

# Viability Criteria for the Lake Ozette Sockeye Salmon ESU



Photo by Caroline Peterschmidt

## *by the Puget Sound Technical Recovery Team*

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*November 20, 2008*

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## **Introduction**

The Puget Sound Technical Recovery Team (PSTRT) was convened by the National Marine Fisheries Service (NMFS) to develop the technical basis for recovery plans for three Pacific salmon (*Oncorhynchus* spp.) evolutionarily significant units (ESUs) listed under the Endangered Species Act (ESA): Lake Ozette sockeye, Puget Sound Chinook, and Hood Canal summer chum. Key tasks of the PSTRT are to identify populations and describe the conditions of viable populations and ESUs. The foundation for accomplishing this for Pacific salmon is described by (McElhany et al. 2000), which discusses delineating populations within an ESU, identifies the key parameters used to describe the status of a population (viable salmon population “VSP” parameters), defines population viability as a probability of persistence over a specified time period, and discusses the means by which ESU delisting criteria can be based on alternative scenarios for the status of populations within the ESU. This report identifies population and ESU viability criteria for the Lake Ozette sockeye salmon (*O. nerka*) 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. 2006). Since the ESU has only one population, the population must be viable in order that the ESU be viable; 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. We consider the conditions for a population to be projected to persist for at least 100 years with a probabilities of 0.95 and 0.99, assuming no immigration or emigration, as bounds for population viability. Because Lake Ozette sockeye are currently below recovered levels and reliable estimates of historical abundance 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 through the adaptive management section of the recovery plan.

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; spatial structure refers to how fish at any life stage are distributed among available or potentially available habitats; and diversity is the variety of genotypes, life histories, morphologies, and other characteristics expressed by individuals within a population. Our task with this report was to develop criteria for each of these characteristics, which, considered together, will describe a viable population and ESU.

Like all 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, in this report abundance is the most well developed. We have used two approaches to determine abundance levels in developing the abundance viability criteria for the Lake Ozette sockeye 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, Munholland, and Scott (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 throughout their life cycle. With such an approach, it is possible to not only determine the abundance criterion for viability, but it is also possible 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 (EDT) model (McConnaha 2001) and the Shiraz model (Sharma et al. 2005, Scheurell et al. 2006) have been applied to the Puget Sound Chinook ESU. Both of these models are data intensive and therefore have not been applied to Lake Ozette sockeye where the necessary information is not available. Instead, the PSTRT considered results from two habitat-based approaches available for Lake Ozette sockeye:

- 1) juvenile habitat rearing capacity approach, which estimates the capacity of Lake Ozette to produce sockeye salmon smolts and 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, and
- 2) spawner habitat capacity approach, which 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 abundance. The criterion is present in terms of a range to include information we have on the population based 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, and it is one of the 4 key population parameters NOAA Fisheries uses to describe viable salmon populations (McElhany et al. 2000). A population that has a greater spatial distribution of individuals 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 3 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 re-colonization (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 re-colonization 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 out throughout the geographic area occupied by the population.

Salmon exhibit considerable diversity within and among populations in their life history, morphological, physiological and genetic traits. Diversity is one of the four key population parameters NOAA Fisheries uses to describe viable salmon populations (McElhany et al. 2000). 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 a population is, the more likely it is 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 (re)colonize newly available habitats. Because salmon regularly face variability in the environments they inhabit, the contributions of diversity to population persistence are critical to consider.

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

## **Methods**

### ***PVA Analysis***

The population viability analysis 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 that the population dynamics will be restored in the future such that 1) the growth rate is stable or increasing ( $\lambda \geq 1$ ) and 2) 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 the analysis performed this way. The first was to estimate  $\sigma^2$  from the observed time series of abundance data using the slope method (Holmes 2001). The second step was to project extinction risk of the population in the future, assuming that the time course of the population approximates a Brownian motion (Dennis, Munholland and Scott 1991). More details on the method are provided below in the section “Parameter Estimation And Population Projection”

### **Data**

Adult return estimates for Lake Ozette sockeye are available for most years from 1977 through 2003 (Haggerty et al. 2007, Appendix A below). These are derived from a variety of census methods and represent the number of adult sockeye entering Lake Ozette each year (Haggerty et al. 2007). 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. (2007) in Appendix A. For Lake Ozette sockeye we use the term “run size” and “escapement” synonymously for Lake Ozette sockeye 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 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, especially lack of reliable information for the years before 1977, we looked at escapement and total recruitment data from other sockeye 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 PVA analyses. However, we completed a detailed analysis for the much longer Lake Quinault run to compare the 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 a species such as salmon. In this method, the variance of the 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 1 to 4. 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 follows the assumptions of the model and also when the population dynamics follows 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 Ozette sockeye, 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 escapements and recruitment with an adjustment for hatchery fish. We did the same for Lake Quinault data, except that a third analysis, for the Lake Quinault time series only, adjusting for both hatchery fish and harvest effects was added. The first estimate uses the Holmes's (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 estimate 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, and 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 four-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's notation) for the 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. We had Lake Quinault catch and escapement data available for 1910- 2005. The full 96-year time series gave us a reasonably long data-set for estimating variability in growth. However, for most of the years before 1973, escapement was estimated as a constant fraction of harvest and was not directly assessed. Therefore, we also computed population parameters for a shorter 33-year dataset (1973-2005) where harvest and escapement were independently estimated (see Appendix B for fuller discussion).

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 depensatory 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 analysis 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 four-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  $N_{QET}$  (the quasi-extinction threshold) 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 value of N (four-year running sum populations 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 an 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 *O. nerka* 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 below citations. A literature review (Haggerty 2006) suggests that salmon production in Lake Ozette is not limited by food availability. He states:

All researchers, (Bortleson and Dion 1979; Dlugokenski et al. 1981; Blum 1988; Beauchamp and LaRiviere 1993) [see also Beauchamp, LaRiviere, and Thomas 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 and concluded that 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 to be the capacity of the lake to support juvenile salmon production based on the plankton productivity of the lake. The Plankton Acre Index (PAI, referred to as API by some authors) was developed by the International Pacific Salmon Fisheries Commission (IPSFC 1972) to estimate the potential sockeye 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 systems 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) (Blum 1988). 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 lake systems used to develop the PAI regression equations.

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

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

Blum notes that, on average, four recruits are produced per spawner in the Fraser systems 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/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: 1) spawners needed for smolt capacity (SSC), 54,000 to 121,500 spawners, and 2) return from the smolt capacity (RSC), 306,000 to 563,000 adult returns. In making these estimates, Blum never gives 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 sockeye in recent years (Tim Tynan, NOAA Fisheries, personal communication). 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 salmon spawners that the lake beaches and tributary streams could accommodate if no other factor were limiting.. Haggerty (2006) developed new estimates of spawner capacity for both beach and tributary habitats and these are explained and reported in the Ozette recovery plan (Haggerty et al. in prep). Recent habitat inventories upon which these estimates are based are documented by Haggerty and Ritchie (2004) and Haggerty (2008). Haggerty (2006) computed spawner capacity 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 three m<sup>2</sup> per female. The numbers of females for both the tributary and beach estimates were converted to total fish assuming a

1:1 male:female ratio. Haggerty's (2006) estimates of the spawner capacity (SpC) range from 11,000 to 15,000 for lake beaches and 80,000 to 106,000 for the three tributaries, for an overall total range of 91,000 to 121,000 for the basin. These are conservative estimates in the sense that, for both beaches and tributaries, there are potentially suitable spawning areas that were not included in the calculations and that would increase the estimates if included (Haggerty 2006 and Haggerty et al. in prep).

### ***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 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 dataset 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.

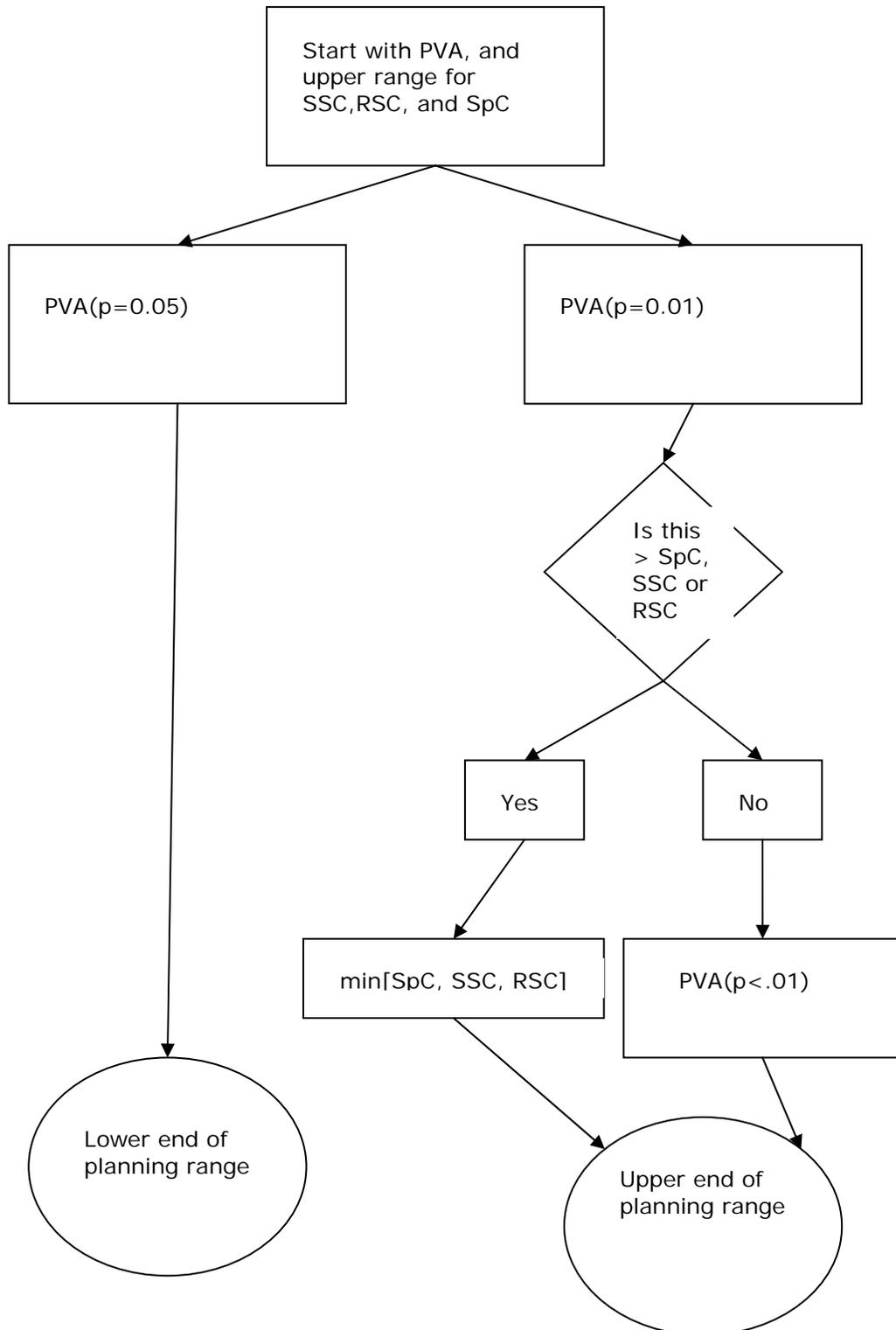


Figure 1. Flow chart showing how demographic and habitat-based analyses were combined with Population Viability Analyses (PVA) to derive planning ranges for equilibrium spawner abundance (based on Ford et al. 2001). SpC = spawner capacity; SSC = spawners needed to produce smolt capacity; RSC = return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

## **Results and Recommendations**

### ***Abundance***

#### PVA Analysis

The estimate of the variance of the population growth rate ( $\sigma^2$ ), 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 (Table 1). We used the 0.1 estimate of  $\sigma^2$  for further analysis.

**Table 1. Estimates of the natural logarithm of the rate of growth ( $\mu$ ) and its variance ( $\sigma^2$ ) for the Lake Ozette sockeye time series, 1977-2007 (30-years) for natural-origin escapement (WEsc), and escapement adjusted for hatchery influence (Hat).**

<b>Ozette</b>		
<b>1977</b>	<b>2007</b>	<b>30 yrs.</b>
	WEsc	Hat
$\mu$	<b>0.027</b>	<b>0.019</b>
$\sigma^2$	<b>0.100</b>	<b>0.0960</b>

Determining minimum population sizes using the population projection simulation requires the following input variables to be specified: population growth rate ( $\lambda$  or its natural logarithm  $\mu$ ), variance of population growth rate ( $\sigma^2$ ), time period for the simulation in years (Y), extinction probability, and quasi-extinction threshold ( $N_{QET}$ ). 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 2). We used 100 years for Y and 0.05 and 0.01 for the extinction probabilities following McElhany et al. (2000). We ran 10000 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 3). Given the estimated  $\sigma^2$  of 0.10 for the 30-year Lake Ozette time series, the minimum population sizes for  $\mu = 0$  is approximately 31,250 for extinction probability ( $p$ ) = 0.05 and 196,250 with  $p = 0.01$  (Table 2).

#### 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 need to produce smolt capacity (SmC) range from 54,000 to 121,500 fish; returns from these spawners would be 306,000 to 563,000 adults. Haggerty's (2006) estimates of the spawner capacity (SpC)

range from 11,000 to 15,000 for lake beaches and 80,000 to 106,000 for tributaries, for an overall total range of 91,000 to 121,000 for the basin.

**Table 2. 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 a probability of extinction (p) less than 0.05 and 0.01. Extinction is determined when the 4-year running sum of abundance declines to a quasi-extinction level ( $N_{qet}$ ) of 250 fish or less over a 100-year period. The estimated  $\sigma^2$  computed from available data for Lake Ozette sockeye (Appendix A) is 0.1. This line is in bold in the table. Numbers were estimated using stochastic simulation modeling as described in the text.**

$\sigma^2$	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
0.06	30,000	7,500	115,000	28,750
0.07	45,000	11,250	200,000	50,000
0.08	65,000	16,250	350,000	87,500
0.09	90,000	22,500	500,000	125,000
<b>0.10</b>	<b>125,000</b>	<b>31,250</b>	<b>785,000</b>	<b>196,250</b>
0.11	160,000	40,000	>800,000	>200,000
0.12	215,000	53,250	>800,000	>200,000

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 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 were appropriate for Lake Ozette, then the viability planning range would be narrower and total abundance value would be smaller. Both the upper and lower ends of the range would be determined by the PVA analysis, and the range would be 11,250 – 47,500 spawners. One could argue that the Lake Quinault dataset is preferable to the Lake Ozette dataset 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 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. 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 multi-age populations, and this expectation is supported by the direction of the difference in the variance estimates of the two populations we looked at. 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. However, 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 refined in order to refine the estimates of viability abundance in the future.

**TRT 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 (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 sockeye estimates which have a realized productivity of around 4 recruits per spawner; if lower productivities were realized, more spawners would be needed and/or fewer adults would return from a fixed smolt capacity, thus changing our adult capacity estimates. As a general rule of thumb, the population growth rate ( $\lambda$ ) 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.

**TRT Recommendation:** *The growth rate for Lake Ozette sockeye, 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 (Haggerty 2004; PSTRT 2006), it is unclear whether the current spatial structure of LOS is the same as the historic structure. Based on the available information however, it

appears that the current spatial structure is mainly tributary-based with less of the population spawning along the lakeshore in fewer lakeshore sites. 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.

**TRT Recommendations:** *A viable sockeye 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 were 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 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 Endangered Species Act, and the resident kokanee salmon, which is not. The genetic differences are large enough between these two groups that they are designated as different evolutionary significant units (Gustafson et al. 1997). Interbreeding between these is possible but genetic data indicate it is rare (Currens et al. 2006). 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 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.

**TRT Recommendation:** *A viable Ozette sockeye 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 as to 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 kokanee salmon in Lake Ozette.*

## **Concluding Remarks**

The PSTRT's viability criteria for Lake Ozette sockeye 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. 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 mean time, 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>1</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 animals is limited. Moreover, the risks from severe environmental events and from more general environmental degradation are high given the population's present limited distribution.

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

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<sup>1</sup> Subpopulation refers here to distinct spawning aggregations and does not necessarily imply a more rigorous genetic distinction.

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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 population in lake Ozette is essential to being 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. 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 used for viability analysis of Lake Ozette sockeye salmon.

Appendix Table A.1. Lake Ozette sockeye data used in viability analysis and source of estimates. Years where we estimated the escapement are italicized. See text for explanation.

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

Run size values from Haggerty (2008) Appendix B are the medians of several values, as explained there. The escapement numbers given above 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. 2007, Table 3.5) by the average ratio of weir counts to overall system estimates

in Appendix B of Haggerty et al. (2007). 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 fraction (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 the table above are from Haggerty (2008) Appendix C and Table 3.9, but reflect only the natural origin portion of the broodstock take. Prior to 2000, the broodstock take was from the beaches and were all natural origin. From 2000 on, the broodstock take was from Umbrella Creek returns and included both natural origin and hatchery origin fish. We used the NOR origin 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, the following estimates of  $\sigma^2$  and  $\mu$  can be computed using the methods described for the Lake Quinault analysis (Appendix B):

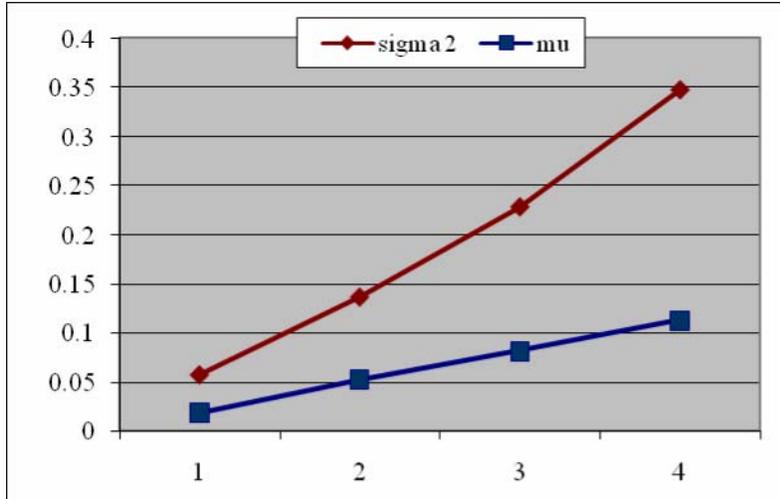
	Tesc	Wesc	Hat
$\mu$	<b>0.033</b>	<b>0.027</b>	<b>0.019</b>
$\sigma^2$	<b>0.098</b>	<b>0.100</b>	<b>0.096</b>

“Tesc” estimates use the time series of estimated total natural escapement, including both natural-origin and hatchery-origin fish that escape to natural spawning areas. “Wesc” estimates use the time series of estimated natural origin escapements obtained by applying the estimated natural origin fraction to the estimated total escapement. “Hat” estimates use the adjustment for hatchery fish described for the Lake Quinault data analysis.

#### Diagnostics

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

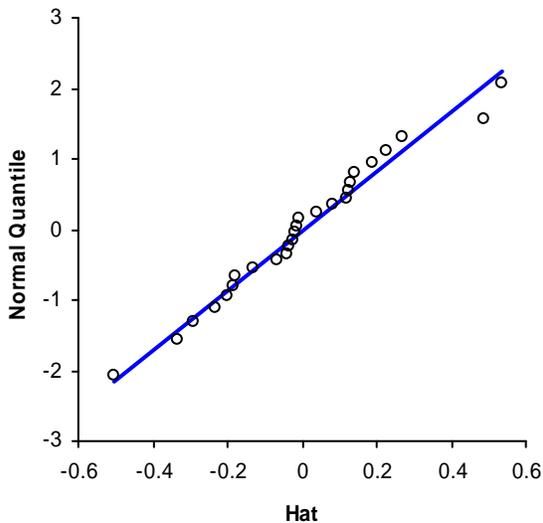
The slope method assumes the relationship of  $\sigma^2$  to  $\tau$  (the lag) is linear. Visual inspection of the graph for the “Hat” adjustment suggests this is the case for these data:



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 three statistical tests do not suggest deviation from the assumption of a normal distribution:

	Coefficient	p
Shapiro-Wilk	0.9786	0.8431
Skewness	0.2567	0.5520
Kurtosis	0.5193	0.4286



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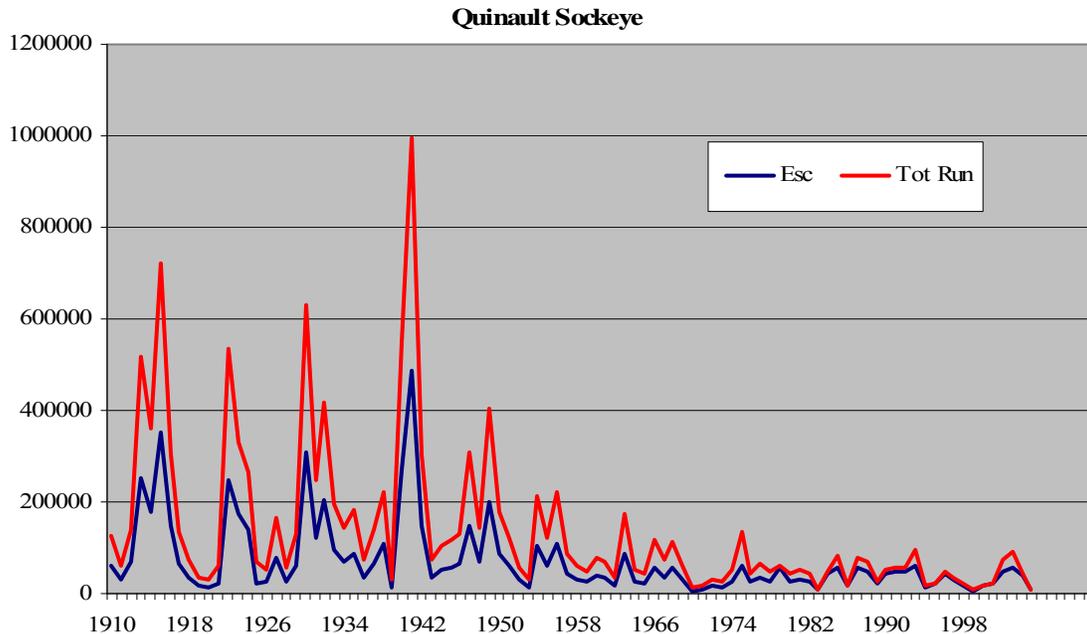
3. *No temporal trend in  $\ln(N_{t+1}/N_t)$  or recruits per spawner.*

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

## **Appendix B. Data and diagnostics for Lake Quinault sockeye viability analysis**

### Data

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



**Figure B.1. Time series of escapement and total runsize for Lake Quinault sockeye, 1910-2005.**

Larry Gilbertson, biologist for the Quinault Nation, supplied the data in Appendix Table B.1, along with the following explanations (personal communication to Kit Rawson, August 2006):

*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 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 estimates for 1953-1965 were taken from WDF Statistical Reports and the Joint Biological Statement (US v Washington). Estimates for 1966-1970 were taken from reports prepared by the Fisheries Assistance Office, U.S. Fish and Wildlife Service for the Quinault Nation. Estimates for 1975-2005 were taken from the Quinault Nation catch reporting system. Harvest numbers for the earlier years were also cited in various publications and government reports (e.g., annual reports of the BIA 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

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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 US 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 1973-78 (mean=0.46) can be used to represent the "norm" for the fishery. Interestingly, the over all mean of 0.51 is near the level of federal policy for stocks under federal management in the early 1900's (e.g., sockeye 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 US Bureau of Fisheries operated a hatchery on Lake Quinault from 1914 to 1947. The Quinault Indian Nation (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 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 broodyear return rate of approximately 0.01. Survival of fry and fingerling 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; e.g., after three decades of operation, only a small hatchery run had been developed (only ~ 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 mid-level survival. This was chosen because of improved hatchery practices and decreased competition from natural origin 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.

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**Appendix Table B.1. Catch and escapement data for Lake Quinault sockeye, 1908-2005.**

YEAR	HARVEST	ESCAPEMENT	RUNSIZE	HATCHERY	HATCH %
1908	75,000	72,059	147,059	0	0.0%
1909					
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%
1955	62,417	59,969	122,386	0	0.0%

*PSTRT Lake Ozette Sockeye Viability Criteria*

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%
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%

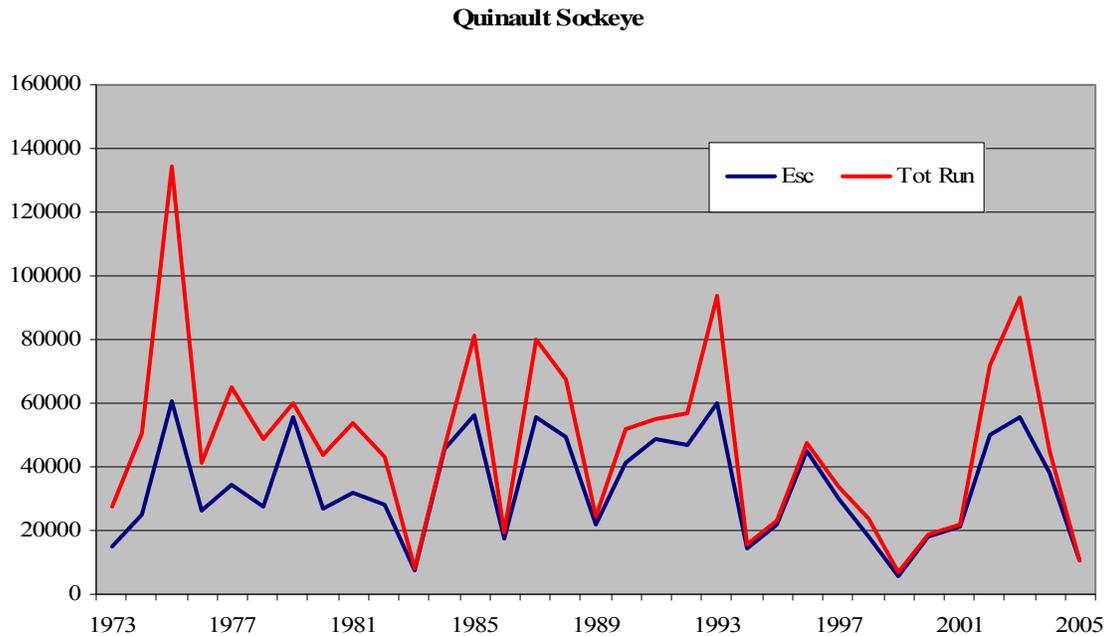


Figure B.2. Time series of escapement and total run size, Lake Quinault sockeye, 1973-2005.

### Basic Data Analysis

We estimated the variance of the growth rate ( $\sigma^2$ ) three ways: using the time series of estimated natural spawning escapements ( $W_{esc}$ ), using this time series with an adjustment for hatchery ( $HatAdj$ ), and using the time series of total recruitment adjusted for both hatchery and harvest ( $HatHarAdj$ ). The first and third estimates use Holmes's (2001) method directly. The third estimate ( $HatHarAdj$ ) uses a modification (Holmes, pers.comm. and McElhany and Payne, in prep.) to account for productivity that would not be evident from looking at escapement data alone. In all cases, a four-year-long unweighted running sums of the appropriate time series was used as the basic input data and lags of 1 through 4 years ( $\tau = 4$  in Holmes's notation) was 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. An 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 1905-2005 (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).

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

Quinault			
1910	2005	96 yrs.	
Fixed	Wesc	HatAdj	HatHarAdj
$\mu$	<b>-0.011</b>	<b>-0.014</b>	<b>0.129</b>
$\sigma^2$	<b>0.163</b>	<b>0.159</b>	<b>0.175</b>

1973	2005	33 yrs.	
Fixed	Wesc	HatAdj	HatHarAdj
$\mu$	<b>0.007</b>	<b>0.000</b>	<b>0.063</b>
$\sigma^2$	<b>0.041</b>	<b>0.038</b>	<b>0.061</b>

Diagnostics

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

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

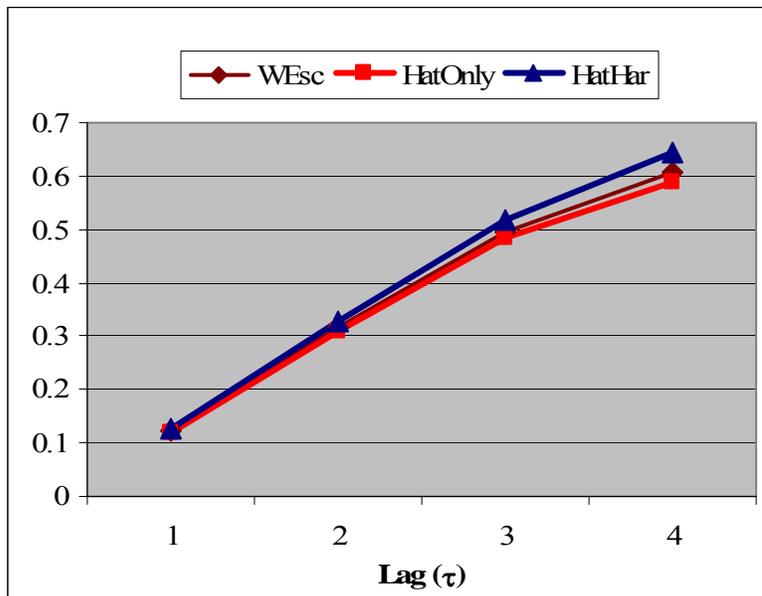


Figure B.3. Graphs of  $\sigma^2$  vs. lag for the 96-year time series.

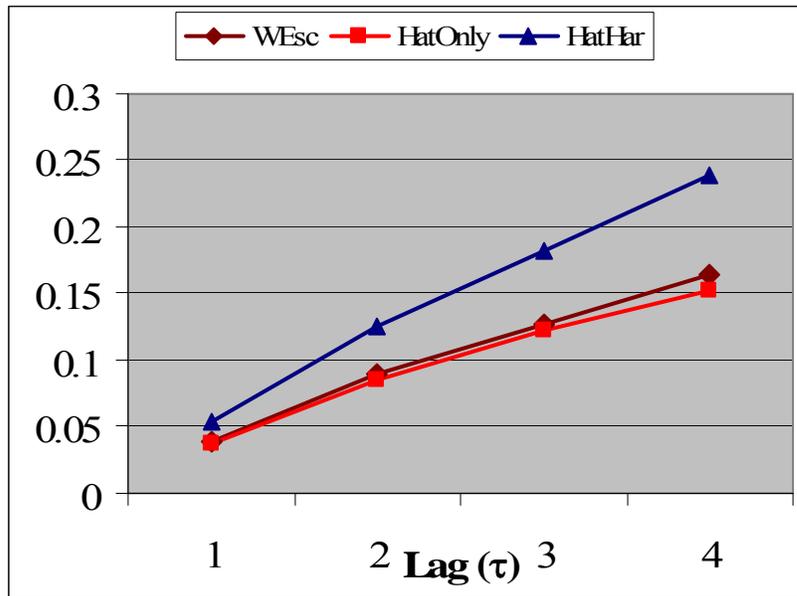


Figure 4. Graphs of  $\sigma^2$  vs. lag for the 33-year time series.

Visual inspection suggests that the relationship of  $\sigma^2(\tau)$  vs.  $\tau$  is linear for both series (Figures B.3 and 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  $\sigma^2$ .

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 (Fig. 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  $p=0.02$ .

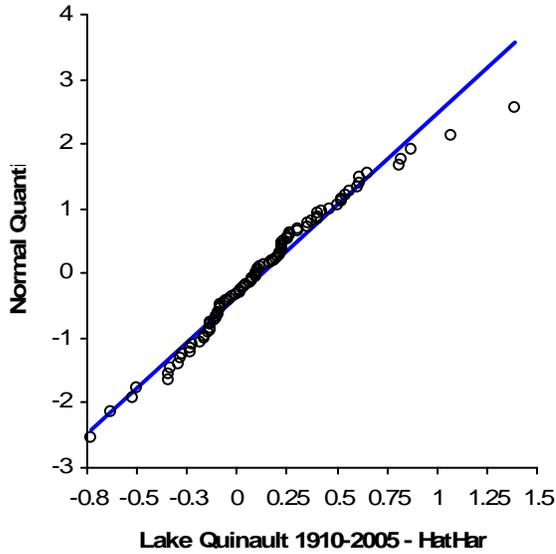


Figure B.5. Normal probability plot of  $\ln(N_{t+1}/N_t)$  for escapement, 96-year time series.

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

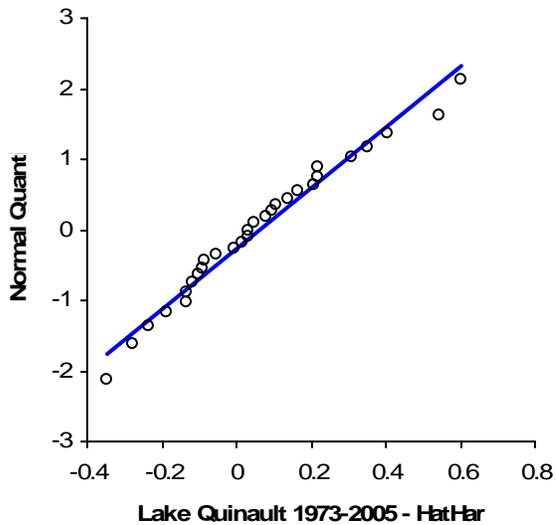
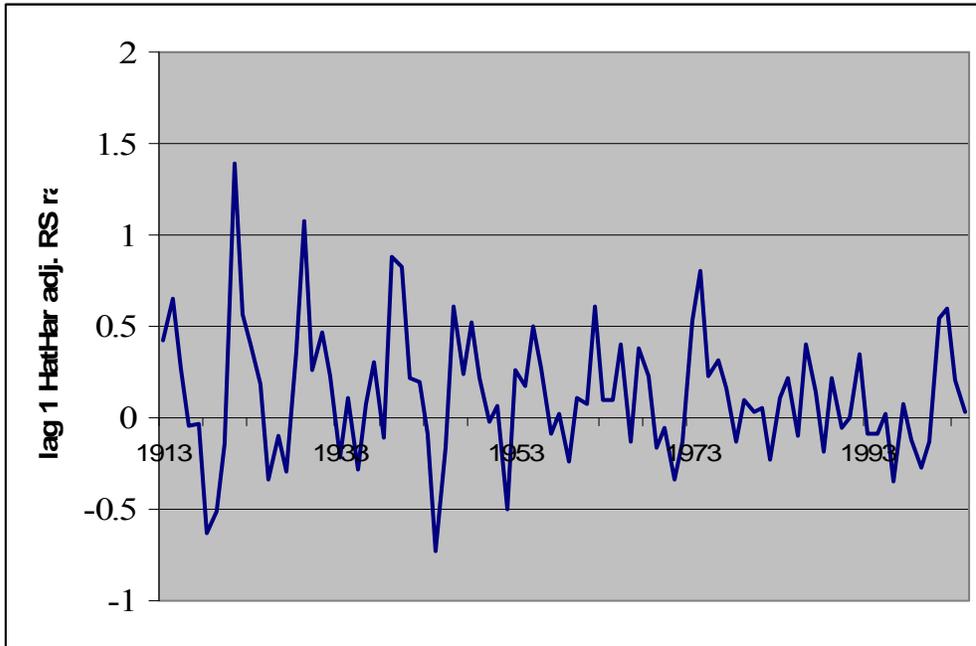


Figure B.6. Normal probability plot of  $\ln(N_{t+1}/N_t)$  for escapement, 33-year time series.

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

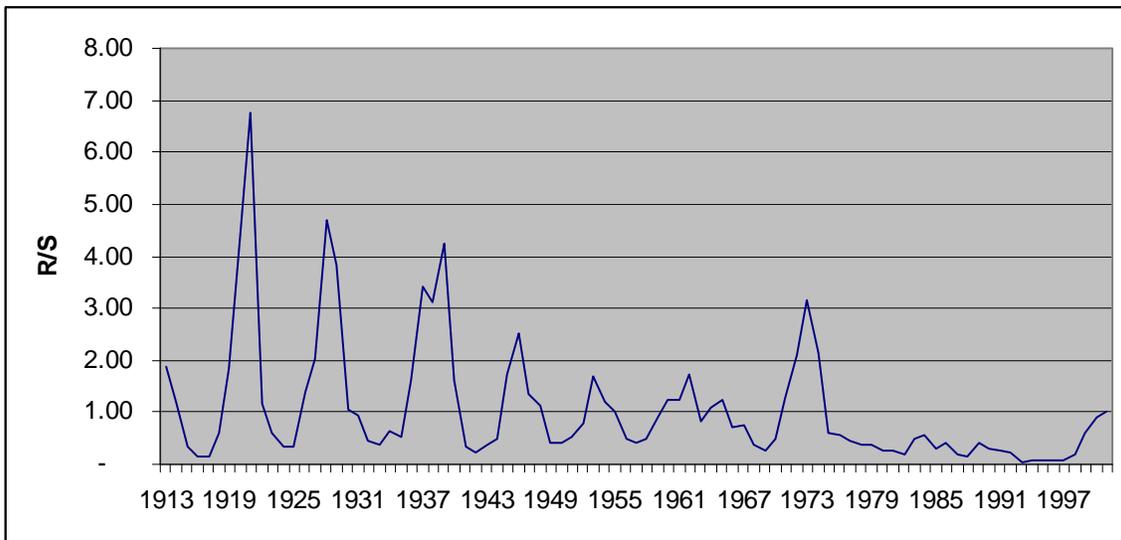
A graph of the time series of  $\ln(N_{t+1}/N_t)$ , adjusted for hatchery and harvest effects, appears to be stationary, although there seems to be a reduction in the absolute values of the extreme high and low values going forward in the 96-year time period (Fig. B.7).



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

*4. No temporal trend in pre-harvest recruits per spawner.*

A graph of the 4-year running sum of recruits (catch plus escapement) divided by the 4-year running sum of natural-origin spawners four years earlier shows a cyclic pattern (high every 7-10 yrs) with decreasing recruits per spawner overall over time (Fig. B.8).



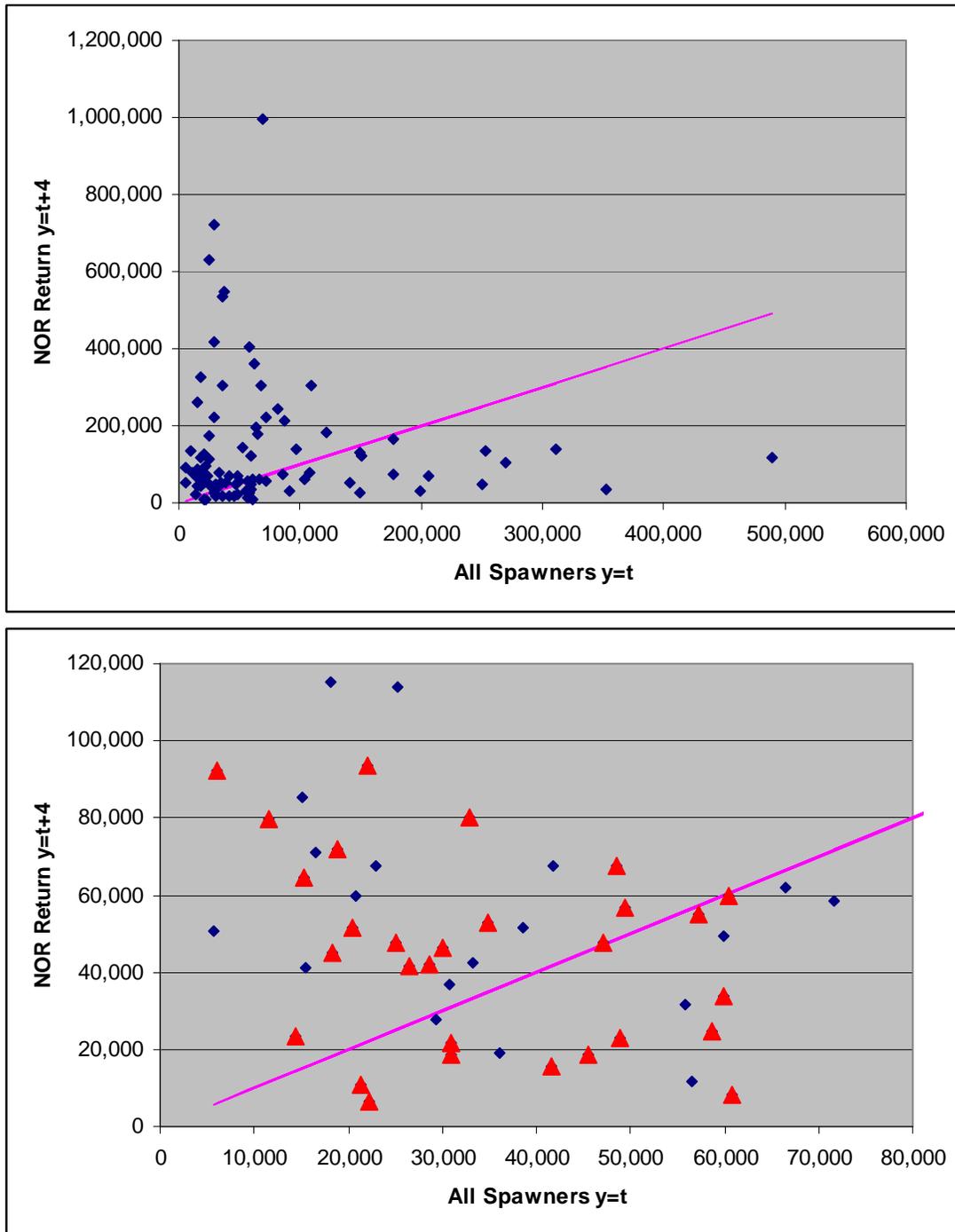
**Figure B.8. Time series of 4-year running sum of catch plus escapement (t+4) divided by 4-year running sum of escapement (t) for the previous 4 years. The x-axis is labeled with the final year of the escapement running sum.**

*5. No density dependence.*

To look for density dependence, the size of the return from the size of the spawning abundance is examined. Assuming an average age of 4, 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). 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, although much less pronounced (Figure B.9 lower).

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

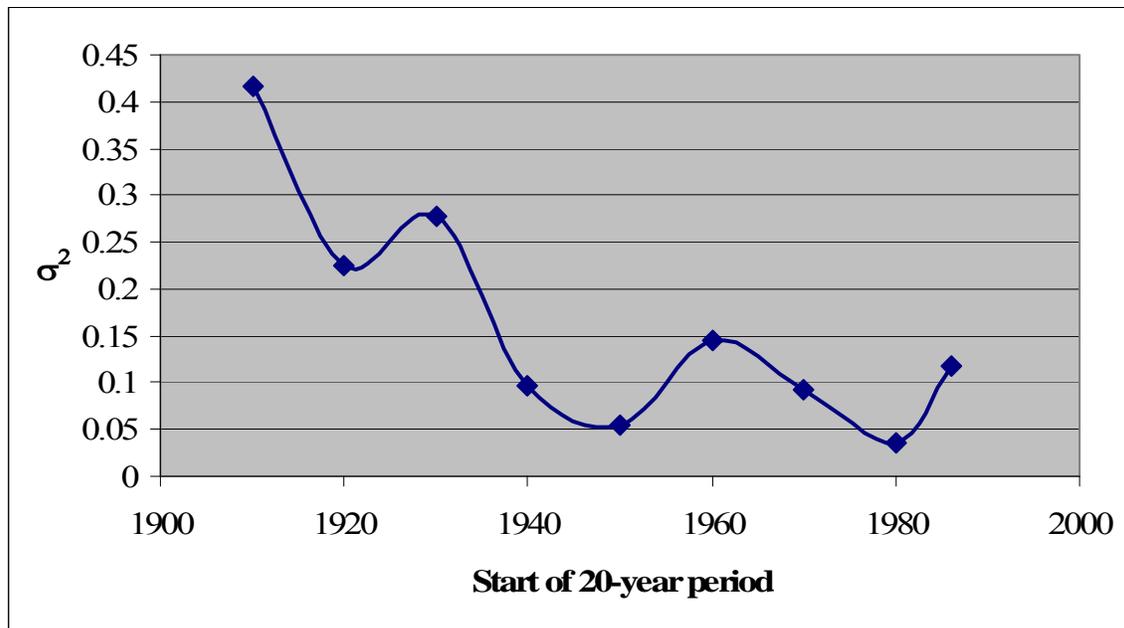
Estimates of  $\sigma^2$  for 20-year segments of the 1910-2005 time series range from 0.036 to 0.417 (Table B.3). The estimates from the Wesc, HatAdj, and HatHar series are nearly identical for the 1910-1969 period because every point before 1973 used the constant .845 catch to escapement ratio (Appendix Table 1). The magnitude of wild stock escapement (Wesc) and the total return (TotR) are both positively correlated with  $\sigma^2$  (computed with the HatHar correction) at  $p < .05$ , and this coincides with a downward trend in both abundance and  $\sigma^2$  over time until about 1960 (Fig. 10). However, for the recent period  $\sigma^2$  appears to be stationary (Fig. 10).



**Figure B.9. Graphs of catch plus escapement (t+4) vs. 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 blue 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 time series.

Years	$\sigma^2$ estimate			Mean Abundance	
	Wesc	HatAdj	HatHarAdj	Natural Origin Escapement	Total Return
1910 1929	0.432	0.424	0.417	100928	208918
1920 1939	0.236	0.228	0.224	95990	200679
1930 1949	0.284	0.272	0.278	132070	272622
1940 1959	0.097	0.096	0.097	104434	214380
1950 1969	0.054	0.054	0.054	47911	97904
1960 1979	0.054	0.054	0.145	33744	65617
1970 1989	0.048	0.049	0.092	30785	49278
1980 1999	0.029	0.020	0.036	33705	44908
1986 2005	0.072	0.070	0.118	33592	43531



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

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.1). 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 provide one of the longest datasets 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 dataset 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 four-year running sums are approximately normally distributed, and there is no indication of major regime shifts.

**Appendix C. “R” functions used for simulation of population dynamics in PVA.**

(NOTE: The default values for these functions are not necessarily the values used in our runs. See methods section.)

```
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(NRRuns=10000, NZero=10000, mu=0, QET=250,
                          Q=.1, Maxn=3*NZero) {
    Extinct <- NULL
    for (i in 1:NRRuns) {
        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/NRRuns))
}

NZero.Test <- function(Low=10000, High=150000, Step=5000, Q=.1,
QET=250, NRRuns=10000) {
    NZero <- Low
    Output.NZero <- NULL
    Output.ExtProb <- NULL
    while (NZero <= High) {
        Output.NZero <- c(Output.NZero, NZero)
        ep <- Dennis.Repeat(NRRuns=NRRuns, 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)
}
```