographic stochasticity becomes important (Morris and Doak 2002). However, in this paper, I demonstrate that the effects of demographic stochasticity differ depending on life-history strategies of organisms. Consequently, the threshold levels (e.g., quasi-extinction threshold and minimum viable population level) in PVA also need to account for the life-history differences.

In an effort to overcome the previous limitations to population viability analysis, I introduce a new population index that is a measure of population size that accounts for the effects of demographic stochasticity, which differ depending on the life-history strategy associated with the population of interest as well as life stages of individuals. This population index was built upon a previously introduced concept of the extinction-effective population size (Caswell 2001: chapter 15.2.7.2), which was specified under unstructured models for the purpose of comparing two or more populations in terms of the risk of population extinction resulting from demographic stochasticity. The extinction-effective population size is the population size of one population that would have the same population extinction probability as a reference population consisting of a certain number of individuals. The new population index, which I call the "extinction-effective population index," differs from the extinction-effective population size in the following regards. First, the new index incorporates a stage structure. Second, the unit of the index is no longer the number of individuals; this results from the fact that the contribution of individuals toward the reduction of population extinction probability differs depending on the life stages of the individuals. Finally, the new index has an analogous interpretation as a similar population size measure recommended by Lande and Orzack (1988).

The extinction-effective population index is a function of the number of individuals in different stages and demographic parameters. This population index is directly related to the probability of population extinction due to demographic stochasticity within a predetermined time. Therefore, the difference in the population index reflects the level of the extinction risk. The population index also accounts for differences in life-history strategy as well as associated demographic parameters, allowing consistent comparisons of extinction risks across populations of different species. It can be used as a baseline population size measure on which other processes can be modeled. In order to complement the count-based PVA, the quasi-extinction threshold also can be determined using the population index by simply choosing an appropriate level of extinction probability and translating the population index to the number of individuals in observed stages.

In the current work, I also derive the formula for the sensitivity and elasticity of the population index to population parameters. This index and its sensitivity are applied to three Pacific salmonid species as examples. The interpretations of the index are also presented. Finally, I derive a measure of demographic stochasticity that is specific to the life-history strategies of organisms. This measure can be used to compare relative importance of demographic stochasticity among different life-history strategies. Both the extinction-effective population index and the measure of demographic stochasticity are expected to become important new tools not only for guiding management decisions but also for aiding theoretical evaluations of sustainability of multiple species within a community.

DERIVATION

In this section, the population index and its sensitivity to demographic parameters are derived. To make the discussion more concrete, the description will refer to a stage structure (Fig. 1) of the chinook salmon (*Onco-*

rhyncus tshawytscha; see Plate 1). The characteristics associated with the life history of the salmon are briefly described in the following section. For the present discussion, please note that the numbers in Fig. 1 indicate different life stages, solid arrows indicate potential transitions of individuals among stages from one year to the next, and dotted arrows indicate fertility (production of eggs and their survival until stage 1). These arrows have associated parameters (Appendix A: Table A1) that are assembled into a population projection matrix, which is commonly used to project a population vector from one year to the next. In the present paper, only the number of females is counted for simplicity. However, a two-sex matrix population model can also be used in the same manner. For more detailed descriptions of the matrix population models, see Caswell (2001). Throughout this paper, the number of offspring is determined by Poisson distribution, which is one of the most commonly used stochastic models to represent reproduction; however, different distributions can be easily incorporated into the model.

Derivation of the population index relies on the notion of lineage extinction probability. Consider a single individual in a given life stage in Fig. 1 at time 0 (individuals in any stage at time 0 are called parents). The parent can potentially survive, transition among stages, and reproduce some time in the future, as shown by the arrows in the life cycle graph (Fig. 1). Similarly, the fates of its juveniles are subject to the processes specified by the arrows. All the descendants from the parent are collectively called offspring; this potentially includes the surviving parent itself, its children, children of children, and so forth. If all descendants from the parent at time 0 disappear by time t, the lineage is considered to have become extinct by time t. The probability of a lineage extinction event between time 0 and t is the lineage extinction probability. This probability is denoted by $q_{i,t}$, where subscript i indicates the stage of the parent at time 0.

The lineage extinction probability differs depending on the stage of a given individual at time 0. For example, juvenile salmon have a higher probability of death compared with adults, so they should have a higher lineage extinction probability than adults. The lineage extinction probability can be calculated using a multi-type branching process assuming that the process is both stationary and "memory-less" and fates of individuals are independent of one another (see Harris 1963, Caswell 2001, Fujiwara and Caswell 2001). The calculation of the lineage extinction probability involves expressing probability-generating functions and iteratively projecting the extinction probability using these functions (Appendix B). The MATLAB (MathWorks 2001) code used to calculate the lineage extinction probabilities from a projection matrix are found in the Supplement. The branching process treats the entries in a population projection matrix as parameters of a probability distribution that determines the fates of
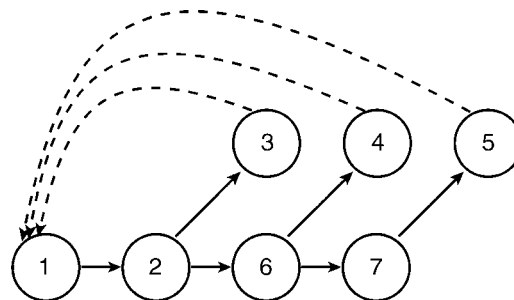

FIG. 1. Diagram of the life cycle of Chinook salmon. Numbers indicate the stage of individuals (1, juvenile; 2, 6, and 7, adults in the ocean; 3–5, spawning adults), solid arrows indicate potential transition of individuals from one year to the next, and arrows with dashed lines indicate reproduction.

individuals. Thus, the number of parameters required for calculating the lineage extinction probability is the same as that in standard matrix population models when the fecundity is modeled with the Poisson process or as a deterministic process (i.e., constant fecundity).

Suppose that there are n_i individuals in stage i ($i = 1, \ldots, 8$ for chinook salmon) at time 0. If this population is to become extinct by time t, all the lineages from every individual at time 0 must disappear by time t. Thus, under the assumption that individuals are independent of one another, the population extinction probability by time t (P_t) from demographic stochasticity is given by

$$P_t = \prod_i (q_{i,t})^{n_i}. \tag{1}$$

Taking the natural log of both sides and multiplying them by -1, we obtain

$$-\log P_t = -\sum_i n_i \log(q_{i,t}). \tag{2}$$

I define this quantity as the extinction-effective population index and denote it by φ_t. Thus the population index is

$$\varphi_t = \sum_i c_{i,t} n_i \tag{3}$$

where $c_{i,t} = -\log(q_{i,t}) \approx 1 - q_{i,t}$. The latter approximation is derived using the Taylor series expansion and holds when the lineage extinction probability is close to 1. The population index is the weighted sum of the number of individuals in each stage, with the weights given by the negative natural log of the lineage extinction probability, which is approximately the probability of lineage persistence at time t. The coefficient $c_{i,t}$ gives the contribution of each individual at time 0 in stage i to reducing the extinction probability of the population by time t and is thus called the extinction-reduction coefficient.

Another beneficial property of the population index is that it is directly related to the population extinction probability from demographic stochasticity:
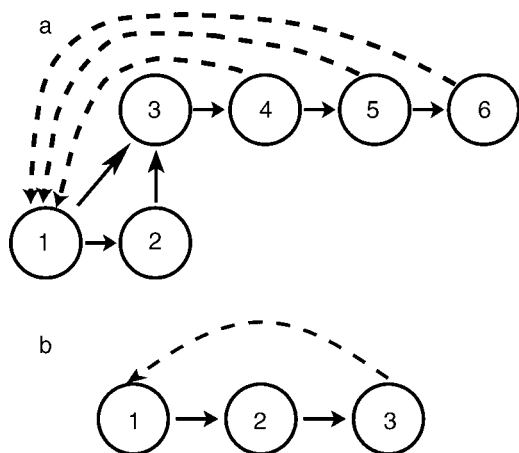
FIG. 2. Diagram of the life cycle of (a) steelhead and (b) coho salmon. For steelhead, only major life-history patterns described in Shapovalov and Taft (1954) are included. Numbers indicate stages of individuals, solid arrows indicate potential transition of individuals from one year to the next, and arrows with dashed lines indicate reproduction. For steelhead, stages are: 1–2, juveniles in a stream; 3, three-year-olds that migrated to the ocean in the previous year; 4, adults in the ocean; 5–7, spawning adults. For coho salmon, numbers correspond to age of individuals in years.

$$P_t = \exp(-\varphi_t). \qquad (4)$$

Because the population index is directly related to the population extinction probability (a common management "currency"), this quantity can be used to compare populations, even among organisms exhibiting different life-history strategies. For example, five mature salmon and five mature whales have different contributions to their populations in terms of the reduction in population extinction probability, but the same changes in φ_t of a salmon population and a whale population are equivalent. This equivalence also holds whether populations are counted before or after breeding events, as long as this information is appropriately incorporated into the population projection matrix.

In actual sampling, individuals in different stages may not be distinguishable or individuals in some stages may be unobservable. To accommodate these situations, the population index can also be expressed in terms of the total population size or the number of individuals in observed stages with an additional assumption in both cases that the population is under a stable stage distribution. Let $N_T(t)$ be the total population size and w_i be the stable stage distribution scaled so that $\Sigma_i w_i = 1$. The population index can be approximated as

$$\varphi_t \approx N_T(t) \sum_i c_{i,t} w_i. \qquad (5)$$

The stable stage distribution is given by the right eigenvector associated with the dominant eigenvalue of the projection matrix (see Caswell 1997). Similarly, when only a subset of stages is observable (e.g., in Fig. 1, total

number of individuals in stages 2, 3, 4, or 5), the population index is approximated as

$$\varphi_t \approx \frac{\sum_j n_j}{\sum_j w_j} \sum_i c_{i,t} w_i \qquad (6)$$

where j and i are stage indices for the observable stages and all stages, respectively.

Finally, the sensitivity of the population index to an entry in the projection matrix can be obtained by taking the derivatives of both sides of Eq. 3:

$$\frac{\partial \varphi_t}{\partial a_{kh}} = -\sum_i \left(\frac{n_i}{q_{i,t}} \frac{\partial q_{i,t}}{\partial a_{k,h}} \right) = -\frac{1}{P_t} \frac{\partial P_t}{\partial a_{kh}} \qquad (7)$$

where a_{kh} is the $\langle k, h \rangle$ entry of the population projection matrix. Similarly, the elasticity of the population index is given by

$$\frac{a_{kh}}{N_e(t)} \frac{\partial \varphi_t}{\partial a_{kh}} = \frac{a_{kh}}{\sum_i n_i \log q_i} \sum_i \left(\frac{n_i}{q_{i,t}} \frac{\partial q_{i,t}}{\partial a_{kh}} \right) \qquad (8)$$

which gives a proportional change in the population index resulting from the proportional change in the parameter. The partial derivatives of the lineage-extinction probability with respect to the matrix entries ($\partial q_{i,t} / \partial a_{kh}$) can be numerically evaluated. The sensitivity of the population index associated with Eqs. 5 and 6 can be derived in the same way by noting that w_i represents the initial population size and is thus unchanged with respect to a_{kh}.

EXAMPLES

The population index adjusts population size based on the contribution of individuals to the reduction in population extinction probability. The level of contribution differs depending on the initial stage of a given individual. A main advantage of the new population index is that it allows comparison of observed sizes of various populations within or across species, even those having different life-history strategies. Here I examine the populations of three different species of Pacific salmonids to demonstrate the index.

The three species of salmonids chosen for comparison are chinook salmon (*Oncorhyncus tshawytscha*), coho salmon (*O. kisutch*), and steelhead (*O. mykiss*). All three species exhibit anadromous behavior, but differ in the timing and/or number of their reproductive events. An individual Chinook salmon reproduces only once in its lifetime (semelparous), and the age of reproduction differs among individuals (indeterminate). In contrast, coho salmon return to their natal streams at a fixed age for a single spawning per individual (determinate semelparous), while each steelhead may reproduce multiple times during its lifetime (iteroparous).

The life histories of these species are depicted in Figs. 1 and 2, and the associated parameters are listed in

TABLE 1. The extinction-reduction coefficients for three species of Pacific salmonids.

Stage i, by species	$c_{i,50}$		
	$\lambda = 0.99$	$\lambda = 1.00$	$\lambda = 1.01$
Chinook salmon			
1	0.0077	0.0102	0.0133
2	0.0130	0.0167	0.0210
3	0.0968	0.1281	0.1660
4	0.1141	0.1509	0.1955
5	0.1331	0.1761	0.2282
6	0.0198	0.0256	0.0323
7	0.0077	0.0339	0.0428
Steelhead			
1	0.0009	0.0012	0.0016
2	0.0004	0.0006	0.0008
3	0.0075	0.0100	0.0131
4	0.0773	0.1015	0.1314
5	0.0952	0.1250	0.1619
6	0.0633	0.0833	0.1084
Coho salmon			
1	0.0033	0.0043	0.0057
2	0.0299	0.0403	0.0538
3	0.0853	0.1126	0.1469

Notes: The coefficient $c_{i,t}$ gives the contribution of each individual at time 0 in stage i to reducing the extinction probability of the population by time t and is thus called the extinction reduction coefficient. Three levels of population growth rate, λ, are modeled.

Appendix A (Tables A1, A2, and A3). These stage structures and parameters were obtained from the existing literature describing different populations of the respective species, and large variations should be expected in both life-history patterns and the parameters among populations within the same species. My goal is to build models that include key features of the life-history strategies of the three species for the purpose of comparisons, rather than trying to formulate accurate models that represent any specific populations. For example, only major life-history patterns of steelhead described in Shapovalov and Taft (1954) were included. Consequently, applications of results herein for management of actual populations need to be done carefully considering sensitivity of the results to the difference between the models and the populations of interests. For details of the life histories of salmonids, readers are referred to Groot and Margolis (1991) and Quinn (2005).

The parameters have been modified as needed (see Appendix A, Tables A1, A2, and A3 for specifications) to adjust the asymptotic annual population growth rate (i.e., the dominant eigenvalue of the projection matrix, denoted by λ) to predetermined values ($\lambda = 0.99$, 1.00, and 1.01) for the purpose of comparison. The adjustment was made to focus on the consequences for the extinction-effective population index of variation in life-history strategy by controlling the effects of an asymptotic population growth rate.

Extinction-reduction coefficients ($t = 50$; see Eq. 3) associated with the three populations were calculated under three different scenarios associated with the asymptotic population growth rate ($\lambda = 0.99$, 1.00, and 1.01). Extinction-reduction coefficients differ among stages within the same species (Table 1). Extinction-reduction coefficients also differ as a function of the asymptotic population growth rate; when the asymptotic population growth rate is low, the population extinction probability is high and the amount of contribution per individual to the unit reduction of population extinction probability is reduced. Extinction-reduction coefficients also differ among similar stages of different species. For example, spawning adult individuals of different species (stages 2–5 of chinook salmon, stage 3 of coho salmon, and stages 5–10 of steelhead) have different coefficients, indicating that we cannot assume that individuals in similar stages of different species are equivalent.

Because extinction-reduction coefficients differ among the three populations, the same number of individuals in each population translates into a different level of population index. For example, suppose that we have 100 spawning adults in each of the three populations, reflecting the fact that salmonids are often counted when they return to their natal streams without distinguishing different age classes. The population indices for the three populations were calculated using Eq. 6 with $t = 50$ (Table 2), assuming the stable stage distribution of the populations. The result shows 100 spawning adults in one population are not equivalent to 100 spawning adults in another in terms of their extinction probabilities. Furthermore, if we base our decisions solely on λ, we might conclude that having 100 Chinook salmon adults under $\lambda = 0.99$ may be in worse condition than having 100 steelhead adults under $\lambda = 1.01$ when, in fact, it is opposite in terms of the extinction probability by $t = 50$.

We might then ask how many spawning coho salmon and steelhead are needed to obtain the same extinction probability as the population consisting of 100 spawning chinook salmon adults. This is an important question in deciding a quasi-extinction threshold. The effective population sizes may be determined by calculating φ_t that corresponds to 100 spawning chinook salmon using

TABLE 2. Population index of three species of Pacific salmonids, each consisting of 100 spawning adults.

Species	φ_{50}		
	$\lambda = 0.99$	$\lambda = 1.00$	$\lambda = 1.01$
Chinook salmon	48	63	82
Steelhead	20	27	34
Coho salmon	25	33	42

Notes: Terms are: φ, extinction-effective population index; λ, population growth rate. The index was calculated for a time span of $t = 50$ years.
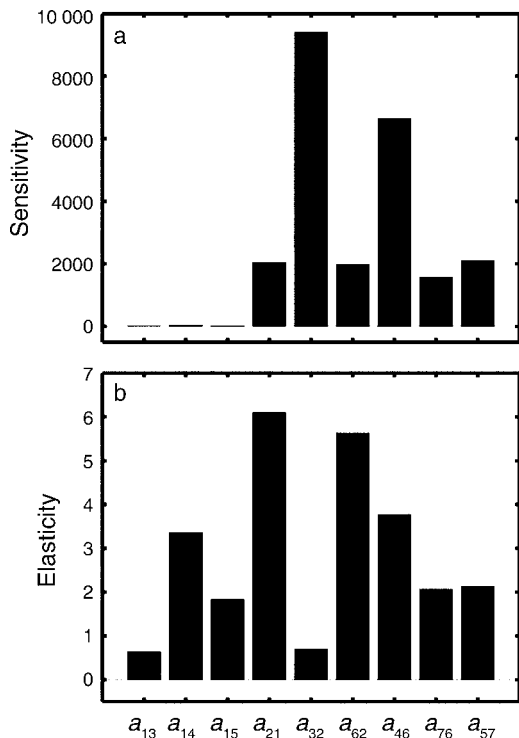
FIG. 3. (a) Sensitivity and (b) elasticity of extinction-effective population index to changes in demographic parameters for chinook salmon population models. The diagram of the life cycle and parameters are shown in Fig. 1 and Appendix Table A1, respectively. The abbreviation a_{1h} is the fertility of individuals in stage h, and a_{kh} (for $k \neq 1$) is the probability of individuals in stage h making a transition into stage k. See *Derivation* for explanations of sensitivity and elasticity.

Eq. 6 and transforming it back to the corresponding spawning adult sizes of coho salmon and steelhead again using Eq. 6 (Appendix C). The results reveal about 190 coho salmon and 238 steelhead are required to achieve the same extinction probability as that of 100 chinook salmon (when considering spawning adults in all cases and $\lambda = 1$). This result remains almost unchanged when calculated using different values of λ as long as the three species being compared experience the same growth rate.

Fig. 3 shows the sensitivity and elasticity of the population index of chinook salmon (under $\lambda = 1.00$ and a total population size of 10 000, distributed according to the stable stage distribution) to changes in demographic parameters. The results reveal that the population index is most sensitive to probabilities of transition into spawning adult stages (Fig. 3a), whereas it is relatively insensitive to changes in reproduction. Elasticity analysis (Fig. 3b) reveals that these differences are partly derived from the differences in the magnitude of the parameters. This type of calculation suggests (1) parameters for which researchers can try to reduce sampling errors by collecting more data and (2) management actions likely to affect the status of populations.

INTERPRETATIONS OF THE EXTINCTION-EFFECTIVE POPULATION INDEX

The population index has an intuitive interpretation; it is a measure of extinction probability given by the weighted sum of number of individuals in each stage, where the weights are determined by the stage-specific lineage extinction probability. This stage-specific lineage extinction probability, in turn, is strongly correlated with the traditional reproductive value (Caswell 2001: section 15.4.7), which is given by the left eigenvector associated with the dominant eigenvalue of the projection matrix. Thus, the extinction-reduction coefficient can be interpreted as a measure of stage-specific reproductive value.

The correlation between the lineage extinction probability and the traditional stage-specific reproductive values are shown with the three salmonid models (Fig. 4). Although Caswell (2001) used the ultimate lineage extinction (i.e., $t = \infty$) and investigated this correlation when the asymptotic growth rate is greater than 1, Fig. 4 reveals that the relationship also holds when the population growth rate is below 1 (this relationship appears to hold as long as t is a sufficiently large finite value relative to the generation time of organisms). However, the slopes of the lines in Fig. 4 differ among the three species. This makes the lineage extinction probability differ from the traditional stage-specific reproductive values. Thus, we cannot simply use the traditional stage-specific reproductive values in place of the lineage extinction probability in Eq. 3.

Reproductive values, in a more general sense, are the stage-specific contributions of individuals to a population. The specific aspect of the population receiving this contribution is reflected partly by the coefficient that scales the reproductive values. When this coefficient is
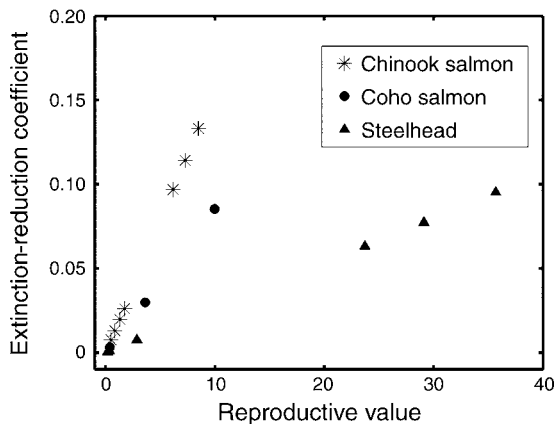

FIG. 4. Relationship between the extinction-reduction coefficient $c_{i,50}$ and the traditional reproductive value. Calculations were done for the three species of salmonids under a population growth rate (λ) = 0.99. The extinction-reduction coefficient gives the contribution of each individual at time 0 in stage i to reducing the extinction probability of the population by time t.

PLATE 1. Spring run chinook salmon (*Oncorhynchus tshawytscha*) and summer run steelhead (*O. mykiss*) in the Crapo Creek cold water refugia on the Salmon River, California, USA. Photo credit: Nat Pennington.

scaled to reduce the population extinction probability, it becomes the extinction-reduction coefficient, which is approximately the probability of lineage persistence.

MEASURE OF DEMOGRAPHIC STOCHASTICITY

The contributions of individuals toward the reduction of the extinction probability from demographic stochasticity differ within a population depending on the initial stage of individuals. These differences are accounted for by the extinction-reduction coefficients. However, the overall effect of demographic stochasticity also differs depending on the life-history strategy of the organism. In other words, organisms using certain life-history strategies suffer from demographic stochasticity more severely than those using other life-history strategies. Here, I derive a measure of life-history-specific effect of demographic stochasticity.

The strong correlation between the traditional reproductive values and the extinction-reduction coefficients suggests that the method in this paper is analogous to the approach suggested by Lande and Orzack (1998) to weight stage count by the reproductive value

$$\eta = \sum_i v_i n_i, \qquad (9)$$

where n_i is the number of individual in stage i and v_i is the traditional reproductive value of an individual in stage i, which is given by the left eigenvector associated with the dominant eigenvalue of a projection matrix (see Caswell 2001).

However, the slope that relates the traditional reproductive value and the extinction-reduction coefficient differs depending on life-history strategy of

organisms (Fig. 4). Therefore, for a given value of λ, the following relationship holds

$$\varphi_t = \delta_{k,t}\eta, \qquad (10)$$

where $\delta_{k,t}$ is a constant specific to life-history strategy (i.e., stage-structure and associated demographic parameters), which is denoted by k, of organisms. Thus, the coefficient $\delta_{k,t}$ can be considered a measure of the life-history-specific effect of demographic stochasticity on the population extinction probability.

The coefficient $\delta_{k,t}$ was calculated for the three species of salmonids (Table 3). The result reveals that the effect of demographic stochasticity differs among these populations, and it reduces the extinction-effective population size of steelhead more than chinook salmon. This is why we need more steelhead adults compared with chinook salmon even though the traditional measure of reproductive value of adult steelhead is higher than that of adult chinook salmon.

DISCUSSION

The development of the extinction-effective population index was motivated by the lack of a consistent

TABLE 3. Life-history-strategy-specific effect of demographic stochasticity ($\delta_{s,50}$) on the population extinction probability within $t = 50$ years.

Species	$\delta_{s,50}$		
	$\lambda = 0.99$	$\lambda = 1.00$	$\lambda = 1.01$
Chinook salmon	0.0157	0.0207	0.0267
Steelhead	0.0027	0.0035	0.0047
Coho salmon	0.0086	0.0114	0.0151

measure of population size, particularly one that could be used for meaningful comparisons among populations exhibiting different life-history strategies and/or demographic parameters. The new index has a monotonic relationship with the population extinction probability, which is a common currency in population management. Thus, this index allows consistent population size comparisons among different populations, in terms of their risks of extinction due to demographic stochasticity when populations are not experiencing density dependence. This property is expected to be particularly useful for cohesive multispecies management.

The lineage extinction probability, which is an ingredient for defining the population index, is related to the traditional reproductive value of a given individual. However, unlike the traditional reproductive value, the lineage extinction probability can be calculated for different time horizons. This adds another dimension to the population index. Furthermore, the population index reflects variation in population growth rate (Table 1) as well as demographic stochasticity. Both the traditional reproductive value and the lineage extinction probability incorporate life-history variations, which play important roles in determining population viability, but have often been ignored in past studies.

When analyzing the viability of a population, we need to consider two types of risks: the risk of the population becoming small and the risk of the population becoming extinct after it has become small (Caughley 1994). The traditional count-based PVA (diffusion model) exclusively deals with the former type of risk. However, the latter type of risk is also important because conservation managers are often interested in comparing the potential risks of extinctions of small populations, for example, for the purposes of allocating conservation effort among endangered populations. The extinction-effective population index presented herein is a measure of population size that incorporates demographic stochasticity, thus allowing its use with small populations.

The population index itself, as described in this paper, does not incorporate environmental stochasticity, which is included in the diffusion model. However, the new index will help in determining consistent quasi-extinction thresholds. I suggest the following procedure: (1) determine the value of the extinction probability and the future time horizon (P_t in Eq. 4) and transform it into the extinction-effective population index using Eq. 4, (2) transform the value of the index into the value of n_i for the observed stage of the population of interest using Eq. 6 (Appendix C), and (3) use it as the threshold value for that population. Steps 2 and 3 can be repeated for different populations to obtain their threshold values. These threshold values in terms of the number of individuals will be different depending on the stage structure, associated parameters, and observed stage. However, at the corresponding population-specific threshold levels, all populations experience the same future extinction probability P_t. This justifies the use of the population-specific threshold values, rather than the same number of individuals across the populations, as quasi-extinction thresholds.

The extinction-effective population index might be criticized because the data required for accurate estimation of demographic parameters used in the index are often not available (Morris et al. 2002). However, although accurate parameter estimates may not be available, the use of crude estimates will allow calculation of the population index. Parameters estimated for different populations exhibiting similar life-history strategies (Caswell et al. 1998) are likely to form adequate starting points for a variety of studies. The sensitivity and elasticity of population indices based on such crude estimates will help identify which parameters would benefit from more accurate estimation, allowing researchers to focus their empirical data collection efforts. Since recent studies (Coulson et al. 2001, Shea and Mangel 2001, Ellner et al. 2002, Shea et al. 2006) have suggested that simply counting individuals in a selected stage over time may not provide sufficient information for management decision-making, and the present study also demonstrates the importance of differences in life-history strategy, I suggest that demographic parameters should be routinely estimated during empirical studies designed for population management. There are sufficient technical capabilities (e.g., Williams et al. 2002, Pine et al. 2003) for this to become standard practice in many animal populations. In this and other ways, the proposed population index may form an important new tool for guiding management decisions.

LITERATURE CITED

Armbuster, P., and R. Lande. 1993. A population viability analysis for African Elephant (*Loxodonta africana*): How big should reserves be? Conservation Biology 7:602–610.

Beissinger, S. R. 2002. Population viability analysis: past, present, future. Pages 5–17 *in* S. R. Beissinger and D. R. McCullough, editors. Population viability analysis. The University of Chicago Press, Chicago, Illinois, USA.

Boyce, M. S. 1992. Population viability analysis. Annual Reviews of Ecology and Systematics 23:481–506.

Caswell, H. 1997. Matrix methods for population analysis. Pages 19–58 *in* S. Tuljapurkar and H. Caswell, editors. Structured-population models in marine, terrestrial, and freshwater systems. Chapman and Hall, New York, New York, USA.

Caswell, H. 2001. Matrix population models, Second edition. Sinauer, Sunderland, Massachusetts, USA.

Caswell, H., S. Brault, A. J. Read, and T. D. Smith. 1998. Harbor porpoise and fisheries: an uncertainty analysis of incidental mortality. Ecological Applications 8:1226–1238.

Caughley, G. 1994. Directions in conservation biology. Journal of Animal Ecology 63:215–244.

Coulson, T., G. M. Mace, E. Hudson, and H. Possingham. 2001. The use and abuse of population viability analysis. Trends in Ecology and Evolution 16:219–221.

De Master, D., R. Angliss, J. Cochrane, P. Mace, R. Merrick, M. Miller, S. Rumsey, B. Taylor, G. Thompson, and R. Waples. 2004. Recommendations to NOAA Fisheries: ESA Listing Criteria by the Quantitative Working Group 10 June 2004. Technical Memo NMFS-F/SPO-67. U.S. Department of Commerce, National Oceanic and Atmospheric Administration, Alaska Fisheries Science Center, Seattle, Washington, USA.

Dennis, B., P. L. Munholland, and J. M. Scott. 1991. Estimation of growth and extinction parameters for endangered species. Ecological Monographs 61:115–143.

Ellner, S. P., J. Fieberg, D. Ludwig, and C. Wilcox. 2002. Precision of population viability analysis. Conservation Biology 16:258–261.

Fujiwara, M., and H. Caswell. 2001. Demography of the endangered North Atlantic right whale. Nature 414:537–541.

Ginzburg, L. R., L. B. Slobodkin, K. Johnson, and A. G. Bindman. 1982. Quasiextinction probabilities as a measure of impact on population growth. Risk Analysis 2:171–181.

Groot, C., and L. Margolis. 1991. Pacific salmon life histories. University of British Columbia Press, Vancouver, British Columbia, Canada.

Harris, T. E. 1963. The theory of branching processes. Prentice-Hall, Englewood Cliffs, New Jersey, USA.

Holmes, E. E. 2001. Estimating risks in declining populations with poor data. Proceedings of National Academy of Sciences (USA) 98:5072–5077.

IUCN [International Union for the Conservation of Nature and Natural Resources]. 2001. IUCN Red List Categories and Criteria. Version 3.1. IUCN Species Survival Commission, IUCN, Gland, Switzerland, and Cambridge, UK.

Lande, R., and S. H. Orzack. 1988. Extinction dynamics of age-structured populations in fluctuating environment. Proceedings of National Academy of Science (USA) 85:7418–7421.

Maschinski, J., R. Frye, and S. Rutman. 1997. Demography and population viability of an endangered plant species before and after protection from trampling. Conservation Biology 11:990–999.

MathWorks. 2001. MATLAB. Version 7.0, release 14. MathWorks, Natick, Massachusetts, USA.

McClure, M. M., E. E. Holmes, B. L. Sanderson, and C. Y. Jordan. 2003. A large-scale, multispecies status assessment: anadromous salmonids in the Columbia River basin. Ecological Applications 13:964–989.

Morris, W. F., P. L. Bloch, B. R. Hudgens, L. C. Moyle, and J. R. Stinchcombe. 2002. Population viability analysis in endangered species recovery plans: past use and future improvements. Ecological Applications 12:708–712.

Morris, W. F., and D. F. Doak. 2002. Quantitative conservation biology: theory and practice of population viability analysis. Sinauer, Sunderland, Massachusetts, USA.

Pine, W. E., K. H. Pollock, J. E. Hightower, T. J. Kwak, and J. A. Rice. 2003. A review of tagging methods for estimating fish population size and components of mortality. Fisheries 28:10–23.

Quinn, T. P. 2005. The behavior and ecology of pacific salmon and trout. University of Washington Press, Seattle, Washington, USA.

Shapovalov, L., and A. C. Taft. 1954. The life histories of the steelhead rainbow trout (Salmo gairdneri gairdneri) and silver salmon (Oncorhynchus kisutch) with special reference to Waddell Creek, California, and recommendations regarding their management. California Department of Fish and Game Fish Bulletin 98:1–375.

Shea, K., and M. Mangel. 2001. Detection of population trends in threatened Coho salmon (Oncorhynchus kisutch). Canadian Journal of Fisheries and Aquatic Sciences 58:375–385.

Shea, K., N. Wolf, and M. Mangel. 2006. The influence of density dependence on the detection of trends in unobserved life history stages. Journal of Zoology 269:442–450.

Tuljapurkar, S. D., and S. H. Orzack. 1980. Population dynamics in variable environments: I. Long-run growth rates and extinction. Theoretical Population Biology 18:314–342.

Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. Analysis and management of animal populations. Academic Press, San Diego, California, USA.

APPENDIX A

Tables of life-history parameters associated with population models depicted in Figs. 1 and 2 (*Ecological Archives* E088-141-A1).

APPENDIX B

Algorithm for calculating the lineage extinction probability (*Ecological Archives* E088-141-A2).

APPENDIX C

Method for transforming a value of the extinction-effective population index into the corresponding value of stage size (*Ecological Archives* E088-141-A3).

SUPPLEMENT

MATLAB source codes used to calculate lineage extinction probability (*Ecological Archives* E088-141-S1).