NOAA Technical Memorandum NMFS

MAY 1999

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NOAA-TM-NMFS-SWFSC-261

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February, 1999

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ABSTRACT

Many populations of Pacific salmon have been listed under the Endangered Species Act (ESA) in recent years, and a formidable task for population ecologists will be application of the rapidly growing field of quantitative conservation biology to specific situations. This review organizes some recent research applicable to this task, including results pertaining to the definition of population structure, the genetic risks posed by reduced population sizes and hatchery stocks, and innovations in population modeling. Where possible, information pertaining to coho salmon is presented as specific examples. The definition of population structure now commonly involves analysis of DNA (mitochrondrial and microsatellite). Genetic risks may be caused by either low population sizes (inbreeding) or hatchery introgression (outbreeding). Analytical population models are increasingly applied to specific populations, and have evolved from random-walk models to include density dependence. Current population viability analysis (PVA) models applied to Pacific salmon vary with respect to data requirements and level of biological detail, and direct application of most existing models to California coho is hindered by a lack of rigorous abundance estimates. A recommended approach is development of matrix population models, and a rudimentary model developed for coho salmon reveals the importance of survival in various habitats (both freshwater and marine) to population growth; such models can be expanded to include relevant biological details. Application to data-poor situations (such as the California coho) will depend upon life history parameters studied in other locations, and Bayesian analysis is a logical approach for assessing parameter uncertainty and incorporating information from other environments. Assessment of population recovery will require effective monitoring of population abundance.

CONTENTS

Introduction

Population viability analysis (PVA) is a process in which a species (or a relevant segment of a species) is identified and the probability of extinction as a function of various risks is assessed. A useful categorization of potential extinction risks was proposed by Shaffer (1981) and includes demographic stochasticity (variation among individuals in, for example, survival and reproduction), environmental stochasticity (temporal variation expected to affect all members of a population equally), genetic stochasticity (changes in gene frequency that could become important at low population sizes), and natural catastrophes (e.g., floods, droughts, etc.). Because the focus of many conservation efforts, such as the ESA, is to preserve genetic diversity (Waples 1991a), early efforts to derive generic guidelines for minimum viable population size were based largely on genetic considerations (Nunney and Campbell 1993). The field of quantitative conservation biology has evolved rapidly in recent years, and important insights have emerged regarding each of the four risk categories above. These results can be expected to influence the application of PVA to specific situations in which the estimation of extinction risks will reflect our knowledge of life history characteristics.

In particular, the application of PVA to Pacific salmon can be expected to produce conceptual insights, as well as being a critically important management procedure. The precise timing of life history events required by the anadromous life history (Allendorf and Waples 1996), the metapopulation structure of spatially separated spawning populations, and the semelparous reproductive strategy (except for steelhead) distinguish salmonids from many other species. The first salmonid population to be listed under the Endangered Species Act (ESA) was the Snake River sockeye in 1989, followed by the winter chinook in the Sacramento River in 1990 and several more recent listing decisions (Table 1). For example, many of the salmon stocks in California are protected under the ESA, and population viability analyses will play a significant role in developing recovery strategies and delisting criteria.

A challenge for population ecologists is applying the growing body of literature in quantitative conservation biology to specific populations for which we may have limited empirical information. Thompson (1991) presents some critical concepts in conservation biology, focusing particularly on the risks associated with environmental stochasticity in population size. More recently, several reviews have discussed the genetic risks facing salmonids (Allendorf and Waples 1996; Lynch, in press), DNA-based techniques for identifying population structure have become more common (Nielsen et al. 1997a), and analytical techniques have been applied to specific populations and compared to simulation results (Cisneros-Mata et al. 1997). However, substantial uncertainty exists regarding extinction risks for most salmonid populations (Allendorf et al. 1997), a situation exemplified by the perhaps extreme case of California coho salmon (Brown et al. 1994). The general recognition of uncertainty has motivated research on evaluating risk, including power analysis and Bayesian techniques.

The purpose of this review is to describe recent developments in theoretical and applied conservation biology, focusing generally on results pertaining to Pacific salmon and, where possible, California coho salmon. A comprehensive review of this broad subject is, of course, not possible in the space here; rather, the goal is to provide the reader with an overview of some general results obtained largely since Thompson's review. I begin by considering the definition of population structure, arguably the first step in a viability analysis. Because several excellent reviews exist regarding genetic risks to salmonids, such material is covered briefly. Developments regarding other risk categories are discussed in the context of specific theoretical and applied models, and five recent PVA models applied to Pacific salmon are discussed in detail. As a departure point, a simple matrix model is developed to summarize our general knowledge of coho salmon life history and illustrate some implications for recovery strategies. Finally, several trends in PVA modeling applicable to salmonid populations at risk are discussed.

Definition of Population Structure

The ESA allows for conservation of organisms at the subspecies level and thus defines "species" as "any subspecies of fish or wildlife or plants, and any distinct population segment of any species of vertebrate fish or wildlife which interbreeds when mature." This definition is pertinent to Pacific salmon because the homing of spawners to natal streams results in many spawning populations. The definition of "distinct populations" needs clarification for applied use, and the policy for Pacific salmon has been to adopt the concept of the Evolutionarily Significant Unit (ESU) originating from systematists (Ryder 1986), which requires that a given population be "substantially" reproductively isolated from conspecific populations and important to the evolutionary legacy of the species (Waples 1991a). Although the extent of reproductive isolation can be estimated with a variety of tools, including external tags, genetic marks or indices, and observation of recolonization or physical barriers to migration (Waples 1991a), a commonly applied measure of reproductive isolation is the frequency of genetically neutral characters, typically measured by allozyme electrophoresis or DNA techniques. These genetic procedures have the advantage of providing measures of gene flow over evolutionary time scales, as well as being relatively easy to apply. In this section, I review the application of these methods to California coho salmon and steelhead populations.

Electrophoretic and tagging studies have revealed that California coho have relatively low gene flow between streams (with straying occurring between adjacent streams) and exhibit marked genetic differences only at broad spatial scales. Bartley et al. (1992a) observed low genetic variability within California coho, based on electrophoretic analysis, and obtained an estimate of gene flow from Wright's (1943) island population model, *Nm*, of 1.3 individuals per population per generation. Although this level of *Nm* exceeds the level necessary to prevent differentiation based upon genetic drift, it is considerably less than the *Nm* of 5.8 for British Columbia coho (Wehrhahn and Powell 1987). In contrast, Shapovalov and Taft (1954) found that 14.9% of tagged coho from Waddell Creek, California, strayed into Scott Creek, located 8 km north, a rate considerably higher than that found in Cowlitz River, Washington (<1.5%; Quinn and Fresh 1988) and Vancouver Island (3.7%; Labelle 1992). Because not all salmon that stray into non-natal streams would be expected to reproduce successfully, tagging studies represent an indirect measure of gene flow; this discrepancy highlights the differences between genetic and demographic population structure. The finding of low genetic diversity by Bartley et al. (1992a) was affected by small sample sizes; recent work analyzing the larger samples within Bartley et al.

(1992a) and Olin (1984) found relatively large genetic distances on broad spatial scales and was instrumental in defining the ESU structure in California (Weitkamp et al. 1995).

Technologies for directly analyzing mitochondrial DNA (mtDNA) and microsatellite DNA have developed rapidly, and often provide increased resolution over allozyme work. Nielsen et al. (1994a) used mtDNA and microsatellite methods to show significant differences in frequency distributions of mtDNA haplotypes and microsatellite alleles for California steelhead (*Oncorhynchus mykiss*), thus allowing separation (based on genetic and oceanographic information) into three regions: (1) north California (Eel River to Gualala River); (2) central California (Russian River to Point Sur); and (3) south California (San Simeon to Santa Monica Bay). Microsatellite and mtDNA data have also shown substantial diversity of nonanadromous *O. mykiss* in southern California freshwater environments, suggesting the importance of this life history pattern and associated habitat in conservation efforts (Nielsen et al. 1997a).

Because different parts of the genome evolve at different rates, the introduction of new genetic techniques may provide results incongruent with previous studies. For example, significant differences in mtDNA haplotype frequency distributions were observed between the four temporal spawning runs of Sacramento River chinook salmon (Nielsen et al. 1994b), whereas allozyme studies were unable to distinguish the four runs (Bartley et al. 1992b). Similarly, microsatellite DNA loci revealed significant differences between summer and winter steelhead from the Middle Fork of the Eel River, but mtDNA did not show distinguishing population structure (Nielsen 1996). Finally, Nielsen et al. (1997b) showed a significant association of mtDNA phylogenic structure of *O. mykiss* with longitude and latitude, although this pattern was not observed in microsatellite alleles. Two features of the salmonid genome, tetraploidy and the organization of microsatellite repeat classes, have hindered development of salmonid microsatellite markers (Nielsen 1996). The tetraploid nature of salmon has led to gene duplication that complicates interpretation of molecular variation (Allendorf and Waples 1996), and knowledge of polymorphic markers with diploid allele expression were rare until recently (Nielsen 1996). Further, the application of previously known microsatellite markers (from mammals) are difficult to apply to salmon because of organizational differences in microsatellites of teleosts. The relation between the three sources of genetic information (allozymes, microsatellite DNA, and mitrochrondrial DNA) remains an important research activity (Nielsen 1996).

Only a small fraction of the genome is examined in DNA analyses, and this limitation is particularly acute in analyses of mtDNA, which is inherited from only the female parent (Avise 1995). For this reason, Cronin (1993) and others recommend using several sources of evidence to assess population structure. Because a small amount of gene flow may genetically homogenize populations that have relatively weak demographic connections, there is a clear need for interpreting results from genetic analyses in terms of demographic population structure. For example, the matrilineal inheritance of mtDNA may yield insights about species that exhibit gender-biased gene flow (Avise 1995). A failure to reject the common null hypothesis of no genetic differentiation does not necessarily imply that a population segment should be managed as a single unit, and power analysis is recommended to evaluate the probability of correctly rejecting the null hypothesis (Dizon et al. 1995; Taylor and Dizon 1996). Finally, while genetic information plays a large role in determining reproductive isolation, the determination of the second ESU criterion of evolutionary importance often depends on information such as phenotypic traits, life history traits, and habitat characteristics (Waples 1991a). For example, genetic information was not available for the ESU determination and eventual ESA listing of Snake River sockeye salmon, and the extraordinary long migration route (~1500 km) and unique freshwater habitat provided substantial evidence of reproductive isolation and a unique life history with evolutionary significance (Waples 1995).

Genetic Risks and the Effect of Hatchery Populations

At small population sizes, the loss of genetic diversity becomes an important issue to consider, and any useful criterion for recovery of endangered populations must reflect population sizes above which genetic risk is minimal (Nunney and Campbell 1993). For an idealized population consisting of randomly mating individuals with a 1:1 sex ratio and a constant population size between discrete generations, the loss of heterozygosity decreases geometrically with a rate of $1-1/(2N)$ per generation; thus, an N of 50 would result in a loss rate of 1% per generation, an acceptable limit in many agricultural applications (Franklin 1980). Departures from the idealized conditions above can be evaluated with the concept of an effective population size, N_e, defined as the size of an ideal population whose genetic composition varies in the same way as an actual population of size N (Gall 1987).

Several factors can influence N_e. Commonly considered factors include nonequal sex ratio, variance in family size, and intergenerational variance in the number of adults. To begin, the unique life history of indeterminate semelparous reproduction can be addressed by relating N_e to the effective number of breeders (N_b) in an idealized population with $N_e = g\ N_b$, where g is the generation length (approximated as the average age of spawning) (Waples 1990). The effective population size is inversely related to the coefficient of variation in family size, which has been observed to be ~ 0.7 for hatchery salmonid populations (Simon et al. 1986, Hedrick et al. 1994). In Alaskan pink salmon, variance in family size reflected not merely random variation, but rather genetic differences that produced phenotypic variation among families. Because the favored phenotype changed from generation to generation, depending on environmental conditions, these results indicate the importance of maintaining genetic diversity (Geiger et al. 1997).

The effect of intergenerational variability in population size may be especially important; the average N_e over t generations can be approximated by the harmonic mean of the effective spawners for each generation:

$$N_e = \frac{1}{\frac{1}{t}\sum_{i=1}^{t}\frac{1}{N_i}} \tag{1}$$

where the N_i in each generation has been adjusted for the effects of sex ratio and variance in family size (Gall, 1987, Gillespie 1998). Under significant variation, N_e will be closer to the minimum N_i than the arithmetic mean is; thus, even a few generations of low N_i can produce a bottleneck. For example, in ten Oregon coho populations the harmonic mean ranged from 30% to 70% of the arithmetic mean (Lynch, in press).

The difficulty of directly estimating N_e for most populations has led to qualitative guidelines for minimum viable population size. Franklin (1980) recommends an effective population size $N_e = 50$ to prevent an unacceptable rate of inbreeding (1%) and $N_e = 500$ to maintain long-term variation; these guidelines are often called the "50/500" rule. Soule (1980, 1987) argues that preservation of long-term evolutionary potential may require a substantially larger N_e and stresses that general guidelines provide only the starting point of a more detailed analysis. Many suggestions of N_e/N ratios for applying Franklin's rule have been made, including 50% by Wilcox (1986), 25%–33% by Soule (1980), and 50% by Salwasser and Malcot (1986). A survey of N_e/N ratios largely from terrestrial data has reveals that variance in population size and family size are the two largest determinants of N_e/N, which averages 0.10 for 102 species; thus the ratios suggested above may be too optimistic for general use (Frankham 1995). For salmonids, however, Lynch (in press) suggests that N_e be estimated as 20% of breeding adults.

Effects of Hatchery Populations

A number of genetic risks may be caused by hatchery supplementation of natural populations; these risks include reduction of effective population size, outbreeding depression, displacement of locally adapted genes, and indirect ecological effects (Waples 1991b, Allendorf and Waples 1996, Lynch in press). A concern with hatchery supplementation is that a relatively small number of hatchery fish will produce much of the succeeding generation, creating an artificial genetic bottleneck (Ryman and Lairke 1991). This process has the greatest chance of lowering the overall effective population size when the hatchery N_e is small relative to the wild N_e and the reproductive contribution from the hatchery component is large; this is a concern for salmonids because hatchery N_e's may be small (Waples and Teel 1990). Simon et al. (1986) found that the N_e of coho salmon in Big Creek hatchery, Oregon, may not be large enough to prevent deleterious effects of inbreeding, despite the seemingly large number of returning adults. The addition of hatchery-reared salmon has not appeared to reduce the overall N_e of Sacramento River winter chinook (Hedrick et al. 1994), in part because the hatchery contribution to the total population is estimated to be relatively small (<20%). Computer simulations suggest that a critical factor affecting the level of inbreeding is whether the supplemented population remained large after stocking was terminated, a function of all the risks that led to the original population decline (Waples and Do 1994).

The survival of hatchery salmonids in the wild is generally less than that of wild salmonids, which may reflect the fostering of potentially deleterious alleles in the hatchery environment (Waples 1991a, Reisenbichler 1997). This suggests that hatchery introgression reduces the fitness of wild salmonids. In ten Mendocino County, California, streams, an inverse relation of geographic distance from the egg-taking station (Noyo River) to estimated genetic flow *(Nm)* from hatchery fish to wild stocks suggests hatchery introgression, although this cannot be stated conclusively without knowledge of the genetic diversity in wild stocks prior to supplementation (Nielsen 1994). Hatchery supplementation may pose risks from ecological interactions such as competition and predation, which may reduce wild population size and production (Waples 1991a). Agonistic encounters between hatchery and coho salmon were observed in the Noyo River, California, immediately following stocking; of wild coho, 83% were displaced from their foraging habitat, and coho production decreased (Nielsen 1994). Finally, hatchery supplementation may support harvest rates in mixed-stock fisheries that are unsustainable for wild stocks and can make assessment of wild stocks difficult by masking their dynamics.

Population Modeling Approaches

Deterministic Models

Although it is clear that extinction of an age-aggregated (or age-structured) population with density-independent growth is a certainty if the growth rate (or dominant eigenvalue of the projection matrix) is less than one, deterministic analyses have yielded insights useful to conservation. Such models follow the general format

$$\mathbf{N}_{t+1} = \mathbf{A}\mathbf{N}_t \qquad (2)$$

where **N** is a vector of population abundances at various ages (or stages), **A** is a $n \times n$ projection matrix that incorporates survival and fecundity, and n is the number of ages (or stages) in the population (Leslie 1945, Lefkovitch 1965). Heppell et al. (1996) use both age- and stage-structured models to conclude that headstarting (the practice of captively rearing turtles through an early part of their life cycle) is unlikely to be effective on the long-lived Kemp's ridley sea turtle. Population growth rate is most sensitive to sub-adult and adult mortality, and efforts to reduce such mortality, such as turtle excluder devices (TEDs), are a more logical focus of conservation efforts; similar models reveal that TEDs should also increase the population sizes of loggerhead turtles (Crowder et al. 1994). Sensitivity analyses of deterministic models have also been applied to the desert tortoise (Doak et al. 1994) and the wandering albatross (Moloney et al. 1994).

Analytical Results of Stochastic Models

A rich array of analytical results has been developed from matrix models when the additional complication of environmental stochasticity is added. Under the assumption of nonperiodic reproduction (where more than one population age class is fecund), the natural logarithm of total population size (X_t) of an age-structured population under serially uncorrelated environmental stochasticity is distributed approximately normally with mean $x_0 + \mu t$ and variance $\sigma^2 t$, where x_0 is the log of initial population size at time t_0, t is the time since t_0, and μ and σ^2 are the long-run growth rates of the mean and variance, respectively (Lande and Orzack 1988, Tuljapurkar 1989). These distribution properties hold for any weighted sum of population sizes at age, including a single age class (Caswell 1989) or the total population size. The logarithmic distribution of N_t results in μ approximating $\log \lambda - \sigma^2/2$ where λ is the dominant eigenvalue of the average projection matrix (or simply the mean population growth rate). Estimation of the critical parameters μ and σ is aided by noting that X_t can be approximated as a diffusion process with drift, which provides a satisfactory approximation under moderate environmental stochasticity (Lande and Orzack 1988). Parameters may be estimated from perturbation of the average projection matrix (Cisneros-Mata et al. 1997) or from an empirical time series of population abundance (Dennis et al. 1991).

The diffusion approximation can also be used to assess the probability and expected time of extinction, with extinction considered as some arbitrarily low population size x_e. As in the deterministic case, extinction is a certainty when $\mu \leq 0$; however, when $\mu \geq 0$ the probability of ultimate extinction given a starting size x_0 is $\exp(-2x_d s)$, where $x_d = x_0 - x_e$ and $s = \mu/\sigma^2$ (Lande and Orzick 1988). For populations doomed to extinction, the time to extinction (T) follows an inverse Gaussian distribution and has expected value $E[T] = x_d/|\mu|$; thus when μ is positive, $E[T]$ is inversely related to μ (Lande and Orzick 1988). This counterintuitive result occurs because a population fated to extinction when μ is positive reaches its fate quickly, before the population can grow substantially.

A critical assumption of the random-walk model above is the lack of density dependence, which leads directly to the counterintuitive inverse relation between $E[T]$ and μ. Recent analytical work has applied diffusion theory to density-dependent models in order to obtain analytical approximations of mean extinction times. A simple formulation imposes an upper bound upon an otherwise density-independent, age-aggregated model, such that

$$N_{t+1} = \begin{cases} A_t N_t & \text{if } A_t N_t \leq N_{\max} \\ N_{\max} & \text{otherwise.} \end{cases} \tag{3}$$

If $a = \log A$ is normally distributed with mean μ_d and variance σ_a, then eventual extinction becomes a certainty and the expected time of extinction, $E[T]$, depends on the initial population size x_o:

$$T(x_0) = \frac{1}{2su_d}\left[e^{2sk}(1-e^{-2sx_0}) - 2sx_0\right] \tag{4}$$

where $s = \mu_d/\sigma_a$ and k is $\log(N_{max})$ (Lande, 1993, Foley 1994, Middleton et al. 1995). Simulations indicate that T is exponentially distributed with a constant rate of extinction $1/E[T]$, and population persistence beyond a few multiples of $E[T]$ is highly unlikely (Foley 1994, Middleton and Nisbet 1997). Middleton and Nisbet (1997) also analyze a more elegant density-dependent formulation, the modified logistic, and Mangel and Tier (1993) present a generalized numerical procedure for obtaining the mean and variance of extinction times in a wide variety of density-dependent systems, including models that may have very complicated dynamics.

The analytical approaches above have focused largely on environmental stochasticity, but a continuous-time model with an upper bound on population size has been used to examine the importance of environmental, demographic, and catastrophic stochasticity (Lande 1993). Demographic stochasticity was modeled by defining the variance of the instantaneous growth rate as V_1/N where V_1 is the variance in individual fitness per unit time; this stems from equating the population growth rate to the mean fitness of individuals at a particular time. Additionally, catastrophic risk was modeled as a Poisson process describing random, proportional decreases in population size. Lande (1993) concludes that moderate population sizes with positive growth rates subject to catastrophic and environmental variation may persist for reasonably long periods, in contrast with the more pessimistic results obtained from a density-independent model (Ewens et al. 1987).

Although the work above has historically remained in the domain of theoretical ecology, it has been applied increasingly to specific populations at risk. Dennis et al. (1991) successfully applied the density-independent model (Eq. 2) to a variety of species, including six bird populations and grizzly bears in Yellowstone Park; extinction times for the latter species were also computed under the bounded model (Eq. 3) (Foley 1994). Cisneros-Mata et al. (1997) created an age-structured Leslie matrix model of *Totoaba macdonaldi*, a long-lived sciaenid fish in the Gulf of California; environmental stochasticity was input either to one of four stages (prerecruits, juveniles, preadults, adults) or to all stages simultaneously with varying degrees of correlation. The probability distributions of extinction time obtained from analytical methods were generally consistent with those obtained from Monte Carlo simulations, with the exception of variations in recruitment; this was attributed to the diffusion approximation being unable to replicate large, random increases in abundance. Application of several models to a specific data set may yield new insights. For example, Middleton and Nisbet (1997) applied three models to an unusually detailed data set for acorn woodpeckers in New Mexico and found that adult survival, which at first appeared density-dependent, actually reflects density-dependent rates of immigration from other subpopulations; this conclusion could not be drawn from simpler model formulations.

Simulation Models

Notwithstanding the elegance of the analytical theory, simulation modeling has emerged as the dominant approach in applied PVA modeling. This trend reflects the extraordinary flexibility inherent in this approach and may be influenced by the "dauntingly technical" nature of the analytical theory (Caswell 1989). Application of analytical results to salmon is complicated by their unique life history, as most of the analytical results assume iteroparity and it is unclear how they translate to the indeterminate semelparous life history of many salmon populations (Botsford and Brittnacher 1997). Many generic simulation programs, such as SIMPOP (Lacy et al. 1989) and its successor VORTEX (Lacy 1993), ALEX (Possingham and Davies 1995), and RAMAS (Ferson 1990) have been developed and applied to a wide range of organisms (see references in Thompson [1991], Lacy [1993], and Lindenmeyer and Possingham [1995]). Such programs often include complexities such as habitat structure and metapopulation movement and may require estimates of numerous parameters. In many cases, the unique life history of salmon as well as the lack of data hinders the application of generic models, and several models specifically tailored to salmon have been formulated recently. In this section, I review five of these models and attempt to illustrate key features that mark recent progress (Table 2).

Example 1: Snake River Spring-Run Chinook Salmon (Emlen 1995)

The primary data used in this analysis were time series of chinook salmon redd counts (1957-1992) from five tributary streams of the Salmon River located within the Snake River spring- and summer-run ESU. The generation of redds by female spawners was modeled with a Ricker function (Ricker 1954), and survival from eggs to spawners was modeled with a Beverton-Holt function (Beverton and Holt 1957); a simple, density-independent measure of straying was also included. The modeled persistence of Snake River chinook salmon was strongly dependent upon density-independent factors but relatively unaffected by the density-dependent factors. Model projections based upon the estimated current level of the Ricker α parameter indicate population recovery within 100 years, although these results are perhaps unduly optimistic because of the lack of modeled genetic or demographic risk.

Example 2: Sacramento River Winter Chinook Salmon (Botsford and Brittnacher 1997)

Extinction of the Sacramento River winter chinook salmon in the near future is a certainty if the long-run rate of decline holds; a pertinent current problem is how to define delisting criteria, assuming population recovery. The primary data for this analysis were a time series of spawner abundances and assumptions regarding fecundity and proportions spawning at age. A simple Leslie matrix was revised to relate current spawners, N_t, to previous spawners:

$$N_t = p_2 r_{t-2} N_{t-2} + p_3 r_{t-3} N_{t-3} + p_4 r_{t-4} N_{t-4} \tag{5}$$

where p_i is the proportion of spawners in age-class $i = \{2,3,4\}$ and r_t is the cohort replacement rate that reflects interannual variation in mortality during the freshwater stage. The values of r_t were estimated by fixing the values of p_i and minimizing the residual errors in N. Two delisting criteria were proposed: the geometric mean growth cohort replacement rate should be ≥ 1, and the probability of extinction within 50 years should be ≤ 0.1. An estimated 13 years of data are needed for estimation of the mean cohort replacement rate when sampling and measurement error are considered, and a population size of 10,000 satisfies the extinction probability criterion. These delisting criteria consider habitat improvements indirectly via their link to the cohort replacement rate and are thus more conservative than a criterion involving population size alone.

Example 3: Stochastic Life-Cycle Model (Lee and Hyman 1992)

An alternative to statistically fitting a simple model to a time series of abundance estimates is explicitly defining the transition between key life history stages; in this sense, the stochastic life-cycle model (SLCM) shares some features with matrix population models (Cisneros-Mata et al. 1997). As in the study of Botsford and Brittnacher (1997), density dependence is incorporated at an early stage (egg-to-presmolt survival), and follows a binomial distribution in which the expected survival (based upon a user-specified density-dependent formulation) is itself a parameter with variation; the resulting beta-binomial distribution can be thought of as incorporating both environmental and demographic stochasticity. SLCM incorporates many other complexities, including separation of natural and hatchery production, a juvenile migration submodel, and submodels describing the fate of adults surviving natural mortality (i.e., harvest [ocean, in-river, or terminal], natural spawning, or hatchery returns). Clearly, this approach requires an extraordinary level of information, including knowledge of stock-recruitment relationships, fecundity, and coded-wire tag data suitable for describing the fate of returning adults; the authors provided example parameter values based upon Snake River fall chinook coded-wire tag recovery data.

Example 4: South Fork Umpqua River Chinook Salmon (Ratner et al. 1997)

The relationship between freshwater habitat and smolt productive capacity has motivated PVA models that explicitly incorporate habitat quality. For example, Ratner et al. (1997) modeled chinook salmon in the South Fork of the Umpqua River with a modified Leslie matrix which incorporates semelparity (Kaitala and Getz 1995), density-dependent changes in first-year survival, and instream mortality of returning adults prior to spawning. Data requirements for this model were similar to those of Botsford and Brittnacher (1997); they included time series of abundance, proportion spawning at age, and fecundity. Demographic stochasticity was incorporated into the spawner sex ratio, instream mortality rate, egg production, and survival of non-spawning adults. First-year survival was affected by environmental and demographic stochasticity, as well as habitat quality and population size; the latter two factors were represented in a multiplicative factor e^{-cN_t} to the first-year survival rate, where c is the density-dependent parameter from a Ricker curve fit to a time series of detrended returning spawner data and N_t is population size. Habitat degradation was interpreted as causing the exponential decline in wild spawner abundance from 1950 to 1983; in the model, it changed the equilibrium population size through changes in c. Projections of future population abundances were made under assumed constant or declining levels of habitat quality. Assuming no further declines in habitat quality, model results project population viability as at least 200 years, based upon current abundances and estimates of model parameters. However, this result may be overly optimistic because lagged effects of detrimental habitat use and the effects of hatchery fish were not modeled.

Example 5: Oregon Coastal Coho Salmon (Nickelson and Lawson 1998)

More detailed measures of habitat quality may allow modeling of individual stream reaches, as in a life-cycle model applied to the Oregon coastal coho (Nickelson and Lawson 1998). The data requirements for this habitat-based approach include knowledge of streambed morphology, its relation to potential fish density, and data on survival and fecundity rates. The capacity of individual reaches to produce smolts was estimated with the Habitat Limiting Factors Model (HLFM) (Nickelson et al. 1992). Empirical data on over-winter survival of first-year juveniles indicate a positive relation with the potential smolt density predicted by HLFM, suggesting that the over-winter survival rate is indicative of overall habitat quality. Additionally, egg-to-parr survival was observed to be strongly inversely related to relative egg density, providing an important empirical density-dependent relationship that led to resiliency in simulated populations. Simulations included density-independent straying of spawners between reaches of an individual stream and the loss of fitness due to genetic drift at low population sizes (<1000). A key model result was that the population contracted into areas of high habitat quality during periods of low marine survival and expanded during periods of high marine survival.

Leslie Matrix Model for Coho Salmon

The focus on habitat degradation of recent PVA models (Ratner et al. 1997, Nickelson and Lawson 1998) is indicative of the essential role that habitat restoration is expected to play in any recovery plan. Because the effectiveness of such restoration efforts depends upon their relation to mortality at key life history stages, it is important to understand not only the relation between habitat quality and mortality but also the population-level impacts of such mortality. The relation between habitat quality and mortality is undoubtably quite complex. For example, Holtby (1988) found that logging increases coho juvenile over-winter survival but may decrease smolt-to-adult survival by altering the timing of smolt migration. Age- or stage-based matrix models can aid in examining the population-level impacts resulting from mortality at specific life history stages.

In this section, the Leslie matrix model is used to summarize the general life history characteristics of coho salmon and implications for conservation. Although the model is simple, it formally expresses the basic life history stages of coho and provides a template which can be modified to other salmon species or more complex situations. The model is used here to illustrate general numerical values of some important life history parameters (e.g, survival, fecundity), and to note that most information of this type comes from studies beyond California (Bradford 1995).

The age-specific, deterministic Leslie model for female coho salmon is given by equation (2) with

$$\mathrm{A} = \begin{bmatrix} 0 & 0 & s_0(f/2) \\ s_1 & 0 & 0 \\ 0 & s_2(1-u) & 0 \end{bmatrix} \tag{6}$$

where N_t is the vector $(N_{1,t}, N_{2,t}, N_{3,t})$, $N_{i,t}$ is the number of female salmon at the end of their *i*th year of life in year *t*, s_i is age *i* to *i+1* survival rate from causes other than fishing, *f* is fecundity (eggs produced per spawning female), and *u* is the exploitation rate (harvested salmon divided by population size). For simplicity, a strict three-year life cycle was assumed and the exploitation rate was set to zero. Age-four spawners have not been observed in California streams (Shapovalov and Taft 1954), although Moring and Lanz (1975) found a small percentage (~3%)

of age four spawners in the Alsea Watershed, Oregon. This minor degree of age structure in returning spawners will not substantially affect the general features illustrated here, although it might have important implications for extinction risk (Botsford and Brittnacher 1997).

Reasonable values of model parameters can be inferred from previous studies of salmonid dynamics. Fecundity was assumed to be 2,500 eggs/female (Moring and Lanz 1975). Bradford (1995) found an average coho egg-fry survival (S_{ef}) of 0.198, whereas the average egg-smolt survival was 0.015, implying a fry-smolt survival (S_{fs}) of 0.0075. Because most marine mortality is expected to occur in the first few months of ocean life (Walters et al. 1978), the overall marine survival S is partitioned into two periods: survival from smoltification to the following December (S_{o1}) and survival in the final year of life (S_{o2}). Matthews and Buckley (1976) estimate $S_{o1} = 0.13$, and Ricker (1976) estimates $S_{o2} = 0.85$.

Under the parameters above, the overall ocean survival rate is estimated as $S = S_{o1} \times S_{o1} = 0.13 \times 0.85 = 0.11$, although recently estimated values for Oregon Production Index coho indicate a mean of approximately 0.05 from 1970 to 1996 (Pearcy 1997). The initial ocean survival rate S_{o1} was adjusted to 0.063 to give a cohort replacement rate (λ) of 1 (an instantaneous growth rate of $\ln(\lambda) = 0$), producing the equilibrium base case used in this illustration. Transforming the stage-specific survival rates to age-specific mortality rates is relatively straightforward, with only the fry-smolt period spanning multiple age groups (Table 3).

A logical focus of conservation efforts is attempting to increase the number of organisms with high reproductive value. Because of significant mortality within the first year of life, the reproductive value (the extent to which animals of a given age will contribute to future generations- Caswell [1989]) is low for age-one salmon. The general feature of reproductive values peaking near the age of first reproduction (Caswell 1989), which for salmon coincides with their terminal year, is observed in this example.

For a density-independent age-structured model, one might expect variation in mortality at any life stage prior to spawning to have an equivalent effect on the population growth rate. The cohort replacement rate for the model is $\lambda = (f/2)s_0 s_1 s_2(1-u)$; thus scaling any of the survival rates does indeed have equal effect on the growth rate. Because the cohort replacement rate is a function of survival in both freshwater and marine environments, this emphasizes the sometimes overlooked point that improvements in freshwater survival may be offset by declines in marine survival (where humans presumably have less control). Ideally, one would attempt to achieve freshwater habitat quality and survival rates that could withstand the decadal fluctuations in marine survival (Lawson 1993).

The discussion above considers the effect of each matrix element separately, although changes in mortality between stages are likely to be correlated. For example, freshwater growth would be expected to play a key role in early ocean survival (Matthews and Buckley 1976, Walters at al. 1978). Such improvements would be multiplicative and could lead to substantial changes in the population growth rate. For example, a 20% increase in any single survival rate among the set S_{ef}, S_{fs}, S_{o1} and S_{o2} would increase cohort replacement rate by the same proportion, whereas the same improvement in two parameters would increase the cohort replacement rate by the factor $(1.2)^2$, or 44%.

For this model to be used for meaningful risk analysis for California coho, it is necessary to evaluate how it addresses the four general risk categories proposed by Shaffer (1981). For example, the extent to which survival at specific stages is density-dependent and the nature of environmental and demographic stochasticity are all features included in previous PVA models and necessary additions to the simple template presented here. Although information regarding model structure and parameter values can be obtained from other environments and used to project model dynamics apart from site-specific empirical data, the most credible analyses will closely integrate empirical observations of the population of interest. In the next section I briefly review the current information available for California coastal coho.

State of Information for California Coho Salmon

Coho salmon are found within California from approximately Monterey Bay northward and are organized by the National Marine Fisheries Service (NMFS) into two ESUs. The central California ESU extends from Monterey Bay, California, to Punta Gorda, California, and was listed as threatened under the ESA in October 1996. The Southern Oregon/Northern California ESU extends from Punta Gorda to Cape Blanco, Oregon, and was listed as threatened under the ESA in May 1997. A status review by Brown et al. (1994) illustrates the lack of information on California streams and includes educated guesses of population size that helped guide the listing decisions. Because escapement estimates are unavailable for coho spawning in natural areas (PFMC 1994), Brown et al. (1994) developed their "20-fish rule": If a stream which historically contained coho lacked recent data, it was assumed to have 20 spawners; if a stream did have recent estimates of run size, it was assumed to have the maximum of 20 spawners or the measured run size. Although these estimates are crude, they are consistent with other estimates (Weitkamp et al. 1995).

The low abundance of coho salmon motivated new data collection beginning in the early 1990s, and most ongoing field programs do not extend before this period. However, the work in California has generally focused upon index-reach sampling of juveniles rather than monitoring spawning escapement or outmigrating smolts, so the basic information that reveals density dependence in egg-to-smolt survival is not obtained. Further, the focus on summer juvenile sampling is inconsistent with the conventional measure of adult escapement used in ESA assessments, and little is known regarding the relationship between abundances at these two life stages. Finally, there is a lack of comprehensive sampling for coastal salmonids and a lack of coordination between existing sampling programs. In short, it is clear that the empirical information necessary to expand the simple model above is not currently available for California coho populations. Further details on the state of information on California coho can be found in Prager et al. (1999).

Future Directions

The paucity of information on California coho poses considerable challenges for making intelligent assessments of the risk of extinction. A simple comparison of the data requirements of currently used salmonid PVA models (Table 2) with the data available for California coho (Brown et al. 1994) reveals that the necessary requirement for application of even the simplest population models, a current time series of abundance estimates, is generally not met; thus managers must make decisions under substantial uncertainty. Although California coho are perhaps an extreme case, the problem of conserving stocks under uncertainty is hardly unique (Allendorf et al. 1997) and will require innovative techniques. Further compounding the situation is the recognition that salmonid PVA work will need to extend beyond simple models and include relevant biological details such as habitat quality and metapopulation dynamics. In this section, I briefly outline some current trends in PVA analyses that can aid model development in data-poor situations.

More Formal Risk Assessment

Risk assessment can be viewed as evaluating the chance of some adverse result's occurrence and ideally should be accomplished with some formal procedure. As previously mentioned in the context of defining population structure, statistical power analysis may be used to assess the risk of falsely failing to reject the null hypothesis (Dizon et al. 1995, Taylor et al. 1996) and should play a greater role in future hypothesis testing. Beyond power analysis, Bayesian analysis provides a fundamentally different approach to examining risk. The merits of frequentist vs. Bayesian statistics remain an active debate in ecology (Dennis 1996, Ellison 1996, Ludwig 1996), although a Bayesian approach does offer clear advantages in PVA work. Because risk assessment typically depends upon a frequency distribution of extinction times, it is critically important to include all factors that affect this distribution, including parameter uncertainty (Goodman, in press). A Bayesian approach provides a formal mechanism for addressing parameter uncertainty, which can have an important effect on PVA results (Taylor 1995). Finally, results from Bayesian analyses can be used directly in formal decision analyses, as is occasionally done in fisheries research (McCallister et al. 1994). Bayesian PVA methods have been applied to the spectacled eider (Taylor et al. 1996) and are the subject of a National Center for Ecological Analysis and Synthesis (NCEAS) working group on California coho.

Because Bayesian analyses merge two types of information (comparative information from other locations and site-specific information) into the analysis, they are conducive to incorporating meta-analytic studies (defined here as attempts to draw inference from a large number of analyses or data sets). When site-specific information is particularly sparse, a logical procedure is to draw inference from data on similar species in similar habitats; this will likely be necessary for California coastal salmonids. For example, the demonstration coho matrix model developed above relies upon the meta-analytical work of Bradford (1995). It is likely that risk assessments for California coastal salmonids will continue to rely upon information derived from similar populations until adequate field observations are available, and a Bayesian approach allows a formal mechanism for inclusion of this information.

Population Dynamics at Larger Spatial Scales

Coastal salmonids are unusual in that the unit of interest for conservation is generally not a species or single population, but rather an ESU that may be composed of several individual populations. Population models that consider the larger-scale ESU dynamics would be most consistent with management purposes, although the review of salmonid PVA models above reveals that most current work typically considers the dynamics of a population within a single river system. The development of metapopulation models has largely been a theoretical exercise (Hastings and Harrison 1994), and models applied to specific field observations often involve terrestrial species for which detailed data exists (Hanski 1994). For salmon, the habitat-based model of Nickelson and Lawson (1998) does consider movement of fish within a single stream. Expanding the Nickelson and Lawson model to consider the dynamics of salmon from several interrelated streams would be a worthwhile research effort.

Application of Several Modeling Approaches

While Bayesian analysis is a logical tool for addressing parameter uncertainty, uncertainty in model structure can also affect our perception of risk. For example, the authors of some of the salmon PVA models reviewed above state that their risk estimates are optimistic because genetic risks, demographic risks, or the effect of hatchery fish are not considered. Given a single data set, a prudent procedure would be to apply a series of viability analyses in which a range of assumptions regarding, for example, straying, compensation, depensation, etc., are evaluated. Approaching the problem from several vantage points will reveal the importance of various assumptions; for example, the assumptions regarding analytical approximations can be evaluated by comparing, when possible, the analytical results with those of simulation modeling (Cisneros-Mata et al. 1997). Additionally, for many salmon populations, the data necessary for detailed quantitative analyses may not exist, thus placing great emphasis on more qualitative assessments (Allendorf et al. 1997). For those systems where both quantitative and qualitative analyses are possible, a comparison between the analyses can aid interpretation of both.

Conclusions

A goal for the many stocks now listed under the ESA is to identify what conditions would improve viability to allow delisting. Recent developments in relating habitat quality to population dynamics (Nickelson and Lawson 1998) and application of analytical models (Cisneros-Mata et al. 1997) will undoubtably aid our understanding. However, the development of appropriate models for California coastal salmonids is hindered by the lack of information on basic site-specific life history parameters (as revealed in Bradford's [1995] analysis of survival rates) and abundance estimates (Brown et al. 1994). Bayesian modeling is a logical tool for addressing uncertainty, but innovative modeling techniques cannot be expected to take the place of empirical observation; unfortunately, the information available for many stocks will allow only qualitative analyses based upon "expert judgments" (Allendorf et al. 1997). A useful intermediate-term goal is to develop more detailed information on life history characteristics, which may differ considerably depending on a population's location relative to the species range (Gaston 1990, Sandercock 1991, Bradford et al. 1997). A useful long-term goal is to develop suitable time series of population abundance indices, a necessary requirement for application of most population models. For the California coho, the call by Brown et al. (1994) for an effective monitoring program is thus more pertinent now than ever before, and until such a program exists the management of endangered and threatened California coastal salmonids will be hindered by a fundamental lack of knowledge regarding abundance and population dynamics.

Acknowledgments

I thank Michael Prager, Steve Lindley, Michael Mohr, and Gareth Penn for comments on earlier drafts of this manuscript. This work was supported by the National Marine Fisheries Service, NOAA, through the Office of Protected Resources and the Southwest Fisheries Science Center.

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Table 1. Pacific salmon and anadromous trout listed under the U.S. Endangered Species Act.

Species–Area	Status	Listing Date
Coho Salmon		
Central California ESU	Threatened	October 1996
Southern Oregon/ Northern California ESU	Threatened	May 1997
Chinook Salmon		
Sacramento River Winter Run	Endangered	January 1994*
Snake River Spring/ Summer Run	Threatened	April 1992
Snake River Fall Run	Threatened	April 1992
Chum Salmon		
Hood Canal Summer Run	Threatened	March 1998
Columbia River ESU	Threatened	March 1998
Sockeye Salmon		
Snake River ESU	Endangered	November 1991
Steelhead		
Southern California ESU	Endangered	August 1997
South-Central California Coastal ESU	Threatened	August 1997
Central California Coastal ESU	Threatened	August 1997
Upper Coulmbia River ESU	Endangered	August 1997
Snake River Basin ESU	Threatened	August 1997
Lower Columbia River ESU	Threatened	August 1997
Central Valley (CA) ESU	Threatened	August 1997
Sea-run Cuttrout Trout		
Umpqua River ESU	Endangered	August, 1997

* Originally listed as threatened in November 1990

Table 2. Summary of five recent population viability models applied to Pacific salmon.

Study	Population(s) modeled	Model features	Principal data used	Modeled variation
Emlen (1995)	Snake River chinook salmon	Density dependence Age structure Sex structure	Time series of redd counts from five index streams	Environmental, demographic
Botsford and Brittnacher (1997)	Sacramento River winter chinook	Density independent Leslie model. Delisting criteria that incorporate sampling variation are developed.	Time series of spawner abundance; proportion spawning at age; fecundity	Environmental
Lee and Hyman (1992)	Representative fall chinook	Density dependent "life-cycle" model.	Fecundity; egg-smolt survival; hatchery-natural fish interactions; age-specific exploitation rates	Environmental, demographic
Ratner et al. (1997)	Umpqua River spring chinook	Leslie matrix, density-dependent first-year survival	Time series of spawner abundance; proportion spawning at age; fecundity	Environmental, demographic
Nickelson and Lawson (1998)	Oregon coastal coho salmon	Density-dependent "life-cycle" model.	Habitat data, capacity of various habitat types to support coho; egg-parr and parr-smolt survival, and their relation to habitat quality and relative coho density, respectively	Environmental, demographic, genetic

Table 3. Estimates of coho salmon survival rates found in previous studies and the derivation of age-structured rates used in the Leslie matrix model. Note that S_{o1} was adjusted to 0.063 to produce an equilibrium model with $\lambda = 1$.

Stage	Approximate Duration (months)	Survival	Reference
Egg-fry	4	$S_{ef} = 0.198$	Bradford (1995)
Fry-smolt	12	$S_{fs} = 0.075$	Bradford (1995)
Ocean (phase 1)	8	$S_{o1} = 0.13$	Mathews and Buckley (1976)
Ocean (phase 2)	12	$S_{o2} = 0.85$	Ricker (1976)

Derivation of age-structured survival rates used in the Leslie model:

$S_0 = S_{ef} * S_{fs}^{\ 8/12} = 0.198 * 0.075^{\ 8/12} = 0.035$

$S_1 = S_{fs}^{\ 4/12} * S_{o1} = (0.0149^{\ 4/12}) * 0.063 = 0.027$

$S_2 = S_{o2} = 0.85$

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