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The behavior of endangered populations in a randomly fluctuating environment.

By

TIM LEE

B.S. (University of California San Diego) 1992

DISSERTATION

Submitted in partial satisfaction of the requirements for the degree of

DOCTOR OF PHILOSOPHY
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in the

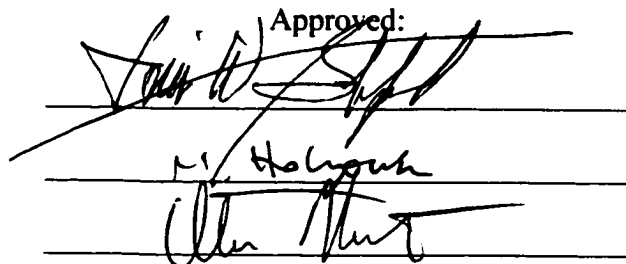
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Beauty and Truth, tho' never found, are worthy to be sought.

-Robert William Buchanan

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Abstract

Frequently wildlife managers must decide how to allocate limited resources amongst a plurality of threatened salmon stocks. In the absence of adequate abundance data, knowledge of stocks life histories might be used to rank risk of extinction thereby allowing more efficient allocation of resources. In Chapter one I assess how differences in life histories contribute to relative risk of extinction using Pacific salmon as an example. Using simulations of coho and chinook salmon, I find increased spawning at multiple ages causes the fate of each cohort to be linked to the success of other cohorts. This novel effect I refer to as cohort coupling.

Since many assume that density dependence is a stabilizing force, Chapter two examines this assumption in terms of extinction risk for coho salmon. Here again I find that life history plays a role in determining risk, along with environmental variation and quasi-extinction threshold. Key also is how density dependence is introduced into the model. I find the widely held view that density dependence is stabilizing is of limited value since density dependence can either increase or decrease probability of extinction.

Chapter three explores the use of a diffusion approximation as a tool for understanding population dynamics of Pacific salmon. Diffusion approximations have a long history in ecology as models of population genetics and population growth. Modeling salmon using a diffusion approximation requires special consideration because salmon are both

semelparous and anadromous. Diffusion estimates of probability of extinction are accurate only for a limited range of life histories.

Since salmon exhibit environmentally influenced variability in spawning age, Chapter four explores the effect variability in spawning age has on probability of extinction. I find that when variability is confined to fraction spawning at a single age, the probability of extinction is proportional to the integrated elasticity of λ for realized fecundity at that age. Additionally simulations indicated that variability in fraction spawning is most important when it affects the dominant age class of a cohort.

Introduction

Exploitation of Pacific salmon in the western United States predates the earliest recorded explorations of the region (Ambrose 1997, Yoshiyama et al. 2000). Originally the salmon runs were so abundant that they were considered inexhaustible. However anthropogenic alteration of breeding habitat (Andrew and Green 1960) combined with a regime shift in the western Pacific (Pearcy 1997) has brought many Pacific salmon stocks to the verge of extinction.

The objectives of this dissertation were to (1) explore the behavior of threatened salmon populations in randomly fluctuating environments and (2) determine how intrinsic and extrinsic factors affected a population's ability to persist over a fixed time frame.

Salmon are unusual in that they are both semelparous and anadromous. Anadromy puts salmon in competition with people for fresh water. This competition makes managing salmon a delicate balancing act weighing the needs of salmon against the needs of an ever-expanding human population. Fisheries managers are particularly interested in issues affecting coho and chinook salmon due to intense competition for freshwater in California. These two species are among the most common salmon species in the California Current.

Female California coho salmon are typically obligate semelparous at age three years, while chinook females are indeterminate semelparous (Groot and Margolis 1991). Chapter one examines how these different types of

semelparity will affect probability of extinction. Using simulations, I determine the conditions under which each breeding structure is more likely to persist.

Chapter two examines the influence of density dependence on probability of extinction. I was interested in testing the widely held belief that density dependence lowered probability of extinction (Ginzburg et al. 1990, Cisneros-Mata et al. 1997, Vucetich et al. 1997, McCallum et al. 2000). I started with a linear simulation model and added density dependence in several fashions that emulate anthropogenic degradation of the environment, i.e. construction of dams, water quality degradation, or loss of spawning habitat.

Chapter three explores several analytical approaches to project population behavior. I projected the growth of the mean and variance of population size using an approach developed by Tuljapurkar (1982, 1989, 1990). Additionally I solved a first crossing problem (Lande and Orzack 1988) to generate projections of probability of extinction.

Chapter four examines the relationship between how a population internalizes environmental variability and probability of extinction. Salmon exhibit environmentally influenced variation in age of maturity (Helle 1979). This variation in age of maturity has the dual effect of influencing both realized survival and realized fecundity. This dual effect leads to a unique influence on population dynamics and ultimately probability of extinction.

Pacific salmon abundance has recently declined precipitously in many western rivers (Nehlsen et al. 1991, Williams et al. 1992, (BRT) 1997, Johnson 1997, Stouder et al. 1997, Myers 1998, Weitkamp et al. 2000). On a number of rivers salmonids are in danger of extinction (Allendorf et al. 1997). Perhaps a better understanding of these low abundance populations will enable better management of these stocks.

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Running Head: Influence of life history on extinction probability.

Chapter 1: The influence of life history characteristics on extinction probability in Pacific salmonids.

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Abstract

A number of Pacific salmon stocks with varying life histories are endangered. Here we assess how differences in life histories contribute to relative risk of extinction in Pacific salmon, using coho (*Oncorhynchus kisutch*) and chinook salmon (*O. tshawytscha*) as examples. Since management is most interested in populations in which there is substantial doubt as to their viability, we focus on populations at low abundance that are neither growing nor declining rapidly. The characteristic of semelparity leads to a novel form of a Leslie matrix, and anadromy leads to an unusual path to population extinction. We found that for obligate semelparous species, the later the age of maturity, the lower the probability of extinction over a fixed time period. This is explained by a shift in time scale of population growth, and an increase in the number of cohorts. For indeterminate semelparous populations in low variability environments, as the distribution of age of maturity becomes broader, the probability of extinction first increases then declines, contrary to previous results. This unexpected result is a consequence of two counter balancing effects. Increased spawning at multiple ages causes the probability of the first reproductive failure to decrease. However the conditional probability of extinction following a single reproductive failure increases dramatically with increased spawning at multiple ages causing all cohorts to go extinct nearly simultaneously when the age structure moves away from obligate semelparity. This novel effect we refer to as cohort coupling. It is the dominant effect at low environmental variability, near the range of observed variability. In real populations cohort coupling would

prevent indeterminate semelparous stocks from having a single lineage missing because as soon as there is a single spawning failure, the entire population would be likely to go extinct. One would expect to see missing lineages only in obligate semelparous species, a phenomenon that is seen in the endangered California stocks of obligate semelparous coho salmon but not in indeterminate semelparous chinook salmon. These results provide managers with baseline indicators of the relative risk of extinction of salmon stocks with differing age structures.

Introduction

Pacific salmonids are an important part of the economic, social, and environmental heritage of western North America. Yet their recent decline in abundance on a number of rivers has put many stocks in danger of extinction. Nehlsen et al (1991), in their review of 214 Pacific salmon stocks, identified 54 not at risk of extinction, but still of special concern, 58 at moderate risk of extinction, and 101 at high risk of extinction. Eighteen of these high risk stocks may already be extinct (Nehlsen et al. 1991). Although the causes of these declines are many, the most significant threats come from the destruction of spawning habitat, alteration of flow regimes in spawning rivers, unfavorable ocean conditions, overfishing, and the influence of hatcheries (Nehlsen et al. 1991, Moyle 1994). Recent declines have been exacerbated by changes in survival in the ocean environment (Pearcy 1997).

Two characteristics of salmon life history are unusual: semelparous reproduction, and an anadromous life cycle. Some stocks are “obligate

semelparous” (Begon et al. 1990), meaning that all females breed at the same age. This is the case for coho salmon in California, where all females breed at 3 years of age. In chinook salmon, individuals in a single population breed at a variety of ages, which is termed “indeterminate semelparous” (Groot and Margolis 1991). In general, female chinook salmon mature between the ages of 3 and 7 years. For female chinook salmon, the standard deviation in the age of maturity ranges from 0.206 to 0.698 years (Groot and Margolis 1991). Male salmon show a much higher variance in the mean age of maturity than females. In Washington, Oregon, and California, variation in both the modal age of reproduction and the distribution around that mode indicate a gradient with later reproduction to the north in Chinook populations (Fig. 1). The life history patterns we use in this paper are appropriate for coho and chinook salmon, the species most common in the California current.

Assessing the relative threat to different stocks is a difficult question but part of the answer lies in differences to be expected due to disparities in life history. A key question for the management of threatened or endangered Pacific salmon is, what are the effects of different age structures on probability of extinction? When planning strategies for recovery, it is useful for managers to know whether some stocks are inherently more prone to extinction by virtue of their spawning age structure. Recent papers have illustrated that accurately determining a population’s probability of extinction is nearly impossible (Ludwig 1996, 1999). An alternative approach is to determine what factors may make one population more vulnerable to

extinction than any other under a given set of conditions, this is the approach we take here.

Because salmon are anadromous, the path to extinction must be defined differently. Our definition is based on the number spawning each year rather than total population abundance for two reasons: (1) Pacific salmon are more vulnerable during the freshwater spawning phase due to increased exposure to anthropogenic effects that decrease survival and (2) density dependent effects take place in freshwater. Some of the latter are associated with breeding, e.g. an Allee effect (Allee 1931) due to the inability of females to find mates at low densities (Lande 1987). Other Allee effects in the freshwater phase include depensatory predation (Neave 1953, Hunter 1959). In years with abundant juveniles the large juvenile populations swamp predators, while at low juvenile densities predators consume a much larger fraction of the juveniles. These Allee effects imply that the appropriate depensatory mechanisms consider numbers in the spawning phase, where only part of the total population is present at one time. Therefore, we modeled extinction as quasi-extinction on the spawning grounds (Ginzburg et al. 1982). Quasi-extinction is one way of allowing for uncertainty in population behavior at low abundances. Our model differed from standard quasi-extinction approaches in that only part of the population, i.e. the spawning run, was considered. In all simulations the quasi-extinction level was set at 100 spawners, the level for which Myers et al. (1995) found convincing evidence for depensation in Pacific salmon. Therefore, in the model, when the

spawning stock reached the quasi-extinction level, there was a reproductive failure for the spawning run and no eggs were produced. The population was considered extinct when there were no individuals remaining in any age class.

Other investigators have broached the issue of dependence of salmon extinction probability on their age structure but there has been no comprehensive analysis. Botsford and Brittnacher (1998) used a linear stochastic model that incorporated quasi-extinction of individual spawning runs. They generated simulations based on the winter run of chinook salmon on the Sacramento River and found that widening the distribution of age of maturity monotonically decreased the probability of extinction for a stock. Higgins (1999) used a stochastic model from Ratner et al. (1997) that incorporated environmental variability by varying survival at each age. He concluded that populations with mixed age cohorts had significantly lower probabilities of extinction than obligate semelparous populations.

Here we assess the dynamics of a single spawning population such as would spawn in a single tributary. We do not include effects of straying and metapopulation dynamics. Since managers are most interested in populations in which there is substantial doubt as to their viability, we focus on populations of low abundance that are not in rapid decline. Populations with a very negative growth rate are clearly going extinct and require no detailed examination.

Simulation model

To model a semelparous population we must account for three key aspects of the stocks life history: survival, fecundity, and the fraction of the stock that spawns at each age. In a standard Leslie matrix a population would be modeled as:

$$\begin{bmatrix} b_0 & b_1 & b_2 & b_3 & b_4 & b_5 \\ p_0 & 0 & 0 & 0 & 0 & 0 \\ 0 & p_1 & 0 & 0 & 0 & 0 \\ 0 & 0 & p_2 & 0 & 0 & 0 \\ 0 & 0 & 0 & p_3 & 0 & 0 \\ 0 & 0 & 0 & 0 & p_4 & 0 \end{bmatrix},$$

where b_i is the fecundity at age i and p_i is survival from age i to $i+1$. This example is of dimension six, but the actual matrix may be of any integer dimension. A dimension of six is adequate for the vast majority of Pacific Salmon. In the case of semelparous Pacific salmon, spawning fraction links fecundity and survival. The appropriate matrix is then,

$$\begin{bmatrix} b_0 \cdot f_0 & b_1 \cdot f_1 & b_2 \cdot f_2 & b_3 \cdot f_3 & b_4 \cdot f_4 & b_5 \cdot f_5 \\ p_0 \cdot (1 - f_0) & 0 & 0 & 0 & 0 & 0 \\ 0 & p_1 \cdot (1 - f_1) & 0 & 0 & 0 & 0 \\ 0 & 0 & p_2 \cdot (1 - f_2) & 0 & 0 & 0 \\ 0 & 0 & 0 & p_3 \cdot (1 - f_3) & 0 & 0 \\ 0 & 0 & 0 & 0 & p_4 \cdot (1 - f_4) & 0 \end{bmatrix}.$$

where f_i is the fraction of females that spawn at age i . In this semelparous matrix, elements in the first row are the product of age-specific fecundity and the fraction of the cohort that breeds at that age. The subdiagonal elements are

the product of the survival at each age and the fraction that does not breed at that age. We iteratively multiplied this matrix by an age structured population vector for the duration of our 100 year simulation period. Our model accounted for females only, assuming that enough males would be present at normal population levels to fertilize eggs.

This matrix illustrates that semelparity affects population dynamics by linking reproduction and survival. Because individuals die following reproduction, survival is affected by the fraction of individuals that breed at each age. Moreover, realized fecundity is a product of age-specific fecundity and the fraction of that age group that breeds. The larger the proportion of an age group that breeds, the higher the realized fecundity at that age, and because salmon die after spawning, the lower the realized survival at that age.

For initial conditions in our simulations, all populations were set to the stable age distribution with the same number of spawners (190 per year) and the same growth rate ($\lambda=1$). In other words, the population without the influence of environmental fluctuations was neither growing nor declining. We chose this value because for stocks with λ much greater or less than 1.0 the probability of extinction is not an issue, it is either zero or one respectively. A population size of 190 spawners was chosen to produce a non-zero probability of extinction. The stable age distribution was chosen for the initial age structure in order to avoid introducing population fluctuations due to variation in initial conditions rather than environmental variability. In the simulations, therefore, fluctuations are due solely to environmental variability.

We simulated Pacific salmon population dynamics in the absence of density dependence. Linear models are applicable at low population densities, which would be the case if population size were reduced by mechanisms that decreased survival, such as over-fishing or mortality due to dams. The linear model is not applicable in the case where population declines are caused by habitat loss because such populations could still be at high densities (Botsford and Brittnacher 1998).

Environmental variability (Athreya and Karlin 1971, May 1973, Keiding 1975, Roughgarden 1975) was assumed to occur in the early ocean phase, where the greatest variation in survival is presumed to occur (Pearcy 1992, 1997). During the simulations all elements of the semelparous matrix were fixed except for first year survival. This was chosen randomly from a Beta distribution with a mean of p_0 in the average matrix and a range of variances. All survivals were set to 0.5 with the exception of p_0 , which was chosen so that the growth rate λ for the average matrix was unity.

To assess the effect of the age specific pattern of maturation on extinction, a variety of population maturation schedules were examined. They ranged from a population based on the California coho salmon in which females are obligate semelparous at age 3 years, to populations where the spawning stock is distributed across a number of age classes similar to California Current chinook salmon. We varied the mean age of maturity from age 3 years to age 5 years. We first assessed behavior of the obligate semelparous case, which has no variation around the mean age of maturity. We then increased the

variation in age of maturity such that the spawning stocks consisted of females of three age groups. The distributions simulated spanned the range from having 0 to 60% of the spawning stock in adjacent age classes (Table 1), i.e. standard deviations in female age of maturity ranging from 0 to 0.774. This range includes the values typically found in coho, near zero, and the values found in chinook, from 0.206 to 0.698 (Healey 1991) (Fig. 1).

Results

Obligate semelparous-effect of age of maturity on probability of extinction.

For obligate semelparous salmon populations, the simulated probability of extinction ($P[E]$) is higher with an earlier age of reproduction (Fig. 2). This can be partially understood based on the earlier results of Lewontin and Cohen (1969). A population that is obligate semelparous at age A is composed of A independent lineages. The dynamics of an obligate semelparous population are described by :

$$n_{t+A} = L_t n_t \quad (1)$$

Where L_t is the population growth rate at time t . The distribution of log of abundance of each lineage is the same as growth of a semelparous population which Lewontin and Cohen (1969) have shown previously to be Gaussian with mean ut and variance $s^2 t$, where u is the mean of the natural logarithm of L and s^2 is the variance of the log of L . Longer lived species of obligate semelparous Pacific salmon are more resilient to extinction over the same time period (Fig. 2) than shorter lived species for two reasons. The first reason

for this longevity effect is that changing the age of maturity changes the time scale of population growth. If a stock is decreasing by a fixed fraction per generation, it is going to take longer for it to reach the quasi-extinction level if the generation time is larger. Therefore we expect populations with a later age of reproduction to have a lower probability of extinction. The second factor in the longevity effect is that increasing A means there are more independent cohorts. Since

$$P[\text{Extinction}] = P[\text{cohort extinction}]^A, \quad (2)$$

increasing A necessarily decreases the probability of extinction.

Effect of semelparous, multiple spawning ages on probability of extinction.

The consequences of moving from an obligate semelparous maturity schedule to one distributed over more than one age are complex (Fig. 3). Simulations for populations with the same deterministic growth rate ($\lambda=1$) indicate that as the variation in age of maturity increases from zero (Table 1), stocks are initially more prone to extinction (Fig. 3). However, as we increase this variance further, the stocks become less prone to extinction. This is unexpected based on previous results and needs to be examined more closely. The probability of extinction for an entire stock is the product of the probability of a single spawning failure and the conditional probability of all the rest of the cohorts being lost given a single spawning failure. As the spawning stock is distributed over an increasing number of age classes, the probability of a first spawning failure decreases as expected (Fig. 4). However the conditional probability of extinction once a spawning failure has occurred

jumps immediately to a high value when spawning is distributed over more than one age class (Fig. 5). That is, for indeterminate semelparous populations, if one cohort goes extinct the entire population will almost certainly go extinct soon after. We refer to this novel effect as cohort coupling. This is the fundamental mechanism underlying the unexpected behavior of a semelparous population with variance in the mean age of reproduction. Although their cohorts may have a lower probability of crossing the quasi-extinction level, once they do the entire population goes extinct. This is not the case for the obligate semelparous populations where cohorts are independent.

Effect of deterministic growth rate on relative probability of extinction.

Thus far we have focused on populations that in the absence of environmental variability would be neither growing nor declining. The next question to address was whether a deterministic decline could cause population dynamics to shift. To address this question we examined simulated populations that were declining rapidly ($\lambda = 0.9550$) from a relatively high initial population value of 10,000 spawners (Table 2). We found that deterministic decline played no role in determining order of jeopardy (compare Figures 3 and 6). At low environmental variability obligate semelparous populations have the lowest probability of extinction whereas at high variability they have the highest (Fig. 6), the same order of jeopardy we found in the absence of a deterministic decline (Fig. 3). That is, as

environmental variability increases there is a crossover in relative probability of extinction.

To determine the source of this effect, we examined the effect of environmental variability on μ , the rate of change of mean of log spawning abundance (Fig. 7). We found that the growth rate of obligate semelparous populations was more sensitive to environmental variability than the growth rate of indeterminate semelparous populations. That is, as variability increases, age structure had a greater effect on obligate semelparous populations than it did on indeterminate semelparous populations. As a result, the obligate semelparous populations declined more rapidly than their indeterminate semelparous counterparts. This would account for obligate semelparous populations having a higher probability of extinction when variability was high. In this situation, the median obligate semelparous population was declining much more rapidly than the median indeterminate semelparous population. As such, the exact mechanics of the extinction process did not determine which populations had the greater probability of extinction. Rather it was the relative rate of decline that was overwhelmingly important.

Further examination of the relationship between μ and probability of extinction revealed that for a similar μ , the obligate semelparous population had a lower probability of extinction (Fig 8). In the case where variability is low and therefore growth rates are similar, the advantage of cohort independence becomes apparent. At low variability, the obligate semelparous

growth rate was still lower than the indeterminate semelparous growth rate, but the difference in growth rates was smaller than it was at high variability. Therefore, although the obligate semelparous cohorts were reaching the quasi-extinction level in greater numbers, the greater number of independent cohorts (three for each obligate semelparous population) more than compensated. The result was a lower probability of extinction for obligate semelparous populations when environmental variability was low, despite the relatively high probability of cohort extinction.

Effect of quasi-extinction level on relative probability of extinction.

Since we examined population dynamics under conditions where quasi-extinction level was relatively large (100 spawners), it is important to characterize the effect that the quasi-extinction level plays in determining population dynamics. We wanted to examine the sensitivity of the result to the assumption that quasi-extinction takes place at 100 spawners. To do so, we generated simulations where the quasi-extinction level was reduced by a factor of five to 20 spawners. To keep the extinction probabilities of comparable magnitude to earlier simulations, we reduced the initial population size by a factor of five as well (Fig. 9). We found that quasi-extinction level played no role in determining relative probability of extinction. The order and magnitude of probabilities of extinction were the same as they were in previous simulations with higher quasi-extinction levels and initial population sizes (Fig. 3). Cohort coupling was still an important force even at lower quasi-extinction levels because indeterminate semelparous cohorts from

different years were still dependent on members of the same recruitment event. Regardless of the magnitude of the quasi-extinction level, when a recruitment class disappeared it affected the success of future cohorts that would have included those recruits.

Effect on probability of extinction from changing both mean and variance of spawning age.

The above results indicate that (1) increasing the mean age of maturity should decrease the probability of extinction for a given population and (2) in a low variability environment increasing variation in age of maturity initially increases, then decreases the probability of extinction. Naturally we would like to know the effects of combining a later age of maturity with varying amounts of age class diversification.

The overall effect of simultaneously varying both the mean and variance of the age of spawning while holding the growth rate constant is interpretable from the effects of varying each separately (Fig. 10 vs. Fig. 3 and Fig. 2, which graph the effect of changing both mean and variance, effect of changing just mean, and effect of changing just variance, respectively). The effects combine linearly. Increasing the mean age of reproduction decreases the probability of extinction for all cases considered (Fig. 10). We would also expect that increasing age class diversification for any given mean age of reproduction would first increase then decrease the probability of extinction. This expectation is supported by the results (Fig. 10). In these examples expected order is maintained with changes in mean, and with changes in variance.

Discussion

The influence of the mean age of maturity on probability of extinction is easily explained, but the effect of variance in age of maturity is more complex. Moving from a population with no variation in female age of maturity to one in which individuals spawn at different ages can either increase or decrease probability of extinction depending on the level of environmental variability. There is a balance of the effects of cohort coupling and the effect of age structure on growth rate, μ ; at high variability the effects of age structure dominate, while at low variability the effects of cohort coupling obscure the effects age structure. Since the spawning run is no longer composed of a single year class, it will initially decline below the quasi-extinction threshold only if multiple year classes are simultaneously weak. That is, if the spawning run is now composed of 3 year classes, all 3 year classes must be weak for a population to decline below the quasi-extinction threshold. Secondly, once a single spawning run fails, the entire population is almost certain to go extinct. The spawning failure affects other cohorts by dramatically reducing the size of any future lineage which would include members of the absent year class. In obligate semelparous populations there would be no future effects on other spawning runs, in indeterminate semelparous populations there can be substantial effects. It is this coupling effect of indeterminate semelparity that is overwhelmingly important in cases where environmental variability is low and therefore growth rates are similar.

Observed levels of variability in ocean survival for Pacific coho range from a coefficient of variation of 0.41 to 0.6 (Beamish et al.2000), placing coho salmon near the range where cohort coupling would dominate population dynamics. At this relatively low level of environmental variability an obligate semelparous population may have a lower probability of extinction than a comparable indeterminate semelparous population. For Pacific coho therefore, an obligate semelparous life history may actually lower its probability of extinction.

In the real world cohort coupling would prevent indeterminate semelparous stocks from having a single lineage missing because as soon as there is a single spawning failure, the entire population would be likely to go extinct. One would expect to see missing lineages only in obligate semelparous species, a phenomenon that is seen in the endangered California stocks of coho salmon but not in chinook salmon (Smith 1998). This is especially important for managers because an obligate semelparous population with a spawning run near the quasi-extinction level may be in much better shape than a non-obligate semelparous population with the same number of annual spawners.

Natural variation in both the mean and variance in the age of maturity can be large (Fig. 1). Some populations are essentially obligate semelparous at age 3 years, others are indeterminate semelparous with a late modal age of maturity, 5 years, and a large variance around that age. These kinds of life history differences can have a dramatic affect on the probability of extinction;

in some cases the differences in probability of extinction based on life history differences alone can be as large as a factor of two (e.g. Fig. 10). An earlier mean age of reproduction increases the probability of extinction. This effect is rooted in the time scale of the problem. Simply stated, any population that is declining a fixed fraction per generation is going to decline more quickly with shorter generation times. The size of the random steps toward extinction is determined by the variance in ocean phase survival, and the number of steps is inversely proportional to the generation time. In the time frame we used, 100 years, a cohort with an average maturity of 4 years will take a random step 25 times in the simulation period. In contrast, a cohort with an average maturity of 5 years will be doing this only 20 times. Obviously the former puts itself at greater risk. In the obligate semelparous case we determined the second factor that comes into play is changing the mean age of reproduction. The earlier the age of reproduction the fewer independent cohorts there are. An obligate semelparous population that breeds at age 2 years would have 2 independent cohorts, whereas an obligate semelparous population that breeds at age 5 years would have 5 independent cohorts. For the first stock to go extinct 2 spawning failures need occur, the latter requires five, which has a much lower probability.

Previous investigations of the effects of age structure on extinction in salmon have not always obtained the same results as ours. In Higgins (1999) there is no longevity affect, that is, longer-lived populations do not have a lower probability of extinction. To understand why there is no longevity affect

in this model it is helpful to return to the random walk metaphor. Recall that each time a lineage passes through an age class with variance in survival it takes a random step. In Higgins' model every lineage takes a random step every year because there is variance in survival at each age. Changing the life expectancy does not change this. In our model a lineage takes a random step once in a lifetime, when passing through the ocean survival phase. A lineage with a 5 year life expectancy will take a random step once every 5 years. A lineage with a 10 year life expectancy will take a random step once every 10 years. By decreasing the frequency of steps we decrease the variance in population abundance.

In previous investigations (Botsford and Brittnacher 1998, Higgins 1999) results showed that in variable environments obligate semelparous populations always had a higher probability of extinction than indeterminate semelparous populations. This apparent inconsistency with our results is easily explained. In these earlier investigations, the level of environmental variability was always very high. We also found that at high variability the obligate semelparous populations had a higher probability of extinction because of the effect of age structure on the growth rate, μ .

Jonsson and Ebenman (2001) examined the effects of delaying reproduction in semelparous populations. They used a stage-structured model consisting of two stages, juveniles and adults. In the case they examined, population extinction occurred instantaneously when quasi-extinction was reached, all juveniles had the same survival probability regardless of age, and

older individuals did not have a higher probability of maturing than younger individuals. These differences make it difficult to compare their results to ours. However, in contrast to what we have found here, they found delaying reproduction in semelparous populations did not decrease probability of extinction when variability was placed in early life history survival. This is likely due to the fact that, in their model, delaying reproduction subjected individuals to longer periods in the variable juvenile stage. This added to the variability in population size and therefore slightly increased probability of extinction. This is in contrast to the case we examined, where variability is confined to first year survival. In this case, delaying reproduction does not increase the time spent in the variable stage.

Recent reviews of applied populations viability analysis (PVA; Gilpin and Soule 1986) emphasize that PVA's can be used to effectively manage a species if two criteria are met (1) data are of sufficiently high quality (2) future vital rates behave similarly to the period in which data was collected (Brook et al. 2000, Coulson et al. 2001). For many salmon stocks it will not be possible to collect data of sufficiently high quality for a PVA before making critical management decisions. Allendorf et al. (1997) examined how to prioritize Pacific salmon stocks for conservation. In their example watershed, they found that available data was of sufficient quality for PVA in three of twenty stocks. Clearly there may be a need to gauge relative extinction probability of stocks before sufficient data can be gathered for a thorough

PVA. Here we have illustrated some guidelines for doing so based on life history characteristics.

Conclusion

The results that managers should be aware of are these. First, given equal amounts of environmental variability we expect short-lived stocks will go extinct more quickly than longer-lived stocks for two reasons: they operate on a shorter time scale, and they have fewer independent cohorts. Secondly, age class diversification has two effects: it brings the probability of any single reproductive failure down, and it couples the cohorts. The effect of this cohort coupling is that reproductive failure in a single year will likely cause the extinction of the entire population. Because of the effects of age class diversification the only populations we would expect to see with a missing cohort are the obligate semelparous populations, and importantly these populations may not be at as high a risk of extinction as comparable indeterminate semelparous populations without a missing age class.

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Tables

Table 1. Semelparous population structures having $\lambda=1.0$. f is fraction spawning. p is survival. b is fecundity in yearlings/spawner. Mean age of maturity is listed at the top of each column.

	Age 3				Age 4				Age 5			
$\sigma_{maturity}$	Age	f	p	b	Age	f	p	b	Age	f	p	b
$= 0$ Spawning distribution 0.0.1	1	0	0.04	0	1	0	0.08	0	1	0	0.16	0
	2	0	0.5	0	2	0	0.5	0	2	0	0.5	0
	3	1	0	50	3	0	0.5	0	3	0	0.5	0
					4	1	0	50	4	0	0.5	0
									5	1	0	50
$= 0.45$ Spawning distribution .1..8...1	Age	f	p	b	Age	f	p	b	Age	f	p	b
	1	0	0.042	0	1	0	0.084	0	1	0	0.168	0
	2	0.0476	0.5	50	2	0	0.5	0	2	0	0.5	0
	3	0.8	0.5	50	3	0.0476	0.5	50	3	0	0.5	0
	4	1	0	50	4	0.8	0.5	50	4	0.0476	0.5	50
					5	1	0	50	5	0.8	0.5	50
									6	1	0	50
$= 0.66$ Spawning distribution .2..6..2	Age	f	p	b	Age	f	p	b	Age	f	p	b
	1	0	0.044	0	1	0	0.088	0	1	0	0.176	0
	2	0.0909	0.5	50	2	0	0.5	0	2	0	0.5	0
	3	0.6	0.5	50	3	0.0909	0.5	50	3	0	0.5	0
	4	1	0	50	4	0.6	0.5	50	4	0.0909	0.5	50
					5	1	0	50	5	0.6	0.5	50
									6	1	0	50
$= 0.77$ Spawning distribution .3..4..3	Age	f	p	b	Age	f	p	b	Age	f	p	b
	1	0	0.046	0	1	0	0.092	0	1	0	0.184	0
	2	0.1304	0.5	50	2	0	0.5	0	2	0	0.5	0
	3	0.4	0.5	50	3	0.1304	0.5	50	3	0	0.5	0
	4	1	0	50	4	0.4	0.5	50	4	0.1304	0.5	50
					5	1	0	50	5	0.4	0.5	50
									6	1	0	50

Table 2. Semelparous population structures where $\lambda=0.9550$. f is fraction spawning. p is survival. b is fecundity in yearlings/spawner. Mean age of maturity is 3 years.

	Age	f	p	b
$\sigma_{maturity} = 0$	1	0	0.03484	0
Spawning	2	0	0.5	0
distribution	3	1	0	50
0,0,1				
$\sigma_{maturity} = .45$	Age	f	p	b
Spawning	1	0	0.03658	0
distribution	2	0.0476	0.5	50
.1..8...1	3	0.8	0.5	50
	4	1	0	50
$\sigma_{maturity} = .66$	Age	f	p	b
Spawning	1	0	0.03832	0
distribution	2	0.09092	0.5	50
.2..6..2	3	0.6	0.5	50
	4	1	0	50
$\sigma_{maturity} = .77$	Age	f	p	b
Spawning	1	0	0.04003	0
distribution	2	0.13044	0.5	50
.3..4..3	3	0.4	0.5	50
	4	1	0	50

Figures

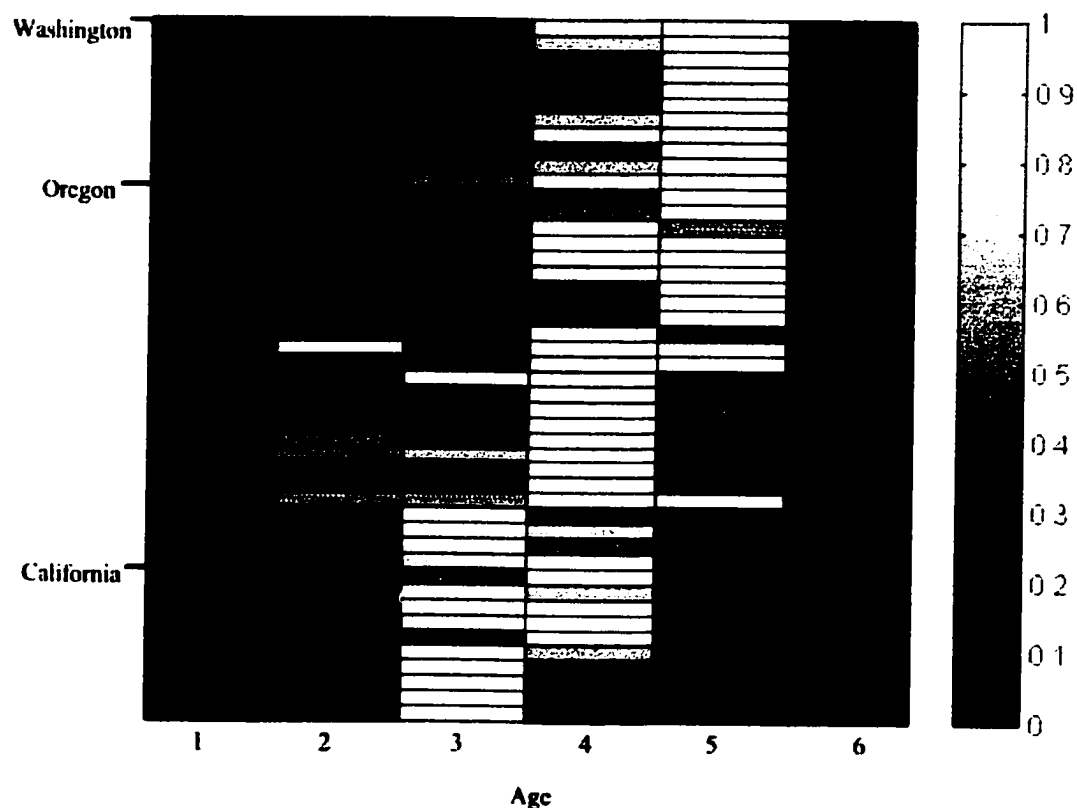


Figure 1. Age frequencies for spawning Chinook in western U.S. river systems. Values are measured as fractions of the mode for each river. From top to bottom the rivers are Hoko R. Fall, Quillayute R. Spring, Quillayute R. Summer, Quillayute R. Fall, Hoh R. Spring/Summer, Queets R. Spring/Summer, Queets R. Fall, Quinalt R. Fall, Humptulips R. Fall, Chehalis R. Fall, Wilapa Bay Fall, Nehalem R. Fall, Wilson R. Fall, Trask R. Fall, Tillamook R. Fall, Nestucca R. Fall, Nestucca R. Summer, Salmon R. Fall, Siletz R. Spring, Siletz R. Fall, Yaquina R. Fall, Alsea R. Fall, Siuslaw R. Fall, Umpqua R. Fall, Umpqua R. Spring, Coquille R. Fall, Sixes R. Fall, Elk R. Fall, Rogue R. Fall, Rogue R. Spring, Pistol R. Fall, Chetco R. Fall, Russian R. Fall, Eel R. Fall, Little R. Fall, Smith R. L. Fall, Klamath R. Fall, Salmon R. Fall, Shasta R. Fall, S. Fall. Trinity Fall, Klamath R. Spring, Trinity R. Fall, Sacramento R. Fall, American R. Fall, San Joaquin R. Fall, Merced R. Fall (Myers et al. 1998).

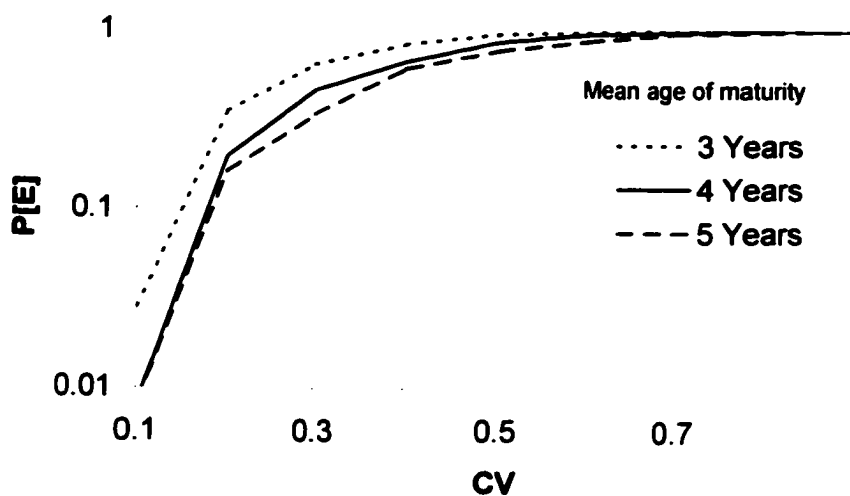


Figure 2. The modeled effect on probability of extinction of mean age of maturity. The series represent obligate semelparous stocks (Table 1). Environmental variation was placed in ocean survival. Quasi-extinction level is 100 spawners and time is 100 years. λ of the average matrix is 1.0. CV is coefficient of variation of environmental variability.

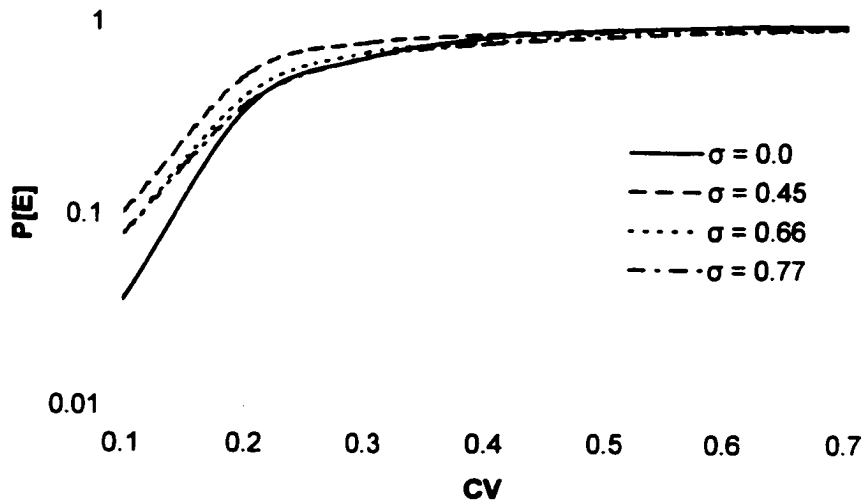


Figure 3. The modeled effect of distributing spawners across three age classes on probability of extinction. The mean age of maturity for all series is 3 years. σ is the standard deviation of age of maturity. Environmental variation was placed in ocean survival. Quasi-extinction level is 100 spawners and time is 100 years. λ of the average matrix is 1.0. CV is coefficient of variation of environmental variability.

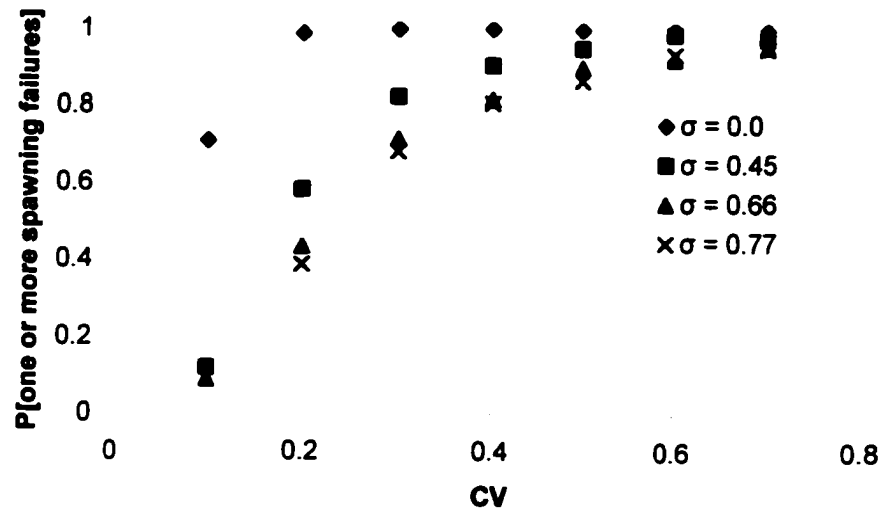


Figure 4. The modeled relationship between the age distribution of spawning stock and the probability of a spawning failure. The mean age of maturity for all series is 3 years. σ is the standard deviation of age of maturity. Environmental variation was placed in ocean survival. Quasi-extinction level is 100 spawners and time is 100 years. λ of the average matrix is 1.0. CV is coefficient of variation of environmental variability.

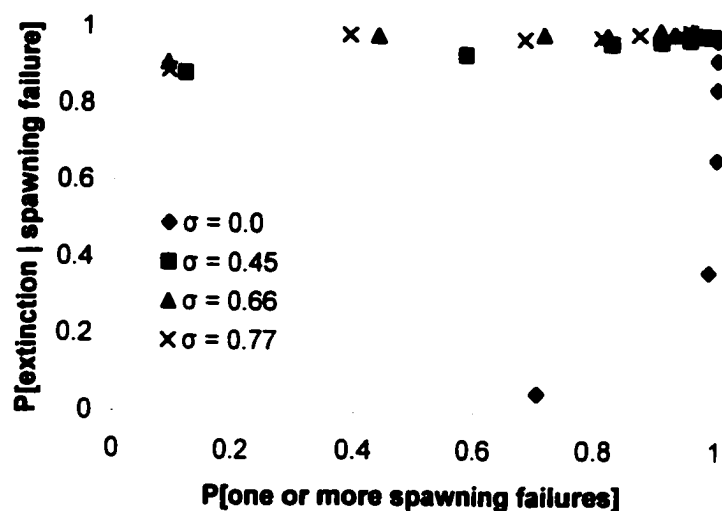


Figure 5. The modeled relationship between age structure and serial extinction events. On the x-axis is the probability of at least one spawning failure event. On the y-axis the probability of population extinction given a spawning failure event has occurred. Note that obligate semelparous population ($\sigma = 0$) has independent extinction events, whereas indeterminate semelparous populations ($\sigma > 0$) do not. Quasi-extinction level is 100 spawners and time is 100 years. λ of the average matrix is 1.0.

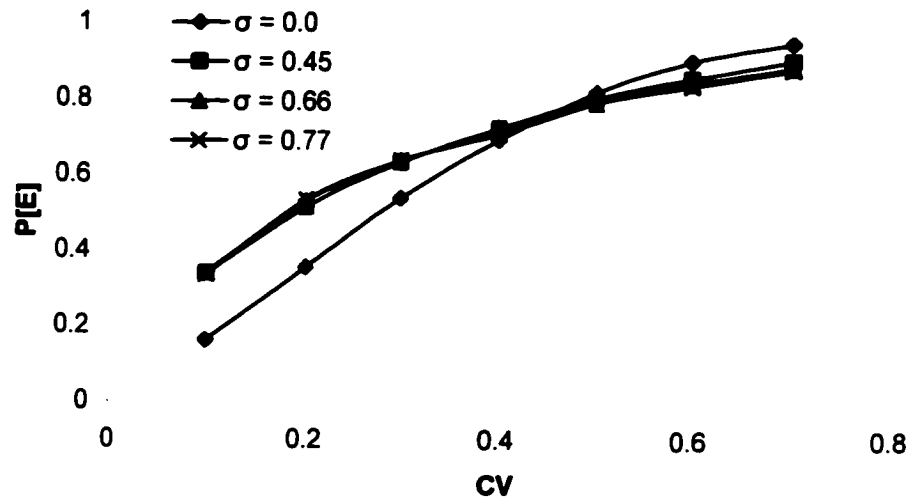


Figure 6. The modeled effect of deterministic decline on probability of extinction. Initial population size is 10,000 spawners. The mean age of maturity for all series is 3 years. σ is the standard deviation of age of maturity. Time is 100 years. λ of the average matrix is 0.9550. CV is coefficient of variation of environmental variability.

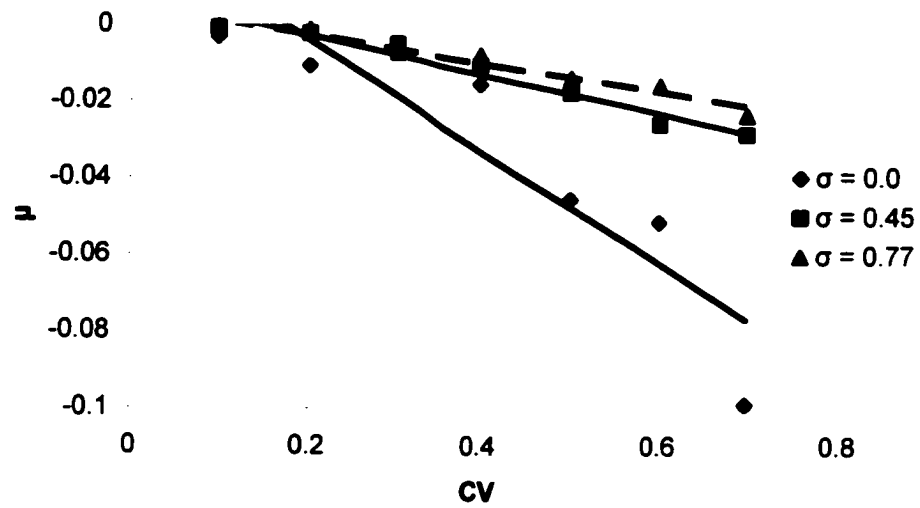


Figure 7. The modeled effect of environmental variability on growth rate, μ . σ is the standard deviation of age of maturity. Time is 100 years. λ of the average matrix is 1.0. Lines represent linear regressions for each of the series. CV is coefficient of variation of environmental variability.

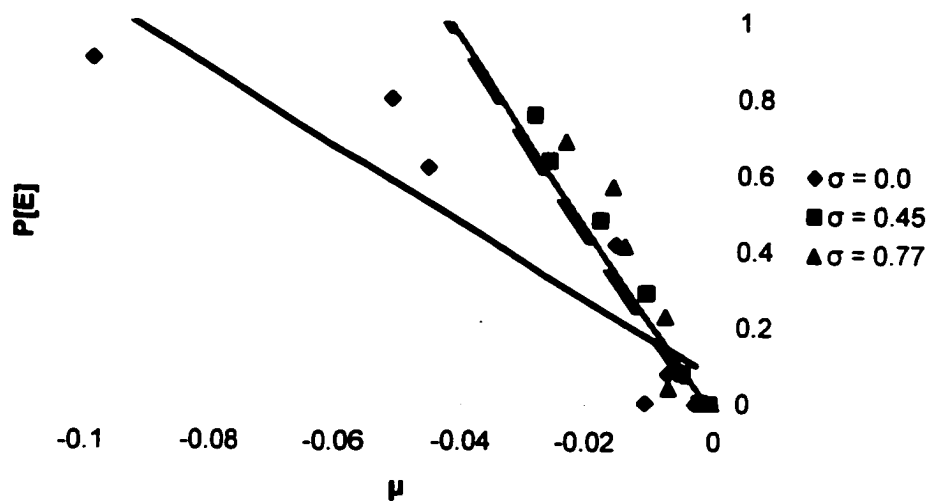


Figure 8. The modeled relationship between the growth rate μ and probability of extinction. σ is the standard deviation of age of maturity. Time is 100 years. λ of the average matrix is 1.0. Lines represent linear regressions for each of the series.

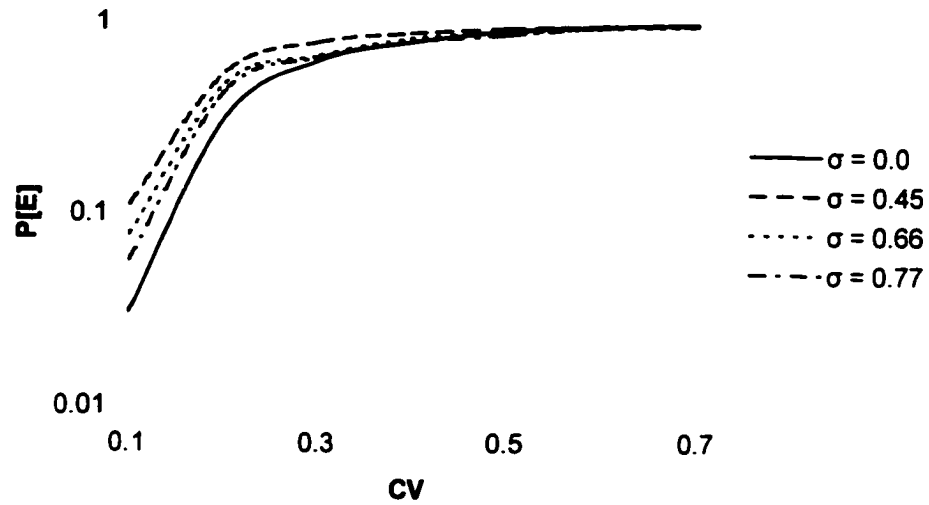


Figure 9. The modeled effect of lowering the quasi-extinction level on probability of extinction. The quasi-extinction level is 20 spawners and the initial population size is 38 spawners. The mean age of maturity for all series is 3 years. σ is the standard deviation of age of maturity. Time is 100 years. λ of the average matrix is 1.0. CV is coefficient of variation of environmental variability.

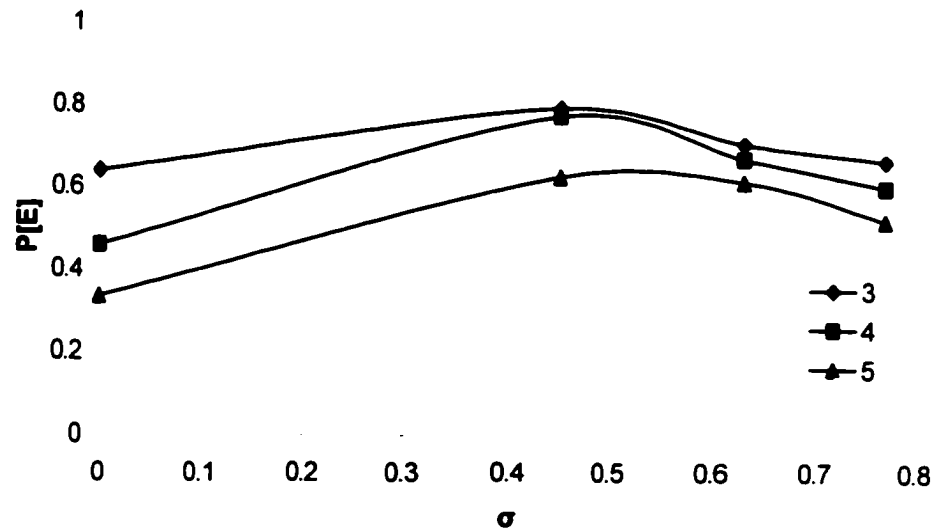


Figure 10. The modeled relationship of increasing both age class diversification and mean age of reproduction on probability of extinction. Each series has a different mean age of maturity 3, 4, or 5, years of age. σ , variability in age of maturity, is represented on the x-axis. For all series the CV of environmental variability is 0.30. Quasi-extinction level is 100 spawners and time is 100 years. λ of the average matrix is 1.0.

Chapter 2: Influence of density dependence on extinction probability: Pacific salmon as an example.

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Abstract

We examined the influence of density dependence on the probability of extinction for threatened populations using Pacific salmon as an example. We generated simulated probabilities of extinction for salmon with compensatory and over-compensatory density dependent relationships. Results showed the influence of density dependence on probability of extinction will vary depending on three factors: (1) how density dependence is introduced (2) the amount of environmental variation present and (3) the quasi-extinction threshold. Increasing compensatory density dependence while holding the equilibrium constant increased risk for a population living in a highly variable environment, while it decreased risk for the same population in a more stable environment. For environments between those two, increasing density dependence first caused an increase then a decrease in risk. Overcompensatory density dependent relationships yielded results similar to compensatory case with the exception that in the highest density dependence region complex dynamics lead to an increase in risk. Increasing density dependence by decreasing carrying capacity, increased population risk. Increasing density dependence by increasing survival at low density, decreased population risk. The widely held view that using density independent models is always conservative is of limited value since no generalizations about the effect of density dependence can be made without consideration of all the aforementioned factors.

Introduction

Density dependence is a phenomenon that is arguably important in all populations (Hanski et al. 1996, Ray and Hastings 1996, Walters and Korman 1999, McCallum et al. 2000). However its relative importance in threatened populations varies with the cause of the decline. In populations that have declined to low levels because of impacts on survival but not carrying capacity such as over-fishing, density dependence would likely not be important and could be ignored. An example is the endangered Sacramento River winter run chinook salmon for which time series of spawners indicate essentially linear behavior (Botsford and Brittnacher 1998). Alternatively, if the population decline was caused by an impact on carrying capacity such as habitat destruction, density dependence could act to keep a population at precariously low levels. In this paper we investigate the effects of density dependence on probability of extinction using Pacific salmon as an example.

Many examples of population viability analysis disregard density dependence based on Ginzburg et al's. (1990) conclusion that ignoring density dependence produces a conservative estimate of probability of extinction, i.e. that risks computed ignoring density dependence are biased high. Ginzburg et al. (1990) compared simulations of *Gadus morhua*, an iteroparous fish, using a linear stock-recruitment relationship with others using a Ricker density dependent relationship and showed that the density-independent simulations gave higher estimates of risk in all cases of practical importance. Here we

examine this issue further using compensatory and overcompensatory density dependent relationships in populations growing in random environments. We show how conclusions regarding the effects of density dependence on probability of extinction depend on the way in which density dependence is introduced into the model and the level of environmental variability. In this context, density dependence can actually increase the probability of extinction within a reasonable range of parameter values.

We formulate this result in terms of endangered Pacific salmon. Many populations of Pacific salmon have declined to historically low abundances and several are listed under the U.S. Endangered Species Act. Causes of decline include destruction of spawning habitat, alteration of flow regimes in spawning rivers, unfavorable ocean conditions, overfishing, and the influence of hatcheries (Nehlsen et al. 1991, Moyle 1994). Most Pacific Salmon consist of metapopulations with low straying rates between sub populations spawning in separate streams. Here we assess the dynamics of a single spawning population such as would spawn in a single tributary. We do not include effects of straying and metapopulation dynamics.

In reexamining Ginzburg et al's. results, we are interested in the effect that different ways of introducing density dependence into a model has on probability of extinction at various levels of environmental variation. Whether density dependence increases or decreases probability of extinction depends on which variable changes and how it changes. One way in which we introduce density dependence is by reducing the carrying capacity of a

compensatory density dependent model. This would represent the case of a salmon population whose breeding grounds had been partially destroyed. To mimic a density dependent population whose fecundity or survival was being affected by a density independent change in cohort survival, such as could be caused by the building of dams or a change in ocean survival, we reduce the model's growth rate at low densities (i.e. slope of the stock recruitment relationship at the origin). Finally we reexamine the fixed equilibrium case analyzed by Ginzburg. When attempting to reconstruct a stock recruitment relationship, there is often a large number of data points around the equilibrium but few data elsewhere. In this case, the equilibrium is established but the shape of the curve around the equilibrium is unknown. The fixed equilibrium case represents the range of models that would give approximately equal fit over a narrow range of data. We explore the relationship of probability of extinction to an increase in density dependence introduced in each of these ways. Furthermore we examine each of these at several levels of random variability, which reflects random survival due to varying ocean conditions.

Methods

Pacific salmon have a range of life history strategies. Some stocks are "obligate semelparous" (Begon et al. 1990), meaning that all females breed at the same age. This is the case for coho salmon in California, where all females breed at age three. In other species such as the chinook salmon, individuals in

a single population breed at a variety of ages, which is termed “indeterminate semelparous” (Groot and Margolis 1991). Here we examine the effects of density dependence on obligate semelparous, indeterminate semelparous, and iteroparous populations.

For the semelparous life histories that we examined (Tables 1 and 2), environmental variability was placed in the early ocean phase, survival from age one to two, where the greatest variation in survival is presumed to occur for Pacific salmon (Pearcy 1992, 1997). Reported survival data indicate that assuming a beta distribution for survival is reasonable (Fig. 1). Therefore the survivals were chosen randomly from beta distributions with a mean of age one survival in the average matrix and coefficients of variation (CV's) from 0.1 to 0.5 (Fig. 2). Marine survivals for hatchery released coho have coefficients of variation ranging from 0.41 to 0.6, corresponding to the highest values we tested (Beamish et al. 2000). The populations were initialized in a stable age distribution with 190 spawners, and simulations lasted 100 years. This initial population size was chosen to produce a non-zero probability of extinction over the simulation period. This represents populations at relatively low abundance, that do not appear to be clearly declining or increasing, a situation in which current jeopardy is an important question.

Because salmon are anadromous, the path to extinction must be defined differently. Our definition is based on the number spawning each year rather than total population abundance for two reasons: (1) Pacific salmon are more vulnerable during the freshwater spawning phase due to increased exposure to

anthropogenic effects that decrease survival and (2) density dependent effects take place in freshwater. Some of the latter are associated with breeding e.g. an Allee due to the inability of females to find mates at low densities (Lande 1987). Other Allee effects in the freshwater phase include depensatory predation (Neave 1953, Hunter 1959). In years with abundant juveniles the large juvenile populations swamp predators, while at low juvenile densities predators consume a much larger fraction of the juveniles. These Allee effects imply that the appropriate depensatory mechanisms consider numbers in the spawning phase, where only part of the total population is present at one time. Therefore, we modeled extinction as quasi-extinction on the spawning grounds (Ginzburg et al. 1982). Quasi-extinction is one way of allowing for uncertainty and Allee effects in population behavior at low abundances. Our model differed from standard quasi-extinction approaches in that each spawning run was considered separately. In all simulations the quasi-extinction level was set at 100 spawners, the level which Myers et al. (1995) found convincing evidence for depensation in Pacific salmon. As soon as the spawning stock reached the quasi-extinction level, there was a reproductive failure for the spawning run and no eggs were produced. The population was considered extinct when there were no individuals remaining in any age class.

Recruitment in salmon is a density dependent function of stock size. To model compensatory density dependence, generally a Beverton-Holt model is used (Quinn and Deriso 1999). This model has the properties of asymptotically approaching a carrying capacity at high densities and an

increase in survival at low densities (as reviewed in Barrowman and Myers 2000). To model over-compensatory density dependence the Ricker relationship is the model of choice (Quinn and Deriso 1999). This model also assumes an increase in survival at low densities but at high densities there is a more dramatic decline in recruitment than in Beverton-Holt relationships. Barrowman and Myers (2000) suggests that a “hockey stick” relationship, i.e. a linear increase in recruitment leveling off at a constant, may be more suitable for modeling the stock recruitment relationship in coho salmon because it is compensatory like the Beverton-Holt, but does not assume an increase in survival for decreasing density.

We modeled compensatory density dependence in recruitment using a Beverton-Holt function,

$$R = \frac{\alpha S}{1 + \frac{\alpha S}{K}} \quad (1).$$

where α is the slope of the stock-recruitment relationship at the origin, S is the stock abundance, K is the carrying capacity, and R is the abundance of recruits. Assuming obligate semelparity and that spawners and recruits are observed at the same age, the equilibrium stock size of a Beverton-Holt relationship is found by setting $S_e = S = R$ in (1),

$$S_e = K(1 - \frac{1}{\alpha}) \quad (2).$$

where S_e is the stock size at equilibrium. To produce a positive equilibrium all values of α tested were greater than one.

We modeled over-compensatory density dependence using a Ricker function:

$$R = aSe^{-bS} \quad (3).$$

Here R is recruitment, S is stock, a is the slope at the origin, and b reflects carrying capacity. The equilibrium stock size of a Ricker density dependence relationship is

$$S_e = \frac{\ln(a)}{b} \quad (4).$$

where S_e is stock size at equilibrium. To limit the equilibrium to positive numbers we tested only values of a greater than 1.0.

We examined the behavior of populations as density dependence was introduced by several different means. Our first model was a Beverton-Holt relationship with a fixed equilibrium but varying α and K . In this case, while the equilibrium was held constant at 163 spawners the propensity toward that equilibrium varied (Fig. 3). We chose this equilibrium level because it was in the range that produced probabilities of extinction that would be of immediate concern to managers. In Figure 3 when $\alpha=1.1$ the population is weakly attracted to the equilibrium, when $\alpha=1.5$ it is moderately attracted to the equilibrium, and when $\alpha=50$ it is strongly attracted to the equilibrium. We refer to this case as the fixed equilibrium Beverton-Holt case. In the second case examined we varied density dependence in the same way but used a Ricker relationship (Fig. 4). We refer to this case as the fixed equilibrium

Ricker case. This is the variable density dependent case used by Ginzburg et al. (1990). The third case examined was a Beverton-Holt relationship with a fixed carrying capacity, but values of α ranging from 1.01 to 1.6 (Fig. 5). We refer to this case as the variable α case. This way of varying the density dependent relationship would represent increasing propensity for growth at low densities. In salmon this propensity for growth at low densities could be altered by the construction of dams, which is believed to affect survival. The fourth case was a Beverton-Holt relationship with fixed α but values of K ranging from 100,000 to 1,200 spawners, which could represent the affects of reducing the carrying capacity of the environment. In Figure 6, $K=5000$ is analogous to a salmon population with a large amount of undisturbed spawning habitat, $K=3000$ represents some deterioration, and $K=1000$ represents a large loss of spawning habitat. We refer to this as the variable carrying capacity case.

To assess whether results for semelparous salmon would be more generally applicable we examined the behavior of an iteroparous breeding structure more reflective of a mammal (Table 3) in the same fixed equilibrium Beverton-Holt scenario that the semelparous population was subjected to. In this case, environmental variability was placed in age one survival. To facilitate meaningful comparison of probability of extinction, the mammal population structure was initialized with a population size equal to the number of spawners in the obligate semelparous population. Since cohort extinction makes little sense for a mammal, we used a more standard quasi-extinction

approach, total number of individuals dropping below the quasi-extinction threshold.

Results

Fixed equilibrium

For the fixed equilibrium Beverton-Holt case, as the shape of the density dependent relationship varied (Fig. 3), we found wide-ranging behavior contingent upon the amount of environmental variability present (Figs. 7 and 8). When environmental variation was low, the probability of extinction decreased as density dependence increased (Fig. 7, $CV=0.1$). This is in concordance with the results of Ginzburg et al. (1990) and is the generally expected behavior: density dependence is “stabilizing”. In an environment with more variability (Fig. 7, $CV=0.2$), the effects of density dependence were no longer monotonic; with increasing strength of density dependence, the probability of extinction first increased then decreased. This unusual behavior was generated from the interaction of environmental variability with the asymmetric influences that come into play as density dependence is increased. When the influence of density dependence was minimal, i.e. α near 1.0 and K nearly infinite, the distribution of population sizes was log. normal (Fig. 9 a), a well-known result for linear models (Tuljapurkar and Orzack 1980). As density dependence increased slightly, the high values of abundance were truncated sharply but the lower values were largely unaffected (Fig. 9 b). The reason for this becomes clear from examination of a similar density dependent

curve (Fig. 3, $\alpha=1.1$). Here we see that at low density the distance between the density dependent curve and the line corresponding to a linear model is minimal. However at high densities difference between the models is large, keeping the populations from becoming numerous. As more density dependence is added, differences in the high and low range are significant (Fig. 9 c), restricting population fluctuations to the area near the equilibrium, and the probability of extinction declines once again. Finally, in high variability environments where CV's for survival are above 0.3 (Figs. 7 and 8 CV=0.3 and CV=0.5) the effect of adding density dependence was to increase the probability of extinction.

It is important to understand this mechanism since Pacific coho survivals have CV's in this range (Beamish et al. 2000). When density dependence is low, the population is free to wander to high levels from which a single bad year cannot cause extinction. However as density dependence increases, the population is held tightly at the equilibrium. Here the distance between equilibrium and quasi-extinction is traversable in a single iteration. A population that is held at the equilibrium tightly will have a probability of extinction proportional to the fraction of the age one survival distribution that allows the population to move to below the quasi extinction level in a single time period. For low variability environments this fraction is zero, so the probability of extinction is zero. For high variability environments this fraction is large resulting in a high probability of extinction. A single bad year in a highly variable environment causes the cohort to go extinct.

The indeterminate semelparous population behaved in a similar fashion to the obligate semelparous population except at the extremes of density dependence. In the very low density dependent regions the indeterminate semelparous population had a higher probability of extinction than the obligate semelparous population because of the effects of cohort coupling, shown in Lee and Botsford (2001). In the very high density dependent regions the indeterminate semelparous population had a lower probability of extinction than the obligate semelparous population. Since the cohort is attracted strongly to the density dependent equilibrium, its only path to extinction is to traverse the gap between equilibrium and quasi-extinction in a single iteration. Cohorts consisting of multiple year classes have less variability in abundance than their single year class counterparts, hence are less likely to traverse that gap.

The result of the fixed equilibrium Ricker case was similar to the result of the fixed equilibrium Beverton-Holt case (Figs. 7 and 10) for values of α and a less than 3. The only difference was the behavior in the region of high density dependence. In the Ricker simulations, cyclic and other complex dynamic behavior occurred from which the populations oscillated below the quasi extinction level (Ginzburg et al. 1990) explaining the increases in the far right hand region of the graph. The Beverton-Holt relationship does not produce cycles and hence did not cause an increase in the probability of extinction in the far right hand region.

When we subjected the iteroparous mammalian life history structure to the same fixed equilibrium Beverton-Holt relationship we subjected the semelparous structures to, we obtained similar results (Fig. 11). In a low variability environment, probability of extinction decreased with increased density dependence. In a high variability environment, probability of extinction increased with increased density dependence. In a mid variability environment the affect of density dependence on probability of extinction was complex. However, there were two key differences between this case and the semelparous case. First, more environmental variability was required to obtain the same extinction pattern. For example, the pattern achieved with $CV = 0.2$ for obligate semelparous requires $CV = 0.43$ in the iteroparous scenario. The reason is that the same amount of environmental variability produces less variation in total population abundance. Since each mammal population consists of three age classes that have passed through the variable stage, population abundance is a sum of random variables, which has a lower coefficient of variation by the Central Limit Theorem. Therefore we have to increase environmental variability substantially to get a similar amount of variability in population size. Second, for a similar amount of variability in population size, the mammalian population has a higher probability of extinction. This is because in our model the mammalian population went extinct when total population abundance reached the quasi-extinction level. In contrast, obligate semelparous extinction requires three independent quasi-extinction events, one for each cohort.

Probability of extinction as carrying capacity varies

When carrying capacity was reduced to simulate the effect that destroying breeding habitat would have on the density dependent relationship, we saw a form of threshold behavior as K was reduced (Fig. 12). For each value of variability, once a critical carrying capacity was breached the probability of extinction began to rise rapidly. That threshold level is determined by a combination of the density dependent curve's slope at the origin (α) and the amount of variability in the environment. Lowering carrying capacity has the dual effect of lowering the population "ceiling", the maximum abundance a population can achieve, and bringing the equilibrium closer to the quasi-extinction level, both of these effects increase a population's probability of extinction.

Probability of extinction as α varies

When α was increased to simulate the effect of a change in survival or fecundity the result was a monotonic decrease in probability of extinction (Fig. 13). Increasing α for a fixed carrying capacity causes two mechanisms to work synergistically to reduce probability of extinction. First, the population equilibrium moves further from the quasi-extinction level (Fig. 5). Secondly the strength of the attraction to the equilibrium increases, preventing the population from "wandering" to quasi-extinction levels. Both of these indicate increasing α should decrease probability of extinction.

Effect of initial abundance on probability of extinction

Since the populations we examine here were characterized by low initial abundance (190 spawners), it is important to characterize the role initial

abundance played in determining probability of extinction. To explore the effect of initial population size on probability of extinction we generated simulations of an obligate semelparous stock (Table 1) where density dependence was held constant while the initial population size varied (Fig. 14). We did this for four Beverton-Holt density dependent relationships: $\alpha=5.0$ and $K=27,000$ yearlings, $\alpha=1.5$ and $K=27,000$ yearlings, $\alpha=1.3$ and $K=27,000$ yearlings, $\alpha=1.1$ and $K=89,826$ yearlings, representing successively weaker strength density dependent relationships. Environmental variability ($CV = 0.2$) and quasi-extinction (100 spawners) were held constant in all cases. For the first two cases, where density dependence was strong or moderate, the probability of extinction was unrelated to the initial population size (Fig. 14). The reason being that the populations were strongly attracted to the equilibrium and therefore population size quickly moved to the equilibrium value. The position of the equilibrium determined the probability of extinction across all initial population sizes. Only in the extreme case where initial population size was below the quasi-extinction level did the probability of extinction vary. Those density dependent relationships with higher equilibrium had lower probability of extinction regardless of initial population size, simply because it was more difficult to drop from a high equilibrium value to the quasi-extinction level. For the third and fourth case ($\alpha=1.3$ $K=27,000$, $\alpha=1.1$, $K=89,826$) where density dependence was weak, initial abundance did influence probability of extinction in the region where initial abundance was below the carrying capacity. Here, probability of

extinction was inversely related to initial abundance because density dependence at the low end of the Beverton-Holt relationship was extremely weak (Fig. 3 $\alpha=1.1$, $K=89,826$). Therefore populations behaved approximately as they do in the absence of density dependence. We concluded that for the bulk of the range examined in this paper, density dependence was relatively strong (Figs. 7, 8, and 11. $\alpha>1.3$); therefore initial abundance would play no role in determining probability of extinction. In the cases where density dependence was weak ($\alpha\leq 1.3$) probability of extinction could possibly be lowered to a small degree by increasing initial abundance.

In a Ricker relationship populations tend to be even more strongly attracted to their density dependent equilibrium. It is expected that the results for a Ricker density dependence relationship would also be largely unaffected by initial population size so long as we stayed out of the region of very high a , where cycles and complex dynamics take hold, or very low a where density dependence is essentially absent.

Discussion

Population viability analysis and conservation biologists in general have relied on Ginzburg et al's (1990) conclusion for their analysis of the influence of density dependence on probability of extinction.

"In general, compared to models with plausible estimates of density dependence, the density independent simulation gives conservative estimates of risk, for most low thresholds".

Ginzburg et al.'s conclusion that we could generate a conservative estimate of probability of extinction by ignoring density dependence and using linear models has been cited frequently in the literature.

"If direct density dependence actually is present, a random walk model will overestimate the risk of extinction. For this reason, some authors (e.g. Ginzburg et al. 1990) recommend that density dependence should be omitted from PVA models, unless there is clear evidence for its inclusion" (McCallum et al. 2000).

We found that this conclusion is not always justified. Ginzburg et al. (1990) based their results on a density dependent model with a fixed equilibrium where the growth rate at low densities was large compared to the random fluctuations in abundance; our results indicate that as the level of variability increases, behavior changes. We found that when environmental variability was high, density dependence can increase probability of extinction. Recall that for a Beverton-Holt stock recruitment relationship, when α is large a population is held tightly to its equilibrium; therefore its only path to extinction is to traverse the gap between equilibrium and quasi-extinction in a single iteration, the result of a particularly bad year in ocean survival. This gap can be impassable in a stable environment, yet easily traversable in a high variability environment such as that of the coho salmon.

Barrowman et al. (2001) examined stock-recruitment data from Pacific coho stocks in an effort to determine their density dependent relationship. In this investigation the equilibrium was reasonably well established but the shape of the curve around the equilibrium was unknown. Using a Beverton-

Holt density dependence relationship they found that 95% of the stocks were estimated to have α values ranging from 30 to 169. This would put the expected behavior into the region of the strongest density dependence relationships we examined. We found that when environmental variability was in the range estimated for Pacific coho ($CV > 0.41$) and density dependence in the range estimated by Barrowman et al. (2001), probability of extinction is actually significantly higher when density dependence is accounted for (Fig. 7). Using linear models in this case could significantly underestimate jeopardy.

The asymmetry of forces around the equilibrium (Fig. 3) for Beverton-Holt density dependence leads to particularly interesting behavior for populations with a fixed equilibrium in a mid variability environment (Figs. 7, 8 and 11). As the strength of density dependence increases, the high values of the population distribution are truncated more rapidly than the low values, the result being an initial increase in the probability of extinction. As density dependence is strengthened further, low values are truncated sufficiently to bring the probability of extinction back down. In this case no generalizations can be made as to whether density dependence is “stabilizing”; rather whether it is stabilizing or destabilizing depends on its strength.

While we have no comprehensive analytical approach to explain all the effects of density dependence, at the extremes of density dependent influence the problem is tractable. When density dependence is very low, below the level at which density dependence is important, a population behaves linearly

and population distributions are log. normal. Here we would expect a typical population's abundance to trend downward while exhibiting considerable variability. At the opposite extreme, where density dependence is strongest, the population is held tightly to the density dependent equilibrium. From here the path to extinction is a single particularly bad year for survival, such that the spawning population falls below the quasi-extinction level. Here a typical population would have no trend in abundance and less long-term variability in abundance.

Obligate semelparous populations tend to reflect environmental variability in abundance much more than their iteroparous or indeterminate semelparous counterparts. Both population structures have the characteristic that their vulnerable stage is composed of multiple age classes each of which is exposed to an independent variable survival condition. Since the sum of independent variables tends towards the mean, the variability in abundance is reduced. The effect on probability of extinction being that more environmental variation is required to produce a similar extinction pattern. For example, to produce an extinction pattern similar to Figure 7 $CV = 0.2$, an iteroparous population requires a much higher variability.

Of particular interest for salmon management, the fixed equilibrium cases demonstrate that adding density dependence to a model can increase probability of extinction significantly, in some cases more than 25%. Practically this means that the use of linear extinction models for particularly vulnerable species may well underestimate the actual risk. If there is a

relatively high probability of extinction without accounting for density dependence, there is likely a higher probability of extinction when it is accounted for. This result holds for both Ricker and Beverton-Holt relationships. Since a semelparous population's abundance will more closely reflect environmental variability than its iteroparous counterpart, it is more sensitive to density dependent increases in probability of extinction. Because the subject of the Ginzburg et al. (1990) model was an iteroparous population, this effect was likely not apparent.

In addition, managers are interested in the effect that degradation or destruction of spawning habitat can have on probability of extinction. It is well known that decline in quality of spawning habitat changes the density dependent relationship by reducing the carrying capacity, which increases the probability of extinction. However, one must consider the strength of the density dependent relationship and environmental variability to determine the amount of reduction in carrying capacity a population can withstand. A healthy population with a high value of α can withstand a greater decline in carrying capacity than its counterpart with a lower value. Likewise a population in a less variable environment can withstand a greater decline in carrying capacity than their counterpart in a highly variable environment. However in all cases the end result is the same, once a threshold carrying capacity is reached, the probability of extinction rises rapidly to unity. It is only the position of this threshold that is changed by the aforementioned factors.

Managers are also interested in the effects that the introduction of dams, and decline in water quality have on probability of extinction for Pacific Salmon. Both of these reduce survival to smoltification (Sandercock 1991) thereby reducing α . Our results show that a significant decline in α will increase probability of extinction regardless of the carrying capacity. For Pacific salmon this means, not surprisingly, that even if there is no damage or destruction of spawning habitat, a decline in the overall river quality can increase the probability of extinction.

A simultaneous decrease in both α and carrying capacity would likely be extremely detrimental to salmon populations. Since reducing α or carrying capacity independently will lower the equilibrium population size, a simultaneous reduction would reduce the equilibrium dramatically. Additionally the reduction in α would mean the population is less strongly attracted to its equilibrium allowing it to wander freely below the quasi extinction level from this lowered equilibrium.

Managers may wish to know whether a decrease in α or a decrease in K is causing the decline they are witnessing. There is little difference between Figures thirteen and fourteen, but we can offer some qualitative guidelines for discerning the two based on the transient response to the change. When α is decreased significantly, we expect populations to exhibit more linear behavior. That is, higher variability in abundance from year to year but a mean tendency towards decline. Effect on abundance of a decline in K should be quite different. In that case the population would drop to a lower value

within a generation's time, but variability in abundance should not increase, more likely it will decrease.

Density dependence can increase the probability of extinction under realistic circumstances. Therefore it is important to incorporate density dependence into extinction models when: (1) population decline is caused by a loss of habitat that would lower the carrying capacity precipitously, (2) there is reason to believe the density dependent equilibrium is low, but there is uncertainty as to the strength of the density dependent relationship, or the amount of environmental variability present, (3) a population's intrinsic growth has been reduced, for example through degradation of habitat quality. In these cases probability of extinction is likely to be significantly higher if one accounts for density dependence.

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Tables

Table 1. Obligate semelparous population structure used in simulations. f is fraction spawning. p is survival probability. b is fecundity measured in yearlings/spawner. Age is measured in years.

Age	f	p	b
1	0	0.04	0
2	0	0.5	50
3	1	0	50

Table 2. Indeterminate semelparous population structure used in simulations. f is fraction spawning. p is survival probability. b is fecundity measured in yearlings/spawner. Age is measured in years.

Age	f	p	b
1	0	0.042	0
2	0.0476	0.5	50
3	0.8	0.5	50
4	1	0	50

Table 3. Iteroparous population structure used in simulations. f is fraction spawning. p is survival probability. b is fecundity measured in yearlings/female. Age is measured in years.

Age	f	p	b
1	0	.585	0
2	0	.9	0
3	1	.9	1
4	1	0	1

Figures

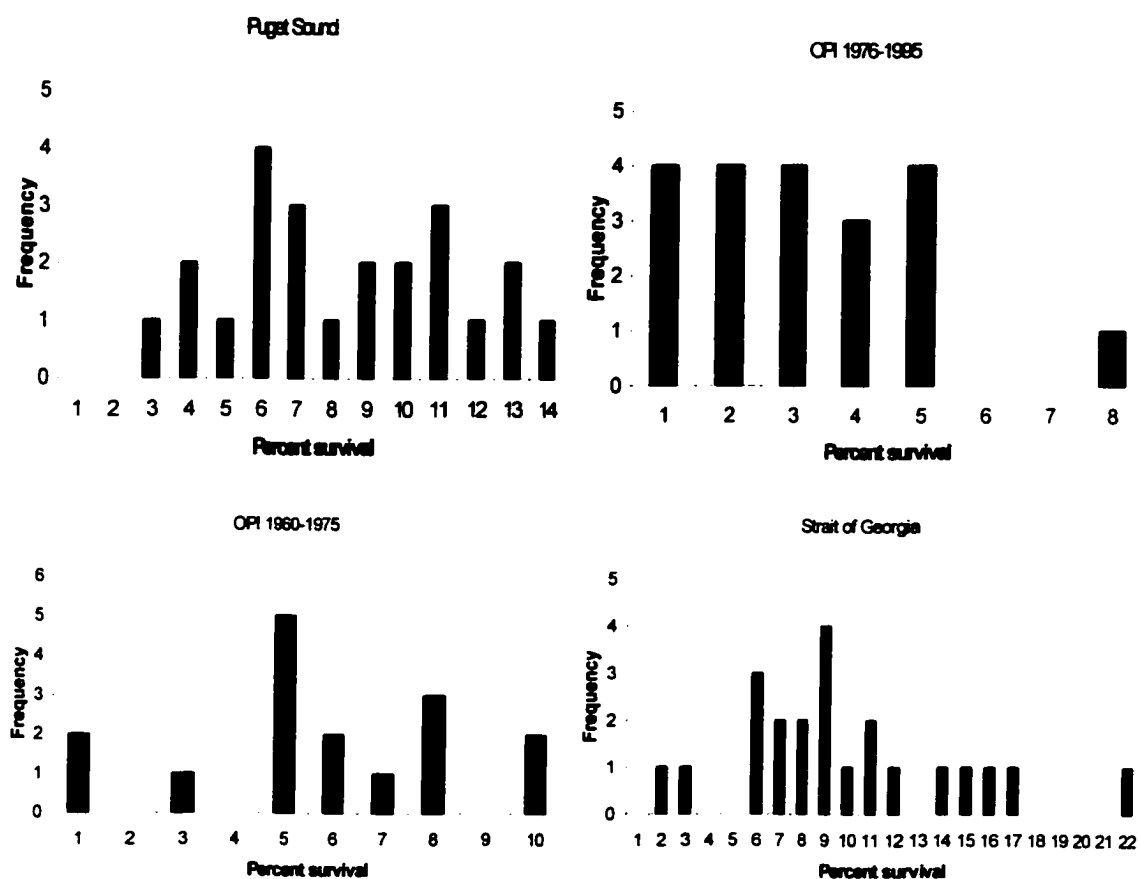


Figure 1. Survival distributions for Pacific coho released from hatcheries (Beamish et al. 2000). Puget sound data is for the years 1972-1995. Straight of Georgia data is for the years 1974-1995. Oregon production index (OPI) is grouped into two time periods (1960-1975 and 1976-1995) to account for a regime shift in ocean conditions in 1975.

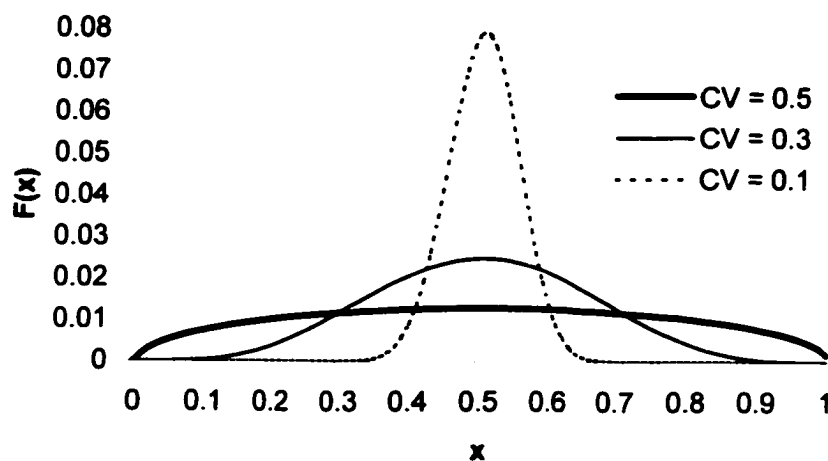


Figure 2. Beta distributions used to model ocean survival. Each distribution has the same mean (0.5) but a different coefficient of variation.

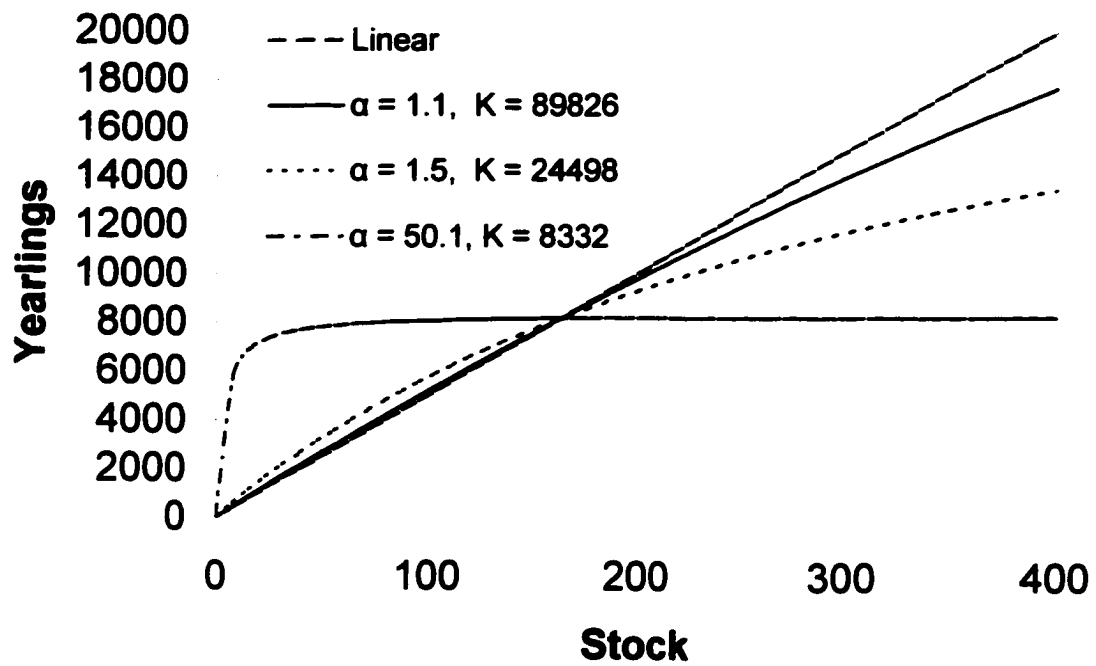


Figure 3. Beverton-Holt density dependence curves having the same equilibrium value, 163 spawners.

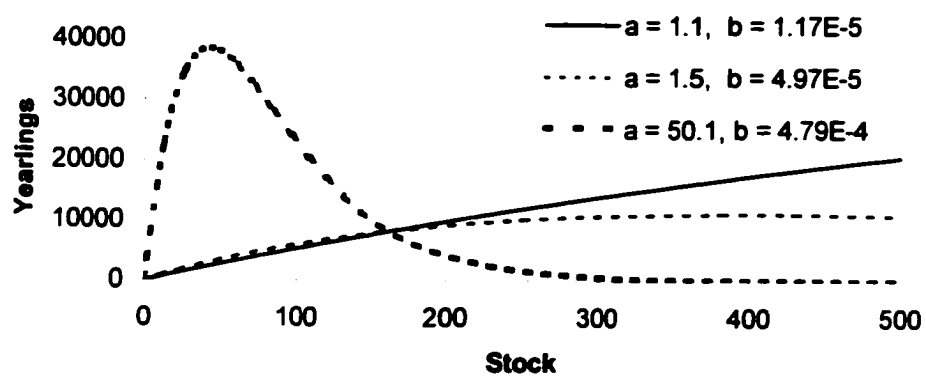


Figure 4. Three Ricker density dependence curves having the same equilibrium value, 163 spawners.

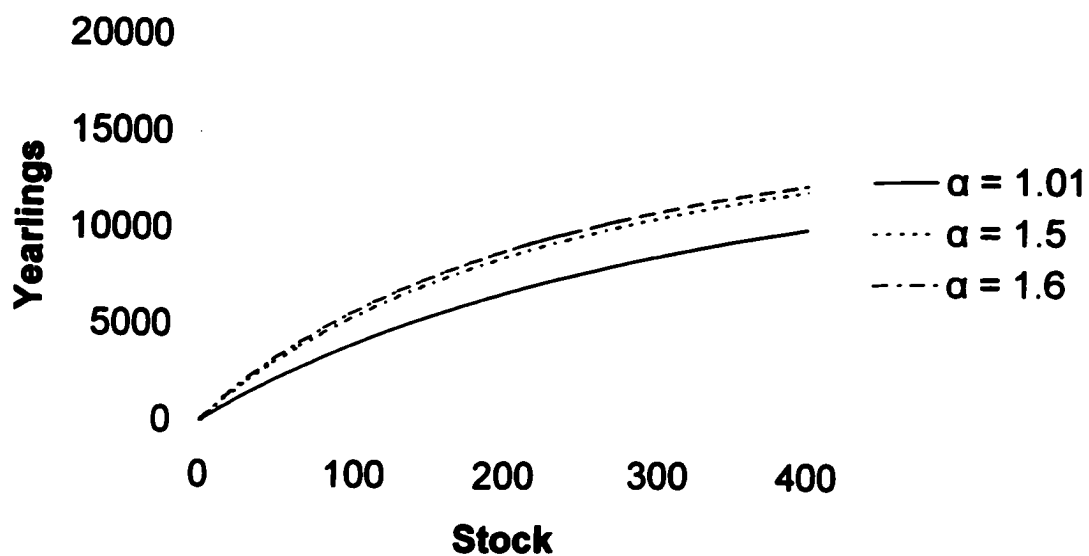


Figure 5. Three Beverton-Holt density dependence curves with the same carrying capacity, 20000 yearlings (400 spawners).

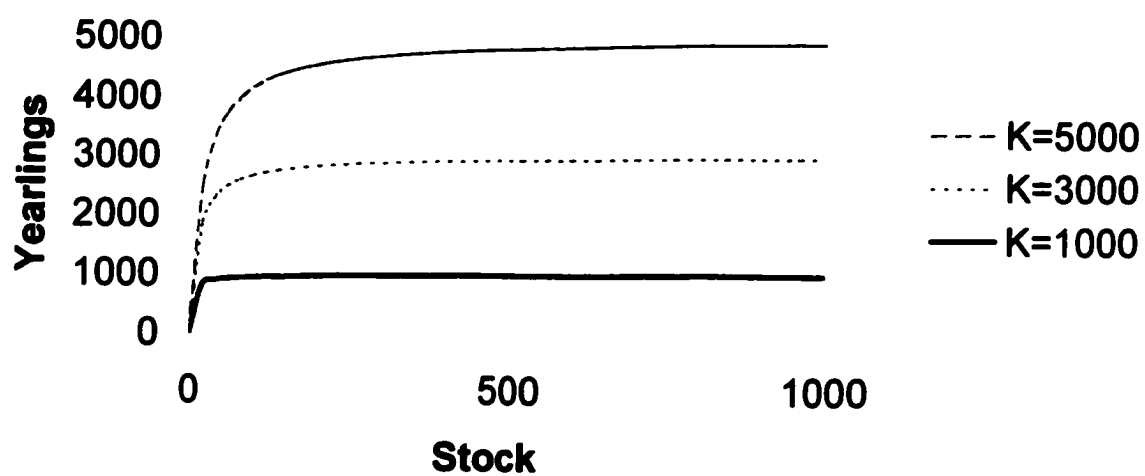


Figure 6. Three Beverton-Holt density dependence curves with the same α , 50.

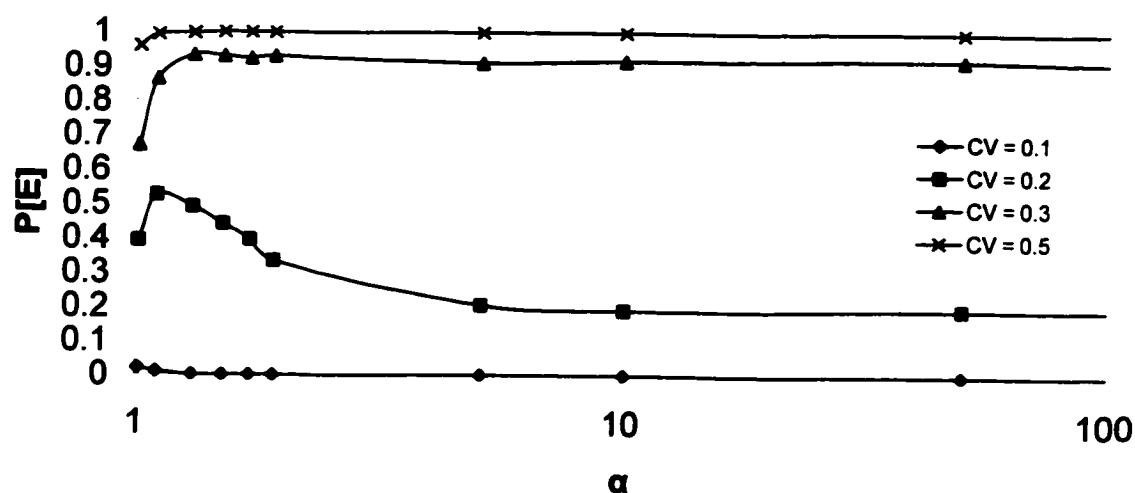


Figure 7. Simulated probability of extinction for obligate semelparous population (Table 1) being subjected to variable strength Beverton-Holt density dependent regulation. The equilibrium is fixed at 163 spawners. Environmental variation is represented by CV, the coefficient of variation of ocean survival. α from (1) is represented on the x-axis. Initial population size is 190 spawners. Quasi-extinction level is 100 spawners. Time is 100 years. λ of the mean matrix is 1.0.

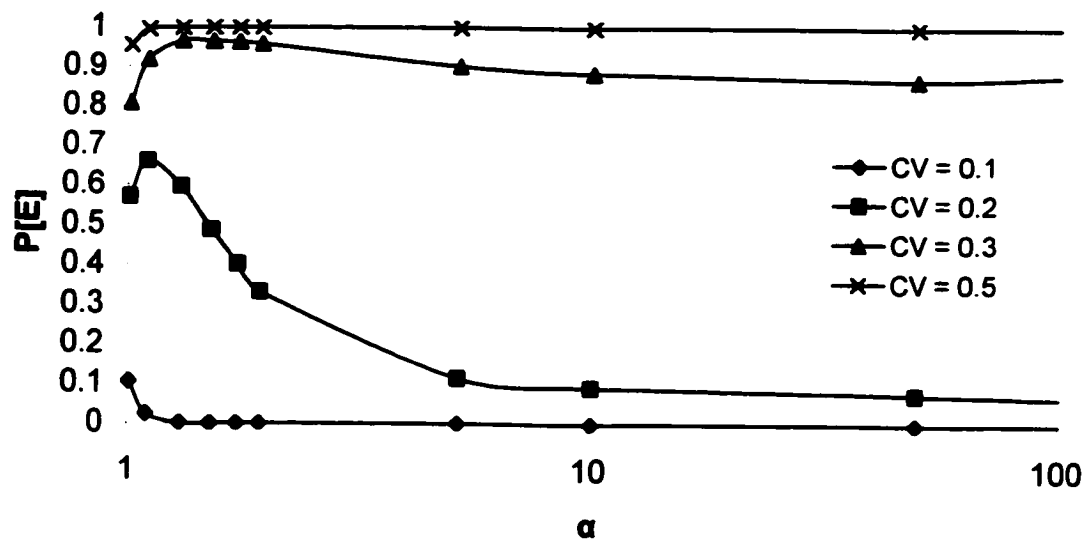
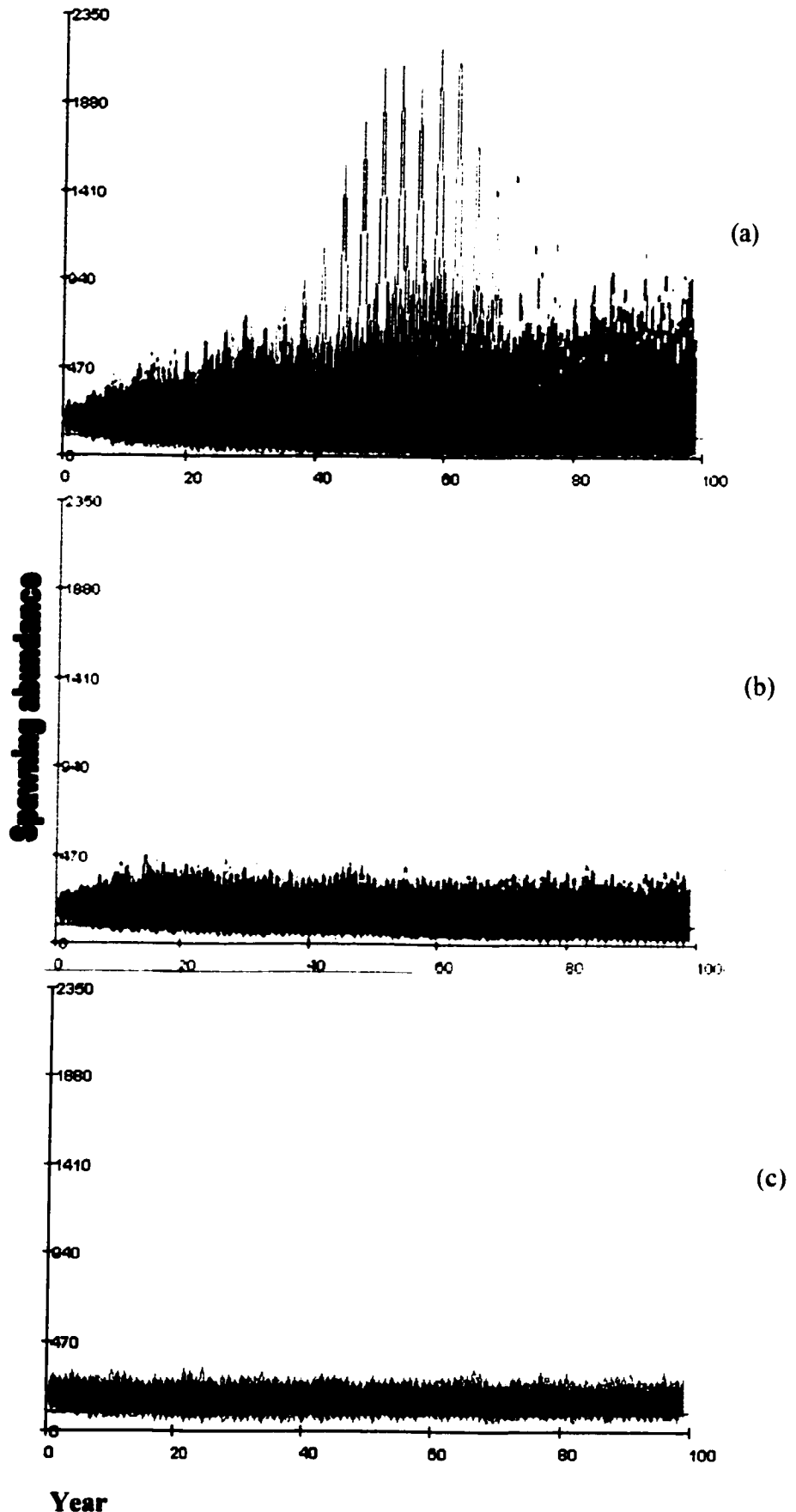


Figure 8. Simulated probability of extinction for indeterminate semelparous population (Table 2) being subjected to variable strength Beverton-Holt density dependent regulation. The equilibrium is fixed at 163 spawners. Environmental variation is represented by CV, the coefficient of variation of ocean survival. α from (1) is represented on the x-axis. Initial population size is 190 spawners. Quasi-extinction level is 100 spawners. Time is 100 years. λ of the mean matrix is 1.0.

Figure 9. Effect of increasing density dependence on distribution of simulated spawning abundance. Each gray line represents the yearly population size of a simulation. Shaded areas are population trajectories. The black line marks the quasi-extinction level in other simulations, abundance = 100 spawners. (a) density dependence is minimal $\alpha=1.01$ $k=16495$ spawners. (b) density dependence is low $\alpha=1.1$ $k=1796$ spawners. (c) density dependence is significant $\alpha=1.7$ $k=397$ spawners. In all simulations the life history modeled is obligate semelparous at age 3 years (Table 1) and coefficient of variation in ocean survival is 0.3. Initial population size is 190 spawners. Time is 100 years. λ of the mean matrix is 1.0.



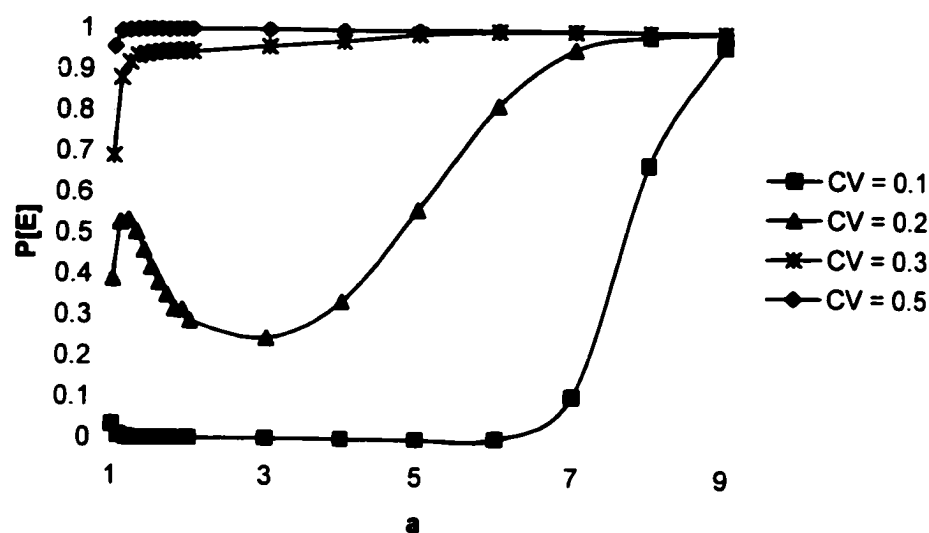


Figure 10. Simulated probability of extinction for obligate semelparous population (Table 1) being subjected to variable strength Ricker density dependent regulation. The equilibrium is fixed at 163 spawners. Environmental variation is represented by CV, the coefficient of variation of ocean survival. a from (3) is represented on the x-axis. Initial population size is 190 spawners. Quasi-extinction level is 100 spawners. Time is 100 years. λ of the mean matrix is 1.0.

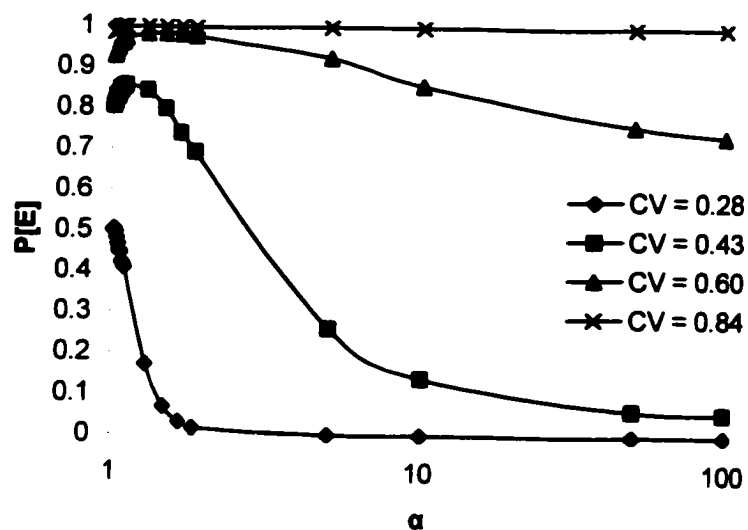


Figure 11. Simulated probability of extinction for iteroparous population (Table 3) being subjected to variable strength Beverton-Holt density dependent regulation. The equilibrium is fixed at 146 individuals. Environmental variation is represented by CV, the coefficient of variation for survival at age 0 years. α from (1) is represented on the x-axis. Initial population size is 190 individuals. Quasi-extinction level is 100 individuals. Time is 100 years. λ of the mean matrix is 1.0.

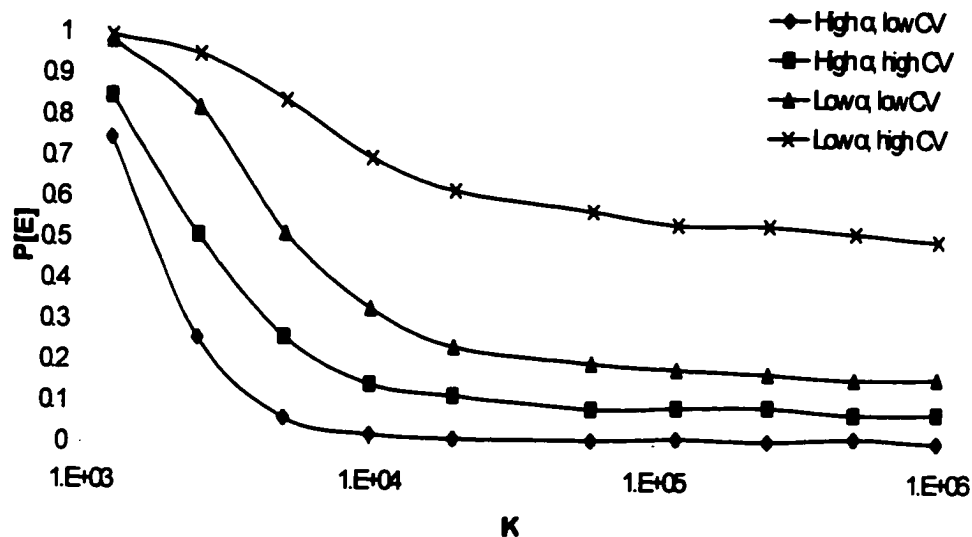


Figure 12. Simulated probability of extinction for obligate semelparous population (Table 1) being subjected to variable strength Beverton-Holt density dependence. Strength of density dependence is modulated by changing the carrying capacity. Environmental variation is represented by CV, the coefficient of variation of ocean survival. Low $\alpha = 1.08$, high $\alpha = 1.2$, low CV = 0.30, high CV = 0.40. K from (1) is measured in number of spawners. Initial population size is 190 spawners. Quasi-extinction level is 100 spawners. Time is 100 years. λ of the mean matrix is 1.0.

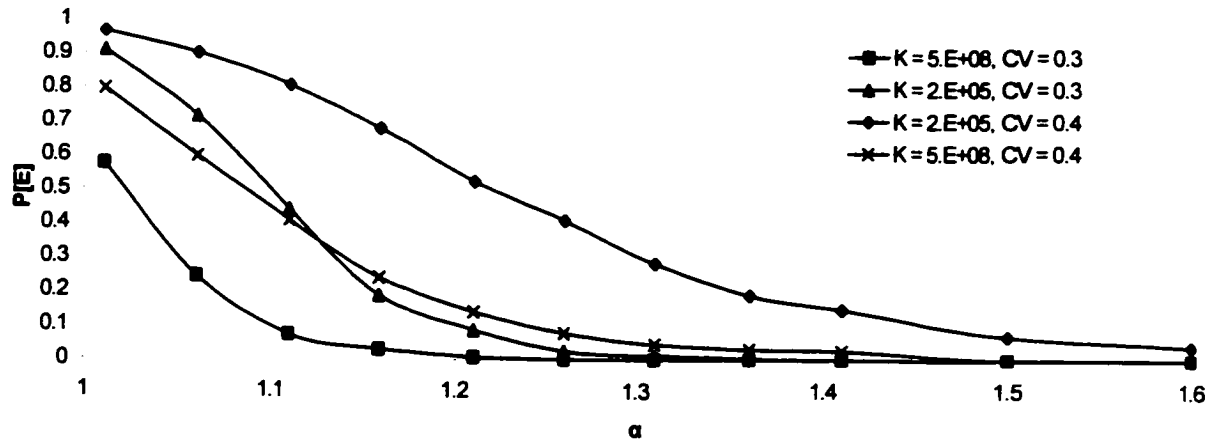


Figure 13. Simulated probability of extinction for obligate semelparous population (Table 1) being subjected to variable strength Beverton-Holt density dependence. Strength of density dependence is modulated by changing α from (1). Environmental variation is represented by CV, the coefficient of variation of ocean survival. Initial population size is 190 spawners. Quasi-extinction level is 100 spawners. Time is 100 years. λ of the mean matrix is 1.0.

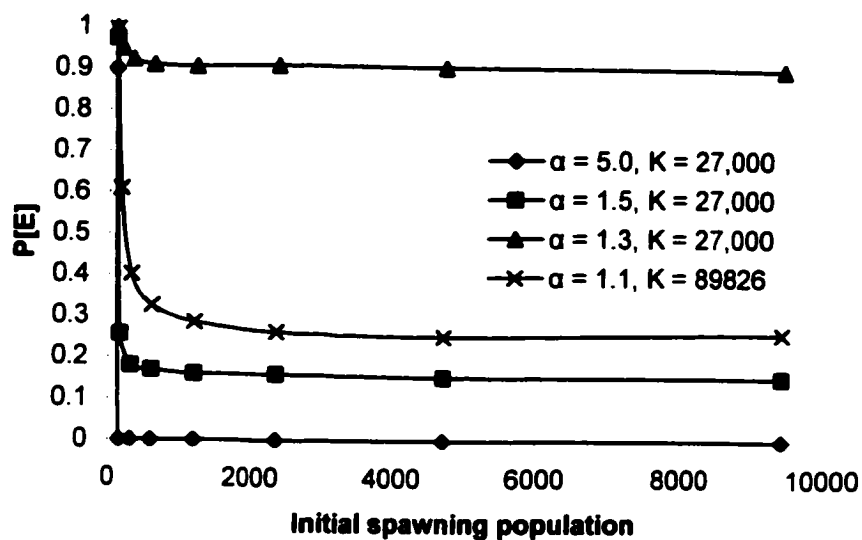


Figure 14. The modeled effect of initial population size on probability of extinction for an obligate semelparous (Table 1) life history. Each series is regulated by a Beverton-Holt density dependent relationship. Coefficient of variation in ocean survival is 0.2. Quasi-extinction level is 100 spawners. Time is 100 years. λ of the mean matrix is 1.0.

Chapter 3: Calculating probability of extinction using first crossing approximation.

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Abstract

Here we assess whether a diffusion approximation developed to model iteroparous populations can accurately model the extinction process for semelparous salmon. We examine the consistency of analytical predictions with existing results and those of our simulations. In salmon the most vulnerable stage is the freshwater breeding cohort. Therefore our simulations model extinction as a process of serial cohort extinctions. In contrast Lande and Orzack's diffusion approximation calculates a cumulative probability that total abundance will decline below a quasi-extinction threshold. Cohort extinction is a good proxy for population extinction for indeterminate semelparous populations where a loss of one cohort results in a loss of all cohorts. Cohort extinction is a poor proxy for population extinction in obligate semelparous populations where each cohort goes extinct independently. For indeterminate semelparous populations with a wide distribution in age of maturity, analytical estimates of probability of extinction were acceptably accurate. However as the distribution in age of maturity narrows, estimates become less accurate for two reasons (1) estimates of the growth rate and variance are less accurate and (2) fluctuations in cohort abundance are larger. For obligate semelparous populations estimates were strongly biased. Therefore the diffusion approximation should not be applied to obligate semelparous populations.

Introduction

Population viability analysis (PVA; Gilpin and Soule 1986) is now commonly used for both determining risk of extinction and managing threatened populations (Carroll et al. 1996). Although the efficacy of population viability analysis has been frequently questioned (Taylor 1995, Ludwig 1996, 1999, Beissinger and Westphal 1998, Chapman et al. 2001, McCarthy et al. 2001), both the World Conservation Union (IUCN 1994) and the U.S. Endangered Species Act urge that population viability be quantitatively evaluated. Most frequently stochastic simulations have been used because of their flexibility (Burgman et al. 1993) and effectiveness in projecting population dynamics (Brook et al. 2000). However stochastic simulations are computationally intensive, subject to programming error, and can be inconsistent due to subjectivity in implementation (Mills et al. 1996, Fagan et al. 1999). Using an analytical approach is less computationally intensive, and yields more consistent predictions. Therefore, it is of interest to investigate whether analytical methods determine a probability of extinction consistent with existing results and our own simulations.

In this chapter we examine life histories typical of coho and chinook salmon (Table 1). Female California coho salmon are typically obligate semelparous at age three years, while chinook females are indeterminate semelparous and mature between the ages of 3 and 7 years (Groot and Margolis 1991). Coho and chinook are two of the most common salmon species in the California current.

Salmon are unusual in that they are both semelparous and anadromous. Because salmon are anadromous, the path to extinction must be defined differently. We modeled extinction as quasi-extinction on the spawning grounds (Ginzburg et al. 1982) for reasons outlined in Chapter one. Myers et al. (1995) found convincing evidence for an Allee effect (Allee 1931) in Pacific salmon at 100 spawners, the level at which we assumed quasi-extinction to occur.

Here we use matrices as the basis of both our simulation and analytical models. Matrix population models are currently a favorite means to assess viability of threatened populations (Crowder et al. 1994, Doak et al. 1994, Cisneros-Mata et al. 1997, Caswell 2001). Projection matrices are assembled from classes of individuals that are presumed to share common demography. Perturbation analysis is then employed to determine which class of individual has the largest impact on growth rate (Crouse et al. 1987). The choice of how individuals are grouped into classes is somewhat arbitrary but important since the choice of classes can affect the sensitivities and elasticities generated by the model (Enright et al. 1995, Wardle 1998). Classes are usually either age-based or stage-based. A stage-based model is preferred when it would be too difficult to age individuals, there is no correlation between age and demography, or the number of age classes is too large to be tractable (Caswell 1989). Since most research on salmon has classified vital rates by age, we have constructed an age-based matrix model.

Using both simulation and analytical models, we compared the effect of variation in salmon's ocean survival on probability of extinction. The simulation model, described in detail in Chapter one, is a stochastic model based on a modified Leslie matrix. The analytical model uses a diffusion approximation to project probability of extinction from a random Leslie matrix. Diffusion models have a long history in ecology, being first applied in the field of population genetics (Fisher 1922, 1930, Wright 1931, Kimura 1955). Later work on population growth (Feller 1951) explored the possibility of using a branching process that converged to a diffusion process to model population dynamics. This work was further developed by many pioneers (Capocelli and Ricciardi 1974, Tuckwell 1974, Keiding 1975). Later work with matrix models established that the distribution of abundance is lognormal for a population growing according to a random Leslie matrix (Tuljapurkar and Orzack 1980). A method for computing the means and variances of these lognormal population distributions was further developed by Tuljapurkar (1982, 1989, 1990). Lande and Orzack (1988) then determined the cumulative probability that such a population will decline to the quasi-extinction level over a specified time period. We use the combination of these results (Tuljapurkar and Orzack 1980, Tuljapurkar 1982, 1989, 1990, Lande and Orzack 1988) to estimate probability of extinction for populations of Pacific salmon growing according to a random Leslie matrix.

Earlier work on iteroparous fish has compared simulations with a diffusion approximation. Cisneros-Mata et al., (1997) compared an analytical

diffusion approximation to a simulation of Totoaba (*Totoaba macdonaldi*) life history and found that when variability was introduced in later life history stages the agreement between the models was good. They also found significant bias in the analytical approximation when the variability was introduced in recruitment.

Our analysis is limited to the dynamics of a single spawning population such as would spawn in a single tributary and ignores the effects of straying and metapopulation dynamics. Since managers are most interested in populations in which there is substantial doubt as to their viability, we focus on populations of low abundance that are not in rapid decline. Populations with a very negative growth rate are clearly going extinct and generally are not modeled to quantify risk of extinction (Cisneros-Mata et al. 1997, Pfister 1998, Jonsson and Ebenman 2001).

Here we determine if the analytical approximation developed by Tuljapurkar, Orzack, and Lande (Tuljapurkar and Orzack 1980, Tuljapurkar 1982, 1989, 1990, Lande and Orzack 1988) gives projections of population dynamics that are consistent with previous results and our own stochastic simulations.

Methods

We compare four breeding structures: one obligate semelparous at age 3 years, and three others that were indeterminate semelparous with mean age of reproduction at 3 years and standard deviation in age of maturity of 0.45, 0.63, 0.77. Environmental variability was placed in the early ocean phase, survival

from age one to two, where the greatest variation in survival is presumed to occur for Pacific salmon (Pearcy 1992, 1997). The deterministic growth rate for all modeled populations was $\lambda=1.0$. The populations were initialized with 10,000 individuals (approximately 190 spawners) in a stable age distribution in both simulation and analytical diffusion models. This initial population size was chosen to produce a non-zero probability of extinction. Since semelparous populations do not exhibit weak ergodicity, the effects of the initial age distribution will not disappear (Tuljapurkar and Orzack 1980). Therefore the stable age distribution was chosen for the initial age structure in order to avoid introducing population fluctuations due to variation in initial conditions rather than environmental variability. In the simulations, therefore, fluctuations are due solely to environmental variability.

Tuljapurkar and Orzack (1980) established that the distribution of abundance of a population growing according to a random Leslie matrix whose vital rates are a Markov sequence is lognormal. A method for computing the means and variances of these lognormal population distributions was further developed by Tuljapurkar (1982, 1989, 1990). The mean and variance of the log of population abundance are μt and $\sigma^2 t$, where those rates of growth are given by

$$\mu = \ln \lambda_0 - \frac{\sigma^2}{2}, \quad (1)$$

and

$$\sigma^2 = \lambda_0^{-2} \delta^T \mathbf{C} \delta. \quad (2)$$

In this set of equations λ_0 is the dominant eigenvalue of the mean Leslie matrix, C is the variance-covariance matrix of the variations about the mean matrix, δ is the vector of sensitivity coefficients $\partial\lambda_0/\partial e_{ij}$ (Lande and Orzack 1988), and δ^T is the transpose of δ . t is time measured in years. The time period we examined here was 100 years.

Sensitivities of the variability in element e_{ij} on λ_0 are given by

$$\frac{\partial\lambda_0}{\partial e_{ij}} = \frac{v_i w_j}{\langle W, V \rangle}, \quad (3)$$

where V is the left eigenvector, W is the right eigenvector, v_i is the i^{th} element of the left eigenvector, w_j is the j^{th} element of the right eigenvector and $\langle W, V \rangle$ is the scalar product of the left and right eigenvectors.

Elements in the left eigenvector are given by

$$v_1 = 1,$$

$$v_i = b_i \lambda^{-1} + p_i v_{i+1} \text{ for } i > 1, \quad (4)$$

where p_i and b_i are the familiar survival and fecundity coefficients from the Leslie matrix.

Elements of the right eigenvector are given by

$$w_1 = 1$$

$$w_j = p_1 p_2 \dots p_{j-1} * \lambda^{-j+1} \text{ for } j > 1. \quad (5)$$

We used a diffusion approximation (Lande and Orzack 1988) for the logarithm of total population abundance to calculate a cumulative probability that a population of size N_0 will decline to N over time t using:

$$P_t[N / N_0] = \Phi\left[\frac{\ln(N / N_0) - \mu t}{\sigma \sqrt{t}}\right] + e^{[2\mu \ln(N / N_0)] / \sigma^2} \left[\frac{\ln(N / N_0) + \mu t}{\sigma \sqrt{t}}\right], \quad (6)$$

where $\Phi(z)$ represents the proportion of a standard normal distribution up to the point z .

This approximation is based on a scenario in which when population abundance reaches the quasi-extinction level, q , the entire population goes extinct. It is expected that the probability of extinction obtained from the diffusion approximation would be different from our simulation results because of the different types of quasi-extinction modeled. In the simulation, when the number of spawners in a cohort drops below the quasi-extinction level no eggs are produced. After all age classes have experienced a reproductive failure the entire population goes extinct. The diffusion model extinction occurs when the entire population abundance falls below the quasi-extinction level, at which point the entire population goes extinct instantaneously. These two mechanisms of extinction are, of course, fundamentally different. One might calculate an equivalent quasi-extinction level for the diffusion approximation by calculating how large the total population would be when the number of spawners is q individuals.

Assuming the population is in a stable age distribution when it goes extinct, total population size N would be

$$N = n_A + n_A m_{A-1} + n_A m_{A-1} m_{A-2} + \dots + n_A \prod_1^{A-1} m_i \quad (7)$$

when the number of spawners is at the quasi-extinction level, where A is the maximum spawning age, and n_A is the number of spawners at age A . Here

$$m_i = \frac{1}{p_i(1-f_i)} \text{ and } n_A = \frac{q s_A}{f_A} \quad (8)$$

where p_i is survival from age i to $i+1$, f_i is the fraction of i year olds who spawn at age i , q is the quasi-extinction level used in the simulation, and s_A is the fraction of the spawning cohort that are age A .

The obligate semelparous case presents additional challenges since each cohort is independent of the others. To model the obligate semelparous extinction process more accurately we needed to account for cohort independence. To do so, we modeled each cohort's extinction separately, and then calculated the probability of extinction as the probability that all cohorts in a population go extinct, i.e.

$$P[E] = P[\text{cohort extinction}]^A. \quad (9)$$

Here cohort extinction is modeled, using equation (6), as occurring when the population size drops from the initial number of spawners in the simulation (190) to q (100).

Results

The diffusion approximation using estimates of μ and σ^2 from equations (1) and (2) generates probabilities of extinction that are in agreement with the simulation model for the life histories with wide distribution of ages of maturity (Fig. 1). For the widest distribution of age of maturity we found that the results from the diffusion approximation were consistently conservative across multiple levels of environmental variability. However not all probabilities of extinction were accurately predicted, as the amount of variability in age of maturity drops, the results become successively less accurate (Fig. 1 $\sigma=0.0$, $\sigma=0.45$). To discover why, we followed results for several examples step by step to see where they break down.

Firstly, equations (1) (2) and (6) are based on the assumption that the distribution of population sizes quickly approach log normality. To test the validity of this assumption for simulated populations, we performed the D test (D'Agostino 1971, 1971) on the results of a simulated log. of abundance. We looked at results from the two life histories for which the we had the poorest fit: obligate semelparous at age three, and indeterminate semelparous with a mean spawning age of three and standard deviation in spawning age of 0.45. Since the results are significant at $\alpha=0.01$ level for both distributions (Table 2), we cannot reject the null hypothesis that these abundances are distributed log normally. This is sufficient evidence that it is not the violation of the

assumption of log normality that is causing the disagreement between simulation and diffusion results.

The next question is whether the mean and the variance of log of abundance change linearly with time as predicted by Tuljapurkar and Orzack (1980). We found that simulation variance did grow linearly, but the accuracy of the analytical estimates varies widely with life history (Fig. 2). The estimates of variance were reasonable for the indeterminate semelparous populations with high variability in age of maturity ($\sigma \geq 0.63$), but much less accurate as variability in age of maturity drops. There was a particularly strong bias in the estimate for the obligate semelparous population. For the obligate semelparous population the growth rate of the variance was one-third the expected rate based on the simulation. To determine the source of this bias, we scrutinized the equations used to estimate μ and σ^2 . Expanding equation (2) showed that when variability is confined to ocean survival the estimate of variance was

$$\sigma^2 = \left(\frac{\partial \lambda}{\partial p_0} \right)^2 \sigma_{p_0}^2 \frac{1}{\lambda^2},$$

which reduced to

$$\sigma^2 = \frac{E[(l - \lambda)^2]}{\lambda^2}, \quad (10)$$

where l is λ plus an infinitesimally small change. Substituting (10) into equation (1) yields an estimate of μ ,

$$\mu = \ln \lambda - \frac{E[(l - \lambda)^2]}{2\lambda^2} \quad (11),$$

which is identical to the Taylor series expansion for the mean of the log of the λ 's of a semelparous annual (Lewontin and Cohen 1969). In other words, equation (2) calculated an estimate of variance for a single cohort. In our case we modeled a population that was obligate semelparous at age 3 years, therefore we have three independent cohorts. Since variances are additive, it followed that our analytical estimate of the variance was off by a factor of three.

Examination of the simulated mean showed that, as predicted, values decreased approximately linearly in the simulation model (Fig. 3). However, the Tuljapurkar model (1982, 1989, 1990) and simulation models produced means that decreased at different rates. There was a positive bias in all indeterminate semelparous populations but the bias was largest in the population with the narrowest distribution in age of maturity. For the obligate semelparous case, μ is positively biased by a factor of three because of the aforementioned bias in the variance estimate.

For the obligate semelparous population, both the bias in the mean and the bias in the variance should lead to a negative bias in the probability of extinction. We found, surprisingly, that this is not the case. In this case the Tuljapurkar approximations (1982, 1989, 1990) overestimated μ and underestimated σ^2 , yet the Lande and Orzack (1988) diffusion approximation overestimated probability of extinction.

To understand why the diffusion approximation gives such a poor fit to simulations of the obligate semelparous life history we examined extinction mechanics. Obligate semelparous populations are composed of multiple breeding cohorts, each of which must go extinct independently. Equation (6) assumes that a population that falls below the quasi-extinction threshold goes extinct as a unit. This extinction mechanism models the indeterminate semelparous life history well. Chapter one showed that when an indeterminate semelparous population loses a cohort, the entire population would almost certainly go extinct within the simulation period, a phenomenon we referred to as cohort coupling. Because of cohort coupling, cohort extinction is a good proxy for population extinction in the indeterminate semelparous case. However it is a poor fit for obligate semelparous populations where each cohort goes extinct independently. To correct for cohort independence we used equation (9). The result being probability of extinction was strongly negatively biased (Fig. 4). Leading to the conclusion that the Lande and Orzack (1988) diffusion approximation will not effectively model cohort extinction in the obligate semelparous case.

Discussion

For indeterminate semelparous populations with a wide distribution in age of maturity, predictions of probability of extinction from the diffusion approximation (Lande and Orzack 1988) were consistent with those of simulations. However the diffusion approximation did not accurately estimate probability of extinction for obligate semelparous populations because (1) it

did not account for cohort independence and (2) large fluctuations in abundance violate the assumptions upon which it was built.

Previous PVA's have used random matrix models to quantify probability of extinction. However not all have utilized the first crossing approach taken here. Doak et al. (1994) developed a PVA for the desert tortoise (*Gopherus agassizii*) using a random stage-based matrix. However their approach was based on confidence intervals rather than first crossings. Confidence intervals only express the distribution of abundance at a particular time; they do not account for populations that have gone extinct up to that time (Cisneros-Mata et al. 1997). Because of this, estimates of absolute probability of extinction were expected to be inaccurate. The first crossing approach we have taken here does not have the same deficiency. We were able to account for all crossings of the quasi-extinction threshold and therefore make more accurate estimates of probability of extinction.

Later PVA's recognized the shortcomings of the confidence limit approach and utilized the more comprehensive first crossing approach. Cisneros-Mata et al., (1997) used a diffusion approximation to estimate probability of extinction for Totoaba (*Totoaba macdonaldi*) a sciaenid fish endemic to the Gulf of California. Using a first crossing approach, they examined the effects of variability in survival of pre-adults, adults, and juveniles as well as variability in recruitment. They found that the diffusion model produced probabilities of extinction that were in agreement with simulations in all cases except one, variability in recruitment. In this case,

because fluctuations in abundance were large, the diffusion model substantially underestimated probability of extinction. Here we have found that for wide distributions of age of maturity diffusion estimates are accurate. However, as distribution of age of maturity narrows, and fluctuations in abundance become larger, the diffusion approximation broke down. Our findings are in agreement with those of Cisneros-Mata et al. (1997).

Other studies utilizing diffusion models on iteroparous populations found good agreement between simulated probability of extinction and diffusion estimates (Lande and Orzack 1988, Fieberg and Ellner 2000). The only discrepancy being a small positive bias due to the simulation operating in discrete time and the diffusion approximation operating in continuous time (Lande and Orzack 1988). Since in these studies the fluctuations in population abundance were proportionally smaller than the fluctuations in cohort abundance modeled here, their results are not surprising. We also found that when fluctuations in abundance were small, the agreement between the diffusion approximation and simulation was good.

In this analysis we have ignored the effects of density dependence. We did this for two reasons: (1) few PVA's include density dependence in their projections and (2) distinguishing density dependent from density independent behavior has proven difficult (Hassell 1986, Gaston and Lawton 1987). Since many forms of density dependence are presumed to dampen fluctuations in population size (Beverton and Holt 1957), it is tempting to speculate that the

agreement between simulation and diffusion approximation may be better in such a case. Future research in this area may prove fruitful.

Conservation biologists have at their disposal an array of options when developing PVA's, among the most popular are individual based models (IBMs; Grimm 1999), matrix models (Van Groenendael et al. 1988, Silvertown et al. 1996, Grand and Beissinger 1997), and state variable models (Tuckwell 1974, Cisneros-Mata et al. 1997). IBMs have the advantage that (1) they make more realistic assumptions about the individuals they model (2) they can explore emergent properties resulting from interactions among the units (Grimm 1999). As a result, IBMs are highly adaptable. However precisely because they use individuals as units, they make it difficult to draw widely applicable conclusions. In contrast, matrix models group individuals of like demography into classes (Caswell 1989). The stochastic Leslie matrix we have used here allowed us to incorporate the relevant level of biological detail (aged based vital rates), without requiring the computational horsepower or individual specifics needed for an IBM. Our matrix approach allowed us to model extinction at a cohort level and follow population trajectories through large changes in abundance. Whereas state variable models such as the diffusion approximation (Lande and Orzack 1988) which treat individuals as identical cannot incorporate this level of relevant detail. The advantage of the state variable approach is the breadth of applicability of the conclusions. However they cannot be tailored to specific situations without losing their generality. Here our need to track (1) extinction at the cohort level and (2)

large fluctuations in abundance, made the diffusion approximation inappropriate. For these reasons we feel stochastic matrix simulations are the better choice for modeling semelparous salmon.

Conclusions

For managers the take home message is this, the analytical approximation (equations (1) (2) and (6)) can be used effectively for indeterminate semelparous populations if one gives due consideration to its domain of applicability. The estimate of probability of extinction is reasonable when there is a wide distribution in age of maturity. However, as the distribution in age of maturity becomes narrower, the estimates become less reliable for two reasons: (1) the estimates of μ and σ^2 are less accurate (Figs. 2 and 3), and (2) the fluctuations in cohort abundance are larger. As the distribution in age of maturity narrows, the fluctuations in cohort abundance approach the amplitude of the fluctuations in a single age class. It has been shown previously that diffusion approximations produce inaccurate results when changes in the state variable are large (Grassman and Ludwig 1983). Further, because these equations assume no density dependence, they can be applied only when population behavior is expected to be linear. Finally, the equations (1) (2) and (6) assume the effects of the initial age distribution will eventually disappear (Tuljapurkar and Orzack 1980). Semelparous populations do not satisfy this condition of weak ergodicity. Therefore, if there are fluctuations in abundance due to the initial age distribution, these approximations are not applicable.

The obligate semelparous case presents additional difficulties. For obligate semelparous populations, the estimate of variance in equation (2) and the probability of extinction from equation (6) account for only one cohort. These biases lead to an unacceptably poor estimate of probability of extinction. In addition the fluctuations in abundance are the largest of any life history examined. Again, diffusion approximations break down when changes in the state variable are large (Grassman and Ludwig 1983). Therefore the Lande and Orzack diffusion approximation is not applicable to an obligate semelparous life history.

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Tables

Table 1. Semelparous population structures. f is fraction spawning. p is survival. b is fecundity. Mean age of maturity is 3 years in all cases.

	Age	f	p	b
$\sigma_{maturity} = 0$	1	0	0.04	0
Spawning	2	0	0.5	0
distribution	3	1	0	50
0,0,1				
$\sigma_{maturity} = 0.45$	Age	f	p	b
Spawning	1	0	0.042	0
distribution	2	0.0476	0.5	50
.1,.8...1	3	0.8	0.5	50
	4	1	0	50
$\sigma_{maturity} = 0.66$	Age	f	p	b
Spawning	1	0	0.044	0
distribution	2	0.09092	0.5	50
.2,.6,.2	3	0.6	0.5	50
	4	1	0	50
$\sigma_{maturity} = 0.77$	Age	f	p	b
Spawning	1	0	0.046	0
distribution	2	0.13044	0.5	50
.3,.4,.3	3	0.4	0.5	50
	4	1	0	50

Table 2. D test for normality of the log of abundance of spawners at time 100 years. Coefficient of variation in ocean survival is 0.3. σ is standard deviation in age of maturity. Mean age of maturity is 3 years in both cases.

	D Value	Critical values $\alpha=.01$
$\sigma=0.0$	0.282645	.2760,.2858
$\sigma=0.45$	0.281707	

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Figures

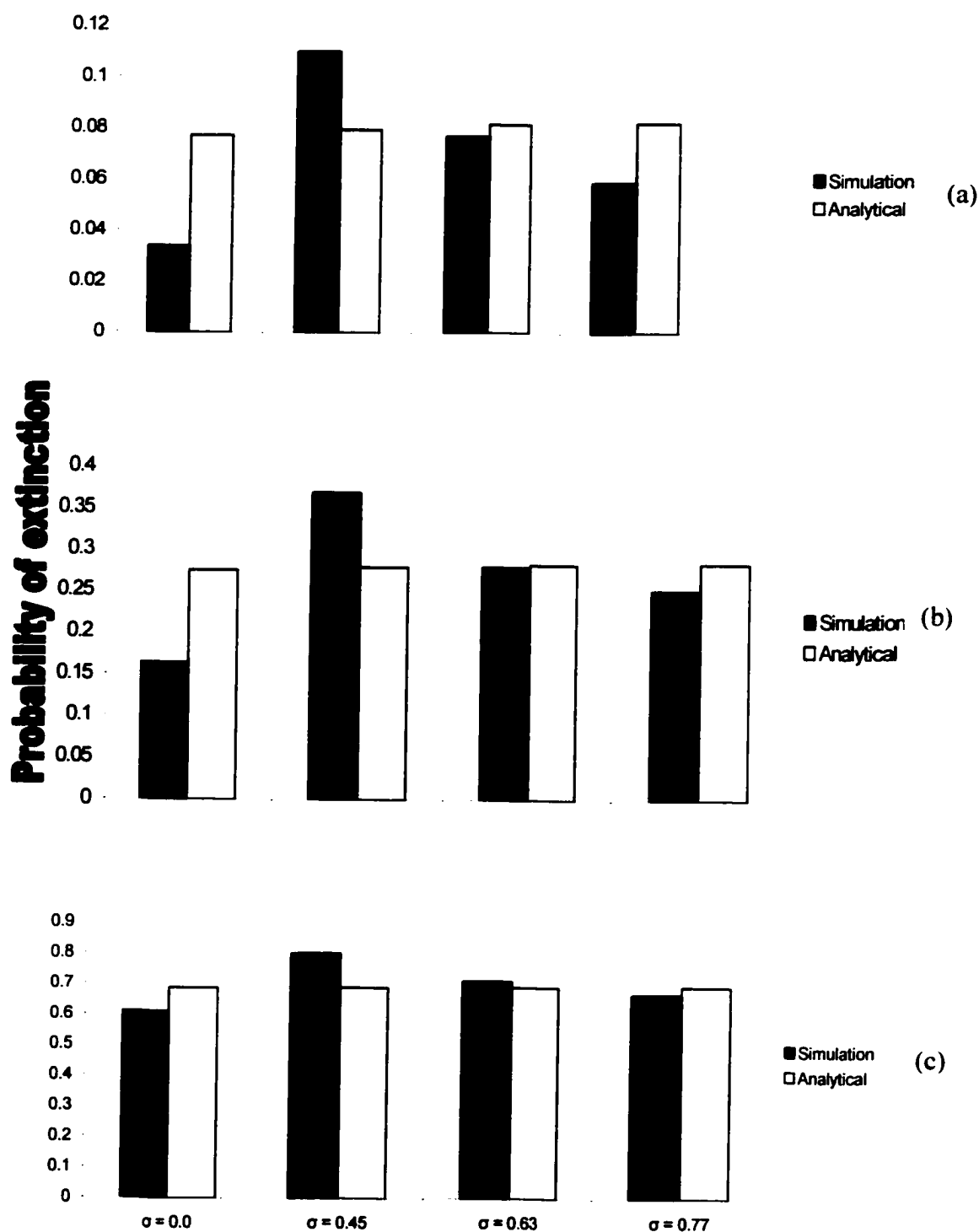


Figure 1. Comparing probabilities of extinction generated by the simulation and analytical models. Environmental variability was placed in survival at age 1 year, the coefficient of variation was 0.1, 0.15, and 0.3 in a, b, and c respectively. Initial population consisted of 10,000 individuals in the stable age distribution, or approximately 190 spawners. λ of the average matrix was 1.0. The time frame examined was 100 years and quasi-extinction level was 100 spawners. All life histories had a mean age of reproduction of 3 years. σ is the standard deviation of age of maturity. Those life histories with higher σ have greater variability in age of maturity.

Figure 2. Comparing the analytical estimates of variance of log abundance with those of the simulation for several life histories. Environmental variability was placed in survival at age 1 year, the coefficient of variation was 0.15. Initial population consisted of 10,000 individuals in the stable age distribution, or approximately 190 spawners. λ of the average matrix was 1.0. Time in years is represented on the x-axis. All life histories had a mean age of reproduction of 3 years. a is obligate semelparous, b, c and d are indeterminate semelparous with a standard deviation in age of maturity of 0.45, 0.63, and 0.77 respectively.

Variance of log abundance

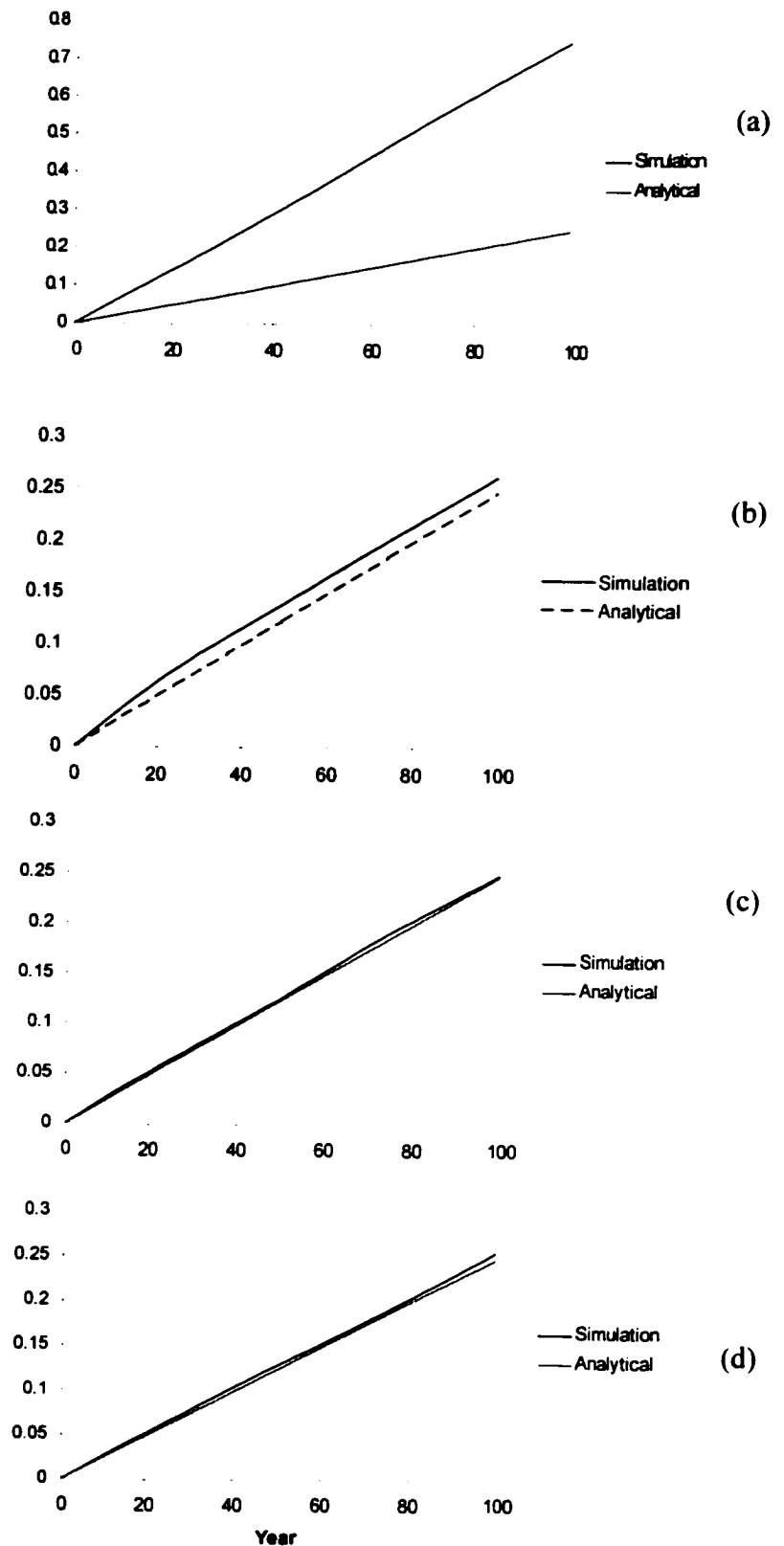
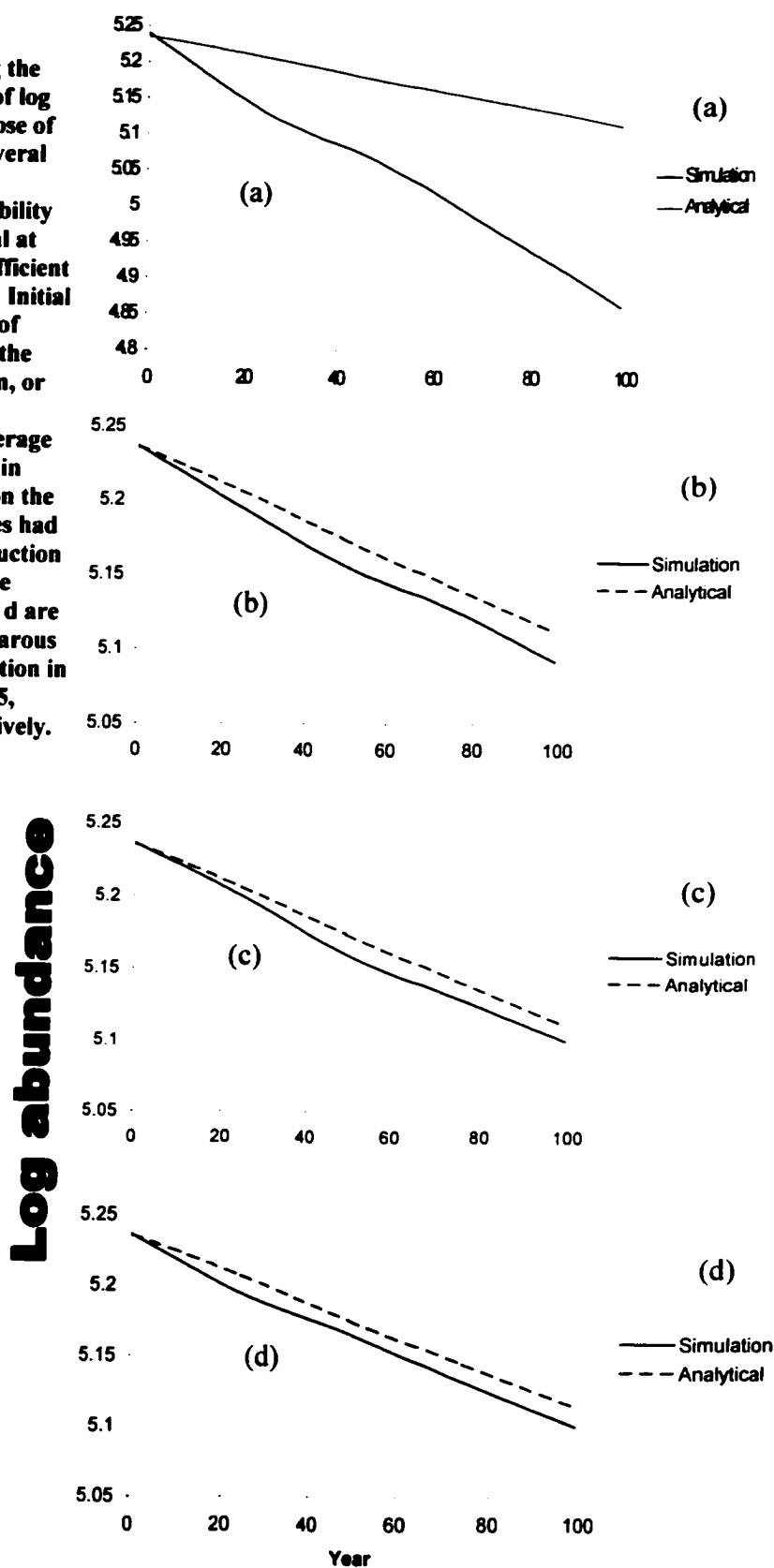


Figure 3. Comparing the analytical estimates of log abundance??with those of the simulation for several life histories.

Environmental variability was placed in survival at age 1 year with a coefficient of variation was 0.15. Initial population consisted of 10,000 individuals in the stable age distribution, or approximately 190 spawners. λ of the average matrix was 1.0. Time in years is represented on the x-axis. All life histories had a mean age of reproduction of 3 years. a is obligate semelparous, b, c and d are indeterminate semelparous with a standard deviation in age of maturity of 0.45, 0.63, and 0.77 respectively.



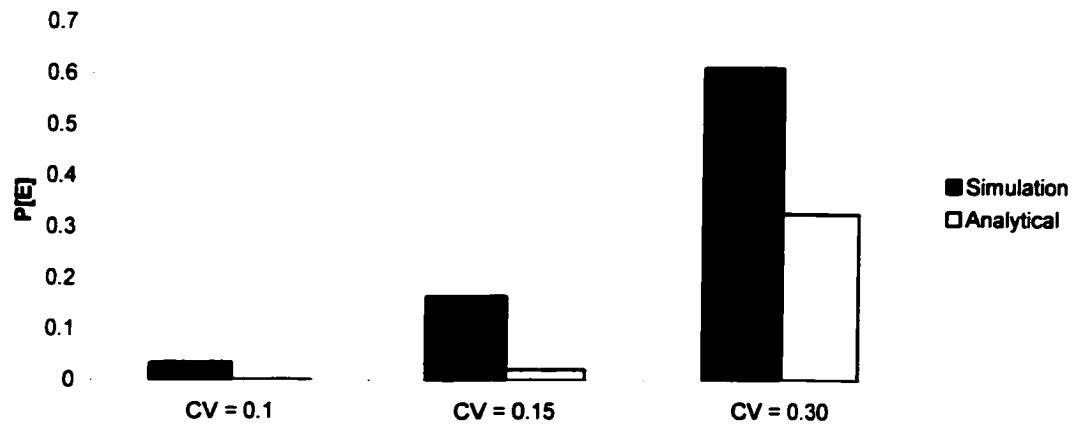


Figure 4. Probabilities of extinction for obligate semelparous populations from analytical and simulation models. Independence of cohorts is corrected for using equation (9). Environmental variability was placed in survival at age 1 year, the coefficient of variation ranged from 0.1 to 0.3. Initial population size consisted of 10,000 individuals in the stable age distribution, or approximately 190 spawners. λ of the average matrix was 1.0. The time frame examined was 100 years and quasi-extinction level was 100 spawners.

Chapter 4: The influence of fraction spawning on extinction probability: Pacific salmon as an example.

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Abstract

Pacific salmon exhibit environmentally influenced variability in spawning age. In years following particularly favorable ocean environments, larger fractions of the population are expected to breed at a younger age. This variation in fraction spawning (the proportion of an age class that matures) affects realized survival, because individuals die after spawning, and realized fecundity because fewer spawners produce fewer progeny. This dual effect leads to a unique influence on probability of extinction. In this chapter we examine the effect of variability in fraction spawning on life histories typical of Pacific chinook using simulation and analytical models. We found that when variability is confined to fraction spawning at a single age, the probability of extinction is proportional to the integrated elasticity of λ for realized fecundity at that age. Simulations showed that probability of extinction is higher when ocean survival varies by an amount equivalent to fraction spawning. Additionally simulations indicated that variability in fraction spawning would result in a probability of extinction proportional to the mean fraction spawning at the age where variability occurs. Therefore variability in fraction spawning is most important when it affects the dominant age class of a cohort.

Introduction

Pacific salmon are endangered or in decline throughout much of their historic North American range (Nehlsen et al. 1991, Williams et al. 1992, (BRT) 1997, Johnson 1997, Stouder et al. 1997, Myers 1998, Weitkamp et al. 2000). This dramatic decline in abundance has had important economic,

social, political, and ecological consequences. Recent evidence has shown that the decline of the salmon is likely to have ecological effects greater than previously hypothesized, since the health of the ecosystem bordering salmon spawning grounds is dependent on abundant salmon runs (Helfield and Naiman 2001). To abate the decline we must understand what makes particular stocks vulnerable to extinction.

Salmon are unusual in that they exhibit semelparous reproduction, and an anadromous life cycle. Semelparity has an important influence on life history because it links reproduction with survival. For many salmon, spawning age is determined by individual growth rates (Groot and Margolis 1991). In years following particularly favorable ocean environments, larger fractions of the population are expected to breed at a younger age (Helle 1979). This variation in fraction spawning affects realized survival, because individuals die after spawning, and realized fecundity because fewer spawners produce fewer progeny. This dual effect leads to a unique influence on probability of extinction.

Because salmon are anadromous, the path to extinction must be defined differently. We modeled extinction as quasi-extinction on the spawning grounds (Ginzburg et al. 1982) for reasons outlined in Chapter one. Myers et al. (1995) found convincing evidence for depensation in Pacific salmon at 100 spawners, the level at which we assumed quasi-extinction to occur.

In this chapter we examine life histories typical of chinook salmon, which are indeterminate semelparous and whose females mature between the ages of 3 and 7 years (Groot and Margolis 1991). Chinook salmon are one of the most common species in the California current.

Other investigations have broached the issue of the influence of life history on probability of extinction but there has been no comprehensive analysis of the influence of variation in fraction spawning in semelparous salmon. While Jonsson and Ebenman (2001) found probability of extinction in semelparous species was very sensitive to variability in growth rate, the stage based model used they used lacked important details of salmon life history. Previous work using salmon models showed that wider distribution of age classes decreased probability of extinction (Botsford and Brittnacher 1998, Higgins 1999). However, none of these previous analyses focused specifically on the influence of variability in fraction spawning on salmon viability.

Here we limit our analysis to the dynamics of a single spawning population such as would spawn in a single tributary and ignore the effects of straying and metapopulation dynamics. Since managers are most interested in populations in which there is substantial doubt as to their viability, we focus on populations of low abundance that are not in rapid decline. Populations with a very negative growth rate are clearly going extinct and require no detailed examination (Cisneros-Mata et al. 1997, Pfister 1998).

Using both simulation and analytical models, we examine the effect of variation in fraction spawning on probability of extinction. The simulation model, described in detail in Chapter one, is a stochastic model based on a modified Leslie matrix. Although stochastic models have been used for many years in biology (Bartlett 1960) their utility has been frequently questioned (Caughley 1994, Mills et al. 1996, Todd et al. 2001). Recent work has shown accurately predicting probability of extinction is nearly impossible (Ludwig 1996, Ludwig 1999). As an alternative, the approach taken here is to determine what makes one population more vulnerable than another under a given set of conditions.

The analytical model we use, described in detail in Chapter three, uses a diffusion approximation to calculate first crossing frequency of a quasi-extinction threshold. Although simulations are more flexible and can incorporate more biological detail than analytical approaches, they cannot create the same level of understanding. Therefore we use an approach that combines both analytical and simulation models.

To ascertain either relative or absolute probability of extinction it is imperative that the influence of all salmon vital rates on population dynamics be understood. Biologists and fisheries managers have devoted considerable effort to quantifying and characterizing the distributions of vital rates for Pacific salmon (Hunter 1959, Burgner 1991, Healey 1991, (BRT) 1997, Johnson 1997). Although survival and fecundity distributions have been quantified, and their effects on probability of extinction characterized, to

model semelparous populations effectively we must also characterize the impact of fraction spawning on population dynamics. Here we determine if age structure can influence probability of extinction when there is variability in fraction spawning. We also seek to quantify the influence variability in fraction spawning has on probability of extinction relative to variability in survival. Finally we seek to quantify the domain of applicability of the diffusion methods developed by Tuljapurkar and Orzack (1980), Tuljapurkar (1982, 1989, 1990), and Lande and Orzack (1988). We first examine the circumstances where diffusion estimates of probability of extinction differ from simulation estimates and second the reason for the differences.

Methods

Pacific chinook (*Oncorhynchus tshawytscha*) exhibit a wide variety of maturation schedules, while in some stocks individuals can mature as early as two years of age, in others individuals mature as late as seven years of age. Despite this variability between chinook stocks, within stocks most individuals mature predominantly at two or three ages (standard deviations in age of maturity ranging from 0.206 to 0.698) (Healey 1991). In this paper we examine three indeterminate semelparous life histories typical of those found in Pacific chinook stocks. At the stable age distribution, these life histories have a mean age of maturity of 3 years and a standard deviation in age of maturity ranging from 0.45 to 0.77 (Table 1).

We compared results from simulation and analytical models at multiple levels of environmental variability. During the simulations all elements of the

semelparous matrix were fixed except for fraction spawning (represented here as f_i , fraction spawning at age i) which we assumed reflected environmental variability (Athreya and Karlin 1971, May 1973, Keiding 1975, Roughgarden 1975). We placed variability alternately in fraction spawning at age 2 years and age 3 years (f_2 and f_3). These were chosen randomly from a beta distribution with a mean of f_i in the average matrix and a range of variances. We examined populations with a coefficient of variation in f_i ranging from 0.1 to 2.5. All survivals were set to 0.5 with the exception of first year survival, which was chosen so that the growth rate λ for the average matrix was unity. In other words, the population without the influence of environmental fluctuations was neither growing nor declining. We chose this value because for stocks with λ much greater or less than 1.0 the probability of extinction is not an issue, it is either zero or one respectively. We further assume that populations are at low enough densities that behavior is essentially linear, and density dependence can be safely ignored. The populations were initialized with 190 spawners in a stable age distribution in both the simulation and analytical models. This initial population size was chosen to produce a non-zero probability of extinction. The stable age distribution was chosen for the initial age structure in order to avoid introducing population fluctuations due to variation in initial conditions rather than environmental variability. In the simulations, therefore, fluctuations are due solely to environmental variability.

Here we assess the dynamics of a single spawning population such as would spawn in a single tributary. We do not include effects of straying and metapopulation dynamics.

Since salmon die following spawning, fraction spawning affects both realized fecundity:

$$B_i = b_i * f_i, \quad (1)$$

and realized survival:

$$P_i = p_i * (1 - f_i), \quad (2)$$

where p_i is survival probability from age i to $i+1$, f_i is fraction spawning at age i and b_i is individual fecundity at age i . This link leads to a covariance between B_i and P_i . Covariance between random variables X and Y is calculated as

$$\text{Cov}(X, Y) = E[(X - \mu_x)(Y - \mu_y)], \quad (3)$$

where μ_x and μ_y are the mean of X and Y . For survival and fecundity, covariance reduces to

$$-b_i p_i * \text{variance}(f_i) \quad (4).$$

The effect of age specific variation in fraction spawning on extinction probability.

Simulation model

Our primary interest was whether age structure could affect probability of extinction when there was variability in fraction spawning. We first examined

the case where variability is in fraction spawning at age two years (f_2). Simulations demonstrated that variability in fraction spawning at this age produced the largest probability of extinction in populations with the widest distribution of age classes in the spawning cohort (Fig. 1 $s=0.77$). This is somewhat surprising since previous work showed that wider distribution of age classes decreased probability of extinction (Botsford and Brittnacher 1998, Higgins 1999). To determine the source of the effect we examined the influence of environmental variability in fraction spawning on population growth rate (Fig. 2), calculated as the change in mean of log. abundance over the simulation period. Clearly the largest impact on growth rate was for those cohorts with a wide distribution of age classes in the spawning cohort. The effect on variance is also most felt in these mixed age cohorts (Fig. 3). These lower growth rates and higher variances translate unsurprisingly into higher probability of extinction (Lande and Orzack 1988).

Cohorts with more age class mixing are more sensitive to changes in fraction spawning at age two because in most years they consist of a large number of two-year-olds. When the two-year-olds are absent it has a dramatic affect on the size and realized fecundity of the cohort. Additionally these missing two-year-olds have the lowest spawning probability at the next age, so they are the least likely to breed the following year. In contrast, cohorts that are not as dependent on two-year-olds for spawning, i.e. predominately three-year-olds, are not as sensitive to their absence. When the two-year-olds are missing, it has the smallest effect on realized fecundity. Additionally these

missing two-year-olds have the highest probability of returning to breed the following year to balance the loss.

To determine whether the age at which environmental variability is expressed would affect relative probability of extinction, we also simulated variability in fraction spawning at age three years. When variability was placed in fraction spawning at age 3 years, we found that the relative probabilities of extinction were in the inverse order they were when variability was in fraction spawning at age two years (Fig. 4). To examine the root of this inversion, we examined the effect of environmental variability on growth rate and variance (Figs. 5 and 6). In contrast to the case where variability was in age two fraction spawning, the lowest growth rates and highest variances were in those life histories with the narrowest distribution of age classes in their cohorts. However, this result is not surprising when one considers the dependency of the spawning cohort on the age class. Those cohorts that normally consist of a large fraction of three-year-olds, narrow distribution, are naturally most sensitive to their absence. Therefore, fluctuations in this age class have the greatest impact on probability of extinction.

Additionally one would like to know if variability in the earlier fraction spawning has the same magnitude of effect as variability in the later. From Figures 1 and 4 we see when equal amounts of variability are placed alternatively in fraction spawning at age two or age three, the greatest probability of extinction results from variability at age three. This holds for all life histories we examined here for a simple reason. The predominant age

class in all the cohorts we examined is the age 3 year class. Naturally we would expect variability in the dominant age class to have the greatest impact on probability of extinction for reasons mentioned above.

Analytical model

Analytical models are considered more intuitive and yield clearer insights into modeled dynamics than simulations. Therefore it is of interest to determine if analytical methods would yield reliable estimates for probability of extinction when variability was in fraction spawning. Two of the most widely used measures to assess the effect of a small change in vital rates on λ are sensitivity and elasticity (Benton and Grant 1999, De Kroon et al. 2000, van Tienderen 2000, Caswell 2001). Perturbation analysis uses these measures to determine the effect of a permanent change in vital rates on λ . Here we use these measures to a different end; to determine the effect variability in a vital rate has on μ and σ^2 and therefore on probability of extinction. In the case where perturbations are in fraction spawning there are effects on two vital rates, realized fecundity and realized survival. Standard perturbation measures do not account for this covariance in vital rates (Caswell 1985). However integrated elasticities (van Tienderen 1995) can express the effect variability in fraction spawning has on μ and σ^2 due to its dual affect on realized survival and realized fecundity. Since we would like to express equation (2) from Chapter three in its simplest form, we used integrated elasticities to reduce the complexity of the expression.

When the relationships amongst the vital rates are approximately linear, as they are in our case, integrated elasticity can be calculated as

$$IE_i = \sum_j r_{ij} e_j CV_j / CV_i, \quad (5)$$

where IE_i is the integrated elasticity of matrix element a_i , r_{ij} is the correlation coefficient between a_i and a_j , e_j is the elasticity of a_j , and CV_j and CV_i the coefficients of variation for matrix elements a_j and a_i respectively (van Tienderen 1995). Here we index the elements of the Leslie matrix from 1 to n^2 rather than by row and column (a_{ij}) to avoid overly complex notation. The correlation coefficient r is defined as

$$r_{xy} = \frac{Cov(x,y)}{\sigma_x \sigma_y}. \quad (6)$$

Correlation between realized survival and realized fecundity can be expanded and simplified. Substitution equation (4) into equation (6) yields

$$r_{B,p_i} = \frac{-b_i p_i \text{var}(f_i)}{\sigma_{B_i} \sigma_{p_i}}. \quad (7)$$

In the case we examine here variability is confined to fraction spawning (f_i) therefore,

$$\sigma_{B_i} = b_i \sigma_{f_i}, \quad (8)$$

and

$$\sigma_{P_i} = p_i \sigma_{f_i}. \quad (9)$$

Substituting equations (8) and (9) into equation (7) yields that in the case when variability is confined to fraction spawning

$$r_{B_i P_i} = -1.0 \quad (10)$$

For variation in realized fecundity and realized survival at age i due to variability in fraction spawning all correlations are zero with the exception of $r_{B_i B_i}$ and $r_{B_i P_i}$. Therefore integrated elasticity reduces to

$$\begin{aligned} IE_i &= r_{B_i B_i} \left(e_{B_i} \frac{CV_{B_i}}{CV_{B_i}} \right) + r_{B_i P_i} \left(e_{P_i} \frac{CV_{P_i}}{CV_{B_i}} \right) \\ &\vdots \\ IE_i &= 1 \left(e_{B_i} \frac{CV_{B_i}}{CV_{B_i}} \right) - 1 \left(e_{P_i} \frac{CV_{P_i}}{CV_{B_i}} \right) \\ IE_i &= e_{B_i} - e_{P_i} \frac{CV_{P_i}}{CV_{B_i}}, \end{aligned} \quad (11)$$

where e_{B_i} and e_{P_i} are the elasticities of B_i and P_i respectively, and CV_{B_i} and CV_{P_i} are the coefficients of variation of B_i and P_i . Elasticities are calculated as

$$e_i = \frac{1}{\lambda} \frac{\partial \lambda}{\partial a_i} \bar{a}, \quad (12)$$

where $\bar{a}$ is the mean value for vital rate a_i . Since all of the variability is due to variability in fraction spawning,

$$CV_{B_i} = CV_{f_i} \quad (13).$$

To transform equation (2) in Chapter three into an expression of integrated elasticities we first expressed it in terms of elasticities.

$$\sigma^2 = \mathbf{e}^T \mathbf{D} \mathbf{e} \quad (14)$$

Here $\mathbf{e}$ is a vector of elasticities of λ with respect to element a_i , and $\mathbf{e}^T$ its transpose. In the case we examine here.

$$\mathbf{e}^T = [e_{B_1}, e_{B_2}, e_{B_3}, e_{B_4}, e_{P_1}, e_{P_2}, e_{P_3}]$$

$$\mathbf{e}^T = \left[\frac{1}{\lambda} \frac{\partial \lambda}{\partial B_1} * \overline{B_1}, \frac{1}{\lambda} \frac{\partial \lambda}{\partial B_2} * \overline{B_2}, \frac{1}{\lambda} \frac{\partial \lambda}{\partial B_3} * \overline{B_3}, \frac{1}{\lambda} \frac{\partial \lambda}{\partial B_4} * \overline{B_4}, \frac{1}{\lambda} \frac{\partial \lambda}{\partial P_1} * \overline{P_1}, \frac{1}{\lambda} \frac{\partial \lambda}{\partial P_2} * \overline{P_2}, \frac{1}{\lambda} \frac{\partial \lambda}{\partial P_3} * \overline{P_3} \right] \quad (15).$$

$\mathbf{D}$ is a symmetric matrix of elements

$$D_i = CV_i CV_j r_{ij} \quad (16)$$

When variability is confined to fraction spawning $\mathbf{D}$ is

$$\begin{array}{ccccccc} CV_{B_1}^2 & 0 & 0 & 0 & -CV_{B_1} CV_{P_1} & 0 & 0 \\ 0 & CV_{B_2}^2 & 0 & 0 & 0 & -CV_{B_2} CV_{P_2} & 0 \\ 0 & 0 & CV_{B_3}^2 & 0 & 0 & 0 & -CV_{B_3} CV_{P_3} \\ 0 & 0 & 0 & CV_{B_4}^2 & 0 & 0 & 0 \\ -CV_{B_1} CV_{P_1} & 0 & 0 & 0 & CV_{P_1}^2 & 0 & 0 \\ 0 & -CV_{B_2} CV_{P_2} & 0 & 0 & 0 & CV_{P_2}^2 & 0 \\ 0 & 0 & -CV_{B_3} CV_{P_3} & 0 & 0 & 0 & CV_{P_3}^2 \end{array} \quad (17)$$

If we further confine variability to fraction spawning at age a single age, i, any element of **D** involving a term other than CV_{B_i} or CV_{P_i} reduces to zero.

Therefore expansion of equation (14) yields that

$$\sigma^2 = e_{B_i}^2 CV_{B_i}^2 - 2CV_{B_i} CV_{P_i} - e_{P_i}^2 CV_{P_i}^2, \quad (18)$$

$$\sigma^2 = (e_{B_i} CV_{B_i} - e_{P_i} CV_{P_i})^2. \quad (19)$$

Substituting (11) into (19) yields

$$\sigma^2 = (IE_i CV_{B_i})^2. \quad (20)$$

Substituting (13) into (20) yields

$$\sigma^2 = (IE_i CV_{f_i})^2. \quad (21)$$

Therefore, those life histories with the largest integrated elasticities should have the largest growth rate of variance and hence the highest probability of extinction. Simulation results support this expectation. Those life histories with the largest integrated elasticities had the highest simulated probability of extinction when variability was placed in fraction spawning. The integrated elasticities accurately predict the order of jeopardy when there was variability in fraction spawning at age two or age three (Figs. 1,4, and 7).

An important question to address was how variability in fraction spawning compares to variability in ocean survival (P_1) in its influence on population dynamics. Again we examined the relationship between integrated elasticity

and σ^2 . When variability was confined to ocean survival, all elements of **D** involving a term other than CV_{P_1} reduce to zero. Therefore equation (14) reduced to,

$$\sigma^2 = (e_{P_1} CV_{P_1})^2. \quad (22)$$

Since variability in P_1 affects only one vital rate, $e_{P_1} = IE_5$. Therefore we can express equation (22) equivalently as

$$\sigma^2 = (IE_5 CV_{P_1})^2. \quad (23)$$

This simplification of the expression reduced the problem of interest to a simple comparison of integrated elasticities. Examination of equations (21) and (23) demonstrated that for equivalent amounts of variability placed alternately in fraction spawning or first year survival, the relative probability of extinction can be determined solely by the integrated elasticities. A comparison of integrated elasticities (Fig. 7) lead to the expectation that variability in early ocean survival (P_1) should have a greater impact on population dynamics than equivalent variability in realized fecundity at any age. Results from Chapter three support this expectation. From Figure three in Chapter three we can see when coefficient of variation of ocean survival is 0.15, σ^2 is approximately 0.025 for all indeterminate semelparous life histories. For a coefficient of variation of 0.15 in fraction spawning at age 2 years or 3 years, σ^2 is much smaller than 0.025 for all life histories we examined (Figs. 3 and 6). Mathematically we can see why fraction spawning

should also have a comparatively lesser impact through the negative covariance term from expression (4). This negative covariance dampens the oscillations in population size and therefore reduces probability of extinction. When an age class has a poor turnout one year, those absent simply age naturally in the ocean environment (rather than spawning and subsequently dying). The following year survivors return to spawn as part of an abnormally large subsequent year class.

Although the diffusion approximation based on analytical estimates of μ and σ^2 was able to correctly predict the relative order of jeopardy, we wanted to further determine if absolute estimates of probability of extinction were in agreement with those of simulations. We found diffusion approximation estimates for probability of extinction when variability was in age two fraction spawning were a poor fit to simulation estimates (Fig. 8). To determine the source of the bias, we examined the accuracy of estimates for μ and σ^2 generated by equation (1) in Chapter three and equation (21) in this chapter (Figs. 9 and 10). Despite relatively good fits between these estimates of μ and σ^2 with those of simulations, the estimates of probability of extinction were strongly negatively biased. This led to the conclusion that the error in the estimate was rooted in Lande and Orzack's (1988) diffusion approximation (equation (1) in Chapter one). One possible explanation for the bias was the violation of assumption of small changes in the state variable implicit in the diffusion approximation. It has been shown previously that diffusion approximations produce inaccurate results when changes in the state variable

are large (Grassman and Ludwig 1983). However the fit was poor across almost all levels of environmental variability. If the poor fit were due solely to the size of changes in abundance we would expect that at low variability the estimates of probability of extinction would be more accurate. This poor fit at all levels of variability was likely due to the inability to effectively equate an extinction process based on multiple cohort extinction (simulation) with that based on a single total population extinction (diffusion approximation) when variability is in fraction spawning. The diffusion approximation determined probability of extinction from estimates of how frequently total population size will make a first crossing of the quasi-extinction threshold. In contrast, the simulation quantified the frequency that all spawning cohorts cross the quasi-extinction threshold. When variability was in fraction spawning, the link between variability in cohort size and population size is especially poor.

The next question to address was if the diffusion approximation based on estimate of μ and σ^2 from the Tuljapurkar equations was more accurate when variability was in a later age class. To address this, we modeled a population where environmental variability was expressed in age three fraction spawning. Once more we compared results of simulation to those of the diffusion approximation and found estimates for probability of extinction were a poor fit to simulation estimates (Fig. 11). In fact, the estimates were worse than for the case where variability was at age two. Once again we examined the estimates of μ and σ^2 from equation (21) and equation (1) in Chapter three. We compared these parameter estimates to those of the simulations in an

effort to determine the source of the error (Figs. 12 and 13). In this case we found that there was a consistent bias to underestimate σ^2 and therefore overestimate μ . Since both a positive bias in μ and a negative bias in σ^2 should result in a negative bias in probability of extinction for the diffusion approximation, these parameter biases could account for the very poor fit that we see here. To determine if the source of the bias was entirely due to poor estimates of μ and σ^2 , we placed corrected values of μ and σ^2 calculated from simulation data into the diffusion approximation (Fig. 14). Although the estimates of probability of extinction using the corrected values were closer to simulation estimates, they were still strongly negatively biased. Leading to the conclusion that the source of this error is most likely rooted in the diffusion approximation. Part of the bias is accounted for by the inability to equate extinction based on multiple cohort extinction events to that based on a single population extinction event. Additionally when variability is in age three fraction spawning the yearly changes in abundance are expected to be larger than when the same amount of variability is placed in age two fraction spawning. The integrated elasticities illustrate this clearly (Fig. 7). Again diffusion approximations have been shown to produce inaccurate results when changes in the state variable are large (Grassman and Ludwig 1983).

Discussion

Variability in fraction spawning leads to a probability of extinction proportional to the integrated elasticity of the age class where it is expressed. For the life histories examined here, integrated elasticity due to variability in

ocean survival is larger than the integrated elasticity due to variability in fraction spawning at any age. Therefore we expect Pacific salmon to be more sensitive to variability in ocean survival than variability in fraction spawning. However, this conclusion is based on elasticity calculations made from point estimates of vital rates typical of salmon life history. Wisdom et al. (2000) have recently highlighted the folly of drawing conclusions from such point estimates. Future work might benefit from the use of life-stage simulation analysis (Wisdom et al. 2000), which would quantify the uncertainty associated with such a conclusion.

A previous population viability analysis combined matrix simulations and a diffusion approximation to estimate probability of extinction as we have done here. Cisneros-Mata et al, (1997) compared diffusion and simulation models of Totoaba (*Totoaba macdonaldi*) life history and found significant negative bias in the diffusion approximation when the variability was introduced in recruitment. In Chapter three we found that when variability was in ocean survival the diffusion approximation produced negatively biased results for populations with a narrow distribution of age of maturity. Here again we find that when variability was in fraction spawning the diffusion approximation produced negatively biased results. Clearly the diffusion approximation does not accurately estimate absolute probability of extinction when (1) spawning abundance is not tightly linked to population abundance or (2) variation in population abundance is large.

Despite the poor fits of the analytical model (Tuljapurkar and Orzack 1980, Tuljapurkar 1982, 1989, 1990, Lande and Orzack 1988) to simulated probability of extinction when variability is in fraction spawning, the analytical model does predict the simulated order of jeopardy correctly. This holds true when variability is in fraction spawning at age two years or three years and includes the order inversion. Since the integrated elasticities (Fig. 7) show an order inversion as well, it is not surprising that the analytical methods correctly inverted probabilities of extinction as variability shifted from age two to age three. However, because we are unable to equate quasi-extinction level based on cohort size with a quasi-extinction level based on population size, the diffusion approximation cannot produce reliable estimates of absolute probability of extinction. Future application of the diffusion approximation to salmon modeling should be limited to determining relative jeopardy.

Integrated perturbation analysis has a short history in ecology. Caswell (1985) in his study of the demography of unitary ramets, utilized integrated sensitivities to measure the direct and indirect affect on λ of an increase in clonal reproduction. In this case there was a trade-off between sexual and clonal reproduction. Van Tienderen (1995) used integrated elasticities in a stage-based model to measure proportional changes in λ to an increase in disease resistance. In this case there was covariation between the healthy and diseased stage in the perennial weed *Plantago lanceolata*. These studies used integrated perturbation analysis to determine the effects of a permanent change in a vital rate on the population growth rate. Here we have illustrated

an additional use for integrated elasticities, to gauge the effect variability in a particular vital rate will have on μ and σ^2 and therefore probability of extinction.

One of the unusual aspects that we examined was the effects of negatively correlated vital rates. Doak et al, (1994) using a stage-based model of the desert tortoise (*Gopherus agassizii*), demonstrated that correlated vital rates could increase variability in abundance and therefore increase probability of extinction. However, in the case they examined positive correlations dominated, leading to an increase of variance in abundance (Chapter 3 equation (2)). Here we have illustrated an example of semelparity leading to negatively correlated vital rates. This negative correlation reduces variability in abundance compared to that due to independent fluctuations in these same vital rates (equation (19)), and consequently reduces probability of extinction.

Jonsson and Ebenman (2001) examined the effects of life history structure on probability of extinction for semelparous populations with many offspring. As outlined in Chapter one discussion, they used a stage-structured model built on different assumptions than those in the age-structured model used here. These differences make it difficult to compare their results to ours. However, in contrast to what we have found here, they found variability in age of maturity had a greater affect on probability of extinction than variability in juvenile survival. This is likely due to the fact that, in their model, delaying reproduction meant that an individual would never mature. The probability of surviving an additional time period as a juvenile, and then

maturing was very low. In this case, delayed reproduction was effectively lethal, and variability in growth rate had a drastic effect on population dynamics. This is in contrast to the case we examined, where individuals who delay reproduction are likely to return in a later time period to breed. For life histories where survival increases substantially with age, as it does in Pacific salmon life history, we would expect that variability in growth rate would have a smaller effect on probability of extinction than variability in survival.

Confidence in population viability analysis has been bolstered by Brook et al (2000) who concluded, "PVA predictions are surprisingly accurate given adequate data." However, collecting accurate data for long lived species such as chinook salmon requires long-term study (Coulson et al. 2001). Certainly this will not be possible for the myriad of endangered salmon stocks (Allendorf et al. 1997). As an alternative, the approach taken here is to determine what makes one population more vulnerable than another under a given set of conditions. This could help prioritize jeopardy without requiring data intensive models for each stock.

Wainwright and Kope (1999) outlined a system for ranking risk of Pacific salmon in which they stated, "methods that allow inclusion of both quantitative and qualitative information are needed." Here we have further developed methodology for qualitatively assessing relative risk based on life history characteristics. Additionally we have illustrated the relative importance of variability in different life history parameters, which should help fisheries managers more effectively allocate research effort. Currently

over 300 stocks of salmonids (*Oncorhynchus* spp.) are at risk of extinction in the Pacific Northwest (Allendorf et al. 1997). Allendorf et al. (1997) suggest prioritizing them by threat of extinction, genetic and evolutionary legacy, and ecological legacy. Our work has focused on prioritizing threat of extinction, leaving the second two criteria to be prioritized by field biologists.

As stated in the introduction, this analysis ignores the effects of straying and metapopulation dynamics. Future research would benefit from an approach which links multiple spawning stocks into a metapopulation and analyzes the viability of both the individual spawning stocks and the greater metapopulation. Interactions between the spawning stocks may lead to emergent properties that will not be evident in this kind of analysis.

Conclusions

Variability in fraction spawning has a substantial impact on probability of extinction. However, when compared to the impact of variability in ocean survival, the greatest effect on probability of extinction is from variability in ocean survival. For managers the short of it is this, if resource limitations dictate that focus must be placed on quantifying only one vital rate, priority should be given to the ocean survival.

Additionally, variability in fraction spawning matters the most when it is the most numerous age class of a cohort that varies. A wider distribution of age classes in the spawning cohort is not helpful or harmful to mitigate risk. Rather the risk comes from variation in abundance in the dominant age class of the spawning cohort.

The diffusion approximation determines probability of extinction from estimates of how frequently total population size will make a first crossing of the quasi-extinction threshold. In contrast, the simulation quantifies the frequency that all spawning cohorts cross the quasi-extinction threshold.

When variability is in fraction spawning, the link between variability in cohort size and population size is especially poor. Although this does not affect the relative order of probability of extinction, the absolute estimates of probability of extinction from the diffusion approximation are unreliable.

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Tables

Table 1. Semelparous population structures. f is fraction spawning. p is survival probability. b is fecundity measured in yearlings/spawner. Age is measured in years. Mean age of maturity is 3 years in all cases. S_{maturity} is standard deviation in age of maturity at the stable age distribution.

	Age	f	p	b
$S_{\text{maturity}} = 0.45$	1	0	0.042	0
Spawning distribution	2	0.0476	0.5	50
.1,.8,.1	3	0.8	0.5	50
	4	1	0	50
$S_{\text{maturity}} = 0.66$	Age	f	p	b
Spawning	1	0	0.044	0
distribution	2	0.09092	0.5	50
.2,.6,.2	3	0.6	0.5	50
	4	1	0	50
$S_{\text{maturity}} = 0.77$	Age	f	p	b
Spawning	1	0	0.046	0
distribution	2	0.13044	0.5	50
.3,.4,.3	3	0.4	0.5	50
	4	1	0	50

Figures

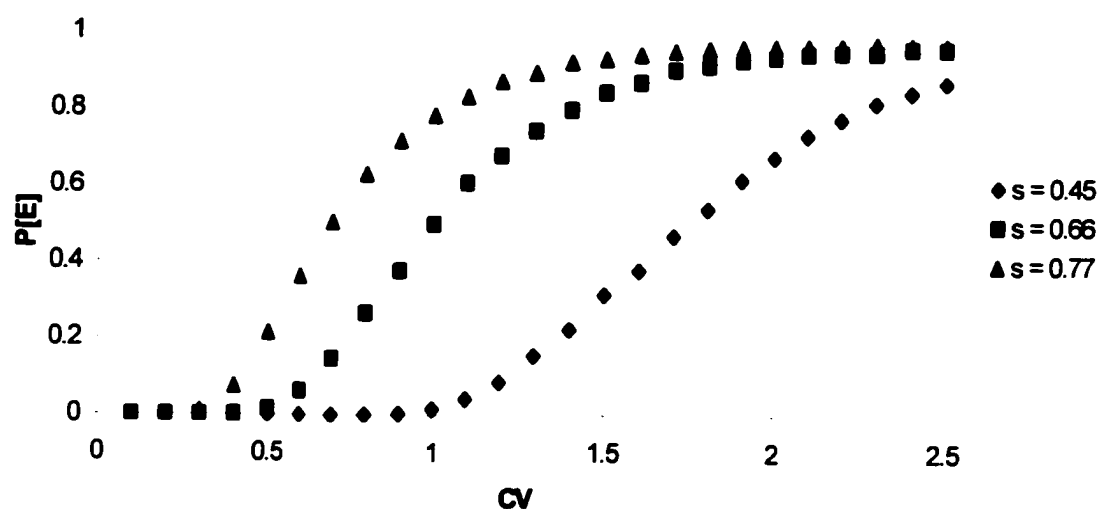


Figure 1. Effect of variation in age two fraction spawning on simulated probability of extinction. Initial population is 190 spawners. Time is 100 years. Quasi-extinction level is 100 spawners. The coefficient of variation in f_2 is represented on the x-axis. s is standard deviation in age of maturity at the stable age distribution (see Table 1).

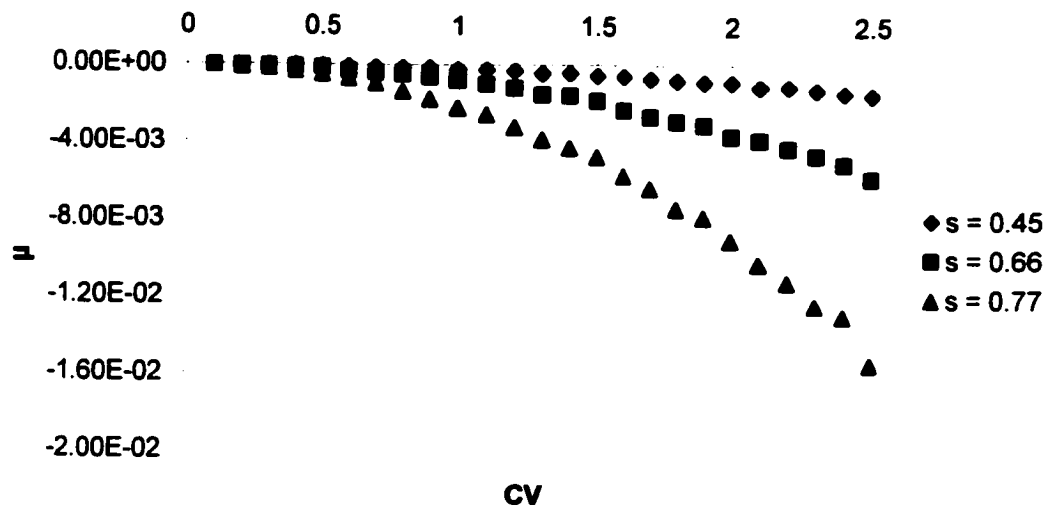


Figure 2. The effect of variation in age two fraction spawning on growth rate. Growth rate is calculated as change in mean of log abundance over the simulation period. The coefficient of variation in f_2 is represented on the x-axis. Time is 100 years. s is standard deviation in age of maturity at the stable age distribution (see Table 1).

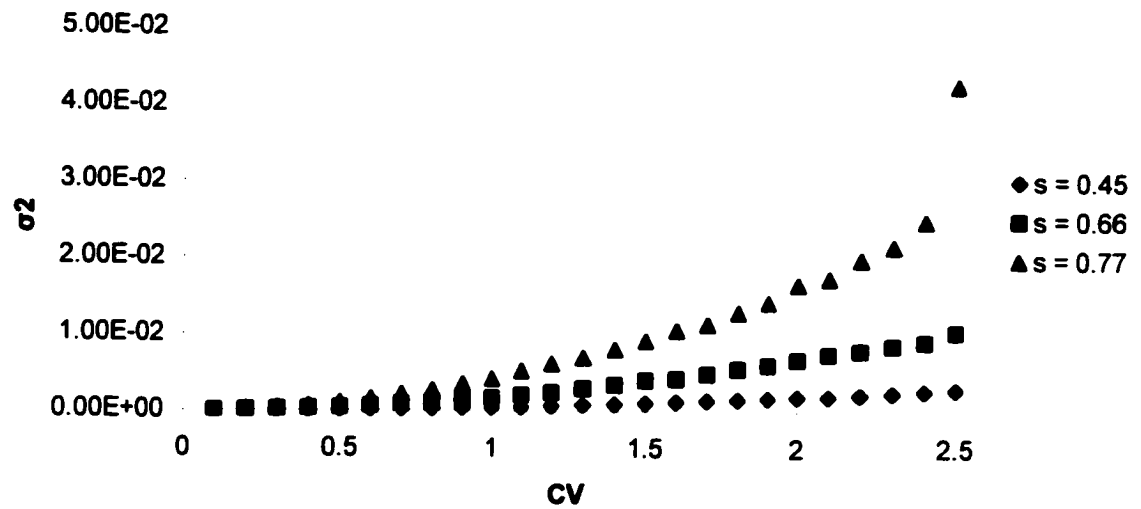


Figure 3. The effect of variation in age two fraction spawning on growth rate of variance. The coefficient of variation in f_2 is represented on the x-axis. Time is 100 years. s is standard deviation in age of maturity at the stable age distribution (see Table 1).

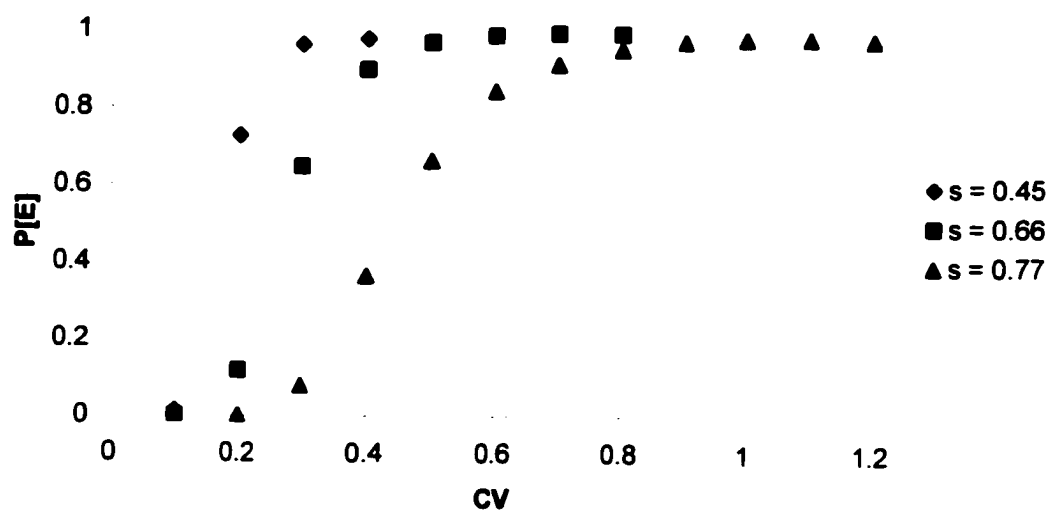


Figure 4. Effect of variation in age three fraction spawning on simulated probability of extinction. Initial population is 190 spawners. Time is 100 years. Quasi-extinction level is 100 spawners. The coefficient of variation in f_3 is represented on the x-axis.

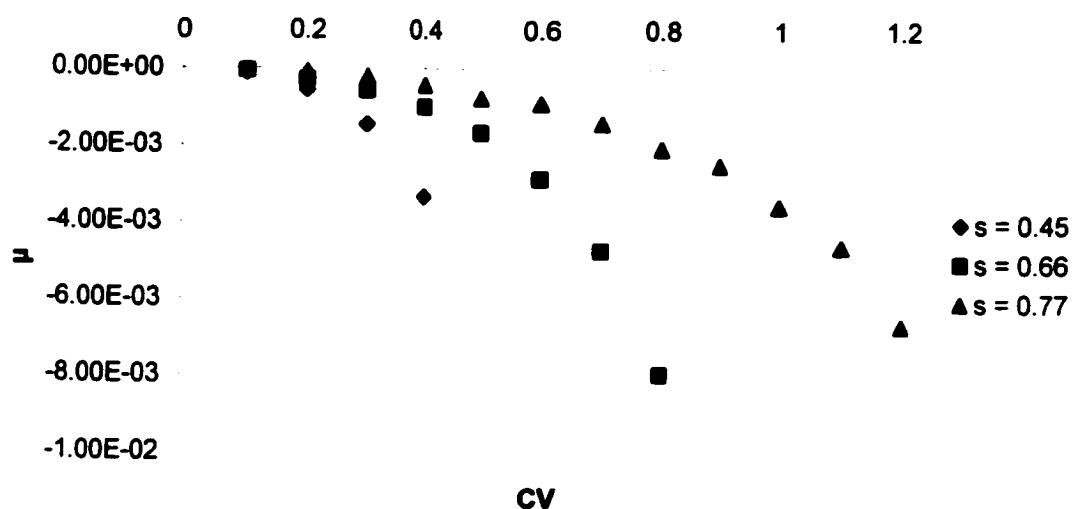


Figure 5. The effect of variation in age three fraction spawning on growth rate. Growth rate is calculated as change in mean of log abundance over the simulation period. The coefficient of variation in f_3 is represented on the x-axis. s is standard deviation in age of maturity at the stable age distribution. CV of 0.4 is maximum variability possible for $s=0.45$. CV of 0.8 is maximum variability possible for $s=0.66$. Time is 100 years.

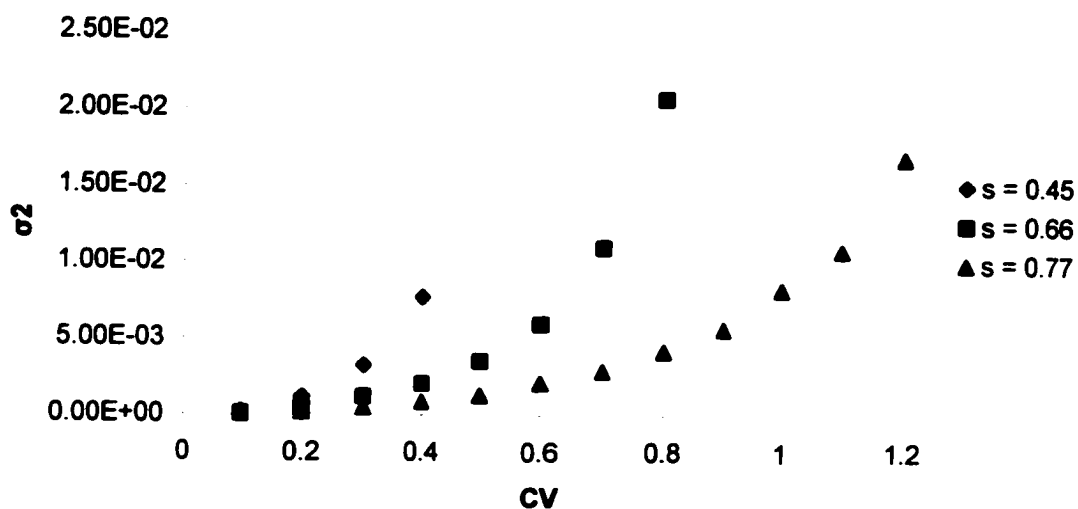


Figure 6. The effect of variation in age three fraction spawning on growth rate of variance. The coefficient of variation in f_3 is represented on the x-axis. s is standard deviation in age of maturity at the stable age distribution. CV of 0.4 is maximum variability possible for $s=0.45$. CV of 0.8 is maximum variability possible for $s=0.66$. Time is 100 years.

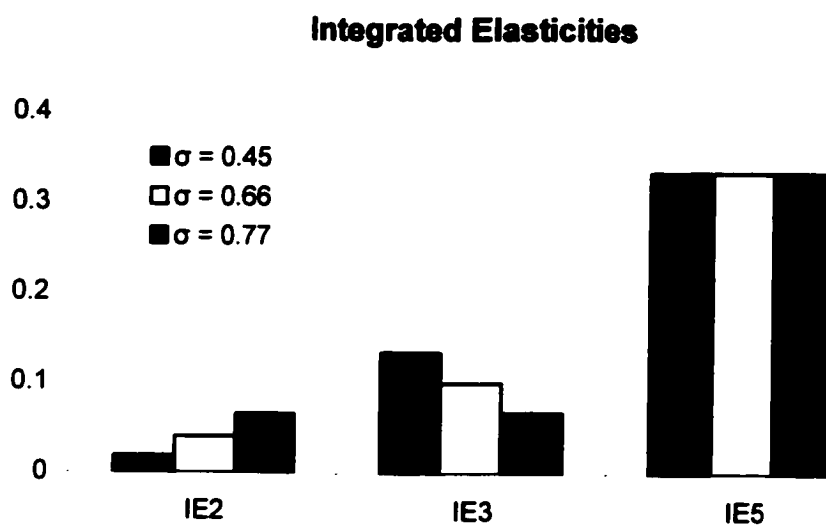


Figure 7. Integrated elasticities of λ to fluctuations in the vital rates. IE_2 is the integrated elasticity of λ due to variability in fraction spawning at age 2 years. IE_3 is the integrated elasticity of λ due to variability in fraction spawning at age 3 years. IE_5 is the integrated elasticity of λ due to variability in first year survival.

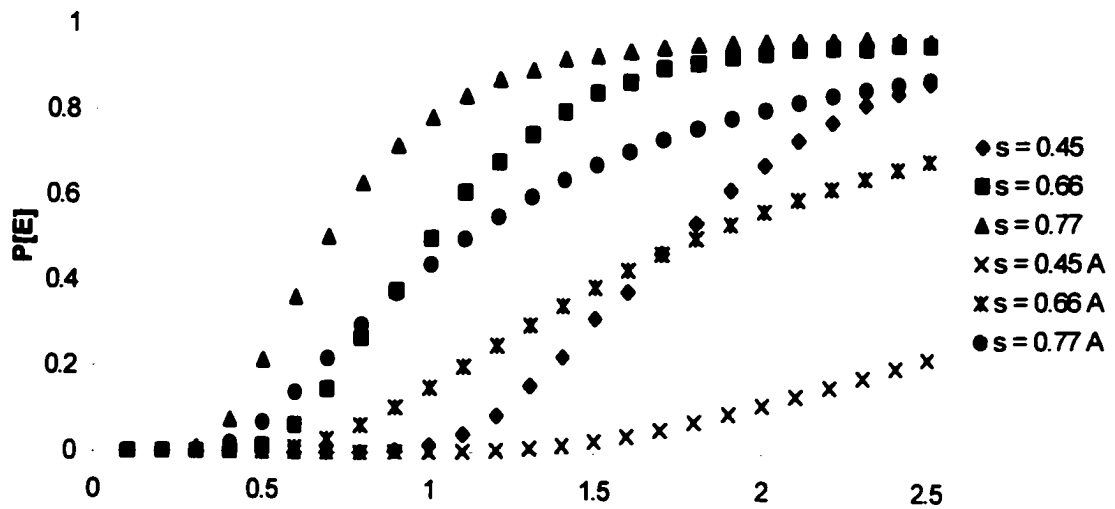


Figure 8. Comparison of probabilities of extinction from simulation and analytical models when variability is in age two fraction spawning. Initial population is 190 spawners. Time is 100 years. Quasi-extinction level is 100 spawners. The coefficient of variation in f_2 is represented on the x-axis. s is standard deviation in age of maturity at the stable age distribution (see Table 1). Analytical estimates are labeled with 'A'.

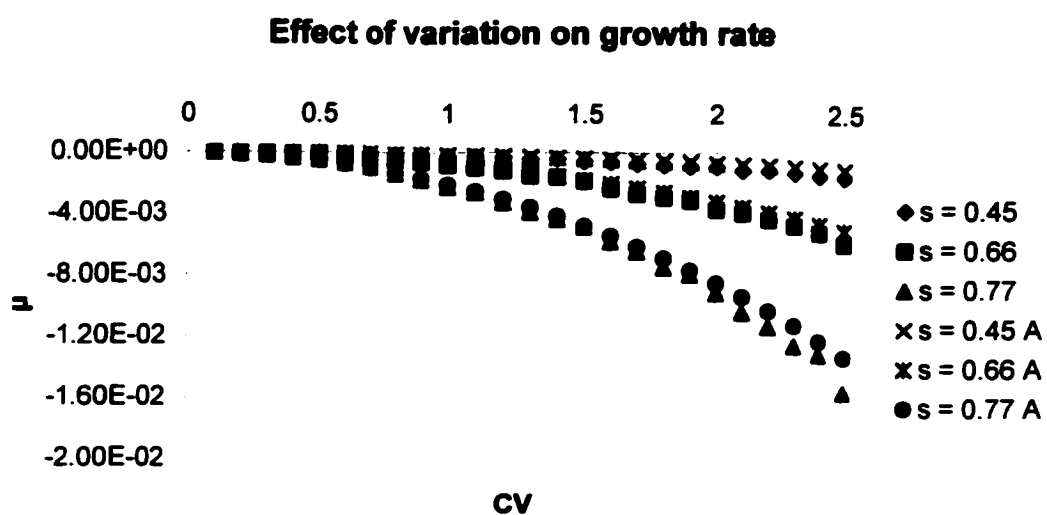


Figure 9. Comparison of the growth rates calculated from analytical method (1) with the simulation values. The coefficient of variation in f_2 is represented on the x-axis. s is standard deviation in age of maturity at the stable age distribution. Time is 100 years. Analytical estimates are labeled with 'A'.

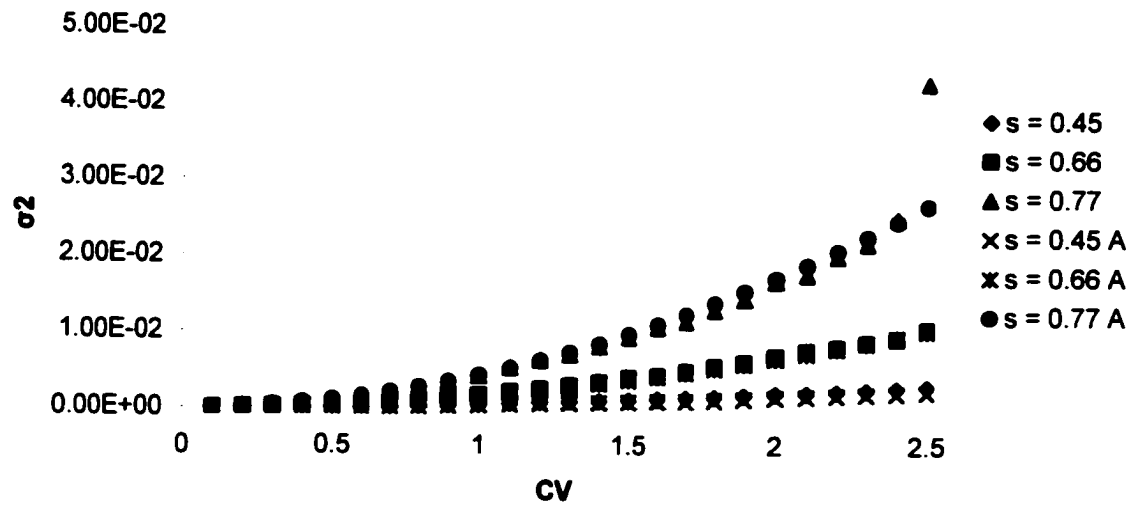


Figure 10. Comparison of growth rate of variance from simulation and analytical models. The coefficient of variation in f_2 is represented on the x-axis. s is standard deviation in age of maturity at the stable age distribution. Time is 100 years. Analytical estimates are labeled with 'A'.

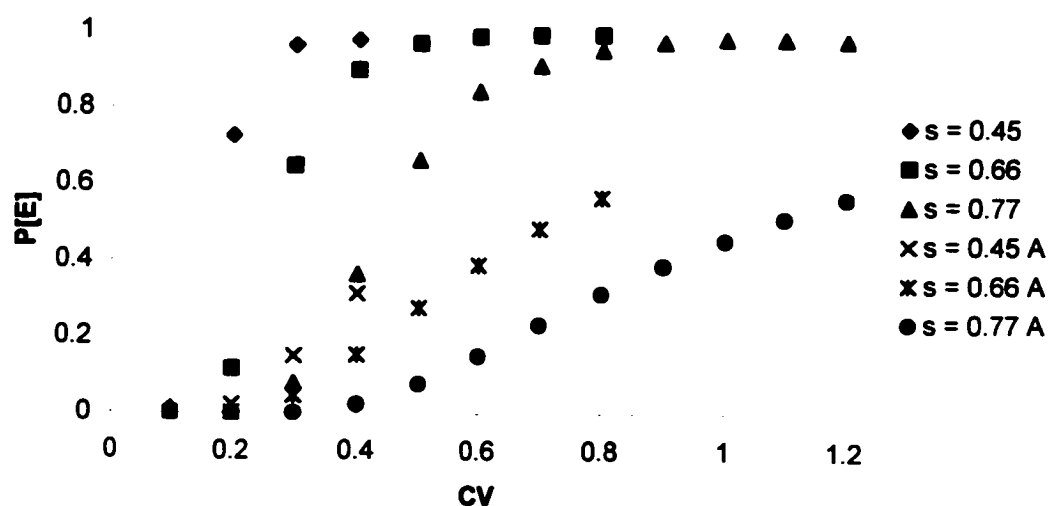


Figure 11. Comparison of simulated probabilities of extinction from simulation and analytical models when variability is in age three fraction spawning. Initial population is 190 spawners. Time is 100 years. Quasi-extinction level is 100 spawners. The coefficient of variation in f_3 is represented on the x-axis. s is standard deviation in age of maturity at the stable age distribution. CV of 0.4 is maximum variability possible for $s=0.45$. CV of 0.8 is maximum variability possible for $s=0.66$. Analytical estimates are labeled with 'A'.

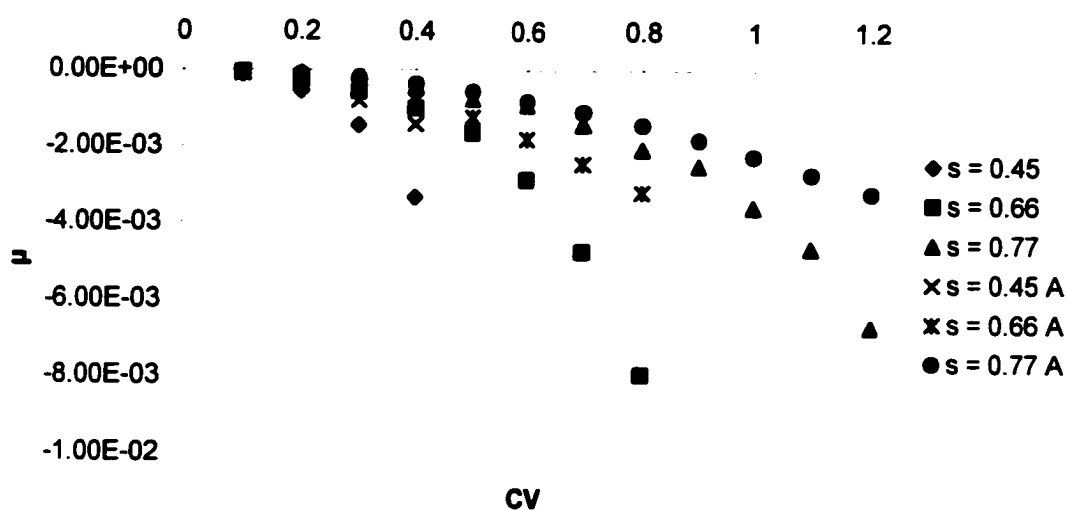


Figure 12. Comparison of the growth rates calculated from analytical method (1) with the simulation values. The coefficient of variation in f_j is represented on the x-axis. s is standard deviation in age of maturity at the stable age distribution. CV of 0.4 is maximum variability possible for $s=0.45$. CV of 0.8 is maximum variability possible for $s=0.66$. Time is 100 years. Analytical estimates are labeled with 'A'.

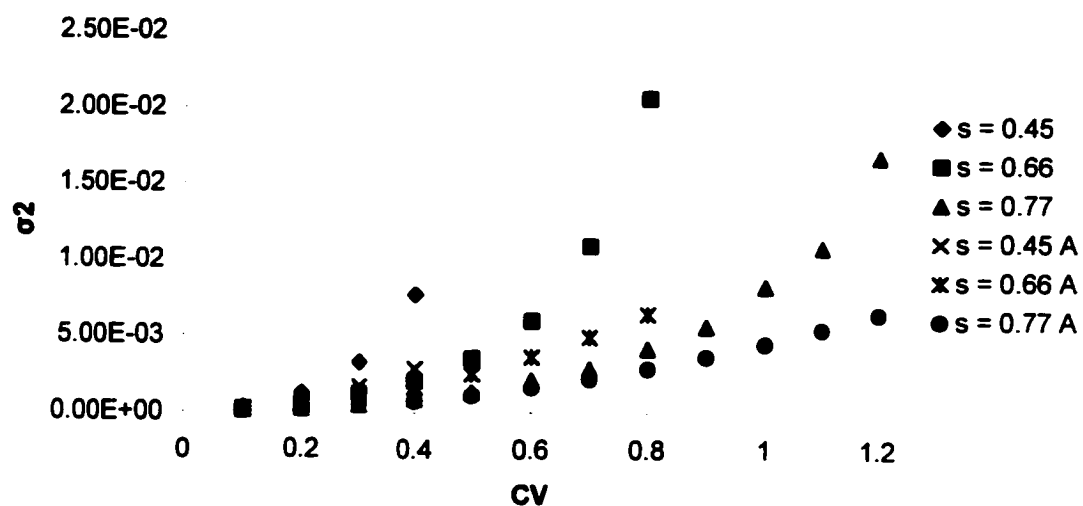


Figure 13. Comparison of growth rate of variance from simulation and analytical models. The coefficient of variation in f_3 is represented on the x-axis. s is standard deviation in age of maturity at the stable age distribution. CV of 0.4 is maximum variability possible for $s=0.45$. CV of 0.8 is maximum variability possible for $s=0.66$. Time is 100 years. Analytical estimates are labeled with 'A'.

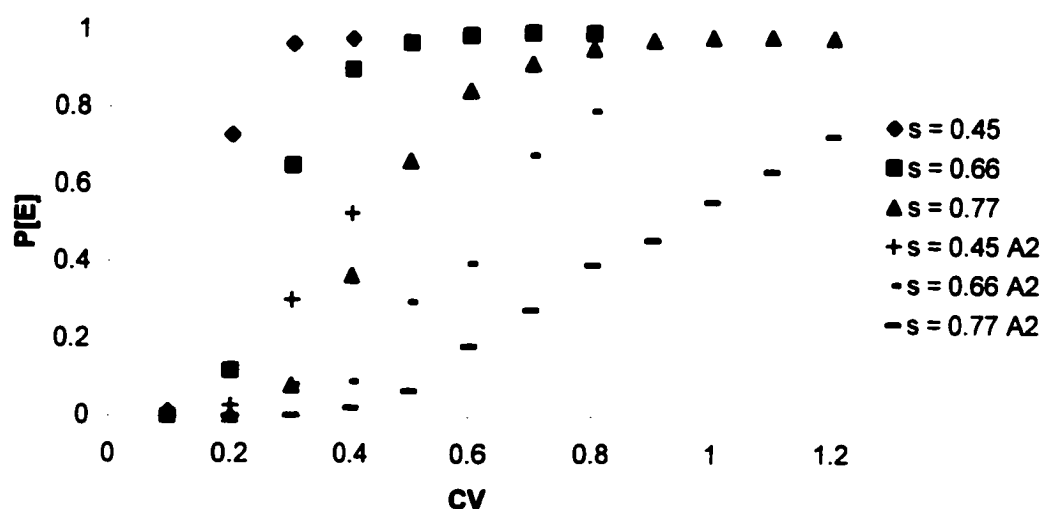


Figure 14. Comparison of simulated and analytical probability of extinction. Analytical model is using values of μ and σ^2 taken from simulation data. Initial population is 190 spawners. Time is 100 years. Quasi-extinction level is 100 spawners. The coefficient of variation in f_j is represented on the x-axis. s is standard deviation in age of maturity at the stable age distribution. CV of 0.4 is maximum variability possible for $s=0.45$. CV of 0.8 is maximum variability possible for $s=0.66$. Analytical estimates are labeled with 'A2'.