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# **Viability Criteria**

## **for the Lake Ozette Sockeye Salmon**

### **Evolutionarily Significant Unit**

April 2009

**U.S. DEPARTMENT OF COMMERCE**  
**National Oceanic and Atmospheric Administration**  
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# Viability Criteria for the Lake Ozette Sockeye Salmon Evolutionarily Significant Unit

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# Executive Summary

A salmon population is considered to be viable if it is expected to persist for at least 100 years with a high probability. Population-based criteria necessary for viable salmonid populations (VSPs) include specific conditions of 1) abundance, 2) productivity, 3) diversity, and 4) spatial structure. The Puget Sound Technical Recovery Team (PSTRT) developed viability criteria for the Lake Ozette sockeye salmon (*Oncorhynchus nerka*) evolutionarily significant unit (ESU), which is comprised of a single population.

## Abundance

Following the general approach we previously applied to Puget Sound Chinook salmon (*O. tshawytscha*), we developed abundance criteria using two methods: a pure demographically based population viability analysis (PVA) and an estimate of the population numbers that the system's available habitat could support if that habitat were in optimal condition. We then combined the PVA and habitat estimates, using an adaptation of a flow chart originally used in Columbia River salmon recovery planning, resulting in upper and lower bounds defining a planning range for the number of Lake Ozette sockeye salmon required for the population to be viable.

The PVA analysis requires an estimate of the variance of the 4-year running sum of the population growth rate. We estimated this parameter using a 30-year data set (1977–2006) of available information for Lake Ozette sockeye salmon abundance. For some years where complete counts of fish were not available, we approximated the population numbers by expanding partial counts. In two cases, where there were no data available for a year, we estimated the abundance by interpolating between values for adjacent years.

We estimated the variance of the growth rate using the “slope method,” which was developed for use with salmon populations where there is a great deal of uncertainty in annual abundance numbers. We conducted standard diagnostic tests and determined that the data met the assumptions of the method. To project the population's extinction probability, we simulated abundance trajectories for 100 years using the estimated variance and assuming a stable (i.e., 1:1) population growth rate. We added an additional constraint that the simulated population abundance could never exceed three times the initial population size. Whenever the population fell below a quasi-extinction threshold of 250 spawners summed over a 4-year period, that run was designated as going extinct. We ran simulations 10,000 times each for a range of starting population sizes between 10,000 and 800,000 (4-year running sum) in steps of 5,000.

We also looked at two habitat-based estimates of the number of sockeye salmon the Lake Ozette system could support, one based on estimates of lake productivity and one based on the amount of available spawning habitat. We combined the habitat and PVA estimates using a flow chart that gives a range of population abundances for viability, with the lower end of the range

being the starting population size that results in an extinction probability of 0.05 with the PVA analysis and the upper end being the smaller of the two habitat-based capacity estimates and the PVA populations size with a 0.01 extinction probability.

The Lake Ozette PVA analysis resulted in a population growth rate variance of 0.1. The population projection analysis using this variance gave a starting population size of 125,000 over a 4-year period (31,250 annual) for a 0.05 extinction probability and a size of 785,000 over 4 years (196,250 annual) for a 0.01 extinction probability. From other work, we had a range of 91,000 to 121,000 for population capacity based on available spawning habitat and numbers of adults much greater than this possible based on lake productivity alone. Therefore, combining the results using our flow chart, the viability abundance range for Lake Ozette sockeye salmon is 31,250 to 121,000 for the annual population size.

We also examined data from nearby Lake Quinault to compare with our results for Lake Ozette, because there is a longer time series and more careful measurement of abundance for Lake Quinault over the years. If we had estimated the variance of the population growth rate using the Quinault data, the viability abundance range for Lake Ozette sockeye salmon would have been 11,250 to 47,500 for the annual population size. In the end, despite a longer and more consistent data set for Lake Quinault, we chose to use the results from the Lake Ozette-specific data because there are important differences between the populations, especially age structure.

**PSTRT Recommendation:** Based on currently available information, a viable sockeye population in Lake Ozette will range in abundance between 31,250 and 121,000 adult spawners.

## Productivity

The PVA method used here assumes the population must be able to sustain itself. In other words, a viable population productivity, on average and after any introduced harvest, must be a 1:1 return of adults per spawner, after the viability level has been achieved. As a general rule of thumb, the population growth rate must be greater than 1:1 for the population to increase in size until the viable abundance threshold is achieved. Given the recent 8-year average Lake Ozette escapement of 4,600 and our abundance target range of 35,000 to 121,000, the growth rates would have to range between an average of 1.04 and 1.06 per year to achieve the abundance targets in 50 years, 1.02 to 1.03 to achieve them in 100 years, and 1.01 to 1.02 to achieve them in 200 years.

**PSTRT Recommendation:** The growth rate for Lake Ozette sockeye salmon, once viability is achieved, should average 1. Until the ESU achieves viability, the growth rate must be greater than 1.

## Spatial Structure

From the historical work done for the population characterization and identification, it is unclear whether the current distribution of Lake Ozette sockeye salmon between lakeshore and tributary spawners is the same as the historic structure. However, it appears that the spatial structure of Lake Ozette sockeye is becoming more tributary based, with less of the population spawning along the lakeshore and in fewer lakeshore sites than in the past. Such a confined

spatial distribution increases the probability of catastrophic harm to the population and likely restricts the population to a narrower (more homogeneous) environmental suite that may reduce adaptive variation. Increasing the spatial structure of the population will reduce environmental risk and abet population variation.

**PSTRT Recommendation:** A viable sockeye salmon population in Lake Ozette includes multiple, spatially distinct and persistent spawning aggregations throughout the historical range of the population. Therefore, a viable population contains multiple spawning aggregations along the lake beaches, which are the known historical spawning areas. The certainty that the population achieves a viable condition would be further increased if spawning aggregations in one or more tributaries to the lake were also established.

## Diversity

Expanding the distribution of sockeye salmon into different habitats may lead to increased life history diversity, including changes in age composition, morphology, and behavior that are different from that now observed in Lake Ozette. For example, such changes in life history could include residualism (i.e., the case where progeny of anadromous sockeye salmon carry out their whole life cycle in freshwater and do not become anadromous).

**PSTRT Recommendation:** A viable Ozette sockeye salmon population includes one or more persistent spawning aggregations from each major genetic and life history group historically present within that population. As there is little information on historical diversity for Ozette sockeye, research is needed on current diversity types and retrospective analyses on the likely historical diversity range. A viable population of sockeye in Lake Ozette also maintains the historical genetic diversity and distinctness between anadromous sockeye salmon and resident kokanee salmon in Lake Ozette.

The PSTRT's viability criteria for Lake Ozette sockeye salmon specify a spatial structure for the population that emphasizes the population's historic distribution and life history characteristics. Unfortunately, the historical distribution and life history diversity is not well documented. Recovery cannot rely solely on the present distribution of spawners within the lake and tributary system or on a simple increase in the tributary subpopulation to the exclusion of a lakeshore subpopulation. Of concern then, is that the present spatial structure and diversity of the population does not well represent the desired characteristics of the viable population.

Our analyses and recommendations for viability criteria for all four VSP parameters were based on the best currently available information for Lake Ozette sockeye salmon. Although we attempted to address important sources of uncertainty in our analyses and recommendations, we were limited by the lack of good historical data. Likewise, because of this uncertainty, recovery strategies focusing exclusively on either tributary or beach spawners alone are also highly uncertain. The only practical solution to this uncertainty is an implemented adaptive management plan. Consequently, we recommend that the recovery plan include an adaptive management component that incorporates improved data monitoring and estimation. This will allow viability criteria to be reevaluated and, if warranted, revised as part of the adaptive management program.



# Introduction

The Puget Sound Technical Recovery Team (PSTRT) was convened by the National Marine Fisheries Service to develop the technical basis for recovery plans for three Pacific salmon (*Oncorhynchus* spp.) evolutionarily significant units (ESUs) in Washington that are listed under the Endangered Species Act (ESA): Lake Ozette sockeye (*O. nerka*), Puget Sound Chinook (*O. tshawytscha*), and Hood Canal summer chum (*O. keta*). Key tasks of the PSTRT are to identify populations and describe the conditions of viable salmonid populations (VSPs) and ESUs. The foundation for accomplishing this for Pacific salmon is described by McElhany et al. (2000), who discuss delineating populations within an ESU, identify the key parameters used to describe the status of a population, define population viability as a probability of persistence over a specified time period, and discuss the means by which ESU delisting criteria can be based on alternative scenarios for the status of populations within the ESU. This PSTRT report identifies population and ESU viability criteria for the Lake Ozette sockeye salmon ESU.

Based on the available information, the PSTRT has concluded that the Lake Ozette sockeye salmon ESU historically was comprised of a single population with several subpopulations (Currens et al. 2009). It follows that the ESU's one population must be viable in order that the ESU be viable; that is, determining population viability criteria is also determining ESU viability for this ESU. The next step was to describe conditions of key population parameters consistent with long-term viability. The team considered the conditions necessary for a population to persist for at least 100 years with probabilities of 0.95 and 0.99, assuming no immigration or emigration, as bounds for population viability. Because Lake Ozette sockeye are currently not meeting viability criteria and because reliable estimates of historical abundance or productivity levels for the population are not available, the viability criteria will need to be reevaluated as measurements of abundance improve, recovery actions take effect, and consequences of recovery actions are evaluated and adapted.

Following McElhany et al. (2000), we describe a population's status using the four viability characteristics: abundance, productivity, diversity, and spatial structure (VSP criteria). Abundance is the number of individuals in the population at a given life stage or time; productivity or growth rate is the actual or potential ratio of abundance in the next generation to current abundance; diversity is the variety of genotypes, life histories, morphologies, and other characteristics expressed by individuals within a population; and spatial structure refers to how fish at any life stage are distributed among available or potentially available habitats. Our task with this report was to develop criteria for each of these characteristics, which considered together will describe a viable population and ESU.

As scientific advisors, the PSTRT has several challenges in developing viability criteria that will be useful to planners, politicians, and the public. Viability criteria are not necessarily recovery goals. Rather, they collectively describe what we believe is necessary to maintain a

viable population and ESU, independent of particular goals for direct or indirect societal benefits from the recovered population.

Of the four VSP criteria, abundance is the most well developed in this report. We have used two approaches to determine abundance levels in developing the abundance viability criteria for the Lake Ozette sockeye salmon population. The first approach, utilizing population viability analysis (PVA) models, is demographically based. Using information derived from population census data combined with simple models of population dynamics, one can estimate extinction probabilities for the population, which can then be used to classify population status. In particular, recovered status can be assigned to those population conditions that result in a suitably low extinction probability. Dennis et al. (1991) first discussed the use of this approach for endangered species recovery planning. McElhany and Payne (in prep.) have developed an application to Pacific salmon, which we previously used for Puget Sound Chinook salmon (Ruckelshaus et al. 2002, Rawson et al. in prep.).

Our second approach to abundance criteria is based on assessing the potential dynamics of the population as related to its natural environment or habitat. This approach requires a means of relating habitat quantity and condition to population performance in terms of abundance, which is challenging when data are scarce. However, the approach has appeal because, if such a linking model can be found, viability estimates can be bounded by reasonable estimates of the intrinsic potential of habitats to support sockeye salmon throughout their life cycle. With such an approach, it is possible to not only determine the abundance criterion for viability, but also to predict the likely contribution of suites of habitat recovery and protection actions to getting there.

Mobrand (1997) described this type of approach in the context of recovery planning for listed Columbia River salmon. Two models linking changes in habitat to salmon population status, the Ecosystem Diagnosis and Treatment model (McConnaha 2001) and the Shiraz model (Sharma et al. 2005, Scheurell et al. 2006), have been applied to the Puget Sound Chinook salmon ESU. Both models are data intensive and therefore have not been applied to Lake Ozette sockeye salmon where the necessary information is not available. Instead, the PSTRT considered results from two habitat-based approaches available for Lake Ozette sockeye:

1. The juvenile habitat rearing capacity approach estimates the capacity of Lake Ozette to produce sockeye salmon smolts, then determines how many returning adults would result from this number of smolts and how many spawners are needed to produce this number of smolts.
2. The spawner habitat capacity approach estimates the maximum number of sockeye salmon spawners that lake beaches and tributary streams could accommodate based on the spawning habitat area and conditions.

Because both the demographic and the habitat approaches have their own strengths and limitations, we explored both approaches to develop the viability criterion for Lake Ozette sockeye salmon abundance. The criterion is presented as a range, which is derived using information on both demographics and habitat. The demographics give us an estimation of a viable spawner abundance level and the habitat-based approach gives us capacity estimates (three estimates from the two approaches given above) which place an upper limit on viability estimates.

Spatial structure is the distribution of individuals in habitats they use throughout their life cycle. A population with a broad spatial distribution at any life stage is more likely to persist than a population whose individuals are concentrated in a few locations. The contribution of spatial structure to population persistence results from three main processes: 1) reduced chance of catastrophic losses of the population (i.e., when groups of individuals are spread out in space), 2) greater chance that locally extirpated or dwindling groups will be rescued by recolonization (i.e., when individual groups are close enough together), and 3) a greater opportunity for long-term demographic processes to buffer a population from future environmental changes.

Collectively, these phenomena commonly are referred to as metapopulation processes. Because of the contrasting benefits of groups of individuals being close enough together for recolonization to occur and yet spread out enough so that all groups do not fall victim to the same catastrophe, spatial structure for a viable population should include multiple clusters of groups that are closely aggregated, with the clusters themselves being spread throughout the geographic area occupied by the population.

Salmon exhibit considerable diversity within and among populations in their life history and their morphological, physiological, and genetic traits. In a spatially and temporally varying environment, there are three main reasons why diversity is important for species persistence: 1) diversity in life history allows a species to use a wider array of environments than a species lacking such diversity, 2) the more diverse the population, the more likely that some individuals will survive and reproduce in the face of environmental variation, and 3) genetically based diversity provides the raw material for surviving long-term environmental changes. Such diversity also allows the population to occupy, and thus potentially adapt to, a wider range of environmental conditions and to colonize or recolonize newly available habitats. Because salmon regularly face variability in the environments they inhabit, the contributions of diversity to population persistence are critical considerations.

In this report, we provide for a viability planning range (upper and lower bounds) for the number of Lake Ozette sockeye salmon needed to achieve the abundance viability criterion given stable growth or productivity. The criteria for spatial structure and diversity for the population and ESU viability are also presented.

# Methods

## PVA

The PVAs we conducted are based on the method of Holmes (2001), Holmes and Fagen (2002), and McElhany and Payne (in prep.). The approach uses an observed time series of abundances to estimate the growth rate ( $\lambda$ ) and the variance of the natural logarithm of the growth rate ( $\sigma^2$ ). Assuming population dynamics will be restored in the future such that the growth rate is stable or increasing ( $\lambda \geq 1$ ) and the variance of the growth rate will remain the same as in the period of the observed time series, it is possible to estimate the minimum initial population size necessary to maintain the probability of extinction at or below a given level over a given number of years. Using this method, the viability criterion is for the population abundance to exceed the minimum size and for the growth rate to exceed  $\lambda = 1$  over the specified time period.

There were two steps in an analysis performed this way. The first step was to estimate  $\sigma^2$  from the observed time series of abundance data using the slope method (Holmes 2001). The second was to project extinction risk of the population in the future, assuming that the time course of the population approximates a Brownian motion (Dennis et al. 1991). More details on the method are provided below in the subsections Parameter Estimation and Population Projection.

## Data

Adult return estimates for Lake Ozette sockeye salmon are available for most years from 1977 through 2003 (Haggerty et al. 2008) (Appendix A). These are derived from a variety of census methods and represent the number of adult sockeye entering Lake Ozette each year (Haggerty et al. 2008). Due to problems with fish counts at the weir, return estimates are not reported for some of the years in this time period. For those years, we interpolated adjacent years or used other information to fill in the missing years to create a complete time series for data analysis. Also, to bring the time series up to date, we used census information for 2004, 2005, and 2006 provided by the Makah Tribe to create estimates of total run for those recent years. We describe methods we used to fill in estimates not provided by Haggerty et al. (2008) in Appendix A.

For Lake Ozette sockeye, we use the term “run size” and “escapement” synonymously over this time period, since there has been no harvest on Lake Ozette sockeye since at least 1973 other than limited ceremonial harvest through 1980 (Haggerty et al. 2008). In this case escapement is not the same as spawning escapement, since there are limited surveys to verify actual spawning numbers. Because we also had data on the numbers of fish removed each year to provide eggs for an artificial production program in Umbrella Creek, we subtracted those

numbers from the estimates of total escapement to estimate the number of fish that spawned naturally.

Because of some uncertainties in the information for Lake Ozette sockeye salmon, especially lack of reliable information for the years before 1977, we looked at escapement and total recruitment data from other sockeye salmon populations along the Pacific coast from Bristol Bay in Alaska to the Washington coast for surrogate estimates of population trends and variability. In the end we chose to use local Lake Ozette data for PVAs. However, we also completed a detailed analysis for the much longer Lake Quinault run to compare variance and other population parameters because of the similar geographic location and ecology, similar proximity of the lake to the ocean, and similar ocean distribution of adults (Appendix B).

### **Parameter Estimation**

The slope method (Holmes 2001) was developed to separate process error (the parameter of interest) from measurement error in the time series of abundance data for species such as salmon. In this method, the variance of population growth rates is estimated as the slope of the regression of the average growth rate over successive lags on the value of the lag, for one to four. Holmes and Fagan (2002) showed that the slope method produces reliable estimates of process error in the face of large measurement error when the population dynamics follow the assumptions of the model and also when the population dynamics follow other forms, including some of the density-dependent spawner-recruit relationships commonly found in salmon. We applied the slope method using 4-year running sums of abundance, based on the 4-year life cycle of Lake Ozette sockeye salmon, to express the returning run size.

We used estimated variance ( $\sigma^2$ ) of growth rate two ways for the Lake Ozette population: using the time series of estimated natural origin (NOR) escapements and recruitment with an adjustment for hatchery fish. We did the same for Lake Quinault data, except that we added a third analysis—for the Lake Quinault time series only—adjusting for both hatchery fish and harvest effects. The first estimate uses the Holmes (2001) method directly to compute the variance of  $\log(N_{t+1}/N_t)$  for a time series, where  $N_t$  is the running sum of natural origin escapement at time  $t$ . The second uses modifications described by McElhany and Payne (in prep.) to adjust for the fact that a portion of each year's return is derived from first generation returns from hatchery releases that escape to natural spawning areas. The third estimate, used in the Lake Quinault analysis only, computes the variance of  $(N_{t+1} + C_{t+1})/N_t$ . Here  $C_{t+1}$  is the running sum of the number of fish that would have returned to spawn in addition to  $N_{t+1}$  had there been zero harvest. In both cases, we used 4-year-long unweighted running sums of the appropriate time series as the basic input data and lags of 1 through 4 years ( $\tau = 4$  in Holmes' notation) for slope estimates.

### **Testing the Assumptions of the Model**

Given the longer-term climatic cycles and ocean regime shifts that govern Pacific salmon population dynamics (Mantua et al. 1997, Pearcy 1992, 1997), variability increases with additional years of data, at least as time series length increases from very short to 30–40 years and as data span distinct ocean regimes. This is true even when the underlying process can be

assumed to be Markovian (McElhany and Payne in prep.), as is the case for the simple model for which this technique was first developed.

To determine if the assumptions underlying the slope method held for the Lake Ozette and Lake Quinault sockeye salmon data, we performed standard diagnostic tests (Holmes and Fagan 2002, McElhany and Payne in prep.). These are presented in Appendices A and B, respectively. None of these flagged a major problem for the 30-year time series for Lake Ozette or the 33-year time series for Lake Quinault, while the 96-year series for Lake Quinault failed several of the tests (Appendix B).

The quasi-extinction threshold ( $N_{QET}$ ) is the population size below which extinction risk is mostly determined by compensatory effects and other factors not included in estimates of  $\sigma^2$  from populations at higher abundance levels. There is no single accepted way to determine this parameter, and the outcome of PVA is highly sensitive to its value. Although a number of processes are important in setting  $N_{QET}$  (Lande 1998), we considered only the potential loss of genetic diversity due to inbreeding. Studies of genetic diversity loss suggest that the probability of losing genetic diversity due to genetic drift increases rapidly at genetic effective population sizes ( $N_E$ ) less than 50 (Soule 1980) and that genetic drift can dominate over natural selection in accounting for changes in gene frequency in salmon populations smaller than 50 to 100 fish effective size (Gall 1987). Allendorf et al. (1997) recommended that Pacific salmon population sizes be above 500 to guard against long-term deleterious genetic change due to genetic drift and above 50 to guard against short-term change. We used the lower end of this range to derive our  $N_{QET}$ .

Typically the census number of fish in a salmon population ( $N_C$ ) is greater than the genetic effective size (Waples 1990). Assuming an  $N_E$  of 50 for a full generation and assuming that  $N_E = 0.2 N_C$ , it follows that an equivalent  $N_C = 250$ . Based on this, we use an  $N_{QET}$  of 250 spawners for a 4-year generation of Lake Ozette sockeye salmon in our analyses.

### **Population Projection**

To project a population's extinction probability, we assumed that a population grows at a lognormally distributed growth rate with a mean of  $\lambda = 1$  and variance of  $\sigma^2$ . The straightforward approach we used is described by McElhany and Payne (in prep.). We simulated population growth using functions written in "R" (R Development Core Team 2008, Appendix C). This program repeatedly simulates population trajectories for  $Y$  years, starting with a population size of  $N$ . The trajectory is assumed to go extinct if the population size ever falls below  $N_{QET}$  during the  $Y$  years. We express population viability criteria as the number of salmon required for a naturally self-sustaining population to have a 0.95 or 0.99 probability of persistence over a  $Y = 100$ -year time period. Our projection method included the additional constraint that the population size can never exceed three times the initial population value in the model simulation. We estimated extinction probabilities by repeating the simulation 10,000 times each for the value of  $N$  (4-year running sum population size) in steps of 5,000.

# Habitat-based Estimates of Adult Capacity

## Adult Capacity Based on Lake Productivity Estimates

Adult capacity based on lake productivity can be expressed as either the maximum number of sockeye salmon adults that Lake Ozette could have produced from estimates of smolt capacity or the number of parent spawners needed to produce smolt capacity levels. This method assumes that no factor other than the capacity of the lake to produce juveniles is limiting and that all juvenile sockeye salmon will be anadromous.

The first step, theoretically, in estimating adult capacity by food availability to juveniles in the lake is to estimate smolt capacity, although this number is never given in the following citations. A literature review suggests that salmon production in Lake Ozette is not limited by food availability. Haggerty (2006) states:

All researchers, (Bortleson and Dion 1979, Dlugokenski et al. 1981, Blum 1988, Beauchamp and LaRiviere 1993) [see also Beauchamp et al. 1995] independent of methodologies, have concluded that Lake Ozette sockeye productivity and survival are not [currently] limited by food availability or competition. No direct estimates of total smolt production capacity of the lake have been developed. Blum (1988) used the Acre Plankton Index (API) model to estimate the carrying capacity of the lake, concluding the lake could support total adult sockeye runs in the range of 306,000 to 563,000 fish.

Smolt capacity as used here is defined as the capacity of the lake to support juvenile salmon production based on the plankton productivity of the lake. The Plankton Acre Index (PAI, also referred to as API) was developed by the International Pacific Salmon Fisheries Commission (IPSFC 1972) to estimate the potential sockeye salmon rearing capacity of Fraser River system lakes based on zooplankton volume in two systems assumed to be at carrying capacity (Shuswap and Chilko lakes).

Blum (1988) adapted the method to develop adult abundance capacity estimates for Lake Ozette. Not having zooplankton volume data, he used regressions with primary productivity indices available for both the Fraser River system lakes and Lake Ozette. The Ozette PAI estimates were derived from regressions on 1) just total dissolved solids (PAI = 0.4) and 2) total dissolved solids and chlorophyll *a* (PAI = 0.9). A PAI of 1 is equivalent to the ability of the lake to support 10 female spawners per acre (IPSFC 1972). Blum's (1988) PAI estimates of 0.4 and 0.9 result in estimates of 27,000 to 60,750 effective female spawners or 54,000 to 121,500 spawners, assuming a female to male spawning ratio of 1:1. Blum (1988) also states that these estimates are based on an assumption of an effective spawn out of 3,000 eggs per female; unstated by Blum, the estimates also assume the same egg to smolt survival on Lake Ozette as experienced in the Fraser River system lakes used to develop the PAI regression equations.

To get the total run estimates of 306,000 to 563,000 sockeye salmon adults, Blum (1988) used a linear regression analysis of total run sizes (Y) of Fraser River system lakes sockeye against mean escapements (X):

$$Y = 3.79 X + 101734.77 \quad (r^2 = 0.741, P < 0.01) \quad (1)$$

Blum notes that, on average, four recruits are produced per spawner in the Fraser River system lakes used; therefore, this same productivity is assumed when applying this regression to Lake Ozette sockeye. These estimates represent potential escapements and returns for Lake Ozette based on plankton productivity measures from the 1970s and 1980s. These potential abundances were not being achieved in either 1988 when Blum did his work or now; limiting factors other than lake capacity were and are controlling current abundances. Therefore, these abundances may be used as upper limits for our viability analysis.

These estimates based on lake capacity give us two adult capacity estimates: spawners needed for smolt capacity (SSC), 54,000 to 121,500 spawners, and return from the smolt capacity (RSC), 306,000 to 563,000 adult returns. In making these estimates, Blum does not give actual smolt numbers or the survival estimates assumed. A 306,000 to 563,000 return from 54,000 to 121,500 spawners, respectively, gives a total egg-to-adult return survival of 0.4% to 0.3%, respectively, given the assumptions of 1:1 female to male spawners and 3,000 viable eggs per female. This total egg-to-adult survival could represent a freshwater survival of about 5% and 4%, respectively, and a marine survival of about 8% (this is the marine survival estimated for Fraser River system lakes sockeye salmon in recent years<sup>1</sup>). Unfortunately, smolt capacity is never actually estimated, and therefore, it is difficult to separate the freshwater and marine survival rates.

### **Adult Spawner Capacity Based on Spawning Habitat Availability**

Spawner capacity (SpC) is the maximum number of sockeye spawners that lake beaches and tributary streams could accommodate if no other factors were limiting. Haggerty (2006) developed new estimates of SpC for lake and tributary habitats; these are explained and reported in the Ozette recovery plan (Haggerty et al. 2009). Recent habitat inventories upon which these estimates are based are documented by Haggerty and Ritchie (unpubl. manusc.) and Haggerty et al. (2008).

Haggerty (2006) computed SpC for Allen's, Olsen's, Umbrella, and Baby Island beaches using various techniques to assess the amount of suitable spawning habitat available under recovered conditions and two methods for projecting the number of females per unit of habitat. For estimates of potential tributary spawner capacity, Haggerty (2006) used habitat surveys from 1999 and 2000 to estimate stream length of suitable habitat in Big River and Umbrella and Crooked creeks. These were converted to suitable spawning area using two different methods. Haggerty converted the tributary spawning area estimates to total spawners assuming 3 m<sup>2</sup> per female. The numbers of females for the lake and tributary estimates were converted to total fish assuming a 1:1 male:female ratio. Haggerty's (2006) estimates of the SpC range from 11,000 to 15,000 spawners for lake beaches and 80,000 to 106,000 spawners for the 3 tributaries, for an overall total range of 91,000 to 121,000 spawners for the basin. These are conservative estimates in the sense that, for both lake beaches and tributaries, potentially suitable spawning areas were not included in the calculations and these would increase the estimates if included (Haggerty 2006, Haggerty et al. 2009).

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<sup>1</sup> Tim Tynan, National Marine Fisheries Service, Olympia, WA. Pers. commun., 9 April 2009.

## Combining Results from the Analyses

We combined the results from the PVA estimates for viability levels and the habitat-based estimates for capacity according to a sequence of decision rules (Figure 1) adapted from an approach originally used in Columbia River recovery planning efforts (Ford et al. 2001, Ruckelshaus et al. 2002). Because of the significant uncertainty in each of the approaches, we used the estimates of viability and capacity to provide upper and lower bounds for the population abundance viability planning ranges rather than a point estimate. The upper and lower bounds are constrained by the different analyses. For example, the PVA estimate of the upper bound for abundance is estimated using an extinction probability of 0.01 (in contrast to the 0.05 used for the lower bound), but this is constrained by the maximum number of fish that could be supported

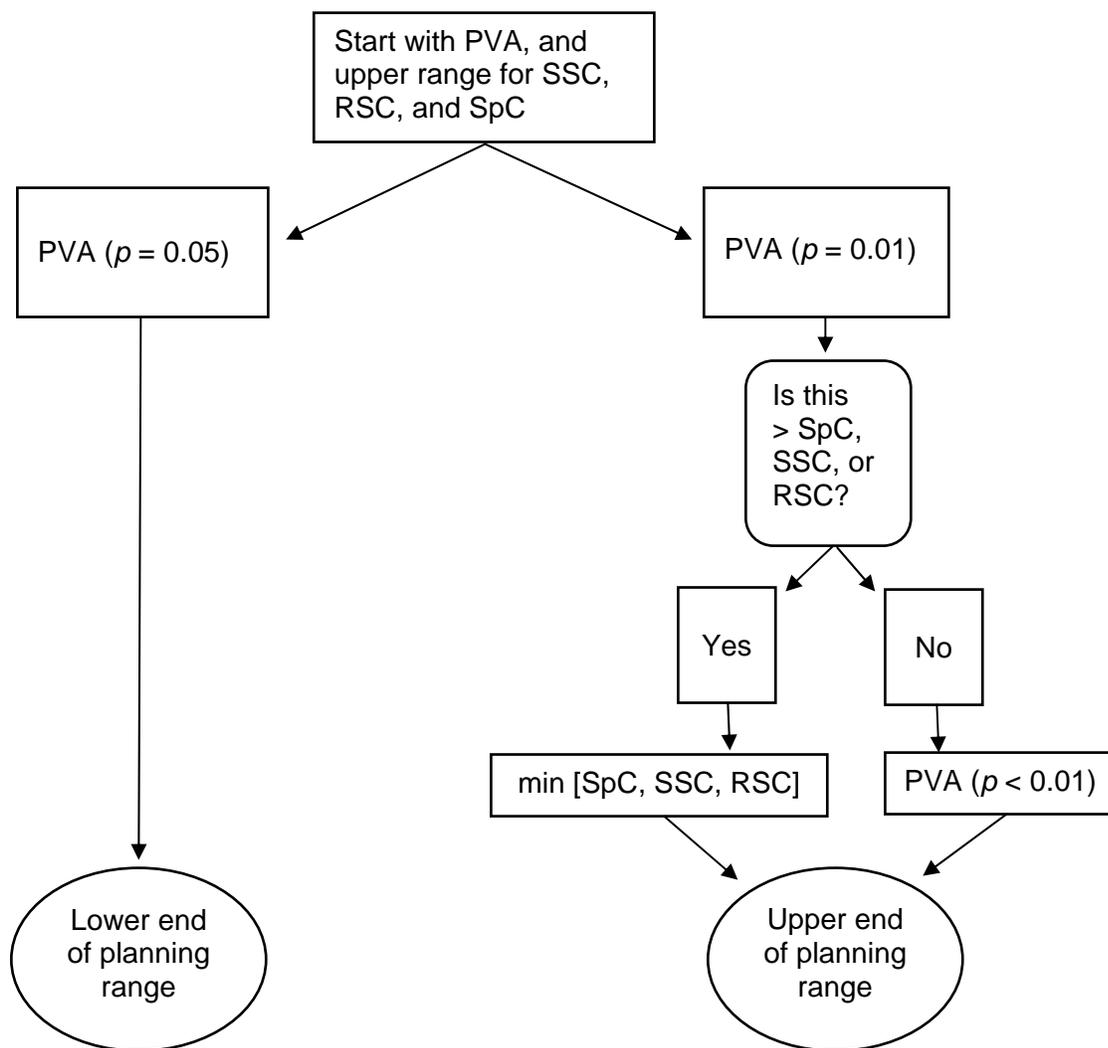


Figure 1. Flow chart showing how demographic and habitat-based analyses were combined with PVAs to derive planning ranges for equilibrium spawner abundance (based on Ford et al. 2001). SSC = spawners needed to produce smolt capacity, RSC = return run size from smolt capacity, and SpC = spawner capacity.

by the available spawning habitat or the available lake rearing capacity under unimpacted habitat conditions. This decision rule approach uses the independent analyses as a series of checks. In this case, the decision tree logic will not allow an upper bound for abundance derived from using demographic data that is greater than estimates of the spawner abundances the recovered habitat could support.

We used the PVA results from the Lake Ozette data set in this decision tree process of combining PVA and habitat-based estimates of viable population sizes. However, because of missing data and other uncertainties in the available Lake Ozette data, we also computed PVA results for data from nearby Lake Quinault. We discuss the implications for the viability ranges if the PVA estimates from the Lake Quinault data were used instead of the direct Lake Ozette information.

# Results and Recommendations

## Abundance

### PVA Analysis

The  $\sigma^2$  estimate, adjusted for the presence of hatchery fish, for the 30-year Lake Ozette time series was 0.1 for the natural escapement time series and 0.096 using the adjustment for the presence of hatchery fish. Shown below are estimates of the natural logarithm of the growth rate ( $\mu$ ) and its variance ( $\sigma^2$ ) for the Lake Ozette sockeye salmon time series, 1977–2007 (30 years) for NOR escapement (Wesc) and escapement adjusted for hatchery influence (Hat).

|            | <u>Wesc</u> | <u>Hat</u> |
|------------|-------------|------------|
| $\mu$      | 0.027       | 0.019      |
| $\sigma^2$ | 0.100       | 0.0960     |

We used the 0.1 estimate of  $\sigma^2$  for further analysis.

Determining minimum population sizes using the population projection simulation requires the following input variables be specified: population growth rate ( $\lambda$  or its natural logarithm  $\mu$ ),  $\sigma^2$ , time period for the simulation in years ( $Y$ ), extinction probability, and  $N_{QET}$ . We set  $\mu = 0$  (indicating that the rate of population increase was stable, i.e., equal to zero) and simulated values of  $\sigma^2$  from 0.04 to 0.12 in increments of 0.01 (Table 1). We used 100 years for  $Y$  and 0.05 and 0.01 for the extinction probabilities following McElhany et al. (2000). We ran 10,000 replicated simulations for each trial parameter value, because we found that fewer replicates led to inconsistent results (i.e., smaller starting population sizes for higher variance in some cases).

With the above input, we produced a table of minimum initial population sizes for ranges of  $\mu$  and  $\sigma^2$  (Table 2). Given the estimated  $\sigma^2$  of 0.10 for the 30-year Lake Ozette time series, the minimum population sizes for  $\mu = 0$  are approximately 31,250 for extinction probability  $p = 0.05$  and 196,250 with  $p = 0.01$  (Table 1).

### Combined Analysis of Abundance Criteria

With the results of the PVA analysis and the habitat-based capacity estimates, we applied the decision rules to generate a viable abundance range for the Lake Ozette sockeye salmon population. Based on Blum's (1988) analyses, spawners needed to produce a smolt capacity (SmC) range 54,000–121,500 fish; returns from these spawners would range 306,000–563,000 adults. Haggerty's (2006) estimates of the spawner capacity (SpC) range 11,000–15,000 for lake beaches and 80,000–106,000 for tributaries, for an overall total range of 91,000–121,000 for the basin.

Table 1. Annual population sizes, given natural logarithm of the population growth of  $\mu = 0$  and over a range of variance ( $\sigma^2$ ) values, that are necessary for  $p < 0.05$  and  $p < 0.01$ . Extinction is determined when the 4-year running sum of abundance declines to a  $N_{\text{qet}}$  of 250 fish or less over a 100-year period. The estimated  $\sigma^2$  computed from available data for Lake Ozette sockeye salmon (Appendix A) is 0.09. The estimated  $\sigma^2$  computed from Lake Quinault data (Appendix B) is 0.06. These lines are in bold in the table. Numbers were estimated using stochastic simulation modeling.

| $\sigma^2$  | $p < 0.05$    |               | $p < 0.01$     |                |
|-------------|---------------|---------------|----------------|----------------|
|             | 4-year        | Annual        | 4-year         | Annual         |
| 0.04        | 12,500        | 3,125         | 45,000         | 11,250         |
| 0.05        | 20,000        | 5,000         | 75,000         | 18,750         |
| <b>0.06</b> | <b>30,000</b> | <b>7,500</b>  | <b>115,000</b> | <b>28,750</b>  |
| 0.07        | 45,000        | 11,250        | 200,000        | 50,000         |
| 0.08        | 65,000        | 16,250        | 350,000        | 87,500         |
| <b>0.09</b> | <b>90,000</b> | <b>22,500</b> | <b>500,000</b> | <b>125,000</b> |
| 0.10        | 125,000       | 31,250        | 785,000        | 196,250        |
| 0.11        | 160,000       | 40,000        | >800,000       | >200,000       |
| 0.12        | 215,000       | 53,250        | >800,000       | >200,000       |

Table 2. Estimates of the natural logarithm of the rate of growth ( $\mu$ ) and its variance ( $\sigma^2$ ) for the Lake Quinault sockeye salmon time series, 1910–2005 (96 years) and 1973–2005 (33 years), for Wesc, adjusted for hatchery influence (HatAdj), and adjusted for both hatchery and harvest influence (HatHarAdj).

| Fixed                       | Wesc   | HatAdj | HatHarAdj |
|-----------------------------|--------|--------|-----------|
| <u>1910–2005 (96 years)</u> |        |        |           |
| $\mu$                       | -0.011 | -0.014 | 0.129     |
| $\sigma^2$                  | 0.163  | 0.159  | 0.175     |
| <u>1973–2005 (33 years)</u> |        |        |           |
| $\mu$                       | 0.007  | 0.000  | 0.063     |
| $\sigma^2$                  | 0.041  | 0.038  | 0.061     |

Following the decision rules in Figure 1, the minimum abundance number is 31,250 from the PVA analysis for a 5% risk of extinction. The PVA estimate for the upper bound is 196,250 (1% risk), but this is larger than the minimum of the upper range of the SSC, RSC, and SpC estimates. Thus the upper end of the viability planning range is determined by the minimum of the upper range of the SSC, RSC, and SpC estimates (Figure 1), which in this case is the SpC estimate of 121,000 spawners. Combining all of this, the current estimate of the viability planning range for Lake Ozette sockeye salmon is 31,250 to 121,000 spawners. It must be remembered that the spawning capacity of 121,000 is likely to be an underestimate if all potential beach and tributary sites were taken into consideration, not just ones currently being used (see Methods section).

We also note that if the estimated variance of the Lake Quinault population was appropriate for Lake Ozette, then the viability planning range would be narrower and the total abundance value would be smaller. Both the upper and lower ends of the range would be determined by the PVA, and the range would be 11,250–47,500 spawners.

One could argue that the Lake Quinault data set is preferable to the Lake Ozette data set for estimating  $\sigma^2$ , because there is a much longer time series available and recent estimates appear to be more precise than those for Lake Ozette. However, fundamental differences between the systems suggest that the Lake Quinault analysis might not be reflective of the Lake Ozette population, and we chose to use the local data for estimating the viability range for Lake Ozette sockeye salmon. The principal reason for this choice is the substantial difference in the age structure of the two populations, with Lake Ozette sockeye returning almost exclusively at age 4, while Lake Quinault sockeye are typically split approximately evenly between age 3 and age 4. We would expect populations that are predominantly of a single age to exhibit greater variability than multiage populations, and this expectation is supported by the direction of the difference in the variance estimates of the two populations we examined. In addition, all Lake Quinault sockeye are tributary spawners while Lake Ozette exhibits both beach and tributary spawners. It is not known what effect this fundamental difference may have on variability in the growth rate of the populations.

Thus we decided to use the available Lake Ozette data to estimate levels of the Lake Ozette population necessary for viability. We recognize that the current estimate of the variance includes a high level of uncertainty, which we expect will be greatly reduced in the future with improved estimates of spawning escapement. However, sampling for and estimation of Lake Ozette abundance and growth rates, and therefore variance, need to be improved in order to refine the estimates of viability abundance in the future.

**PSTRT Recommendation:** Based on currently available information, a viable sockeye salmon population in Lake Ozette will range between 31,250 and 121,000 adult spawners.

## Productivity

The PVA method used here assumes the population must be able to sustain itself (i.e., not be declining) at the viability abundance level. In other words, a viable population productivity, on average and after any introduced harvest, must be at a 1:1 return of adults per spawner, after the viability level has been achieved. The capacity estimates based on smolt capacity are derived from Fraser River system lakes sockeye salmon estimates that have a realized productivity of approximately four recruits per spawner; if lower productivities were realized, more spawners would be needed or fewer adults would return from a fixed smolt capacity, thus changing our adult capacity estimates. As a general rule of thumb, the  $\lambda$  must be greater than 1.0 for the population to increase in size until the viable abundance threshold is achieved. Given the recent 8-year average Lake Ozette escapement of 4,600 and our abundance target range of 35,000 to 121,000, the growth rates would have to range between an average of 1.04 and 1.06 per year to achieve the abundance targets in 50 years, 1.02 to 1.03 to achieve them in 100 years, and 1.01 and 1.02 to achieve them in 200 years.

**PSTRT Recommendation:** The growth rate for Lake Ozette sockeye salmon, once viability is achieved, should average 1. Until the ESU achieves viability, the growth rate must be greater than 1.

## Diversity

Expanding the distribution of sockeye salmon into different habitats may lead to increased life history diversity, including changes in age composition, morphology, and behavior that are different from what is observed now in Lake Ozette. For example, such changes in life history could include residualism (i.e., the case where progeny of anadromous sockeye salmon carry out their whole life cycle in freshwater and thus do not become anadromous).

Dramatic differences in diversity within the *O. nerka* species in Lake Ozette occur between the anadromous sockeye salmon population, which is listed under the ESA, and the resident kokanee salmon, which is not. The genetic differences are large enough between these two groups that they are designated as different ESUs (Gustafson et al. 1997). Interbreeding between the two is possible but genetic data indicate it is rare (Currens et al. 2009). Changing tributary habitats and expansion in the distribution of tributary spawning anadromous sockeye salmon could increase the likelihood of interbreeding, which would have the undesired impact of increasing homogeneity between the two groups. Any life history changes that do occur in the Lake Ozette sockeye population should be separately tracked and not confused with the genetically distinct kokanee salmon residing in Lake Ozette and its tributaries. Research is needed on current diversity types and retrospective analyses on the likely historical diversity range.

**PSTRT Recommendation:** A viable Lake Ozette sockeye salmon population includes one or more persistent spawning aggregations from each major genetic and life history group historically present within that population. Since there is little historical diversity information for Lake Ozette sockeye, research is needed on current diversity types and retrospective analyses on the likely historical diversity range. A viable population of sockeye in Lake Ozette also maintains the historical genetic diversity and distinctness between anadromous sockeye salmon and resident kokanee salmon in Lake Ozette.

## Spatial Structure

From the historical work done for population characterization and identification (Currens et al. 2009), it is unclear whether the current spatial structure of Lake Ozette sockeye salmon is the same as the historic structure. Based on the available information of current spawning activity, however, it appears that the spatial structure of Lake Ozette sockeye is becoming more tributary-based, with less of the population spawning along the lakeshore and in fewer lakeshore sites than in the past. Such a confined spatial distribution increases the probability of catastrophic harm to the population and probably restricts the population to a narrower (more homogeneous) environmental suite that may reduce adaptive variation. Increasing the spatial structure of the population will reduce environmental risk and abet population variation.

**PSTRT Recommendation:** A viable sockeye salmon population in Lake Ozette includes multiple, spatially distinct and persistent spawning aggregations throughout the historical range of the population. Therefore, a viable population contains multiple spawning aggregations along the lake beaches, which are the known historical spawning areas. The certainty that the population achieves a viable condition would be further increased if spawning aggregations in one or more tributaries to the lake were also established.

# Conclusion

The PSTRT's viability criteria for Lake Ozette sockeye salmon specify a spatial structure for the population that emphasizes the population's historic distribution and life history characteristics. Unfortunately, the historical distribution and life history diversity are not well documented. Little is known about the distribution of the historic (pre-1950s) population, and the role played by Lake Ozette tributaries in the spatial structure of the species. Data available since the 1950s (and prior to adult returns from the tributary hatchery programs) indicate that the population was generally lake-centric, mainly shoreline spawners with some smaller contribution by the tributaries. Research is needed on current diversity types and retrospective analyses on the likely historical diversity and spatial ranges. In the meantime, under the recovery process, it is advantageous to increase spatial distribution from where it was when the ESU was listed. The recovery of multiple persistent spawning aggregations along the lakeshore and in tributaries can only increase the robustness of the population.

Recovery cannot rely solely on the present distribution of spawners within the lake and tributary system or on a simple increase in the tributary subpopulation<sup>2</sup> to the exclusion of a lakeshore subpopulation. Managing the transition from current population attributes to the attributes of the viable population will require care and attention to the status of the various components of the population and to habitat and watershed conditions in the tributaries and the lake. Care must be taken to begin the process of habitat recovery in the lake at the same time as restoration proceeds in the tributaries so that the attributes of the remaining lake aggregations are not lost altogether.

Of concern then, is that the present spatial structure and diversity of the population does not well represent the desired characteristics of the viable population. Currently, the population is not well-distributed, either within the tributaries or the lake or across the watershed. This relatively confined spatial structure (considering both the distribution of spawners and the abundance of each of the spawning groups) probably also confines the expression of life history diversity, especially if the adaptive regime experienced by the fish is limited. Moreover, given the population's present limited distribution, the risks from severe environmental events and from more general environmental degradation are high.

Our analyses and recommendations for viability criteria for all four VSP parameters were based on the best currently available information for Lake Ozette sockeye salmon. Although we attempted to address important sources of uncertainty in our analyses and recommendations, we were limited by the lack of good historical data (e.g., spawner abundances, distribution over lake beaches and between lake and tributary spawning areas, and life history diversity). Likewise because of this uncertainty, recovery strategies focusing exclusively on either tributary or beach spawners alone are also highly uncertain. The only practical solution to this uncertainty is an implemented adaptive management plan. Consequently, we recommend that the recovery plan include an adaptive management component that incorporates improved data monitoring and estimation. Better data about the sockeye salmon population in Lake Ozette is essential to being

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<sup>2</sup> Subpopulation refers here to distinct spawning aggregations and does not necessarily imply a more rigorous genetic distinction.

able to recognize changes in the status as a result of recovery actions and will allow reanalysis of the population to get better estimates of annual results. This will allow viability criteria to be reevaluated and, if warranted, revised as part of the adaptive management program.

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# Appendix A: Data and Diagnostics for Viability Analysis of Lake Ozette Sockeye Salmon

## Data

Run size values from Haggerty et al. (2008, their Appendix B) in Table A-1 below are the medians of several values, as explained there. The escapement numbers given are the run size minus the broodstock take. Years with no run size estimates available were filled in by expanding weir counts (Haggerty et al. 2008, their Table 3.5) by the average ratio of weir counts to overall system estimates (Haggerty et al. 2008, their Appendix B). Because the expansion factor seemed to be generally larger before 1991 and smaller after that, we used the pre-1991 average of 2.37 for the years before 1991 and the post-1991 average of 1.46 for the later years. We also used a factor of 1.46 to expand weir count data for 2004, 2005, and 2006 provided to us by Caroline Peterschmidt of the Makah Tribe. By this method, we were able to fill in all years except 1985 and 1987, for which there were no weir counts available; they were estimated as the average of the escapement from the year before and the year after. Note that in each case, one of the two years averaged was also an estimate for missing data, but based on the expansion factor.

Estimates of the natural origin (NOR) fraction of the total escapement were derived from NOR estimates of the Umbrella Creek returns provided by the Makah Tribe to reflect the proportion of the total Ozette return that are NOR.

The broodstock take given in Table A-1 is from Haggerty et al. (2008, their Appendix C and Table 3.9), but reflects only the NOR portion of the broodstock take. Prior to 2000, the broodstock take was from the beaches and was all NOR. From 2000 on, the broodstock take was from Umbrella Creek returns and included both NOR and hatchery origin fish. We used the NOR proportions given us by the Makah Tribe (see previous paragraph) to determine the NOR fish in the broodstock take.

From the escapement time series in Table A-1, estimates of variance ( $\sigma^2$ ) and growth rate ( $\mu$ ) can be computed using the methods described for the Lake Quinault data analysis (Appendix B) as shown below, providing estimates of  $\mu$  and  $\sigma^2$  for natural escapement (Tesc), NOR escapement (Wesc), and hatchery adjusted escapement (Hat).

|            | <u>Tesc</u> | <u>Wesc</u> | <u>Hat</u> |
|------------|-------------|-------------|------------|
| $\mu$      | 0.033       | 0.027       | 0.019      |
| $\sigma^2$ | 0.098       | 0.100       | 0.096      |

Tesc estimates use the time series of estimated total natural escapement, including both NOR and hatchery-origin fish that escape to natural spawning areas. Wesc estimates use the

Table A-1. Lake Ozette sockeye salmon data used in viability analysis and source of estimates. Years where we estimated the escapement are italicized.

| Year        | Escapement   |            | NOR fraction | Escapement data source           |
|-------------|--------------|------------|--------------|----------------------------------|
|             | Spawning     | Broodstock |              |                                  |
| 1977        | 2,752        | 0          | 100%         | Haggerty et al. 2008, Appendix B |
| 1978        | 2,398        | 0          | 100%         | Haggerty et al. 2008, Appendix B |
| 1979        | 1,335        | 0          | 100%         | Haggerty et al. 2008, Appendix B |
| 1980        | 1,054        | 0          | 100%         | Haggerty et al. 2008, Appendix B |
| 1981        | 858          | 0          | 100%         | Haggerty et al. 2008, Appendix B |
| 1982        | 4,131        | 0          | 100%         | Haggerty et al. 2008, Appendix B |
| <i>1983</i> | <i>828</i>   | <i>14</i>  | <i>100%</i>  | <i>Expanded from weir count</i>  |
| 1984        | 2,474        | 0          | 100%         | Haggerty et al. 2008, Appendix B |
| <i>1985</i> | <i>2,054</i> | <i>40</i>  | <i>100%</i>  | <i>Interpolated</i>              |
| <i>1986</i> | <i>1,566</i> | <i>43</i>  | <i>100%</i>  | <i>Expanded from weir count</i>  |
| <i>1987</i> | <i>5,542</i> | <i>123</i> | <i>100%</i>  | <i>Interpolated</i>              |
| 1988        | 9,696        | 193        | 95%          | Haggerty et al. 2008, Appendix B |
| 1989        | 1,520        | 6          | 95%          | Haggerty et al. 2008, Appendix B |
| 1990        | 709          | 33         | 95%          | Haggerty et al. 2008, Appendix B |
| 1991        | 1,932        | 175        | 95%          | Haggerty et al. 2008, Appendix B |
| 1992        | 4,010        | 109        | 95%          | Haggerty et al. 2008, Appendix B |
| <i>1993</i> | <i>320</i>   | <i>32</i>  | <i>92%</i>   | <i>Expanded from weir count</i>  |
| 1994        | 949          | 54         | 93%          | Haggerty et al. 2008, Appendix B |
| <i>1995</i> | <i>363</i>   | <i>94</i>  | <i>63%</i>   | <i>Expanded from weir count</i>  |
| 1996        | 3,931        | 200        | 95%          | Haggerty et al. 2008, Table 3.6  |
| 1997        | 1,404        | 263        | 79%          | Haggerty et al. 2008, Table 3.6  |
| 1998        | 1,882        | 88         | 91%          | Haggerty et al. 2008, Table 3.6  |
| 1999        | 2,620        | 29         | 84%          | Haggerty et al. 2008, Table 3.6  |
| 2000        | 4,851        | 170        | 87%          | Haggerty et al. 2008, Table 3.6  |
| 2001        | 4,151        | 149        | 93%          | Haggerty et al. 2008, Table 3.6  |
| 2002        | 3,822        | 116        | 88%          | Haggerty et al. 2008, Table 3.6  |
| 2003        | 4,876        | 193        | 99%          | Haggerty et al. 2008, Table 3.6  |
| <i>2004</i> | <i>6,461</i> | <i>190</i> | <i>92%</i>   | <i>Expanded from weir count</i>  |
| <i>2005</i> | <i>2,997</i> | <i>144</i> | <i>77%</i>   | <i>Expanded from weir count</i>  |
| <i>2006</i> | <i>3,044</i> | <i>29</i>  | <i>63%</i>   | <i>Expanded from weir count</i>  |

time series of estimated NOR escapements obtained by applying the estimated NOR fraction to the estimated total escapement. Hat estimates use the adjustment for hatchery fish in progeny escapement as described for the Lake Quinault data analysis (Appendix B). Unlike the Quinault system, there is no harvest on Ozette sockeye salmon.

## Diagnostics

We examined three diagnostic tests.

1. Slope of  $\sigma^2(\tau)$  versus  $\tau$  (the lag) is linear.

The slope method assumes the relationship of  $\sigma^2$  to  $\tau$  is linear. Visual inspection of the graph for the Hat adjustment suggests this is the case for the data in Figure A-1.

2. Distribution of  $\ln(N_{t+1}/N_t)$  is approximately normal.

The slope method also assumes that the distribution of the natural logarithm of the 4-year running sums, lagged one year, is approximately normal. The data used in all three of these analyses fit this assumption well. For example, for the Hat analysis, results of three statistical tests, giving the coefficient value and probability ( $p$ ) and testing the Ozette sockeye salmon data for normality, were as follows.

|              | <u>Coefficient</u> | <u><math>p</math></u> |
|--------------|--------------------|-----------------------|
| Shapiro-Wilk | 0.9786             | 0.8431                |
| Skewness     | 0.2567             | 0.5520                |
| Kurtosis     | 0.5193             | 0.4286                |

The  $p$  values are all high, indicating no identifiable deviation from normality (Figure A-2).

3. No temporal trend in  $\ln(N_{t+1}/N_t)$  or recruits per spawner.

The Ozette time series is also relatively stationary over the 30-year period used here, which satisfies another assumption of the slope method.

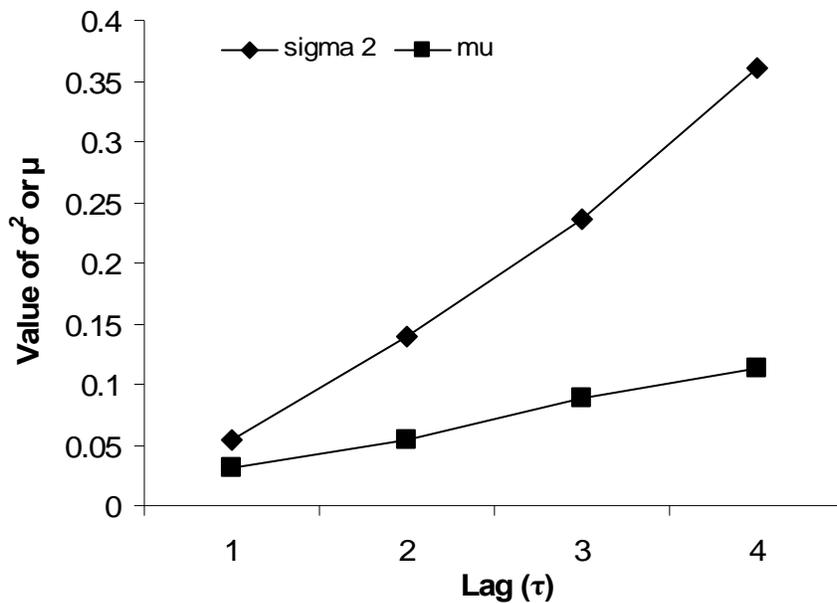


Figure A-1. Graph for  $\sigma^2$  ( $\sigma^2$ ) and  $\mu$  versus lag for the 30-year time series.

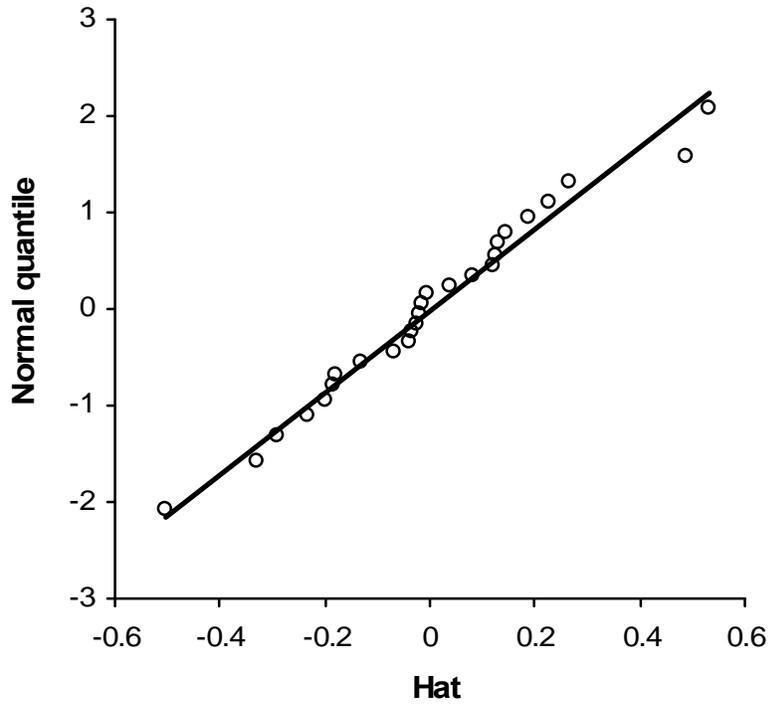


Figure A-2. Normal probability plot of  $\ln(N_{t+1}/N_t)$  for the Hat analysis.

# Appendix B: Data and Diagnostics for Viability Analysis of Lake Quinault Sockeye Salmon

## Data

The time series of escapement and catch plus escapement for Lake Quinault sockeye salmon, 1908–2005, is shown in Figure B-1 and the available data are given in Table B-1.

Larry Gilbertson, biologist for the Quinault Indian Nation (QIN), supplied the data in Table B-1, along with the following explanations:<sup>3</sup>

**Harvest.** The harvest estimates come from historic and current records and catch accounting systems. The estimate for 1908 came from an article in the New York Sun Times (July 19, 1908). The estimates for 1910–1952 came from a Washington Department of Fisheries (WDF) publication (R. S. Robison, 1953, *The Quinault River Indian Fishery with statistics of the catch.*). Harvest numbers for 1910–1934 were estimated based on an average of 7.5 fish per case of 48 half-pound cans. The estimates for 1935–1952 came from the WDF catch reporting system. The

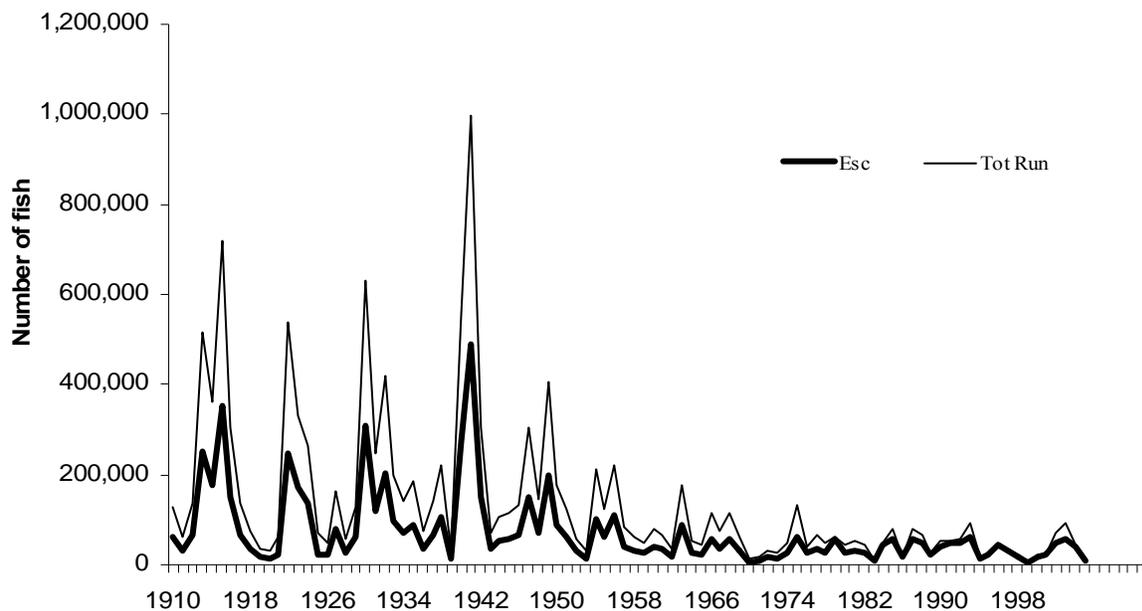


Figure B-1. Time series of escapement (Esc) and total run size (Tot Run) for Lake Quinault sockeye salmon, 1910–2005.

<sup>3</sup> Larry Gilbertson, Quinault Indian Nation, Taholah, WA. Pers. commun., August 2006.

Table B-1. Catch and escapement data for Lake Quinault sockeye salmon, 1908–2005. The number and percentage of hatchery fish in the escapement are also given.

| <b>Year</b> | <b>Harvest</b> | <b>Escapement</b> | <b>Run size</b> | <b>Hatchery</b> | <b>Hatchery %</b> |
|-------------|----------------|-------------------|-----------------|-----------------|-------------------|
| 1908        | 75,000         | 72,059            | 147,059         | 0               | 0.0%              |
| 1910        | 65,250         | 62,691            | 127,941         | 0               | 0.0%              |
| 1911        | 30,465         | 29,270            | 59,735          | 0               | 0.0%              |
| 1912        | 70,500         | 67,735            | 138,235         | 0               | 0.0%              |
| 1913        | 263,198        | 252,877           | 516,075         | 0               | 0.0%              |
| 1914        | 184,110        | 176,890           | 361,000         | 0               | 0.0%              |
| 1915        | 367,260        | 352,858           | 720,118         | 0               | 0.0%              |
| 1916        | 154,725        | 148,657           | 303,382         | 0               | 0.0%              |
| 1917        | 69,120         | 66,409            | 135,529         | 0               | 0.0%              |
| 1918        | 37,350         | 35,885            | 73,235          | 0               | 0.0%              |
| 1919        | 18,660         | 17,928            | 36,588          | 2,566           | 7.0%              |
| 1920        | 15,665         | 15,051            | 30,716          | 2,566           | 8.4%              |
| 1921        | 38,850         | 22,892            | 61,742          | 0               | 0.0%              |
| 1922        | 288,195        | 249,545           | 537,740         | 2,625           | 0.5%              |
| 1923        | 156,810        | 176,503           | 333,313         | 6,756           | 2.0%              |
| 1924        | 125,595        | 141,042           | 266,637         | 5,432           | 2.0%              |
| 1925        | 49,695         | 20,854            | 70,549          | 2,791           | 4.0%              |
| 1926        | 25,935         | 24,918            | 50,853          | 1,490           | 2.9%              |
| 1927        | 84,300         | 80,994            | 165,294         | 2,184           | 1.3%              |
| 1928        | 30,000         | 28,824            | 58,824          | 4,937           | 8.4%              |
| 1929        | 66,735         | 64,118            | 130,853         | 4,381           | 3.3%              |
| 1930        | 323,040        | 310,372           | 633,412         | 3,362           | 0.5%              |
| 1931        | 127,140        | 122,154           | 249,294         | 3,697           | 1.5%              |
| 1932        | 213,945        | 205,555           | 419,500         | 2,792           | 0.7%              |
| 1933        | 101,310        | 97,337            | 198,647         | 3,240           | 1.6%              |
| 1934        | 74,400         | 71,482            | 145,882         | 5,264           | 3.6%              |
| 1935        | 95,094         | 91,365            | 186,459         | 5,747           | 3.1%              |
| 1936        | 39,060         | 37,528            | 76,588          | 5,257           | 6.9%              |
| 1937        | 71,890         | 69,071            | 140,961         | 3,899           | 2.8%              |
| 1938        | 113,594        | 109,139           | 222,733         | 2,460           | 1.1%              |
| 1939        | 17,127         | 16,455            | 33,582          | 3,641           | 10.8%             |
| 1940        | 280,422        | 269,425           | 549,847         | 3,730           | 0.7%              |
| 1941        | 509,140        | 489,174           | 998,314         | 1,446           | 0.1%              |
| 1942        | 155,247        | 149,159           | 304,406         | 1,986           | 0.7%              |
| 1943        | 37,410         | 35,943            | 73,353          | 2,378           | 3.2%              |
| 1944        | 54,686         | 52,541            | 107,227         | 1,889           | 1.8%              |
| 1945        | 60,129         | 57,771            | 117,900         | 2,135           | 1.8%              |
| 1946        | 68,068         | 65,399            | 133,467         | 2,145           | 1.6%              |
| 1947        | 156,941        | 150,786           | 307,727         | 2,391           | 0.8%              |
| 1948        | 74,631         | 71,704            | 146,335         | 2,288           | 1.6%              |
| 1949        | 207,473        | 199,337           | 406,810         | 2,072           | 0.5%              |
| 1950        | 91,008         | 87,439            | 178,447         | 1,816           | 1.0%              |
| 1951        | 62,442         | 59,993            | 122,435         | 718             | 0.6%              |
| 1952        | 29,928         | 28,754            | 58,682          | 0               | 0.0%              |
| 1953        | 15,644         | 15,031            | 30,675          | 0               | 0.0%              |
| 1954        | 107,579        | 103,360           | 210,939         | 0               | 0.0%              |

Table B-1 continued. Catch and escapement data for Lake Quinault sockeye salmon, 1908–2005. The number and percentage of hatchery fish in the escapement are also given.

| <b>Year</b> | <b>Harvest</b> | <b>Escapement</b> | <b>Run size</b> | <b>Hatchery</b> | <b>Hatchery %</b> |
|-------------|----------------|-------------------|-----------------|-----------------|-------------------|
| 1955        | 62,417         | 59,969            | 122,386         | 0               | 0.0%              |
| 1956        | 112,646        | 108,229           | 220,875         | 0               | 0.0%              |
| 1957        | 43,545         | 41,837            | 85,382          | 0               | 0.0%              |
| 1958        | 32,036         | 30,780            | 62,816          | 0               | 0.0%              |
| 1959        | 25,288         | 24,296            | 49,584          | 0               | 0.0%              |
| 1960        | 40,159         | 38,584            | 78,743          | 0               | 0.0%              |
| 1961        | 34,551         | 33,196            | 67,747          | 0               | 0.0%              |
| 1962        | 18,828         | 18,090            | 36,918          | 0               | 0.0%              |
| 1963        | 89,674         | 86,157            | 175,831         | 0               | 0.0%              |
| 1964        | 26,210         | 25,182            | 51,392          | 0               | 0.0%              |
| 1965        | 21,648         | 20,799            | 42,447          | 0               | 0.0%              |
| 1966        | 58,872         | 56,563            | 115,435         | 0               | 0.0%              |
| 1967        | 37,556         | 36,083            | 73,639          | 0               | 0.0%              |
| 1968        | 58,010         | 55,735            | 113,745         | 0               | 0.0%              |
| 1969        | 30,576         | 29,377            | 59,953          | 0               | 0.0%              |
| 1970        | 5,987          | 5,752             | 11,739          | 0               | 0.0%              |
| 1971        | 9,701          | 9,321             | 19,022          | 0               | 0.0%              |
| 1972        | 16,185         | 15,550            | 31,735          | 0               | 0.0%              |
| 1973        | 12,369         | 15,200            | 27,569          | 0               | 0.0%              |
| 1974        | 25,629         | 25,000            | 50,629          | 0               | 0.0%              |
| 1975        | 73,612         | 60,487            | 134,099         | 0               | 0.0%              |
| 1976        | 14,904         | 26,420            | 41,324          | 0               | 0.0%              |
| 1977        | 30,400         | 34,900            | 65,300          | 774             | 1.2%              |
| 1978        | 21,022         | 28,586            | 49,608          | 1,826           | 3.7%              |
| 1979        | 4,666          | 60,800            | 65,466          | 5,865           | 9.0%              |
| 1980        | 16,653         | 30,000            | 46,653          | 4,964           | 10.6%             |
| 1981        | 21,743         | 32,949            | 54,692          | 2,002           | 3.7%              |
| 1982        | 15,329         | 30,909            | 46,238          | 4,266           | 9.2%              |
| 1983        | 679            | 11,546            | 12,225          | 4,046           | 33.1%             |
| 1984        | 947            | 48,550            | 49,497          | 3,118           | 6.3%              |
| 1985        | 24,736         | 58,700            | 83,436          | 3,313           | 4.0%              |
| 1986        | 1,894          | 20,516            | 22,410          | 3,607           | 16.1%             |
| 1987        | 24,347         | 57,186            | 81,533          | 1,861           | 2.3%              |
| 1988        | 18,186         | 49,492            | 67,678          | 168             | 0.2%              |
| 1989        | 2,691          | 22,017            | 24,708          | 88              | 0.4%              |
| 1990        | 10,106         | 41,536            | 51,642          | 0               | 0.0%              |
| 1991        | 6,158          | 48,820            | 54,978          | 0               | 0.0%              |
| 1992        | 9,797          | 47,162            | 56,959          | 0               | 0.0%              |
| 1993        | 33,681         | 59,832            | 93,513          | 0               | 0.0%              |
| 1994        | 1,194          | 14,407            | 15,601          | 0               | 0.0%              |
| 1995        | 828            | 22,147            | 22,975          | 0               | 0.0%              |
| 1996        | 2,230          | 45,527            | 47,757          | 231             | 0.5%              |
| 1997        | 3,690          | 30,973            | 34,663          | 894             | 2.6%              |
| 1998        | 5,476          | 18,801            | 24,277          | 705             | 2.9%              |
| 1999        | 760            | 5,967             | 6,727           | 111             | 1.6%              |
| 2000        | 250            | 18,364            | 18,614          | 70              | 0.4%              |

Table B-1 continued. Catch and escapement data for Lake Quinault sockeye salmon, 1908–2005. The number and percentage of hatchery fish in the escapement are also given.

| Year | Harvest | Escapement | Run size | Hatchery | Hatchery % |
|------|---------|------------|----------|----------|------------|
| 2001 | 284     | 21,302     | 21,586   | 0        | 0.0%       |
| 2002 | 21,800  | 50,000     | 71,800   | 0        | 0.0%       |
| 2003 | 37,131  | 56,612     | 93,743   | 1,292    | 1.4%       |
| 2004 | 6,973   | 39,942     | 46,915   | 2,076    | 4.4%       |
| 2005 | 517     | 12,022     | 12,539   | 1,773    | 14.1%      |

estimates for 1953–1965 were taken from WDF Statistical Reports and the Joint Biological Statement (U.S. v Washington). Estimates for 1966–1970 were taken from reports prepared by the U.S. Fish and Wildlife Service, Fisheries Assistance Office, for the QIN. Estimates for 1975–2005 were taken from the QIN catch reporting system. Harvest numbers for the earlier years were also cited in various publications and government reports (e.g., annual reports of the U.S. Bureau of Indian Affairs agent at Taholah) that differ from the estimates reported by Robison.

**Escapement.** We have escapement estimates made directly from counts for two time periods, 1921–1925 and 1973–2005. The early estimates were made from weir counts at a Bureau of Fisheries weir constructed at the mouth of Lake Quinault. Escapement estimates since 1973 have been made using acoustic methods in Lake Quinault. The weir counts were “corrected” for days that the weir was not operated and for years when the weir started operations late or ended operations early. The estimates for other years were based on assuming a fixed harvest rate (see below).

**Harvest rates.** The basic structure of the fishery was established in 1915, based on recommendations contained in a report by Special Agent Dorrington of the U.S. Indian Service. Fishing ground locations were formally established with specific gear limitations for each. This basic structure has survived to the present and is still enforced. A system of fishing seasons and schedules was also established early in the period of record. As a result, the fishery operated in a fairly consistent way from 1915 through 1978. Much of the structure was already in place prior to 1915 and was enforced by the power of tradition. After 1978, management was changed from a set-season-gear-restriction approach to an escapement goal approach. The harvest rates during 1921–25 (mean = 0.56) and 1973–1978 (mean = 0.46) can be used to represent the “norm” for the fishery. Interestingly, the overall mean of 0.51 is near the level of federal policy for stocks under federal management in the early 1900s (e.g., sockeye salmon in Alaska). This was not Dorrington’s intent; it is just a fortuitous result of the structured fishery.

**Hatchery contribution.** Hatchery releases of sockeye salmon have occurred in Lake Quinault from two facilities during two time periods. The U.S. Bureau of Fisheries operated a hatchery on Lake Quinault from 1914 to 1947. The QIN has operated a facility on the lake since 1972. Broodstock for the bureau hatchery came mostly from spawning grounds distant from the facility. A few adults were taken at the facility toward the end of its operation, but the on-station egg takes amounted to

only 10–12% of the total each year. Broodstock for the QIN hatchery has come from spawning grounds. The fingerling releases from the bureau hatchery were fed fry held into the summer period prior to release. The fingerling releases from the QIN facility were fish fed for accelerated growth and released in early summer as 0-age smolts.

The only direct estimates of return rates for the sockeye salmon releases comes from the 0-age smolt releases from the QIN facility. Marked fish from the 1973–1976 broodyear releases were recorded during catch sampling. These data were used to estimate a total brood year return rate of approximately 0.01. Survival of fry and fingerlings from the bureau facility were likely on the low side of the published range. The hatchery practices were not advanced and there was little sign of success; for example, after three decades of operation, only a small hatchery run had been developed (only  $\approx 100$  females/year). The 0-age smolt rate was used for yearlings simply for lack of something better. The return rate for QIN facility fry is based on midlevel survival. This was chosen because of improved hatchery practices and decreased competition from natural origin (NOR) fry. A high survival rate was not used because of degraded habitat conditions.

Based on the above, the time series from 1973 through 2005 (Figure B-2) includes the best time series of data having independent estimates of both harvest and escapement.

### Basic Data Analysis

We estimated the variance of the growth rate ( $\sigma^2$ ) in three ways: 1) using the time series of estimated natural origin spawning escapements (Wesc), 2) using this time series with an

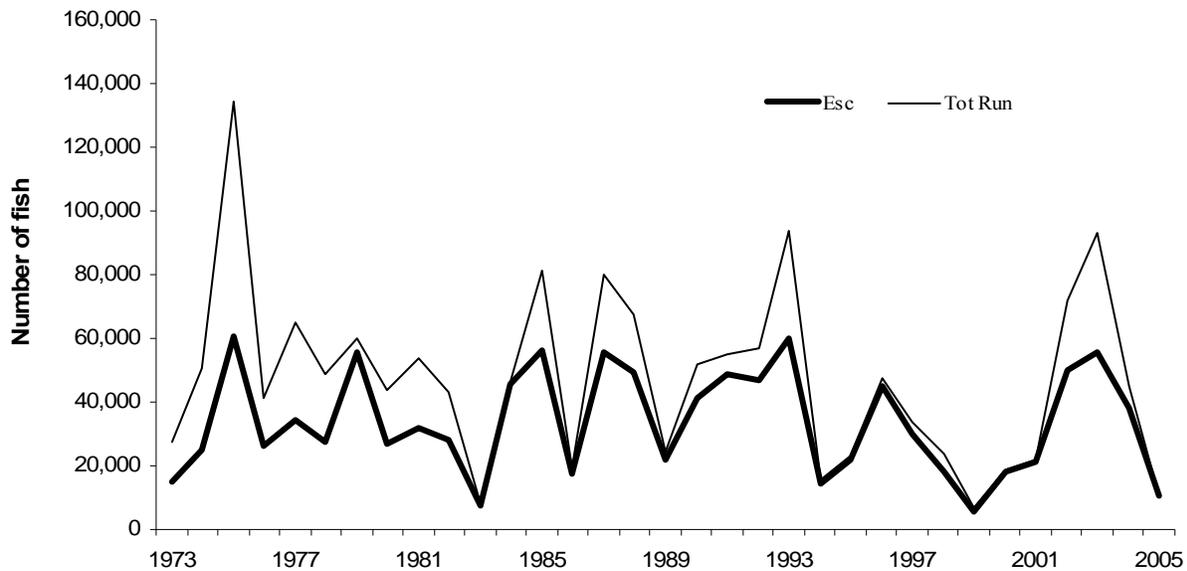


Figure B-2. Time series of Esc and Tot Run for Lake Quinault sockeye salmon, 1973–2005.

adjustment for hatchery (HatAdj), and 3) using the time series of total recruitment adjusted for both hatchery and harvest (HatHarAdj). The first and second estimates use Holmes' (2001) method directly. The third estimate, HatHarAdj, uses a modification (McElhany and Payne in prep.) to account for productivity that would not be evident from looking at escapement data alone.

In all cases, 4-year-long unweighted running sums of the appropriate time series were used as the basic input data and lags of 1 through 4 years ( $\tau = 4$  in Holmes' notation) were used for the slope estimates. The HatAdj estimate requires average age of reproduction as an input parameter and, lacking specific data for the Quinault population, we used an average age of 3.5 years. A Microsoft Excel spreadsheet was developed to compute these estimates rather than the SimSalmon computer program, because the spreadsheet approach facilitates manipulation of the data to conduct the diagnostic tests.

The computations were conducted on the entire 1910–2005 (96-year) time series and on the 1973–2005 (33-year) subset, during which time we have independent estimates of escapement and catch.

For the 96-year time series,  $\sigma^2$  was estimated to be between 0.159 and 0.175 for the Wesc, HatAdj, and HatHarAdj analyses (Table B-2). For the 33-year time series,  $\sigma^2$  was estimated to be between 0.038 and 0.061 for the three analyses (Table B-2).

## Diagnostics

We examined seven diagnostic tests, which look at assumptions of the method, suggested by Paul McElhany as follows.

1. Slope of  $\sigma^2(\tau)$  versus  $\tau$  is linear.

Visual inspection suggests that the relationship of  $\sigma^2(\tau)$  versus  $\tau$  is linear for both series (Figure B-3 and Figure B-4). For the three, 96-year HatAdj analyses, there is a possible deviation from linearity at  $\tau = 4$ . Reducing the maximum lag to 3 from 4 for the 96-year time series would increase the estimates of  $\sigma^2$ .

Table B-2. Estimates of  $\mu$  and  $\sigma^2$  for the two Lake Quinault sockeye salmon time series, 1910–2005 (96 years) and 1973–2005 (33 years).

| Fixed                | Wesc   | HatAdj | HatHarAdj |
|----------------------|--------|--------|-----------|
| 1910–2005 (96 years) |        |        |           |
| $\mu$                | –0.011 | –0.014 | 0.129     |
| $\sigma^2$           | 0.163  | 0.159  | 0.175     |
| 1973–2005 (33 years) |        |        |           |
| $\mu$                | 0.007  | 0.000  | 0.063     |
| $\sigma^2$           | 0.041  | 0.038  | 0.061     |

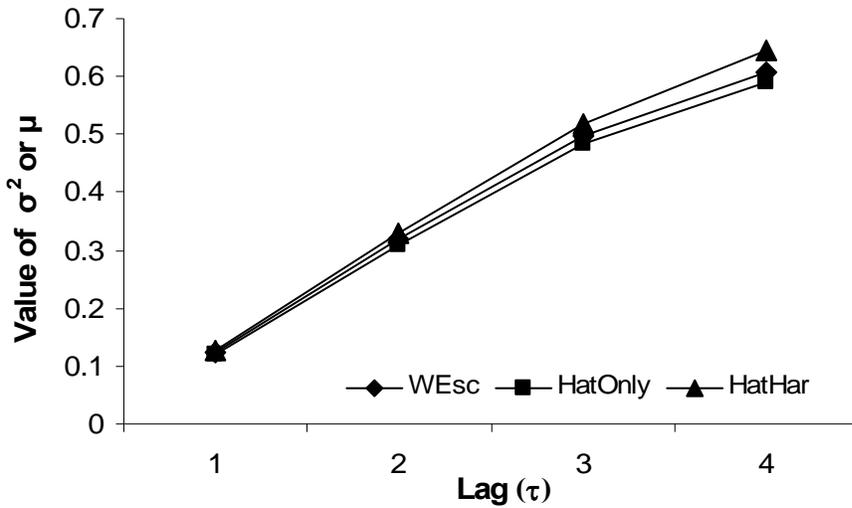


Figure B-3. Graphs of  $\sigma^2$  versus lag for the 96-year time series.

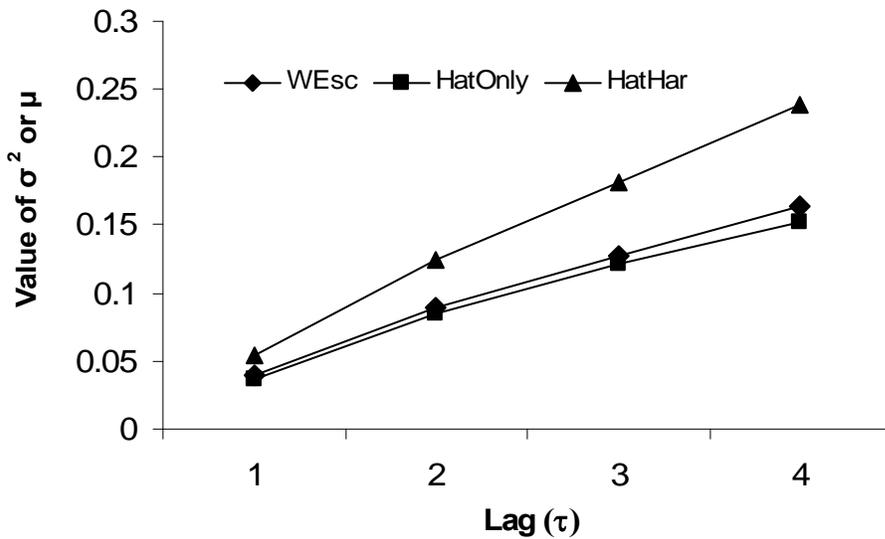


Figure B-4. Graphs of  $\sigma^2$  versus lag for the 33-year time series.

2. Distribution of  $\ln(N_{t+1}/N_t)$  is approximately normal.

Inspection of a normal probability plot of the natural log interannual ratios of the 4-year running sums shows significant deviation from a normal distribution in some cases. For example, the 96-year HatHar adjusted series (Figure B-5) differs from normality at  $p = 0.06$  by the Shapiro-Wilk test and has a coefficient of skewness significantly different from 0 at  $p = 0.02$ .

The comparable series for the 33-year period (Figure B-6) fits the normal distribution better, with a Shapiro-Wilk coefficient at  $p = 0.63$  and a skewness coefficient different from 0 at  $p = 0.2$ .

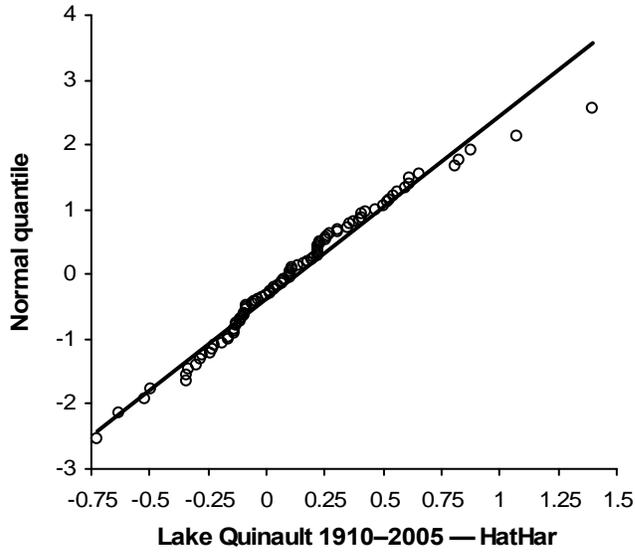


Figure B-5. Normal probability plot of  $\ln(N_{t+1}/N_t)$  for escapement, 96-year time series.

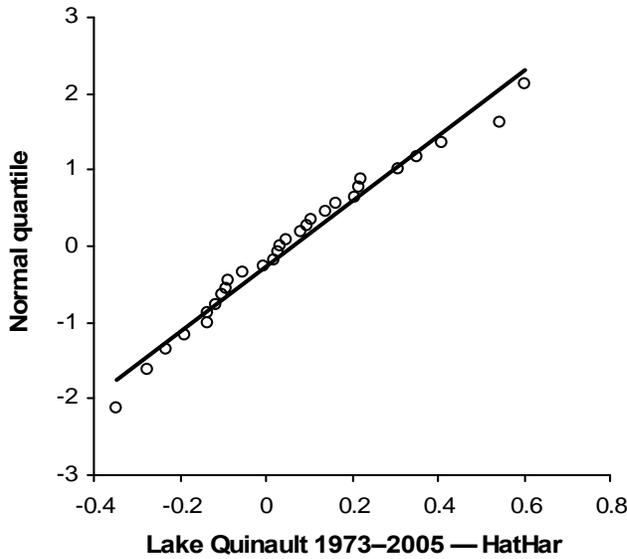


Figure B-6. Normal probability plot of  $\ln(N_{t+1}/N_t)$  for escapement, 33-year time series.

3. No temporal trend in  $\ln(N_{t+1}/N_t)$ .

A graph of the time series of  $\ln(N_{t+1}/N_t)$ , adjusted for hatchery and harvest effects, appears to be stationary, although there seems to be a reduction in the absolute values of the extreme high and low values going forward in the 96-year time period (Figure B-7).

4. No temporal trend in preharvest recruits per spawner.

A graph of the 4-year running sum of recruits (catch plus escapement) divided by the 4-year running sum of NOR spawners 4 years earlier shows a cyclic pattern (high every 7–10 years) with decreasing recruits per spawner overall over time (Figure B-8).

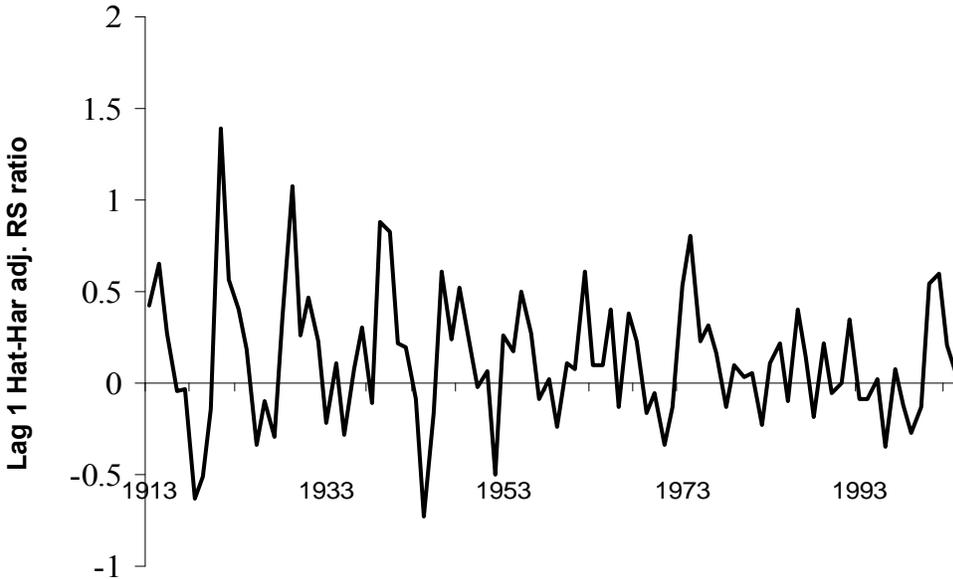


Figure B-7. Graph of natural logarithm of lag 1 ratios of 4-year running sums of spawning escapements, 96-year time series. The year on the x-axis is the final year of the running sum in the denominator.

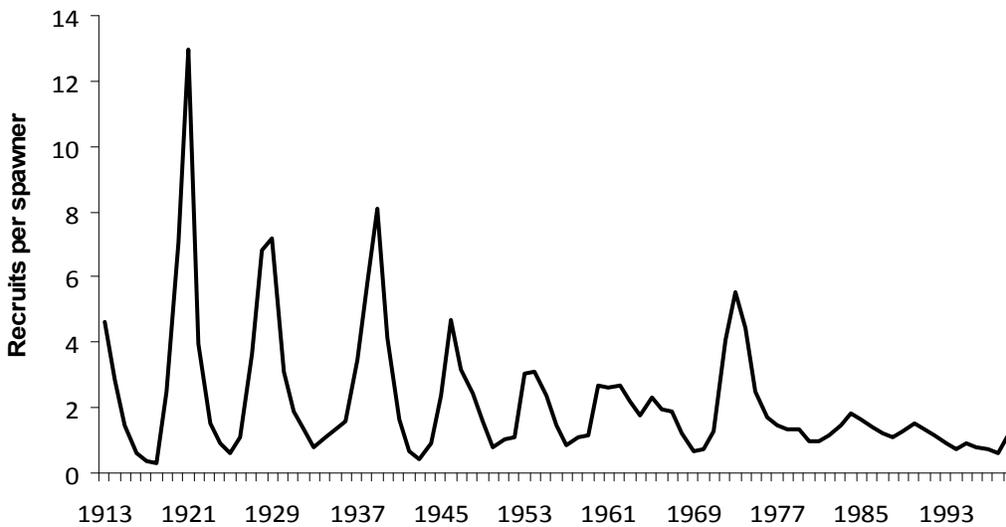


Figure B-8. Time series of 4-year running sum of catch plus escapement ( $t+4$ ) divided by 4-year running sum of escapement ( $t$ ) for the previous 4 years. The x-axis is labeled with the final year of the escapement running sum.

## 5. No density dependence.

To look for density dependence, we examined the size of the return from the size of the spawning abundance. Assuming an average age of 4 years, we compared escapement in year  $t$  with the catch plus escapement 4 years later for the years 1910–2001; there is a definite pattern of density dependence (Figure B-9 upper graph). If we only look at recent abundance (1973–2001), although the range of escapements and returns is much reduced, the pattern of density dependence is still notable, but much less pronounced (Figure B-9 lower graph).

## 6. No temporal trend or changes in $\sigma^2$ .

Estimates of  $\sigma^2$  for 20-year segments of the 1910–2005 time series range from 0.020 to 0.432 (Table B-3). The estimates from the Wesc, HatAdj, and HatHar series are nearly identical for the 1910–1969 period because every estimate of total returns before 1973 used the constant 0.845 catch to escapement ratio (Table B-1). The magnitude of Wesc and the total return are both positively correlated with  $\sigma^2$  (computed with the HatHar correction) at  $p < 0.05$ , and this coincides with a downward trend in both abundance and  $\sigma^2$  over time until about 1960 (Figure B-10). However for the recent period,  $\sigma^2$  appears to be stationary (Figure B-10).

## 7. Data should not encompass regime shifts.

Major regime shifts (long-term changes in overall survival or productivity) could affect the estimate of  $\sigma^2$ , which is meant to be the variance of growth rate on a relatively short-term basis. There is no good statistical test for this, but any major regime shifts should be apparent from a graph of the escapement over time (Figure B-10). There appears to be an earlier period of higher abundance, followed by a more recent period of lower abundance. The 1973–2005 period encompasses part of this more recent period of low abundance and appears to be within a single production regime.

# Conclusions

The Quinault Lake sockeye salmon provide one of the longest data sets available within or near our domain. However, only the data from 1973 through the present are useful for estimating the variance in growth rate during a period of stable growth.

The 1973–2005 data series for Lake Quinault appears to be a reliable data set and is usable for our purpose. The relationships of  $\sigma^2$  to  $\tau$  are approximately linear, the time series of the log growth rate and recruits per spawner appear to be stationary, the natural log ratios of the 4-year running sums are approximately normally distributed, and there is no indication of major regime shifts.

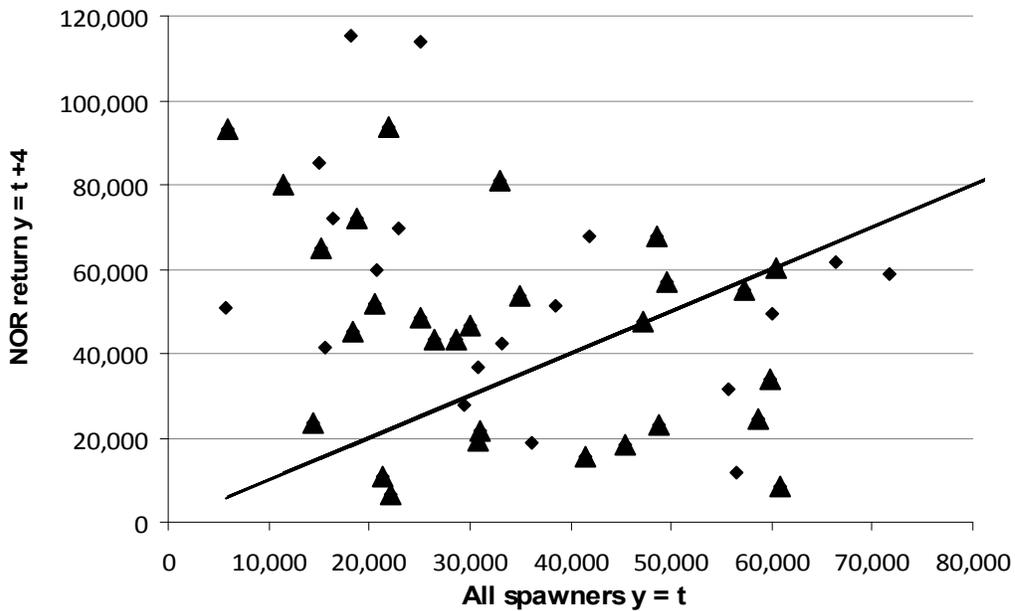
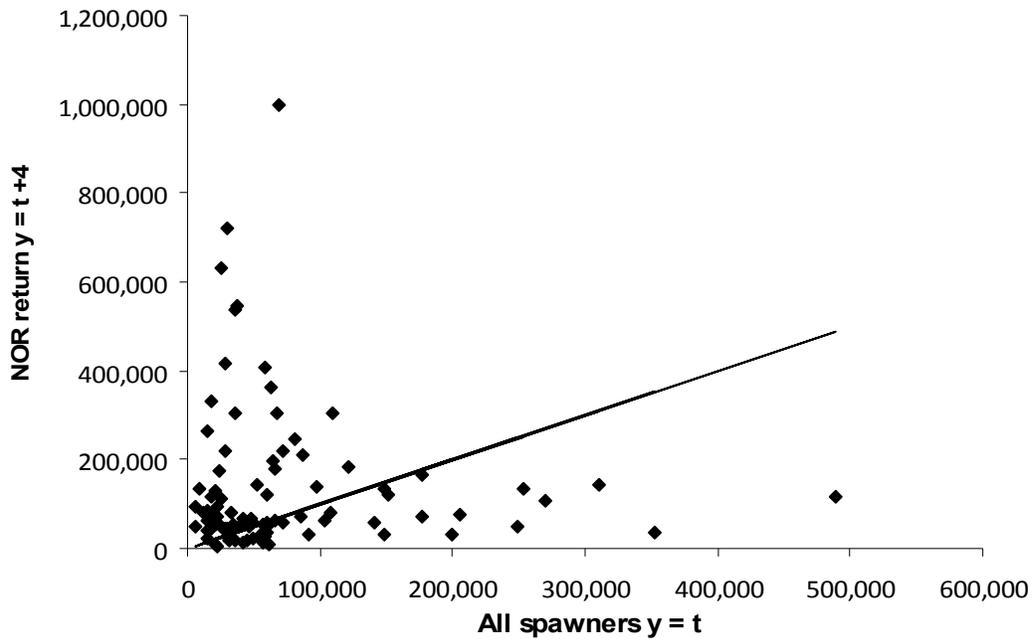


Figure B-9. Graphs of catch plus escapement ( $t+4$ ) versus escapement ( $t$ ). The upper graph is for the entire time series, 1910–2001, and the lower graph is the same plot with the axes reduced to emphasize the recent year time series, 1973–2001, with triangles representing those years and the small diamonds being early years that fall in the same range within the graph. In both graphs, the linear line is the replacement line (i.e., 1:1 return per spawner).

Table B-3. Estimates of  $\sigma^2$  and mean abundance for 20-year segments of the Quinault sockeye salmon time series.

| Years |      | $\sigma^2$ estimate |        |           | Mean abundance |              |
|-------|------|---------------------|--------|-----------|----------------|--------------|
|       |      | Wesc                | HatAdj | HatHarAdj | NOR escapement | Total return |
| 1910  | 1929 | 0.432               | 0.424  | 0.417     | 100,928        | 208,918      |
| 1920  | 1939 | 0.236               | 0.228  | 0.224     | 95,990         | 200,679      |
| 1930  | 1949 | 0.284               | 0.272  | 0.278     | 132,070        | 272,622      |
| 1940  | 1959 | 0.097               | 0.096  | 0.097     | 104,434        | 214,380      |
| 1950  | 1969 | 0.054               | 0.054  | 0.054     | 47,911         | 97,904       |
| 1960  | 1979 | 0.054               | 0.054  | 0.145     | 33,744         | 65,617       |
| 1970  | 1989 | 0.048               | 0.049  | 0.092     | 30,785         | 49,278       |
| 1980  | 1999 | 0.029               | 0.020  | 0.036     | 33,705         | 44,908       |
| 1986  | 2005 | 0.072               | 0.070  | 0.118     | 33,592         | 43,531       |

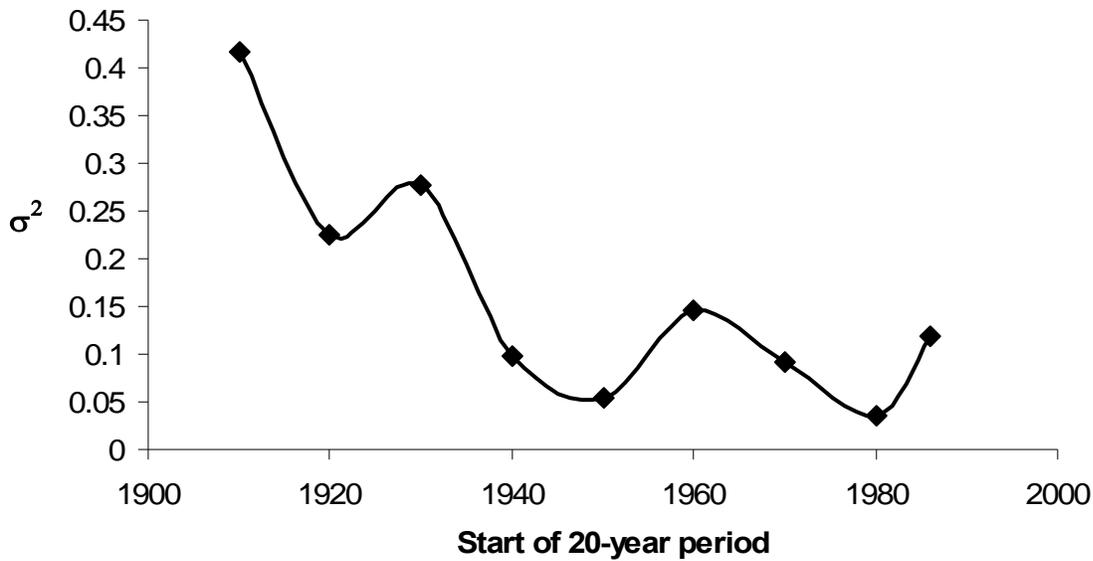


Figure B-10. Trend in  $\sigma^2$  (HatHar) computed for 20-year period with different starting dates.

## Appendix C: “R” Functions Used for Simulation of Population Dynamics in PVA

This appendix provides the computer code for the “R” functions. (Note: The default values for these functions are not necessarily the values used in our runs; see Methods section of this report.)

```
Dennis <- function(mu=0, Q=.1, NZero=10000, T=100, QET=250,
Maxn=3*NZero, randomMax=FALSE) {
    # mu = log growth rate, Q = variance of mu
    N <- NULL
    n <- NZero
    eta <- rnorm(T, 0, sqrt(Q))
    z <- rnorm(T, 0, sqrt(Q))
    for (i in 1:T) {
        n <- n * exp(mu + eta[i])
        if (n < QET) n <- 0
        if (n > Maxn)
            if (randomMax) n <- MaxN*exp(z[i]) else n <- Maxn
        N <- c(N,n)
    }
    return(N)
}

Dennis.Repeat <- function(NRuns=10000, NZero=10000, mu=0, QET=250,
                          Q=.1, Maxn=3*NZero) {
    Extinct <- NULL
    for (i in 1:NRuns) {
        Pop <- Dennis(T=100, mu=mu, QET=QET, NZero=NZero, Q=Q,
                      Maxn=Maxn, randomMax=FALSE)
        p <- min(Pop)
        if (p <= 0)
            Extinct <- c(Extinct, TRUE)
        else Extinct <- c(Extinct, FALSE)
    }
    E <- sum(Extinct)
    return (c(NZero, E/NRuns))
}

NZero.Test <- function(Low=10000, High=150000, Step=5000, Q=.1,
QET=250, NRuns=10000) {
    NZero <- Low
    Output.NZero <- NULL
    Output.ExtProb <- NULL
    while (NZero <= High) {
```

```
Output.NZero <- c(Output.NZero, NZero)
ep <- Dennis.Repeat(NRuns=NRuns, NZero=NZero, Q=Q, QET=QET,
                    Maxn=3*NZero)
Output.ExtProb <- c(Output.ExtProb, ep[2])
NZero <- NZero + Step
}
Output <-
data.frame("NZero"=Output.NZero, "ExtProb"=Output.ExtProb)
return(Output)
}
```

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