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POPULATION VIABILITY OF THE SNAKE RIVER CHINOOK SALMON (*Oncorhynchus Tshawytscha*)

Recovery Issues for Threatened and Endangered Snake River Salmon
Technical Report 11 of 11

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**POPULATION VIABILITY OF THE SNAKE RIVER
CHINOOK SALMON (Oncorhynchus tshawytscha)**

**Recovery Issues for Threatened and Endangered Snake River Salmon
Technical Report 11 of 11**

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EXECUTIVE SUMMARY

A stochastic simulation model of **spring** chinook population dynamics was **parameterized** using 36 years of redd count **data from** five index streams on the middle fork of the Salmon **River** in Idaho. Two versions of the **model**, one in which spawning age structure was presumed to follow an evolutionarily stable strategy and another in which spawning age structure was constrained to observed values were examined. The models were then used to generate 1000 statistically representative population projections over the next 100 years to assess risk of extinction and prospects for stock rebuilding. Current levels of production and mortality appear to suffice for maintaining the status quo, virtually assuring persistence over the next 100 years, barring **catastrophes**, but providing no hope for rebuilding. A doubling of the current population level over the next 100 years can be expected to follow an increase in a (density independent mortality or fry production) of 5 to **25%**, but rebuilding to the population levels prevailing in the 1950's will require an increase in a of at least 37%.

Population Viability of the Snake River Chinook Salmon (Oncorhynchus tshawytscha)

Part of any endangered species recovery plan should be a risk assessment in which the probabilities of extinction over some finite period are related to various management **options**. Such a risk **assessment** consists of two steps: (1) relating management options to their impact on demographic parameters, and (2) determining the **relationship** between the demographic parameter changes and prognosis for population persistence. The latter step is generally **referred** to as **population viability analysis** (PVA) and **it** involves the application of **population** models utilizing the best information on life history of the species in question. The work presented here reports on a PVA for the Snake River spring chinook salmon (Oncorhynchus tshawytscha).

The purpose of this work is three-fold; first to utilize existing time sequence **datasets** on redd numbers in several **Idaho "index streams"** on the middle fork of the Salmon River **to parameterize** a Snake River spring chinook salmon population dynamics model; second, to use **the parameterized** model for assessing probabilities of extinction over the **next 100 years**; and third, to evaluate the effects on extinction **probabilities of altering** model parameter values manipulable through **appropriate** management. Data were supplied by the Idaho Department of **Fish and Game**, and **cover** a period from **1957 to 1992**.

Because the precise trajectory of a population depends on a series of stochastic events... **environmental** fluctuations, **deviations** in sex ratio about a mean, variations **from mean** straying **rates**... **any** appropriate model of necessity must be stochastic in nature. As such, each run can be thought of as a random selection from a universe of possible population trajectories specific to the **values of the parameters** used and the initial population conditions. **If, over (say) 100 runs, 80 result in extinction** within **100 years**, then the probability of persistence over **100 years** is estimated at 20%.

THE MODEL

General Form: PVA has at its **disposal** a number of classes of population model. At one extreme are **the** so-called "systems" models, **which incorporate** significant detail in the processes to **be modelled**. The Salmon Life Cycle Model (SLCM, Lee and **Hyman** 1992) which includes considerable life history detail and into which still more detailed submodels can be plugged, is such a model. At the other extreme are the holistic models which, in theory, trade complexity for generality of application. The theoretical models of Goodman (**1987**), Ewens et al. (**1987**) and the Dennis model (Dennis **et al.** 1991) are of this type. Both extremes have their advantages and drawbacks. With precise and complete knowledge of parameter values, the systems models should be the most accurate. Unfortunately, in the case of the Snake River chinook **salmon** (and, for that matter, most species), many parameter values are little more than educated guesses. This opens the **possibility of** cascading errors in the projection of future population values. The simpler, holistic models are far less parameter-intensive, and the Dennis model permits **parameterization** using time sequence data (see below). **But** these models generally are too simplistic to be of use except **under** rather... limited circumstances. The Dennis model, for example, does **not consider** density dependence. Thus its applicability to populations that may, on

occasion, rise close to carrying capacity is shaky. (A later, still unpublished model corrects 'for this factor. Dennis, Univ. Idaho, pers. comm.). The Dennis model also uses a mathematical convergence that may be misleading over periods of time as short as 100 years.

For the purposes of this PVA, a model of intermediate complexity is used. In keeping with standard practice in fisheries biology/the basic model structure incorporates both early life, instantaneous density feedback (Ricker 1958) and continuous hatch-to-adult density feedback (Beverton and Holt 1954). The model also incorporates age structure.

Define the following terms:

$n_f(t)$, $n_m(t)$, $n(t)$ are numbers of spawners in year t , female, male and total

$N(t)$ is the number of redds produced in year t

$p(t)$ is the proportion of fish spawned in year t surviving to age 2 that are female.

$q_{fi}(t)$ is the proportion of females hatched in year t that return to spawn at age i

$q_{mi}(t)$ is the equivalent for males

$g(t)$ is the Ricker beta for fish spawning in year t

$\xi_f(t)$ is the ratio of female fish surviving to age 2 to the number of redds from which they arose in year t

$\xi_m(t)$ is the ratio of spawning male fish surviving to age 2 to the number of redds from which they arose in year t

$\mu(t)$ is a Beverton-Holt constant

$\delta(t)$ is the ratio of females to the redds they produce in year t before the influence of density feedback.

It follows from the above that

$$N(t) = n_f(t)/\delta(t)$$

in the absence of density feedback. After Ricker-type feedback,

$$N(t) = n_f(t)e^{-\mu N(t)}/\delta(t) \quad (1)$$

These redds subsequently produce fry which rear in tributaries where they experience continuing (Beverton-Holt type) density influences, migrate to sea, then return to spawn at age 2 (males only), or 3, 4, or 5 years. The number of fish surviving to age 2 that are female, divided by the number of redds giving rise to them is $\xi_f(t)p(t)$, and the fraction of these that return to spawn at age i is $q_{fi}(t)$. Also the number of female spawners returning in year $t+5$ are drawn from the pool of females produced in years t , $t+1$, $t+2$. Incorporating the Beverton-Holt feedback term and noting that the initial number of fry in year t is proportional to the number of redds from which they arose,

$$n_f(t+5) = \frac{\xi_f(t)N(t)q_{f5}(t)p(t)}{1+\mu(t)N(t)} t. + \frac{\xi_f(t+2)N(t+2)q_{f3}(t+2)p(t+2)}{1+\mu(t+2)N(t+2)} \quad (2a)$$

Similarly,

$$n_m(t+5) = \frac{\xi_m(t)N(t)q_{m5}(t)[1-p(t)]}{1+\mu(t)N(t)} t. + \frac{\xi_m(t+3)N(t+3)q_{m2}(t+3)[1-p(t+3)]}{1+\mu(t+3)N(t+3)} \quad (2b)$$

The number of parameters describing these dynamics is already unwieldy and with the addition of stochastic parameters, would make best fit estimates unreliable. Accordingly, I simplify the model at this point in either of two ways. For the first, the "fitted age" model, I make use

of the concept of the evolutionary stable strategy (ESS). Suppose females, on average, made the greatest genetic contribution to future generations by returning to spawn at age-4. Then there would be selection pressure favoring predilections to return at that age. However, as more and more females return at age 4 the population becomes increasingly at risk from "putting all its eggs in one basket;" if the corresponding year were characterized by bad environmental conditions, the entire year class might be lost. There is, therefore, a selective advantage in the fish evolving a genetic program that favors temporal dispersion in age at return. Furthermore, unless there is no density feedback among individuals of a year class spawning in the same year, individuals returning at any one age should, on average, contribute equally to those returning at any other age; else natural selection would favor a lowered frequency of return at the age which, on average, contributed least. Thus (on average), the evolutionarily stable strategy (ESS) is given by

$$\frac{\xi_f(t)N(t)q_{f5}(t)}{1+\mu(t)N(t)} = \frac{\xi_f(t+1)N(t+1)q_{f4}(t+1)}{1+\mu(t+1)N(t+1)} = \dots$$

But the various terms in the above expression are either constants or uncorrelated. Thus, where E[] denotes expectation,

$$E[\xi_f(t)q_{f5}(t)] = E[\xi_f(t+1)q_{f4}(t+1)] = \text{etc.}$$

The same argument holds for males. Denote $\xi_f(t)q_f(t)$ with $\tau_f(t)$, and $\xi_m(t)q_m(t)$ by $\tau_m(t)$. Then equations (2) may be rewritten

$$n_f(t+5) = \frac{\tau_f(t)N(t)p(t)}{1+\mu(t)N(t)} \cdot \dots \cdot \frac{\tau_f(t+2)N(t+2)p(t+2)}{1+\mu(t+2)N(t+2)} \quad (3a)$$

$$n_m(t+5) = \frac{\tau_m(t)N(t)[1-p(t)]}{1+\mu(t)N(t)} \cdot \dots \cdot \frac{\tau_m(t+3)N(t+3)[1-p(t+3)]}{1+\mu(t+3)N(t+3)} \quad (3b)$$

The alternate approach, the "forced age" model, calculates $n_f(t+5)$, $n_m(t+5)$ as above, but weights each term according to observed spawning age **bundance** (Chapman et al., 1990).

Now τ_f and τ_m vary according to climatic and other temporally varying factors. After Peterman (1981), I therefore write

$$\tau_j(t) = \hat{\tau}_j e^{-\sigma w(t)} : w(t) \sim N(0, 1) \quad (4a)$$

where j is either f or m. Similarly,

$$\mu(t) = \hat{\mu} e^{-\sigma' w'(t)} \quad (4b)$$

The parameters $\hat{\tau}_f$ and $\hat{\tau}_m$ can be telescoped into one if we only note that the **difference** arises because some males return at age 2 while females do not, and because of possible sex-specific mortality differences. Thus, if we set $\hat{\tau}_f = \hat{\tau}_m$ and calculate $n_f(t+5)$, $n_m(t+5)$ using equations (3), we will end up with a disproportionate number of one sex. This can be rectified as follows. Denote the contributions of the different aged spawners to $n(t+5) = n_f(t+5) + n_m(t+5)$, respectively, by n_5 ,

n_4 , n_3 , and n_2 . Then add equations (3a) and (3b) to calculate $n(t+5)$ using a common $\hat{\tau}$. Assume an expected sex ratio of 1:1. Because only males return at age 2 we can now "correct" the expected proportion of females in the spawning population age 3 and above, from 0.5 to

$$\frac{(n_5+n_4+n_3+n_2)}{(n_5+n_4+n_3+n_2)+(n_5+n_4+n_3)}$$

The values of $n_f(t+5)$, $n_m(t+5)$ are then determined by drawing from the full population of $n(t+5)$ according to a binomial distribution with parameter equal to the above female proportion. Finally, if, either $n_f(t+5)$ or $n_m(t+5)$ are zero, there can be no reproduction. If both are non-zero, reproduction occurs as described in equation (1).

Equations (1), (3), and (4), along with the above binomial calculation for sex ratio define the general model except for two last considerations. Environmental fluctuations are more complex than simple white noise. It is therefore appropriate to allow for a certain amount of temporal autocorrelation in the process $w(t)$ (see eqn. [4a]). Too much generality would reintroduce many more parameters, so we compromise by allowing for a single, one-year lag correlation, writing

$$w(t) = \lambda w(t-1) + \sqrt{1-\lambda^2} w''(t) \quad (5)$$

for use in equation (4a), where λ is the autocorrelation coefficient and $w(0), w''(t) \sim N(0,1)$.

Finally, fishing pressures on these populations have been light and not well tracked. Hence, year-to-year changes in density independent mortality (reflected in τ) cannot be incorporated reliably into the model. On the other hand, effects of dam turbines and screens have been studied by Raymond (1988). Using his data, a regression of percent return (y) to the Snake River on number of turbine units (x_T) and screens (x_S) yields

$$y = 8.229 - 0.0976x_T + 0.0890x_S : R^2 = 0.596. \quad (6)$$

This relation was used to rescale $\hat{\tau}$ ($\hat{\tau}_{used} = \hat{\tau}_{equation 4} * y$) on a year-to-year basis. $\hat{\tau}$, as so calculated from the last year of data (1992) was used in subsequent population projections.

Metapopulation Considerations: Spring chinook spawn and rear (largely) in tributaries. Therefore, fish inhabiting each tributary might be thought of as comprising a single population unit. However, even if no fish returned to a tributary over a 5-year period (meaning all year classes have died out), recolonization from other tributaries via straying may stave off extinction.

There is a philosophical issue re. recolonization by strays that has not been dealt with satisfactorily in the WA literature. If recolonization is by individuals of different genetic constitution from those whose home turf is being invaded, resulting in genetic change of the native stock, is that native stock enhanced or compromised? In particular, if extinction is avoided by virtue of gradual replacement of the native population by immigrants, should the local stock nevertheless be considered extinct because its genome no longer exists? How different must the native and immigrant stocks be before we reach this conclusion?

This matter is probably not of concern where only natural, wild populations exist, because current stray rates are likely ~~to be~~ similar to the historic patterns that, in fact, defined the local stocks (unless some significant anthropogenic habitat alteration has taken place), but the presence of hatchery strays is problematic. To avoid such nasty issues, the current work focuses on "index" streams largely free of hatchery influence (Bear Valley Creek, Elk Creek, Marsh Creek, Sulphur Creek and Upper Big Creek in the middle fork Salmon River drainage in Idaho).

Given the paucity of data, straying has to be dealt with in a somewhat simplistic fashion. For example, no consideration is given in this treatment to variations in stray rate among close vs. more distant tributaries, and no consideration is given as to whether immigration is more or less likely into areas of low or high resident population density. These simplifications might have significant impacts on **the conclusions** reached in this report.

Quinn and Fresh (1984) showed that straying from a local spring chinook population increased with age of the fish and decreased with population size. The relations are close to linear. Hence, we modelled outmigration using the function

$$\theta = \text{Number of outmigrants} = \gamma t \kappa x - \phi n \quad (7)$$

where x is average age in the population, n is population size (number of potential spawners), and γ , κ and ϕ are parameters to be fit with real time sequence data.

Model Parameterization: For each of the five index streams named above, equations (3), and (4) were applied to observed redd counts over four consecutive years ($t-5$, $t-4$, $t-3$, $t-2$) to calculate number of spawners in year t . Then equation (7) was used to calculate probability of emigration, θ , for each population. Number of emigrants was determined with a binomial distribution with parameter θ , and randomly split among the sexes. Finally, number of immigrants, male and female separately, were randomly (binomially) determined for each population from the total pool of outmigrants. The resulting spawner population was then used (eqn. [1]) to calculate number of redds produced in year t . This was compared to the observed number, and the cumulative sums of squared errors was calculated over all data years for each population separately. A non-linear best fit routine (Kupferschmid and Ecker 1983) was used to estimate the various model parameters. Constraints utilized in the fitting procedure involved holding γ , β , μ , σ , σ' , λ and outmigration rate over all years non-negative, and $0 < \lambda < 1$. Initial parameter input values for 3 were based on estimated alpha values for these index streams as reported by Schaller et al. (1993), which varied about 1.9 to 2.8. Because λ applies to each of four male and three female age classes whose contributions are added, λ should be roughly one seventh the value of α . Initial input value used in the nonlinear best fit routines was 0.35. Schaller et al. (1993) estimate beta values for these streams as .0008 to .0026. The input value used in data fitting for this paper was .002. The initial estimate of μ was obtained by estimating historic number of redds at 200 two to four times present levels. Then, if Beverton-Holt feedback reduced the population at those levels by, say, 8-10%, $\hat{\mu} = -\ln(.92)/200 = .0004$. With respect to σ and σ' , suppose, as a first cut, that environmental fluctuations result in a 95% confidence swing of 20% about

the average values of $\hat{\tau}$ and $\hat{\mu}$. Then the values of σ and σ' must be on the order of 0.17. The value of the environmental autocorrelation must lie between 0 and 1; a pure guess of **0.4** was used. Data collected on spring chinook spawners and redds on the middle fork of the Salmon River in **1988** (Bjornn, Univ. Idaho, pers. comm.) suggest a redd-to-spawning female ratio of 3.5 to 4. Under present densities of about 40-80 redds per stream, and a beta value of **.002**, this translates to a delta value of **.20** to **.26**. I used an initial value of 0.25. A regression of the fraction of the population comprised of strays at Cowlitz hatchery (Quinn and Fresh, **1984**) on average age at return and escapement level provided initial estimates of γ , κ , and ϕ of -0.6, **1.00**, and **-.0002**, respectively.

Because results depend on the precise stochastic sequence (values of $w(t)$, $w'(t)$, $w''(t)$, binomially determined sex ratio, migration and distribution of immigrants) used in a simulation, **100** different runs were made, each with a different sequence. The results from all **100** provide a multivariate probability distribution for the parameters, permitting calculation of expected (mean) values and confidence limits.

An initial set of runs, designed to find values for all **10** parameters proved insensitive to initial input values of β , $\hat{\mu}$, and ϕ . . . that is, over a range of one fifth to five times the initial estimates given above, the best fit output estimates did not differ appreciably from the initial input estimates. This probably is due to the fact that populations since the **1950's** have been well below carrying capacity, therefore rendering the effects governed by these density feedback all but meaningless. Subsequently, the values of these three parameters were set at their initial input values and the best fit routine rerun to evaluate the remaining 7 parameters. Results of these later runs, the parameter solution sets for the five index streams, are shown in Table 1.

Population Projections: Because the five index streams do not comprise the full story of the metapopulation represented, results of subsequent population projections and estimates of population survival and size might be biased by limiting simulations to them. It seems likely, because the five populations are highly correlated ($r=0.826$) with respect to year-to-year redd counts, and well below carrying capacity, that their dynamics are, in fact, nearly independent. That is, **metapopulation structure** seems likely to prove a minimal factor in population projections, at least so long as the **population** remains well below **historic** levels. To test this expectation, simulations were run, ten replicates for each of the **100** parameter solution sets, for $\hat{\tau}$ set at 0.75 **its estimated** true value (to assure a fair number of extinctions for comparison purposes) and various stray rates.

There is some question as to accuracy of the redd counts. The **impact of** such measurement error on accuracy of **population** projections can be explored, **at least** crudely, as follows. Because **redd counts** are constrained to be positive, it is, not **unlikely that the measurement error** term should be approximately **lognormally distributed**. Thus, **measurement error** affects redd count in the same **manner** as environmental **fluctuations** and can be incorporated into the σ term. Population projections were run using σ equal to zero (equivalent, to a situation in which all "environmental" error is, in fact, measurement error), equal to its estimated true value (no measurement error), and equal to one **half** its estimated true value.

Following the above sensitivity tests, simulations were run, again

with ten replicates for each of the 100 parameter solution sets, varying the value of τ from 0.75 to 1.5 times its estimated true value. Results are provided in Figures 2 and 3.

RESULTS

Although the mean best fit parameter values were quite similar to their initial estimates, there was considerable variation among the 100 solution sets. This raised the possibility that there might be different sets of solutions corresponding to different local optima on the response surface. To check this possibility, scatter diagrams of τ vs $\hat{\sigma}$ were constructed to look for any apparent discontinuities or evidence of multiple peaks. There is no such evidence.

Simulations with the ESS model, regardless of the stray rate used or the values of σ and $\hat{\tau}$, predicted a spawning age structure with jacks comprising 30-45% of all males and 3, 4, and 5 year-olds of both sexes occurring in a ratio of roughly 1:1.1:1.2. In fact, observed age structure has jacks at less than 5%, essentially no spawning 3 year-olds., and a ratio of 4 to 5 year-olds of between 1:3 and 1:4 (Chapman et al., 1990; W. Miller, Fisheries Assistance Office, U.S. Fish and Wildlife Service, Dwarshak Fish Hatchery). The forced age model utilized these observed values, setting jack rate at 5% and the 3:4:5 year-old ratio for both sexes at 0:20:75. Interestingly, population persistence projections based on these two variants of the model were almost identical, (see below), although predicted redd counts in year 100 average about twice as high for the forced age model.

Roth model versions predict stray rates of approximately 5%. Data on actual stray rates are poor for the Salmon River middle fork, but the expected rate for spring chinook spawning at the Cowlitz hatchery, projected for the population density levels and spawning age structure seen in the index streams, is about 4% (based on the aforementioned regression of percent strays on population size and age-at-return (Quinn and Fresh 1984). The estimates are very close.

Results of the sensitivity analysis for stray rate are presented in Figure 1. With respect to the ESS model, it is clear that stray rate has virtually no effect on either population persistence or size. The forced age model (Figure 1b) suggests that both- likelihood of persistence and, expected redd abundance to decline as stray rate rises. In the vicinity of the estimated true stray rate and below, however, neither persistence probability nor redd count in year 100 vary significantly with stray rate. Therefore, both models indicate that, so long as stray rates do not exceed the estimated value, metapopulation structure has little effect on the population dynamics. That is to say, the data obtained from the five index streams can be used, with minimal bias, to estimate impacts on future trends of varying management practices.

With respect to bias introduced by errors in redd count data (Table 2), measurement error appears to have a small negative effect on number of redds in year 100, and to elevate slightly the probability of persistence. The forced age model indicates the same increase in expected redd number as measurement error falls, and no effect on likelihood of persistence. It is reasonable to conclude that unless the bulk of fluctuations described by the σ term are due to measurement error, population projections, at least concerning likelihood of persistence, are not greatly affected by inaccuracy in redd counts.

$\hat{\tau}$ measures, among other things, density-independent survival and

reproductive output. Thus it is proportional to the more familiar Ricker alpha (α). It is convenient, then, to **speak** of proportional changes in α rather than \hat{r} . Varying \hat{r} (or α , Figures 2 and 3) clearly has a profound influence on both likelihood of persistence and expected redd **count in the 100th year**. It appears that the present estimated α value is sufficient to virtually assure population persistence over the next **100 years**, although the corresponding number of redds in the system at the end of that period shows no recovery whatsoever (for the ESS model). That is, after **100 years**, the projected redd count is **only** about the level found between **1988 and 1992**, the lowest **5-year** counts on record. The present α level, then, represents a kind of threshold above which the population may increase, but below which it can be expected to plummet; note how rapidly probability of persistence drops when τ falls below the estimated true value.

DISCUSSION

While the present α value may all but assure persistence, it needs considerable boosting if the population is to recover to higher levels. Figure 3 indicates that a doubling of the low **1988-1992** levels over the next **100 years** will require an increase in α of 525% (depending on which model version one considers most reliable). A recovery to **1957-1962** levels (average over the 5 years of 1575 redds) within **100 years** will require an increase in α of at least 37%. It should be borne in mind when reading these predictions, however, that as the population grows with increased α , the role of density feedback parameters, β , μ and ϕ become increasingly strong. **Because** of the insensitivity of population dynamics to these parameters at present densities, the values obtained for them using the best fit routines may be inaccurate. Projections of redd counts with **high** α values, therefore, must be considered tenuous; projections might be either 'overly pessimistic or overly rosy, and given present data it is impossible to say which.

The analyses and conclusions presented here account for temporal and other stochastic variation, as indicated over the period between **1957 and 1992**. They do not **address** risk arising from **catastrophies**. The effects of a series of unusually low water years, 'a **toxicant** spill, or any other major environmental disruption, might well fall outside the range of fluctuations implied by events over those 36 years and implicitly incorporated into the **100 year** projections. Thus the predictions **given in** Figures 2 and 3 are, perhaps, overly optimistic. Good management will reflect this possibility.

CONCLUSIONS

Simulation, using a general stochastic population dynamics model with density feedback, age structure and autocorrelated environmental fluctuations, parameterized for best fit over 36 years of **redd** count data in five Idaho **index** streams, indicates that probability of persistence (over **100 years**) of the Snake River spring chinook salmon population depends **critically** on density-independent mortality. **Two** model versions, one in which spawning age structure **is** predicted as an **evolutionarily** stable strategy, the other in which observed age structure is imposed as a constraint, both give comparable results. The two model versions provide different predictions vis a vis redd counts to be expected **100 years** in the future, thus suggesting a range in the extent to which density-independent mortality must be raised to achieve recovery. Rearing

habitat improvement, predator control, **curtailing** of fishing pressure- and improved dam passage all would enhance density-independent survival, The current **value** of α should, barring catastrophes, provide for a continuation of the status quo. A doubling in population within 100 years can be expected to follow a **5-to-25%** increase in survival, and a 100 year climb to **1950's** levels can be expected to require at least a 37% survival increase. This latter prediction must be considered tenuous in light of inadequate information on the importance of density feedback and **metapopulation structure** at high population densities.

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TABLE 1

Fitted Parameter Values

Parameter	Population					
	1	2	3	4	5	
$\hat{\tau}$	Fitted age model	.222	.224	.234	.269	.218
	Forced age model	.208	.212	.234	.252	.235
β		.002	.002	.002	.002	.002*
$\hat{\mu}$.0004	.0004	.0004	.0004	.0004*
σ		.177	.169	.174	.208	.182
		.170	.175	.188	.224	.196
λ		.408	.417	.398	.465	.371
		.398	.393	.434	.476	.438
δ		.233	.241	.233	.400	.320
		.238	.251	.251	.388	.380
σ'		.160	.176	.184	.214	.174
		.167	.183	.187	.190	.172
γ		-.661	-.575	-.542	-.389	-.583
		-.632	-.545	-.608	-.490	-.545
κ		1.062	1.045	1.139	1.439	1.131
		1.253	1.183	1.187	1.436	1.272
ϕ		.0002	.0002	.0002	.0002	.0002*

* Fixed values

TABLE 2

Sensitivity to Stray Rate

	Stray Rate Relative to Estimated True Value	Probability of Persistence	Number of Redds in Year 100
	0	.698	22.872 ± 2.49
Fitted Age Model	0.5	.571	26.08 ± 3.33
	1.0	.574	30.87 ± 3.65

	0	.483	38.56 ± 7.59
Forced Age Model	0.5	.471	36.94 ± 7.11
	1.0	.492	46.76 ± 6.57

$\sigma = 0$ implies all "noise" is redd count error

$\sigma = 1$ implies **all** "noise" is due to environmental
fluctuations

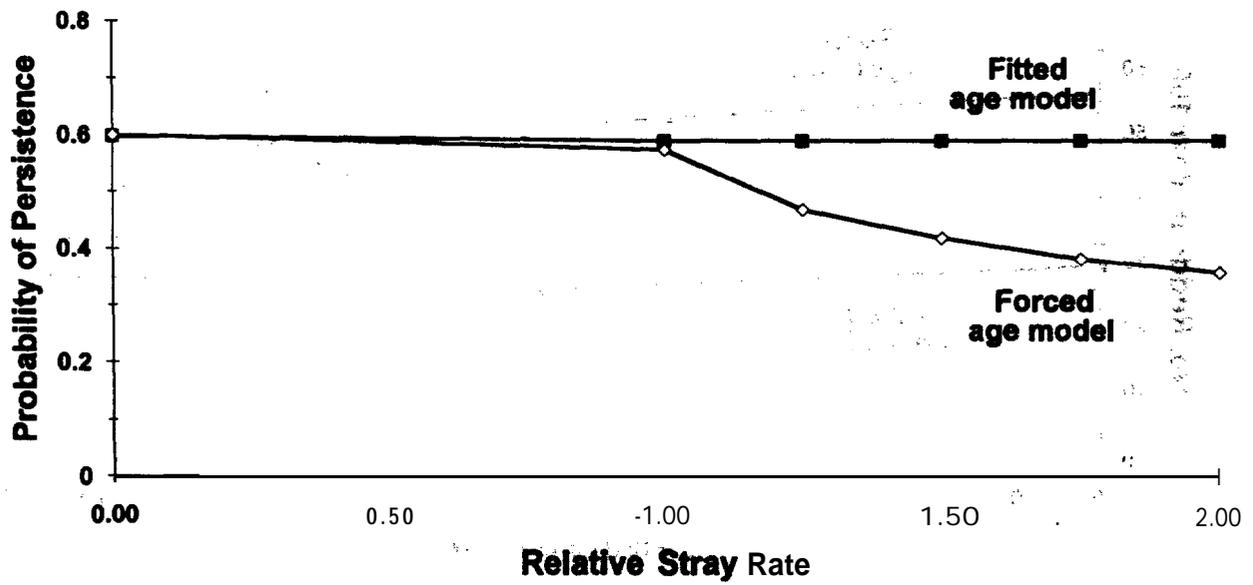


Fig. 1a Sensitivity analysis showing effect of stray rate (relative to estimated existing value) on the probability of population persistence over 100 years.

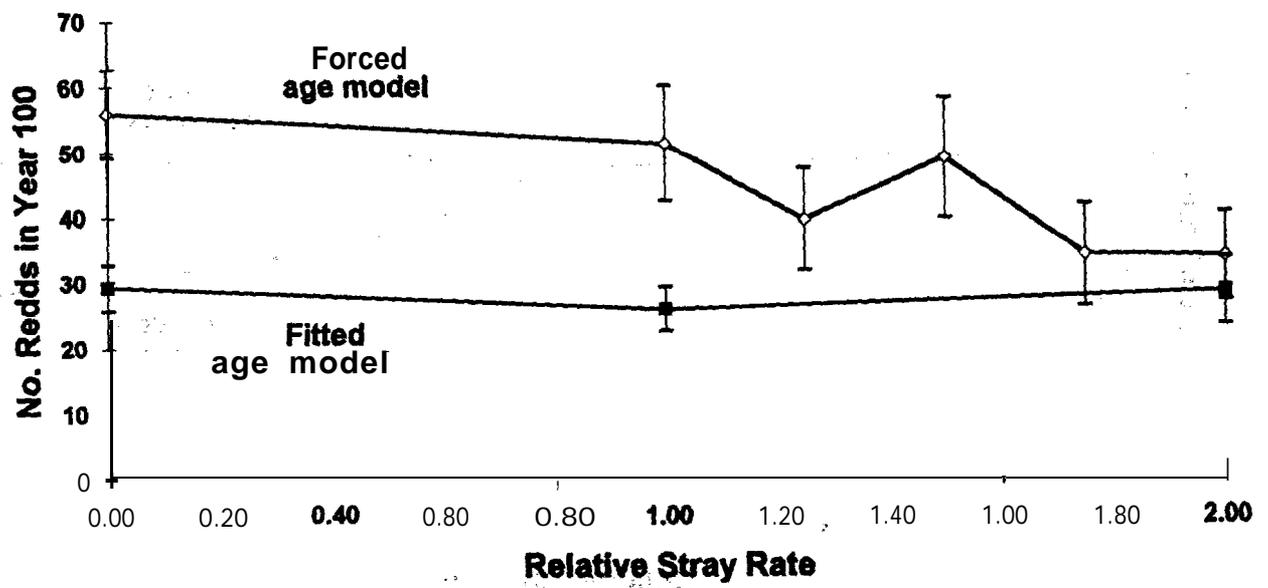


Fig. 1b Sensitivity analysis showing effect of stray rate (relative to estimated existing value) on the total number of redds in year 100 of the simulation.

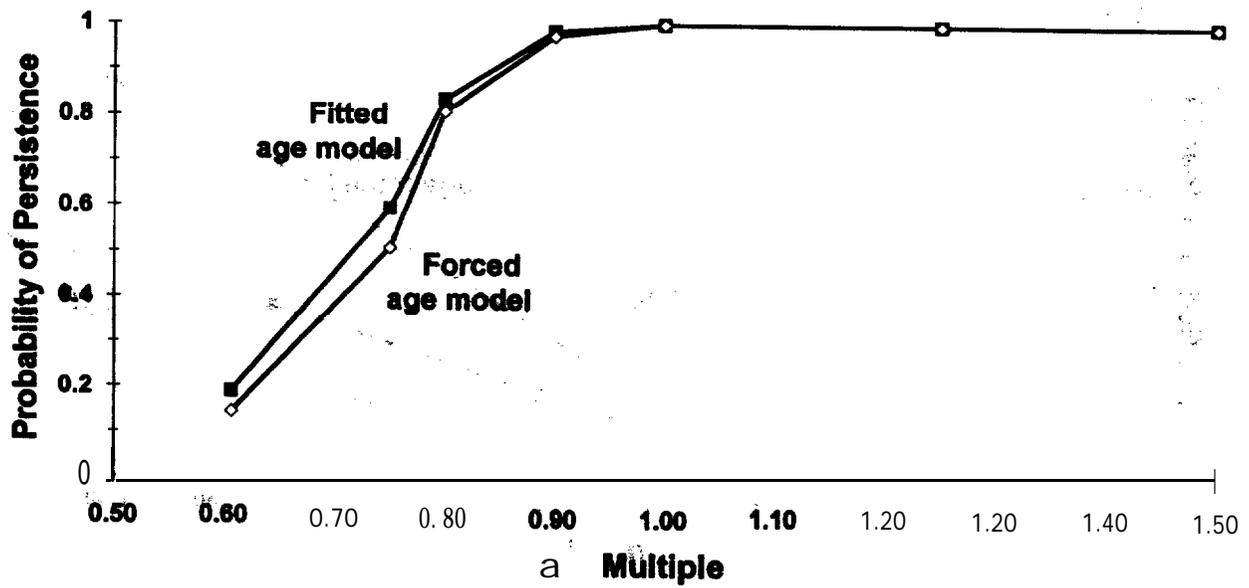


Fig. 2 Probability of population persistence over 100 years as a function of α (density independent survival or fry production). α multiple is the value of α relative to its current, estimated value.

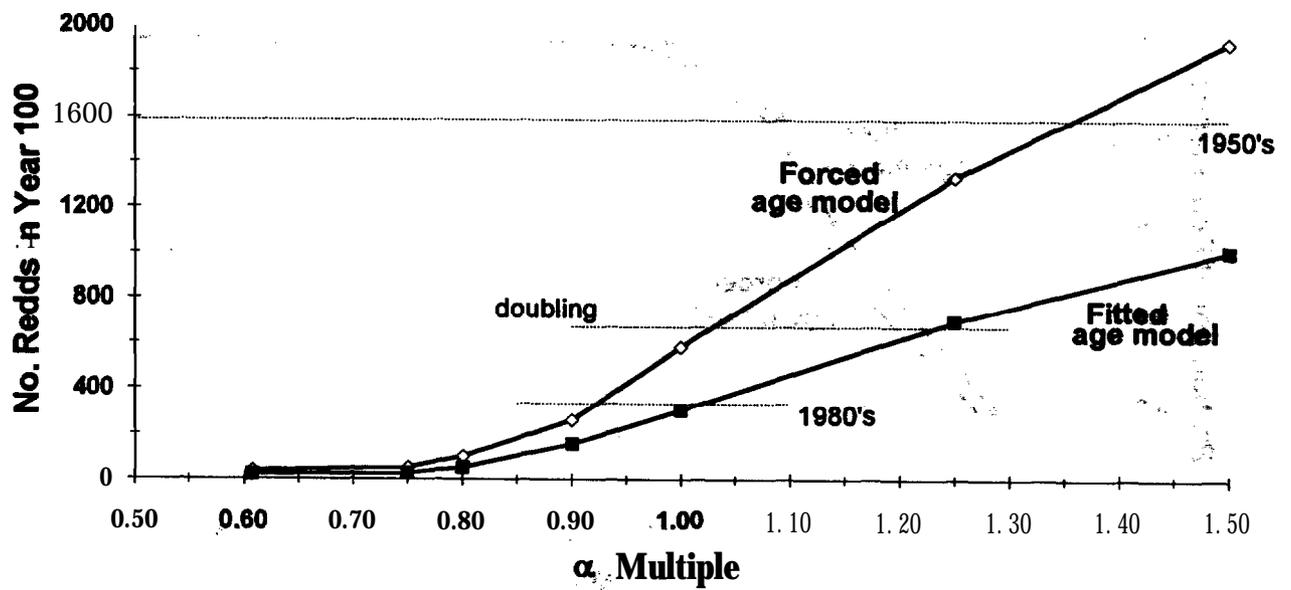


Fig. 3 Total number of redds in year 100 as a function of α (density independent survival or fry production). α multiple is the value of α relative to its current, estimated value.