

Viability Criteria for Puget Sound Steelhead

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Dedication

Robert August Hayman (27 February 1952 – 20 December 2011)

During the development and writing of this document the Puget Sound Steelhead Technical Recovery Team was saddened by the death of one of its members, Bob Hayman. His contributions to the TRT went beyond his extensive knowledge of the Skagit River Basin; it was his determination that the TRT process be logical, consistent, and transparent that ensured its work would meet the highest standards. Bob's good-natured and humble manner made him likeable, even when he was challenging your thinking. He was a tireless worker, and the determination he displayed in both his professional endeavors and in battling cancer was inspiring. He will be missed by all of us.

DRAFT

Executive Summary

Introduction

Under the U.S. Endangered Species Act (ESA), the National Oceanographic and Atmospheric Administration's National Marine Fisheries Service is required to identify measurable and objective delisting criteria as part of recovery planning. These delisting criteria must describe the conditions under which a listed species or Distinct Population Segment (DPS) is no longer in danger of extinction (endangered) or likely to become so in the foreseeable future (threatened). We define a viable DPS as one that is unlikely to be at risk of extinction in the foreseeable future; for this purpose, we adopt the Viable Salmonid Populations (VSP) criterion of a 100-year timeline (McElhany et al. 2000) to evaluate risk of extinction. Ultimately, the identification of delisting criteria requires the consideration of technical analyses relating to viability, which are contained in this document, and policy decisions such as acceptable levels of risk, which are not. This document presents the recommended biological viability criteria recommended by the Puget Sound Steelhead Technical Recovery Team (TRT). The framework and the analyses it supports do not set targets for delisting or recovery, nor do they explicitly identify specific populations or groups of populations for recovery priority. Rather, the framework and associated analyses are meant to provide a technical foundation for those charged with recovery of listed steelhead in Puget Sound from which they can develop effective recovery plans at the watershed scale (and higher) that are based on biologically meaningful criteria.

This document develops viability criteria for the Puget Sound Steelhead DPS as identified in the National Marine Fisheries Service's (NMFS) status review for Puget Sound steelhead (Hard et al. 2007). The DPS was listed as a threatened species under the ESA in May 2007. Under the ESA, a threatened species is "any species which is likely to become an endangered species within the foreseeable future throughout all or a significant portion of its range." An endangered species is "any species which is in danger of extinction throughout all or a significant portion of its range." The viability of a threatened species is therefore at some risk, and in an attempt to quantify this risk this document was developed by the Puget Sound Steelhead TRT, which was composed of scientists from federal, state, tribal, and local government agencies with expertise in steelhead biology and management.

Viability is a term intended to characterize a population's, or other group's, capacity to persist in its environment. For example, a viable population is one that is unlikely to disappear over the foreseeable future, but instead has sufficient abundance, productivity, diversity, and spatial distribution to sustain itself, though these characteristics may vary considerably during that period. In NMFS's VSP report, McElhany et al. (2000) defined a viable population in this way:

"We define a viable salmonid population as an independent population of any Pacific salmonid (genus *Oncorhynchus*) that has a negligible risk of extinction due to threats from demographic variation, local environmental variation, and genetic diversity changes over a 100-year time frame. We define an independent population as any collection of one or more local breeding units whose population dynamics or extinction risk over a

100-year time period are not substantially altered by exchanges of individuals with other populations.”

In this report, we develop viability criteria for threatened Puget Sound steelhead with this definition in mind. The threatened status of Puget Sound steelhead under the ESA means that the viability of this DPS as a whole is low and that increasing its viability to an acceptable level is a prerequisite to delisting. Our criteria were developed to inform conservation and recovery objectives for threatened steelhead in Puget Sound. In developing these criteria, the TRT reviewed several documents, including both published and draft reports of several other TRTs from the Pacific Northwest and California. In addition, the TRT has had numerous interactions with staff of the Washington Department of Fish and Wildlife (WDFW) and tribal fishery resource managers in Washington that collect information and manage harvest and escapement of steelhead in Puget Sound.

The primary purpose of this report is to recommend objective, measurable biological criteria for assessing the recovery, and progress toward recovery, of the Puget Sound steelhead DPS. In doing so, we apply these criteria to an assessment of the current biological status of the DPS. We do not provide comprehensive recommendations for biological criteria for listing or delisting of the DPS under the ESA, nor do we evaluate whether the DPS should or should not be listed. In addition to evaluating the biological requirements presented here, listing and delisting decisions require evaluations regarding particular listing factors and conservation measures, which are beyond the scope of this report. Thus, the criteria presented here provide a necessary, but not a sufficient, set of criteria to determine the ESA listing status of the DPS.

Approach to Developing the Criteria

We develop viability criteria based on the considerations laid out in the VSP (McElhany et al. 2000), which identifies four key population parameters that influence the persistence of populations. These attributes are:

- population size—the abundance of all life stages of the species (often only measured as adults);
- population growth rate (productivity)—production over the entire life cycle, often measured as recruits or returns per spawner, or as long-term population growth rate (λ);
- spatial structure—distribution of individuals among spawning and rearing habitat areas, and connectivity among those areas; and
- diversity—variation in traits (phenotypic and genetic) among individuals within and among populations in the DPS.

The goal of recovery is not merely to meet a set of defined criteria, but rather to restore or repair ecological processes that lead to long-term sustainability of the resource. Our approach views the DPS as a complex structure with important processes operating at scales ranging from individual breeding aggregations to the entire DPS. Along this continuum, we identify three hierarchical units for defining attributes related to biological processes that characterize DPS status, from

smallest to largest: demographically independent populations (DIPs), major population groups (MPGs), and the entire DPS. We develop VSP-based criteria that pertain to each of these units.

Analysis of Viability

To achieve full recovery, steelhead populations in the Puget Sound DPS need to be robust enough to withstand natural environmental variation and even some catastrophic events, and they should be resilient enough to support harvest and habitat loss due to human population growth. Recovery therefore requires sufficient abundance and productivity of the DPS and diversity among and within its constituent populations distributed across the DPS's range. Achieving ESA goals requires biological sustainability into the foreseeable future (as well as the absence of threats, not discussed in this report). DPS sustainability implies that the number and distribution of sustainable populations are sufficient and that DPS-level diversity is conserved. Avoiding endangerment requires biological persistence, i.e., assurance that all significant parts of the DPS have a high likelihood of persisting over a VSP time horizon—i.e., for 100 years. Achieving viability at each level implicitly requires meeting all criteria for the lower levels.

Our analysis of steelhead viability rests on two primary components, one component focused on evaluating the quantitative abundance information available for individual populations, and the other component aimed at assessing viability at multiple hierarchical scales (DIP →MPG→DPS) by incorporating both qualitative and quantitative information pertaining to all four VSP criteria. For the first component—a quantitative analysis of individual population data—we apply two distinct population viability analyses (PVAs) to the DIPs that have sufficient information on abundance and productivity to support them. The first of these PVAs is based loosely on a conventional spawner-recruit analysis and estimates extinction risk from combinations of abundance and productivity across the parameter space. The second of these PVAs is based on an autoregressive state-space analysis of abundance time series, and uses estimates of demographic stochasticity to predict future abundance and extinction risk.

For the second component, we develop a knowledge-based decision support system (DSS) to incorporate these PVAs into a framework to characterize viability that can 1) accommodate both quantitative and qualitative information, including habitat-based (rather than strictly biological) metrics and 2) estimate viability at multiple hierarchical scales, i.e., DIPs, MPGs, and the entire DPS. This framework is based on a Bayesian Network (also known as a Bayesian belief network or a Bayes net; Newton et al. 2007) of probabilities that links the key aspects of viability—abundance, productivity, diversity, and spatial structure—across the DPS and all its constituent populations.

Development of a Bayesian Network to Assess Viability at Multiple Scales

A complete assessment of the biological condition of the DPS is necessarily multifaceted, including a variety of interrelated criteria, with varying data availability and quality. These criteria relate to biological processes at a variety of time and space scales, with processes varying from individual stream reaches to the entire range of the DPS. To track this large suite of data and criteria in a transparent and logically consistent framework, we developed a DSS based on a series of Bayesian Networks.

A DSS is a computer-based tool that can analyze and compare numerous types of data, producing results that assist managers in making decisions (Turban and Aronson 2001). These systems allow decision-makers to perform complex evaluations quickly, present a consistent assessment that draws from a variety data sources, and track large sets of information accurately, thus improving the choices made by decision-makers without overriding human judgment (Rauscher 1999). A system evaluating ecological conditions may contain substantial uncertainty about the precise conditions that are optimal for the target organisms because of gaps in information and the lack of perfect knowledge about the interrelationships among relevant factors (Reynolds et al. 2000).

The DSS we designed uses a network framework to link criteria at a variety of scales and aggregate them from population-level criteria, through major population group (MPG, equivalent to biogeographic stratum)-level criteria, to criteria for the entire DPS. This DSS is structured as a Bayesian Network (BN), a decision tool that provides a transparent, graphical framework for characterizing relationships among a diverse set of variables. Accurately characterizing the viability of Puget Sound steelhead over a series of hierarchical levels and across a diverse set of criteria requires an approach that can explicitly incorporate uncertainty into the evaluation and can deal with available information of variable quality for all four VSP criteria. We sought a method that could accommodate these types of information in a transparent, consistent way. A Bayesian Network meets this need.

A BN incorporates likelihoods (conditional probabilities) for each of its input variables, typically by using discrete uniform distributions to treat all values of a finite set of possible values as equally probable. This property makes BNs effective models of reasoning under uncertainty (Jensen 2001). A BN is a probabilistic graphical model (e.g., Lee and Rieman 1997, Marcot et al. 2001, Peterson et al. 2008) designed to efficiently represent a probability distribution underlying a set of variables that influence each other, but that is too complex to be represented using a series of tables and equations. A main feature of a BN is that there is only one probability distribution that satisfies the structure of the BN (as reflected in the constraints among variables in the form of probabilistic conditional dependencies), and this distribution can be estimated by ‘testing’ the BN by locking values of the variables at particular probabilities (a process known as *instantiation*). The primary objective of a BN is to characterize the dependencies among its constituent variables (depicted by *nodes*) given the influences between them (depicted by *edges*). Each node represents a variable that can take any of several values, either as discrete states or as represented by a continuous function. Each edge connecting two nodes represents probabilistic dependencies among these nodes (the arrow indicates the direction of influence). In a BN, the conditional probabilities that reflect these dependencies are estimated from Bayes’ theorem (Bayes and Price 1763, Gelman et al. 1995).

A BN is intended to directly incorporate estimates of uncertainty into evaluating the relationships between variables. As a decision support system, it can be as simple or as complex as one feels is supportable. It has the advantage that its components—its *criteria*—can easily be constructed through simple verbal guidelines, through actual data, or estimated functional relationships. A BN has some features that can favor its use over other decision tools:

- a BN can lay out parameters and how they interact transparently in a clear decision framework;
- a BN explicitly depicts uncertainty as prior probabilities, which lends itself well to risk analysis; and
- a BN can be used to help identify key factors that influence the outcome of interest or to help prioritize research, monitoring, or other actions.

Given the input variables and the prior probabilities associated with their states, a BN estimates the probabilities that its constituent populations, MPGs, and the whole DPS are viable. The prior probabilities can easily be modified, based on new or corrected information, to see how these probabilities change. This property of a BN makes it very useful in determining which factors have the greatest influence on the viability estimates, and it also lends itself well to evaluating alternative scenarios. One simple example of such an exercise would be to ask, “if freshwater survival increased from x% to y% due to habitat improvements, how much would population viability be expected to increase, with all other factors held constant?” Manipulating a BN in this way by changing the probabilities associated with a particular factor—a kind of formal sensitivity analysis—can illuminate the salient factors that influence viability, and can therefore be very useful in evaluating alternative scenarios aimed at improving viability, or in identifying key viability criteria. That said, a BN is not intended as a substitute for human judgment or as a means of “making” decisions, but rather to support decision-making processes by integrating available information and human judgment into a sensible conceptual framework.

Identification and Application of Viability Criteria

Identifying viability criteria is largely accomplished through use of a series of Bayesian Networks. At its highest level, the BN estimates the viability of the DPS and is constructed to represent its hierarchical population structure. Demographically independent populations are grouped into major population groups (MPGs, equivalent to biogeographic strata), which together make up the DPS; there are subsidiary BNs for each of these populations and MPGs. Within this hierarchical structure we estimate the contributions of abundance, productivity, diversity, and spatial structure to viability of each DIP, and then integrate these estimates into evaluations of viability of each MPG within the DPS.

For each DIP, the components of population-level diversity are, for (1) VSP abundance: adult and juvenile abundance relative to estimated capacity, and the probability that abundance would reach a specified quasi-extinction threshold (QET; a specified abundance considered to be tantamount to functional extinction) within 100 years; (2) VSP productivity: the number of smolts per spawner and the number of adults per smolt (both of which influence long-term population growth rate), and the frequency of repeat spawners; (3) VSP diversity: the degree of hatchery influence, variation in adult run timing, the fraction of smolts from resident fish, and current age structure relative to the historic distribution; and (4) VSP spatial structure: the fraction of intrinsic potential rearing and spawning habitat occupied, where intrinsic potential is the area of habitat suitable for steelhead rearing or spawning, at least under historical conditions.

The BN constructed for each DIP estimates DIP viability from each of these VSP parameters using Bayesian probabilities. The BNs for each DIP are then combined to produce a composite BN for estimating the viability of each MPG, with weights provided to consider DIP

representation of each major life-history type (summer- versus winter-run). The composite BNs for each MPG are then combined to estimate the viability of the DPS as a whole, with the contribution of each MPG weighted equally. In combination with the requirement that all MPGs within a viable DPS must be viable, this approach ensures that for an DPS to be viable, a sufficient fraction of its constituent DIPs spread across all its MPGs, representing each major life-history types, must be viable.

In defining viability criteria and metrics, we use the DSS to provide an assessment of the current status of the DPS by applying the metrics to data available through 2010. This analysis is provided for illustration to demonstrate how the criteria might be used in the future to assess progress toward recovery. The assessment framework evaluates viability using objective measures of spawner abundance, productivity, hatchery influence, spawner and juvenile distribution, and several measures of population diversity (e.g., resident fish contribution, spawn timing, and relative effective population size). Some of these measures are estimated from physical habitat data, in particular metrics extracted from Geographic Information Systems (GIS) data layers that measure intrinsic potential steelhead production. (The algorithm used by the TRT to estimate intrinsic potential spawning or rearing area and potential steelhead production is described in Appendix C). Fully quantifiable criteria are not available for the several metrics, so we used TRT members' judgment to evaluate those. In evaluating DIP-level viability, we gave the combined diversity and spatial structure metrics equal weight of the more quantifiable abundance and productivity metrics. We then used recent observations of population performance (primarily trends in abundance) to evaluate how certain we can be that the Puget Sound Steelhead DPS is sustainable under current conditions.

The TRT considered two issues specific to steelhead viability for which little information is available in Puget Sound populations: the demographic contributions of a resident life history and the degree of iteroparity. The Biological Review Team (BRT; Good et al. 2005) explained in general terms how to conduct an overall risk assessment for a DPS that includes both resident and anadromous populations, particularly when the resident fish may outnumber the anadromous ones but their biological relationship is unclear or unknown. The question Good et al. (2005) considered was: Under what circumstances when associated resident fish are abundant would one conclude that a steelhead DPS was not in danger of extinction or likely to become endangered? The BRT identified the required conditions as:

- The resident forms are capable of maintaining connectivity among populations to the extent that the DPS's historical evolutionary processes are not seriously disrupted, and
- The anadromous life history is not permanently lost from the DPS but can be regenerated from the resident forms.

In determining the viability of steelhead DIPs in the Puget Sound DPS, the TRT considered the potential influence of co-occurring resident *O. mykiss* on anadromous steelhead demographics. The TRT concluded that in basins where anadromous *O. mykiss* abundance is below the QET threshold, the risk of extinction is not necessarily 100% if resident *O. mykiss* are present below natural, long-standing migration barriers. Inclusion of resident fish in the viability criteria is dependent, however, on several conditions. First, the abundance of resident fish must be large enough to be self-sustaining (this will be largely dependent on the numbers of resident females). Second, there must be some evidence of interbreeding between the anadromous and

resident forms (this will most likely be established by genetic analysis of the relationship between the resident fish and the most proximate anadromous population). To accommodate these considerations, we included in the Bayesian Network for DIP viability a diversity node describing the proportional contribution of smolts from resident fish.

A comprehensive risk assessment must consider the effect of resident *O. mykiss* that have anadromous access on the viability of the entire DPS. Good et al. (2005) concluded if the anadromous life history form in an ESU/a DPS is extirpated or critically depressed, it is unlikely the resident life history form alone is capable of maintaining the productivity, connectivity, and diversity necessary for a viable *O. mykiss* DPS/ESU (NMFS 2003). In a review of currently listed steelhead ESUs, the Northwest Fisheries Science Center (NWFSC) concluded “None of these DPPs/ESUs is likely to persist in total into the foreseeable future because substantial parts of the ESUs are at risk of extinction” (Varanasi 2004).

The Puget Sound steelhead TRT concluded that an *O. mykiss* population expressing a combination of migratory strategies (freshwater resident, anadromous) and a heritable propensity to produce both types of progeny means that residents can serve as a buffer when anadromous productivity is low—extinction risk is lower when residents are relatively abundant. But it is important to remember that while a population of residents may indeed provide a genetic reservoir to produce anadromous migrants, these fish may have reduced adaptive potential to cope with the marine environment and smolt production may entail a cost in fitness. This is an active area of research that merits immediate attention to help guide development of conservation strategies for steelhead.

Iteroparity, or repeat spawning, is another primary characteristic of *O. mykiss* with potentially substantial demographic consequences. Simulation analyses of the demographic consequences of iteroparity were conducted by Nick Gayeski of the Wild Fish Conservancy at the request of the TRT and with its cooperation; these analyses rely on an approach that develops a suite of age-structured matrix population projection models with annual time-steps that incorporate density dependence, varying levels of repeat spawning, and varying levels of density-independent stochasticity, and harvest mortality. The stochastic models were used to evaluate the influence of varying levels of repeat spawning on population abundance and age structure under varying levels of harvest.

From his modeling, Gayeski concluded that the average proportion of repeat spawners in an adult steelhead population is relevant to population abundance and stream capacity in two ways. First, relative to a population with no repeat spawners, for a given average capacity of juveniles, a population with repeat spawners will have a larger average adult spawning population. Second, a given average number of adult spawners can be sustained by fewer juveniles when repeat spawners are present than when they are not. It is therefore likely that viable populations (DIPs) of steelhead can be sustained in smaller stream basins than is the case for semelparous Pacific salmon.

Gayeski also concluded that when population resilience to environmental variation and/or harvest mortality is measured in terms of either the probability of declining below specific levels of annual spawner abundance or the expected frequency of the spawning population declining

below some threshold of concern (quasi-extinction), repeat spawning provides increased levels of resilience compared to populations without repeat spawning. When both harvest mortality and environmental variation in smolt survival are present, repeat spawning increases population resilience. The precise extent to which resilience is increased is sensitive to the harvest rate and to both the magnitude of the average value of life-stage survival rates subject to environmental variation and the amount of variation in the rate as measured by the coefficient of variation. From a recovery, population rebuilding perspective, it appears that for small population sizes such as the ones considered in this modeling exercise, the value of specific levels of repeat spawning to population resilience (and repeat spawning) are most likely to be realized under a zero harvest scenario, regardless of the level of environmental variation (at least for the range and kind of variation employed in the models).

These analyses are exploratory, but these analyses as well as the Integral Projection Model (IPM) analysis applied to a wild Alaskan steelhead population in Appendix F, tend to reinforce the TRT's conviction that iteroparity is an important consideration in a comprehensive evaluation of viability for anadromous coastal steelhead. We therefore included in the Bayesian Network for DIP viability a productivity node describing the influence of iteroparity on aspects of viability.

Viability Criteria for Puget Sound Steelhead

The listed unit under the ESA for *Oncorhynchus mykiss*, including anadromous steelhead, is the DPS, and this is the unit that must be considered for delisting. Thus, delisting criteria must ultimately address the extinction risk of the DPS. In approaching the development of criteria for assessing viability of (and, subsequently, delisting) DPSs, we have relied on the language in the ESA, information described in the listing decision, concepts outlined in the VSP document by McElhany et al. (2000), which can be found online at <http://www.nwfsc.noaa.gov/pubs/tm/tm42/tm42.pdf>, and in published research describing salmon populations and their past or potential responses to environmental changes. The ESA lists five potential factors for decline that must be considered in species listing decisions (ESA Section 4.2.1):

1. the present or threatened destruction, modification, or curtailment of its habitat or range;
2. overutilization for commercial, recreational, scientific, or educational purposes;
3. disease or predation;
4. the inadequacy of existing regulatory mechanisms; and
5. other natural or manmade factors affecting its continued existence.

NMFS identified all five factors as contributing to the endangerment of Pacific salmonids, including steelhead. In considering how viability criteria might inform population delisting requirements, the TRT also attempted to consider these factors for decline. The TRT approach evaluates the extinction risks facing the DPS by assessing the viability of the individual populations (DIPs) and Major Population Groups (MPGs) within that DPS. The TRT recommended population-level biological viability criteria based on a combination of the four

parameters identified in the VSP document—productivity, abundance, spatial structure, and diversity, and information about the habitat requirements of the listed fish.

From the analyses in this report, building from these population-level criteria, the TRT identified viability criteria for Puget Sound steelhead that take into account these key VSP parameters and incorporate hierarchical viability criteria for MPGs and for the entire DPS.

NMFS's Population Recovery Approach for threatened Puget Sound Chinook salmon (NMFS 2010; see also Ruckelshaus et al. 2006) identified six delisting criteria for this Evolutionarily Significant Unit (ESU):

1. The viability status of all populations in the ESU is improved from current conditions.
2. At least two and up to four Chinook salmon populations in each of five biogeographical regions (i.e., major population groups) within the ESU achieve viability, depending on the historical biological characteristics and acceptable risk levels for populations within each region.
3. At least one population from each major genetic and life history group historically present within each of the five biogeographical regions is viable.
4. Tributaries to Puget Sound not identified as primary freshwater habitat for any of the 22 identified populations are functioning in a manner that is sufficient to support an ESU-wide recovery scenario.
5. Production of Chinook salmon from tributaries to Puget Sound not identified as primary freshwater habitat for any of the 22 identified populations occurs in a manner consistent with an ESU recovery.
6. Populations that do not meet the viability criteria for all VSP parameters (i.e., abundance, productivity, spatial structure and diversity) are sustained to provide ecological functions and preserve options for ESU recovery.

For the Puget Sound Steelhead DPS, in this document the TRT has developed criteria for recovery of steelhead that share some similarities:

1. The viability (as reflected in abundance, productivity, diversity, and spatial structure) of a majority of steelhead populations in each of the Major Population Groups (MPGs) across the DPS is detectably higher than currently, using conventional population viability analysis.
2. At least 40% of steelhead populations in each of the three MPGs within the DPS achieve viability, depending on the historical biological characteristics and acceptable risk levels for populations within each region. (The threshold of 40% corresponds to an average probability of DIP viability of 64% if the DIPs that are not viable have probabilities of viability of 50%.)

3. At least 40% of populations from each major life history type (summer-run, winter-run) historically present within each of the MPGs is viable using these criteria.
4. Natural production of steelhead from tributaries to Puget Sound not identified as primary spawning or rearing habitat for any of the 32 identified populations is sustained to provide ecological diversity and productivity sufficient to support DPS-wide recovery.

The viability analyses in this report indicate that abundance and productivity from each major life history type in a sufficient fraction of populations spread spatially across each MPG are critical to the viability of each MPG—which DPS viability depends on. Diversity and spatial structure—which are also limited throughout the DPS—make essential contributions to MPG (and therefore DPS) viability as well.

From these considerations, the Puget Sound Steelhead TRT developed a simple construct for developing viability criteria. The TRT developed these criteria using the Puget Sound Steelhead DPS population structure identified in its “population identification” document. In that document the TRT identified 3 MPGs containing a total of 32 historically present DIPs, including at least one considered to be functionally extinct (i.e., below a defined quasi-extinction threshold of abundance). The criteria for viability for each unit within the DPS follow simple “traffic light” rule sets: using a three-bin classification (low = “not viable”, “intermediate”, high = “viable”), the DIPs in an MPG are scored at each of the four VSP criteria with 1 (red, downward triangle), 2 (yellow square), or 3 points (green, upward triangle), corresponding to the contributions of these scores to DIP viability. These scores reflect probabilities that DIP viability is influenced by the VSP criteria, ranging from < 40%, 40-85%, or $\geq 85\%$, respectively. For a DIP to be considered viable, its probability of viability must be at least 85%, as calculated by the Bayesian Network for viability. To estimate this value, the mean abundance and productivity criteria for the candidate DIP are each double-weighted; this produces DIP viability scores ranging from 6 to 18 points. DIPs with viability scores < 1 are considered not viable; those with viability scores between 11 and 14 are considered to have intermediate viability; and those with viability scores ≥ 14 ($\geq 85\%$, rounded up) are considered viable.

MPG viability depends on two criteria. First, a minimum of 40% of the DIPs in the MPG that exhibit each of the two distinct life-history strategies (summer-run versus winter-run) must be viable using the same “traffic light” rule set (i.e., score = 3). Second, the DIPs in the MPG must have a geometric mean score of at least 2.2, a value the TRT determined based on consideration of the first criterion and examining how MPG viability under the traffic light rule set varies. This score is the minimum achieved across a range of MPG sizes (with number of DIPs ranging from 8 to 16) with a sufficient fraction of DIPs having viabilities of 85%. Following these two criteria, to be viable an MPG with 8 DIPs must have at least 4 viable DIPs (score = 3) and no more than one DIP that is considered not viable (score = 1). An MPG with 11 winter-run and 5 summer-run DIPs must have at least 5 viable winter-run and 2 viable summer-run DIPs and no more than 1 DIP of each life-history type that is considered not viable.

DPS viability depends only on one criterion: that each of its component MPGs is considered viable. The viability criteria for each level within the DPS are summarized below.

DIP Viability

1. Using a simple three-bin classification (not viable, intermediate, viable), a DIP is scored 1, 2, or 3, depending on whether the probability of viability as computed by its viability Bayesian Network is $< 40\%$, $40\text{-}85\%$, or $\geq 85\%$, respectively. For a DIP to be considered viable, its probability of viability must be at least 85% ; the TRT considered this estimate to be sufficiently high to insure persistence over 100 years. To estimate this value, the mean abundance and productivity criteria for the candidate DIP are each double-weighted; this produces DIP viability scores ranging from 6 to 18 points. DIPs with viability scores < 1 are considered not viable; those with viability scores between 11 and 14 are considered to have intermediate viability; and those with viability scores ≥ 14 ($\geq 85\%$, rounded up) are considered viable.

MPG Viability

2. An MPG is considered viable if 40% (rounded up) of its DIPs (including extinct as well as extant historical populations) are viable and mean DIP viability exceeds a threshold for viability.
 - a. DIPs exhibiting distinct life-history strategies (i.e., summer-run versus winter-run) will be considered separate components of the MPG. Therefore, a minimum of 40% of summer-run *and* 40% of winter-run populations within an MPG must be viable to achieve MPG viability.
 - b. DIPs containing both winter- and summer-run subpopulations predominantly exhibit the winter-run life-history strategy in Puget Sound and will be considered winter-run for the purpose of estimating 2a.
 - c. A viable MPG must, in addition to the criterion outlined in 2a and 2b, have a geometric mean (averaged over all its DIPs) score of at least 2.2 to be considered viable.

DPS Viability

3. A DPS is considered viable only if **all** its component MPGs are viable.

The TRT applied the criteria to the 32 DIPs in the Puget Sound steelhead DPS to provide a status assessment of the current viability of these units. This assessment indicates low viability for many DIPs, all MPGs, and the DPS as a whole. Nearly all DIPs have insufficient current abundance and productivity scores to be considered viable. Most DIPs also have low scores for diversity and spatial structure, largely because of extensive hatchery influence, low breeding population sizes, and freshwater habitat fragmentation or loss.

Based on a combination of quantitative population viability analyses, collective judgment of qualitative information, and use of habitat-based metrics to estimate intrinsic potential, the TRT developed and applied a comprehensive framework incorporating Bayesian Networks to evaluate the current biological status of the Puget Sound Steelhead DPS. The TRT applied the framework to the Puget Sound Steelhead DPS to evaluate the status of the DPS and with the intent to assist in guiding recovery actions. Despite the lack of quantitative information for several aspects of diversity and spatial structure, the TRT considers these VSP criteria to be

essential for DPS viability into the future, and recommends the use of a framework that encompasses all four criteria to evaluate viability. This framework and the analyses it supports do not set recovery targets at any of the three levels, nor do they explicitly identify specific populations or groups of populations for recovery priority. Rather, the framework and associated analyses are meant to provide a technical foundation for those charged with recovery of listed steelhead in Puget Sound from which they can develop effective recovery plans at the watershed scale (and higher) that are based on biologically meaningful criteria. They are also meant to highlight the data that are needed in future monitoring and evaluation studies to improve these efforts.

The Puget Sound Steelhead Distinct Population Segment is not considered to be viable by the TRT. The TRT concludes that the DPS is currently at very low viability; most of the 32 DIPs, all 3 MPGs, and the DPS as a whole are at low viability. Nearly all DIPs in both the South Puget Sound and the Hood Canal and Strait of Juan de Fuca MPGs are not viable. Most of the DIPs score low for all four VSP criteria, and nearly all DIPs have insufficient current abundance and productivity scores to be considered viable. Most DIPs also have low scores for diversity and intermediate scores for spatial structure. The pattern of low viability is widespread throughout Puget Sound, across all three MPGs, and includes both summer- and winter-run populations. The populations with highest viability—and those with highest abundance and diversity—are in northeastern Puget Sound (Northern Cascades MPG).

The TRT's Bayesian Network framework provides a means of evaluating steelhead viability with explicit reference to estimates of historical abundance, productivity, diversity, and spatial distribution steelhead in this region. This framework provides a systematic and transparent mechanism to evaluate viability of the DPS and its component MPGs and DIPs, and lends itself to evaluating alternative recovery scenarios and the effects of specific recovery actions, especially those operating at the watershed scale.

Viability Criteria for Puget Sound Steelhead

Introduction

The goal of recovery and restoration is to restore or repair ecological processes that lead to long-term sustainability of natural resources. The Puget Sound Steelhead Technical Recovery Team (TRT) is charged with developing criteria for viability of steelhead in Puget Sound that contribute to the long-term sustainability of these fish. Puget Sound steelhead have a complex, hierarchical structure affected by ecological processes operating at scales ranging from individual spawning aggregations up to the entire Distinct Population Segment (DPS). Along this continuum, we (the TRT) identified three scales as important for defining attributes related to biological processes that define status: independent populations, major population groups, and the entire DPS. We developed viability criteria at each scale. The TRT also developed attribute sets for each scale to assess viability status.

The framework and the analyses it supports described in this report do not set targets for delisting or recovery of steelhead, nor do they explicitly identify specific populations or groups of populations for recovery priority. Rather, the framework and associated analyses are meant to provide a technical foundation for those charged with recovery of listed steelhead in Puget Sound from which they can develop effective recovery plans at the watershed scale (and higher) that are based on biologically meaningful criteria.

Our approach to assessing viability of Puget Sound steelhead adhered to the Viable Salmonid Populations (VSP) criteria originally described by McElhany et al. (2000) to address conservation and recovery of Pacific salmonids under the Endangered Species Act (ESA). According to McElhany et al. (2000), four parameters form the key to evaluating viability status at the population scale. We slightly modify their description of these parameters here:

- **population size (abundance)**—the abundance of all life stages of the species;
- **population growth rate (productivity)**—production over the entire life cycle, often measured as recruits or returns per spawner, or as long-term population growth rate (λ);
- **diversity**—phenotypic and genetic variation in traits among individuals in a population and among populations in the conservation unit; and
- **spatial structure**—distribution of individuals among spawning and rearing habitat areas, and connectivity among those areas.

In considering recovery of salmon and steelhead units (Evolutionarily Significant Units [ESUs] in the case of Pacific salmon and Distinct Population Segments [DPSs] in the case of steelhead and Atlantic salmon), the National Marine Fisheries Service focuses on these parameters for three reasons. First, they are reasonable predictors of avoiding extinction risk, which reflects the ability of a population to persist into the future (i.e., its viability). We adopt here the VSP approach of considering a conservation unit's viability primarily as its ability to persist over a 100-year time frame. Second, they reflect general processes that are important to all populations of all species. Third, the parameters are measurable.

Population size, or abundance, is recognized as an important parameter because, all else being equal, small populations are at greater risk of extinction than large populations, primarily because several processes that affect population dynamics operate differently in small populations than they do in large populations. These processes are deterministic density effects, environmental variation, genetic processes, demographic stochasticity, ecological feedback, and catastrophes. McElhany et al. (2000) provided guidelines relating minimum abundance to each of these processes at both the “viable” and “critical” levels, where a critical level implies a high risk of extinction over a short time period.

Population growth rate (i.e., productivity over the entire life cycle) and factors that affect population growth rate provide information on how well a population is “performing” in the natural habitats it occupies during the life cycle. Estimates of population growth rate that indicate a population is consistently failing to replace itself demonstrate increased extinction risk. Although the overall focus is on population growth rate over the entire life cycle, estimates of stage-specific productivity—particularly productivity during freshwater life-history stages—are also important to comprehensive evaluation of population viability. Other measures of population productivity, such as intrinsic productivity and the intensity of density dependence, may provide important additional information for assessing a population’s viability. McElhany et al.’s (2000) guidelines for population growth rate are closely linked with those for abundance.

Several steelhead traits exhibit considerable diversity within and among populations, and this variation can have important effects on population viability. In a spatially and temporally varying environment, there are three general reasons why biological diversity is important for population (and DPS) viability. First, diversity allows a population to use a wider array of environments than they could without it. Second, diversity protects against short-term spatial and temporal changes in the environment. Third, genetic diversity provides the raw material for adapting to long-term environmental change.

Finally, when evaluating population viability, it is important to take spatial structure into account for two main reasons: 1) because there is a time lag between changes in spatial structure and species (DPS)-level effects, overall extinction risk at the 100-year time scale may be affected in ways not readily apparent from short-term observations of abundance and productivity, and 2) population spatial structure affects evolutionary processes and may therefore alter a population’s ability to respond to environmental change. Spatially structured populations in which subpopulations occupy habitat patches connected by some low to moderate migration rates are often generically referred to as “metapopulations.” A metapopulation’s spatial structure depends fundamentally on habitat quality and spatial configuration, and demographic dynamics as well as the dispersal characteristics of individuals in sub-populations. Pacific salmonids such as steelhead are generally recognized to have some degree of metapopulation structure. Our criteria for steelhead population spatial structure attempt to account for this structure.

Population viability is typically estimated as some correlate of the probability that a low-abundance threshold, known as a quasi-extinction threshold (QET), will be reached within 100 years. With sufficient quantitative data on abundance or productivity, this can be estimated using a variety of statistical approaches that involve analysis of time series. Incorporating information on population diversity and spatial structure is also important in assessing viability in a larger,

holistic sense, but combining this information with abundance and productivity data in a statistical analysis of extinction risk remains a major challenge in evaluating viability in a conservation framework.

However, the Endangered Species Act is not concerned with the viability of populations per se, but rather with the extinction risk faced by an entire conservation unit (i.e., an ESU or DPS). A key question is how the viabilities of a suite of constituent populations and major population groups are related to the sustainability of the entire unit. Three factors need to be considered when relating VSP parameters to viable conservation units: 1) catastrophic events, 2) long-term demographic processes, and 3) long-term evolutionary potential. McElhany et al. (2000) provided several guidelines related to these factors with an emphasis on risks from catastrophic events:

1. **Conservation units should contain multiple populations.** If an ESU (or DPS) is made up of multiple populations, it is less likely that a single catastrophic event will cause it to become extinct. Also, these conservation units may function as “metapopulations” over the long term and the existence of multiple populations would be necessary for the operation of sustainable population-level extinction/recolonization processes. In addition, multiple populations within a unit increase the likelihood that a diversity of phenotypic and genotypic characteristics will be maintained, thus allowing natural evolutionary processes to operate and increasing the unit’s viability in the long term. Obviously, this guideline does not apply to units that appear to contain a single population. In units containing a single population, Guideline 6 below becomes more important.
2. **Some populations in a conservation unit should be geographically widespread.** Spatially correlated environmental catastrophes are less likely to drive a widespread unit to extinction. This guideline also directly relates to the ESA mandate of protecting a species in a “significant portion of (its) range.”
3. **Some populations should be geographically close to each other.** On long temporal scales, conservation units may function as “metapopulations” and having populations geographically close to one another facilitates connectivity among existing populations. Thus, a viable unit composed of multiple populations requires both widespread (Guideline 2) AND spatially close populations.
4. **Populations should not all share common catastrophic risks.** A conservation unit containing populations that do not share common catastrophic risks is less likely to be driven to extinction by correlated environmental catastrophes. Maintaining geographically widespread populations is one way to reduce risk associated with correlated catastrophes (Guideline 2), but spatial proximity is not the only reason why multiple populations could experience a correlated catastrophic risk.
5. **Populations that display diverse life-histories and phenotypes should be maintained.** When a conservation unit’s populations have a fair degree of life-history diversity (or other phenotypic diversity), the unit is less likely to go extinct as a result of correlated environmental catastrophes or changes in environmental conditions that occur too rapidly

for an evolutionary response. In addition, assuming phenotypic diversity is caused at least in part by genetic diversity, maintaining diversity allows natural evolutionary processes to operate within a unit.

6. **Some populations should exceed VSP viability criteria.** In other words, some constituent populations should have a high probability of persistence for longer than the criteria required for viability of an entire conservation unit. Larger and more productive (“resilient”) populations may be able to recover from a catastrophic event that would cause the extinction of a smaller population. A conservation unit that contains some populations in excess of VSP threshold criteria for abundance and population growth rate is less likely to go extinct in response to a single catastrophic event that affects all populations. It is important to note that the abundance guidelines do not take catastrophes into account. If a unit consists of a single population or a small number of populations, the viability criteria for them should be stronger than the viability criteria for populations within a unit composed of many populations.
7. **Evaluations of a conservation unit’s status should take into account uncertainty about unit-level processes.** Our understanding of unit-level spatial and temporal process is very limited. Conservation units are believed to have been historically self-sustaining and the historical number and distribution of populations serves as a useful “default” goal in maintaining viable units.

Approaches to Assessing Viability

We considered several approaches to assessing the viability of the Puget Sound steelhead Distinct Population Segment (DPS). Population viability analysis (PVA; Beissinger and McCullough 2002) is a set of quantitative or semi-quantitative methods used to estimate the probability that a population, or collection of populations, will persist for a defined period of time in a particular environment. The seminal papers by Dennis et al. (1991) and Thompson (1991) described some of these methods. PVA can assist with evaluating viability at the population level but it can be challenging to extend this analysis to evaluate viability at higher spatial scales involving multiple populations (but see, e.g., Ward et al. 2010). We therefore explored additional tools, including Decision Support Systems (DSSs), to conduct a more comprehensive and hierarchical assessment of Puget Sound steelhead viability (see “Decision Support Systems as Tools for Assessing Viability”, p. 101).

In recent status review updates for Pacific salmon and steelhead (e.g., Good et al. 2005), Biological Review Teams (BRTs) have adopted a risk assessment method that has been used for Pacific salmon recovery planning and is outlined in the VSP report (McElhany et al. 2000). In this approach, risk assessment is addressed first at the population level, then at the overall ESU or DPS level.

In this approach, individual populations are assessed according to the four VSP viability criteria: abundance, growth rate/productivity, spatial structure, and diversity. The condition of individual populations is then summarized at the ESU or DPS level, and the patterns of abundance, distribution, and diversity of populations are considered in evaluating the status of

the ESU or DPS as a whole. These larger scale patterns include the total number of viable populations, geographic distribution of these populations (to ensure inclusion of major life history types and to buffer the effects of regional catastrophes), and connectivity among these populations (to ensure appropriate levels of gene flow and recolonization potential in case of local extirpations). The considerations are reviewed in McElhany et al. (2000).

The revised risk matrix integrates the four major population VSP viability criteria directly into the risk assessment process. After reviewing all relevant biological information for the ESU, each evaluator assigns a risk score (see below) to each of the four criteria. The scores are tallied and reviewed by the evaluation team before making its overall risk assessment. Although this process helps to integrate and quantify a large amount of diverse information, there is no simple way to translate the risk matrix scores directly into an assessment of overall risk. For example, simply averaging the values of the various risk factors would not be appropriate; an ESU or DPS at high risk for low abundance would be at high risk even if there were no other risk factors.

Scoring population viability criteria: Risks for each population viability factor are ranked on a scale of 1 (very low risk) to 5 (very high risk):

1. **Very low risk.** Unlikely that this factor contributes significantly to risk of extinction throughout all or a significant portion of the range, either by itself or in combination with other factors.
2. **Low risk.** Unlikely that this factor contributes significantly to risk of extinction throughout all or a significant portion of the range by itself, but some concern that it may, in combination with other factors.
3. **Moderate risk.** This factor contributes significantly to long-term risk of extinction throughout all or a significant portion of the range, but does not in itself constitute a danger of extinction in the near future.
4. **High risk.** This factor contributes significantly to long-term risk of extinction throughout all or a significant portion of the range and is likely to contribute to short-term risk of extinction in the foreseeable future.
5. **Very high risk.** This factor by itself indicates danger of extinction throughout all or a significant portion of the range in the near future.

Recent events: The “recent events” category considers events that have predictable consequences for ESU or DPS status in the future but have occurred too recently to be reflected in the population data. Examples include a climatic regime shift or El Niño event that may be anticipated to result in increased or decreased marine productivity in subsequent years. This category is scored as follows:

++ (double plus)	expect a strong improvement in status of the ESU or DPS,
+ (single plus)	expect some improvement in status,
0	neutral effect on status,

- (single minus) expect some decline in status,
- – (double minus) expect strong decline in status.

This analysis of overall risk to the ESU or DPS, throughout all or a significant portion of its range, has used categories that correspond to definitions in the ESA: in danger of extinction, likely to become endangered in the foreseeable future, or neither. These evaluations do not consider protective efforts, and therefore are not recommendations regarding listing status. The overall risk assessment reflected professional judgment by each evaluation team member. This assessment was guided by the results of the risk matrix analysis as well as expectations about likely interactions among factors. For example, a single factor with a high risk score might be sufficient to result in an overall score of “in danger of extinction throughout all or a significant portion of the range,” but a combination of several factors with more moderate risk scores could also lead to the same conclusion.

To allow for uncertainty in judging the actual risk facing the ESU or DPS, the evaluation team has often adopted a “likelihood point” method, often referred to as the FEMAT method because it is a variation of a method used by scientific teams evaluating options under former President Clinton’s Forest Plan (Forest Ecosystem Management: An Ecological, Economic, and Social Assessment Report of the Forest Ecosystem Management Assessment Team, or FEMAT). In this approach, each team member distributes 10 likelihood points among the three ESU/DPS risk categories, reflecting his opinion of how likely that category correctly reflects the true ESU/DPS status. Thus if a member were certain the ESU or DPS was in the “not at risk” category, all 10 points could be assigned to that category. A reviewer with less certainty about ESU/DPS status could split the points among two or even three categories. This method has been used in all status review updates for anadromous Pacific salmonids since 1999.

Assessing a population’s viability in a comprehensive way requires consideration of all four VSP criteria. That being said, relating the contribution of lost diversity or eroded spatial structure quantitatively to extinction risk is no trivial matter. We therefore adopted methods that can accommodate both qualitative and quantitative information to assess viability and develop viability criteria. These methods are explained in detail below.

However, we first describe our approaches to evaluating current viability at the population level using quantitative criteria. For this effort we relied on two different methods: viability curve analysis and evaluation of abundance data time series.

Viability Assessment Methods

The TRT adopted methods described by Good et al. (2005) to evaluate data that affect the four VSP parameters in the Puget Sound Steelhead DPS; these methods are described briefly below. State and tribal comanagers provided data on abundance, the fraction of hatchery origin spawners (where available), harvest, age structure, and hatchery releases to the TRT. Data on adult returns were obtained from a variety of sources, including time series of freshwater spawner surveys, redd counts, and historical catch data. Time series of estimated abundance were assembled and analyzed for each population that had sufficient data. Estimates of harvest were

provided for several populations. In the next section we describe basic methods used for analysis of abundance data.

Recent Abundance

Recent abundance of natural spawners is reported as the geometric mean (and range) of the most recent data to be consistent with previous coastwide status reviews of steelhead. Geometric means were calculated to represent the recent abundance of natural spawners for each DIP within the DPS. Geometric means were calculated for the most recent five years; this time frame was selected to correspond with modal age at maturity. Zero values in the data set were replaced with a value of 1, and missing data values within a multiple-year range were excluded from geometric mean calculations. The geometric mean is the n th root of the product of the n data:

$$\overline{X}_G = \sqrt[n]{N_1 N_2 N_3 \dots N_n}$$

where N_t is the abundance of natural spawners in year t . Arithmetic means (and ranges) were also calculated for the most recent abundance data:

$$\overline{X}_A = \left(\sum_{t=1}^n N_t \right) / n$$

where N_t is the abundance of natural spawners in year t .

Trends in Abundance

Short-term and long-term trends were calculated from time series of the total number of adult spawners. Short-term trends were calculated using data from 1995 to the most recent year (2010). Long-term trends were calculated using all the data in a time series. Trend was calculated as the slope of the regression of the number of natural spawners (log-transformed) over the time series. To mediate for zero values, 1 was added to natural spawners before transforming the data. Trend was reported in the original units as exponentiated slope, such that a value greater than 1 indicates a population trending upward, and a value less than 1 indicates a population trending downward. The regression was calculated as

$$\ln(N + 1) = \beta_0 + \beta_1 X + \varepsilon$$

where N is the natural spawner abundance, β_0 is the intercept, β_1 is the slope of the equation, and ε is the random error term.

Confidence intervals (95%) for the slope, in their original units of abundance, were calculated as

$$\exp(\ln(b_1) - t_{0.05(2),df} s_{b_1}) \leq \beta_1 \leq \exp(\ln(b_1) + t_{0.05(2),df} s_{b_1})$$

where b_1 is the estimate of the true slope, β_1 , $t_{0.05(2),df}$ is the two-sided t -value for a confidence level of 0.95, df is equal to $n - 2$, n is the number of data points in the time series, and s_{b_1} is the standard error of the estimate of the slope, b_1 .

Population Growth Rate

In addition to analyses of trends in natural spawners, the median short-term population growth rate (λ) of natural origin spawners was calculated where possible as a measure for comparative risk analysis. Lambda more accurately reflects the biology of steelhead, as it incorporates overlapping generations and calculates running sums of cohorts. It is an essential parameter in viability assessment, as most population extinctions are the result of steady declines, $\lambda < 1$. It has been developed for data sets with high sampling error and age-structure cycles (Holmes 2001). These methods have been extensively tested using simulations for both threatened and endangered populations as well as for stocks widely believed to be at low risk (Holmes 2004), and cross-validated with time series data (Holmes and Fagan 2002).

Ideally, the λ of natural-origin spawners would be calculated on the basis of natural production alone. Nearly all Puget Sound steelhead abundance data series are based on redd counts to which an average number of fish per redd is applied. Counts or proportions of hatchery fish contributing to natural production typically were not available. Thus, it is possible that our computation of λ includes a mixture of hatchery and natural-origin spawners. A multistep process based on methods developed by Holmes (2001) and Holmes and Fagan (2002) and described in McClure et al. (2003) was used to calculate estimates for λ , its 95% confidence intervals, and its probability of decline [$P(\lambda < 1)$]. The first step was calculating 4-year running sums (R) for natural origin spawners as

$$R_t = \sum_{i=1}^4 N_{t-i+1}$$

where N_t is the number of natural-origin spawners in year t . A 4-year running sum window was used, as the analysis by McClure et al. (2003) indicates this is an appropriate window for a diverse range of salmonid life histories.

Next, an estimate of μ , the rate at which the median of R changes over time (Holmes 2001), was calculated as

$$\hat{\mu} = \text{mean} \left(\ln \left(\frac{R_{t+1}}{R_t} \right) \right)$$

the mean of the natural log-transformed running sums of natural origin spawners. The point estimate for λ was then calculated as the median annual population growth rate,

$$\hat{\lambda} = e^{\hat{\mu}}$$

Confidence intervals (95%) were calculated for $\hat{\lambda}$ to provide a measure of the uncertainty associated with the growth rate point estimate. First, an estimate of variability for each population was determined by calculating an estimate for using the slope method (Holmes 2001). The slope method formula is

$$\hat{\sigma}_{pop}^2 = \text{slope of the regression of } \text{var} \left(\ln \left(\frac{R_{t+\tau}}{R_t} \right) \right) \text{ vs. } \tau$$

where τ is a temporal lag in the time series of running sums.

Individual population variance estimates were highly uncertain, so a more robust variance estimate, $\hat{\sigma}_{avg}^2$, was obtained by averaging the $\hat{\sigma}_{pop}^2$ estimates from all the populations in the DPS. This average variance estimate was then applied as the variance for every population in the DPS. The degrees of freedom associated with the average variance estimate are obtained by summing the degrees of freedom for each of the individual population variance estimates. The degrees of freedom for the individual population estimates were determined using the method of Holmes and Fagan (2002), which identifies the adjusted degrees of freedom associated with slope method variance estimates. The calculation for the adjusted degrees of freedom is

$$d = 0.212n - 1.215$$

where n is the length of the time series. Using the average variance estimate and the summed degrees of freedom, the 95% confidence intervals for λ were calculated as

$$\exp(\hat{\mu} \pm t_{0.05(2),df}) \sqrt{\hat{\sigma}_{slp}^2 / (n - 4)}$$

Recruitment

Recruits, or spawners in the next generation, from a given brood year were calculated as

$$C_t = \sum_{i=1}^{MaxAge} N_{t+i} A(i)_{t+i}$$

where C_t is the number of recruits from brood year t , N_t is the number of natural origin spawners in year t , and $A(i)_t$ is the fraction of age i spawners in year t . The estimate of preharvest recruits is similarly

$$C(preHarvest)_t = \sum_{i=1}^{MaxAge} P_{t+i} A(i)_{t+i}$$

where $C(preHarvest)_t$ is the number of preharvest recruits in year t , P_t is the number of natural origin spawners that would have returned in year t if there had not been a harvest, and $A(i)_t$ is the fraction of age i spawners in year t had there not been a harvest. (Because P_t is in terms of the

number of fish that would have appeared on the spawning grounds had there not been a harvest, it can be quite difficult to estimate; thus, simplifying assumptions are often made) (see Hard et al. 2007).

Demographic Data and Analyses

Abundance and Trends

The data considered in this report include estimates of steelhead natural escapement, as calculated from index redd count statistics obtained from the Washington Department of Fish and Wildlife. These data are for winter-run steelhead primarily (the sole summer-run exception is from the Tolt River), and date from as early as 1977. The 20 populations under analysis are considered by the Technical Recovery Team to be potential Demographically Independent Populations (DIPs). However, sufficient quantitative abundance data were not available for other populations among the 32 total candidate DIPs. The DIPs for which insufficient quantitative data were available for analysis are: Drayton Harbor winter-run, Nooksack River winter-run, South Fork Nooksack River summer-run, Nookachamps Creek winter-run, Baker River summer- and winter-run, Sauk River summer- and winter-run, Canyon Creek summer-run, Deer Creek summer-run, North Fork Skykomish River summer-run, North Lake Washington tributaries winter-run, South Sound tributaries winter-run, and East Kitsap Peninsula winter-run steelhead. We present basic analyses of natural escapement data in Tables 1-3 below; these analyses focus on a) data from the entire time series, b) data since 1995, and c) from the most recent five years.

Data from the entire series—Since 1977, Puget Sound steelhead abundance has shown a widespread declining trend over much of the DPS (Table 1). None of the 21 populations evaluated exhibit estimates of long-term population growth rate ($\lambda = R_0 = e^r$, where R_0 is the net birth rate and r is the intrinsic geometric growth rate) that are significantly positive; only two of these has a point estimate of $\lambda > 1$ (indicating positive population growth): Samish River and Snohomish/Skykomish River winter-run. In fact, no estimates of population growth rate were significantly different from 1, indicating no evidence for population trend, but statistical power is limited by missing data and high variability. The highest growth rates over the entire series were estimated in the Northern Cascades MPG, and the lowest rates were estimated in South Sound MPG. Data from redd counts in the Nooksack River in 2010 and 2011 indicated abundances of 1901 and 1774 spawners, respectively, but no data series was available to estimate trend.

Table 1. Estimates of exponential trend in the natural logarithm (\ln) of natural spawners (λ) for populations (DIPs) of steelhead in the Puget Sound DPS over the entire data series. Tahuya River winter-run is part of the South Hood Canal winter-run DIP, and Morse Creek winter-run is part of the Strait of Juan de Fuca Independent Tributaries winter-run DIP. Where necessary, data were interpolated between adjacent years (max. $n = 3$) for some populations to estimate the 95% CIs. NC, not calculated.

Population	Exp. trend $\ln(\text{nat. spawners})$ (95% CI)
Northern Cascades (South Salish Sea) MPG	
Drayton Harbor winter-run	NC
Nooksack R. winter-run	NC
S.F. Nooksack R. summer-run	NC
Samish R. winter-run (1979-2011)	1.031 (0.915 - 1.160)
Nookachamps Cr. winter-run	NC
Baker R. summer- & winter-run	NC
Sauk R. summer- & winter-run	NC
Skagit R. summer- & winter-run (1978-2011)	0.997 (0.921 - 1.079)
Canyon Cr. summer-run	NC
Pilchuck R. winter-run (1981-2011)	0.984 (0.879 - 1.101)
Stillaguamish River winter-run (1985-2011)	0.963 (0.879 - 1.055)
Deer Cr. summer-run	NC
Snohomish/Skykomish R. winter-run (1981-2011)	1.012 (0.887 - 1.156)
N.F. Skykomish R. summer-run	NC
Snoqualmie R. winter-run (1981-2011)	0.967 (0.902 - 1.037)
Tolt R. summer-run (1985-2011)	0.973 (0.801 - 1.182)
Central and South Puget Sound MPG	
Cedar R. winter-run (1981-2011)	0.774 (0.592 - 1.010)
N. Lake Washington tributaries winter-run	NC
Green R. winter-run (1978-2011)	0.975 (0.885 - 1.074)
Puyallup/Carbon R. winter-run (1983-2011)	0.939 (0.860 - 1.026)
White R. winter-run (1983-2011)	0.974 (0.888 - 1.068)
Nisqually R. winter-run (1980-2011)	0.938 (0.853 - 1.031)
South Sound tributaries winter-run	NC
East Kitsap Peninsula winter-run	NC
Hood Canal and Strait of Juan de Fuca MPG	
South Hood Canal winter-run (1998-2011)	0.904 (0.431 - 1.896)
Tahuya R. winter-run* (1981-2011)	0.991 (0.877 - 1.121)
East Hood Canal winter-run (1981-2011)	0.985 (NC)
Skokomish R. winter-run (1982-2011)	0.975 (0.867 - 1.097)
West Hood Canal winter-run (1997-2011)	0.860 (0.624 - 1.184)

Table 1. Continued.

Hood Canal and Strait of Juan de Fuca MPG	
Dungeness R. summer- & winter-run (1988-1996)	0.935 (NC)
Strait of Juan de Fuca Indep. winter-run (1998-2010)	0.921 (0.501 - 1.692)
Morse Cr. winter-run* (1984-2010)	0.972 (0.907 - 1.042)
Elwha R. summer- & winter-run (1986-1997)	0.864 (NC)

* one component of a DIP

Data since 1995—Since 1995, Puget Sound winter-run steelhead abundance has also shown a widespread declining trend over much of the DPS (Table 2). No estimates of population growth rate were significantly different from 1, indicating no evidence for population trend, but the statistical power of those estimates was even lower in this shorter dataset. For most populations, the point estimates of population growth are even more negative in this recent period. Only one of the 20 populations evaluated exhibit a point estimate of growth rate that was positive (Skokomish River winter-run), but it was not significantly so.

Table 2. Estimates of exponential trend in the natural logarithm (\ln) of natural spawners (λ) for populations (DIPs) of steelhead in the Puget Sound DPS since 1995. Tahuya River winter-run is part of the South Hood Canal winter-run DIP, and Morse Creek winter-run is part of the Strait of Juan de Fuca Independent Tributaries winter-run DIP. Where necessary, data were interpolated between adjacent years (max. $n = 3$) for some populations to estimate the 95% CIs. NC, not calculated.

Population	Exp. trend $\ln(\text{nat. spawners})$ (95% CI)
Northern Cascades (South Salish Sea) MPG	
Drayton Harbor winter-run	NC
Nooksack R. winter-run	NC
S.F. Nooksack R. summer-run	NC
Samish R. winter-run	0.993 (0.592 - 1.666)
Nookachamps Cr. winter-run	NC
Baker R. summer- & winter-run	NC
Sauk R. summer- & winter-run	NC
Skagit R. summer- & winter-run	0.966 (0.494 - 1.891)
Canyon Cr. summer-run	NC
Pilchuck R. winter-run	0.928 (0.413 - 2.085)
Stillaguamish River winter-run	0.895 (0.729 - 1.098)
Deer Cr. summer-run	NC
Snohomish/Skykomish R. winter-run	0.953 (0.220 - 4.123)
N.F. Skykomish R. summer-run	NC

Table 2. Continued.

Population	Exp. trend ln(nat. spawners) (95% CI)
Central and South Puget Sound MPG	
Cedar R. winter-run	0.678 (0.434 - 1.060)
N. Lake Washington tributaries winter-run	NC
Green R. winter-run	0.902 (0.703 - 1.157)
Puyallup/Carbon R. winter-run	0.928 (0.700 - 1.229)
White R. winter-run	0.987 (0.794 - 1.228)
Nisqually R. winter-run	0.965 (0.615 - 1.514)
South Sound tributaries winter-run	NC
East Kitsap Peninsula winter-run	NC
Hood Canal and Strait of Juan de Fuca MPG	
South Hood Canal winter-run	0.904 (0.431 - 1.896)
Tahuya R. winter-run*	0.974 (0.743 - 1.276)
East Hood Canal winter-run	0.985 (NC)
Skokomish R. winter-run	1.007 (0.720 - 1.408)
West Hood Canal winter-run	0.887 (0.709 - 1.111)
Strait of Juan de Fuca trib. winter-run	0.887 (0.709 - 1.111)
Dungeness R. summer- & winter-run	NC
Strait of Juan de Fuca Indep. winter-run	0.921 (0.501 - 1.692)
Morse Cr. winter-run*	0.948 (0.830 - 1.083)
Elwha R. summer- & winter-run	NC

* one component of a DIP

Data from the most recent five years—Over the most recent five years where data were available, Puget Sound winter-run steelhead abundance has been low over much of the DPS, with a geometric mean less than 250 fish annually for eight of the 20 populations evaluated (Table 3). One of these is in the Northern Cascades MPG (Tolt River summer-run), one is in Central and South Puget Sound MPG (Cedar River winter-run), and six are in the Hood Canal and Strait of Juan de Fuca MPG (South Hood Canal, East Hood Canal, West Hood Canal, Strait of Juan de Fuca Lowland Tributaries, Strait of Juan de Fuca Independent Tributaries winter-runs, and Elwha River summer/winter-run). Only seven populations had a geometric mean greater than 500 fish—Nooksack River, Samish River, Skagit River, Pilchuck River, Snohomish River/Skykomish River, Snoqualmie River, and Green River winter-runs—and all but one of these are in the Northern Cascades MPG. The Cedar River winter-run population is extremely low in abundance. Eleven populations have no quantitative abundance estimates, and an additional two (Dungeness and Elwha River summer/winter-run) have no recent quantitative estimates.

Table 3. Geometric means of natural spawners for populations (DIPs) of steelhead in the Puget Sound DPS over the most recent five years of available data. Tahuya River winter-run is part of the South Hood Canal winter-run DIP, and Morse Creek winter-run is part of the Strait of Juan de Fuca Independent Tributaries winter-run DIP. Where necessary, data were interpolated between adjacent years (max. missing n = 1) for some populations to estimate the 95% CIs. NC, not calculated.

Population	Geometric mean (95% CI)
Northern Cascades (South Salish Sea) MPG	
Drayton Harbor winter-run	NC
Nooksack R. winter-run (2010-2011)	1820.8 (NC)
S.F. Nooksack R. summer-run	NC
Samish R. winter-run (2007-2011)	581.3 (467.7 - 694.9)
Nookachamps Cr. winter-run	NC
Baker R. summer- & winter-run	NC
Sauk R. summer- & winter-run	NC
Skagit R. summer- & winter-run (2007-2011)	4078.0 (3578.2 - 4577.8)
Canyon Cr. summer-run	NC
Pilchuck R. winter-run (2007-2011)	512.0 (390.0 - 634.1)
Stillaguamish River winter-run (2007-2011)	301.3 (240.5 - 362.1)
Deer Cr. summer-run	NC
Snohomish/Skykomish R. winter-run (2007-2011)	917.5 (785.3 - 1049.7)
N.F. Skykomish R. summer-run	NC
Snoqualmie R. winter-run (2009-2011)	591.9 (NC)
Tolt R. summer-run (2007-2011)	70.7 (58.4 - 82.9)
Central and South Puget Sound MPG	
Cedar R. winter-run (2007-2011)	1.9 (0.6 - 3.2)
N. Lake Washington tributaries winter-run	NC
Green R. winter-run (2007-2011)	660.3 (456.6 - 864.1)
Puyallup/Carbon R. winter-run (2007-2011)	394.2 (340.9 - 447.6)
White R. winter-run (2007-2011)	366.2 (275.9 - 456.5)
Nisqually R. winter-run (2007-2011)	367.8 (280.4 - 455.2)
South Sound Tributaries winter-run	NC
East Kitsap Peninsula winter-run	NC
Hood Canal and Strait of Juan de Fuca MPG	
South Hood Canal winter-run (2007-2011)	101.8 (74.8 - 128.9)
Tahuya R. winter-run* (2007-2011)	84.3 (58.3 - 110.4)
East Hood Canal winter-run (2007-2011)	30.1 (15.5 - 44.7)

Table 3. Continued.

Population	Geometric mean (95% CI)
Hood Canal and Strait of Juan de Fuca MPG	
Strait of Juan de Fuca Trib. winter-run (2007-2011)	17.1 (11.4 - 22.9)
Dungeness R. summer- & winter-run (1992-1996)**	304.0 (289.4 - 318.6)
Strait of Juan de Fuca Indep. winter-run (2006-2010)	176.4 (133.8 - 219.0)
Morse Cr. winter-run* (2007-2011)	56.9 (NC)
Elwha R. summer- & winter-run (1993-1997)**	125.1 (82.0 - 168.1)

* one component of a DIP

** note that these are the most recent 5 years of data

Collectively, these data indicate that several populations are at low abundance (13 of 20 populations with fewer than 500 spawners annually) and suggest that nearly all populations exhibit declining trends (low power and high variability precludes detection of clear trends in many cases using these simple measures). Natural escapement of winter-run steelhead throughout Puget Sound is currently far below historical estimates, particularly in southern Puget Sound and on the Olympic Peninsula.

Population Viability Analysis

The abundance trends and numbers described above alone do not always give a clear picture of population viability. Small salmonid populations can be viable if not trending downward. In addition, these data address only two of the four VSP criteria. Evaluating the viability of populations, or aggregates of populations, that are perceived to be at high risk of extinction—usually the case with threatened and endangered species—is typically challenging. Such populations are often characterized by meager data on abundance or productivity. Ideally, when such data do exist, a population viability analysis (PVA), complete with estimates of extinction risk and minimum viable population sizes, will be conducted. But even if a detailed PVA is not done, an attempt to describe the population's likely future trajectory is crucial to identifying population status and recovery options. Identifying a population or conservation unit's current state and likely future state is valuable in informing managers as to how much improvement in abundance and productivity is necessary to arrest a declining trend (Holmes 2001). Such an exercise can be instrumental in helping to identify priorities among different populations with different trends and to quantify the short-term risks until better information is acquired. A now widely used estimator for population extinction was proposed by Dennis et al. (1991), in which treating a time series of abundance as a diffusion process can yield estimates of extinction risk. A key advantage of this approach is that it requires only two parameters to estimate the state of the population into the future, based on past censuses: the arithmetic mean and variance of the log population growth rate; this variance accounts for sources of variability of abundance, including environmental and demographic stochasticity and observation error (Dennis et al. 1991). The approach makes analysis of time series tractable, in part because it treats a population's trajectory as though it is at stochastic equilibrium, subject primarily to

random variation, with a state at a particular time little influenced by previous states (especially as the interval increases). However, this method has difficulty capturing the ability of populations at high risk of extinction to recover from very low levels.

Evaluating the viability of Demographically Independent Populations (DIPs) of steelhead was made challenging by the lack of quantitative abundance and productivity data for many of them. Additionally, some data sets describe multiple DIPs within a single basin. For DIPs that had quantitative or semi-quantitative abundance estimates, we employed a combination of viability curves developed from stock-recruitment analysis and autoregressive state-space models to analyze population viability.

Viability curves such as those depicted in Figure 1 are useful in illustrating the current extinction or quasi-extinction risk of a population under recent conditions of abundance and productivity. They require a demographic model to forecast future population viability from available trends in abundance and productivity.

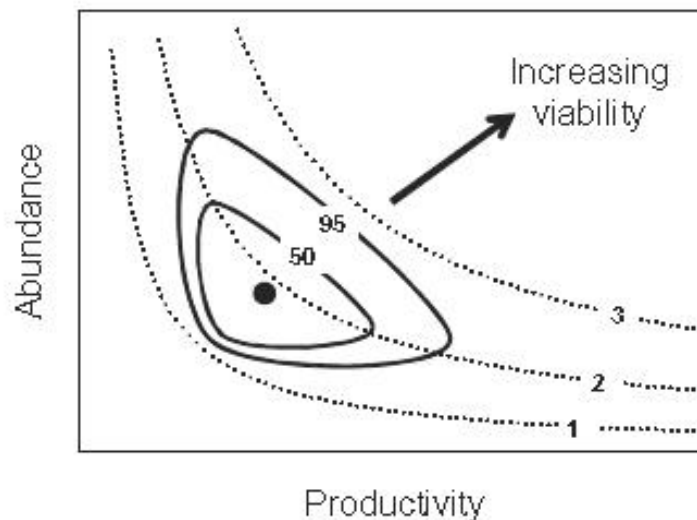


Figure 1. Viability as a function of abundance and productivity. The dotted curves depict isopleths of equivalent extinction risk along different combinations of abundance and productivity and corresponding to different viability categories (1, 2, or 3). For a given abundance, viability increases with increasing productivity, and conversely, for a given productivity, viability increases with increasing abundance. The black dot and solid lines estimate the current risk of extinction and its 50% and 95% confidence ellipses for a hypothetical population. Adapted from McElhany et al. (2007) and Waples et al. (2010).

For 20 of the 32 steelhead DIPs, we used viability curves to characterize the relationship between population abundance, productivity, and quasi-extinction risk (or conversely, the probability of persistence; see Tables 4 and 5). DIPs for which we could not conduct such

analyses included Drayton Harbor Tributaries winter-run, Nooksack River winter-run, South Fork Nooksack summer-run, Sauk River summer- and winter-run, Baker River winter-run, Canyon Creek summer-run, Nookachamps Creek winter-run, North Fork Skykomish River summer-run, Deer Creek summer-run, South Sound Tributaries winter-run, and East Kitsap Peninsula winter-run. The viability curve approach was developed in an effort to establish recovery criteria for threatened salmon and steelhead populations and was first described in McElhany et al. (2003). The points that describe a viability curve reflect combinations of abundance and productivity that generate the same probability of reaching or exceeding a quasi-extinction threshold (Figure 2). The quasi-extinction threshold is established for each population by first considering the potential of the freshwater habitat to support steelhead rearing and spawning, and then applying a minimal marine survival rate to estimates of smolt production that would produce an abundance of spawners considered to be too low for sustained viability. Populations with productivity and abundance combinations above (to the right) the curve have a lower extinction risk than those along the curve, while those below (to the left) the curve have a higher risk. Relating abundance, productivity and extinction risk is accomplished using a simulation model with a stochastic recruitment function having terms for productivity, carrying capacity, recruitment variability, age structure, future harvest rate, and a reproductive failure threshold (RFT). To estimate extinction risk for any particular set of input parameters, the model is run thousands of times to determine the fraction of simulations that drop below a critical risk threshold (CRT). A viability curve is drawn by determining combinations of productivity and capacity (abundance) that are associated with a given level of risk. Drawing the curve for any particular group of fish requires appropriate estimates of recruitment variability, age structure, future harvest rate, and RFT. Note that the curve is not calculated from empirical estimates of productivity and abundance—instead, a range of hypothetical abundances and capacities (abundances) are explored to produce a curve. The viability curve can be thought of as a target for population abundance and productivity to achieve a certain level of extinction risk; it is not a comprehensive evaluation of population status (McElhany et al. 2003). We apply it to Puget Sound steelhead to evaluate status relative to desirable levels of abundance and productivity, and compare these results to other methods to assess population viability (described in a later section).

Table 4. Population persistence categories (McElhany et al. 2006).

Population persistence category	Probability of population persistence over 100 yr	Probability of population extinction in 100 yr	Description
0	0-40%	60-100%	Either extinct or very high risk of extinction
1	40-75%	25-60%	Relatively high risk of extinction in 100 years
2	75-95%	5-25%	Moderate risk of extinction in 100 years
3	95-99%	1-5%	Low (“negligible”) risk of extinction in 100 years (viable salmonid population)
4	>99%	<1%	Very low risk of extinction in 100 years

Table 5. Population abundance (number of spawners) relative to persistence category and population size category (after McElhany et al. 2007). The Chinook salmon data were used to construct the viability curves in Figure 2.

Species	Size category	Persistence category				
		0	1	2	3	4
Chum salmon	Small	<250	250-300	300-500	500-1000	>1000
	Medium	<500	500-600	600-700	700-1000	>1000
	Large	<700	700-850	850-1000	1000-1200	>1200
Chinook salmon	Small	<100	100-200	200-500	500-1000	>1000
	Medium	<350	350-450	450-600	600-1000	>1000
	Large	<600	600-750	750-1000	1000-1300	>1300

Table 5.
Continued.

Species	Size category	Persistence category				
		0	1	2	3	4
Coho salmon	Small	<500	500-700	700-1000	1000-1300	>1300
	Medium	<1000	1000-1400	1400-2000	2000-2400	>2400
	Large	<1600	1600-2000	2000-3000	3000-3600	>3600
Steelhead	Small	<100	100-200	200-500	500-750	>750
	Medium	<200	200-250	250-500	500-1000	>1000
	Large	<400	400-450	450-500	500-1000	>1000

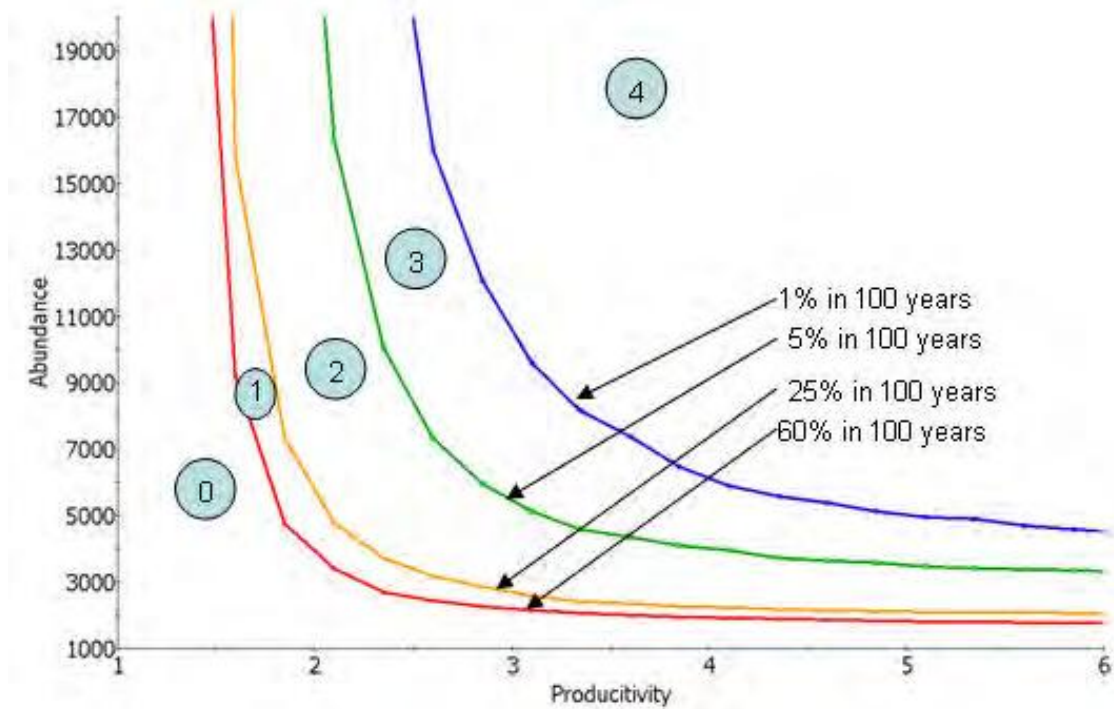


Figure 2. Hypothetical viability curves showing the relationship between levels of extinction risk and population persistence categories. The example is based on the Chinook salmon values in Table 5. Each of the curves indicates a different risk level corresponding to a combination of abundance (y-axis) and productivity (x-axis, here as recruits per spawner). The numbers in the circles are the persistence categories associated with each region of the plot (i.e., the area between adjacent curves). For example, a population with risk category of 0 is described as a population that is nearly extinct and a population with a risk category of 3 (or 4) is described as viable (Table 4).

In order to evaluate a particular population's status relative to a viability curve estimate, the population's abundance and productivity must be estimated. We used the MeanRS method described by McElhany et al. (2006) to estimate these parameters. Productivity is a measure of a population's resilience or tendency to return to higher abundance if the population declines to low abundance. Using the MeanRS method, this tendency is estimated as the geometric mean recruits per spawner for the brood years with the lowest half of spawner abundances. The abundance is estimated as the geometric mean recruitment over the time series. The characteristics of the MeanRS method compared to other possible approaches are described in McElhany et al. (2006). The MeanRS methods are solidly based on the empirical data because they do not depend on extrapolation outside the observe ranges of recruitment and abundance. Estimating a population's abundance and productivity requires input data on population spawner abundance, the fraction of hatchery origin spawners, harvest rates and the population age structure. All of these parameters are estimated with error, sometimes considerable error. This

error is incorporated into the analysis by using a Monte Carlo approach of simulating many equally plausible data sets based on our understanding of the measurement errors and then calculating the MeanRS output for each simulated data set. This gives a distribution of possible abundance and productivity combinations for the current state of the population, which can be depicted in the form of probability contours. We used the Salmon Population Analyzer (SPAz) computer program to generate viability curves and current status probability contours (McElhany and Payne 2006).

Stochastic Population Viability Analysis

We used a stochastic population viability model incorporated into a set of computer programs termed SPAz (Salmon Population AnalyZer v. 1.3.4; McElhany and Payne 2006) to characterize viability of populations for which we had temporal estimates of relative abundance (typically, number of spawners estimated from redd counts), using estimates of population abundance and productivity under different demographic models. SPAz can estimate extinction risk, minimum viable population size, and population change criteria. The program estimates stock-recruitment parameters from spawner-recruit data and incorporates environmental stochasticity, in the form of random uncorrelated environmental variation, and parameter uncertainty, in the form of random variation in parameter estimates. These estimates can be obtained in SPAz using any of a variety of stock-recruitment models, including constant recruitment, random walk (with or without drift), stochastic exponential (with ceiling), stochastic hockey stick, running sum growth, stochastic (logistic) Ricker, and Beverton-Holt models (Myers et al. 1994, Barrowman and Myers 2000).

The SPAz program has the capability of incorporating observation error and process error into the analyses. Observation error, assumed to be normally distributed in SPAz, is measurement error that contributes to uncertainty in estimating abundance at any given time, but it does not accumulate or contribute to future uncertainty. Process error, on the other hand, is random error that contributes to temporal variation in population dynamics but is not directly accounted for by the model. It can result from a number of sources, including genetic or demographic stochasticity (sampling effects) or environmental stochasticity (random environmental variation). It can accumulate and contribute to future uncertainty. In SPAz it is treated with a lognormal distribution and is considered temporally auto-correlated.

We used SPAz to generate estimates of relative risk of a population reaching a low-abundance threshold, termed a quasi-extinction threshold (QET), under simple stock-recruitment models such as the random walk with drift and the stochastic hockey stick. Using these risk estimates, we generated viability curves for steelhead populations that depict the risk of these populations reaching a particular QET within 100 years, given a range of particular combinations of current abundance and population growth rate. An example of the results of this type of PVA is given in Figure 3, showing how the joint estimate of population abundance and productivity, depicted by the colored probability contours at lower left, relates to a series of four viability curves representing different levels of abundance and productivity that correspond to the projections of the population reaching a quasi-extinction threshold (e.g., QET = 2, 20, 50, or 100 spawners in a given year) within 100 years with 5% probability.

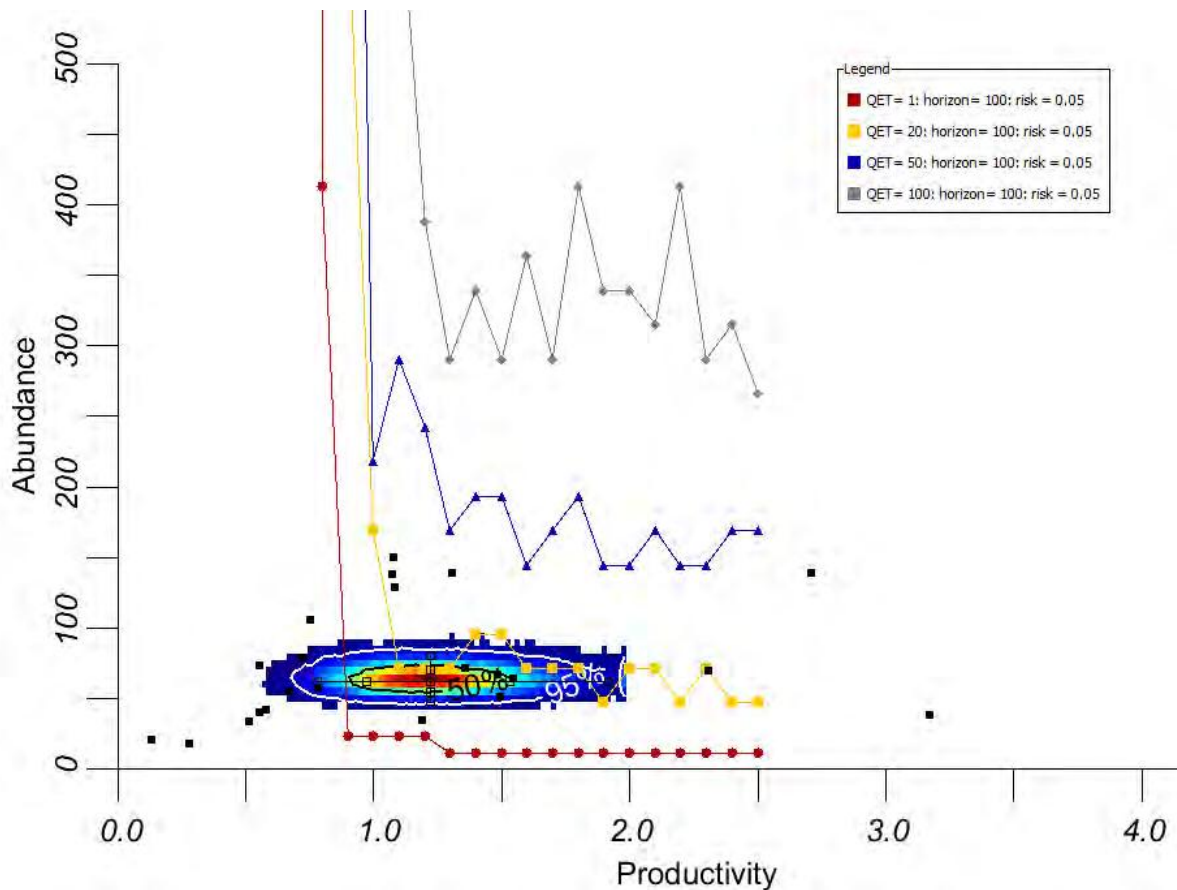


Figure 3. An example of the results of a population viability analysis (PVA) conducted with the program SPAz (McElhany and Payne 2006). The plot depicts a joint estimate of population abundance (y-axis) and productivity (recruits per spawner, x-axis), represented by the connected open squares (showing the approximate 50% and 95% probability centroids of projected abundance and productivity) overlain by colored probability contours. Actual abundance and estimated productivity data are given by the black squares (for the wild Snow Creek winter-run steelhead population in Washington State, 1978-2011). The joint estimates and the data are portrayed in relation to four viability curves representing different combinations of abundance and productivity that correspond to the projections of the population reaching a quasi-extinction threshold (QET = 2, 20, 50, or 100 spawners in a given year) within 100 years with 5% probability. Assumptions of this PVA include no harvest and stationarity of conditions into the future. The PVA relies on a hockey stick recruitment model and uses the geometric mean of recruits per spawner to estimate productivity over the observed data. The bootstrapped estimates incorporate a range of uniform priors for population growth rate, number of recruits, and process error. Comparison with the values in Table 5 and Figure 2 suggest that this population is at a high risk of quasi-extinction over the next 100 years, and that this risk is posed by both low abundance and high variance in productivity.

Applying Stochastic PVA to Puget Sound Steelhead Populations—Of the 32 DIPs of Puget Sound steelhead we identified (Table 1), we applied PVA to 16 of them for which we had sufficient abundance time series (Figures 4-25). For each of these PVAs we made the following assumptions:

1. We based these PVAs on available natural escapement data, which were available for 20 of the 32 DIPs for most years from 1977-2011 (with some notable exceptions), as too few populations provided total run size (harvest plus escapement) information. Such PVAs will tend to underestimate extinction risk if temporal declines in total run size are steeper than those for escapements. Additional characteristics of the escapement data are briefly summarized in Table 6).
2. We had empirical age structure data available for only three populations in the Puget Sound DPS. We used the two datasets that were longest to determine a fixed average age structure for each Puget Sound DIP and apply it across its abundance time series. For DIPs in northern and southern Puget Sound and Hood Canal drainages, we used the estimated average age structure from the Green River winter-run steelhead population, available from a WDFW 28-year time series between 1978 and 2005. The age structure applied was 0.1% age-2, 5.8% age-3, 49.8% age-4, 45.3% age-5, 4.0% age-6, and 0.3% age-7 adults. For DIPs in Strait of Juan de Fuca drainages, we used the estimated average age structure from the Snow Creek winter-run steelhead population, available from a WDFW 34-year time series between 1977 and 2011. This age structure was similar, except that more age-4 and fewer age-5 fish are represented (0.2% age-2, 6.3% age-3, 70.2% age-4, 21.9% age-5, 1.4% age-6, and <0.1% age-7 adults). We applied normally distributed random error around these estimates.
3. For most of the DIPs we applied a running sum growth model (McElhany and Payne 2006) to initiate the analysis of abundance and productivity, which relied on 4-year running sums of spawner counts. We fitted a hockey-stick recruitment model (Barrowman and Myers 2000) to these data. The estimation of both the growth parameter, μ , and the process error, σ^2 , using the slope method (Holmes 2001) was done on the (corrected) running sums. A “meanRS” bootstrap method was then used to calculate recruits per spawner, a growth curve was fit to the data, and population projections were used to estimate extinction risk for a set of four fixed quasi-extinction thresholds. For Dungeness River, Strait of Juan de Fuca Independents, and Elwha River winter-run steelhead we relied a simpler, random-walk-with-trend model to estimate minimum viable population sizes from their shorter time series of abundance.
4. We did not account for differences in reproductive fitness between hatchery and natural spawners (see discussion in Araki et al. 2008), but simply assumed that all adults identified as natural spawners in the data were of wild origin.
5. We ran 100,000 bootstrap replicates using estimates of intrinsic growth rate, maximum number of recruits, and process error. These were drawn from uniform distributions with ranges of 0.5-4.0, 1-30, and 0.2-4.0, respectively.
6. We ran 1000 risk projections for several QET values that always included 1 and a habitat-based estimate of QET that we derived from our intrinsic potential metrics (with 5% probability of reaching QET over a 100-year time horizon).
7. We did not account for non-anadromous (resident) recruits of steelhead spawners. For example, precocious male offspring of steelhead are known to participate in steelhead

spawning, and to sire anadromous offspring. Most of the empirical escapement data we used are based on redd counts multiplied by a uniform spawners per redd number, which may or may not adequately account for resident spawners. Not accounting for resident recruits may underestimate productivity, and potentially lead to overestimates of extinction risk.

The results of the SPAz analyses indicate that two of the seven populations that could be evaluated in the Northern Cascades MPG are at moderate to high levels of risk of reaching QET. The two populations at moderate to high quasi-extinction risk in this MPG—Stillaguamish River winter-run and Tolt River summer-run—are at risk primarily because of high variance in productivity. For the Central and South Puget Sound MPG, the SPAz analyses indicate that a much higher fraction of populations are at high risk: four of the five populations that could be evaluated are at high levels of risk of reaching QET. The three populations at high quasi-extinction risk in this MPG—Cedar River/North Lake Washington, Puyallup/Carbon River, White River, and Nisqually River winter-run—are at risk primarily because of very low productivity (the Lake Washington population is also at very low abundance). For the Hood Canal and Strait of Juan de Fuca MPG, the SPAz analyses indicate that 6 of the 8 populations that could be evaluated are at moderate to high levels of risk of reaching QET. The four populations clearly at high quasi-extinction risk in this MPG—South Hood Canal, East Hood Canal, West Hood Canal, and Strait of Juan de Fuca Lowland Tributaries winter-run—are at risk primarily because of low productivity; two others—Dungeness River and Elwha River winter-run—are also at low or unknown recent abundance. Because the abundance data used in the SPAz analyses are generally indexes of natural escapement rather than reasonably precise estimates of natural run size, these analyses are likely to underestimate risk to viability from low abundance or productivity. The conclusions are further tempered by the rather restrictive assumptions described above, which may not apply to all these populations except in broad terms.

Table 6. Description of WDFW natural escapement data available for Puget Sound steelhead populations and their relationship to the TRT-designated Demographically Independent Populations (DIPs). WSH, winter-run steelhead; SSH, summer-run steelhead; SaSI, Salmonid Stock Inventory (a WDFW database accessible through its “Salmonscape” website at <http://wdfw.wa.gov/mapping/salmonscape/>).

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DIP name	Drainages included in DIP	Drainages R. represented in escapement data	Important contrasts between DIP and escapement data	Escapement data type
Nooksack R. WSH	mainstem Nooksack R. and all major tributaries and many side channels	mainstem, north fork, middle fork, south fork, tributaries, and side channels	Escapement data are from 2010 and 2011 only, and 2011 data were made by expanding off the 2010 data	for R.edds in mainstem index areas and associated tributaries based on aerial counts and AUC estimation
Samish R. WSH	Samish R. and four creeks entering Bellingham Bay	mainstem Samish and Samish tributary Friday Creek		total escapement estimates based on cumulative R.edd counts
Skagit R. SSH/WSH	mainstem Skagit R. and all tributaries except Baker R., Sauk R., and entire Stillaguamish Basin except Deer and Canyon creeks	mainstem Skagit R. (RM 22.5 to 94.1), Alder, Diobsud, R.ocky, North Fork Stillaguamish and its tributaries upstream of Deer Cr.	SaSI data include Sauk R. escapement, and Sauk R. SSH/WSH is a South Fork Stillagaumish escapements are NOT included in SaSI data	total escapement estimates based on cumulative R.edd counts
Snohomish-Skykomish WSH	mainstem Snohomish, Skykomish basin	mainstem Snohomish to R.M 51.5 on S.F. Skykomish; Wallace		total escapement estimates based on R.edd counts
Pilchuck R. WSH	Pilchuck R.	mainstem Pilchuck R. from R.M 0.0 to 15.3, and Worthy, Dubuque		total escapement estimates based on R.edd counts
Snoqualmie R. WSH	mainstem Snoqualmie R. and its tributaries	mainstem Snoqualmie upstream to Snoqualmie Falls (RM 40.5),		total escapement estimates based on R.edd counts
Tolt R. SSH	North and South Forks of Tolt R.	South Fork Tolt R.iver, R.M 3.3 to 7.8	no estimates for N.F. Tolt in SaSI data	total escapement estimates based on R.edd counts February

Table 6. Continued.

DIP name	Drainages included in DIP	Drainages R. represented in escapement data	Important contrasts between DIP and escapement data	Escapement data type
Cedar R. WSH	Cedar R.	Cedar R.iver and Issaquah and Bear creeks	Cedar and Lake Washington data combined	total escapement estimates based on R.edd counts
N Lake Washington WSH	Bear, Issaquah and Swamp creeks and other tributaries	data are NOT available separately from Cedar R.		
Green R. WR	Green R.	Green R. mainstem spawning areas and index R.eaches in Soos		total escapement estimates based on cumulative R.edd counts
Puyallup/Carbon WSH	Puyallup (excluding White R.) and Carbon R.ivers	mainstem Puyallup R.iver and its tributaries, excluding White R.;	Puyallup and Carbon are separate SaSI stocks; data were combined to 2009 to 2011 counts at Buckley Trap included R.eturning adults from	total escapement estimates based on R.edd counts in all counts of steelhead at USACE adult trap at the Buckley Dam (RM 24.3)
White R. WSH	White R.	Important Note: data are from Fish Managemnet staff, which combines Nisqually R. and some tributaries such as Mashel R. are now		total escapement estimates based on R.edd counts
Nisqually WSH	Nisqually R.			total escapement estimates based on R.edd counts
East Hood Canal WSH	Dewatto R., Big Beef and Anderson creeks; other small west Kitsap	Dewatto R. only	SaSI data for Dewatto R. only	index escapement estimates based on R.edd counts from R.M
South Hood Canal WSH	Tahuya and Union R.ivers, Mission Cr, other small south Hood	Tahuya and Union R.ivers. [Also, Tahuya data provided separately	SaSI data for Tahuya and Union only. Tahuya and Union are separate	index escapement estimates based on R.edd counts from
Skokomish WSH	Skokomish R.	mainstem Skokomish, North Fork and South Fork Skokomish		total escapement estimates based on R.edd counts in index

Table 6. Continued.

DIP name	Drainages included in DIP	Drainages R. represented in escapement data	Important contrasts between DIP and escapement data	Escapement data type
West Hood Canal WSH	Hamma Hamma, Duckabush, Dosewallips, Big and Little Quilcene	Hamma Hamma, Duckabush, Dosewallips, and Little Quilcene	SaSI data do not include Big Quilcene R. or Tarboo Cr.	index escapement estimates based on R.edd counts in Hamma
Strait of Juan de Fuca Lowland Tributaries WSH	Snow, Salmon and Jimmycomelately creeks and other streams	Snow Cr. (Discovery Bay stream)	SaSI data only for Snow Cr. population	total escapement estimates based on Snow Cr. trap counts and on
Dungeness WSH	Dungeness R.	Dungeness R. (no R. recent data series available)		index escapements based on R.edd counts in index areas. Escapement
Strait of Juan de Fuca Independent Tributaries WSH	Ennis, White, Morse, Siebert and McDonald creeks	Morse and McDonald creeks. [Also, Morse data provided separately	SaSI data only for Morse and McDonald creeks	total escapement estimates based on R.edd counts in Morse
Elwha R. WSH	Elwha R.	Elwha R. within 4.9 miles downstream of (former) Elwha Dam.		total escapement estimates based on hatchery/wild R. atios in

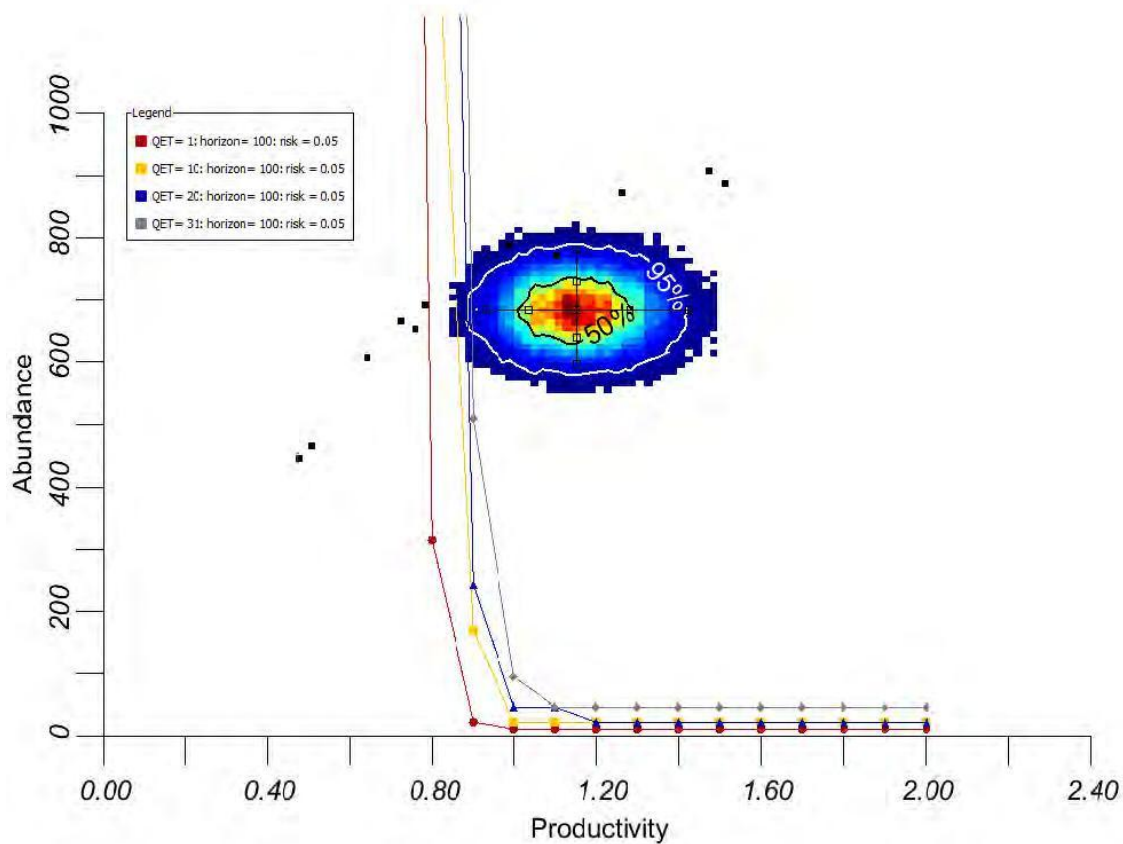


Figure 4. Population viability analysis (PVA) for Samish River winter-run steelhead, conducted with the program SPAz (McElhany and Payne 2006). The plot depicts the joint estimate of population abundance (y-axis) and productivity (recruits per spawner, x-axis), represented by the connected open squares (showing the approximate 50% and 95% probability centroids of projected abundance and productivity) overlain by colored probability contours. Actual abundance and productivity data are given by the solid black squares. The joint estimate and the data are overlaid onto four viability curves representing different combinations of abundance and productivity that correspond to a 5% risk of reaching a quasi-extinction threshold (QET) of 1, 10, 20, or 31 spawners (the habitat-based estimate of QET for this population) in a given year over a 100-year time horizon. The PVA relies on a hockey stick recruitment model and uses the geometric mean of running sums of recruits per spawner to estimate productivity over the observed data. Comparison with the values in Table 5 and Figure 2 suggests that this population is at a low risk of quasi-extinction over the next 100 years.

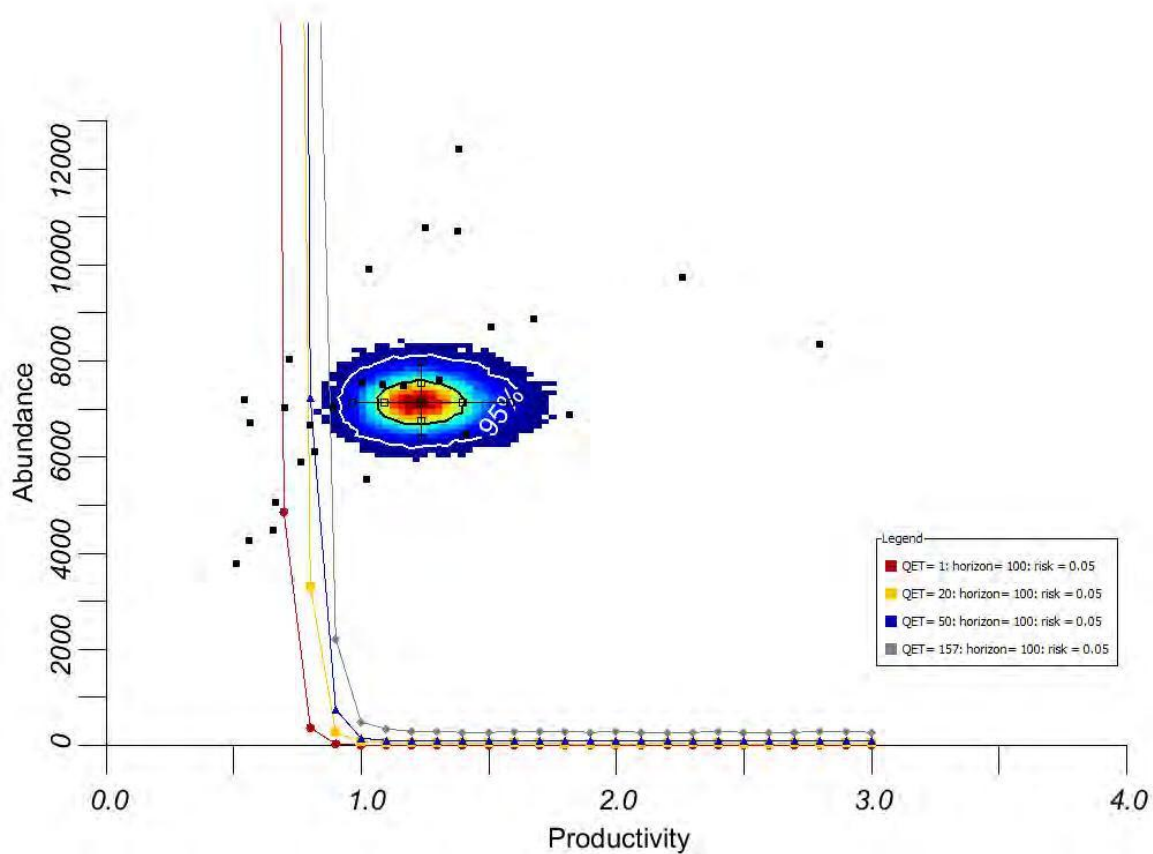


Figure 5. Population viability analysis (PVA) for Skagit River summer- and winter-run steelhead, conducted with the program SPAz (McElhany and Payne 2006). The plot depicts the joint estimate of population abundance (y-axis) and productivity (recruits per spawner, x-axis), represented by the connected open squares (showing the approximate 50% and 95% probability centroids of projected abundance and productivity) overlain by colored probability contours. Actual abundance and productivity data are given by the solid black squares. The joint estimate and the data are overlaid onto four viability curves representing different combinations of abundance and productivity that correspond to a 5% risk of reaching a quasi-extinction threshold (QET) of 1, 20, 50, or 157 spawners (the habitat-based estimate of QET for this population) in a given year over a 100-year time horizon. The PVA relies on a hockey stick recruitment model and uses the geometric mean of running sums of recruits per spawner to estimate productivity over the observed data. Comparison with the values in Table 5 and Figure 2 suggests that this population is at a low risk of quasi-extinction over the next 100 years.

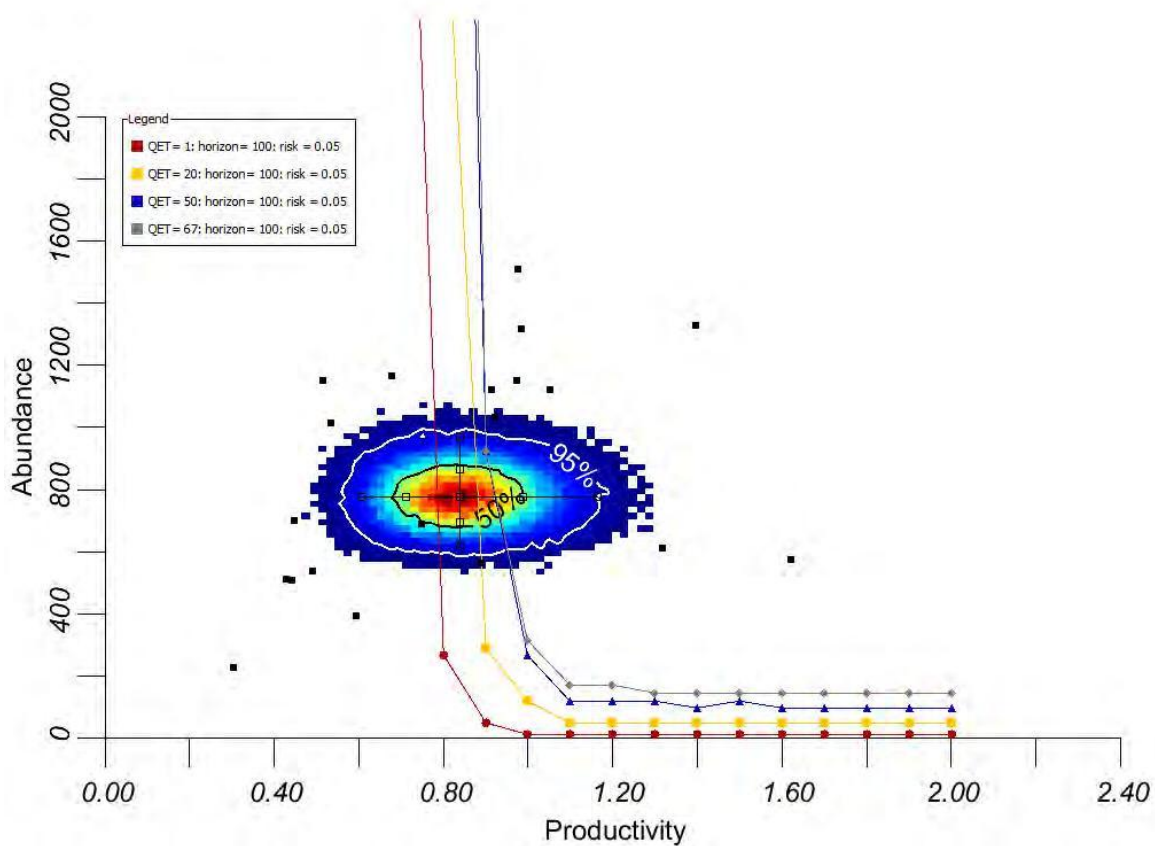


Figure 6. Population viability analysis (PVA) for Stillaguamish River winter-run steelhead, conducted with the program SPAz (McElhany and Payne 2006). The plot depicts the joint estimate of population abundance (y-axis) and productivity (recruits per spawner, x-axis), represented by the connected open squares (showing the approximate 50% and 95% probability centroids of projected abundance and productivity) overlain by colored probability contours. Actual abundance and productivity data are given by the solid black squares. The joint estimate and the data are overlaid onto four viability curves representing different combinations of abundance and productivity that correspond to a 5% risk of reaching a quasi-extinction threshold (QET) of 1, 20, 50, or 67 spawners (the habitat-based estimate of QET for this population) in a given year over a 100-year time horizon. The PVA relies on a hockey stick recruitment model and uses the geometric mean of running sums of recruits per spawner to estimate productivity over the observed data. Comparison with the values in Table 5 and Figure 2 suggests that this population is at a very high risk of quasi-extinction over the next 100 years.

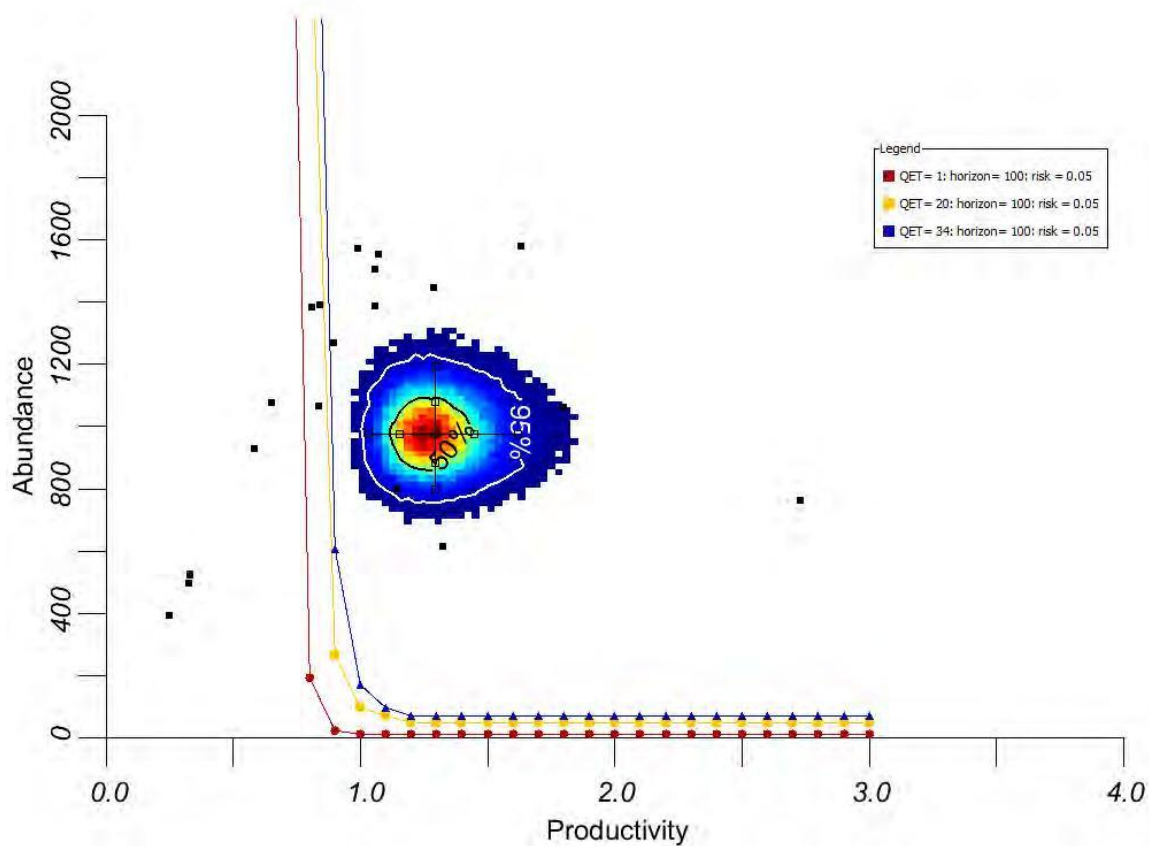


Figure 7. Population viability analysis (PVA) for Pilchuck River winter-run steelhead, conducted with the program SPAz (McElhany and Payne 2006). The plot depicts the joint estimate of population abundance (y-axis) and productivity (recruits per spawner, x-axis), represented by the connected open squares (showing the approximate 50% and 95% probability centroids of projected abundance and productivity) overlain by colored probability contours. Actual abundance and productivity data are given by the solid black squares. The joint estimate and the data are overlaid onto four viability curves representing different combinations of abundance and productivity that correspond to a 5% risk of reaching a quasi-extinction threshold (QET) of 1, 20, or 34 spawners (the habitat-based estimate of QET for this population) in a given year over a 100-year time horizon. The PVA relies on a hockey stick recruitment model and uses the geometric mean of running sums of recruits per spawner to estimate productivity over the observed data. Comparison with the values in Table 5 and Figure 2 suggests that this population is at a very low risk of quasi-extinction over the next 100 years.

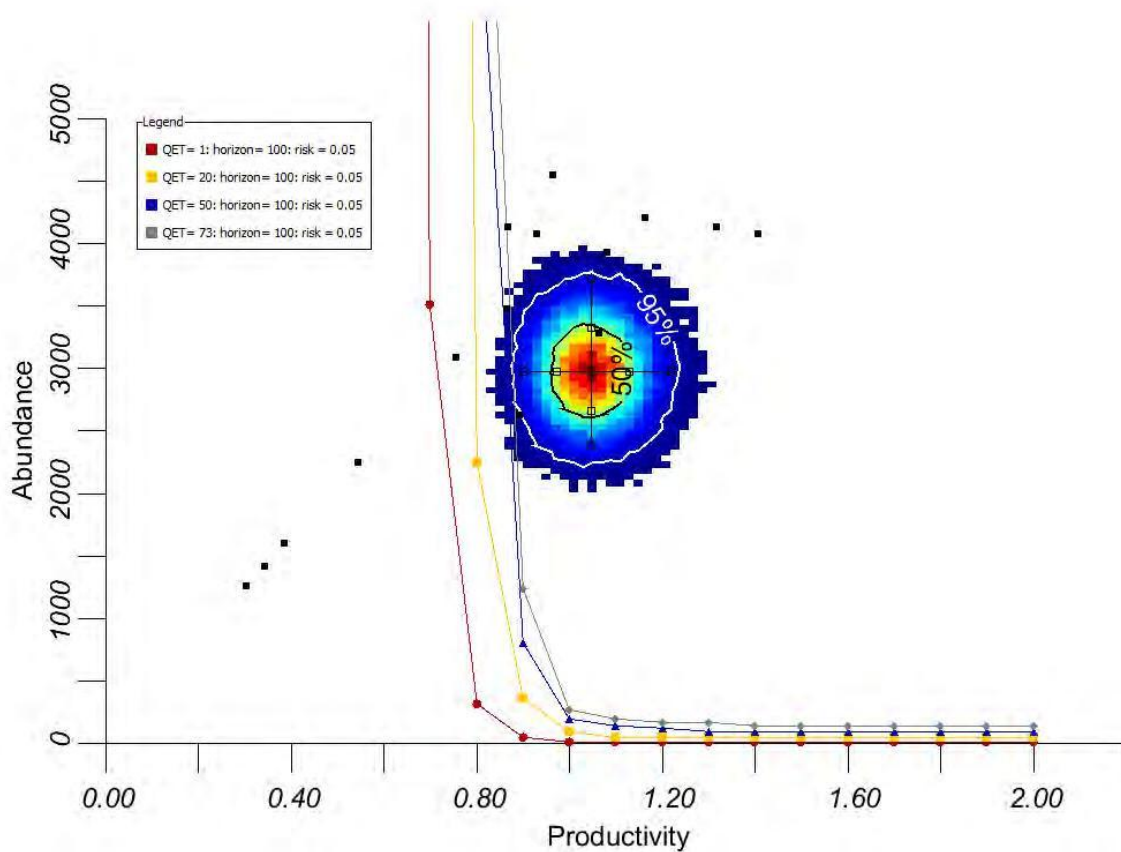


Figure 8. Population viability analysis (PVA) for Snohomish/Skykomish River winter-run steelhead, conducted with the program SPAz (McElhany and Payne 2006). The plot depicts the joint estimate of population abundance (y-axis) and productivity (recruits per spawner, x-axis), represented by the connected open squares (showing the approximate 50% and 95% probability centroids of projected abundance and productivity) overlain by colored probability contours. Actual abundance and productivity data are given by the solid black squares. The joint estimate and the data are overlaid onto four viability curves representing different combinations of abundance and productivity that correspond to a 5% risk of reaching a quasi-extinction threshold (QET) of 1, 20, 50, or 73 spawners (the habitat-based estimate of QET for this population) in a given year over a 100-year time horizon. The PVA relies on a hockey stick recruitment model and uses the geometric mean of running sums of recruits per spawner to estimate productivity over the observed data. Comparison with the values in Table 5 and Figure 2 suggests that this population is at a low risk of quasi-extinction over the next 100 years.

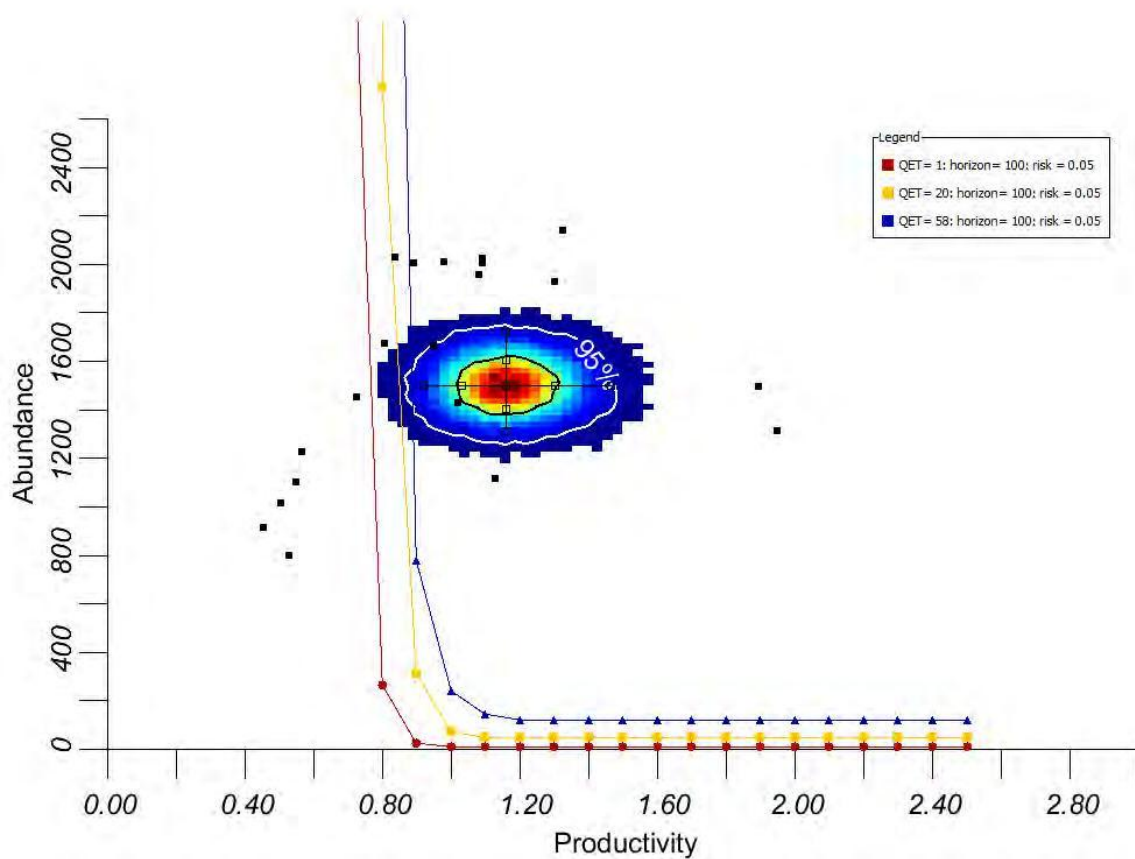


Figure 9. Population viability analysis (PVA) for Snoqualmie River winter-run steelhead, conducted with the program SPAz (McElhany and Payne 2006). The plot depicts the joint estimate of population abundance (y-axis) and productivity (recruits per spawner, x-axis), represented by the connected open squares (showing the approximate 50% and 95% probability centroids of projected abundance and productivity) overlain by colored probability contours. Actual abundance and productivity data are given by the solid black squares. The joint estimate and the data are overlaid onto four viability curves representing different combinations of abundance and productivity that correspond to a 5% risk of reaching a quasi-extinction threshold (QET) of 1, 20, or 58 spawners (the habitat-based estimate of QET for this population) in a given year over a 100-year time horizon. The PVA relies on a hockey stick recruitment model and uses the geometric mean of running sums of recruits per spawner to estimate productivity over the observed data. Comparison with the values in Table 5 and Figure 2 suggests that this population is at a moderate risk of quasi-extinction over the next 100 years.

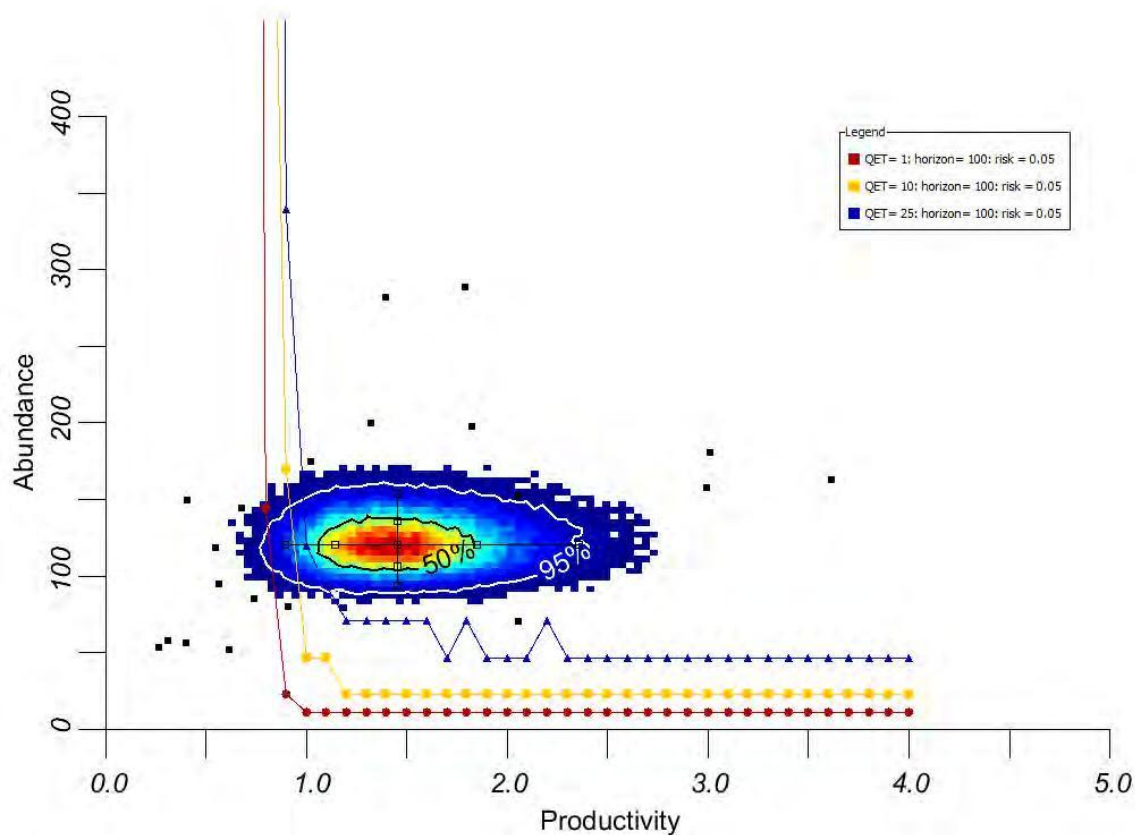


Figure 10. Population viability analysis (PVA) for Tolt River summer-run steelhead, conducted with the program SPAz (McElhany and Payne 2006). The plot depicts the joint estimate of population abundance (y-axis) and productivity (recruits per spawner, x-axis), represented by the connected open squares (showing the approximate 50% and 95% probability centroids of projected abundance and productivity) overlain by colored probability contours. Actual abundance and productivity data are given by the solid black squares. The joint estimate and the data are overlaid onto four viability curves representing different combinations of abundance and productivity that correspond to a 5% risk of reaching a quasi-extinction threshold (QET) of 1, 10, or 25 spawners (the habitat-based estimate of QET for this population) in a given year over a 100-year time horizon. The PVA relies on a hockey stick recruitment model and uses the geometric mean of running sums of recruits per spawner to estimate productivity over the observed data. Comparison with the values in Table 5 and Figure 2 suggests that this population is at a high risk of quasi-extinction over the next 100 years.

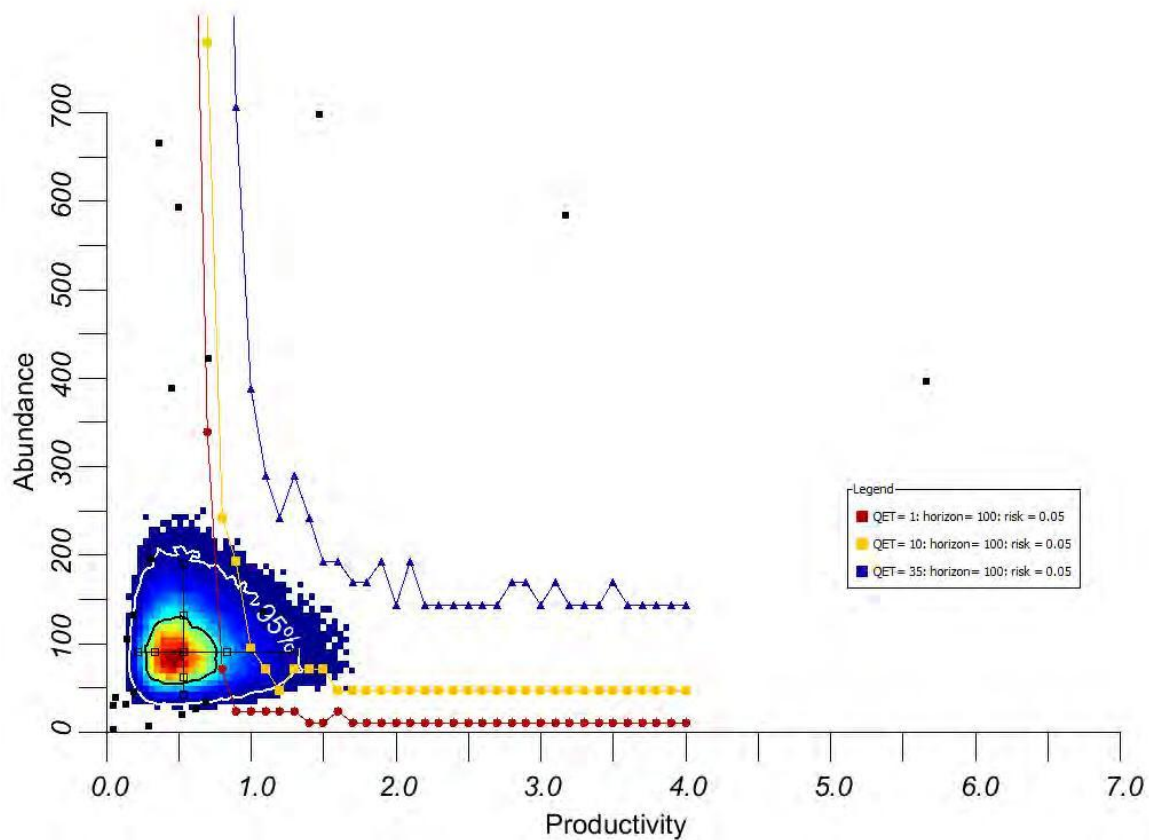


Figure 11. Population viability analysis (PVA) for Cedar River summer- and winter-run steelhead, conducted with the program SPaZ (McElhany and Payne 2006). The plot depicts the joint estimate of population abundance (y-axis) and productivity (recruits per spawner, x-axis), represented by the connected open squares (showing the approximate 50% and 95% probability centroids of projected abundance and productivity) overlain by colored probability contours. Actual abundance and productivity data are given by the solid black squares. The joint estimate and the data are overlaid onto four viability curves representing different combinations of abundance and productivity that correspond to a 5% risk of reaching a quasi-extinction threshold (QET) of 1, 10, or 35 spawners (the habitat-based estimate of QET for this population) in a given year over a 100-year time horizon. The PVA relies on a hockey stick recruitment model and uses the geometric mean of running sums of recruits per spawner to estimate productivity over the observed data. Comparison with the values in Table 5 and Figure 2 suggests that this population is at a very high risk of quasi-extinction over the next 100 years.

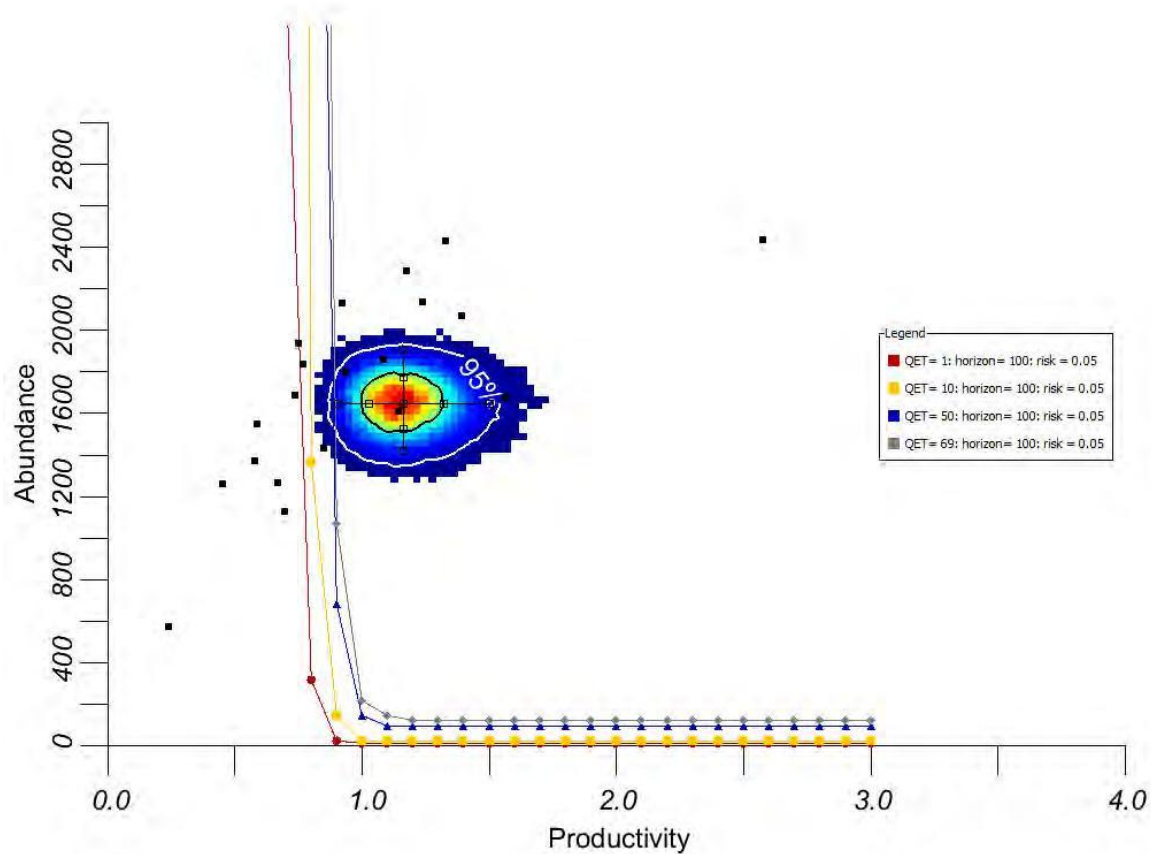


Figure 12. Population viability analysis (PVA) for Green River winter-run steelhead, conducted with the program SPAz (McElhany and Payne 2006). The plot depicts the joint estimate of population abundance (y-axis) and productivity (recruits per spawner, x-axis), represented by the connected open squares (showing the approximate 50% and 95% probability centroids of projected abundance and productivity) overlain by colored probability contours. Actual abundance and productivity data are given by the solid black squares. The joint estimate and the data are overlaid onto four viability curves representing different combinations of abundance and productivity that correspond to a 5% risk of reaching a quasi-extinction threshold (QET) of 1, 20, 50, or 69 spawners (the habitat-based estimate of QET for this population) in a given year over a 100-year time horizon. The PVA relies on a hockey stick recruitment model and uses the geometric mean of running sums of recruits per spawner to estimate productivity over the observed data. Comparison with the values in Table 5 and Figure 2 suggests that this population is at a moderate risk of quasi-extinction over the next 100 years.

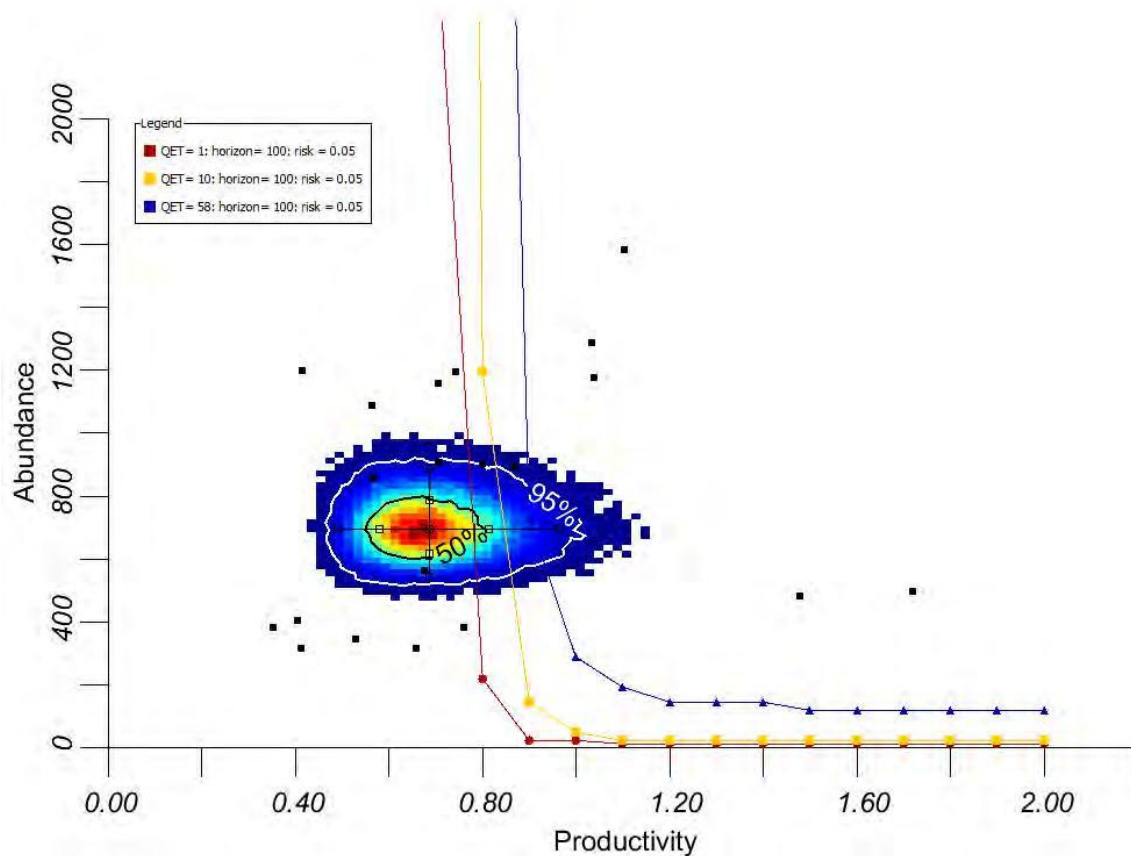


Figure 13. Population viability analysis (PVA) for Puyallup/Carbon River winter-run steelhead, conducted with the program SPAz (McElhany and Payne 2006). The plot depicts the joint estimate of population abundance (y-axis) and productivity (recruits per spawner, x-axis), represented by the connected open squares (showing the approximate 50% and 95% probability centroids of projected abundance and productivity) overlain by colored probability contours. Actual abundance and productivity data are given by the solid black squares. The joint estimate and the data are overlaid onto four viability curves representing different combinations of abundance and productivity that correspond to a 5% risk of reaching a quasi-extinction threshold (QET) of 1, 10, or 58 spawners (the habitat-based estimate of QET for this population) in a given year over a 100-year time horizon. The PVA relies on a hockey stick recruitment model and uses the geometric mean of running sums of recruits per spawner to estimate productivity over the observed data. Comparison with the values in Table 5 and Figure 2 suggests that this population is at a very high risk of quasi-extinction over the next 100 years.

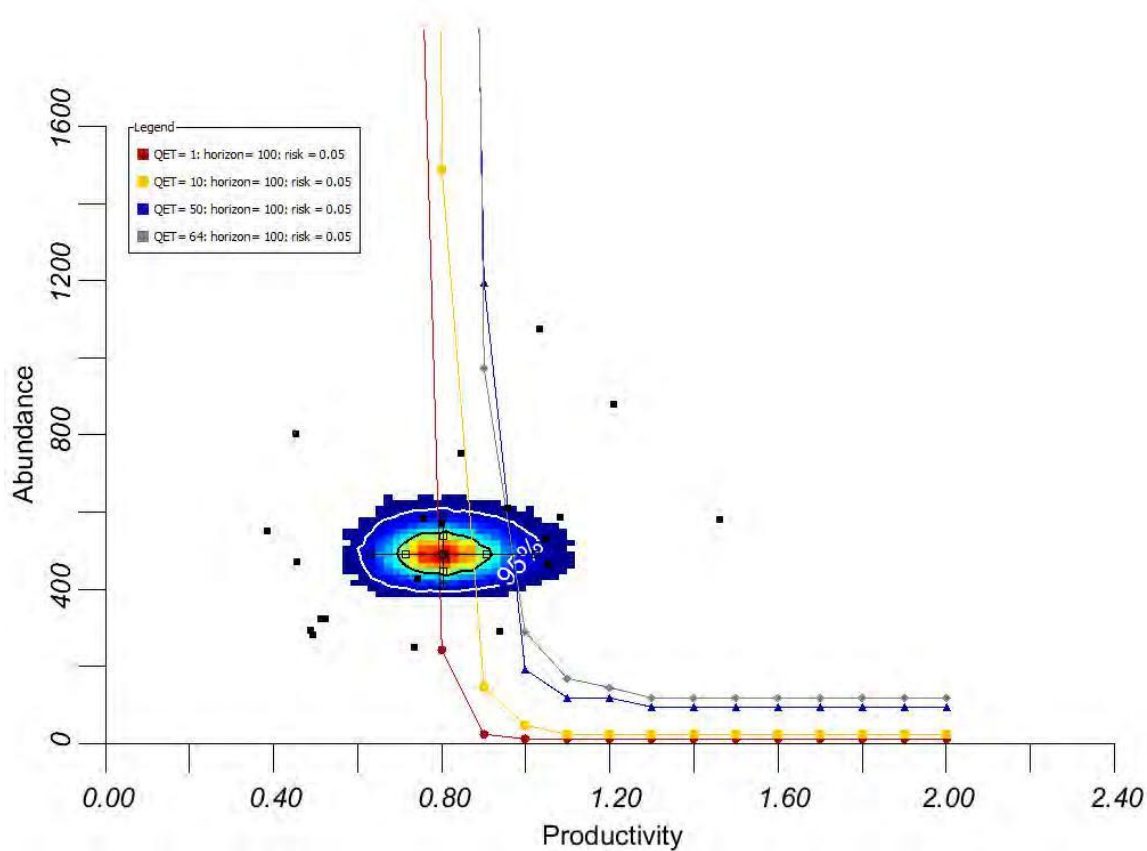


Figure 14. Population viability analysis (PVA) for White River winter-run steelhead, conducted with the program SPAz (McElhany and Payne 2006). The plot depicts the joint estimate of population abundance (y-axis) and productivity (recruits per spawner, x-axis), represented by the connected open squares (showing the approximate 50% and 95% probability centroids of projected abundance and productivity) overlain by colored probability contours. Actual abundance and productivity data are given by the solid black squares. The joint estimate and the data are overlaid onto four viability curves representing different combinations of abundance and productivity that correspond to a 5% risk of reaching a quasi-extinction threshold (QET) of 1, 10, 50, or 64 spawners (the habitat-based estimate of QET for this population) in a given year over a 100-year time horizon. The PVA relies on a hockey stick recruitment model and uses the geometric mean of running sums of recruits per spawner to estimate productivity over the observed data. Comparison with the values in Table 5 and Figure 2 suggests that this population is at a very high risk of quasi-extinction over the next 100 years.

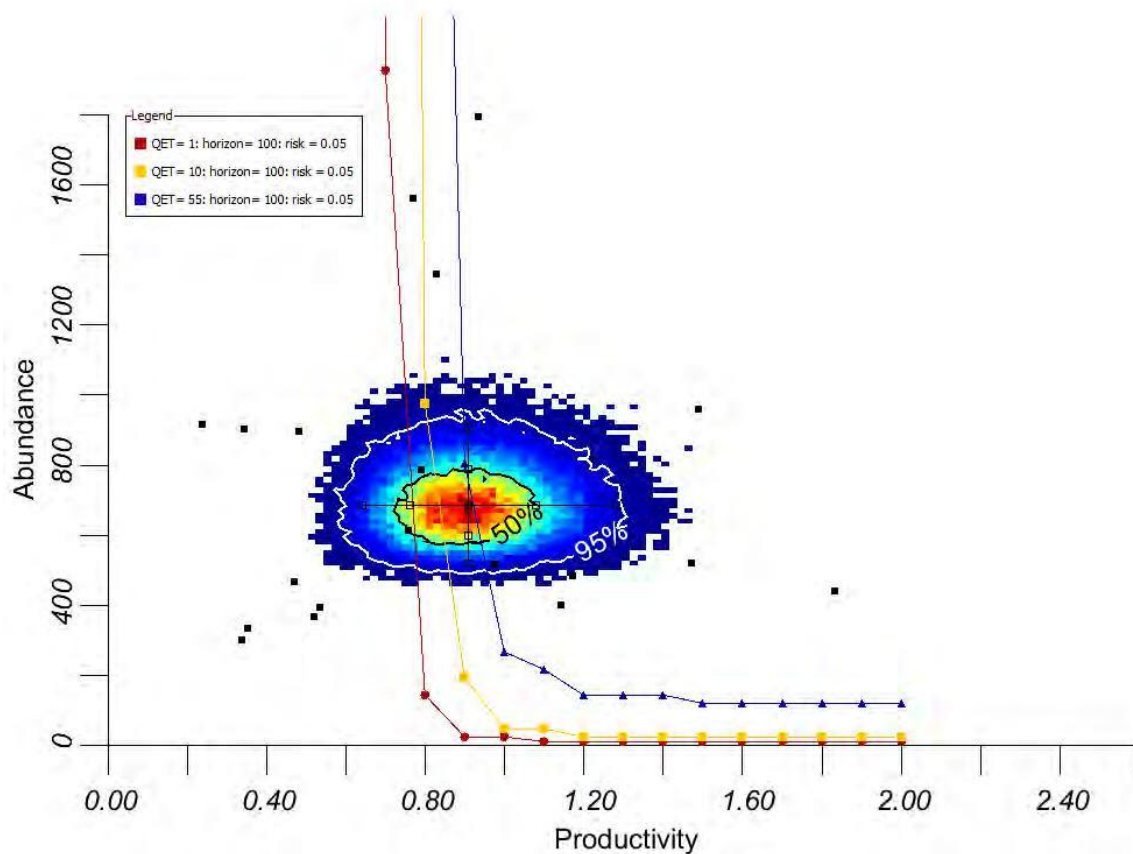


Figure 15. Population viability analysis (PVA) for Nisqually River winter-run steelhead, conducted with the program SPAz (McElhany and Payne 2006). The plot depicts the joint estimate of population abundance (y-axis) and productivity (recruits per spawner, x-axis), represented by the connected open squares (showing the approximate 50% and 95% probability centroids of projected abundance and productivity) overlain by colored probability contours. Actual abundance and productivity data are given by the solid black squares. The joint estimate and the data are overlaid onto four viability curves representing different combinations of abundance and productivity that correspond to a 5% risk of reaching a quasi-extinction threshold (QET) of 1, 10, or 55 spawners (the habitat-based estimate of QET for this population) in a given year over a 100-year time horizon. The PVA relies on a hockey stick recruitment model and uses the geometric mean of running sums of recruits per spawner to estimate productivity over the observed data. Comparison with the values in Table 5 and Figure 2 suggests that this population is at a very high risk of quasi-extinction over the next 100 years.

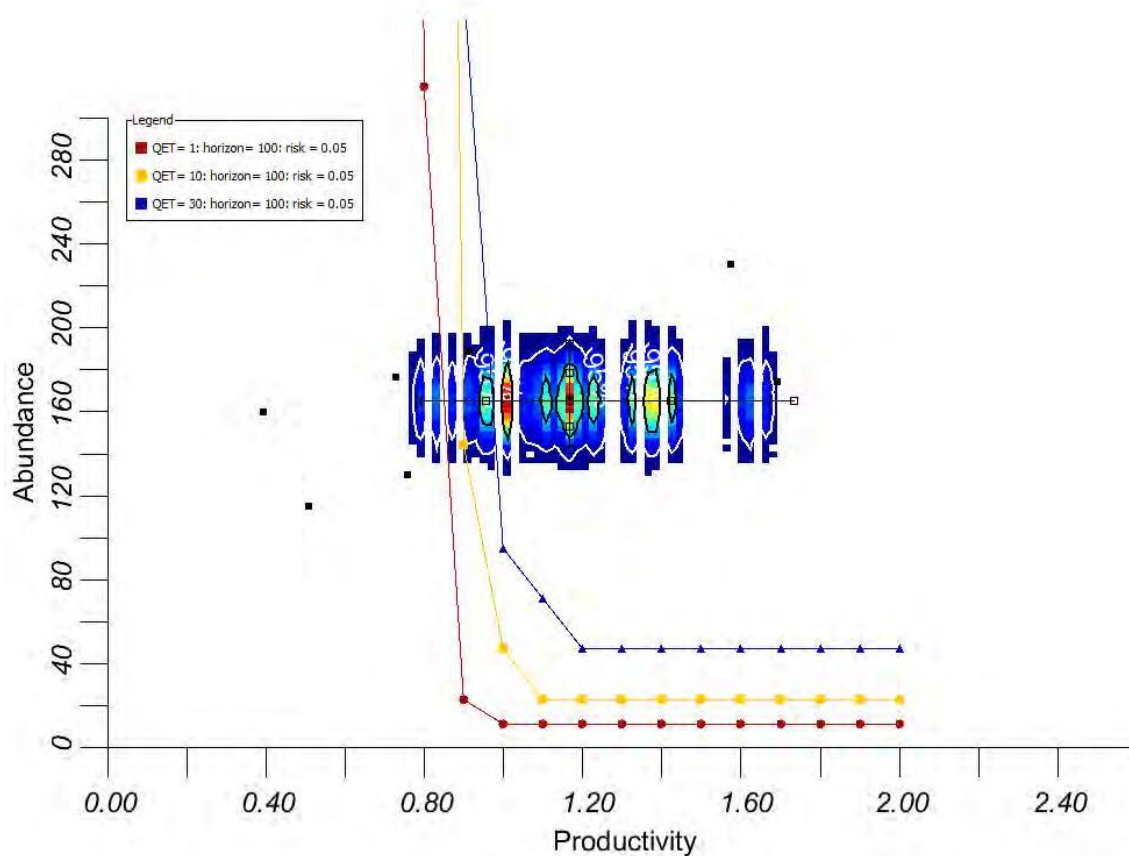


Figure 16. Population viability analysis (PVA) for South Hood Canal winter-run steelhead, conducted with the program SPAz (McElhany and Payne 2006). The plot depicts the joint estimate of population abundance (y-axis) and productivity (recruits per spawner, x-axis), represented by the connected open squares (showing the approximate 50% and 95% probability centroids of projected abundance and productivity) overlain by colored probability contours. Actual abundance and productivity data are given by the solid black squares. The joint estimate and the data are overlaid onto four viability curves representing different combinations of abundance and productivity that correspond to a 5% risk of reaching a quasi-extinction threshold (QET) of 1, 10, or 30 spawners (the habitat-based estimate of QET for this population) in a given year over a 100-year time horizon. The PVA relies on a hockey stick recruitment model and uses the geometric mean of running sums of recruits per spawner to estimate productivity over the observed data. Comparison with the values in Table 5 and Figure 2 suggests that this population is at a high risk of quasi-extinction over the next 100 years.

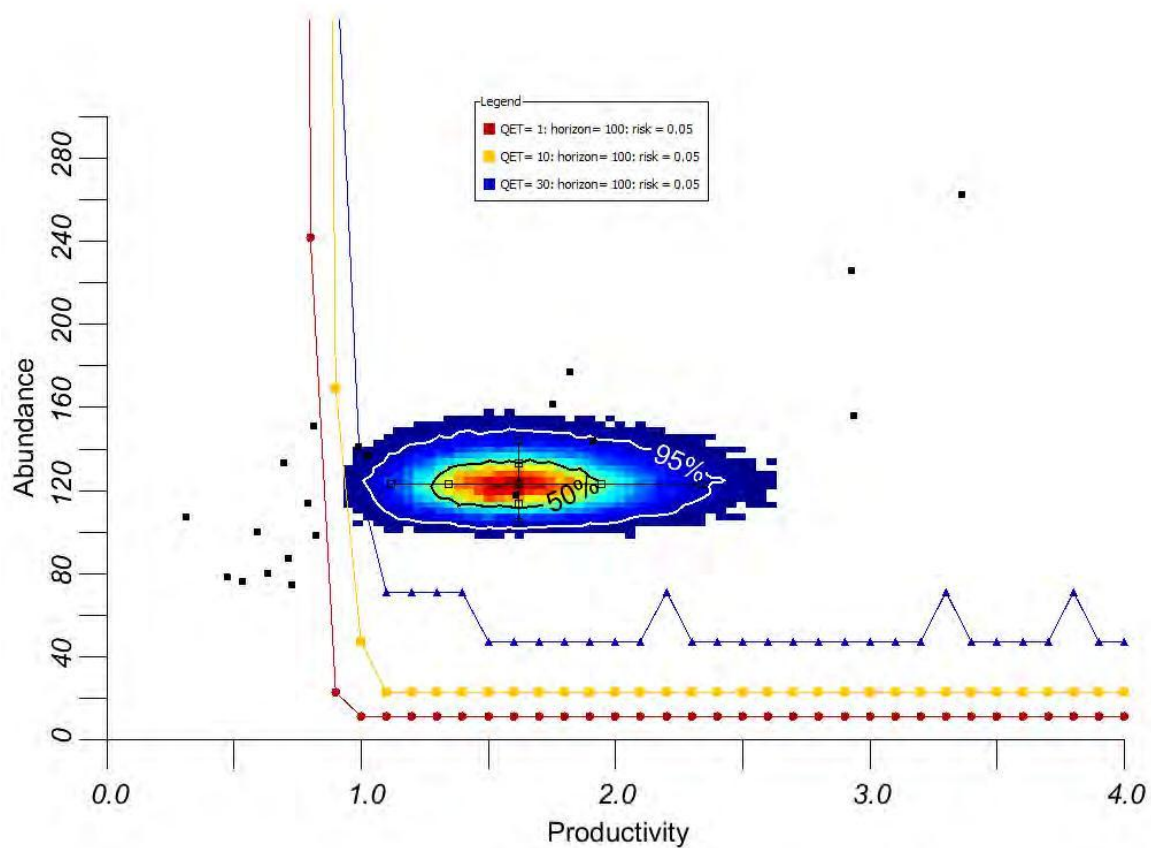


Figure 17. Population viability analysis (PVA) for Tahuya River winter-run steelhead, part of the South Hood Canal DIP, conducted with the program SPAz (McElhany and Payne 2006). The plot depicts the joint estimate of population abundance (y-axis) and productivity (recruits per spawner, x-axis), represented by the connected open squares (showing the approximate 50% and 95% probability centroids of projected abundance and productivity) overlain by colored probability contours. Actual abundance and productivity data are given by the solid black squares. The joint estimate and the data are overlaid onto four viability curves representing different combinations of abundance and productivity that correspond to a 5% risk of reaching a quasi-extinction threshold (QET) of 1, 10, or 30 spawners (the habitat-based estimate of QET for this population) in a given year over a 100-year time horizon. The PVA relies on a hockey stick recruitment model and uses the geometric mean of running sums of recruits per spawner to estimate productivity over the observed data. Comparison with the values in Table 5 and Figure 2 suggests that this population is at a low risk of quasi-extinction over the next 100 years.

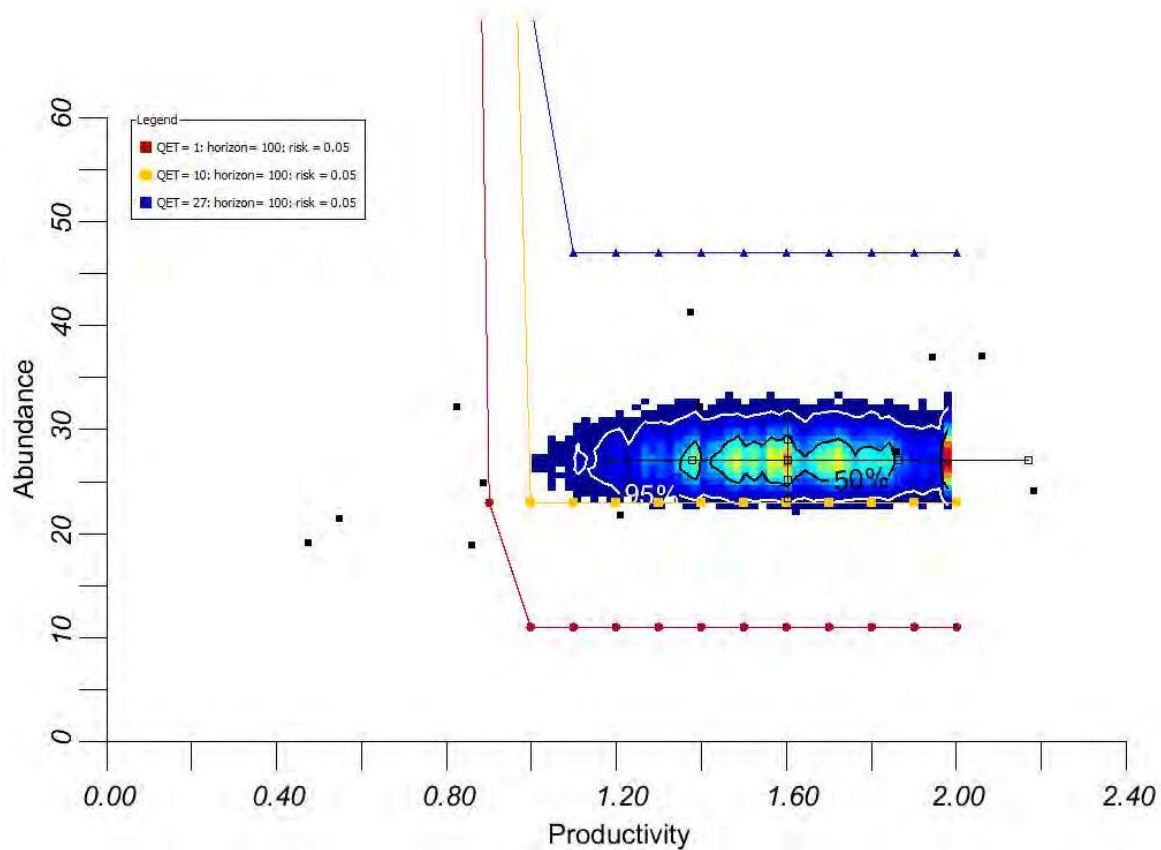


Figure 18. Population viability analysis (PVA) for East Hood Canal winter-run steelhead conducted with the program SPAz (McElhany and Payne 2006). Only Dewatto River population data are available for this DIP. The plot depicts the joint estimate of population abundance (y-axis) and productivity (recruits per spawner, x-axis), represented by the connected open squares (showing the approximate 50% and 95% probability centroids of projected abundance and productivity) overlain by colored probability contours. Actual abundance and productivity data are given by the solid black squares. The joint estimate and the data are overlaid onto four viability curves representing different combinations of abundance and productivity that correspond to a 5% risk of reaching a quasi-extinction threshold (QET) of 1, 10, or 27 spawners (the habitat-based estimate of QET for this population) in a given year over a 100-year time horizon. The PVA relies on a hockey stick recruitment model and uses the geometric mean of running sums of recruits per spawner to estimate productivity over the observed data. Comparison with the values in Table 5 and Figure 2 suggests that this population is at a high risk of quasi-extinction over the next 100 years.

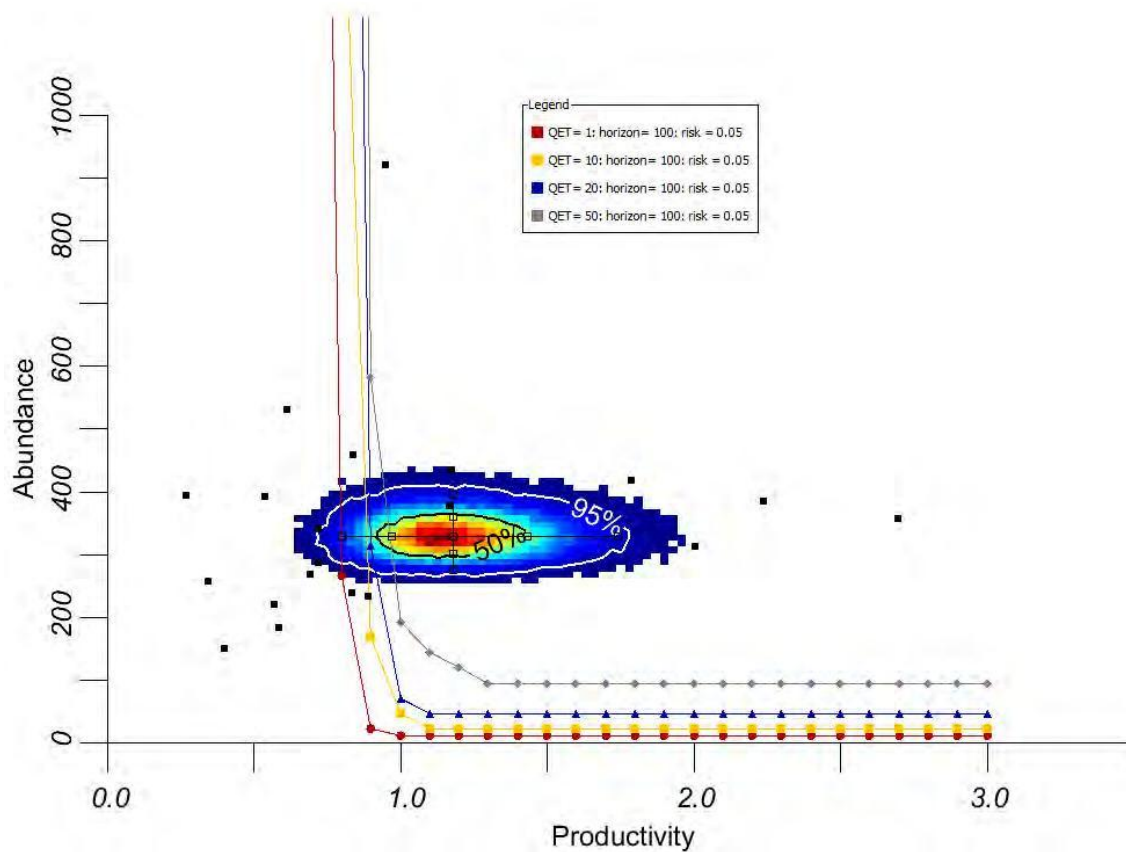


Figure 19. Population viability analysis (PVA) for Skokomish River winter-run steelhead conducted with the program SPAz (McElhany and Payne 2006). The plot depicts the joint estimate of population abundance (y-axis) and productivity (recruits per spawner, x-axis), represented by the connected open squares (showing the approximate 50% and 95% probability centroids of projected abundance and productivity) overlain by colored probability contours. Actual abundance and productivity data are given by the solid black squares. The joint estimate and the data are overlaid onto four viability curves representing different combinations of abundance and productivity that correspond to a 5% risk of reaching a quasi-extinction threshold (QET) of 1, 10, 20, or 50 spawners (the habitat-based estimate of QET for this population) in a given year over a 100-year time horizon. The PVA relies on a hockey stick recruitment model and uses the geometric mean of running sums of recruits per spawner to estimate productivity over the observed data. Comparison with the values in Table 5 and Figure 2 suggests that this population is at a high risk of quasi-extinction over the next 100 years.

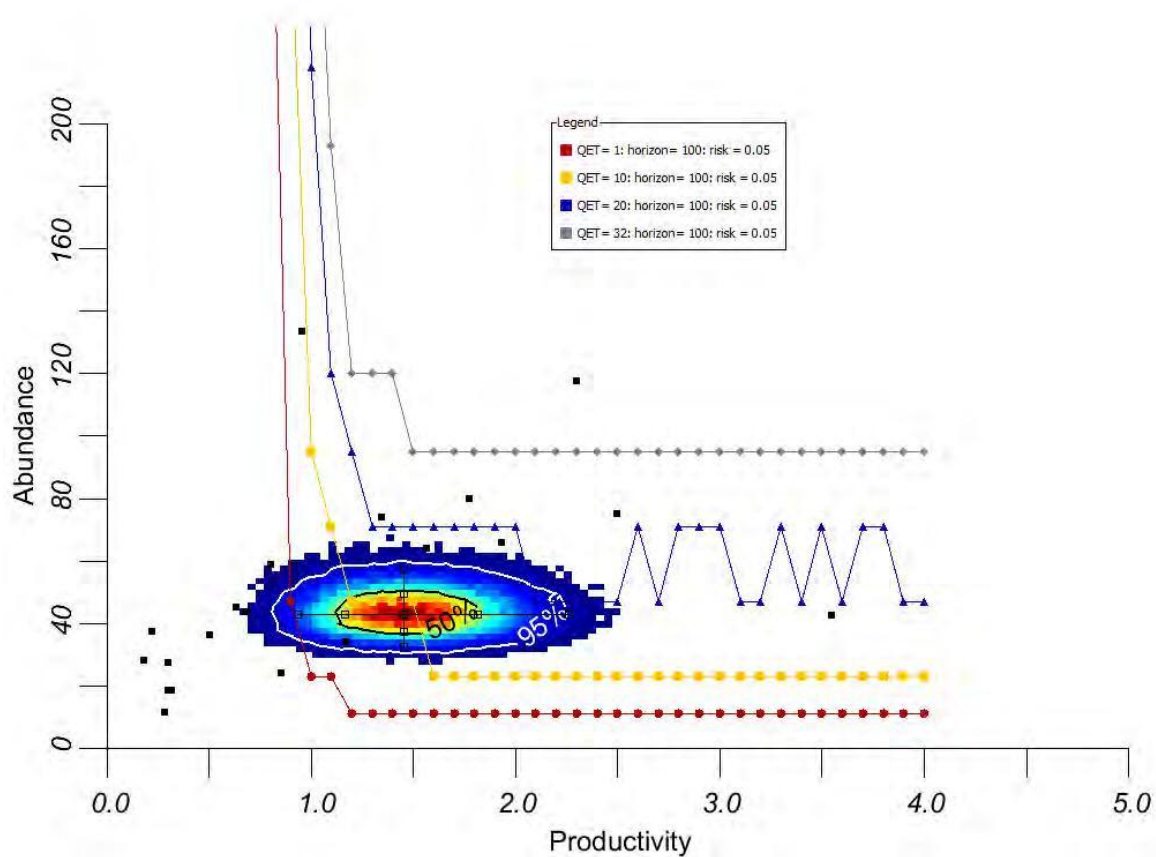


Figure 20. Population viability analysis (PVA) for West Hood Canal winter-run steelhead conducted with the program SPAz (McElhany and Payne 2006). The plot depicts the joint estimate of population abundance (y-axis) and productivity (recruits per spawner, x-axis), represented by the connected open squares (showing the approximate 50% and 95% probability centroids of projected abundance and productivity) overlain by colored probability contours. Actual abundance and productivity data are given by the solid black squares. The joint estimate and the data are overlaid onto four viability curves representing different combinations of abundance and productivity that correspond to a 5% risk of reaching a quasi-extinction threshold (QET) of 1, 10, 20, or 32 spawners (the habitat-based estimate of QET for this population) in a given year over a 100-year time horizon. The PVA relies on a hockey stick recruitment model and uses the geometric mean of running sums of recruits per spawner to estimate productivity over the observed data. Comparison with the values in Table 5 and Figure 2 suggests that this population is at a very high risk of quasi-extinction over the next 100 years.

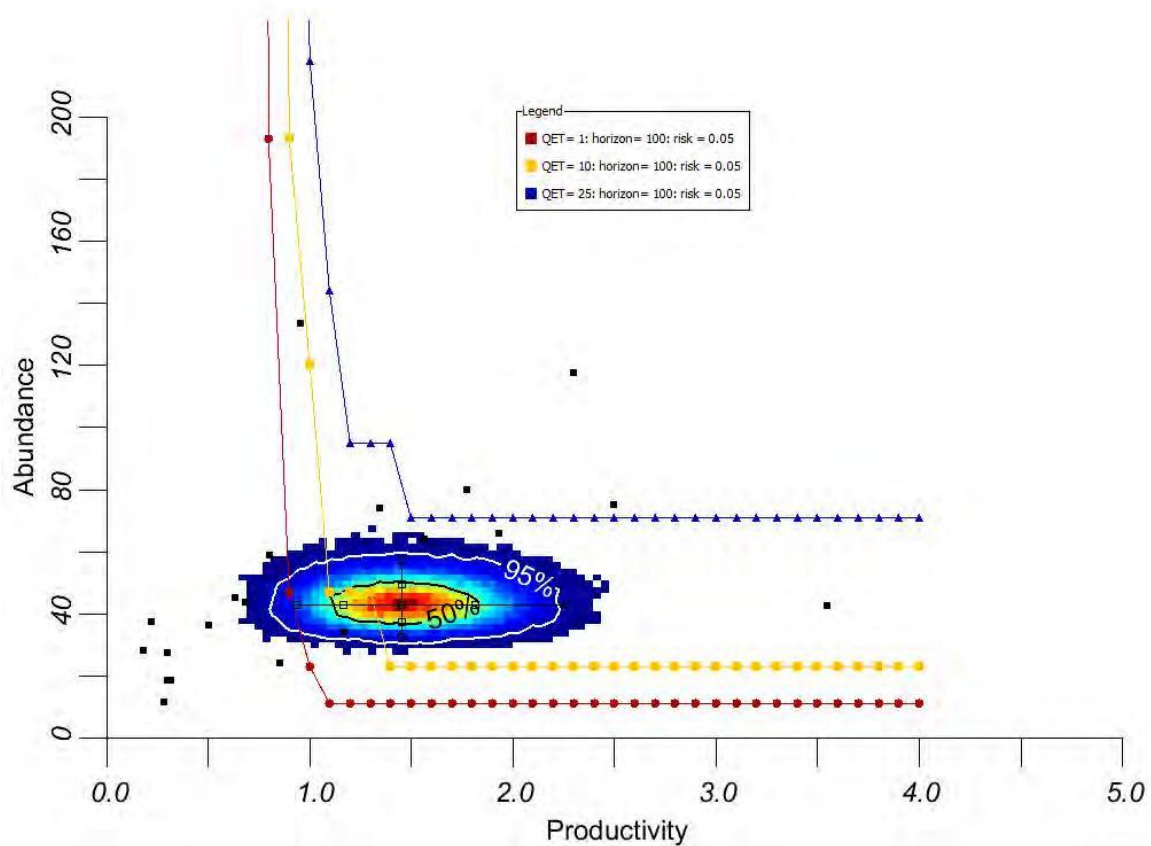


Figure 21. Population viability analysis (PVA) for Strait of Juan de Fuca lowland tributaries (Sequim/Discovery Bay tributaries; data available only for Snow Creek) winter-run steelhead conducted with the program SPAz (McElhany and Payne 2006). The plot depicts the joint estimate of population abundance (y-axis) and productivity (recruits per spawner, x-axis), represented by the connected open squares (showing the approximate 50% and 95% probability centroids of projected abundance and productivity) overlain by colored probability contours. Actual abundance and productivity data are given by the solid black squares. The joint estimate and the data are overlaid onto four viability curves representing different combinations of abundance and productivity that correspond to a 5% risk of reaching a quasi-extinction threshold (QET) of 1, 10, or 25 spawners (the habitat-based estimate of QET for this population) in a given year over a 100-year time horizon. The PVA relies on a hockey stick recruitment model and uses the geometric mean of running sums of recruits per spawner to estimate productivity over the observed data. Comparison with the values in Table 5 and Figure 2 suggests that this population is at a high risk of quasi-extinction over the next 100 years.

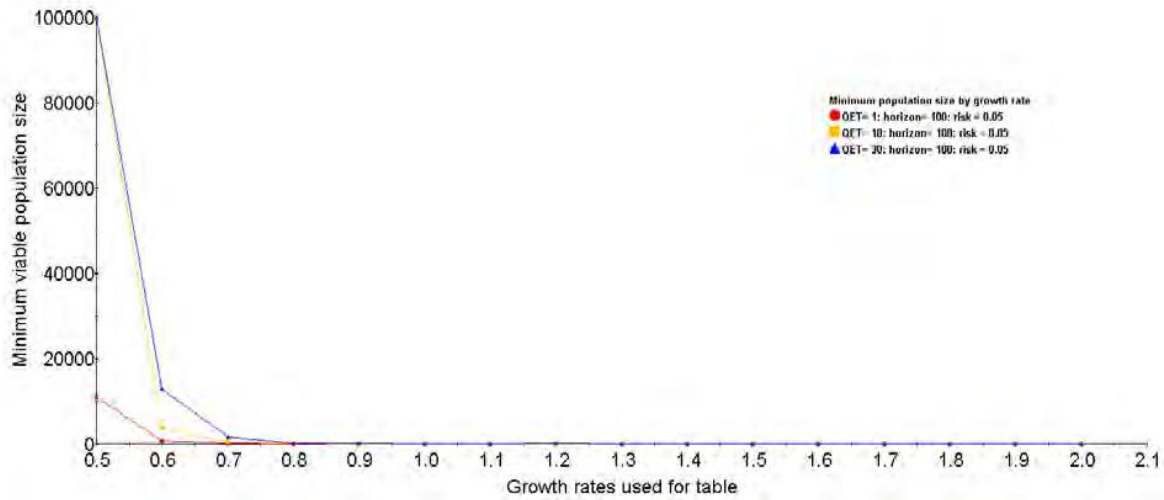


Figure 22. Population viability analysis (PVA) for Dungeness River summer- and winter-run steelhead conducted with the program SPAz (McElhany and Payne 2006). The plot depicts the estimates of minimum viable population size (MVP, y-axis) as a function of population growth rate (x-axis). The estimates of MVP correspond to a 5% risk of reaching a quasi-extinction threshold (QET) of 1, 10, or 30 spawners (the habitat-based estimate of QET for this population) in a given year over a 100-year time horizon. The PVA relies on a random walk with trend model to estimate productivity over the observed data. Comparison with the available abundance data (from the 1980s and 1990s) and the values in Table 5 and Figure 2 suggests that this population is at a very high risk of quasi-extinction over the next 100 years.

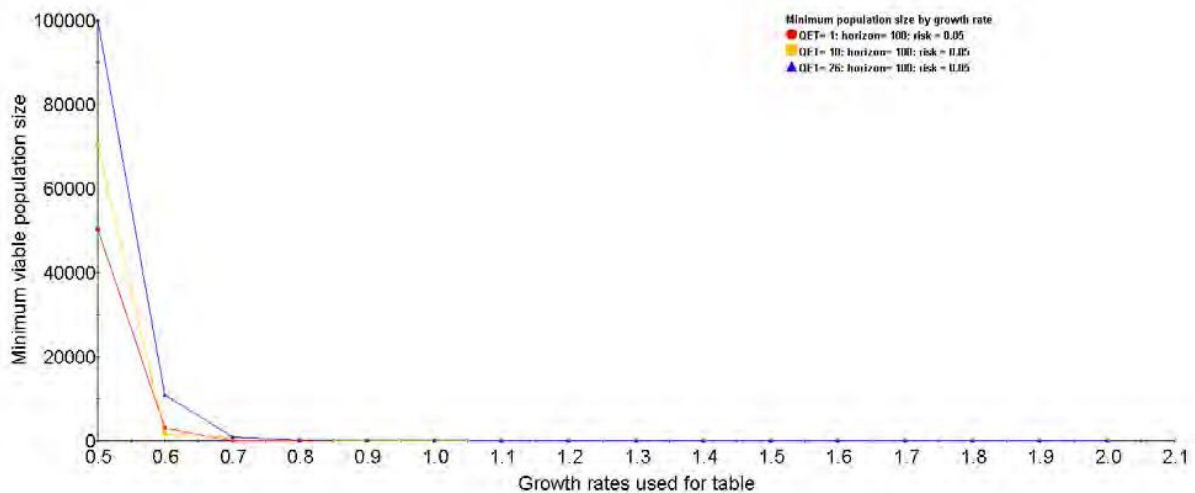


Figure 23. Population viability analysis (PVA) for Strait of Juan de Fuca Independents winter-run steelhead conducted with the program SPAz (McElhany and Payne 2006). The plot depicts the estimates of minimum viable population size (MVP, y-axis) as a function of population growth rate (x-axis). The estimates of MVP correspond to a 5% risk of reaching a quasi-extinction threshold (QET) of 1, 10, or 26 spawners (the habitat-based estimate of QET for this population) in a given year over a 100-year time horizon. The PVA relies on a random walk with trend model to estimate productivity over the observed data. Comparison with the available abundance data (from the 1980s and 1990s) and the values in Table 5 and Figure 2 suggests that this population is at a very high risk of quasi-extinction over the next 100 years.

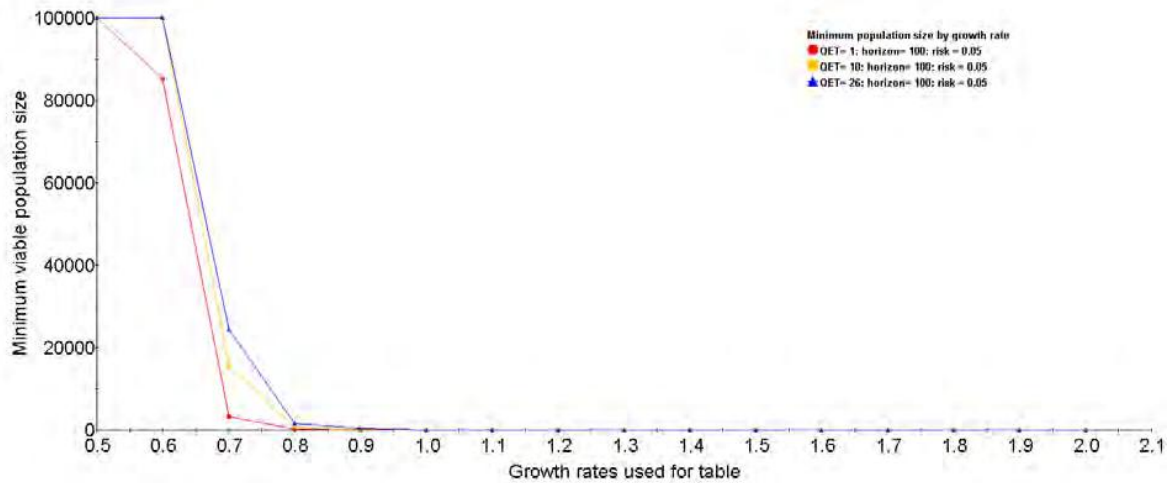


Figure 24. Population viability analysis (PVA) for Morse Creek winter-run steelhead, part of the Strait of Juan de Fuca Independents DIP, conducted with the program SPAz (McElhany and Payne 2006). The plot depicts the estimates of minimum viable population size (MVP, y-axis) as a function of population growth rate (x-axis). The estimates of MVP correspond to a 5% risk of reaching a quasi-extinction threshold (QET) of 1, 10, or 26 spawners (the habitat-based estimate of QET for this population) in a given year over a 100-year time horizon. The PVA relies on a random walk with trend model to estimate productivity over the observed data. Comparison with the available abundance data (from the 1980s and 1990s) and the values in Table 5 and Figure 2 suggests that this population is at a very high risk of quasi-extinction over the next 100 years.

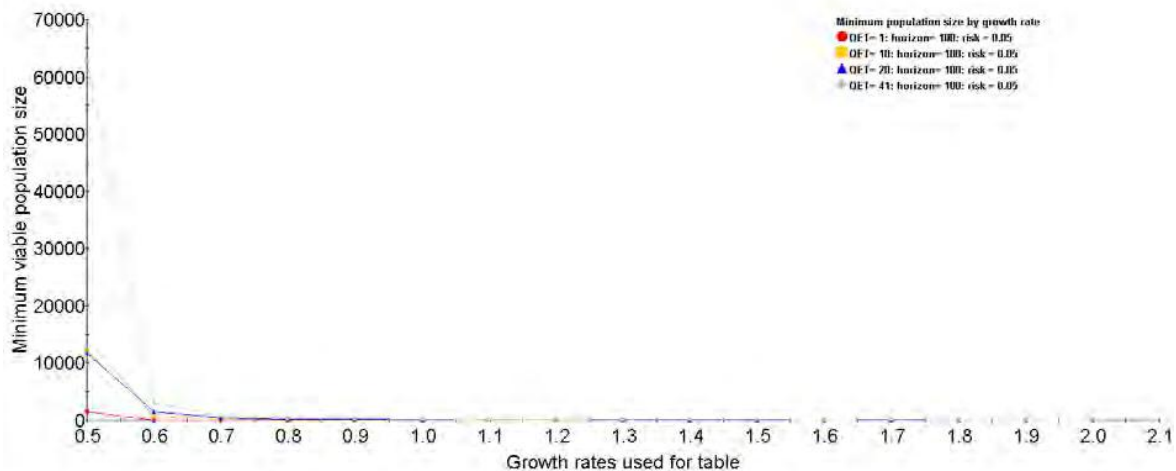


Figure 25. Population viability analysis (PVA) for Elwha River summer- and winter-run steelhead conducted with the program SPAz (McElhany and Payne 2006). The plot depicts the estimates of minimum viable population size (MVP, y-axis) as a function of population growth rate (x-axis). The estimates of MVP correspond to a 5% risk of reaching a quasi-extinction threshold (QET) of 1, 10, 20, or 41 spawners (the habitat-based estimate of QET for this population) in a given year over a 100-year time horizon. The PVA relies on a random walk with trend model to estimate productivity over the observed data. Comparison with the available abundance data (from the 1980s and 1990s) and the values in Table 5 and Figure 2 suggests that this population is at a very high risk of quasi-extinction over the next 100 years.

If we accept the assumptions underlying these analyses as reasonable and conclude that estimates based on index redd counts for these steelhead populations are tightly correlated with total natural spawning abundance (and that for about last 10 years spawning abundance and total run size have been similar), the analyses indicate that the majority (considerably more than half) of steelhead populations in the Puget Sound DPS are at high levels of quasi-extinction risk. These analyses have been applied to populations for which semi-quantitative estimates of abundance and productivity exist (or can be roughly inferred). For populations for which we have no quantitative information, we hypothesize that they would likely show a similar pattern because the few data available for these populations show them either to be very small or to have declined precipitously from historic sizes. The risk of quasi-extinction of steelhead in Puget Sound appears to be highest in the Central and South Puget Sound and the Hood Canal and Strait of Juan de Fuca MPGs. In the Northern Cascades MPG, two of the seven populations that could be evaluated are at high levels of risk of reaching QET. One of these is a summer-run population (Tolt River). For the Central and South Puget Sound MPG, four of the five populations that could be evaluated are at high levels of risk of reaching QET. The populations at high quasi-extinction risk are at risk primarily because of very low productivity (the Lake Washington population is also at very low abundance). For the Hood Canal and Strait of Juan de Fuca MPG, all eight populations appear to be at high levels of risk of reaching QET. These risk assessments may underestimate true risk levels because of the nature of the data available. It is also important to recognize that these analyses do not explicitly incorporate uncertainty into the risk assessment; they do not fully describe a risk “envelope.”

The populations at high QET risk are spread geographically across the DPS. Very little information exists for many populations in the DPS, in particular in Central and South Sound DIPs where steelhead once occurred in abundance in smaller streams and rivers, based largely on punch card data collected by the Washington Department of Game in the first half of the 20th century. Collectively, these analyses provide strong evidence that most steelhead populations in the Puget Sound DPS are at low levels of viability in terms of abundance and productivity.

Population Viability Analysis With Auto-Regressive State-Space Models

The above analyses make some assumptions about population demography that may be too restrictive in evaluating extinction risk. In particular, they assume that the population census data are accurate, and they apply a particular stock-recruitment model and an average estimate of adult age distribution that may not apply to all populations or reflect temporal changes in age structure. In addition, as described above the steelhead data themselves are typically based on indexes of redd counts rather than precise estimates of total run size. Consequently, we also evaluated population viability by applying approaches based on maximum-likelihood estimation to analyze the time series reflecting indices of abundance and infer underlying population dynamics without making such restrictive assumptions. We used the state-space framework described by Hinrichsen and Holmes (2009) and Ward et al. (2010), and implemented in the program MARSS version 2.3 (Multivariate Auto-Regressive State-Space, Holmes and Ward 2011) in the R statistical environment (R Development Core Team 2009), to estimate parameters describing population dynamics over time from basic abundance data. The state-space framework has a distinct advantage in evaluating ecological applications such as time series of abundance because they can accommodate missing data and can account for both intrinsic

biological factors (process error) and measurement error (non-process error) in terms of their contributions to the variability observed in the time series.

State-space models have some other advantages. They explicitly incorporate consideration of uncertainty in forecasts of future population trends, assuming that current conditions persist. They do not require an assumption of a specific underlying demographic structure (e.g., a specific spawner-recruit relationship). The MARSS models used here are fit iteratively to the data via maximum likelihood, using a Kalman filtered Expectation-Maximization (EM) algorithm. This algorithm is especially well suited to dynamic systems where hidden random variables occur in the model. The Kalman filter, which is widely applied to the analysis of time series, uses diffusion approximation methods (see p. 36) to solve for the expected values of the hidden states (of the multivariate auto-regressive processes), conditioned on the data over the entire time series. This approach is appropriate for steelhead abundance data for Puget Sound because these data include primarily observed redd counts, often from index stream reaches, which makes estimation of total abundance challenging.

State-space models have been applied frequently to time series of ecological data because they are able to separate these sources of error, while requiring less information than some other methods (such as estimates of age structure), in the absence of estimates of observation error or replicated observations. Widely used in ecology using both maximum-likelihood and Bayesian frameworks, state-space models have focused primarily on analysis of single time-series (e.g., Staples et al. 2004, Dennis et al. 2006) but are capable of handling higher-dimension data as well. The basic form of a univariate state-space model with Gaussian (normally distributed) errors is:

$$x_t = x_{t-1} + \mu + e_t$$

which is closely related to a stochastic, discrete-time Gompertz model (Ives et al. 2003, Dennis et al. 2006). In these equations x_t is abundance in year t , x_{t-1} is abundance in the previous year, μ is a parameter estimating population growth rate (e.g., intrinsic rate of increase), and e_t is the process error in year t (e_t is distributed multivariate normal [MVN] with mean = 0 and variance = σ^2). The term x_{t-1} can be multiplied by a parameter to reflect the strength of density dependence. The multivariate version of the MARSS model, which can accommodate n multiple populations, takes the form (Holmes and Ward 2011):

$$\mathbf{x}_t = \mathbf{x}_{t-1} + \boldsymbol{\mu} + \mathbf{e}_t$$

$$\mathbf{y}_t = \mathbf{a} + \mathbf{Z}\mathbf{x}_t + \boldsymbol{\varepsilon}_t$$

The first of these equations models the population process, and the second the observation process. In these equations, \mathbf{x}_t and \mathbf{x}_{t-1} are $n \times 1$ vectors of true population sizes in years t and $t-1$, $\boldsymbol{\mu}$ is an n -element vector of population growth rates, \mathbf{e}_t is an n -element vector of process errors in year t (\mathbf{e}_t is distributed MVN with mean = 0 and covariance matrix \mathbf{Q}), \mathbf{y}_t is an n -element vector of observations in year t , \mathbf{a} is an n -element vector that represents bias in observation errors, \mathbf{Z} is an $n \times n$ matrix of 0s and 1s that translates the n sizes in year t to n observations in year t , and $\boldsymbol{\varepsilon}_t$

is an n -element vector of observation errors in year t (ϵ_t is distributed MVN with mean = 0 and covariance matrix R).

The state-space based PVAs were computed from the same data used for the SPAz analyses: estimates of natural escapement (rather than run size) for most of the Puget Sound steelhead populations. The PVAs provide estimates of process and measurement error, and use these to compute probabilities of extinction risk and associated confidence intervals. Process error is particularly significant in this context because it reflects variability resulting from intrinsic natural processes, such as demographic stochasticity. The PVAs estimated by MARSS do not account for density dependent effects on productivity and abundance, but this is a frequent assumption of PVA when applied to small or declining populations. If habitat capacity is changing or if Allee effects expressed at low abundance are important influences on population trends, they are not detected by these methods. Although missing data are not strictly limiting to the approach (so long as sufficient data are present in the time series), the PVAs do assume that a population is stationary through time, i.e., trends are constant and environmental conditions affecting mortality and production (including harvest) persist. Because it is a state-space approach, a MARSS analysis can provide more precision in estimates of trend because observation error is explicitly included in the analysis (ignoring observation error tends to lead to inflated estimates of process error). The state-space framework partitions the total variance into process and observation variance, which can yield more constrained, realistic estimates of process error and, as a result, more precise estimates of viability metrics. The model also allows estimation of a risk “envelope” that directly incorporates uncertainty resulting from the variability inherent in the time series into the risk projection.

Some concern has been expressed with this approach (and with the slope method), centering on potential bias in overestimating the precision of population growth rate from the analysis of trend in abundance data. However, this concern is based primarily on an assumption that an analysis is estimating the observation variance, not the process variance. The slope and state-space (e.g., MARSS) methods separate process and observation errors and estimate the process variance, so that extinction risk can be forecast from a model of population variability that is free of observation variance.

An example of the results of a PVA using MARSS applied to a time series of population abundance data is shown in Figure 26. The key features and assumptions of this analysis include the following:

- The state-space model uses a diffusion approximation approach;
- No specific demographic structure (e.g., age structure) is assumed;
- Process error due to demographic stochasticity, etc., is partitioned from observation error, and estimated;
- Density independence of the population’s trajectory and stationarity (meaning that an underlying trend that is a function solely of time can be removed, leaving a stationary process) are assumed; and
- Dispersions around estimates are obtained from a Hessian matrix (a numerically estimated square matrix of second-order partial derivatives of the function describing the population trajectory).

In this example, the abundance data are plotted over time with the fitted state-space estimate at top left; MARSS estimated the annual change in abundance (μ_{est}) at -0.057, reflecting a decline of 5.7% per year and corresponding to a growth rate ($\lambda = e^{\mu_{\text{est}}}$) of 0.944. A quasi-extinction threshold (QET) of 10% of the current abundance (21 in 2009 and 10 in 2010) was used to plot the probability of reaching a QET of 2 over time; MARSS estimated that this probability reached 80% by about year 60, and a plot of the probability density function (PDF) of the time to reach this threshold (middle plot at left) shows the distribution of this time to reach QET, given that it *is* reached. At middle right is a plot of the probability of reaching QET within 100 years as a function of variation in current abundance N_e (the red vertical line shows the actual data).

Several sample projections for the population as a function of years into the future are plotted at lower left, showing low variability among the projections. Finally, at lower right MARSS has plotted a risk envelope, along with the estimates of annual change in abundance (μ_{est}) and process error (Q_{est} , or s_p^2 —s_p² in the figure—a reflection of variability resulting from intrinsic natural processes, such as demographic stochasticity). In this plot, the y-axis ($x_e = \log_{10}(N_0/N_e)$) can be considered to represent the expected rate of decline in abundance from current (N_e) to that at the end of the projection (N_0), plotted against the time projection in years on the x-axis. The red and green hatched areas represent parameter spaces where rates of population decline over specific time periods are estimated with 95% or higher confidence, with the green area reflecting minimum time horizons for specified rates of decline, and the red area reflecting maximum time horizons for those rates. The gray areas encompass the uncertainty in estimating probabilities of reaching the specified quasi-extinction threshold. So, for example, in this plot one could conclude with 95% confidence that an expected rate of decline of 50% in this population ($y = -1.0$) is not likely to occur within 100 years; a rate of decline of 90% is not likely before 8-10 years (and a decline of 99% is not likely before 18-20 years). However, beyond the near term the precise level of extinction risk is uncertain, and highly uncertain after about 20 years (for a specified decline of 90%).

Applying Stochastic PVA to Puget Sound Steelhead Populations—We applied autoregressive state space models to abundance time series for 16 Puget Sound steelhead populations identified as DIPs. The next several multi-plots summarize MARSS analyses that evaluate the trends in estimated wild abundance for putative DIPs of Puget Sound steelhead over the entire estimated escapement data series, project population trends 100 years into the future, and where possible evaluate these projections against specified viability criteria.

For each population, the graphs in this section provide two plots summarizing the population viability analyses (PVAs). The left panel plots the observed counts against year, giving the MARSS maximum-likelihood estimate of fit to the abundance data (red curve), the estimated long-term population growth rate (u_{est} , equivalent to $\ln(\lambda)$), and the estimate of process error (Q_{est}). The right panel plots the probability that the population will reach a particular quasi-extinction threshold (QET) abundance within the next 100 years (with approximate 95% confidence intervals). The QETs applied here (Table 7) are based on a low average of 24 spawners for Snow Creek winter-run steelhead measured over four consecutive years, then scaling by the ratio of the estimate of intrinsic potential for the watershed supporting the

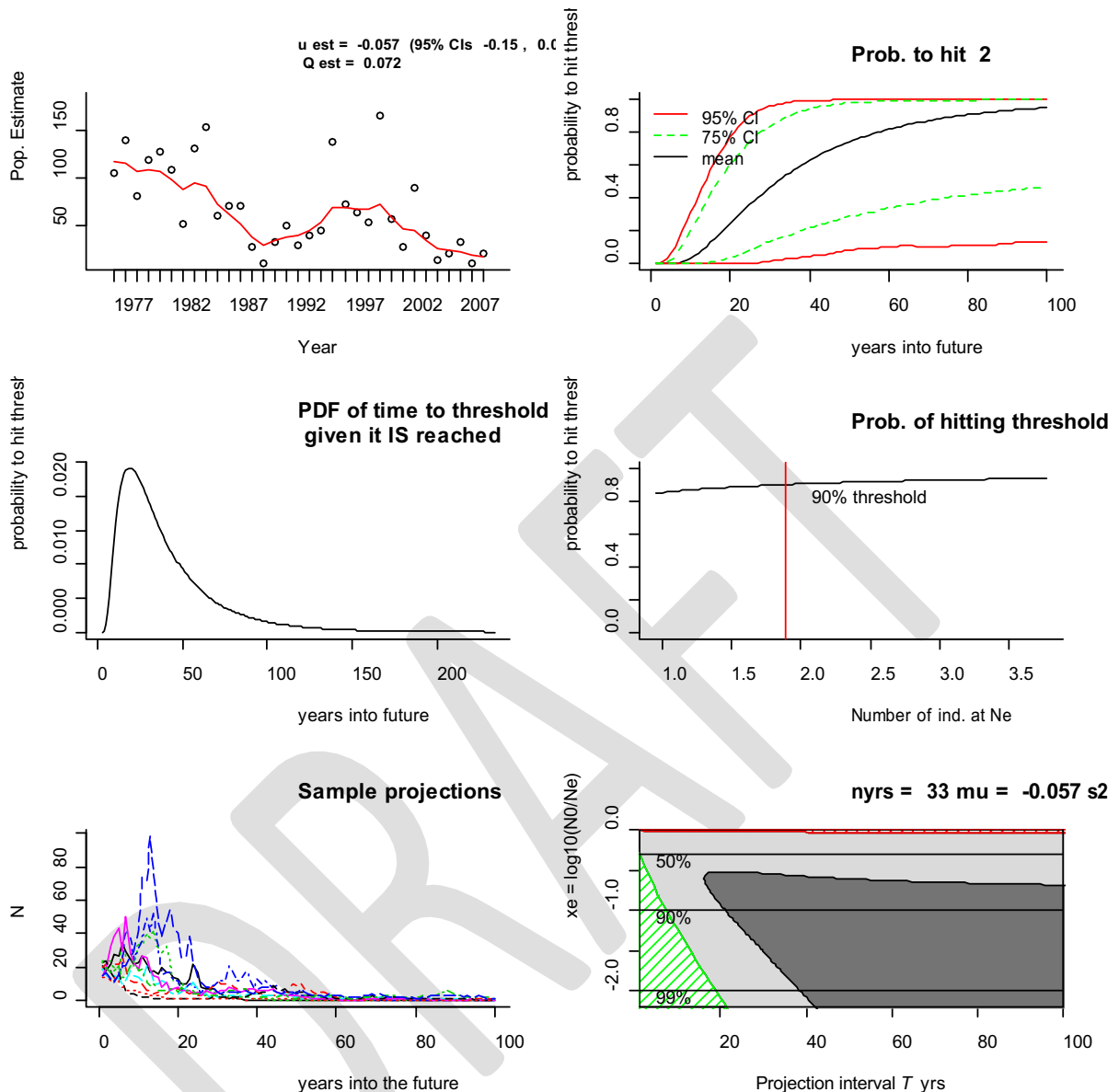


Figure 26. Population viability analysis output from MARSS (Holmes and Ward 2011) as applied to a time series of wild steelhead population abundance (Snow Creek winter-run steelhead on the Olympic Peninsula in Washington). Top left: time series of abundance data, showing estimated annual change in abundance (u_{est} , or $\ln(\lambda)$) and process error (Q_{est} , or s_p^2). Top right: estimated probability of reaching a quasi-extinction threshold (QET) of 10% of the current abundance (21 in 2009 and 10 in 2010). Middle left: plot of the probability density function (PDF) of the time to reach QET, given that it *is* reached. Middle right: plot of the probability of reaching QET within 100 years as a function of variation in current abundance N_e . Lower left: sample projections for the population as a function of years into the future. Lower right: plot of the risk envelope (Ellner and Holmes 2008), showing the expected rate of decline in abundance as a function of time projection in years. The red and green hatched areas represent parameter spaces where rates of population decline over specific time periods are estimated with 95% or higher confidence, with the green area reflecting minimum time horizons for specified rates of decline, and the red area reflecting maximum time horizons for those rates. The gray areas encompass the uncertainty envelope for estimating extinction risk ($P < 0.95$).

candidate DIP (intrinsic potential is the area of habitat suitable for steelhead rearing or spawning, at least under historical conditions) to that of Snow Creek. The Snow Creek winter-run steelhead population was chosen because it is a natural anadromous population with sustained wild production in a relatively stable watershed, and provides accurate estimates of adult escapement, smolt production, and intrinsic potential to serve as a basis for estimating QETs throughout the Puget Sound steelhead DPS.

Table 7. Estimated quasi-extinction thresholds (QET) for adult steelhead in Puget Sound. SSH, summer-run steelhead; WSH, winter-run steelhead. Intrinsic potential is total area across habitat categories suitable for steelhead use (see text).

Puget Sound steelhead DIP	Intrinsic potential (m ²)	Estimated QET
Drayton Harbor tribs	597409	26
Nooksack R WSH	11119563	73
SF Nooksack R SSH	795382	27
Samish R/Bellingham Bay tribs WSH	1616020	31
Nookachamps R WSH	870466	27
Skagit R WSH/SSH	30038382	157
Baker R WSH/SSH	2850284	36
Sauk R WSH/SSH	17894638	103
Stillaguamish R WSH	9814400	67
Deer Cr SSH	1575597	31
Canyon Cr SSH	91697	24
Snohomish R/Skykomish R WSH	11175208	73
Pilchuck R WSH	2446486	34
Snoqualmie R WSH	7738534	58
NF Skykomish R SSH	414682	25
Tolt R SSH	231883	25
N Lk Washington/Sammamish R WSH	2840214	36
Cedar R WSH/SSH	2545580	35
Green R WSH	10170477	69
Puyallup R/Carbon R WSH	7779880	58
White R WSH	9070004	64
Nisqually R WSH	7069169	55
South Sound WSH	4253116	42
E Kitsap Penin WSH	256617	25
E Hood Canal WSH	676924	27
South Hood Canal WSH	1496762	30
Skokomish R WSH	6041453	50
W Hood Canal WSH	1815949	32
SJF Lowland Tributaries Bay WSH	228335	25
Dungeness R WSH/SSH	1449576	30
SJF Independents WSH	627758	26
Elwha R WSH/SSH	3915221	41

Additional PVA results for each DIP, including the plots provided in this section, are described in Appendix A, where a full set of MARSS plots is provided.

Figure 27 depicts population trends for Samish River winter-run steelhead. Steelhead counts (primarily redd counts) in the Samish River have varied considerably with a decline over the past decade but have generally declined. The estimated mean population growth rate (u_{est}) is 0.048 ($\lambda = 1.049$) and process error (Q_{est}) is 0.260, with no significant evidence for a population trend. Assuming that these counts are a reasonable reflection of spawner abundance, the estimated probability that this steelhead population would decline to a QET of 31 fish is relatively low—about 30% within 100 years.

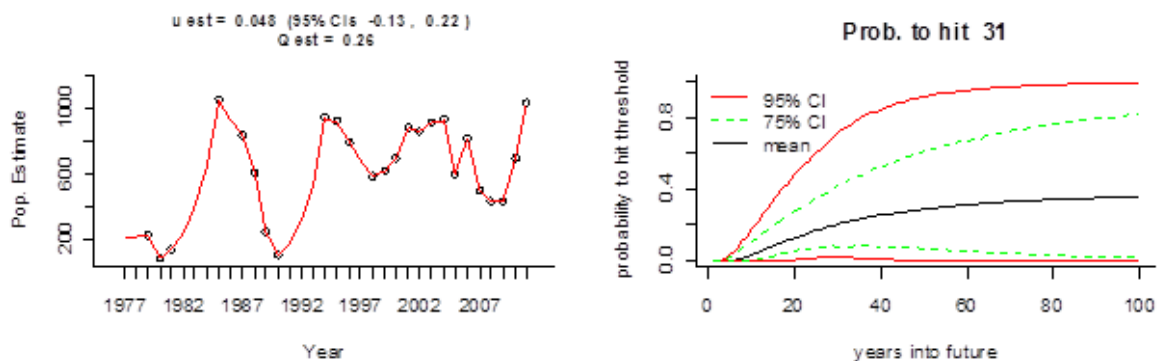


Figure 27. Summary of a MARSS-based (Holmes and Ward 2011) population viability analysis (PVA) for Samish River winter-run steelhead. See text for description.

Figure 28 depicts population trends for Skagit River summer- and winter-run steelhead. Steelhead counts in the Skagit River have been highly variable but have declined since the low 1980s. The estimated mean population growth rate is -0.002 ($\lambda = 0.998$) and process error is 0.033, with no significant evidence for a population trend. Assuming that these counts are a reasonable reflection of spawner abundance, the estimated probability that this steelhead population would decline to a QET of 157 fish is very low—less than 10% within 100 years.

Figure 29 depicts population trends for Stillaguamish River winter-run steelhead. Steelhead counts in the Stillaguamish River (represented by North Fork Stillaguamish River counts only) have declined steadily since the early 1980s. The estimated mean population growth rate is -0.075 ($\lambda = 0.928$) and process error is < 0.001 , with clear evidence of a decline (though the significance could not be calculated). Assuming that these counts are a reasonable reflection of spawner abundance, the estimated probability that this steelhead population would decline to a QET of 67 fish is high—about 90% within 25 years.

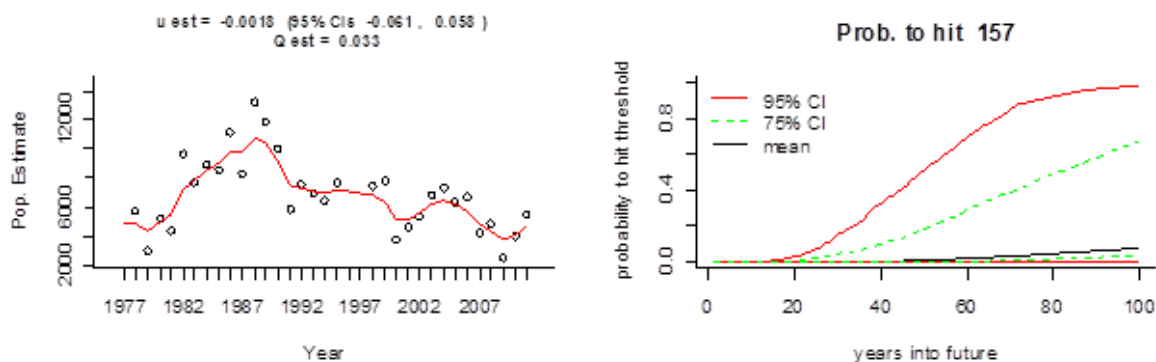


Figure 28. Summary of a MARSS-based (Holmes and Ward 2011) population viability analysis (PVA) for Skagit River summer- and winter-run steelhead. See text for description.

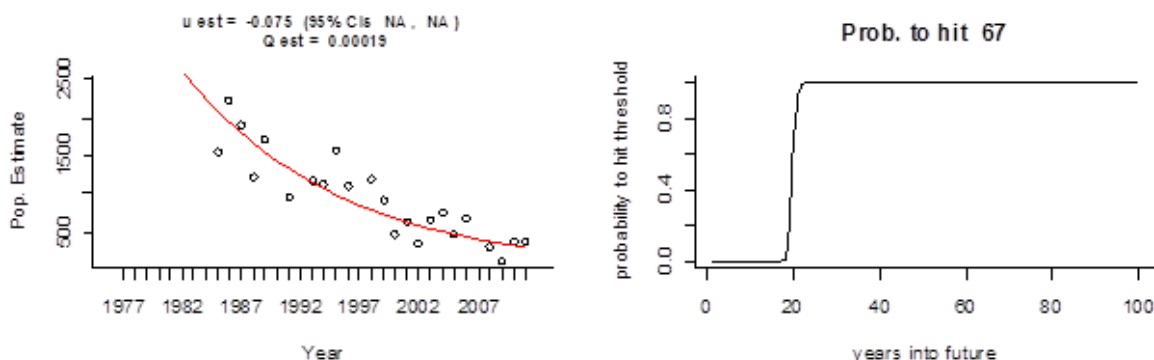


Figure 29. Summary of a MARSS-based (Holmes and Ward 2011) population viability analysis (PVA) for Stillaguamish River winter-run steelhead. See text for description.

Figure 30 depicts population trends for Pilchuck River winter-run steelhead. Steelhead counts in the Pilchuck River have declined detectably from levels during the late 1980s and early 1990s, and been relatively low in most years since 2000. The estimated mean population growth rate of -0.006 ($\lambda = 0.994$) and process error is 0.097 , with no significant evidence for a population trend. Assuming that these counts are a reasonable reflection of spawner abundance, the estimated probability that this steelhead population would decline to a QET of 34 fish is relatively low—about 40% within 100 years.

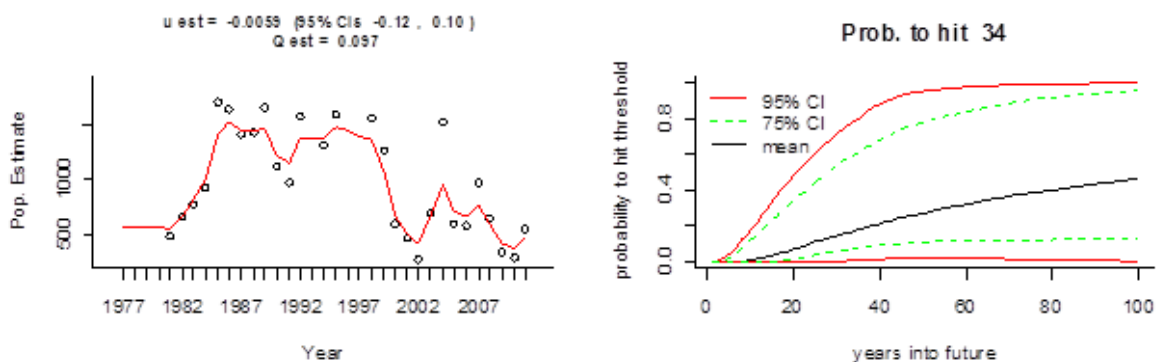


Figure 30. Summary of a MARSS-based (Holmes and Ward 2011) population viability analysis (PVA) for Pilchuck River winter-run steelhead. See text for description.

Figure 31 depicts population trends for Snohomish River winter-run steelhead. Steelhead counts in the Snohomish River have generally declined since the early 1990s but have varied widely. The estimated mean population growth rate is -0.005 ($\lambda = 0.995$) and process error is 0.120 with no significant evidence for a population trend. Assuming that these counts are a reasonable reflection of spawner abundance, the estimated probability that this steelhead population would decline to a QET of 73 fish is low—about 40% within 100 years.

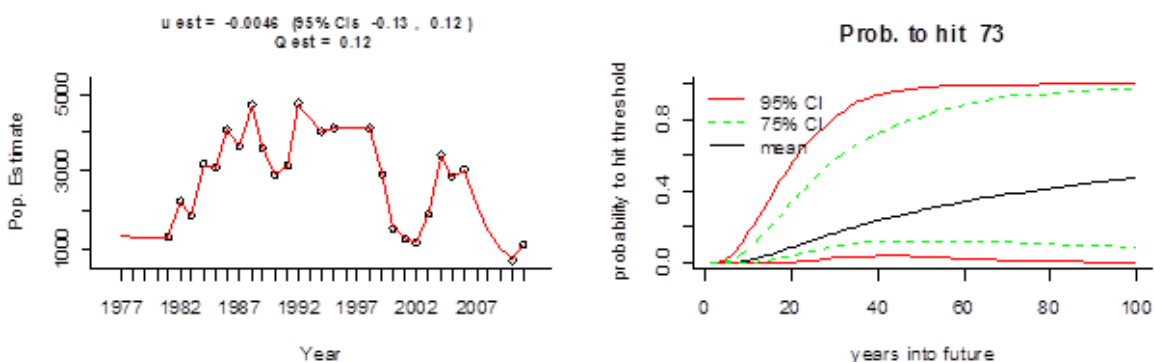


Figure 31. Summary of a MARSS-based (Holmes and Ward 2011) population viability analysis (PVA) for Snohomish River winter-run steelhead. See text for description.

Figure 32 depicts population trends for Snoqualmie River winter-run steelhead. Steelhead counts in the Snoqualmie River have declined since the early 1990s. The estimated mean population growth rate is -0.027 ($\lambda = 0.973$) and process error is 0.030 , with no significant evidence for a population trend (although a decline is evident). Assuming that these counts are a reasonable reflection of spawner abundance, the estimated probability that this steelhead population would decline to a QET of 58 fish is relatively high—nearly 70% within 100 years.

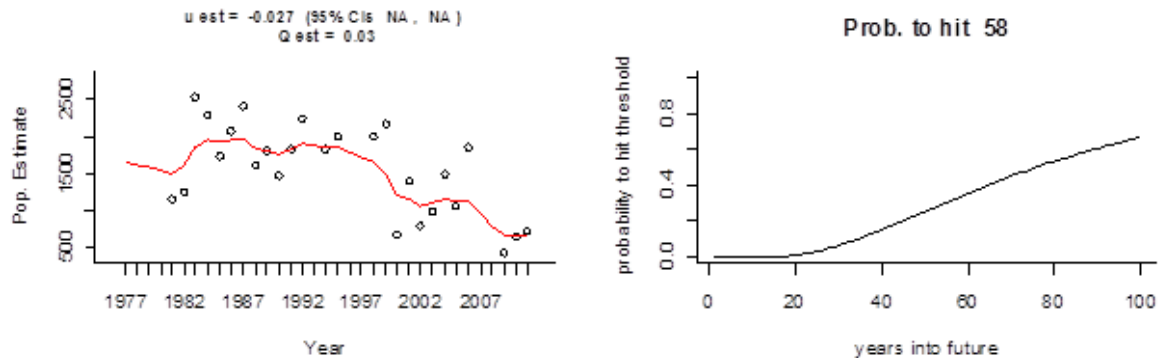


Figure 32. Summary of a MARSS-based (Holmes and Ward 2011) population viability analysis (PVA) for Snoqualmie River winter-run steelhead. See text for description.

Figure 33 depicts population trends for Tolt River summer-run steelhead. Steelhead counts in the Tolt River have varied since the 1980s, declining from a modest high in the late 1990s. The estimated mean population growth rate is -0.013 ($\lambda = 0.987$) and the process error is 0.077 , with no significant evidence for a population trend. Assuming that these counts are a reasonable reflection of spawner abundance, the estimated probability that this steelhead population would decline to a QET of 25 fish is high—about 80% within 100 years.

Figure 34 depicts population trends for Cedar River summer- and winter-run steelhead. Steelhead counts in the Lake Washington watershed, including the Cedar River, have declined sharply since the early 1980s and have been very low since the early 1990s. The estimated mean population growth rate is -0.210 ($\lambda = 0.811$) and process error is 0.280 , with clear evidence for a population decline. Assuming that these counts are a reasonable reflection of spawner abundance, the estimated probability that this steelhead population would decline to a QET of 36 fish is high—at least 90% within the next few years. Note that this population's abundance is nearly at this level already.

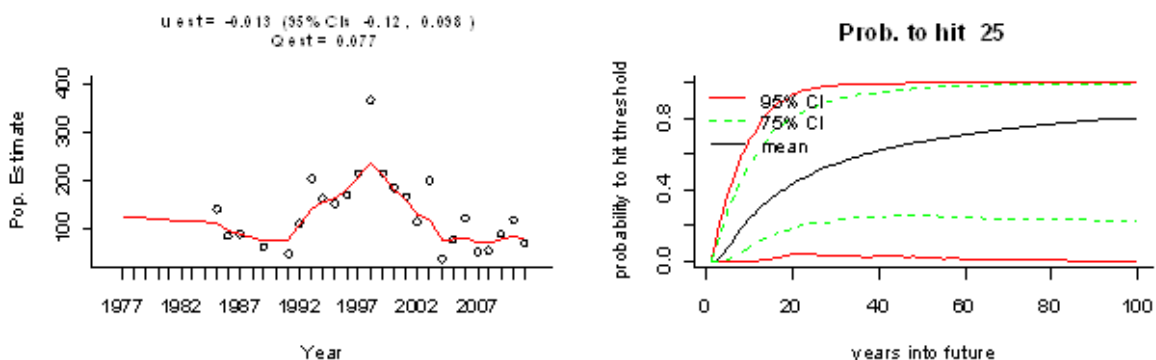


Figure 33. Summary of a MARSS-based (Holmes and Ward 2011) population viability analysis (PVA) for Tolt River summer-run steelhead. See text for description.

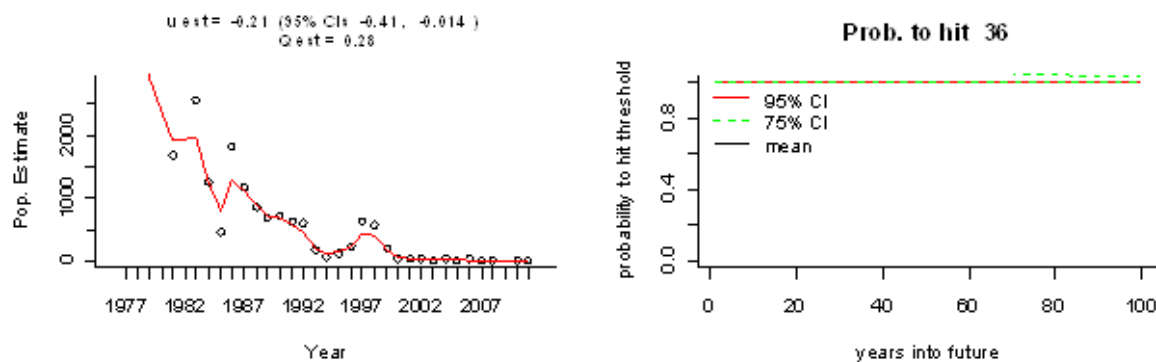


Figure 34. Summary of a MARSS-based (Holmes and Ward 2011) population viability analysis (PVA) for Cedar River summer- and winter-run steelhead. See text for description.

Figure 35 depicts population trends for Green River winter-run steelhead. Steelhead counts in the Green River have been variable but have exhibited a clear decline in recent years. The estimated mean population growth rate is -0.018 ($\lambda = 0.982$) and process error is 0.066 , with no clear evidence for a population trend. Assuming that these counts are a reasonable reflection of spawner abundance, the estimated probability that this steelhead population would decline to a QET of 69 fish is moderately high—about 50% within 100 years.

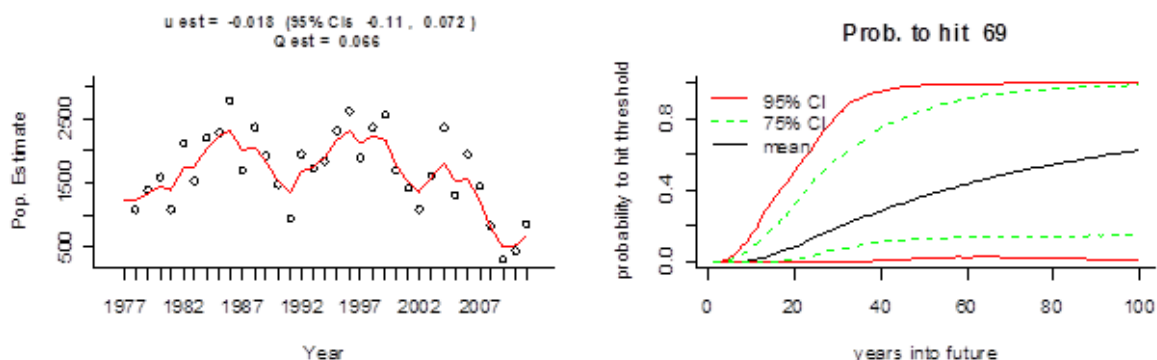


Figure 35. Summary of a MARSS-based (Holmes and Ward 2011) population viability analysis (PVA) for Green River winter-run steelhead. See text for description.

Figure 36 depicts population trends for Puyallup/Carbon River winter-run steelhead. Steelhead counts in the Puyallup River have declined steadily since the 1980s. The estimated mean population growth rate is -0.071 ($\lambda = 0.931$) and process error is <0.001 , with clear evidence for a declining trend (although the significance of the trend could not be calculated). Assuming that these counts are a reasonable reflection of spawner abundance, the estimated probability that this steelhead population would decline to a QET of 58 fish is high—about 90% within 30 years.

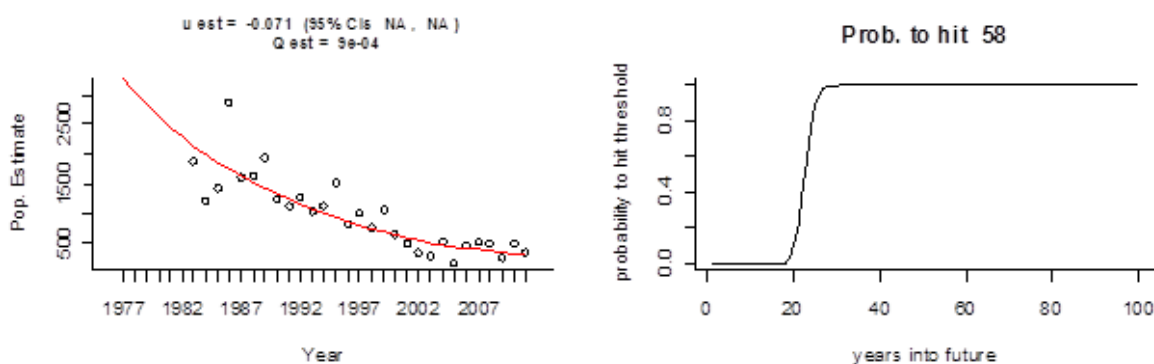


Figure 36. Summary of a MARSS-based (Holmes and Ward 2011) population viability analysis (PVA) for Puyallup/Carbon River winter-run steelhead. See text for description.

Figure 37 depicts population trends for White River winter-run steelhead. Steelhead counts in the White River have declined steadily since the 1980s. The estimated mean population growth rate is -0.003 ($\lambda = 0.997$) and process error is 0.055 , with no significant evidence for a population trend. Assuming that these counts are a reasonable reflection of spawner abundance, the estimated probability that this steelhead population would decline to a QET of 64 fish is relatively low—about 40% within 100 years.

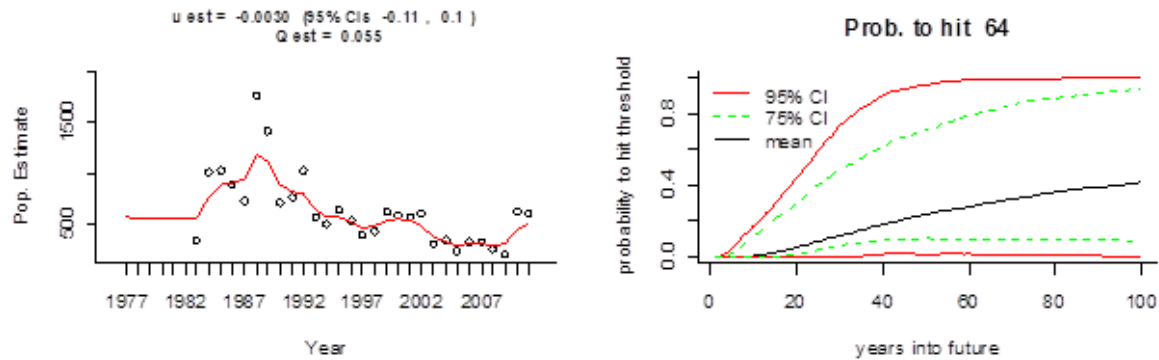


Figure 37. Summary of a MARSS-based (Holmes and Ward 2011) population viability analysis (PVA) for White River winter-run steelhead. See text for description.

Figure 38 depicts population trends for Nisqually River winter-run steelhead. Steelhead counts in the Nisqually River declined steadily since about 1990 and have remained low since then. The estimated mean population growth rate is -0.075 ($\lambda = 0.928$) and process error is <0.001 , with clear evidence of a declining trend (although its significance could not be calculated). Assuming that these counts are a reasonable reflection of spawner abundance, the estimated probability that this steelhead population would decline to a QET of 55 fish is high—about 90% within 25 years.

Figure 39 depicts population trends for South Hood Canal winter-run steelhead, represented by data for the Tahuya and Union rivers only. Steelhead counts in South Hood Canal declined steadily since the late 1990s. The estimated mean population growth rate is -0.097 ($\lambda = 0.908$) and process error is 0.049 , with clear evidence of a declining trend (although its significance could not be calculated). Assuming that these counts are a reasonable reflection of spawner abundance, the estimated probability that this steelhead population would decline to a QET of 30 fish is high—about 90% within 20 years.

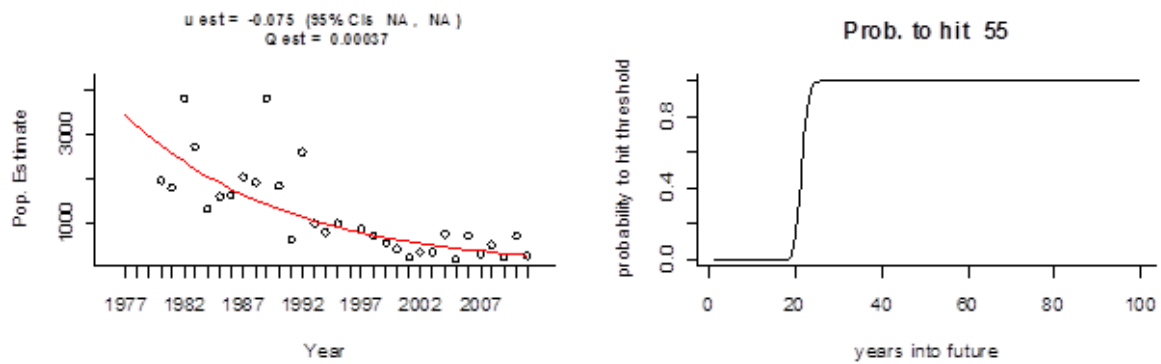


Figure 38. Summary of a MARSS-based (Holmes and Ward 2011) population viability analysis (PVA) for Nisqually River winter-run steelhead. See text for description.

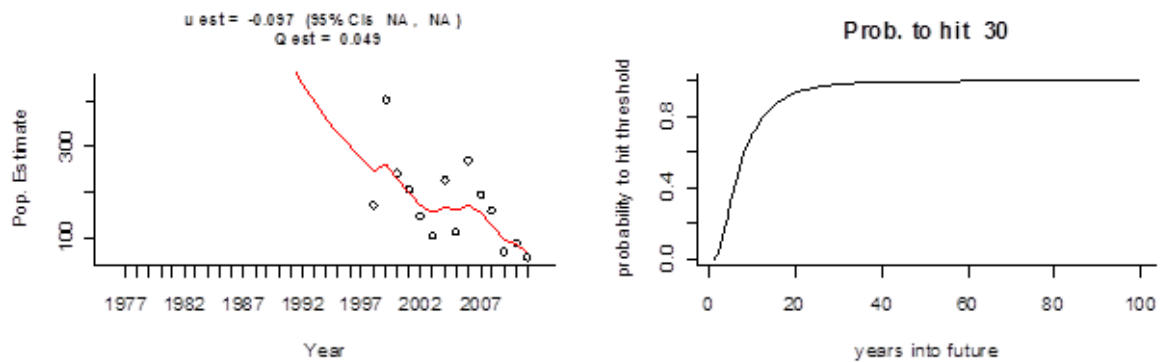


Figure 39. Summary of a MARSS-based (Holmes and Ward 2011) population viability analysis (PVA) for South Hood Canal (including the Dewatto and Union rivers) winter-run steelhead. See text for description.

Figure 40 depicts population trends for Tahuya River winter-run steelhead, which we analyzed because of the longer time series available compared to Tahuya and Union rivers combined data. Steelhead counts in the Tahuya River have varied and often been quite low but there has been no distinct trend since the 1980s. The estimated mean population growth rate is -0.016 ($\lambda = 0.984$) and process error is 0.083, with no significant evidence for a population trend. Assuming that these counts are a reasonable reflection of spawner abundance, the estimated

probability that this steelhead population would decline to a QET of 21 fish is relatively high—over 80% within 100 years.

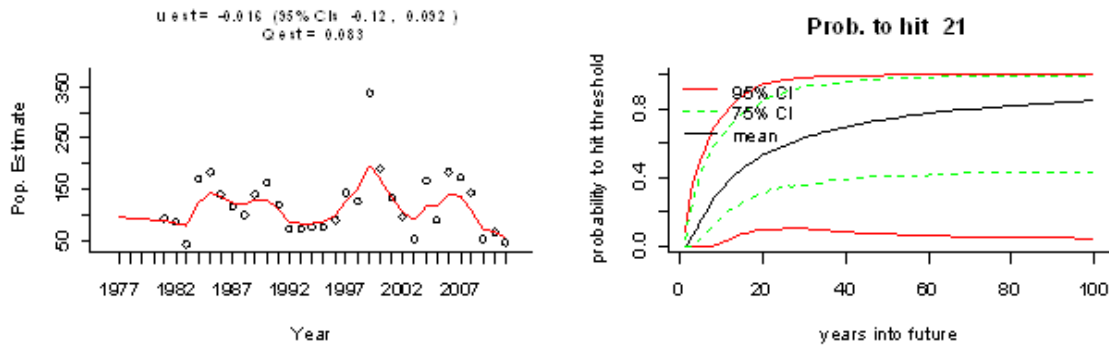


Figure 40. Summary of a MARSS-based (Holmes and Ward 2011) population viability analysis (PVA) for Tahuya River winter-run steelhead. See text for description.

Figure 41 depicts population trends for East Hood Canal winter-run steelhead, represented by Dewatto River data only. Steelhead counts in East Hood Canal have varied and often been quite low but there has been no distinct trend since the 1980s. The estimated mean population growth rate is 0.006 ($\lambda = 1.006$) and process error is < 0.001 , with no significant evidence for a population trend. Assuming that these counts are a reasonable reflection of spawner abundance, the estimated probability that this steelhead population would decline to a QET of 27 fish is relatively low—about 40% within 100 years.

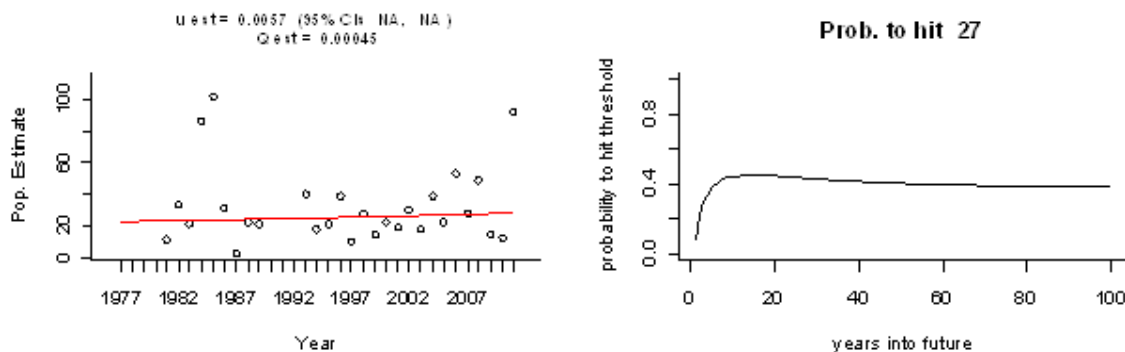


Figure 41. Summary of a MARSS-based (Holmes and Ward 2011) population viability analysis (PVA) for East Hood Canal winter-run steelhead, represented by Dewatto River data only. See text for description.

Figure 42 depicts population trends for Skokomish River winter-run steelhead. Steelhead counts in the Skokomish River have declined since the 1980s. The estimated mean population growth rate is -0.029 ($\lambda = 0.971$) and process error is 0.042 , with no significant evidence for a population trend. Assuming that these counts are a reasonable reflection of spawner abundance, the estimated probability that this steelhead population would decline to a QET of 50 fish is relatively high—over 70% within 100 years.

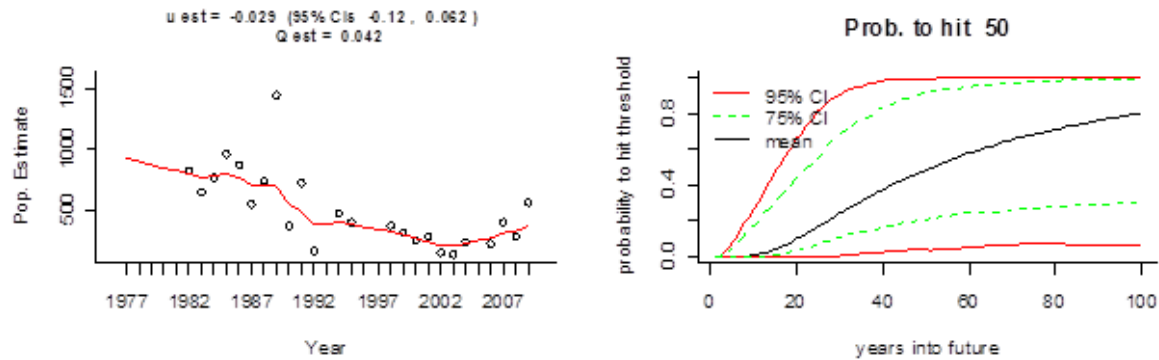


Figure 42. Summary of a MARSS-based (Holmes and Ward 2011) population viability analysis (PVA) for Skokomish River winter-run steelhead. See text for description.

Figure 43 depicts population trends for West Hood Canal winter-run steelhead. Steelhead counts in West Hood Canal have tended to increase since the mid 1990s but variability in abundance has been high. The estimated mean population growth rate is 0.035 ($\lambda = 1.096$) and process error is 0.048 , with no significant evidence for a population trend over this short time series. Assuming that these counts are a reasonable reflection of spawner abundance, the estimated probability that this steelhead population would decline to a QET of 32 fish is low—less than 20% within 100 years. One issue with this analysis is the inclusion of supplementation fish in the returns for the Hamma Hamma River, where the contribution of local-stock hatchery fish to overall abundance is out of proportion to the wild population size or basin size.

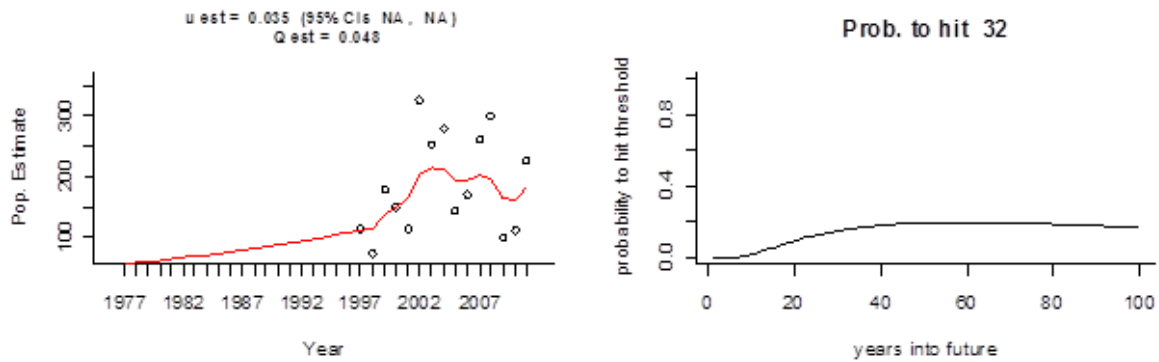


Figure 43. Summary of a MARSS-based (Holmes and Ward 2011) population viability analysis (PVA) for West Hood Canal winter-run steelhead. See text for description.

Figure 44 depicts population trends for Strait of Juan de Fuca lowland tributaries winter-run steelhead, represented by Snow Creek data only. Steelhead counts have varied considerably since the 1980s but generally have declined and recently have been very low. The estimated mean population growth rate is -0.054 ($\lambda = 0.947$) and process error is 0.074 , with no significant evidence for a population trend. Assuming that these counts are a reasonable reflection of spawner abundance, the estimated probability that this steelhead population would decline to a QET of 25 fish is high—about 90% within 100 years.

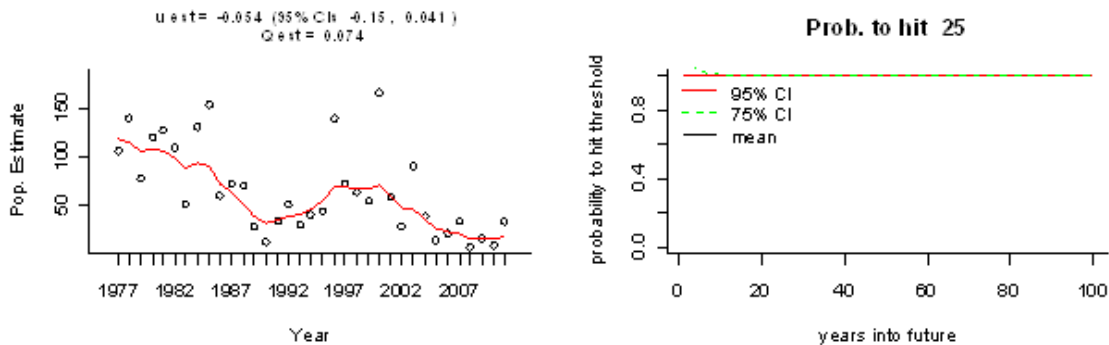


Figure 44. Summary of a MARSS-based (Holmes and Ward 2011) population viability analysis (PVA) for Strait of Juan de Fuca lowland tributaries winter-run steelhead (Snow Creek data only). See text for description.

Figure 45 depicts population trends for Dungeness River summer- and winter-run steelhead. Steelhead counts in the Dungeness River declined steeply between the late 1980s and the late 1990s. Accurate counts in more recent years are not available. The estimated mean population growth rate is -0.064 ($\lambda = 0.938$) and process error is < 0.001 , with clear evidence of a declining trend (although its significance could not be calculated). Assuming that these counts are a reasonable reflection of spawner abundance, the estimated probability that this steelhead population would decline to a QET of 30 fish is high—about 90% within 20 years. However, the lack of data in recent years means that the population's viability is uncertain.

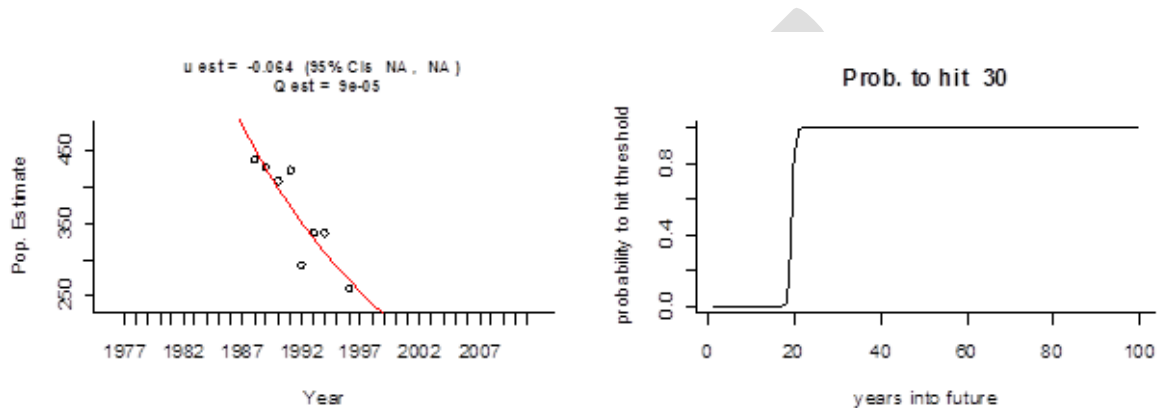


Figure 45. Summary of a MARSS-based (Holmes and Ward 2011) population viability analysis (PVA) for Dungeness River summer- and winter-run steelhead. See text for description.

Figure 46 depicts population trends for Strait of Juan de Fuca Independent Tributaries winter-run steelhead (represented by Morse and McDonald creeks data). Steelhead counts in this area have declined steeply since the late 1990s. Based on the limited time series, the estimated mean population growth rate is -0.067 ($\lambda = 0.935$) and process error is 0.046 , with clear evidence of a declining trend (although its significance could not be calculated). Assuming that these counts are a reasonable reflection of spawner abundance, the estimated probability that this steelhead population would decline to a QET of 26 fish is high—about 90% within 60 years.

Figure 47 depicts population trends for Morse Creek winter-run steelhead, which we analyzed because of the longer time series available compared to Morse and McDonald creeks combined data. Steelhead counts in Morse Creek have declined, albeit at a slower rate than combined data representing the Strait of Juan de Fuca Independent Tributaries DIP as a whole (Figure 46), since the mid 1980s. The estimated mean population growth rate is -0.041 ($\lambda = 0.960$) and process error is 0.037 , with no significant evidence for a population trend. Assuming that these counts are a reasonable reflection of spawner abundance, the estimated probability that this steelhead population would decline to a QET of 11 fish is high—almost 90% within 100 years.

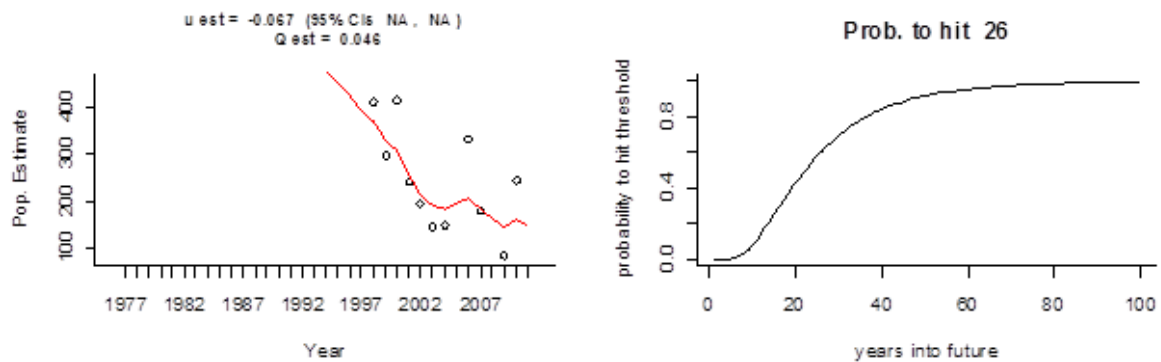


Figure 46. Summary of a MARSS-based (Holmes and Ward 2011) population viability analysis (PVA) for Strait of Juan de Fuca Independent Tributaries winter-run steelhead (Morse and McDonald creeks data only). See text for description.

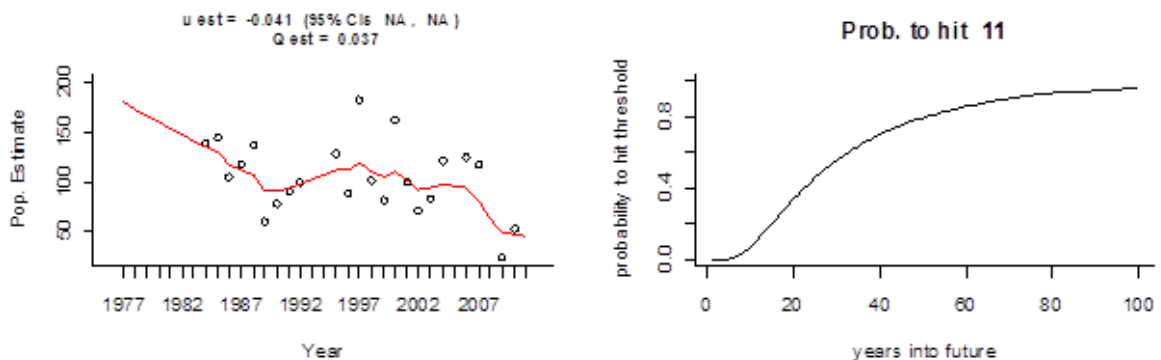


Figure 47. Summary of a MARSS-based (Holmes and Ward 2011) population viability analysis (PVA) for Morse Creek winter-run steelhead. See text for description.

Figure 48 depicts population trends for Elwha River summer- and winter-run steelhead. Like Dungeness River steelhead counts, steelhead counts in the Elwha River declined steeply between the 1980s and late 1990s, after which data are not available. Based on the limited count data, the estimated mean population growth rate is -0.17 ($\lambda = 0.844$) and the process error is

0.046, with no significant evidence for a population trend (although a clear decline between the 1980s and 1990s is evident). Assuming that these counts are a reasonable reflection of spawner abundance, the estimated probability that this steelhead population would decline to a QET of 41 fish is high—at least 90% currently. However, the lack of data in recent years means that the population's viability is uncertain.

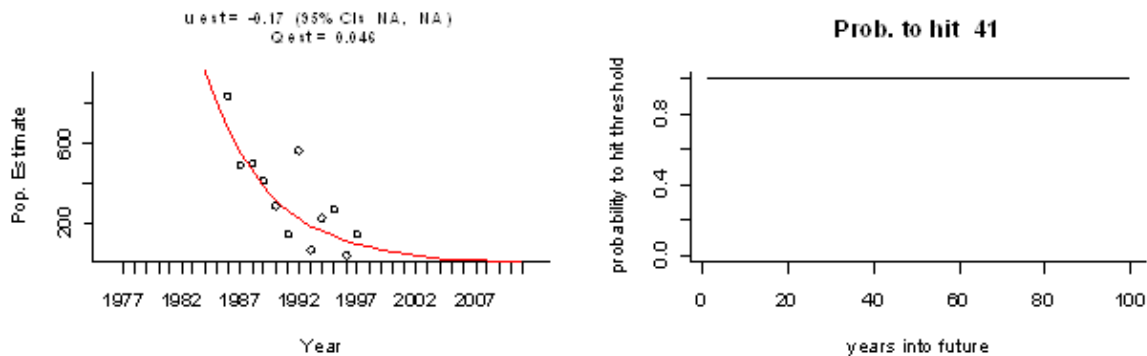


Figure 48. Summary of a MARSS-based (Holmes and Ward 2011) population viability analysis (PVA) for Elwha River summer- and winter-run steelhead. See text for description.

Summary of Population Viability Analyses Using MARSS

As did the SPAz analyses, the MARSS PVAs indicate that the majority of steelhead populations in the Puget Sound DPS are at moderate to high levels of quasi-extinction risk. The risk appears to be high throughout the DPS, but especially in the Central and South Puget Sound MPG and in tributaries to the Strait of Juan de Fuca. Although the variability in the data meant that nearly all the estimates of population growth did not differ significantly from 1 (i.e., a stable trend; the sole exception in these analyses was the Cedar River winter-run DIP), collectively the trends in abundance point to declining abundance and low productivity. In the Northern Cascades MPG, all but one of the seven populations that could be evaluated show evidence of long-term negative population growth, based on the point estimates ($\lambda < 1$), and three of these populations exhibit probabilities of reaching their specified QET within 100 years that exceed 50%. In this MPG, the Stillaguamish River winter-run, Snoqualmie River winter-run, and Tolt River summer-run populations had the lowest productivities and steepest declines in abundance. Only the Samish River winter-run population showed evidence of positive population growth and a low QET risk. For the Central and South Puget Sound MPG, all of the five populations that could be evaluated show evidence of long-term negative population growth, and four of these exhibit probabilities of reaching their specified QET within 100 years that exceed 50% (three of these are $> 90\%$). In this MPG, the Cedar River summer- and winter-run, Puyallup/Carbon River winter-run, and Nisqually River winter-run populations had the lowest productivities and

steepest declines in abundance. Only the White River winter-run population showed evidence of nearly neutral population growth ($\lambda \sim 1$) and a low QET risk ($\sim 40\%$ in 100 years). For the Hood Canal and Strait of Juan de Fuca MPG, six of the eight populations show evidence of long-term negative population growth, and these also exhibit probabilities of reaching their specified QET within 100 years that exceed 50%. In this MPG, the South Hood Canal and Strait of Juan de Fuca Independent Tributaries winter-run populations, and Dungeness River, and Elwha River summer-/winter-run populations had the lowest productivities and steepest declines in abundance. Only the East and West Hood Canal winter-run populations showed evidence of neutral or positive population growth ($\lambda \geq 1$) and a low QET risk ($\leq 40\%$ in 100 years).

Examination of the uncertainty surrounding the risk projections in the MARSS plots in Appendix A indicates that precise characterization of viability is not possible for most populations after a couple of decades. Nevertheless, the overarching trends are clear and viability appears generally to be low throughout most of the DPS. Because these abundance data in most cases are indexes of natural escapement rather than reasonably precise estimates of natural run size, we emphasize that these estimates of viability for the DIPs are likely to overestimate their true viabilities in most cases.

The populations at high QET risk are spread geographically across the DPS. Collectively, these PVAs conducted with SPAz and MARSS provide strong evidence that most steelhead populations in all three MPGs within the Puget Sound DPS are at low levels of viability with respect to abundance and productivity, and many populations—probably at least a quarter of them—are at high risk of reaching specified quasi-extinction thresholds.

Analyses at the Major Population Group level

The following six graphs (Figures 49-54) examine the trends in estimated natural escapement for Puget Sound steelhead over the entire data series (1985-2011), including their residuals (Figures 50, 52, and 54), for 20 DIPs combined into three putative MPGs in the DPS: Northern Cascades, Central and South Puget Sound, and Hood Canal and Strait of Juan de Fuca. In each case, the graphs plot the maximum-likelihood estimate of log(total number of natural steelhead) for the candidate populations in the MPG against the observed data, assuming that 1) each population time series follows a single MPG trajectory and are simply scaled up or down relative to it, and 2) variances in the observation errors for each time series are multivariate normal but are allowed to be unique for each population. The estimate of the log(total MPG count) (solid black curve) has been scaled relative to the first population at the top of the legend (i.e., Samish River for the Northern Cascades MPG, Cedar River/Lake Washington for the Central and South Puget Sound MPG, and East Hood Canal for the Hood Canal and Strait of Juan de Fuca MPG). The 95% confidence intervals (CI) around the total MPG estimate are given by the red dashed curves (note: these are not the confidence intervals around the observed data, which are expected to fall outside the CI depending on the degree of population-specific non-process error, but are instead around the composite estimate; Holmes and Ward 2011). The approximate CIs were computed using either a numerically estimated Hessian matrix (a square matrix of second-order partial derivatives of the function) or via parametric bootstrapping (see Holmes and Ward 2011). The relatively tight CIs arise because the estimate of composite process

error is small and because all the time-series data are fit to a single “population” trajectory. The total MPG estimate accounts for the bias estimated for the first population time series.

The Northern Cascades MPG shows a clearly declining trend in natural spawner abundance (Figure 49). The average long-term MPG growth rate (u_{est} , equivalent to $\ln(\lambda)$; see Tables 1 and 2) is estimated from the slope of the regression. This growth rate is negative (-0.039), corresponding to an estimated loss in abundance of 3.9% per year and a λ of 0.962. The process error (Q_{est}), which is the temporal variability in population growth rate arising from demographic stochasticity, is estimated from the variance of residuals around the regression line (Figure 50), and is 0.024. The Central and South Puget Sound MPG also shows a clearly declining trend in wild abundance (Figures 51 and 52). Its estimated long-term MPG growth rate is negative, with a loss of 6.9% per year ($\lambda = 0.933$), and its estimated process error is <0.001 . The Hood Canal and Strait of Juan de Fuca MPG shows a negative long-term population growth rate of 1.3% per year ($\lambda = 0.987$), with an estimated process error of 0.096 (Figures 53 and 54). All three MPGs contain populations with trending residuals in abundance (Figures 50, 52, and 54), which indicates that the population dynamics of these populations are following different demographic processes or trajectories, suggesting that each MPG is not functioning demographically as a single, cohesive metapopulation but, rather, contains distinctly different demographically independent populations that reflect the DIP identifications. This type of diversity is natural for a complex unit like an MPG and we do not investigate further here its demographic substructure.

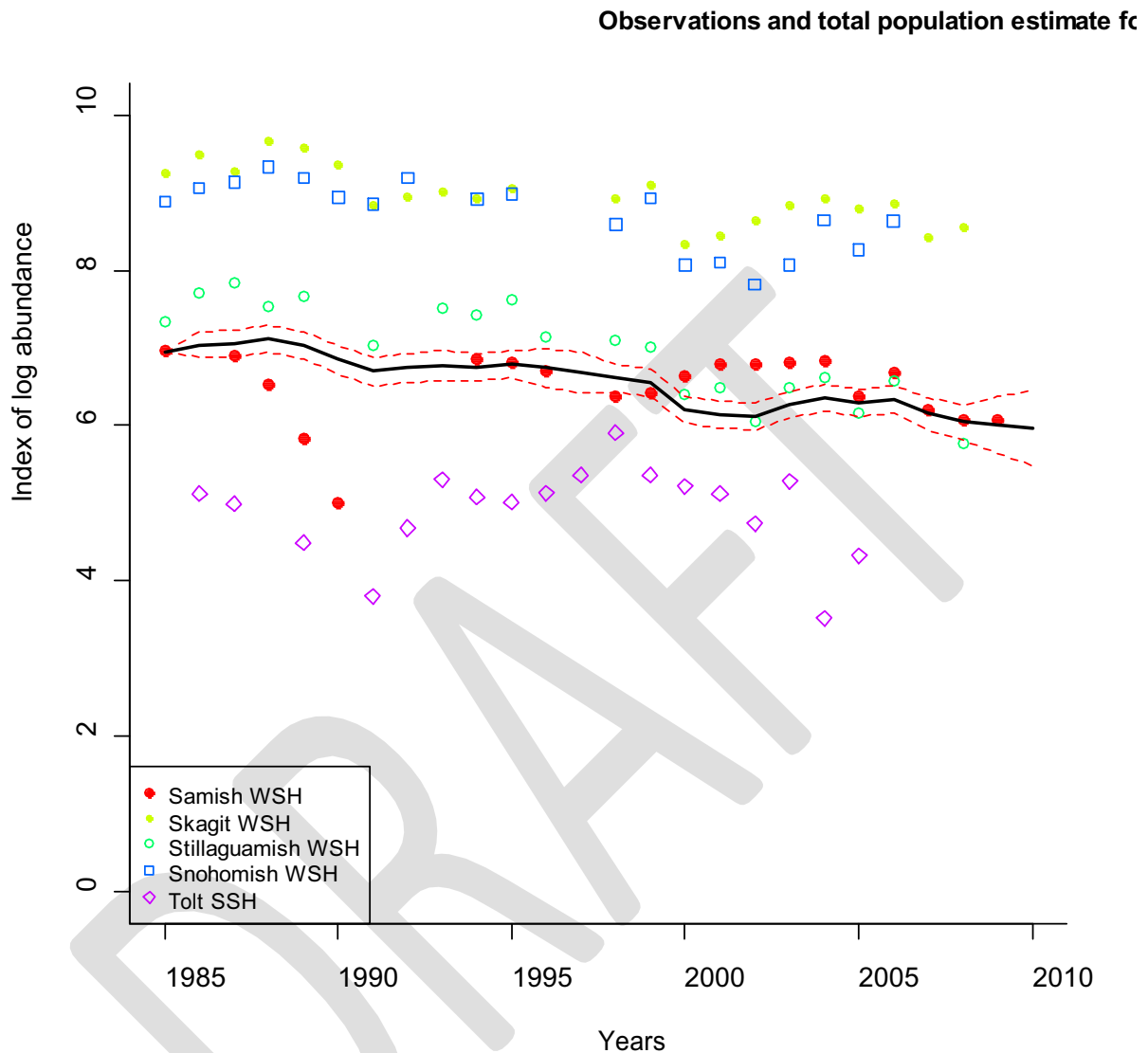


Figure 49. Plot of the trend in estimated total Puget Sound winter-run, one summer/winter-run (Skagit River), and one summer-run (Tolt River) steelhead population for a putative Northern Cascades Major Population Group (MPG). The graph plots the maximum-likelihood estimate of $\log(\text{total no. steelhead})$ in the MPG against the observed data, assuming a single population model for the MPG. The estimate of the $\log(\text{total MPG count})$ (solid black line) has been scaled relative to the Samish River population. The 95% confidence intervals (CI) around the total MPG estimate are given by the red dashed lines (note: these are not the confidence intervals around the observed data, which are expected to fall outside the CI, depending on population-specific non-process error). See text for details.

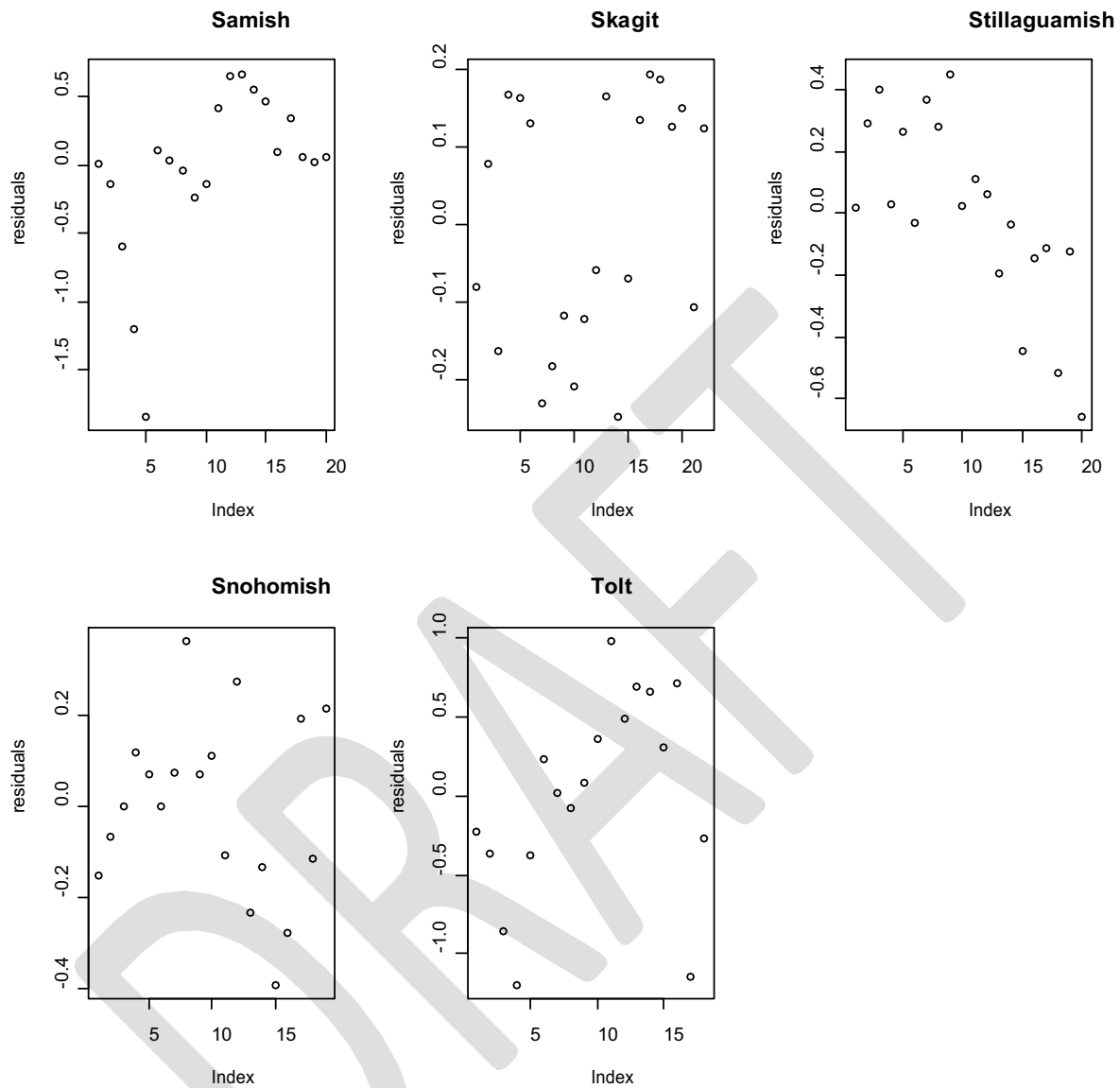


Figure 50. Plots of the residuals from regression of steelhead counts over time for five populations in the Northern Cascades Major Population Group (MPG). Note the increasing trend for Samish River winter-run steelhead and the declining trend for Stillaguamish River winter-run steelhead.

Observations and total population estimate for

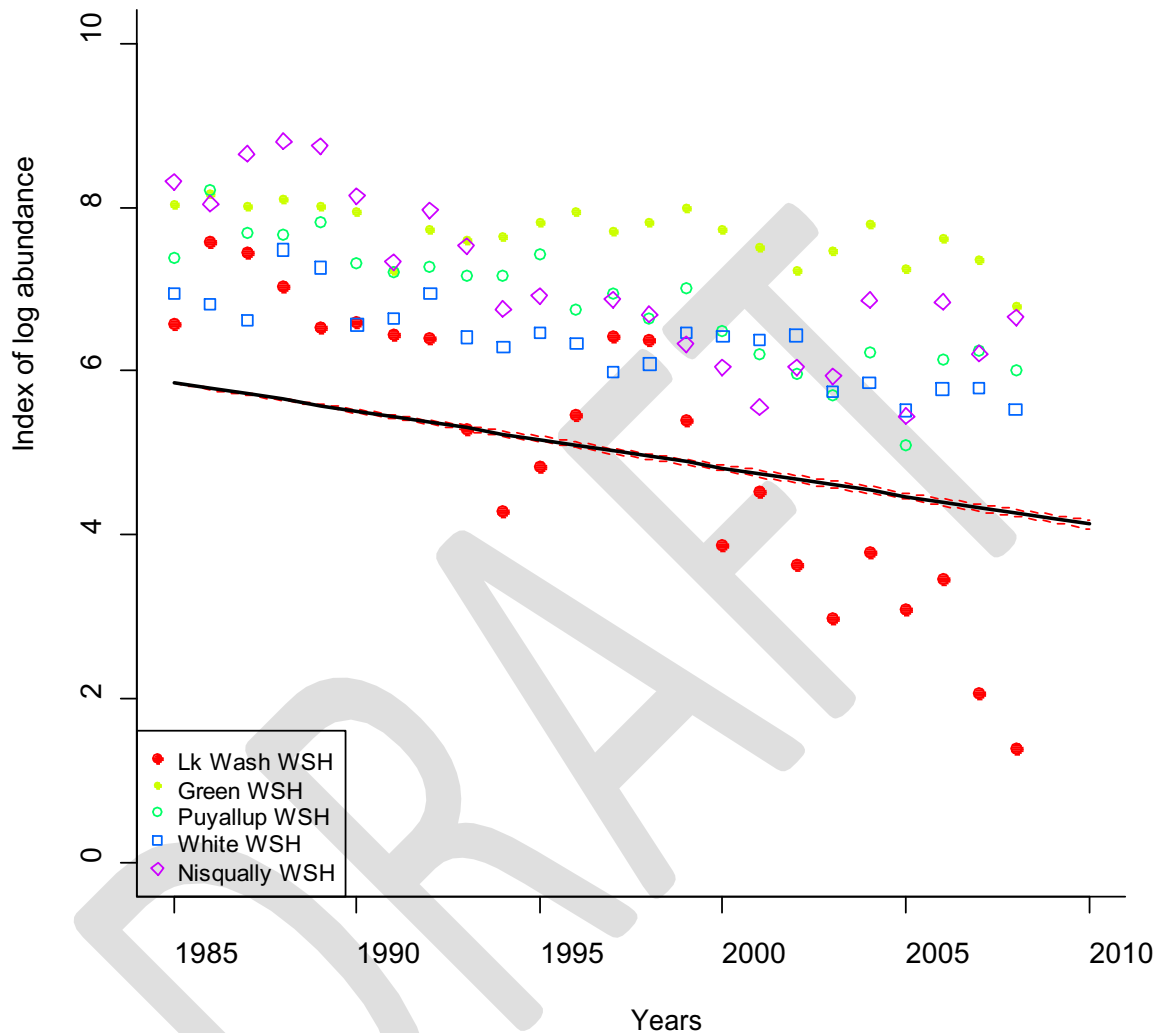


Figure 51. Plot of the trend in estimated total Puget Sound winter-run steelhead for a putative Central and South Puget Sound Major Population Group (MPG). The graph plots the maximum-likelihood estimate of $\log(\text{total no. steelhead})$ in the MPG against the observed data. The estimate of the $\log(\text{total MPG count})$ (solid black line) has been scaled relative to the Cedar/Lake Washington population. The 95% confidence intervals (CI) around the total MPG estimate are given by the red dashed lines (note: these are not the confidence intervals around the observed data, which are expected to fall outside the CI, depending on population-specific non-process error). See text for details.

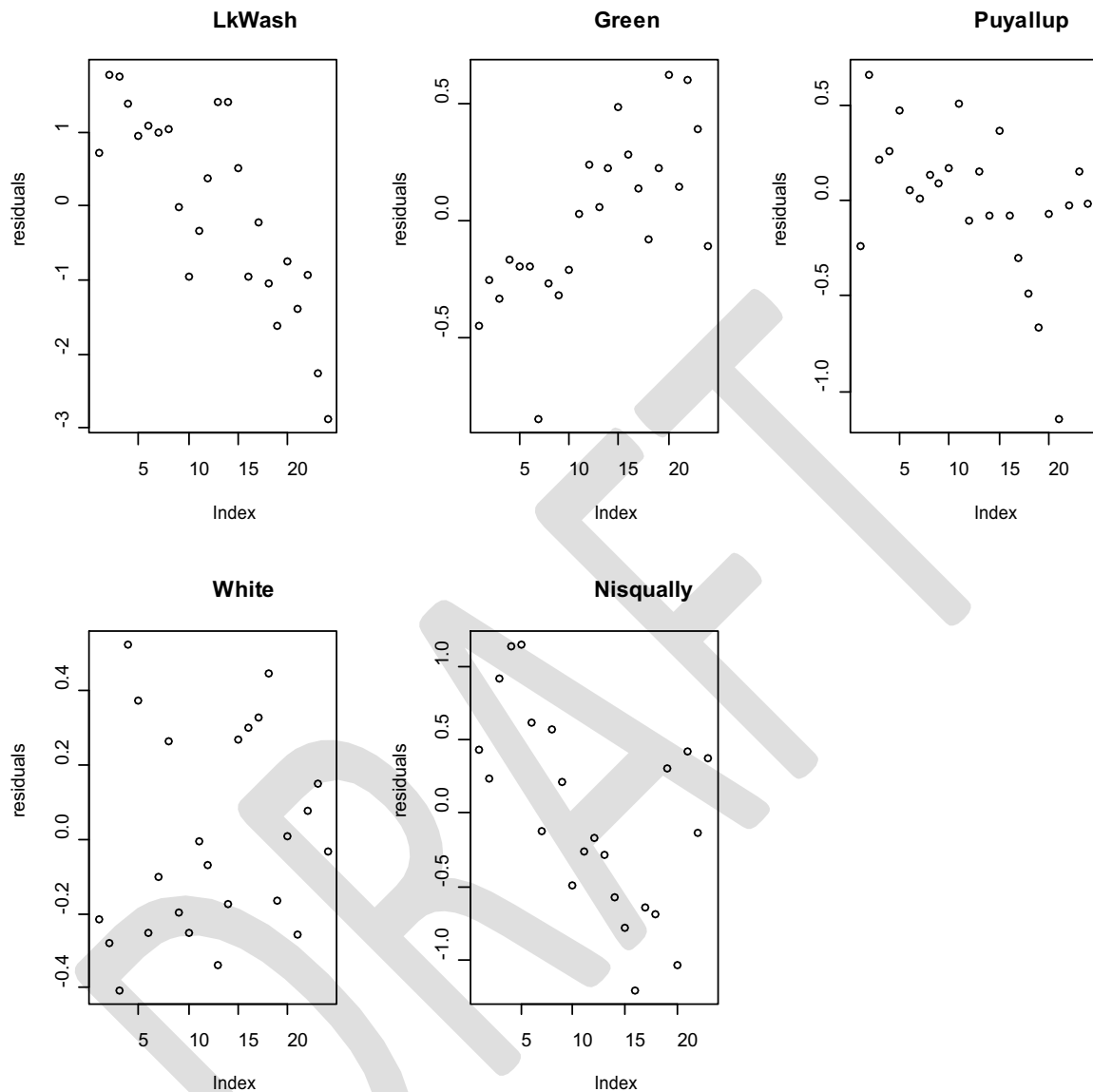


Figure 52. Plots of the residuals from regression of steelhead counts over time for five winter-run populations in the Central and South Puget Sound Major Population Group (MPG). Note the declining trends for Cedar River/Lake Washington and Nisqually River winter-run steelhead and the increasing trend for Green River winter-run steelhead.

Observations and total population estimate for

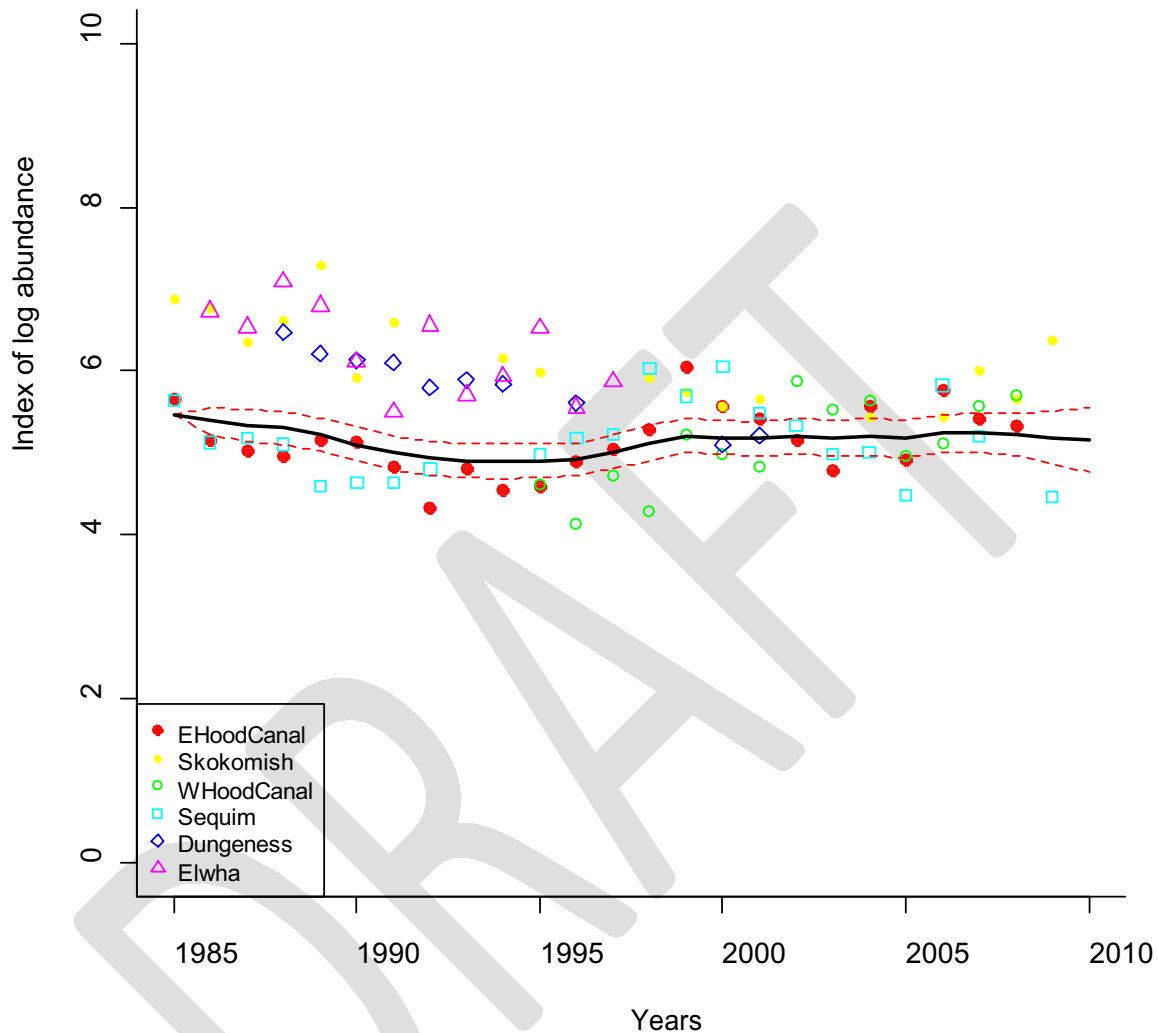


Figure 53. Plot of the trend in estimated total Puget Sound winter-run and summer/winter-run steelhead for a putative Hood Canal and Strait of Juan de Fuca Major Population Group (MPG). The graph plots the maximum-likelihood estimate of $\log(\text{total no. steelhead})$ in the MPG against the observed data. The estimate of the $\log(\text{total MPG count})$ (solid black line) has been scaled relative to the Elwha River population. The 95% confidence intervals (CI) around the total MPG estimate are given by the red dashed lines (note: these are not the confidence intervals around the observed data, which are expected to fall outside the CI, depending on population-specific non-process error). See text for details.

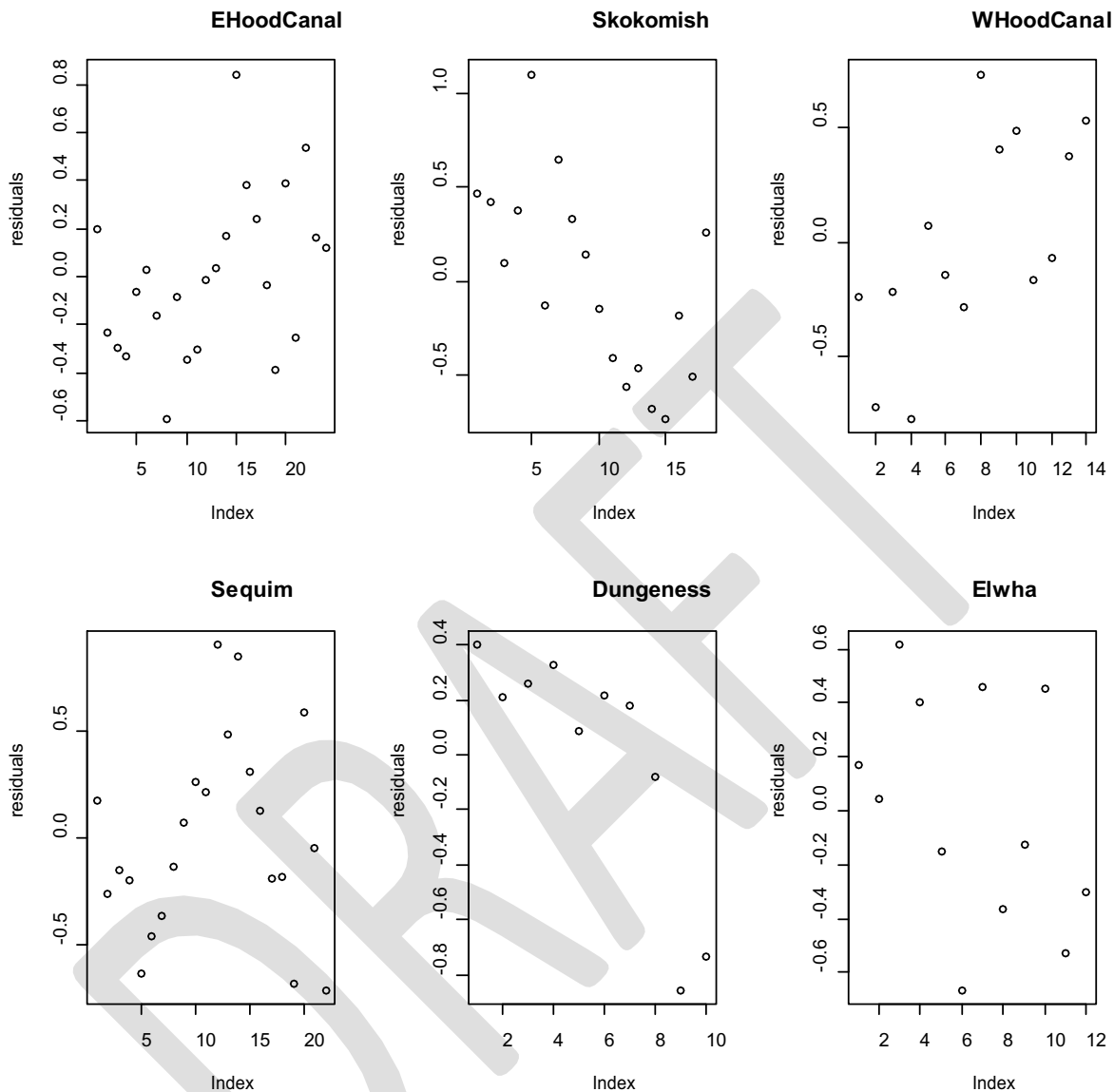


Figure 54. Plots of the residuals from regression of steelhead counts over time for six winter-run or summer/winter-run populations in the Hood Canal and Strait of Juan de Fuca Major Population Group (MPG). Note the declining trends for Skokomish and Dungeness River steelhead and the increasing trend for West Hood Canal winter-run steelhead.

Summary

All three steelhead MPGs exhibit declining trends in abundance, and estimated composite long-term growth rates are negative, ranging from about 1-7% annually. For all but a few of the

demographically independent populations of steelhead in these MPGs, estimates of mean population growth rates obtained from observed spawner or redd counts are declining—typically 3 to 10% annually—and extinction risk within 100 years for most populations in the DPS is estimated to be moderate to high, especially for most populations in the Central and South Puget Sound MPG and the Hood Canal and Strait of Juan de Fuca MPG. Collectively, these analyses indicate that steelhead in the Puget Sound DPS remain at risk of extinction throughout all or a significant portion of their range in the foreseeable future, but are not currently in danger of imminent extinction.

DPS Viability Assessment Methods

The viability of a DPS is dependent on the viability of all of its component MPGs, which in turn are evaluated based on the combined status of their component DIPs. The TRT adopted methods described by Good et al. (2005) to evaluate data that affect the four VSP parameters for each DIP in the Puget Sound Steelhead DPS. State and tribal co-managers provided data on abundance, harvest, age structure, and hatchery releases to the TRT. Data on adult returns were obtained from a time series of freshwater spawner surveys, and redd and trap counts. Where possible, time series were assembled and analyzed for each population that had sufficient data.

In addition, a comprehensive assessment of viability at each level also depends on consideration of diversity and spatial structure as well as abundance and productivity, but these factors are typically much more difficult to quantify. In this section we review the four VSP components and describe the metrics the TRT considered most useful for each component. The utility of a metric is based on its biological relevance and its availability.

Abundance

Population size, or abundance, is recognized as an important parameter because, all else being equal, small populations are at greater risk of extinction than large populations, primarily because several processes that affect population dynamics operate differently in small populations than they do in large populations. These processes are deterministic density effects (e.g., depensation at low density), environmental variation, genetic processes (e.g., genetic drift), demographic stochasticity, ecological feedback, and susceptibility to catastrophe. McElhany et al. (2000) provided guidelines relating minimum abundance to each of these processes at both the “viable” and “critical” levels, where a critical level implies a high risk of extinction over a short time period.

Metrics: Adult spawners, expanded from redd counts; weir, trap, or dam counts of adult fish.

Productivity

Population growth rate (i.e., productivity over the entire life cycle) and factors that affect population growth rate provide information on how well a population is “performing” in the habitats it occupies during the life cycle. Estimates of population growth rate that indicate a population is consistently failing to replace itself are an indicator of increased extinction risk.

Although the overall focus is on population growth rate over the entire life cycle, estimates of stage-specific productivity—particularly productivity during freshwater life-history stages—are also important to comprehensive evaluation of population viability. Other measures of population productivity, such as intrinsic productivity and the intensity of density dependence, may provide important information for assessing a population's viability. McElhany et al.'s (2000) guidelines for population growth rate are closely linked with those for abundance.

Metrics: Lambda, recruits/spawner estimates, smolt or parr to adult survival estimates, trend analysis; freshwater habitat-based intrinsic potential (parr production) estimates.

Diversity

Several salmonid traits exhibit considerable diversity within and among populations, and this variation has important effects on population viability. In a spatially and temporally varying environment, there are three general reasons why diversity is important for species and population viability. First, diversity allows a species to use a wider array of environments than they could without it. Second, diversity protects a species against short-term spatial and temporal changes in the environment. Third, genetic diversity provides the raw material for surviving long-term environmental change. In order to conserve the adaptive diversity of salmonid populations, it is essential to 1) conserve the environment to which they are adapted, 2) allow natural process of regeneration and disturbance to occur, and 3) limit or remove human-caused selection or straying that weakens the adaptive fit between a salmonid population and its environment or limits a population's ability to respond to natural selection.

Metrics: Age structure, repeat spawning rate, spawn timing range (within run types), and contribution of resident *O. mykiss* to anadromous production; hatchery introgression (in contrast to competition).

Spatial Structure

When evaluating population viability, it is important to take within-population spatial structure into account for two main reasons: 1) because there is a time lag between changes in spatial structure and species-level effects, overall extinction risk at the 100-year time scale may be affected in ways not readily apparent from short-term observations of abundance and productivity, and 2) population structure affects evolutionary processes and may therefore alter a population's ability to respond to environmental change. Spatially structured populations in which subpopulations occupy habitat patches connected by low to moderate stray rates are often generically referred to as "metapopulations." A metapopulation's spatial structure depends fundamentally on habitat quality, spatial configuration, and dynamics as well as the dispersal characteristics of individuals in the population. Pacific salmonids, including steelhead, are generally recognized as having metapopulation structure and the guidelines for spatial structure describe general rules of thumb regarding metapopulation persistence.

Metrics: Accessible habitat (present vs. historical), proportion of spawning or rearing habitat occupancy.

Applying Viability Analyses to Multiple Spatial Scales

Assessing the viability of a DPS is rooted in the evaluation of demographically independent population VSP parameters. From a recovery planning standpoint, recommended biological delisting criteria for Puget Sound steelhead are more easily understood from a DPS to DIP perspective. The Puget Sound Steelhead TRT has recommended a number of biological viability criteria for the DPS; individual DIP viability criteria are less fully developed, although the general assessment approach has been outlined. In this section we present the DPS and MPG-based viability criteria. These criteria were developed using the Puget Sound Steelhead DPS population structure identified by the TRT in its “Pop ID” document (PSSTRT 2013). In that document the TRT identified 3 MPGs containing a total of 32 historically present steelhead DIPs (Figure 55). The existing configuration of the Puget Sound Steelhead DPS is based on information compiled to date, and it is possible that future analyses of new data will suggest additional changes. It is unlikely that these changes will affect the number or configuration of the MPGs, but most probably would result in identification of additional DIPs. The following DPS viability criteria would be unaffected by changes in the number of DIPs.

DPS Viability

1. The DPS is considered viable only if all of its component MPGs are considered viable.

MPG Viability

2. An MPG is considered viable if at least 40% (rounded up) of its component DIPs are considered viable.
 - a. DIPs exhibiting major life history strategies (e.g., summer-run vs. winter-run) will be considered separate components within an MPG. Therefore, 40% of summer-run populations and 40% of winter-run populations within an MPG that contains both life history types must be viable.
 - b. DIPs containing winter- and summer-run subpopulations predominantly exhibit the winter-run life history strategy and will be considered winter-run for the purpose of 2a.
3. Within an MPG, those DIPs that do not meet the VSP criteria for viability must be maintained at a level such that the probability of reaching a specified QET within 100 years is no greater than 0.25 (the geometric mean of all populations in the MPG).
 - a. Where a DIP is below QET, but a self-sustaining resident population of *O. mykiss* is present in the accessible anadromous zone, the QET risk cannot be greater than 0.90.
4. Viability criteria for DIPs within an MPG cannot be allowed to degrade to the point where an MPG is no longer viable.

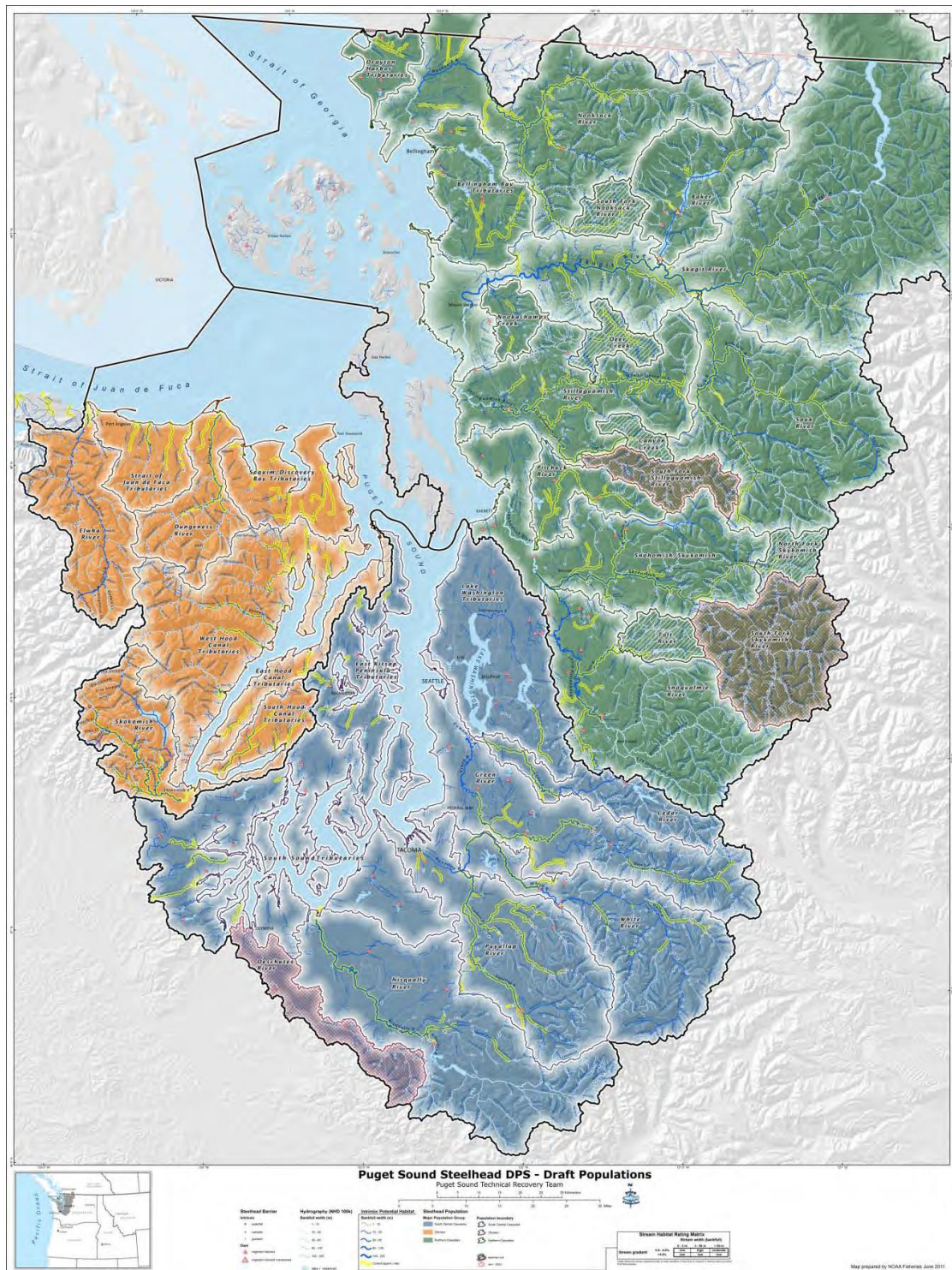


Figure 55. Three major population groups (MPGs) for the Puget Sound steelhead DPS: Northern Cascades (green), Central and South Puget Sound (blue), and Hood Canal and Strait of Juan de Fuca (orange). Areas currently occupied by out-of-DPS steelhead introduced into historically inaccessible areas are in brown or purple (e.g., Chamber’s Creek winter run steelhead introduced (via fish ladder) above Tumwater Falls in the Deschutes River); crosshatched DIPs identify summer-run populations.

Decision Support Systems as Tools for Assessing Viability

Evaluating the viability of Puget Sound steelhead at the level of Major Population Groups (MPGs) and the entire Distinct Population Segment (DPS) requires methods that can accommodate both qualitative and quantitative information and information of varying quality. In the following sections we describe some of these methods.

Decision support systems are increasingly being employed to assess status and viability when uncertainty about variables influencing viability is considered extensive (McCann et al. 2006; Newton et al. 2007; Newton 2010). A complete assessment of the biological condition of a complex entity such as a DPS is necessarily multifaceted, including a variety of interrelated criteria, with varying data quality. These criteria relate to biological processes at a variety of time and space scales, with processes varying from individual stream reaches to the entire range of the DPS. To track this large suite of data and criteria in a transparent and logically consistent framework, we used a knowledge-based Decision Support System (DSS).

A DSS is a computer-based tool that can analyze and compare numerous types of data, producing results that assist managers in making a decision (Turban and Aronson 2001). DSSs, which include decision trees and approximate logic models, allow decision-makers to perform complex evaluations quickly, present a consistent assessment that draws from a variety data sources, and track large sets of information accurately, thus improving the choices made by decision-makers without overriding human judgment (Rauscher 1999). A system evaluating ecological conditions may contain substantial uncertainty about the precise conditions that are optimal for the target organisms because of gaps in information and the lack of perfect knowledge about the interrelationships among relevant factors (Reynolds et al. 2000).

One type of DSS incorporates approximate logic (popularly referred to as “fuzzy logic”; Zadeh 1965, Reynolds et al. 2000) to assist evaluation of conditions and functional relationships based on imprecise information. These DSSs typically rely on function relationships between influence variables and response variables referred to as Truth Membership Functions. These functions can take any form, from linear, to a threshold or sigmoidal relationship, to nonlinear—so long as one is confident that the available information supports that characterization.

A DSS of this type was employed by Wainwright et al. (2008) to identify viability criteria for threatened Oregon coast coho salmon (*O. kisutch*). Their DSS used a “fuzzy logic” network framework to link criteria at a variety of scales and aggregate them from fine-scale watershed-level criteria, through population-level criteria and major population group-level criteria, to criteria for the entire coho salmon ESU. We attempted to adapt this tool for Puget Sound steelhead viability but ultimately did not employ it because the lack of quantitative information available for Puget Sound steelhead made it difficult to develop robust truth membership functions to parameterize the model.

The Puget Sound Steelhead TRT opted instead to develop a novel tool for this purpose, another DSS model based on Bayesian Networks (BN) (Marcot et al. 2001, Newton et al. 2007). Bayesian Networks represent a decision tool that provides a transparent, graphical framework for characterizing relationships among a diverse set of variables. Because these networks usually

incorporate likelihoods (conditional probabilities) for each of the input variables, typically by using discrete uniform distributions to treat all values of a finite set of possible values as equally probable, they are effective models of reasoning under uncertainty (Jensen 2001). They also have the advantage that they can readily incorporate new information as it becomes available to reduce uncertainty in the decision process.

Bayesian Networks for Evaluation of Viability

Evaluating viability of Puget Sound steelhead at the level of DIP, MPG, and DPS requires an approach that can explicitly incorporate uncertainty into the evaluation and can deal with available information of variable quality for all four VSP criteria. We sought a method that could accommodate these types of information in a transparent, consistent way. We elected to construct a series of Bayesian Networks (also known as Bayesian belief networks or Bayes nets; Newton et al. 2007) to assess viability at these multiple scales and to ascertain the influence of factors on viability. A BN is a probabilistic graphical model (e.g., Lee and Rieman 1997, Marcot et al. 2001, Peterson et al. 2008) designed to efficiently represent a probability distribution underlying a set of variables that influence each other, but that is too complex to be represented using a series of tables and equations. A main feature of a BN is that there is only one probability distribution that satisfies the structure of the BN (as reflected in the constraints among variables in the form of probabilistic conditional dependencies), and this distribution can be estimated by ‘testing’ the BN by locking values of the variables at particular probabilities (a process known as *instantiation*). The objective of a BN is to characterize the dependencies among its constituent variables (depicted by *nodes*) given the influences between them (depicted by *edges*).

A BN is composed of nodes and edges. Each node represents a variable that can take any of several values, either as discrete states or as represented by a continuous function. Each edge connecting two nodes represents probabilistic dependencies among these nodes (the arrow indicates the direction of influence). In a BN, the conditional probabilities that reflect these dependencies are estimated from Bayes’ theorem. In its simplest form, Bayes’ theorem states that the probability of event *b* occurring given that event *a* has occurred, $P(b|a)$, is:

$$P(b|a) = \frac{P(a|b) \times P(b)}{P(a)}$$

where $P(a)$ is the probability of *a*, $P(b)$ is the probability of *b*, $P(a|b)$ is the probability of *a* given that *b* has occurred (Bayes and Price 1763, Gelman et al. 1995). We can demonstrate this relationship with a simple example. Suppose that we know from previous studies that slowly growing (‘event’ *b*) juvenile steelhead (i.e., progeny of steelhead parents) adopt a freshwater resident life history (‘event’ *a*), $P(a|b)$, about 10% of the time. Suppose we also know that the average probability of a growth rate sufficiently low to induce residency in this population, $P(b)$, is 0.3, and the probability of sampling a resident *O. mykiss* in this population which has anadromous access to the ocean is 1 in 5 (so, $P(a)$ is 0.2). We want to know how likely it is that a juvenile *O. mykiss* born of steelhead parents will become resident as a result of slow growth—i.e., how likely is it that depressed growth (*b*) will result in residency (*a*) in this population? We can use Bayes’ theorem to compute the probability that residency results from depressed growth, given this information:

$$P(b|a) = \frac{0.1 \times 0.3}{0.2} = 0.15$$

Under these conditions, we would predict that if a fish born of anadromous parents becomes resident, then the likelihood that this is caused by depressed growth is 15%.

Another way of expressing Bayes' theorem is one that includes a hypothesis (H), evidence (E), and prior knowledge or past experience (K), so that the probability that a hypothesis is true given the evidence and past experience is:

$$P(H|E, K) = \frac{P(H|K) \times P(E|H, K)}{P(E|K)}$$

where $P(H|K)$ is the probability of the hypothesis given prior knowledge, $P(E|K)$ is the probability of the evidence given prior knowledge, and $P(E|H, K)$ is the probability of the evidence given the hypothesis is true and prior knowledge. The term $P(H|E, K)$ is the *posterior probability*, or the probability of hypothesis H after considering the effect of the evidence E on prior knowledge K . The term $P(H|K)$ is the *prior probability* H given K alone. The term $P(E|H, K)$ is the *likelihood* and gives the probability of E given that both H and K are true. The term $P(E|K)$ is independent of H and is usually regarded as a normalizing or scaling constant (Gelman et al. 1995).

A Bayesian Network (BN) is intended to directly incorporate estimates of uncertainty into evaluating relationships between variables. As a decision support system, it can be as simple or as complex as one feels is supportable. It has the advantage that its components—its *criteria*—can easily be constructed through simple verbal guidelines, through actual data, or estimated functional relationships. A BN has some features that can favor its use over other decision tools:

- BNs can lay out parameters and how they interact transparently in a clear decision framework;
- BNs explicitly depict uncertainty as prior probabilities, which lend themselves well to risk analysis; and
- BNs can be used to help identify key factors that influence the outcome of interest or to help prioritize research, monitoring, or other actions.

BNs are not intended as a substitute for human judgment or as a means of “making” decisions, but rather to support decision-making processes by integrating available information and human judgment into a sensible conceptual framework.

Example: A Simple Bayesian Network

Figure 56 depicts an example of a simple BN to evaluate viability of a population based on current abundance and estimated population growth rate. For this example and other analyses using BN in this report, we used the program Netica v. 5.09 (Norsys Software Corporation,

Vancouver, BC, <http://www.norsys.com>) to construct and evaluate the networks. In this BN, one parent node, “Population abundance,” summarizes an assessment of the current abundance of the population relative to a low-abundance threshold that would trigger concern (or remedial action); the other parent node, “Average population growth,” summarizes an assessment of the population’s growth rate (e.g., an estimate of the annual % change in abundance). In this simple BN, we assume that these two factors alone determine “Population viability,” the child node of interest, and they do so independently.

For each parent node in the BN, the black bars and corresponding numbers depict prior probabilities of each state. In this example, we are using discrete states to describe each variable in the BN. For example, the assessment of current population abundance reflected in Figure 56 is that current abundance is larger than the population’s low-abundance threshold with a probability of 85%. However, because this estimate is likely to be obtained from sampling, it incorporates some uncertainty. To capture this uncertainty, in this case we have estimated that the probability that the population is much larger than this threshold (say, 10 times the threshold abundance) is 5%, and the probability that the population is smaller than this threshold is 10%. Similarly, the assessment of the population’s growth (based, say, on an estimate of linear trend in abundance) is that the population is stable, but with a modest probability of 50%. We believe that there is some likelihood that the population is increasing (e.g., 1 or 2% annually) or rapidly increasing (> 5% annually)—here estimated at 16%, and we also believe that there is some likelihood that the population is declining or rapidly declining—here estimated at 34%. Note that the probabilities of each variable state must sum to 1.

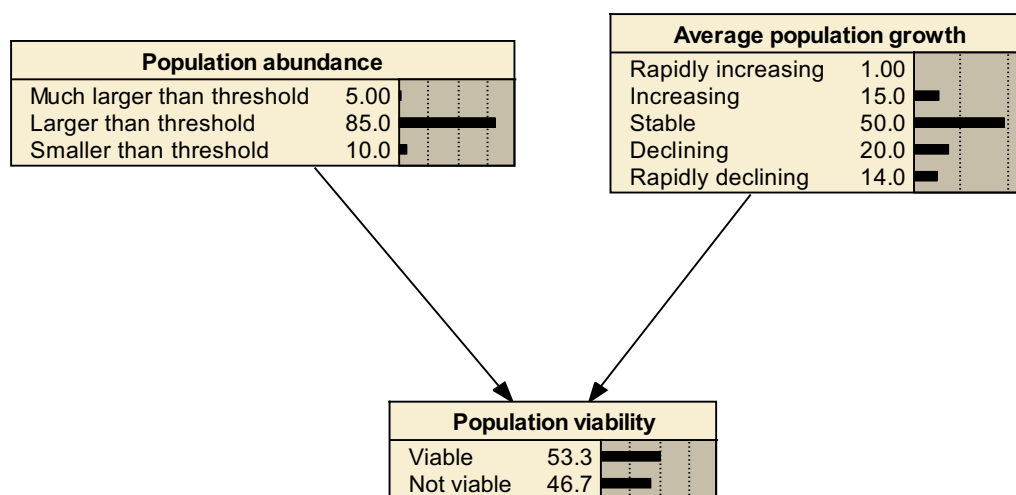


Figure 56. A simple Bayesian Network depicting the influence of three discrete states of population abundance and five discrete states of average population growth on a dichotomous estimate of population viability. The bars and values in the two parental nodes (Population abundance and Average population growth) show estimates of the probabilities of each state for these factors; the bars and values in the child or outcome (“decision-aiding”) node (Population viability) depict resulting estimates of the probabilities of each viability state. The joint probabilities of all possible combinations of these states of population abundance and average population growth, which are inputs from the user, are given in Table 8.

The population viability node is an output node; it represents the results of a decision-aiding model. Here we have depicted the probability that the population is viable or not, given the probability distributions for population abundance and growth rate described above. The Bayesian calculations underlying the BN, parameterized with the probabilities given in the parent nodes for population abundance and annual population growth and with a set of conditional probabilities that represent all the combinations of states for population abundance and growth (Table 8), result in the probabilities estimated for population viability (53.3%) or non-viability (46.7%) given in the child node for population viability in Figure 56. The prior information that the population is thought to be somewhat larger than the low-abundance threshold and stable, albeit with some uncertainty, leads to a BN outcome that we are uncertain that the population is viable, with probability 53.3%.

Table 8. Conditional probability table (CPT) underlying the outcome node of population viability for the Bayesian Network (BN) given in Figure 56, representing the joint probabilities of all possible combinations of states of population abundance and population growth described in the BN's parent nodes.

Population abundance	Average population growth	Viable	Not viable
Much larger than threshold	Rapidly increasing	0.99	0.01
Much larger than threshold	Increasing	0.95	0.05
Much larger than threshold	Stable	0.90	0.10
Much larger than threshold	Declining	0.75	0.25
Much larger than threshold	Rapidly declining	0.50	0.50
Larger than threshold	Rapidly increasing	0.80	0.20
Larger than threshold	Increasing	0.70	0.30
Larger than threshold	Stable	0.60	0.40
Larger than threshold	Declining	0.45	0.55
Larger than threshold	Rapidly declining	0.35	0.65
Smaller than threshold	Rapidly increasing	0.50	0.50
Smaller than threshold	Increasing	0.40	0.60
Smaller than threshold	Stable	0.30	0.70
Smaller than threshold	Declining	0.05	0.95
Smaller than threshold	Rapidly declining	0.01	0.99

What if we are more certain about the population's state, e.g., because of new information? One can *instantiate* the BN to correspond to particular states of the variables and examine how viability is affected by this additional information. Instantiation is the term used to indicate that node states are set at particular values and is important in conducting sensitivity analyses for a BN (see below). For example, if additional information led us to conclude that the population is in fact larger than the low-abundance threshold (probability = 100%) and its growth

is positive (e.g., $\lambda > 1$, probability = 100%), the BN estimates that the probability the population is viable is now 70% (Figure 57a). It turns out that if we are certain that the population is much larger than the threshold and its growth is positive, the probability that the population is viable rises to 95%. If, on the other hand, additional information led us to conclude that the population is in fact smaller than the low-abundance threshold (probability = 100%) and its growth is negative (e.g., $\lambda < 1$, probability = 100%), the BN estimates that the probability the population is viable is now only 5% (Figure 57b). From these results it is easy to see that the estimates directly reflect the corresponding values in the CPT (Table 8).

To determine the most likely configuration of probabilities in the network given the evidence, we can estimate the Most Probable Explanation (MPE) for this network. The MPE is a complete variable instantiation across the entire network that gives the highest probability, given the current evidence (distributions of conditional probabilities). The MPE is equivalent to the Maximum A-Posteriori Probability (MAP), which asks the question “Given the values at some nodes, what are the most likely findings across the network?” In a Bayesian sense, it can be considered an estimate of the most plausible explanation of the data. It is computed as follows. The probability of a complete variable instantiation \mathbf{x} is:

$$\Pr(\mathbf{x}) = \prod_{\mathbf{x}u \sim \mathbf{x}} \theta_{\mathbf{x}|u}$$

where \sim is the compatibility among instantiations (i.e., $\mathbf{x}u$ is compatible with \mathbf{x}). A most probable explanation is a complete variable instantiation given evidence \mathbf{e} that has the highest probability:

$$\begin{aligned} \text{MPE}(\mathbf{e}) &\stackrel{\text{def}}{=} \arg\max_{\mathbf{x} \sim \mathbf{e}} \Pr(\mathbf{x}) \\ &= \arg\max_{\mathbf{x} \sim \mathbf{e}} \prod_{\mathbf{x}u \sim \mathbf{x}} \theta_{\mathbf{x}|u} \end{aligned}$$

Note that there may be more than one MPE for a network (i.e., more than one complete instantiations with the same probability).

For the network in Figure 56, the MPE is shown in Figure 58. It indicates that, given the data, our best guess is that the population abundance is larger than the threshold, that its dynamics are stable (growth rate near zero), and that the population is viable. However, although the MPE indicates that the population is most likely viable (i.e., that probability is instantiated at 100%), the estimated probability that the population is not viable is still rather high (66.7%) given the MPE, reflecting the considerable uncertainty about the population’s status in both size and, especially, growth rate. Note that under MPE the “probabilities” given within a node in a

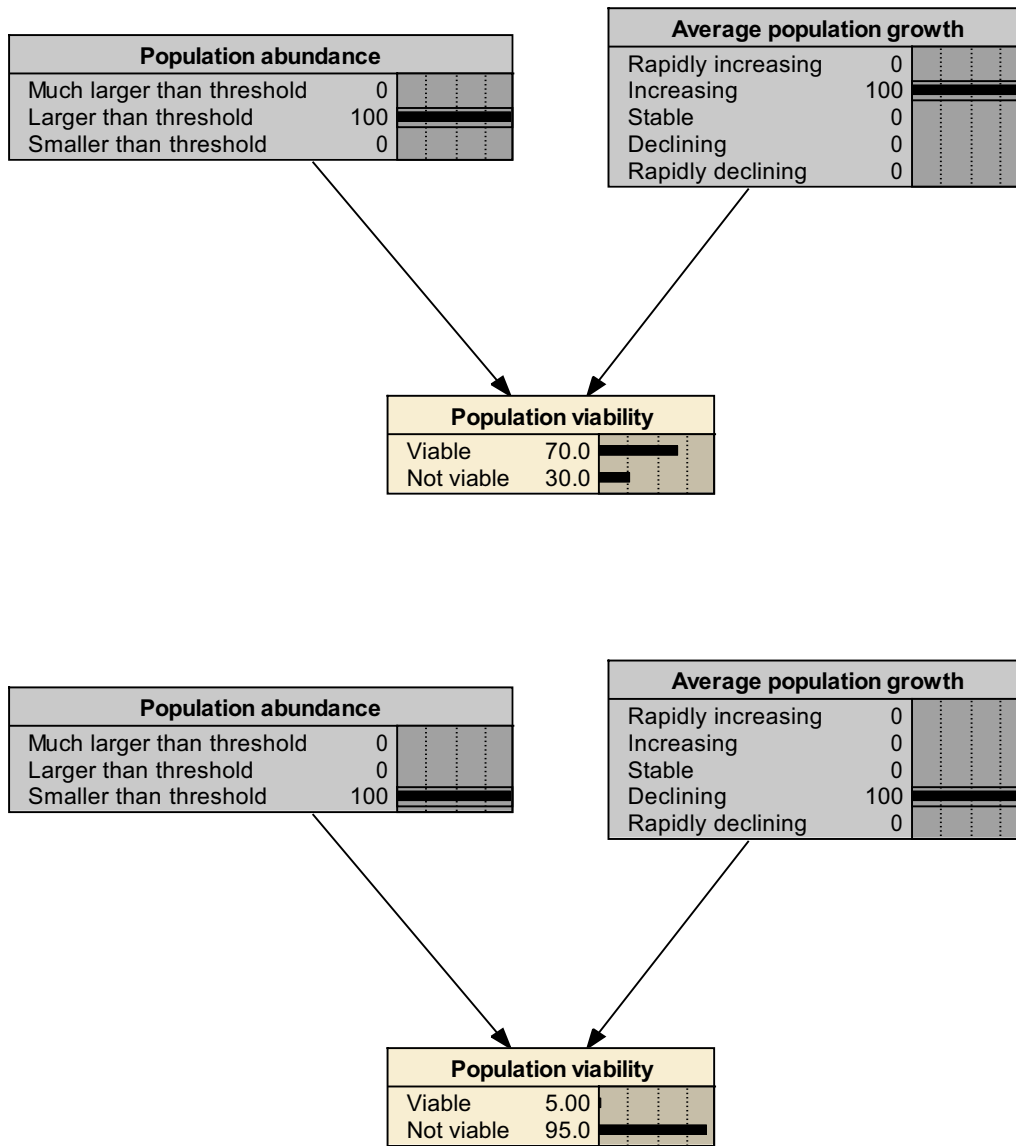


Figure 57. (a) The Bayesian Network in Figure 56 instantiated at particular states of population abundance and growth, depicting certainty that the population is larger than the low-abundance threshold and increasing in size. Note how this additional knowledge has altered the assessment of viability, given these prior probabilities and the conditional probability table (CPT) given in Table 8. (b) The Bayesian Network in Figure 56 instantiated at different states for population abundance and growth, depicting certainty that the population is smaller than the low-abundance threshold and declining in size.

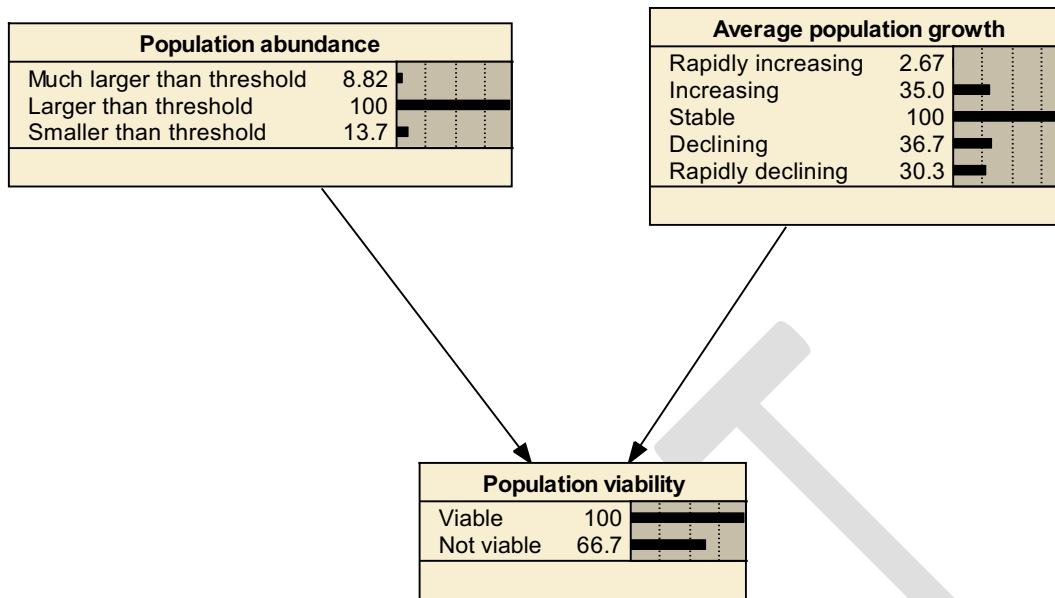


Figure 58. Most probable explanation (MPE) for the Bayesian Network in Figure 56.

network are not additive. The reason for this is that in computing MPE across the network, Netica represents the MPE probability within each node as a full bar (i.e., probability = 100%); the actual probability for that state given the evidence is given by the uninstantiated network without computing MPE. Figure 56 indicates that this value is 53.3%. Figure 58 indicates that the MPEs for abundance, growth, and viability are “Larger than threshold,” “Stable,” and “Viable,” respectively. These states do correspond to the largest probabilities for these respective nodes (85%, 50%, and 53.3%, respectively) in the uninstantiated network in Figure 56. In computing the MPE for the network, Netica simply estimates the probabilities of the alternate states at each node given that the other nodes are in their most probable configurations (and scaling by the same factor that was used to bring the MPE bar to 100%). Since MPE is computed and probabilities are adjusted at each node, complex networks can be difficult to characterize simply. This is the primary value of MPE in a Bayesian Network—it identifies the most likely states of each variable given the evidence, and quantifies their likelihoods relative to those of the other states.

As expected, the viability outcome directly depends on the set of probabilities used to parameterize the BN. It is important to remember that these probabilities, including those in the CPT, can represent estimates obtained from best judgement (belief), from actual data, or a combination of these sources of information, and they can be revised when additional information becomes available (Marcot et al. 2006b, Newton et al. 2007).

We can conduct a sensitivity analysis of the BN to determine how sensitive the population viability results are to changes in the states of population abundance and growth. This sensitivity is often measured by estimating the *entropy reduction* (or reduction in *mutual information*) or *belief variance* (expected reduction in real variance) resulting from the degree to which findings at a node are influenced by the findings at another node, given the findings that are entered into the network. In information theory, entropy is a measure of the uncertainty of a random variable(s). Mutual information corresponds to the reduction in the entropy of a variable achieved by learning the state of another variable. In a BN, entropy reduction (in the case of discrete or categorical variable states) or variance reduction (in the case of continuous variables) is the expected reduction in variation at an output node due to a finding at an input node (Marcot et al. 2006b). It is calculated by

$$I = H(Q) - H(Q|F) = \sum_q \sum_f \frac{P(q,f) \log_2 [P(q,f)]}{P(q)P(f)}$$

where I is the entropy reduction, $H(Q)$ is the entropy of output node Q before any new findings from input node F , $H(Q|F)$ is the entropy of Q after new findings from F , $P(q,f)$ is the probability of finding q at node Q given finding f at node F , and $P(q)$ and $P(f)$ are the probabilities of findings q and f , respectively (Marcot et al. 2006b, Appendix B). In structuring a BN, one seeks to maximize entropy of the entire network, which corresponds to maximizing the mutual information among the variables. For example, an entropy reduction of 5% at node Q resulting from a new finding at node F reflects a reduction in mutual information of 5%; this means that the uncertainty in the state of Q is reduced by 5% by knowing the state of F .

The results of a sensitivity analysis (Table 9) show that the estimate of viability is sensitive to variation in both population abundance and growth rate, but slightly more sensitive to changes in abundance for this particular BN; the entropy reduction for sensitivity of viability to change in abundance was 4.27%, whereas that for sensitivity to change in productivity was 4.07%. This is largely because the population's viability changes considerably when population size drops below the low-abundance threshold, as depicted by the probabilities in the CPT (Table 8).

Table 9. Results of a sensitivity analysis of the Bayesian Network (BN) given in Figure 56, showing the sensitivity of population viability to changes in the states of population abundance and growth rate.

Sensitivity of 'Population viability' to findings at 'Population abundance':

Probability ranges:	Min	Current	Max	RMS Change
Viable	0.2264	0.533	0.8224	0.1179
Not viable	0.1776	0.467	0.7736	0.1179
Entropy reduction	= 0.0426 (4.27 %)			

Table 9. Continued.

Belief Variance	= 0.01389 (5.58 %)			
Sensitivity of 'Population viability' to findings at 'Average population growth':				
Probability ranges:	Min	Current	Max	RMS Change
Viable	0.3235	0.533	0.7795	0.1174
Not viable	0.2205	0.467	0.6765	0.1174
Entropy reduction	= 0.0406 (4.07 %)			
Belief Variance	= 0.01379 (5.54 %)			

Sensitivity of 'Population viability' to a finding at another node:

Node	Mutual Info	Percent	Variance of Beliefs
Population viability	0.99686	100	0.2489136
Population abundance	0.04260	4.27	0.0138948
Average population growth	0.04060	4.07	0.0137896

Use of Bayesian Networks to Incorporate Viable Salmonid Populations Criteria into a Viability Assessment Framework

We constructed a Bayesian Network (BN) to characterize the influence of a number of features of coastal steelhead biology and estimates of the four VSP parameters (abundance, productivity, diversity, and spatial structure) for individual populations on viability at the level of the DIP, the MPG, and the entire DPS. We developed the BN using Netica software (Norsys Software Corp., Vancouver, BC) following the general guidelines recommended by Marcot et al. (2006). In essence, a BN is a set of variables (nodes) linked by probabilities that represent their interdependence. Our objective in building the BN model was to evaluate the net effects of several features of steelhead populations related to VSP parameters and their habitat on the viability of populations across the entire Puget Sound DPS. We did so by synthesizing available information and expert knowledge on abundance, productivity, diversity, and spatial structure of Puget Sound steelhead. The BN that determines DPS viability is composed of three subnetworks that determine the viability of each MPG. Each of these MPG subnetworks is composed of a series of subnetworks that determine the viability of each DIP in the constituent MPG. A

representative BN to characterize the viability of a typical winter-run steelhead population in Puget Sound is depicted in Figure 59.

Our goal was to construct each such network to minimize its complexity while still retaining the capacity to evaluate the influence of all four VSP parameters on viability: abundance, productivity, diversity, and spatial structure. We aimed to keep the number of nodes small but to include key variables that we either had available information for, or else thought might become available later and could assist with viability assessment and future recovery planning. Consequently, some nodes can be considered “placeholders” with underlying conditional probabilities that reflect considerable uncertainty. As indicated by Figure 59, the effect of DIP abundance on DIP viability incorporates influences of adult and juvenile abundance relative to capacity for production, and quasi-extinction risk (as estimated from a population viability analysis, if available). The effect of DIP productivity on DIP viability incorporates influences of population growth rate and frequency of repeat spawning; in the network, population growth rate is influenced by both freshwater survival (smolts per spawner) and marine survival (adults per smolt). Next, the influence of DIP diversity on DIP viability incorporates influences of the distribution of run timing, influence of hatchery fish on natural diversity, the adult age distribution, and the proportion of migrant smolts produced by resident adults. Finally, the influence of DIP spatial structure on DIP viability incorporates influences of the fraction of intrinsic potential (IP) habitat occupied by rearing juveniles and the fraction of intrinsic potential habitat occupied by spawning adults.

In this network, the values for the input nodes and the conditional probabilities underlying each node were assigned by TRT members after considering available data, opinions and comments from other steelhead biologists, reviews of other models and analyses, reports, and similar approaches in the scientific literature (see References and Appendix A). In most cases, the intermediate and output conditional probabilities pertain to steelhead demographic and life history responses that are poorly understood; in these cases, we attempted to account for this uncertainty by assigning moderate to high levels of spread in the conditional probabilities. In general, probability values were chosen to produce a linear relationship between the score for a VSP category and the DIP viability (with a consequent distribution of probability of being viable ranging from 0-100%), with all VSP criteria weighted equally in the network. A description of the nodes in the network for DIP viability in Figures 59 and 60 is given in Table 10. The probabilities that underlie the network are given in Tables 11 and 12.

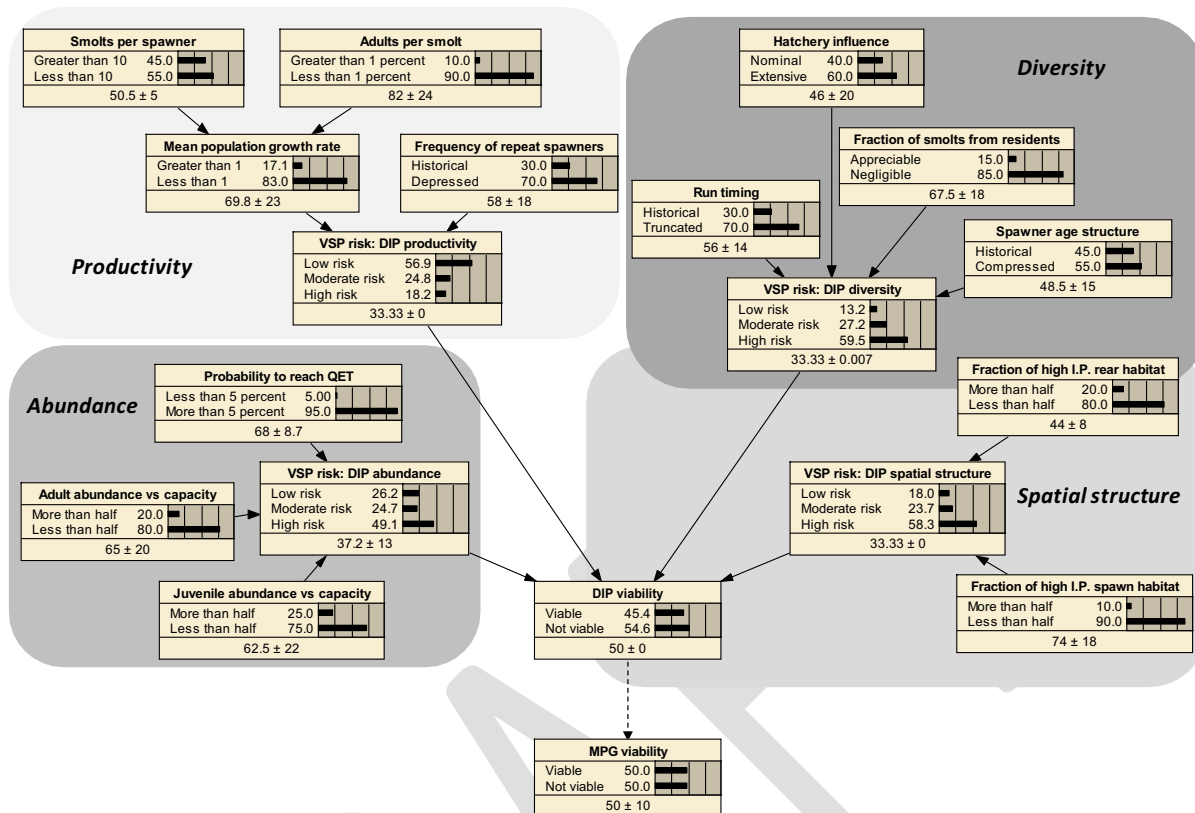


Figure 59. A Bayesian Network to characterize the viability of a hypothetical Demographically Independent Population (DIP) of winter-run steelhead in the Puget Sound DPS. The network is intended to be minimally complex while estimating the influence of all four Viable Salmonid Population (VSP) parameters (abundance, productivity, diversity, and spatial structure) on population viability. The influence of the DIP’s abundance on its viability is represented by the “VSP risk: DIP abundance” node (lower left) that incorporates influences of adult abundance, juvenile abundance, and quasi-extinction risk (as estimated from a population viability analysis, if possible) on DIP viability. The influence of the DIP’s productivity on its viability is represented by the “VSP risk: DIP productivity” node (upper left) that incorporates influences of population growth rate and frequency of repeat spawning on DIP viability; the node for population growth rate is itself influenced by freshwater survival (smolts per spawner) and marine survival (adults per smolt). The influence of the DIP’s diversity on its viability is represented by the “VSP risk: DIP diversity” node (upper right) that incorporates influences of the distribution of run timing, influence of hatchery fish on natural diversity, the adult age distribution, and the proportion of migrant smolts produced by resident adults. The influence of the DIP’s spatial structure on its viability is represented by the “VSP risk: DIP spatial structure” node (lower right) that incorporates influences of the fraction of intrinsic potential habitat occupied by rearing juveniles and the fraction of intrinsic potential habitat occupied by spawning adults. This network is a subnetwork that then determines the viability of the corresponding Major Population Group (MPG), as indicated by the dashed arrow at bottom; similar subnetworks for the viability of each DIP in the MPG combine to influence the MPG’s overall viability. A description of the nodes in the network is given in Table 10. The underlying conditional probability tables for this subnetwork are given in Tables 11 and 12.

Table 10. Titles and descriptions of the input, intermediate, and decision nodes in the Bayesian Networks describing population viability of steelhead. See the main text for a description of how the input probabilities were calculated for these nodes, and Tables 11 and 12 for the final input probabilities used.

Node title	Node description	States
Adult abundance vs capacity	<i>Input Nodes: VSP abundance</i> The probability that the fraction of estimated spawner carrying capacity represented by the current geometric mean adult abundance in the DIP is less than 25% or more than 25%	More than 25% Less than 25%
Juvenile abundance vs capacity	The probability that the fraction of estimated rearing capacity represented by the current mean parr or smolt abundance in the DIP is less than 25% or more than 25%	More than 25% Less than 25%
Probability to reach QET	The probability that the quasi-extinction threshold (QET) estimated for this DIP will be reached within 100 years (from a population viability analysis, if available)	Less than 20% More than 20%
Intermediate Node: VSP abundance	The probability that the DIP’s abundance poses a risk to DIP viability	Low risk Moderate risk High risk
Mean population growth rate	<i>Input Nodes: VSP productivity</i> The probability that the mean population growth rate estimated for this DIP is less than one (declining population size) or greater than one (increasing population size). This metric is influenced by two major components: smolts per spawner and adults per smolt (below)	Greater than 1 Less than 1

Table 10. Continued.

Node title	Node description	States
Smolts per spawner	A measure of productivity in freshwater (and a component of population growth rate), it is the probability that the number of smolts produced per spawner in the DIP is less than 50 or more than 50	Greater than 50 Less than 50
Adults per smolt	A measure of productivity in the ocean (and a component of population growth rate), it is the probability that the smolt to adult survival rate in the DIP is less than 2% or more than 2%	Greater than 2% Less than 2%
Frequency of repeat spawners	The probability that the frequency of repeat spawning in this DIP is historical (e.g., 10-20%) or compressed (< 10%)	Historical Depressed
<i>Intermediate Node: VSP productivity</i>	The probability that the DIP's productivity poses a risk to DIP viability	Low risk Moderate risk High risk
Run timing	<i>Input Nodes: VSP diversity</i> The probability that the current distribution of spawn timing (within a run type) in the DIP is historical vs truncated or altered	Historical Altered
Hatchery influence	The probability that hatchery influence from Chambers Cr. WSH or Skamania SSH stock in the DIP is nominal or extensive (e.g., hatchery plants have occurred for >5 years and/or involved more than 500,000 fish)	Nominal Extensive
Fraction of smolts from residents	The probability that the fraction of smolts produced by residents in the DIP is appreciable or negligible (e.g., the fraction of smolts produced by residents is more than 10% or less than 10%)	Appreciable Negligible

Table 10. Continued.

Node title	Node description	States
	<i>Input Nodes: VSP spatial structure</i>	
Fraction of IP spawning habitat	The fraction of estimated available steelhead spawning habitat area in the DIP (IP), under historical conditions, utilized by the current distribution of spawners. In the network's current form, this is the estimated fraction (%) of accessible spawning habitat that is occupied	Greater than 20% Less than 20%
Fraction of IP rearing habitat	The fraction of estimated available steelhead rearing habitat area in the DIP (IP), under historical conditions, utilized by the current distribution of rearing juveniles. In the network's current form, this is the estimated fraction (%) of accessible rearing habitat that is occupied	Greater than 20% Less than 20%
<i>Intermediate Node: VSP spatial structure</i>	The probability that the DIP's spatial structure poses a risk to DIP viability	Low risk Moderate risk High risk
<i>Decision Node: DIP viability</i>	The probability that the DIP is viable (based on the collective influence of the four VSP parameters on DIP viability)	Viable Not viable
<i>Decision Node: MPG viability</i>	The probability that the MPG is viable (based on the collective influence of the viabilities of each of its composite DIPs)	Viable Not viable

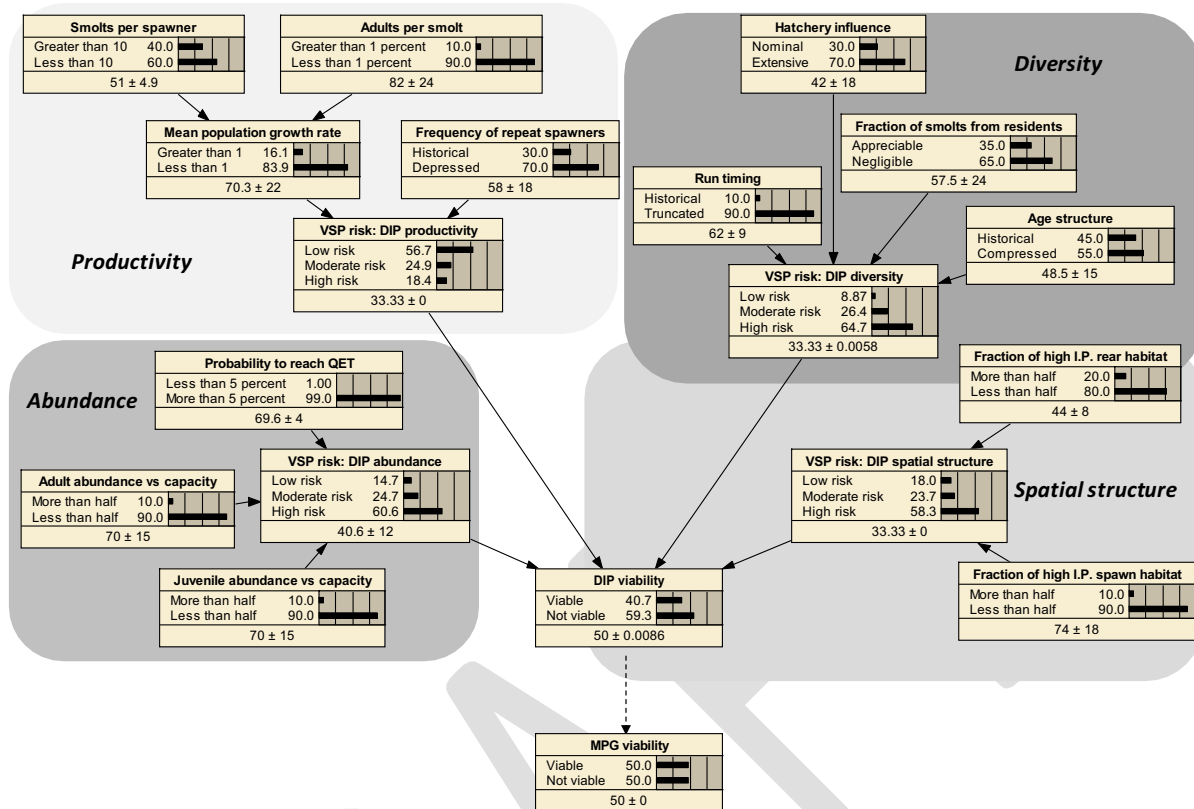


Figure 60. A Bayesian Network to characterize the viability of a hypothetical Demographically Independent Population (DIP) of summer-run steelhead in the Puget Sound DPS. The primary differences between this BN and that for winter-run steelhead are in the conditional probabilities underlying abundance, productivity, and diversity (especially the run timing and hatchery influence nodes). See the caption for Figure 59 for details.

We weighted abundance and productivity criteria equally with diversity and spatial structure criteria in our network CPTs even though the evidence was that DIP viability for Puget Sound steelhead was somewhat more dependent on how current abundance compared with historical estimates, based on preliminary networks constructed before weighting (Figure 61). Comparisons of estimates of relative viability for Puget Sound steelhead DIPs between current (“depressed”) and historical estimates of the four VSP parameters (abundance, productivity, diversity and spatial structure) point to the primary importance of abundance to DIP viability. Therefore, after constructing each network, in assessing final categories of viability for each DIP we weighted mean abundance and productivity criteria more heavily than mean diversity and spatial structure criteria for this reason and because more quantitative demographic information was available (see “Viability Criteria” section, p. 164).

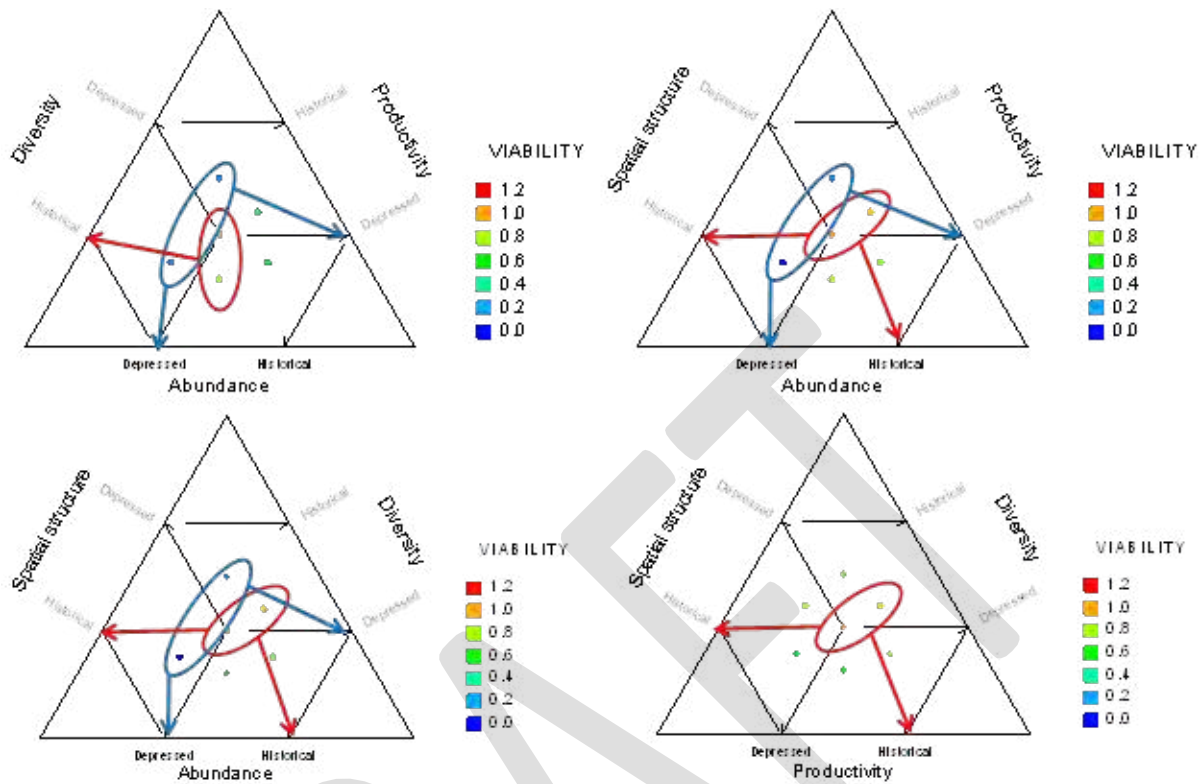


Figure 61. Comparisons of estimates of relative viability for Puget Sound steelhead DIPs between current (“depressed”) and historical estimates of VSP parameters (abundance, productivity, diversity and spatial structure). The red ovals encompass the highest estimates of DIP viability; the blue ovals encompass the lowest estimates. Note that the blue ovals tend to be shifted to the left of the red ovals, indicating the important contribution of abundance to DIP viability.

Table 11. Conditional probability table (CPT) for the input nodes describing risk for each VSP parameter for the Bayesian Networks describing viability of Puget Sound steelhead populations (DIPs). The probabilities input for each DIP were estimated from data, PVA results, and expert opinion as described in the text.

Abundance			Risk			Productivity		Risk			
Adult abundance vs capacity	Juvenile abundance vs capacity	P(QET)	Low	Moderate	High	Mean growth rate	Frequency repeats	Low	Moderate	High	
More than 25%	More than 25%	Less than 10%	90	9	1	Greater than 1	Historical	90	9	1	
More than 25%	More than 25%	More than 10%	75	15	10	Greater than 1	Depressed	70	20	10	
More than 25%	Less than 25%	Less than 10%	60	15	25	Less than 1	Historical	40	40	20	
More than 25%	Less than 25%	More than 10%	40	20	40	Less than 1	Depressed	1	9	90	
Less than 25%	More than 25%	Less than 10%	15	25	60						
Less than 25%	More than 25%	More than 10%	10	20	70						
Less than 25%	Less than 25%	Less than 10%	15	20	65						
Less than 25%	Less than 25%	More than 10%	1	9	90						
							Population growth rate	Value			
							Adults per smolt	Smolts per spawner	Greater than 1	Less than 1	
							Greater than 2%	Greater than 50	95	5	
							Greater than 2%	Less than 50	40	60	
							Less than 2%	Greater than 50	20	80	
							Less than 2%	Less than 50	5	95	

Table 11. Cont'd.

Diversity				Risk			Spatial structure		Risk		
Run timing	Fraction smolts from residents	Age structure	Hatchery influence	Low	Moderate	High	Fraction IP rear habitat	Fraction IP spawn habitat	Low	Moderate	High
Historical	Appreciable	Historical	Nominal	90	9	1	Greater than 20%	Greater than 20%	70	25	5
Historical	Appreciable	Historical	Extensive	69	20	11	Greater than 20%	Less than 20%	50	20	30
Historical	Appreciable	Compressed	Nominal	60	30	10	Less than 20%	Greater than 20%	50	20	30
Historical	Appreciable	Compressed	Extensive	54	25	21	Less than 20%	Less than 20%	5	25	70
Historical	Negligible	Historical	Nominal	40	40	20					
Historical	Negligible	Historical	Extensive	39	30	31					
Historical	Negligible	Compressed	Nominal	20	50	30					
Historical	Negligible	Compressed	Extensive	19	40	41					
Altered	Appreciable	Historical	Nominal	10	50	40					
Altered	Appreciable	Historical	Extensive	9	40	51					
Altered	Appreciable	Compressed	Nominal	10	40	50					
Altered	Appreciable	Compressed	Extensive	9	30	61					
Altered	Negligible	Historical	Nominal	5	35	60					
Altered	Negligible	Historical	Extensive	4	25	71					
Altered	Negligible	Compressed	Nominal	5	20	75					
Altered	Negligible	Compressed	Extensive	1	9	90					

Table 12. Conditional probability table (CPT) describing the influence of each of the four VSP parameters on DIP viability for the Bayesian Networks describing viability of Puget Sound steelhead. Note that the values in the first four columns are risk values, e.g., a value of “Low” for DIP abundance implies a low risk to DIP viability posed by abundance in the DIP. The values were chosen to produce a linear relationship between VSP category and DIP viability (with a consequent distribution of probability of being viable ranging from 0-100%), with all VSP criteria weighted equally. The viability scores for this BN are graphed in the bar plots for various combinations of DIP abundance, DIP productivity, DIP diversity, and DIP spatial structure in Figure 64.

DIP abundance	VSP risk			DIP viability	
	DIP productivity	DIP diversity	DIP spatial structure	Viable	Not viable
Low	Low	Low	Low	100.0	0.0
Low	Low	Low	Moderate	91.7	8.3
Low	Low	Low	High	83.3	16.7
Low	Low	Moderate	Low	91.7	8.3
Low	Low	Moderate	Moderate	83.3	16.7
Low	Low	Moderate	High	75.0	25.0
Low	Low	High	Low	83.3	16.7
Low	Low	High	Moderate	75.0	25.0
Low	Low	High	High	66.7	33.3
Low	Moderate	Low	Low	83.3	16.7
Low	Moderate	Low	Moderate	75.0	25.0
Low	Moderate	Low	High	66.7	33.3
Low	Moderate	Moderate	Low	75.0	25.0
Low	Moderate	Moderate	Moderate	66.7	33.3
Low	Moderate	Moderate	High	58.3	41.7
Low	Moderate	High	Low	66.7	33.3
Low	Moderate	High	Moderate	58.3	41.7
Low	Moderate	High	High	50.0	50.0
Low	High	Low	Low	66.7	33.3
Low	High	Low	Moderate	58.3	41.7
Low	High	Low	High	50.0	50.0
Low	High	Moderate	Low	58.3	41.7
Low	High	Moderate	Moderate	50.0	50.0
Low	High	Moderate	High	41.7	58.3
Low	High	High	Low	50.0	50.0
Low	High	High	Moderate	41.7	58.3
Low	High	High	High	33.3	66.7
Moderate	Low	Low	Low	83.3	16.7
Moderate	Low	Low	Moderate	75.0	25.0

Table 12.
Cont’d.

Moderate	Low	Low	High	66.7	33.3
Moderate	Low	Moderate	Low	75.0	25.0
Moderate	Low	Moderate	Moderate	66.7	33.3
Moderate	Low	Moderate	High	58.3	41.7
Moderate	Low	High	Low	66.7	33.3
Moderate	Low	High	Moderate	58.3	41.7
Moderate	Low	High	High	50.0	50.0
Moderate	Moderate	Low	Low	66.7	33.3
Moderate	Moderate	Low	Moderate	58.3	41.7
Moderate	Moderate	Low	High	50.0	50.0
Moderate	Moderate	Moderate	Low	58.3	41.7
Moderate	Moderate	Moderate	Moderate	50.0	50.0
Moderate	Moderate	Moderate	High	41.7	58.3
Moderate	Moderate	High	Low	50.0	50.0
Moderate	Moderate	High	Moderate	41.7	58.3
Moderate	Moderate	High	High	33.3	66.7
Moderate	High	Low	Low	50.0	50.0
Moderate	High	Low	Moderate	41.7	58.3
Moderate	High	Low	High	33.3	66.7
Moderate	High	Moderate	Low	41.7	58.3
Moderate	High	Moderate	Moderate	33.3	66.7
Moderate	High	Moderate	High	25.0	75.0
Moderate	High	High	Low	33.3	66.7
Moderate	High	High	Moderate	25.0	75.0
Moderate	High	High	High	16.7	83.3
High	Low	Low	Low	66.7	33.3
High	Low	Low	Moderate	58.3	41.7
High	Low	Low	High	50.0	50.0
High	Low	Moderate	Low	58.3	41.7
High	Low	Moderate	Moderate	50.0	50.0
High	Low	Moderate	High	41.7	58.3
High	Low	High	Low	50.0	50.0
High	Low	High	Moderate	41.7	58.3
High	Low	High	High	33.3	66.7
High	Moderate	Low	Low	50.0	50.0
High	Moderate	Low	Moderate	41.7	58.3
High	Moderate	Low	High	33.3	66.7
High	Moderate	Moderate	Low	41.7	58.3
High	Moderate	Moderate	Moderate	33.3	66.7
High	Moderate	Moderate	High	25.0	75.0

Table 12.
Cont’d.

High	Moderate	High	Low	33.3	66.7
High	Moderate	High	Moderate	25.0	75.0
High	Moderate	High	High	16.7	83.3
High	High	Low	Low	33.3	66.7
High	High	Low	Moderate	25.0	75.0
High	High	Low	High	16.7	83.3
High	High	Moderate	Low	25.0	75.0
High	High	Moderate	Moderate	16.7	83.3
High	High	Moderate	High	8.3	91.7
High	High	High	Low	16.7	83.3
High	High	High	Moderate	8.3	91.7
High	High	High	High	0.0	100.0

Our approach to parameterizing the BNs for each DIP was as follows. For the abundance criterion, we first computed each DIP’s geometric mean abundance over the most recent five years from available abundance data. For DIPs which have no recent abundance data, we used the mean geometric mean abundance for all DIPs within the MPG, scaled by the estimate of total intrinsic potential (IP) area for that DIP, as the input variable. (For the Northern Cascades MPG, we excluded the Skagit River basin for these calculations for DIPs with no abundance data because of its uniquely large size among drainages within the MPG.) We computed the probability that the DIP would reach its estimated quasi-extinction threshold (QET) abundance within 100 years; the QET for each DIP was based on the DIP habitat’s estimate of intrinsic potential, the empirical Puget Sound steelhead parr densities computed by Gibbons et al. (1985) (using an estimate of 0.0754 parr/m²), and the Chapman (1981) estimate of parr to smolt survival of 0.30 to estimate smolt productivity at 0.023 smolts/m². For each DIP we calculated the probability of reaching QET using auto-regressive state-space (MARSS) algorithms applied to the abundance data as described in an earlier section (see “Population Viability Analysis With Auto-regressive State-Space Models”). For those DIPs for which we could not calculate QETs, we used the mean QET computed for the associated MPG as the input variable.

We used the IP metrics (i.e., the sum of low, medium and high IP areas in reaches accessible by steelhead) and the juvenile steelhead densities estimated by Gibbons et al. (1985) and Chapman (1981) for each DIP to calculate parr and smolt densities and spawner abundances based on 1%, 5%, and 20% marine survival rates; we considered these minimum, viable, and capacity abundances, respectively (see Appendix C). We then parameterized the influence of abundance on probabilities of viability in the BNs for each DIP using a compound rule: if the estimated geometric mean abundance was < 25% of the adult abundance calculated from occupied IP area at a density of at least 1 fish/km at a marine survival rate < 1%, the probability of viability was 20%; if the abundance was less than that for 1 fish/km at a marine survival rate < 5%, the probability was 40%; if the abundance was less than that for 1 fish/km at a marine

survival of 20%, the probability was 80%; otherwise, the probability was 90%. Using this rule the probabilities of DIP viability based on abundance alone ranged from 20-90%. In addition, we used the output from the PVAs for available DIPs to estimate the probability that a population was near its QET abundance. We did so in this way: if the ratio of the recent (last five years) geometric mean abundance to the QET was greater than 10, the probability that abundance was near QET was 10%; if this ratio was greater than 8, the probability was 20%; if this ratio was greater than 6, the probability was 40%; if this ratio was greater than 4, the probability was 60%; if this ratio was greater than 2, the probability was 80%; otherwise, the probability was 90%. We applied these probabilities to both adult and juvenile abundances because we had almost no information on historical or current juvenile abundances. These probabilities were then entered into each BN's conditional probability table for the abundance criterion and combined with the other probabilities in Table 11 to determine the overall contribution of abundance to DIP viability.

For the productivity criterion, we relied primarily on the long-term population growth rate (λ) estimated by the PVAs from MARSS. For DIPs that we could calculate this metric for we used the mean growth rate computed for all DIPs within the MPG. We parameterized the influence of productivity on probabilities of viability in the BNs for each DIP in this way: if the point estimate of growth rate was greater than 1.1, the probability of viability was 90%; if the growth rate was between 1.0 and 1.1, the probability of viability was 80%; if the growth rate was between 0.99 and 1.0, the probability was 70%; if the growth rate was between 0.95 and 0.99, the probability was 50%; if the growth rate was between 0.90 and 0.95, the probability was 30%; if the growth rate was between 0.85 and 0.9, the probability was 20%; otherwise, the probability was 10%. We selected values of smolts per spawner and adults per smolt to approximate the specified growth rates estimated from the PVAs, so that freshwater and marine influences on productivity could be accounted for separately in the network. Probabilities for the influence of frequency of iteroparity on viability through productivity were determined by consensus among TRT members. All these probabilities were then entered into the CPTs in Table 11 to determine the overall contribution of productivity to DIP viability.

For the diversity criterion, we relied primarily on two considerations: 1) the potential influence of hatchery-produced steelhead, most of which are either highly domesticated (Chambers Creek winter-run) or out-of-basin source stocks (Skamania River summer-run), on wild fish; and 2) evidence for an alteration in natural spawn timing from historical patterns. Iteroparity was under consideration as a factor influencing diversity because of its importance as a temporal risk-spreading strategy, but the TRT decided to consider iteroparity under productivity because of its strong influence on population growth rate. To assess hatchery influence, each DIP we looked at the number of years of hatchery plants and the cumulative number of hatchery fish planted, based on historical hatchery records. We parameterized the influence of this diversity element on probabilities of viability in the BNs for each DIP in this way: if the number of years of hatchery plants was fewer than five, the probability of extensive hatchery influence was 10%; if there were no hatchery plants, the probability was 5%. If, however the number of years of hatchery plants was five or more, we calculated the average annual number of hatchery fish planted by dividing the cumulative number of hatchery fish planted by the number of years planted. This number was then divided by the estimated intrinsic potential area and multiplied by 1000. If this metric was greater than 60, the probability of

extensive hatchery influence from this diversity criterion was 90%; if it was between 40 and 60, the probability was 80%; if it was between 30 and 40, the probability was 60%; if it was between 20 and 30, the probability was 40%; if it was between 10 and 20, the probability was 20%; otherwise, the probability was 10%.

To assess whether spawn timing was altered, we examined current spawn timing distributions relative to available documentation for historical distributions from unpublished reports and the published literature (see the reference list at the end of Appendix F; “Selected Steelhead Documents,” p. 366). We parameterized the influence of this diversity element on probabilities of viability in the BNs for each DIP in this way: if there was evidence that the current distribution had changed (e.g., shifted earlier or become compressed) relative to the historical distribution for a particular DIP, the probability of viability was 60%; if there was no evidence for change, the probability was 95%. Probabilities for other diversity factors affecting viability (fraction of smolts from resident fish and age structure) were determined by consensus among TRT members. There are no available data on the first factor for Puget Sound steelhead, but the TRT considered it important to include because resident fish that are sympatric with anadromous fish are known from studies of several steelhead populations to be capable of producing smolts, which could provide a demographic buffer, especially for small populations. There are some age data available for selected Puget Sound steelhead populations. All these probabilities, including those for effects of hatchery fish production, were then combined with those in Table 11 to determine the overall contribution of diversity to DIP viability.

Finally, for the spatial structure criterion, we first examined how steelhead DIPs tended to be related according to habitat characteristics, estimating a Gower similarity coefficient (Gower 1971) that incorporated maximum elevation, current spawnable area, mean bankfull width, mean stream gradient, maximum mean temperature, and presence of permanent snowpack. The Gower index clustered the DIPs according to the dendrogram in Figure 62 with an agglomerative coefficient of 0.93. Three primary clusters are evident in the dendrogram: one for high elevation areas of moderate to high gradient and influenced by snowpack (left), one for low gradient areas with little or no snowpack influence (right), and one for streams with intermediate characteristics (middle).

We determined probabilities of viability in the BNs for each DIP by first determining occupancy of adult steelhead in reaches within distinct habitat classes incorporating steelhead IP area as described in Appendix C. We further categorized stream reaches by whether they were mainstem or tributary, and whether the hydrograph was influenced by snowpack or not (intersection of the reach with a 0°C contour in January).

We then performed a series of regressions and multivariate analyses (employing principal components analysis, or PCA) to examine the relationships between observed steelhead productivity and habitat occupancy. These analyses revealed weak but significant relationships between drainage-wide productivity, as measured by population growth rate (λ) or exponential trend in abundance, and steelhead occupancy of smaller mainstem and larger tributary reaches influenced by snowpack. Linear regressions of λ or exponential trend in abundance on occupancy of particular habitat classes incorporating steelhead IP area revealed that these productivity metrics increased most strongly with occupancy of tributary reaches influenced by snowpack; the relationships were relatively weak ($r^2 = 0.1-0.2$) but this reflected primarily a rise

in productivity when a small fraction of the total IP represented by that habitat class was occupied (10-15% or more).

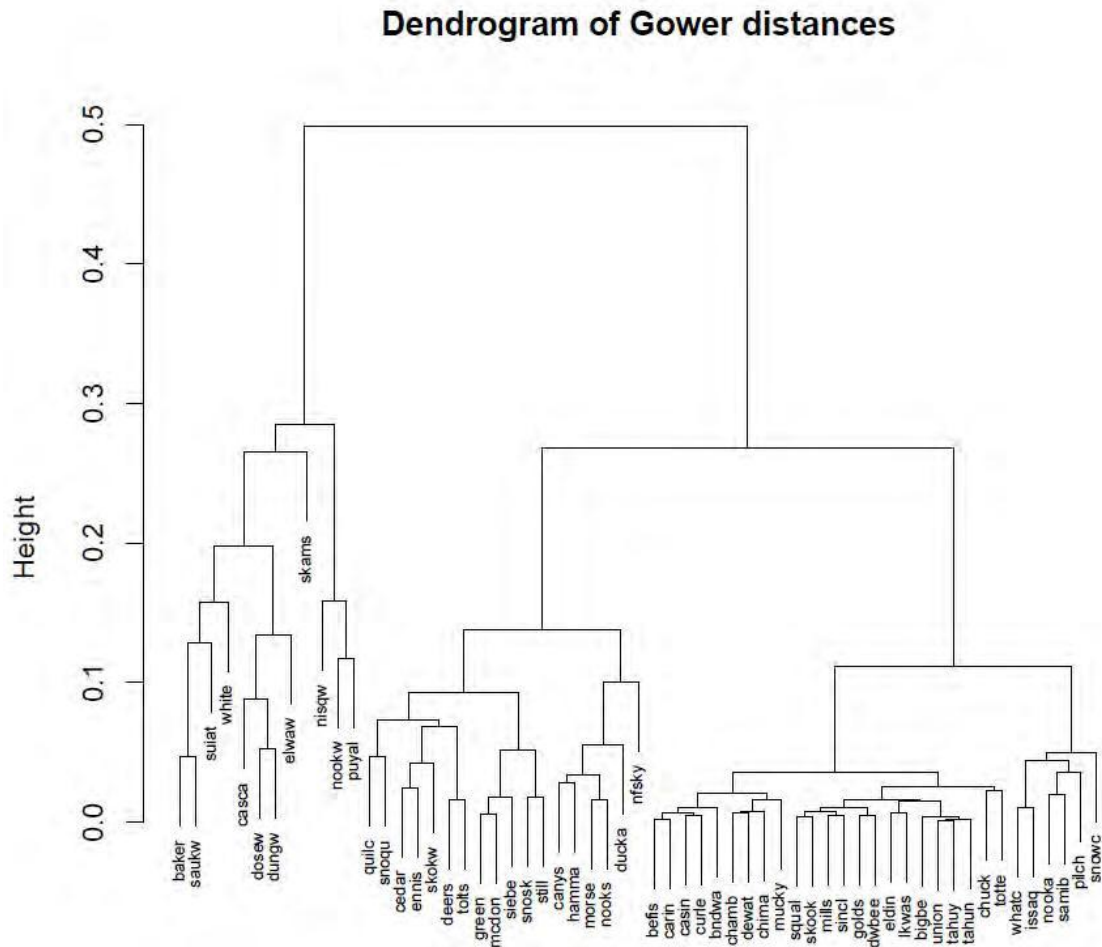


Figure 62. Relationships among steelhead DIPs with the Puget Sound DPS based on a Gower similarity index (Gower 1971) computed from six habitat variables: maximum elevation, current spawnable area, mean bankfull width, mean stream gradient, maximum mean temperature, and presence of permanent snowpack. The agglomerative coefficient is 0.93. Three primary clusters are evident in the dendrogram: one for high elevation areas of moderate to high gradient and influenced by snowpack (left), one for low gradient areas with little or no snowpack influence (right), and one for streams with intermediate characteristics (middle).

For example, a PCA (with varimax rotation of principal components) of spawner occupancy (fraction of total IP area occupied by spawning steelhead) and population growth rate across various habitat categories (mainstem vs tributary, three stream width classes, three stream gradient classes, and snowpack vs no snowpack influence) produced eight eigenvectors with eigenvalues > 1.0 , explaining 85.8% of the variation. Although the relationships were complex, many of the higher loadings on the first 2-3 principal components were associated with snowpack (more positive values) vs no snowpack (more negative values), with higher productivity also associated with occupancy of stream reaches of particular widths and gradients.

A PCA of a subset of the data focusing on smaller mainstem and larger tributary reaches (3-20 m) of moderate to high gradient ($> 0.25\%$) revealed two principal components that explained 73.5% of the variation and showed that population growth rate was most closely associated with steelhead occupancy of reaches influenced by snowpack. A PCA of tributary reaches alone revealed two principal components that explained 77.9% of the variation and showed that population growth rate was highly associated with steelhead occupancy of reaches with snowpack. Finally, a PCA of tributary reaches influenced by snowpack revealed two principal components that explained 84.6% of the variation and showed that population growth rate was highly associated with steelhead occupancy of larger reaches with moderate to high gradient.

We used this information to parameterize the influence of the spatial structure element on probabilities of viability in the BNs for each DIP in a simple way: if the proportion of occupied IP habitat area in mainstem reaches < 20 m bankfull width and influenced by snowpack and in tributary reaches > 3 m bankfull width and influenced by snowpack was less than 20%, the probability of viability was 40%; if the proportion was 20% or more, the probability of viability was 80%. We used 20% of historical area as our baseline because the regressions of population growth rate on occupancy rate indicated a positive change in productivity of steelhead if occupancy of these habitat areas exceeded this rate. We applied these probabilities to both spawning and rearing occupancies because we had almost no information on rearing occupancy. These probabilities were then combined with those in Table 11 to determine the overall contribution of spatial structure to DIP viability.

We determined the overall viability of each DIP from each DIP-level BN using the conditional probabilities shown in Table 12. Supplementary data describing each DIP are summarized in Appendix D. For many DIPs, some specific viability assessments are based on little or no quantitative information. Although some critics might argue that the criteria these assessments are assigned to can be considered “placeholders” and should be left out of a Bayesian network framework until better information becomes available, we include them for three reasons:

- Eliminating such factors from the network, when they are thought to be important to an overall assessment, defeats the purpose of creating an informative network;
- Bayesian networks are designed to accommodate both factors that can be quantified and those that are evaluated based on collective judgement in the absence of more definitive information, which can be updated when more information becomes available; and
- Eliminating such factors tends to place higher importance on factors with better information, regardless of whether those factors are more critical to viability or not.

DIP viability—The conditional probabilities underlying the BN for the hypothetical winter-run steelhead population in Puget Sound (Figure 59; Tables 11-12) lead to the conclusion that the viability of this DIP is relatively low (45.4%); the probability that the DIP is viable should be on the order of 90% or higher to be confident of viability. If additional information led us to conclude that the population is in fact larger than the low-abundance threshold (adult abundance, probability = 100%) and its growth is positive (i.e., $\lambda > 1$, probability = 100%), the BN estimates that the probability that the population is viable rises to 60.4%. If, on the other hand, additional information led us to conclude that the population is in fact smaller than the low-abundance threshold (probability = 100%) and its growth is negative ($\lambda < 1$, probability = 100%), the BN estimates that the probability the population is viable drops to 41.9%. Certainty that hatchery influence is nominal and that resident fish produce an appreciable fraction of smolts, with no instantiation at any other node in the network, prompts the estimate of probability that the population is viable to increase to 48.9%. Certainty that more than half the high intrinsic potential spawning habitat is at capacity for adults, with no instantiation at any other node, prompts the probability that the population is viable to rise to 51.2%. Meeting most of the criteria for the positive contribution of VSP parameters in the network to DIP viability goes a long way to increasing probability that the DIP is viable; for example, if all of the lowest-level parent nodes in the network except for iteroparity and resident smolt production are instantiated at the highest levels, the probability that the DIP is viable rises to 84.2%. If all such criteria are satisfied, the probability that the DIP is viable is 92.5%. The reason it is no higher is because of uncertainty in the overall contribution of risk for each VSP parameter, reflected by the distribution of probabilities there. This uncertainty is not zero because not all factors that can influence risk for each VSP parameter are considered in the network.

Similarly, the conditional probabilities underlying the BN for the hypothetical summer-run steelhead population in Puget Sound (Figure 60, Tables 11-12) lead to the conclusion that the viability of this DIP is low (40.7%). Instantiating the network at the adult low-abundance threshold (probability = 100%) and positive population growth ($\lambda > 1$, probability = 100%) causes the probability that the population is viable rises to 58.8%. Instantiating at the adult low-abundance threshold (probability = 100%) and negative population growth ($\lambda < 1$, probability = 100%) causes the probability the population is viable to drop to 38.3%. As for the winter-run steelhead BN, meeting most of the criteria for the positive contribution of VSP parameters in the network to DIP viability goes a long way to increasing probability that the DIP is viable; if all of the lowest-level parent nodes in the network except for iteroparity and resident smolt production are instantiated at the highest levels, the probability that the DIP is viable rises to 85.1%. (cf. 84.2% for the winter-run case). If all such criteria are satisfied, the probability that the DIP is viable is again 92.5%. The results of the sensitivity analyses for this BN are essentially identical to those for the winter-run case (Table 13).

The Most Probable Explanation, or MPE, for a BN is an estimate of the most likely network, given the current evidence (i.e., the distributions of conditional probabilities). In other words, it is the most plausible explanation of the data given the evidence. The MPEs for these BNs indicate that neither of these DIPs is viable. The MPEs also indicate that for each network, the risk of DIP abundance to viability is high, that the risk of DIP productivity to viability is low, that the risk of DIP diversity to viability is high, and that the risk of DIP spatial structure to viability is high. These MPE estimates are consistent with the probability distributions for these

nodes depicted in Figures 59 and 60. Under MPE, the uncertainty that each DIP is not viable is relatively high; the probability that each DIP is viable is 49.9%.

Table 13. Results of a sensitivity analysis of the influence of three components of DIP abundance to the VSP risk posed by DIP abundance in the Bayesian Network (BN) given in Figure 60.

Sensitivity of ‘DIP abundance’ to findings at ‘Juvenile abundance’:

Probability ranges:	Min	Current	Max	RMS Change
Low risk	0.1565	0.262	0.5785	0.1827
Moderate risk	0.2349	0.247	0.251	0.006972
High risk	0.1866	0.491	0.5925	0.1758
Mean of Real Value:	27.95	37.2	40.29	5.343
Variance reduction	= 28.54 (16.7 %)			
Entropy reduction	= 0.1335 (8.85 %)			

Table 13. Continued.

Belief Variance	= 0.0247 (6.03 %)			
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Sensitivity of ‘DIP abundance’ to findings at ‘Adult abundance’:

Probability ranges:	Min	Current	Max	RMS Change
Low risk	0.1806	0.262	0.5875	0.1628
Moderate risk	0.1949	0.247	0.26	0.02605
High risk	0.2176	0.491	0.5594	0.1367
Mean of Real Value:	28.48	37.2	39.38	4.361
Variance reduction	= 19.02 (11.1 %)			
Entropy reduction	= 0.0945 (6.26 %)			
Belief Variance	= 0.01889 (4.61 %)			

Sensitivity of ‘DIP abundance’ to findings at P(QET):

Probability ranges:	Min	Current	Max	RMS Change
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Table 13. Continued.

Low risk	0.255	0.262	0.395		0.03051
Moderate risk	0.24	0.247	0.3795		0.0304
High risk	0.2255	0.491	0.505		0.06092
Mean of Real Value:	30.56	37.2	37.55		1.523
Variance reduction	= 2.321 (1.36 %)				
Entropy reduction	= 0.01133 (0.751 %)				
Belief Variance	= 0.001594 (0.389 %)				
Sensitivity of 'DIP abundance' to a finding at another node:					
Node	Variance Reduction	Percent	Mutual Info	Entropy Reduction	Belief Variance
Juvenile abundance	28.54	16.7	0.13347	8.85	0.0247045
Adult abundance	19.02	11.1	0.09450	6.26	0.0188911
P(QET)	2.321	1.36	0.01133	0.751	0.0015942

Figure 63 shows how the four different VSP criteria combine to affect the probability that a representative steelhead DIP in Puget Sound is viable. In this example, abundance and productivity have the greatest influences on viability, approximately twice those of diversity and spatial structure. The contributions of the four VSP criteria to the probability of viability for all 32 candidate DIPs, as estimated from the BNs, are summarized in Figure 64.

The Bayesian Networks for viability for each of the 32 candidate DIPs identified by the TRT for the Puget Sound DPS indicate that population viabilities vary appreciably both within and among MPGs, but these viabilities are all low (each of the 32 BNs is given in Appendix B). Over the entire DPS, the probabilities that a DIP was viable are estimated from the BNs to range from 33.4 to 60.2%, with an average of 44.1%. Average DIP viability is 47.9% in the Northern Cascades MPG, 39.9% in the Central and South Puget Sound MPG, and 40.6% in the Hood Canal and Strait of Juan de Fuca MPG. Average DIP viability for winter-run populations (or those that include both winter- and summer-run fish) across the DPS is 42.7%; average viability for summer-run populations across the DPS is 52.7%. In most cases, these viabilities reflect the substantial influence of all four VSP criteria, but especially of abundance and diversity, as components of the BN models.

To illustrate how viability of the 32 candidate steelhead DIPs varies with respect to the influence of each of the four VSP criteria, we plot estimated DIP viability as a function of the influence of pairs of these criteria. Figure 63 depicts the influence of the values of abundance and productivity on the estimate of viability. Higher values of the VSP components indicate higher influence on viability. Viabilities are computed from the DIP-level Bayesian Networks in Appendix B.

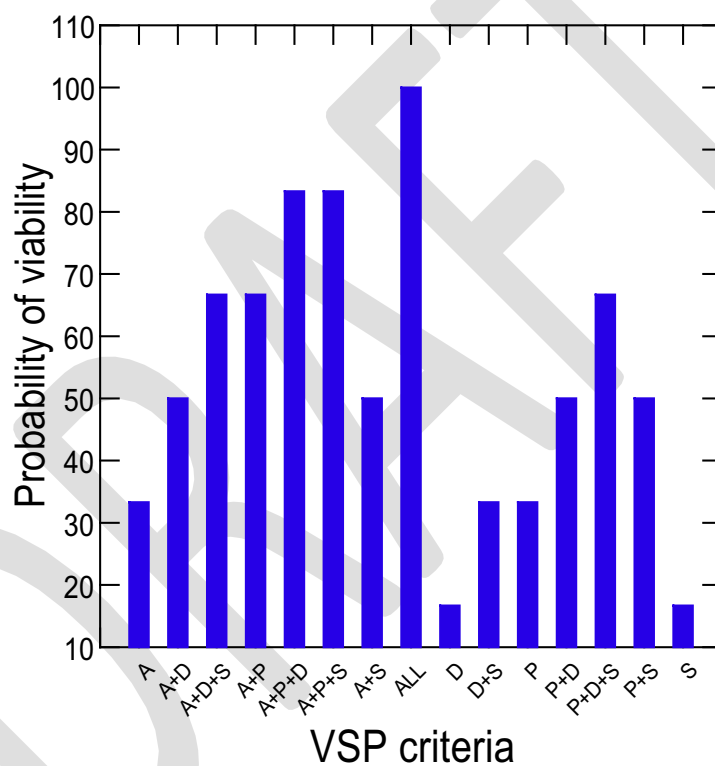


Figure 63. Bar plot showing how the probabilities of viability for a representative Demographically Independent Population (DIP) of Puget Sound steelhead vary with the contribution to risk from different combinations of viable Salmonid Population (VSP) criteria. Probabilities were derived from the Bayesian Network model of steelhead population viability. In this example, abundance and productivity criteria are weighted twice those for diversity and spatial structure. A = abundance, P = productivity, D = diversity, and S = spatial structure.

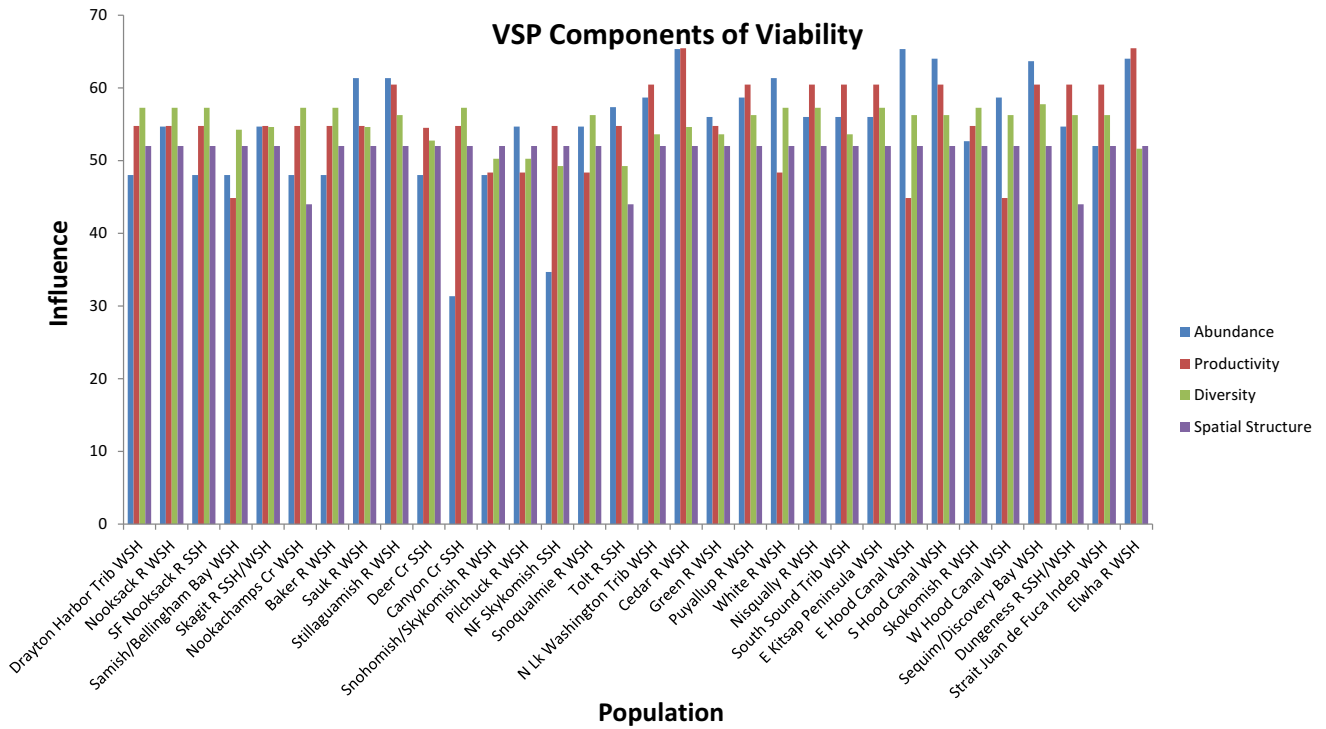


Figure 64. Bar plot of the relative influences of the four Viable Salmonid Populations (VSP) parameter estimates (abundance, productivity, diversity, and spatial structure) applied to the viabilities of each of the 32 candidate Demographically Independent Populations of steelhead in the Puget Sound Distinct Population Segment. These values are estimated from the respective Bayesian Networks.

The plots reveal interesting geographical patterns in population viability and how it varies with the VSP criteria. With respect to the combination of VSP abundance and productivity, viability is generally highest for DIPs in the Northern Cascades MPG (Figure 65). The BN models indicate that viability with respect to abundance and productivity is highest for a few Northern Cascades DIPs (e.g., Canyon Creek summer-run and North Fork Skykomish summer-run; probabilities of viability = 55-60%). The viabilities of these DIPs are influenced more by productivity than by abundance. Most other populations in this MPG with lower viabilities are influenced more by low abundance. Viabilities are lower in the Central and South Puget Sound and Hood Canal and the Strait of Juan de Fuca MPGs, in general, and were lowest in the Central and South Puget Sound MPG, where most populations are at low abundance (e.g., Cedar River and Puyallup River winter-run; probabilities of viability 30-40%). In the latter MPG, only the White River winter-run DIP shows modest viability. The decline in DIP viability with declining abundance and productivity is clearly nonlinear, and viability seems to be somewhat more sensitive to productivity than to abundance. Most DIPs in the DPS exhibit low probabilities of viability with respect to abundance and productivity (40-50%).

With respect to the combination of VSP abundance and diversity, there is less variation evident for the influence of diversity on DIP viability (Figure 66). For DIPs in both the Central and South Puget Sound and the Hood Canal and Strait of Juan de Fuca MPGs, where viabilities are lower, populations are influenced by both low abundance and low diversity. DIPs in the Northern Cascades MPG tend to show a wider range of viabilities and, on average, viabilities are higher with respect to these criteria. The change in DIP viability with abundance and diversity is highly variable. As for abundance and productivity, most DIPs in the DPS exhibit low probabilities of viability with respect to abundance and diversity (40-50%).

With respect to the combination of VSP abundance and spatial structure, the two summer-run DIPs with highest viabilities (Canyon Creek and North Fork Skykomish River) show a strong influence of spatial structure (Figure 67). Only Nookachamps Creek winter-run and Tolt River summer-run in the Northern Cascades MPG and Dungeness River summer- and winter-run in the Hood Canal and Strait of Juan de Fuca MPG showed a relatively modest influence of spatial structure on viability. Most DIPs throughout the DPS showed an appreciable influence of both abundance and spatial structure on viability.

The influences of VSP productivity and diversity on DIP viability are more variable than those for the previous combinations of VSP parameters (Figure 68). The DIPs with the lowest viabilities (e.g., Sequim/Discovery Bay winter-run and Elwha River winter-run, Cedar River winter-run) indicate the very high influence of low productivity. Those with the highest viabilities (e.g., Canyon Creek summer-run and North Fork Skykomish summer-run) show a more consistent influence of productivity than of diversity. Viability appears to be most sensitive to low productivity.

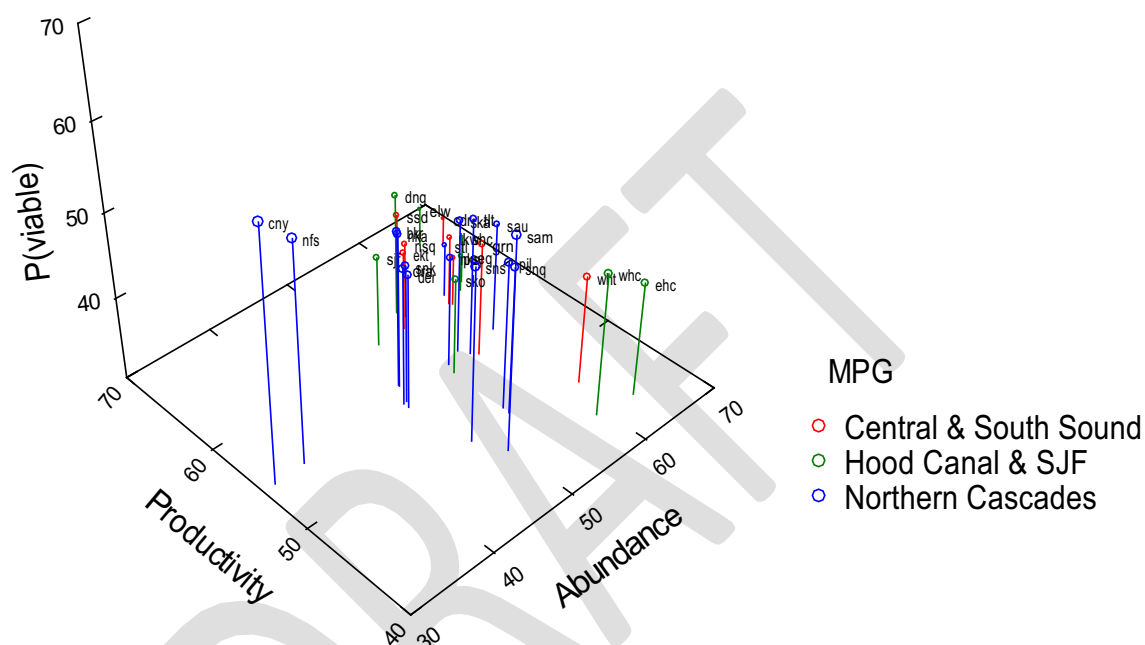


Figure 65. Scatter plot of the viabilities of each of the 32 candidate Demographically Independent Populations of steelhead in the Puget Sound Distinct Population Segment as a function of their Viable Salmonid Populations (VSP) parameter estimates of influence of abundance and productivity. Viabilities are computed from the DIP-level Bayesian Networks in Appendix A. Abundance and productivity scores are estimated from intermediate metrics computed by the DIP-level Bayesian Networks. The DIP symbols (WSH, winter-run steelhead; SSH, summer-run steelhead) are color coded by MPG: blue, Northern Cascades; red, Central and South Puget Sound; green, Hood Canal and Strait of Juan de Fuca. Three-letter DIP codes are: dra, Drayton Harbor Tributaries WSH; nks, Nooksack R. WSH; sns, S. Fk. Nooksack R. SSH; sam, Samish R./Bellingham Bay WSH; ska, Skagit R. SSH/WSH; nka, Nookachamps Cr. WSH; bkr, Baker R. SSH/WSH; sau, Sauk R. SSH/WSH; stl, Stillaguamish R. WSH; der, Deer Cr. SSH; cny, Canyon Cr. SSH; snk, Snohomish/Skykomish R. WSH; pil, Pilchuck R. WSH; nfs, N. Fk. Skykomish R. SSH; snq, Snoqualmie R. WSH; tlt, Tolt R. SSH; lkw, N. Lk. Washington/Sammamish WSH; cdr, Cedar R. WSH; grn, Green R. WSH; puy, Puyallup/Carbon R. WSH; wht, White R. WSH; nsq, Nisqually R. WSH; ssd, South Sound Tributaries WSH; ekt, East Kitsap Peninsula WSH; ehc, East Hood Canal WSH; shc, South Hood Canal WSH; sko, Skokomish R. WSH; whc, West Hood Canal WSH; seq, Strait of Juan de Fuca lowland (Sequim/Discovery Bay) Tributaries WSH; dng, Dungeness R. SSH/WSH; sjf, Strait of Juan de Fuca Independents WSH; elw, Elwha R. SSH/WSH.

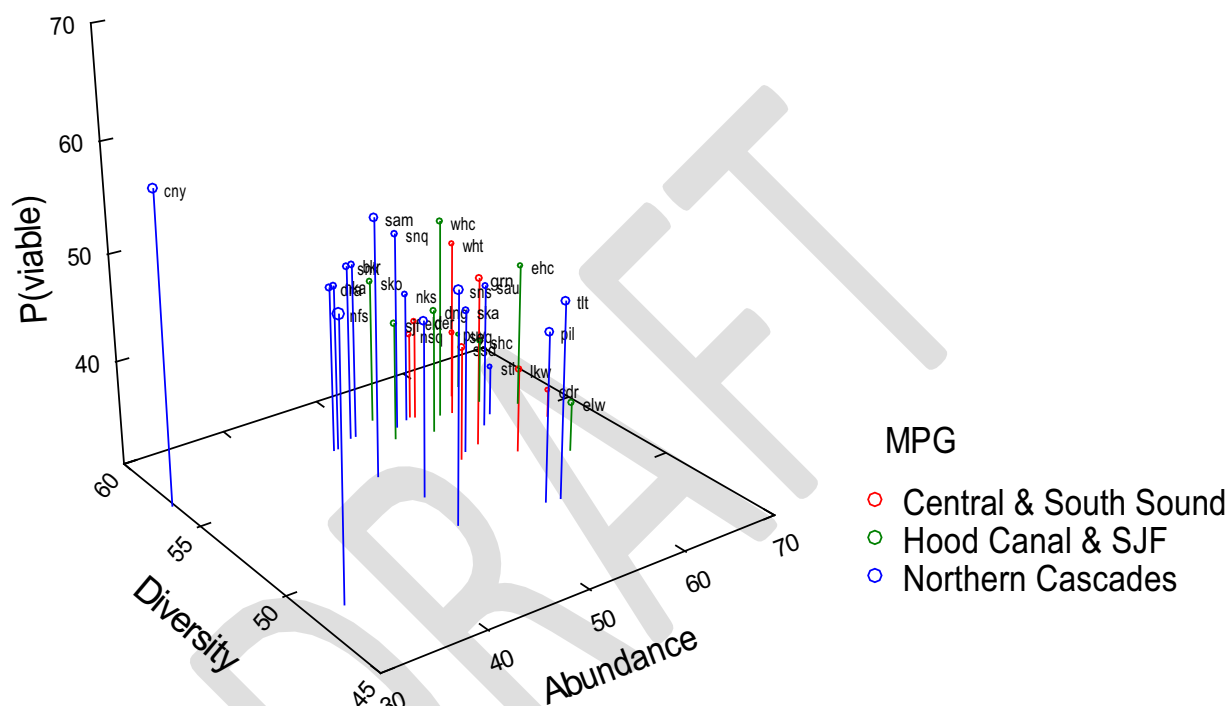


Figure 66. Scatter plot of the viabilities of each of the 32 candidate Demographically Independent Populations of steelhead in the Puget Sound Distinct Population Segment as a function of their Viable Salmonid Populations (VSP) parameter estimates of influence of abundance and diversity. Viabilities are computed from the DIP-level Bayesian Networks in Appendix A. Abundance and diversity scores are estimated from intermediate metrics computed by the DIP-level Bayesian Networks. The DIP symbols (WSH, winter-run steelhead; SSH, summer-run steelhead) are color coded by MPG: blue, Northern Cascades; red, Central and South Puget Sound; green, Hood Canal and Strait of Juan de Fuca. Three-letter DIP codes are as in Figure 65.

When considered with productivity, spatial structure has a modest influence on population viability; for DIPs with a high influence of spatial structure on viability, the DIPs with lowest viabilities were influenced heavily by low productivity (Figure 69). In general, DIP viability declines steeply when productivity is low. For the few DIPs that have a modest influence of spatial structure on viability (Nookachamps Creek winter-run, Tolt River summer-run, and Dungeness River summer- and winter-run), viability tends to be moderate. The pattern of viability with respect to the combination of VSP diversity and spatial structure is similar the pattern with respect to productivity and spatial structure (Figure 70).

According to the BN models, a typical DIP's viability is lowest whenever abundance and productivity are limiting (probabilities of viability < about 30%). As a representative example, for the Samish River/Bellingham Bay winter-run DIP in the Northern Cascades MPG, the sensitivity of viability to DIP abundance (entropy reduction, 6.7%), DIP productivity (entropy reduction, 5.2%), DIP diversity (entropy reduction, 1.3%, primarily a result of hatchery fish influence), and DIP spatial structure (entropy reduction, 1.6%) indicated that Samish River steelhead viability is limited primarily by both abundance and productivity. For the abundance criterion, the most important contributing factor was adult abundance (entropy reduction, 2.1%), followed by juvenile abundance (entropy reduction, 0.1%) and by the probability of reaching the specified QET (entropy reduction, < 0.1%). For the productivity criterion, the most important contributing factor was population growth rate (entropy reduction, 2.0%), followed by iteroparity (entropy reduction, 0.3%). Other factors contributing to DIP viability included marine survival rate (entropy reduction, 1.2%), both spatial structure criteria (total entropy reduction for spawning and rearing area occupied, 0.5%), and altered spawn timing (entropy reduction, 0.3%). Hatchery influence and alteration of age structure had minor influences on viability. The mutual information provided by the BN model for this DIP was > 0.99. The Most Probable Explanation for the viability of this DIP is that it is not viable, but there is considerable uncertainty around this MPE: the probability that this DIP could be viable is estimated at 69.2%.

By comparison, for the Nisqually River winter-run DIP in the Central and South Puget Sound MPG, the sensitivity of viability to DIP abundance (entropy reduction, 6.0%), DIP productivity (entropy reduction, 6.9%), DIP diversity (entropy reduction, 1.3%), and DIP spatial structure (entropy reduction, 1.7%) indicated that Nisqually River steelhead viability is limited more by productivity. For the abundance criterion, the most important contributing factor was adult abundance (entropy reduction, 1.2%), followed by the probability of reaching the specified QET (entropy reduction, 0.2%) and by juvenile abundance (entropy reduction, < 0.1%). For the productivity criterion, the most important contributing factor was population growth rate (entropy reduction, 2.8%), followed by iteroparity (entropy reduction, 1.4%). Other factors contributing to viability included marine survival rate (entropy reduction, 1.5%) and spawn timing (entropy reduction, 0.3%) and both spatial structure criteria (total entropy reduction for spawning and rearing area occupied, 0.5%). Hatchery influence and alteration of age structure had minor influences on viability. The mutual information provided by the BN model for this DIP was 0.96. The Most Probable Explanation for the viability of this DIP is that it is not viable, and there is little uncertainty around the MPE, because the probability that it could be viable is estimated at only 11.9%.

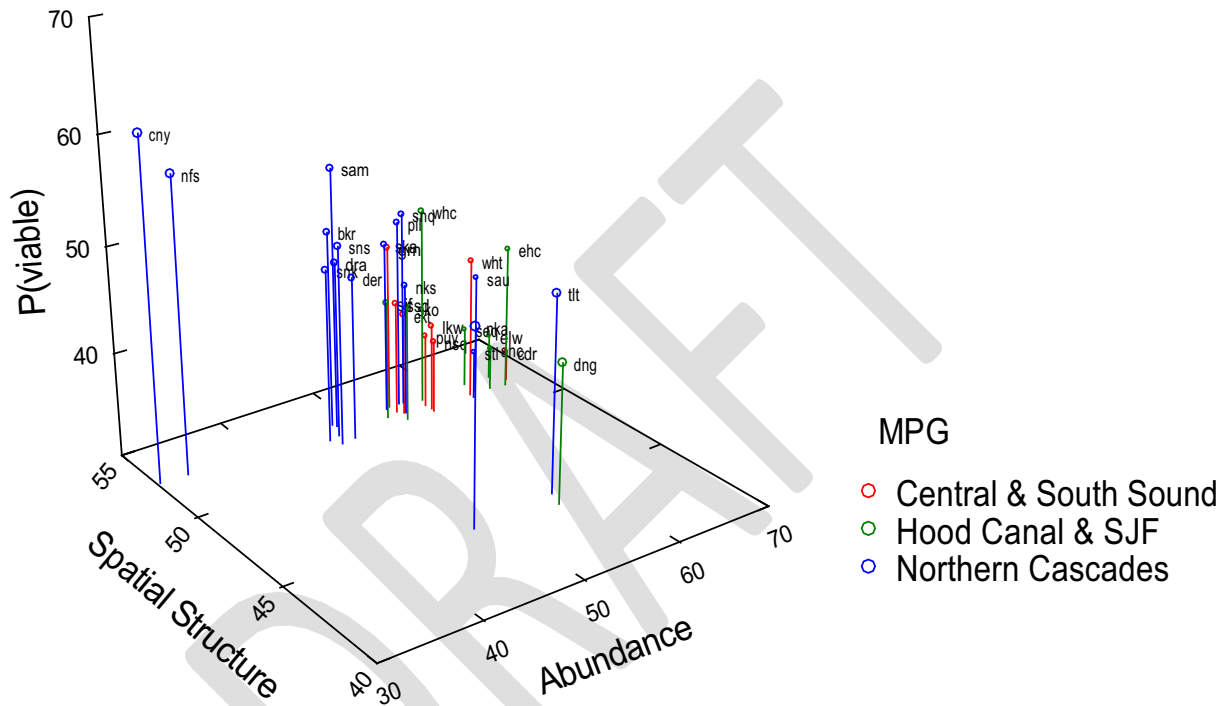


Figure 67. Scatter plot of the viabilities of each of the 32 candidate Demographically Independent Populations of steelhead in the Puget Sound Distinct Population Segment as a function of their Viable Salmonid Populations (VSP) parameter estimates of influence of abundance and spatial structure. Viabilities are computed from the DIP-level Bayesian Networks in Appendix A. Abundance and spatial structure scores are estimated from intermediate metrics computed by the DIP-level Bayesian Networks. The DIP symbols (WSH, winter-run steelhead; SSH, summer-run steelhead) are color coded by MPG: blue, Northern Cascades; red, Central and South Puget Sound; green, Hood Canal and Strait of Juan de Fuca. Three-letter DIP codes are as in Figure 65.

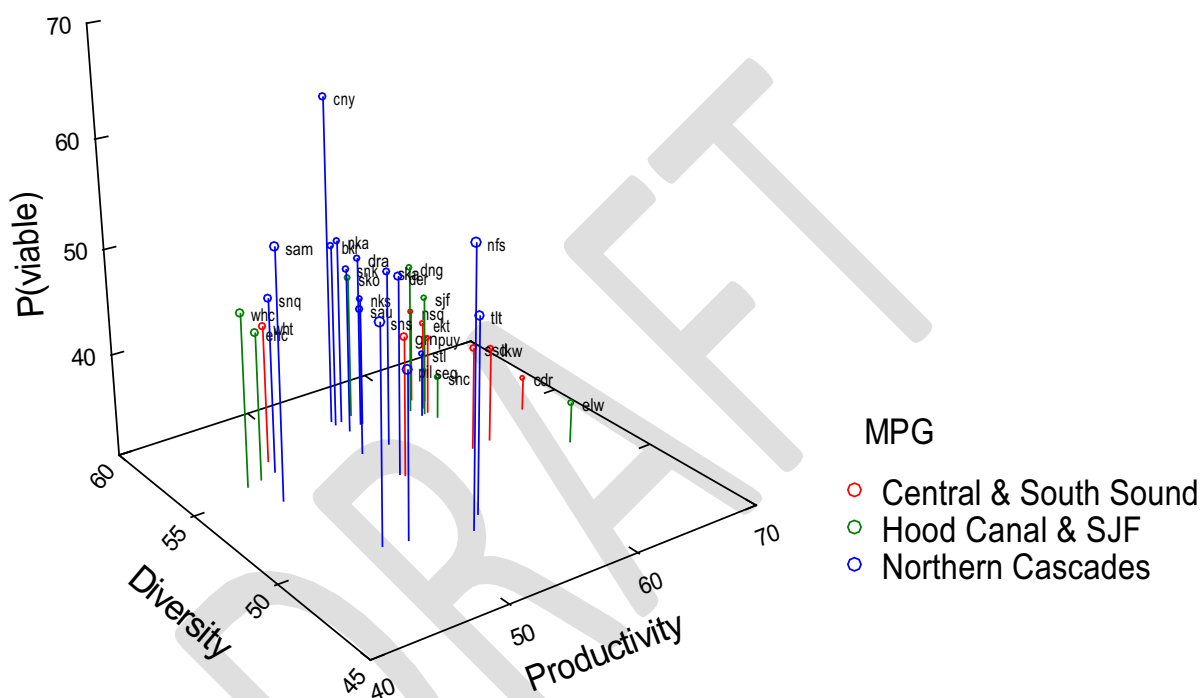


Figure 68. Scatter plot of the viabilities of each of the 32 candidate Demographically Independent Populations of steelhead in the Puget Sound Distinct Population Segment as a function of their Viable Salmonid Populations (VSP) parameter estimates of influence of productivity and diversity. Viabilities are computed from the DIP-level Bayesian Networks in Appendix A. Productivity and diversity scores are estimated from intermediate metrics computed by the DIP-level Bayesian Networks. The DIP symbols (WSH, winter-run steelhead; SSH, summer-run steelhead) are color coded by MPG: blue, Northern Cascades; red, Central and South Puget Sound; green, Hood Canal and Strait of Juan de Fuca. Three-letter DIP codes are as in Figure 65.

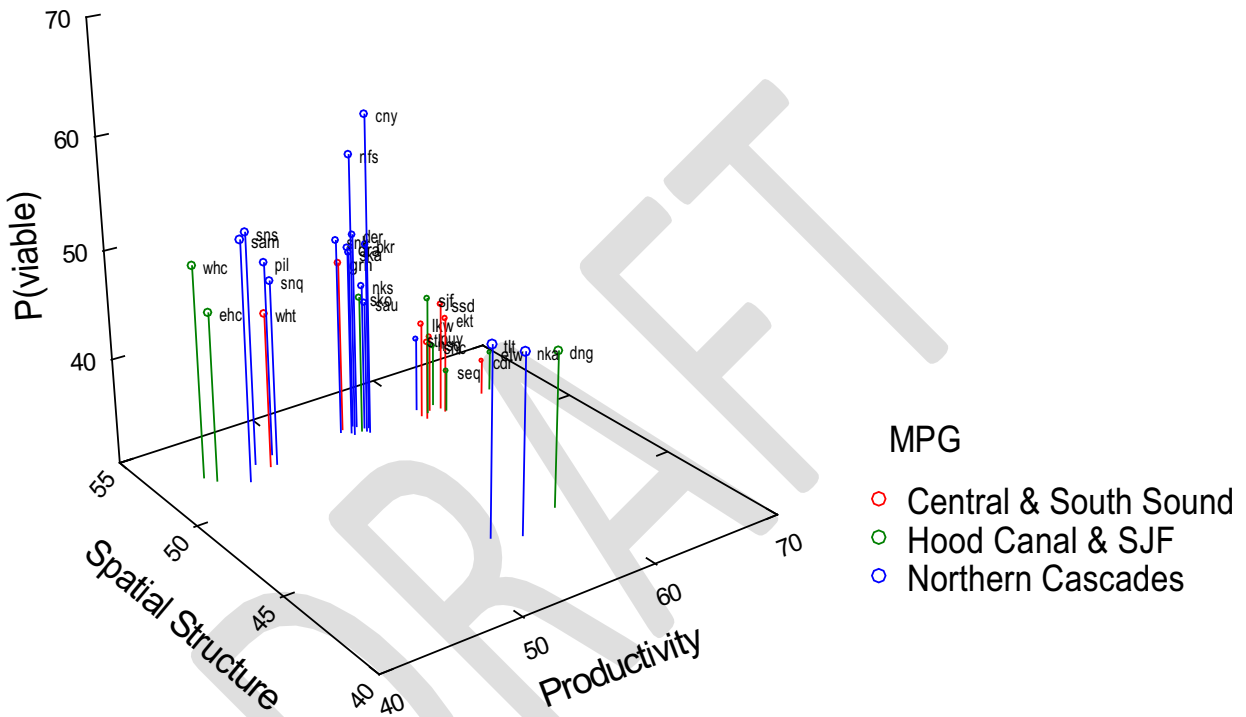


Figure 69. Scatter plot of the viabilities of each of the 32 candidate Demographically Independent Populations of steelhead in the Puget Sound Distinct Population Segment as a function of their Viable Salmonid Populations (VSP) parameter estimates of influence of productivity and spatial structure. Viabilities are computed from the DIP-level Bayesian Networks in Appendix A. Productivity and spatial structure scores are estimated from intermediate metrics computed by the DIP-level Bayesian Networks. The DIP symbols (WSH, winter-run steelhead; SSH, summer-run steelhead) are color coded by MPG: blue, Northern Cascades; red, Central and South Puget Sound; green, Hood Canal and Strait of Juan de Fuca. Three-letter DIP codes are as in Figure 65.

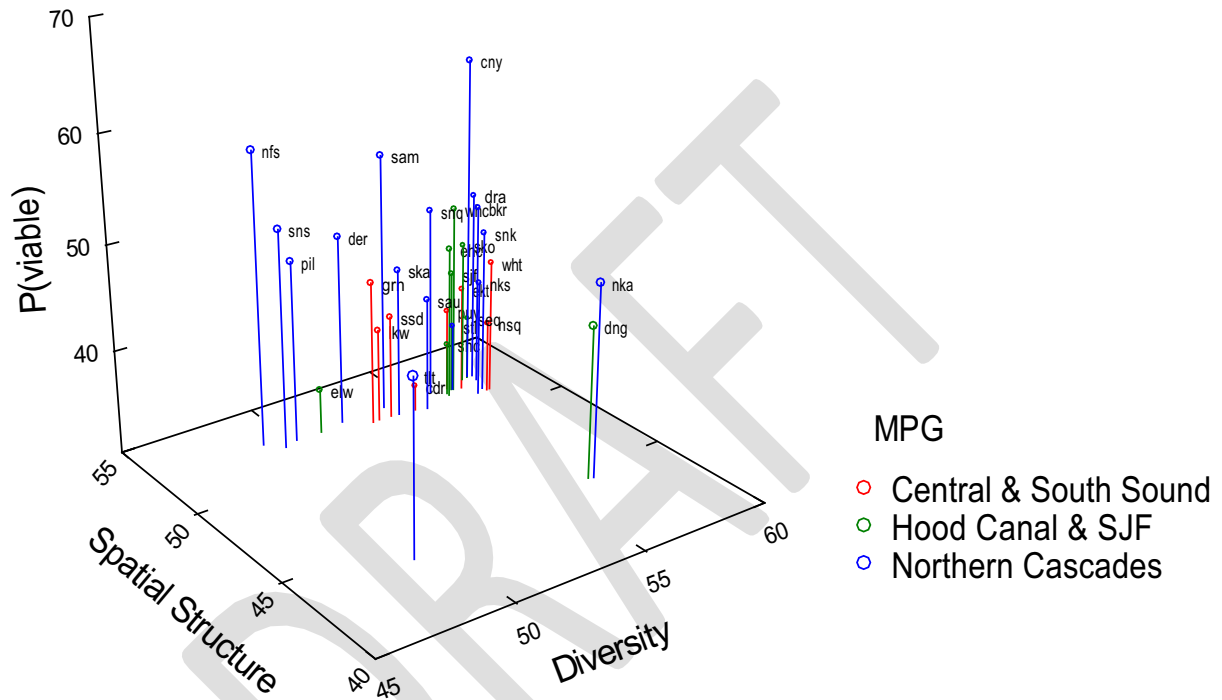


Figure 70. Scatter plot of the viabilities of each of the 32 candidate Demographically Independent Populations of steelhead in the Puget Sound Distinct Population Segment as a function of their Viable Salmonid Populations (VSP) parameter estimates of influence of diversity and spatial structure. Viabilities are computed from the DIP-level Bayesian Networks in Appendix A. Diversity and spatial structure scores are estimated from intermediate metrics computed by the DIP-level Bayesian Networks. The DIP symbols (WSH, winter-run steelhead; SSH, summer-run steelhead) are color coded by MPG: blue, Northern Cascades; red, Central and South Puget Sound; green, Hood Canal and Strait of Juan de Fuca. Three-letter DIP codes are as in Figure 65.

As an example for a summer-run population, for the Tolt River DIP in the Northern Cascades MPG, the sensitivity of viability to DIP abundance (entropy reduction, 6.2%), DIP productivity (entropy reduction, 6.8%), DIP diversity (entropy reduction, 1.3%), and DIP spatial structure (entropy reduction, 1.1%) indicated that Tolt River steelhead viability is limited by both abundance and productivity. For the abundance criterion, the most important contributing factor was adult abundance (entropy reduction, 2.1%), followed by juvenile abundance (entropy reduction, 0.3%) and the probability of reaching the specified QET (entropy reduction, 0.1%). For the productivity criterion, the most important contributing factor was population growth rate (entropy reduction, 3.2%), followed by iteroparity (entropy reduction, 0.9%). Other factors contributing to viability included marine survival rate (entropy reduction, 1.8%) and spawn timing (entropy reduction, 0.3%); hatchery influence, age structure, and adult and juvenile occupancy of IP areas had minor influences on viability. The mutual information provided by the BN model for this DIP was > 0.99 . The Most Probable Explanation for the viability of this DIP is that it is not viable, but this MPE has a high level of uncertainty: the probability that it could be viable is estimated to be as high as 62.8%.

The BNs for the remaining 29 steelhead DIPs yield similar conclusions for DIP viability, as well as the range of influence of VSP parameters on DIP viability. Throughout the DPS, the probability that a DIP is viable does not exceed about 60%; for the DIP with the highest estimated viability, Canyon Creek summer-run steelhead in the Northern Cascades MPG, the MPE is that this DIP is viable, although there is considerable uncertainty around the MPE: the probability that this DIP could be inviable is 85%.

MPG viability—We evaluated the viability of each of the three Puget Sound steelhead MPGs by combining the DIP-level Bayesian Networks for each MPG into an encompassing network with an edge connecting each node determining DIP viability to a single node for MPG viability. Figure 69 depicts such a network for one of the smaller MPGs—the Hood Canal and Strait of Juan de Fuca MPG. The conditional probability table (CPT) describing the influence of DIP viability on MPG viability for this BN is given in Table 14 (similar CPTs, not shown, underlie the BNs for the Northern Cascades and the Central and South Puget Sound MPGs). In this table of probabilities and the corresponding values for other MPGs, the MPG is considered viable only if 40% or more of the constituent DIPs are considered viable as an outcome of the DIP viability BN analyses *and*, if summer-run DIPs are present, at least 40% of these populations are also considered viable.

Under these conditions, a BN analysis computes that the probability of viability for the Hood Canal and Strait of Juan de Fuca MPG as a whole is only 16.4% (Figure 71). Average DIP probability of viability is 40.6% in this MPG. The BN for the Hood Canal and Strait of Juan de Fuca MPG indicates that the probability that this MPG is viable would rise to 100% if at least one DIP from each of the four major regions of the MPG (i.e., Strait of Juan de Fuca [4 DIPs], East Hood Canal [1 DIP], South Hood Canal [2 DIPs], and West Hood Canal [1 DIP]) was viable with certainty (i.e., by instantiating certainty of viability for these DIPs). MPG viability would rise to 89.5% if all four DIPs on the Strait of Juan de Fuca were instantiated at fully viable. A sensitivity analysis (output not shown) indicates that the mutual information provided by the BN model for viability of this MPG was 0.64. The entropy reduction contributed by the viability of its constituent DIPs varied from 5.2% (Sequim/Discovery Bay tributaries winter-run)

to 10.5% (Dungeness summer- and winter-run). The Most Probable Explanation (MPE) for the viability of this MPG is that it is not viable, and there is little uncertainty around this MPE: the probability that the MPG could be viable is 1.3%.

A BN analysis for the Central and South Puget Sound MPG shows that the probability of its viability is also low: 17.2%. Average DIP probability of viability in this MPG is 39.9%. The BN for the MPG indicates that the probability that this MPG is viable would rise to at least 87.7% if at least one DIP from each of the four major regions of the MPG (i.e., Central Sound [3 DIPs], Southeast Sound [3 DIPs], South Sound tributaries [1 DIP], and East Kitsap Peninsula [1 DIP]) were viable. A sensitivity analysis (output not shown) indicates that the mutual information provided by the BN model for viability of this MPG was 0.66. The entropy reduction contributed by the viability of its constituent DIPs showed little variation, ranging from 6.6% (Cedar River winter-run) to 6.7% (North Lake Washington tributaries winter-run). The MPE for the viability of this MPG is that it is not viable, and there almost no uncertainty around this MPE: the probability that the MPG could be viable is < 0.1%.

A BN analysis for the Northern Cascades MPG indicates a probability of viability of 36.3%. Average DIP probability of viability in this MPG is the highest of the three MPGs at 47.9%. Although this MPG contains twice as many DIPs as the other two in the DPS (16 versus 8 for both the Hood Canal and Strait of Juan de Fuca and Central and South Puget Sound MPGs), its viability is also low because not enough of its constituent DIPs within each major life-history type are at reasonable levels of viability. The BN for this MPG indicates that its viability would rise to at least 88.7% if at least half of the DIPs in this MPG were viable. Given the conditions specified by the underlying CPT, the BN also indicates that the probability that this MPG is viable would rise to 87.9% if at least half (6 of 11) of the winter-run and at least half (3 of 5) of the summer-run DIPs in the MPG were viable (spread geographically across the MPG, and including the Skagit River summer- and winter-run). It indicates as well that the probability that this MPG is viable would rise to 85.9% if all five summer-run DIPs and the Skagit River summer- and winter-run DIP in this MPG were viable (100% if all five summer-run and three winter-run DIPs were viable). A sensitivity analysis (output not shown) indicates that the mutual information provided by the BN model for viability of this MPG was 0.94. The entropy reduction contributed by the viability of its constituent DIPs showed considerable variation, ranging from 0.6% (Stillaguamish River winter-run) to 7.6% (Snoqualmie River winter-run and Tolt River summer-run). The MPE for the viability of this MPG is that it is not viable, and there little uncertainty around this MPE: the probability that the MPG could be viable is only 4.0%.

Despite the low uncertainty about viability for all three MPGs, we also assessed the reliability of the BNs to predict MPG viability by simulating 1,000 random networks in each case. We used two metrics to assess the quality of the information provided by the networks: an error rate measured by a “confusion matrix,” which assesses how often the beliefs produced by the network fail to line up with the actual assignments to node categories based on the conditional probabilities; and a “quality of test,” which estimates the fraction of correctly predicted cases given a specified cut-off probability. In all cases we used the recommended value for the cut-off probability (40% for the Northern Cascades MPG, 20% for the Central and South Puget Sound MPG, and 20% for the Hood Canal and Strait of Juan de Fuca MPG). For the

Northern Cascades MPG, the analysis indicated that the BN was a mediocre predictor of MPG viability from the data. The confusion matrix indicated an error rate of 36.3%, and the ability of the test to predict correct viability results was only 63.7% at a cut-off probability of 40% or higher (100% at a cut-off probability of 0%). For the Central and South Puget Sound MPG, the BN was a better predictor of MPG viability; the confusion matrix indicated an error rate of 17.2%, and the ability of the test to predict correct viability results was 82.8% at a cut-off probability of 20% or higher. In the case of the Hood Canal and Strait of Juan de Fuca MPG, the BN's predictive power for viability was similar to that for the Central and South Puget Sound MPG. The confusion matrix indicated an error rate of 16.4%, and the ability of the test to predict correct viability results was 83.6% at a cut-off probability of 20% or higher. These results suggest that the networks for the two smaller MPGs provide reasonable frameworks that capture most of the variation contributing to MPG viability across these complex groups of constituent populations. The larger size and complexity of the Northern Cascades MPG contributes to the diminished capability of its network to predict how variation in its VSP parameters contributes to this MPG's viability.

Collectively, these analyses indicate that all three steelhead MPGs are at very low viability. One implication of these analyses is that increasing the abundance and productivity of DIPs of both major life-history types (summer- and winter-run) and spread geographically across each MPG is essential to bringing all MPGs to viable condition. Maintaining life-history diversity and the spatial distribution of steelhead in IP stream reaches across DIPs within the MPGs would also be essential to elevating viability in each of them.

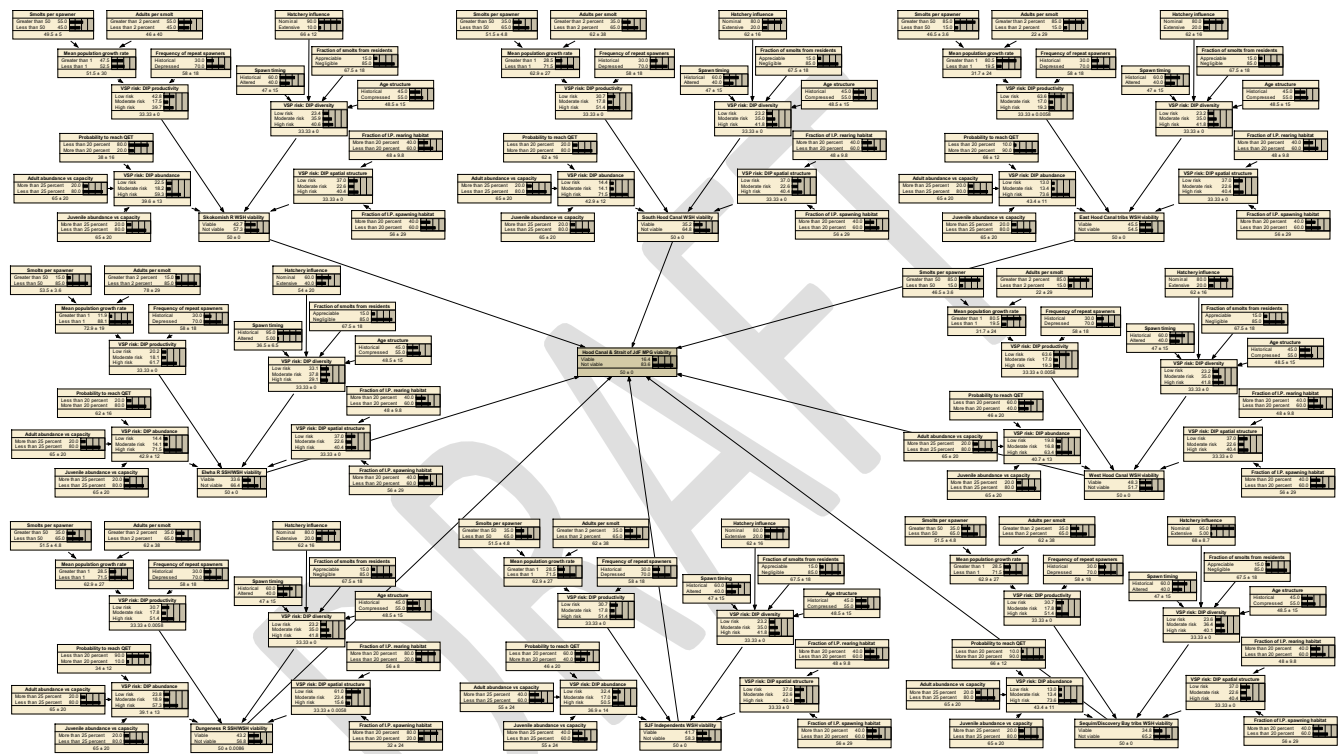


Figure 71. Bayesian Network (BN) used to characterize the viability of the Hood Canal and Strait of Juan de Fuca steelhead MPG. The conditional probability table (CPT) describing the influence of DIP viability on MPG viability is given in Table 14.

Table 14. Conditional probability table (CPT) describing the influence of DIP viability on MPG viability for the Bayesian Network in Figure 71. Similar CPTs were used to parameterize the Northern Cascades and Central and South Puget Sound MPGs, which contain 16 and 8 steelhead DIPs, respectively. The Northern Cascades MPG contains twice as many DIPs as the other MPGs but we used an analogous CPT to characterize the influence of DIP viability on MPG viability, which explicitly requires > 40% viable DIPs of each distinct life-history type (summer-run, winter-run or combined summer-run/winter-run) for MPG viability.

DIP viability								MPG viability	
E Hood Canal WSH	S Hood Canal WSH	Skokomish R WSH	W Hood Canal WSH	Sequim/Disc. Bay Tribs WSH	Dungeness R SSH/WSH	SJF Indep. Tribs WSH	Elwha R SSH/WSH	Viable	Not viable
Viable	Viable	Viable	Viable	Viable	Viable	Viable	Viable	100	0
Viable	Viable	Viable	Viable	Viable	Viable	Viable	Not viable	100	0
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DPS viability—As was described previously, the viability of the DPS as a whole critically depends on the combined viability of all its constituent MPGs; a DPS with even a single inviable MPG cannot be viable. The BN depicted in Figure 72 shows how the viability of the entire DPS depends on MPG viability.

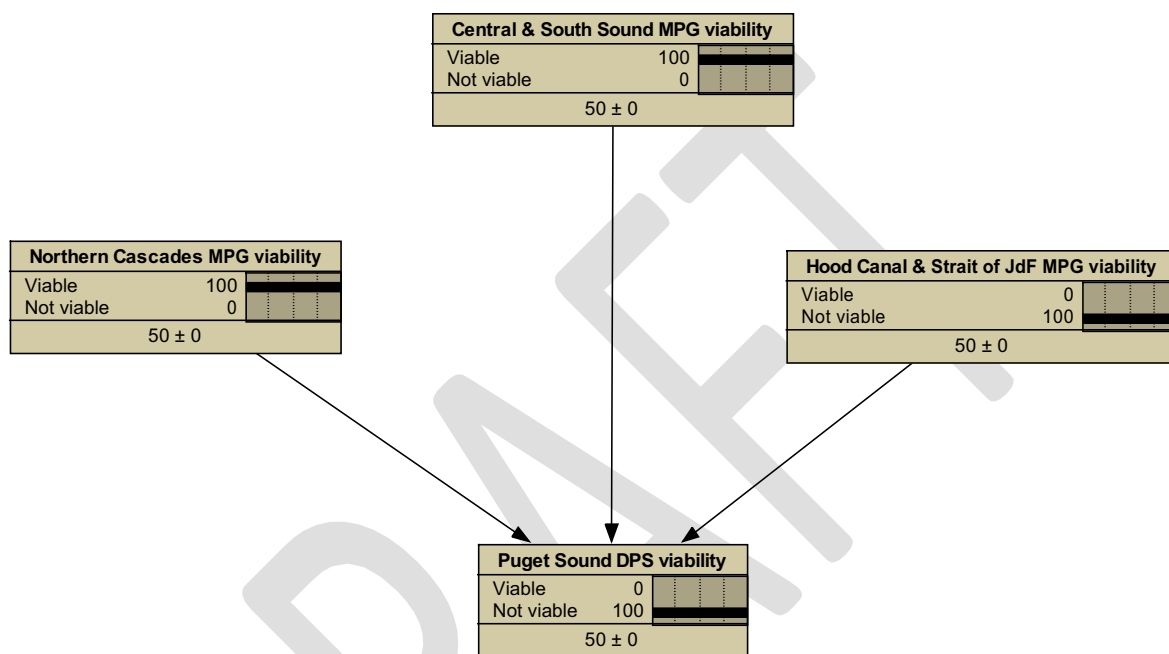


Figure 72. Highest-level Bayesian Network (BN) used to characterize the viability of the Puget Sound steelhead DPS. DPS viability requires that each MPG be viable (see Table 15); in this case, instantiation shows that one MPG that is not viable (e.g., Hood Canal and Strait of Juan de Fuca) leads to the situation where the DPS is also not viable. The viability of each MPG is estimated using BNs like that in Figure 71.

Table 15. Conditional probability table (CPT) describing the influence of MPG viability on DPS viability for the Bayesian Network in Figure 72.

N Cascades MPG	C & S Puget Sound MPG	HC & Strait J de F MPG	Puget Sound DPS	DPS state	
				Viable	Not viable
Viable	Viable	Viable	Viable	100	0
Viable	Viable	Not viable	Not viable	0	100
Viable	Not viable	Viable	Not viable	0	100
Viable	Not viable	Not viable	Not viable	0	100
Not viable	Viable	Viable	Not viable	0	100
Not viable	Viable	Not viable	Not viable	0	100
Not viable	Not viable	Viable	Not viable	0	100
Not viable	Not viable	Not viable	Not viable	0	100

Combining the Bayesian Networks for each MPG to create a network for the entire DPS (as outlined in Figure 72), and following the conditional probabilities in Table 15, indicates that the DPS is not viable: the probability of DPS viability computed by the network is 1.0%. A sensitivity analysis (output not shown) indicates that the mutual information provided by the BN model for viability of the DPS was only 0.082. The entropy reduction contributed by the viability of the Northern Cascades MPG is 18.3%; the entropy reduction contributed by the viability of the Central and South Puget Sound MPG is 32.0%, and that for the Hood Canal and Strait of Juan de Fuca MPG is 32.9%. We assessed the ability of these networks to predict DPS viability by simulating 1,000 random networks in each case. The ability of the combined network to predict DPS viability was very high; the confusion matrix indicated an error rate of 1.0% and the ability of the test to predict correct viability results was > 98.9% at a cut-off probability of 2% or more. This result is not unexpected, as there is little uncertainty about the condition of steelhead in any of the MPGs constituting the Puget Sound DPS using these networks.

We also used a simpler modification of these combined networks to evaluate the viability of the DIPs, MPGs, and DPS relying on only abundance and productivity criteria. The basis for this exercise is to address the question “What if we rely primarily on quantitative demographic information to assess steelhead viability?” To do so, we created subsets of each of the DIP BNs that included only the abundance and productivity nodes, and eliminated the iteroparity criterion from the productivity node. We used the same underlying CPTs for the abundance and productivity criteria as in the more comprehensive BNs, and as before we used MPG-wide averages for abundance and productivity where these data were not available for individual DIPs. This analysis substantially increased the probabilities of viability at each level. Probabilities of viability for DIPs varied from a low of 64.9% for Stillaguamish River winter-run to a high of 86.8% for Canyon Creek summer-run in the Northern Cascades MPG. The Most Probable Explanation for Stillaguamish River winter-run was that it is viable, but there was a 75% probability that this DIP is not viable; the MPE for Canyon Creek summer-run was that it is

viable, and there was only a 5.5% probability that this DIP is not viable. For the Central and South Puget Sound MPG, probabilities of DIP viability varied from a low of 61.3% for Cedar River winter-run to a high of 69.5% for White River winter-run. The MPE for Cedar River winter-run was that it is viable, but there was a 75% probability that this DIP is not viable; the MPE for White River winter-run was that it is viable, but the probability that this DIP is not viable was estimated at 49.9%. For the Hood Canal and Strait of Juan de Fuca MPG, probabilities of DIP viability varied from a low of 61.8% for Elwha River summer- and winter-run to a high of 72.0% for West Hood Canal winter-run. The MPE for Elwha River summer- and winter-run was that it is viable, but there was a 75% probability that this DIP is not viable; the MPE for West Hood Canal winter-run was that it is viable, but the probability that this DIP is not viable was estimated at 49.9%.

Under this analysis, the probabilities of viability for the three MPGs were 89.9% for the Northern Cascades MPG, 74.6% for the Central and South Puget Sound MPG, and 70.5% for the Hood Canal and Strait of Juan de Fuca MPG. The MPEs for MPG viability were that all three MPGs are viable, with probabilities that each MPG is not viable of 12.4%, 31.6%, and 56.2%, respectively. Finally, the probability of viability for the entire DPS was 42.3%; the MPE was that the DPS is viable, with a probability that the DPS is not viable equal to 56.2%.

This exercise illustrates how the structure of a Bayesian Network can strongly influence the inference about viability at nodes throughout the network. If we rely on the more quantifiable and readily available of the VSP criteria alone, estimates of steelhead viability are higher throughout the DPS for two main reasons: the TRT's largely qualitative assessment of diversity and spatial distribution of steelhead is that the widespread state of these factors in Puget Sound steelhead poses risk to sustainability, and the TRT's more quantitative assessment of demography (abundance and productivity) is conservative with respect its influence on risk to persistence. If one were to accept this analysis (and its underlying probability theory) as a reasonable evaluation of the status of Puget Sound steelhead, one would still have to conclude that there is substantial uncertainty in the status of at least two of the MPGs and of the entire DPS. Furthermore, the main problem with this analysis is that it is at odds with the threatened status of the DPS and with concerns about continued risks to persistence and sustainability of many of its populations. It also indicates that the existing BNs may be too benign with respect to risk of quasi-extinction; the viabilities for several DIPs and all the MPGs are at odds with the outcomes of several of the PVAs, in part because of the MPG-wide averaging for DIPs with no quantitative information. It is also probably due in part to the fact that this analysis does not consider the effects of factors that are known to be risks to wild Puget Sound steelhead, including limited availability of productive rearing and spawning habitat, the widespread use of Chambers Creek and Skamania River hatchery fish throughout the DPS, and perceived changes in aspects of diversity for several populations.

The TRT considers the networks that encompass all four VSP criteria to more accurately reflect the current status of Puget Sound steelhead. The vast majority of steelhead populations throughout Puget Sound do not appear to be viable, regardless of where one looks; most are declining steeply from historical levels and many are very small. Despite the lack of demographic information for many of the populations, and the lack of clarity regarding the precise states of diversity and spatial structure for nearly all of them, these BNs appear to

provide a framework that assesses the broad-sense viability of steelhead with reasonable confidence. The TRT considers these networks to represent a reasonable starting point for identifying the major criteria for effective recovery of Puget Sound steelhead, and believes that they help to identify key gaps in knowledge that must be addressed if further declines in steelhead viability are to be arrested.

Diversity Considerations for Steelhead Viability: Resident Life History and Iteroparity

In this section we briefly consider how the presence of freshwater resident *O. mykiss* and the degree of iteroparity may affect viability of steelhead. Both factors may mitigate extinction risk, but few analyses are available in the published literature to guide their consideration in a viability analysis of anadromous fish. We briefly describe previous considerations of these factors by NMFS and outline an approach and justification for including them in our overall assessment of viability.

Resident Fish as a Factor Influencing Viability

Oncorhynchus mykiss exhibits varying degrees of anadromy. Nonanadromous forms are usually called rainbow trout. Although the anadromous and nonanadromous forms have long been taxonomically classified within the same species, in any given area the exact relationship between the forms is not well understood.

The Biological Review Team (BRT; Good et al. 2005) had to consider in more general terms how to conduct an overall risk assessment for a DPS that includes both resident and anadromous populations, particularly when the resident fish may outnumber the anadromous ones but their biological relationship is unclear or unknown. Some guidance is found in Waples (1991), which outlines the scientific basis for the NMFS Evolutionarily Significant Unit (ESU) policy. That paper suggested that an ESU (or equivalently, a DPS) that contains both forms could be listed based on a threat to only one of the life history traits “if the trait were genetically based and loss of the trait would compromise the ‘distinctiveness’ of the population” (p. 16). That is, if anadromy were considered important in defining the distinctiveness of the ESU, loss of that trait would be a serious ESA concern. In discussing this issue, the NMFS ESU policy (NMFS 1991a) affirmed the importance of considering the genetic basis of life history traits such as anadromy and recognized the relevance of a question posed by one commenter: “What is the likelihood of the nonanadromous form giving rise to the anadromous form after the latter has gone locally extinct?” To focus the issue, Good et al. (2005) considered a hypothetical scenario that has varying degrees of relevance to individual steelhead ESUs/DPSs. In this scenario, the once-abundant and widespread anadromous life history is extinct, or nearly so, but relatively healthy native populations of resident fish remain in many geographic areas. The question the BRT (Good et al. 2005) had to consider was: Under what circumstances would one conclude that such a DPS was not in danger of extinction or likely to become endangered? The BRT identified the required conditions as

- The resident forms are capable of maintaining connectivity among populations to the extent that the DPS's historical evolutionary processes are not seriously disrupted.
- The anadromous life history is not permanently lost from the DPS but can be regenerated from the resident forms.

The task faced by the Puget Sound Steelhead TRT ideally involves a finer-scale evaluation of the contribution of resident fish to the viability of individual anadromous DIPs. While Good (2005) developed generalized guidelines to evaluate the relationship between the two life history forms, despite differences in that relationship for both coastal and interior steelhead DPSs, the TRT was able to focus on coastal *O. mykiss* in Puget Sound. Additionally, the TRT benefited from a number of recent studies on the interactions between Puget Sound resident and anadromous *O. mykiss*. In general, there appeared to be a relatively close relationship between sympatric resident and anadromous forms below long-standing natural barriers. This may be due, in part, to the relatively short geologic time period since the Pleistocene glaciations. It may also be that, below impassable barriers, truly resident populations do not exist. Rather, the degree of anadromy in an *O. mykiss* DIP may be somewhat plastic, with environmental and ecological cues influencing the relative rate of anadromy. For example, in the Lake Washington Basin (including the Cedar River) the anadromous populations of *O. mykiss* and cutthroat trout (*O. clarki*) have dwindled to near zero levels, yet resident fish of both species are widely abundant. This is thought to be due, in part, to changes (improvements) in the productivity of Lake Washington and Lake Sammamish.

In determining the viability of steelhead DIPs in the Puget Sound DPS, the TRT considered the potential influence of co-occurring resident *O. mykiss* on anadromous steelhead demographics. Based on recent studies, it is clear that there is some degree of interaction between resident and anadromous. This interaction can be both genetic and ecological (competition, predation, etc.) and has the potential to be a positive or negative influence on steelhead viability. Interactions between resident and anadromous fish can be especially beneficial when the abundance of anadromous fish is especially low, near QET. Thus, resident fish may be most important not in bringing a DIP to full viability, but in preventing a DIP from being extirpated. Any reduction in risk of extinction would be directly linked the genetic relationship between resident and anadromous *O. mykiss* and the sustainability of the resident population. Resident *O. mykiss* could be the result of non-native introductions from other basins within Puget Sound or from outside of the DPS (most prominently in northern California). Alternatively, resident fish may be emigrating into anadromous accessible areas from upstream of impassable stream structures. In either case where substantial genetic differences exist between resident and anadromous fish, it is unlikely that interbreeding between these two life history forms will be beneficial to the fitness of steelhead. Where genetic differences between the two forms are more moderate, the two life history forms may have recently diverged or may co-exist with continued gene exchange.

If resident *O. mykiss* are a potential reservoir of the anadromous genetic legacy in a steelhead population, they can play an important role in the viability of that population. This is especially important in areas that historically contained anadromous *O. mykiss*, but have been rendered inaccessible to upstream migration post-European contact. The TRT concluded that in basins where anadromous *O. mykiss* abundance is below the QET threshold, the risk of

extinction is not necessarily 100% if resident *O. mykiss* are present below long-standing migration barriers. Inclusion of resident fish in the viability criteria is dependent, however, on several conditions. First, the abundance of resident fish must be large enough to be self-sustaining (this will be largely dependent on the numbers of resident females). Secondly, there must be some evidence of interbreeding between the anadromous and resident forms (this will most likely be established by genetic analysis of the relationship between the resident fish and the most proximate anadromous population). Identifying resident fish that contain the genetic legacy of their historical anadromous population is an important step in potentially reestablishing anadromous *O. mykiss* to some basins and subbasins.

A comprehensive risk assessment must consider the effect of resident *O. mykiss* that have anadromous access on the viability of the entire DPS. This task is especially difficult because little or no information is available about the abundance and distribution of resident fish, or about the extent and nature of their interactions with anadromous populations. The 2003 BRT incorporated information about rainbow trout populations into their analyses of the four VSP criteria and their assessments of extinction risk for *O. mykiss* ESUs (Good et al. 2005). In several ESUs, Good et al. (2005) concluded the presence of relatively numerous rainbow trout populations reduced risks to ESU abundance. However, there is considerable scientific uncertainty regarding the potential of the resident form to contribute to the productivity, spatial structure/connectivity and diversity of steelhead ESUs (Varanasi 2004).

Good et al. (2005) underscored the importance of the anadromous life history form in reducing risks to these latter three VSP parameters, and thus in contributing to a viable *O. mykiss* ESU or DPS in total. Although there is the potential for rainbow trout populations to generate steelhead migrants, it may be short-lived if the reproductive success of steelhead offspring is low. Finally, the BRT concluded if the anadromous life history form in an ESU is extirpated or critically depressed, it is unlikely the resident life history form alone is capable of maintaining the productivity, connectivity, and diversity necessary for a viable *O. mykiss* ESU (NMFS 2003).

Subsequent to the conclusions of the 2003 BRT, NMFS solicited opinions from two expert panels to review the issue of viability in listing units that contain both rainbow trout and steelhead (note that the language below refers to ESUs, although listing units for *O. mykiss* are now considered DPSs). The independent Recovery Science Review Panel (RSRP) identified anadromy as “an evolutionarily significant component of *O. mykiss* diversity” (RSRP 2004). In its review of available information the panel concluded “resident populations by themselves should not be relied upon to maintain long-term viability of an ESU.” Similarly, the Independent Scientific Advisory Board (ISAB) found the long-term consequences of the extirpation of a major life history form would have deleterious consequences on the entire ESU (ISAB 2005):

To be viable an ESU or DPS needs more than simple persistence over time; it needs to be sustained in an ecologically and evolutionarily functional state. Evaluation of ESU/DPS viability should not only rest on the numbers of component populations or on the abundance and productivity of those individual populations, but also should be based on the integration of population dynamics within the ecosystem as a whole.

This concept of ESU/DPS viability does not accommodate the loss of populations or the anadromous or resident life history form from any given ESU/DPS, because that loss would represent a loss in diversity for the ESU/DPS that would put its long-term viability at risk.

Where both life history forms are present, the ISAB considered that the resident forms contribute to the overall abundance and diversity of an ESU/DPS, but were unsure of the contribution by resident fish to connectivity and spatial structure. Overall, the presence of both resident and anadromous life history forms is “critical for conserving the diversity of steelhead/rainbow trout populations and, therefore, the overall viability of ESUs.”

In a 2004 review of currently listed steelhead ESUs, the Northwest Fisheries Science Center (NWFSC) concluded that “None of these ESUs is likely to persist in total into the foreseeable future because substantial parts of the ESUs are at risk of extinction” (Varanasi 2004). The NWFSC review supported the 2003 BRT conclusions that the ESUs were at risk of extinction, now or in the foreseeable future, because the anadromous life history represented a “significant portion of the species ‘range,’ such that its loss is a direct threat to the ESUs” (Varanasi 2004).

Courter et al. (2010) conducted deterministic simulation modeling of population viability for an interior population of *O. mykiss* with both resident and anadromous life history types (Upper Yakima River) and concluded that extinction risk was low when production of steelhead from both resident and anadromous fish was accounted for. Viability was highly sensitive to the quasi-extinction risk thresholds for both resident spawners and anadromous steelhead, but Courter et al. (2010) found that natural variation in stage-specific survival rarely caused steelhead abundance to drop below 25 spawners over four consecutive years, but almost always caused abundance to drop below 100 spawners. The modeling indicated that after 1,000 iterations, steelhead abundance dropped below a QET of 50 spawners in about one quarter of the simulated scenarios. Courter et al. (2010) stated that “our modeling as well as historic fish counts reveal that a reduction in steelhead below 50 spawners across four or more consecutive years does not lead to extinction when resident rainbow trout are abundant in the population.” They concluded that their data highlights the sensitivity of steelhead abundance to marine survival and demonstrates that when resident fish are highly abundant and contribute sufficient smolts, steelhead can be maintained in the population at low abundance.

These results are consistent with the evidence for plastic and genetic influences on migratory life history in this species. In at least some coastal systems, smolt production from resident fish has been documented, although the two forms can sometimes be genetically differentiated. Pearse et al. (2009) found evidence for rapid evolution of a resident life history in a coastal California steelhead population above a natural migration barrier in response to selection against seaward migration. In cases where anadromous steelhead abundance is very low in a population that also harbors a resident life history, smolt production from resident fish may contribute substantially to steelhead viability. In their controlled breeding study of *O. mykiss* from Sashin Creek, Alaska, Thrower et al. (2004) found that resident fish there can produce substantial numbers of smolts, albeit with lower marine survival (see also Thrower and Hard 2009). They concluded that “the judicious use of freshwater sequestration merits consideration as a temporary component of a comprehensive strategy for the maintenance of

endangered anadromous populations of *O. mykiss* in cases where the likelihood of rapid restoration of freshwater habitats for anadromous fish is low.”

An *O. mykiss* population expressing a combination of migratory strategies (freshwater resident, anadromous) and a heritable propensity to produce both types of progeny means that residents can serve as a buffer when anadromous productivity is low—extinction risk is lower when residents are relatively abundant. But it is important to remember that while a population of residents may indeed provide a genetic reservoir to produce anadromous migrants, these fish may have reduced adaptive potential to cope with the marine environment and smolt production may entail a cost in fitness. This is an active area of research that merits immediate attention to help guide development of conservation strategies for steelhead. For our analysis, we simply assumed that the presence of locally adapted, resident fish with an opportunity to interact with steelhead in Puget Sound (e.g., in the Cedar River watershed) limited extinction risk for steelhead to a level not exceeding 90% in 100 years.

Iteroparity as a Factor Influencing Viability

Steelhead are iteroparous anadromous salmonids. It is widely thought that this ability to reproduce repeatedly over the lifespan can contribute significantly to population productivity and provide a temporal buffer in demographic and environmental stochasticity. In the Pacific Northwest, the current frequency of repeat spawners appears to be low, generally less than 10% and frequently much lower, and rates appear to be declining in several populations in recent decades (e.g., Figure 73). A systematic analysis of the contribution of repeat spawning to population dynamics has not, to our knowledge, been undertaken for coastal steelhead. Nevertheless, a comprehensive evaluation of population viability must consider this contribution, and that is a primary reason why iteroparity is a component of the Bayesian Networks for viability developed in the previous section of this report.

In this section of the report we summarize some preliminary analyses that incorporate the proportion of repeat spawners in adult populations as a viability parameter influencing productivity. These unpublished analyses, conducted by Nick Gayeski of the Wild Fish Conservancy in coordination with and reviewed by the TRT, rely on an approach that develops a suite of age-structured matrix population projection models with annual time-steps that incorporate density dependence, varying levels of repeat spawning, and varying levels of density-independent stochasticity, and harvest mortality. The models were used to evaluate the influence of varying levels of repeat spawning on population abundance and age structure under varying levels of harvest.

Gayeski's models incorporated iteroparity under deterministic and stochastic conditions, with and without harvest mortality. Gayeski's models simulated a winter-run steelhead population with six age classes and three ages at maturation, with age of first maturation at age 4. The entire population was assumed to be anadromous and had no interactions with resident fish. Smolts were assumed to be all age 2, and repeat spawners were limited to one repeat spawning event in the year following the year of first reproduction. Therefore, repeat spawners were either 5 or 6 years old. All harvest mortality occurred on mature fish following river entry and prior to spawning. Sex ratio was 0.5.

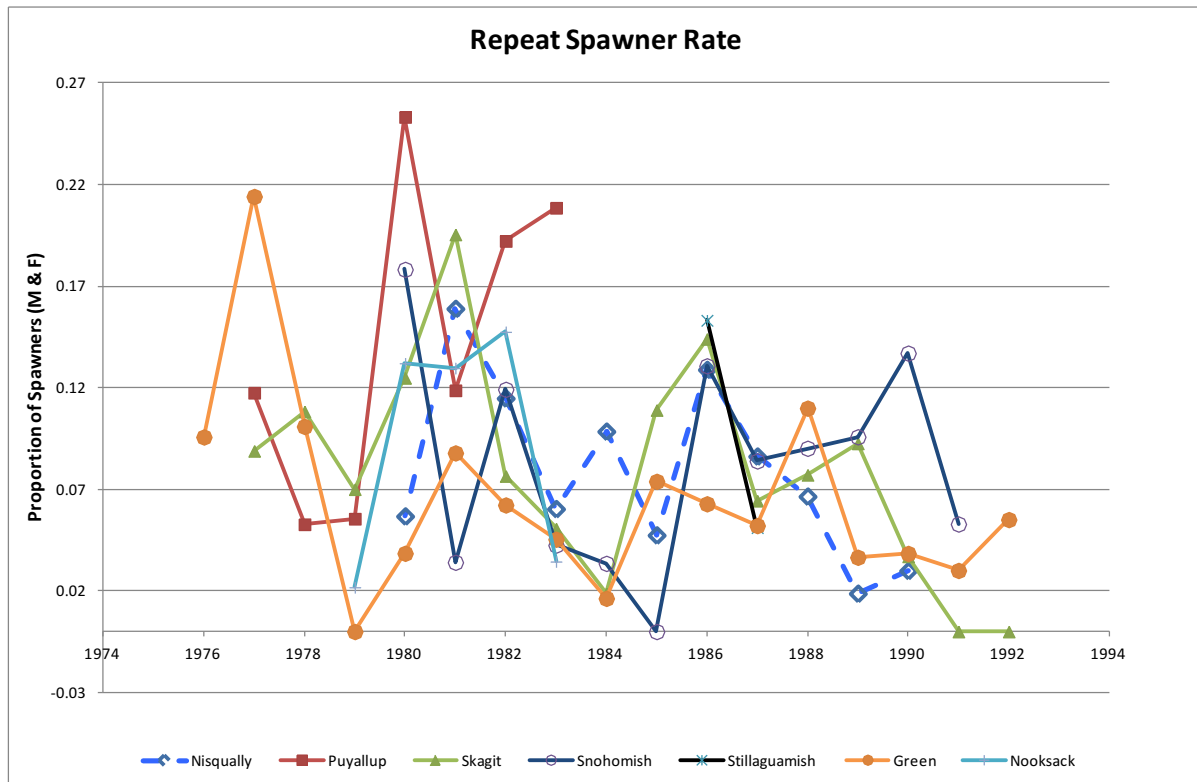


Figure 73. Temporal changes between the 1970s and 1990s in the estimates of repeat spawning rates for seven winter-run steelhead populations from the Northern Cascades and Central and South Puget Sound MPGs.

Female fecundity scaled with size and Kamchatka wild steelhead data were used to determine individual fecundities. First-time spawners were assumed to deposit more eggs than repeat spawners of the same age, reflecting the assumption that repeat spawners pay a cost in fecundity due to the costs of first spawning and to having less time available for growth in the ocean after spawning. This fecundity/growth cost is in addition to a survival cost that is paid for having matured and spawned at a younger age rather than remaining in the ocean and maturing one or two years later.

Density-dependence was modeled as a Beverton-Holt functional response. There is a scarcity of data on age- and stage-specific survival or mortality rates for adult and juvenile steelhead. The model employed values from a few of the steelhead studies available and theoretical considerations based on life-history theory and allometry to produce estimates for both juvenile and adult survival rates (Ward and Slaney 1993, McGurk 1996, Quinn 2005).

The effect of stochasticity was evaluated by modeling random variation in the smolt-to-age 3 transition rate as a random variable drawn from a Beta distribution with specific mean and coefficient of variation. Two ocean survival scenarios were evaluated that span reasonable levels of favorable and unfavorable variation in this transition rate.

Figure 74 summarizes some of the deterministic model results under a 20% harvest rate, assuming smolt to adult survival rates of 15% and a variety of repeat spawning rates. The median abundance declines from 330 for a population with 25% repeat spawners (which is more than 100 adults lower than without harvest) to just above 250 with no repeat spawners.

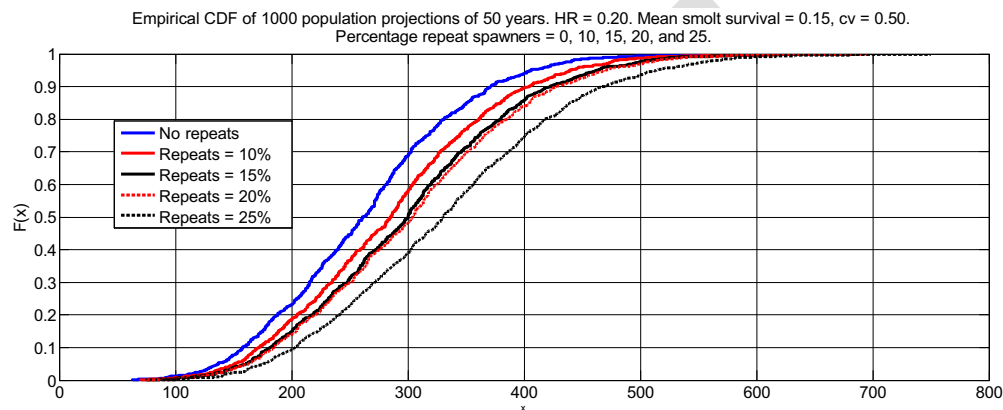


Figure 74. Empirical cumulative densities (CDF) of 1000 deterministic population projections over 50 years for steelhead exposed to a harvest rate of 20% under a mean smolt survival of 15% with a coefficient of variation (CV) of 50%. The different curves represent different repeat spawning rates ranging from 0-25%.

From his modeling, Gayeski concluded that:

1. The average proportion of repeat spawners in an adult steelhead population is relevant to population abundance and stream capacity in two ways: first, relative to a population with no repeat spawners, for a given average capacity of juveniles, a population with repeat spawners will have a larger average adult spawning population. Second, a given average number of adult spawners can be sustained by fewer juveniles when repeat spawners are present than when they are not. It is therefore likely that viable populations (DIPs) of steelhead can be sustained in smaller stream basins than is the case for Pacific salmon.
2. When population resilience to environmental variation and/or harvest mortality is measured in terms of either the probability of declining below specific levels of annual spawner abundance or the expected frequency of the spawning population declining below some threshold of concern (quasi-extinction), repeat spawning provides increased levels of resilience compared to populations without repeat

spawning. However, the impact of harvest mortality on the average proportion of repeat spawning confounds understanding of precisely how much resilience a given mean level of repeat spawning (measured under deterministic conditions) affords a population, especially at low levels of total abundance. The significance of repeat spawning may be weakened (and/or underestimated) when small population sizes are considered.

3. When both harvest mortality and environmental variation in smolt survival are present, repeat spawning increases population resilience. The precise extent to which resilience is increased is sensitive to the harvest rate and to both the magnitude of the average value of life-stage survival rates subject to environmental variation and the amount of variation in the rate as measured by the coefficient of variation.
4. From a recovery, population rebuilding perspective, it appears that for small population sizes such as the ones considered in this modeling exercise, the value of specific levels of repeat spawning to population resilience (and repeat spawning) are most likely to be realized under a zero harvest scenario, regardless of the level of environmental variation (at least for the range and kind of variation employed in the models).

These analyses reinforce the TRT's conviction that iteroparity is an important consideration in a comprehensive evaluation of viability for steelhead. Iteroparity is also arguably an important factor for diversity (and also for population persistence through temporal risk spreading), but the TRT did not consider this issue quantitatively. The degree of iteroparity is likely to be especially influential on viability in small populations during periods when marine mortality varies widely (see also the Integral Projection Model analysis of a small wild steelhead population described in Appendix F).

Viability Criteria for Puget Sound Steelhead

Under the ESA, NMFS is required to identify measurable and objective delisting criteria as part of recovery planning. These delisting criteria must describe the conditions under which a listed species or DPS is no longer in danger of extinction (endangered) or likely to become so in the foreseeable future (threatened). We define a viable DPS as one that is unlikely (with less than an estimated 5% probability) to be at risk of extinction in the foreseeable future; for this purpose, we adopt the VSP criteria of a specified quasi-extinction threshold and a 100-year timeline (McElhany et al. 2000) to evaluate risk of extinction. Ultimately, the identification of delisting criteria requires the consideration of technical analyses relating to viability, which are contained in this document, and policy decisions such as acceptable levels of risk, which are not. This document presents the Puget Sound Steelhead TRT's recommended biological viability criteria.

The listed unit under the ESA for *Oncorhynchus mykiss*, including anadromous steelhead, is the DPS, and this is the unit that must be considered for delisting. Thus, delisting criteria must ultimately address the extinction risk of the DPS. In approaching the development of criteria for assessing viability of (and, subsequently, delisting) DPSs, we have relied on the language in the ESA, information described in the listing decision, concepts outlined in the VSP document by McElhany et al. (2000), which can be found online at <http://www.nwfsc.noaa.gov/pubs/tm/tm42/tm42.pdf>, and in published research describing salmon populations and their past or potential responses to environmental changes. The ESA lists five potential factors for decline that must be considered in species listing decisions (ESA Section 4.2.1):

1. the present or threatened destruction, modification, or curtailment of its habitat or range;
2. overutilization for commercial, recreational, scientific, or educational purposes;
3. disease or predation;
4. the inadequacy of existing regulatory mechanisms; and
5. other natural or manmade factors affecting its continued existence.

NMFS identified all five factors as contributing to the endangerment of Pacific salmonids, including steelhead. In considering how viability criteria might inform population delisting requirements, the TRT also attempted to consider these factors for decline. NMFS's Population Recovery Approach for threatened Puget Sound Chinook salmon (NMFS 2010; see also Ruckelshaus et al. 2006) identified six delisting criteria for this Evolutionarily Significant Unit (ESU):

1. The viability status of all populations in the ESU is improved from current conditions.
2. At least two and up to four Chinook salmon populations in each of five biogeographical regions (i.e., major population groups) within the ESU achieve viability, depending on the historical biological characteristics and acceptable risk levels for populations within each region.

3. At least one population from each major genetic and life history group historically present within each of the five biogeographical regions is viable.
4. Tributaries to Puget Sound not identified as primary freshwater habitat for any of the 22 identified populations are functioning in a manner that is sufficient to support an ESU-wide recovery scenario.
5. Production of Chinook salmon from tributaries to Puget Sound not identified as primary freshwater habitat for any of the 22 identified populations occurs in a manner consistent with an ESU recovery.
6. Populations that do not meet the viability criteria for all VSP parameters (i.e., abundance, productivity, spatial structure and diversity) are sustained to provide ecological functions and preserve options for ESU recovery.

The TRT approach evaluated the extinction risks facing the DPS by assessing the viability of the individual populations (DIPs) and Major Population Groups (MPGs) within that DPS. The TRT identified population-level viability criteria based on a combination of the four parameters identified in the VSP document—productivity, abundance, diversity, and spatial structure—and information about the habitat requirements of the listed fish. From the analyses in this report, and building from these population-level criteria, the TRT identified viability criteria for the Puget Sound steelhead DPS that take into account these key VSP parameters and incorporate hierarchical viability criteria for MPGs and for the entire listed unit. Some of these criteria for steelhead share similarities to NMFS' Population Recovery Approach criteria for Puget Sound Chinook salmon listed above:

1. The viability (as reflected in abundance, productivity, diversity, and spatial structure) of a majority of steelhead populations in each of the Major Population Groups (MPGs) across the DPS is detectably higher than currently, using an accepted form of population viability analysis and additional tools like those described in this report.
2. At least 40% of steelhead populations in each of the three MPGs within the DPS achieve viability, depending on historical biological characteristics and acceptable levels for risk to population persistence within each region. To be viable, an MPG's constituent DIPs must have a mean viability above a specified threshold (described in the next section, p. 166).
3. A minimum of 40% of summer-run *and* 40% of winter-run populations historically present within each of the MPGs must viable using the VSP-based criteria described in this report.
4. Natural production of steelhead from tributaries to Puget Sound not identified as primary spawning or rearing habitat in any of the 32 identified populations is sustained to provide sufficient ecological diversity and productivity to support DPS-wide recovery.

The viability analyses described in an earlier section indicate that sufficient abundance and productivity from each major life history type in a sufficient fraction of populations spread spatially across each MPG are critical to the viability of each MPG—which DPS viability depends on. That said, diversity and spatial structure—which also appear to be limited throughout the DPS, based on limited data—make essential contributions to MPG (and therefore DPS) viability as well.

From these considerations, the Puget Sound Steelhead TRT developed the simple viability criteria framework outlined below. The TRT developed these criteria using the Puget Sound Steelhead DPS population structure identified in its “population identification” document (PSSTRT 2013) and implemented here: a DPS composed of 3 MPGs containing a total of 32 historically present DIPs. The configuration of the Puget Sound Steelhead DPS adopted in this report is based on information compiled to date, and it is possible, perhaps likely, that additional data will suggest future changes. These changes would most likely involve the number of DIPs identified rather than the number or configuration of the MPGs.

The criteria for viability for each unit within the DPS follow basic “traffic light” rule sets (summarized in Figures 75-77). Using a three-bin classification (low = “not viable”, “intermediate”, high = “viable”), the DIPs in an MPG are scored at each of the four VSP criteria with 1 (red, upside-down triangle), 2 (yellow square), or 3 points (green, upright triangle), corresponding to the contributions of these scores to DIP viability. These scores reflect probabilities that DIP viability is influenced by the VSP criteria, ranging from < 40%, 40-85%, or $\geq 85\%$, respectively (Figure 75). For a DIP to be considered viable, its probability of viability must be at least 85%, as calculated by the Bayesian Network for viability (see Appendix B). To estimate this value, the mean abundance and productivity criteria for the candidate DIP are each double-weighted; this produces DIP viability scores ranging from 6 to 18 points. DIPs with viability scores < 11 are considered to be not viable; those with viability scores between 11 and 14 are considered to have intermediate viability; and those with viability scores > 14 ($\geq 85\%$, rounded up) are considered to be viable.

MPG viability depends on two criteria. First, as indicated in Figure 76, a minimum of 40% of the DIPs in the MPG that exhibit each of the two distinct life-history strategies (summer-run versus winter-run) must be viable using the same “traffic light” rule set (i.e., score = 3). (The threshold of 40% corresponds to an average probability of DIP viability of 64% if the DIPs that are not viable have probabilities of viability of 50%.) Second, the DIPs in the MPG must have a geometric mean score of at least 2.2, a value the TRT determined based on consideration of the first criterion and examining how MPG viability under the traffic-light rule set varies. This score is the minimum achieved across a range of MPG sizes (with number of DIPs ranging from 8 to 16) with a sufficient fraction of DIPs having viabilities of 85%. Following these two criteria, to be viable an MPG with 8 DIPs must have at least 4 viable DIPs (score = 3) and no more than one DIP that is considered not viable (score = 1). An MPG with 11 winter-run and 5 summer-run DIPs must have at least 5 viable winter-run and 2 viable summer-run DIPs and no more than 1 DIP of each life-history type that is considered not viable.

Figure 75. Framework for establishing viability criteria for Demographically Independent Populations (DIPs) of Puget Sound steelhead. See text for description.

		DIP viability					
		VSP Parameter					
		Abundance	Productivity	Diversity	Spatial structure	Viability	
		▼	▼	▼	▼	▼	6
		▲	▼	▼	▼	▼	10
		▼	▲	▼	▼	▼	10
		▼	▼	▲	▼	▼	8
		▼	▼	▼	▲	▼	8
		▲	▲	▼	▼	■	14
		▲	▼	▲	▼	■	12
		▲	▼	▼	▲	■	12
		▼	▲	▲	▼	■	12
		▼	▲	▼	▲	▼	10
		▲	▲	▲	▼	▲	
							16
		▲	▲	▼	▲	▲	16
		▲	▼	▲	▲	■	14
		▼	▲	▲	▲	■	14
		▲	▲	▲	▲	▲	18

Key:	
▼	Low < 40%
■	Moderate 40-85%
▲	High > 85%

Figure 76. Framework for establishing viability criteria for Major Population Groups (MPGs) of Puget Sound steelhead based on the viability of component DIPs containing distinct life-history types (summer- or winter-run steelhead). Key is as in Figure 75. See text for description.

MPG viability						
	<40% viable DIPs (S or W)	>40% viable DIPs (S)	>40% viable DIPs (W)	>40% viable DIPs (S + W)		Viability
	■	-	-	-		▼
	-	■	-	-		▼
	-	-	■	-		▼
	-	-	-	■		▲

Finally, DPS viability depends only on one criterion: that each of its component MPGs is considered viable (Figure 77).

The viability criteria for each level within the DPS are summarized below.

DIP Viability

- Using a simple three-bin classification (not viable, intermediate, viable), a DIP is scored 1, 2, or 3, depending on whether the probability of viability as computed by its viability Bayesian Network is < 40%, 40-85%, or ≥ 85%, respectively. For a DIP to be considered viable, its probability of viability must be at least 85%. To estimate this value, the mean abundance and productivity criteria for the candidate DIP are both double-weighted; this produces DIP viability scores ranging from 6 to 18 points. DIPs with viability scores < 11 are considered not viable; those with viability scores between 11 and 14 are considered to have intermediate viability; and those with viability scores > 14 (≥ 85%, rounded up) are considered viable.

Figure 77. Framework for viability criteria for the entire Distinct Population Segment (DPS) of Puget Sound steelhead. Key as in Figure 75. See text for description.

		DPS viability							
		MPG 1		MPG 2		MPG 3		Viability	
		▼		▼		▼		▼	
		▲		▼		▼		▼	
		▼		▲		▼		▼	
		▼		▼		▲		▼	
		▲		▲		▼		▼	
		▲		▼		▲		▼	
		▼		▲		▲		▼	
		▲		▲		▲		▲	

MPG Viability

2. An MPG is considered viable if 40% (rounded up) of its DIPs (including extinct as well as extant historical populations) are viable and mean DIP viability exceeds the specified threshold for viability (Table 16).
 - a. DIPs exhibiting distinct life-history strategies (summer-run versus winter-run) will be considered separate components of the MPG. Therefore, a minimum of 40% of summer-run *and* 40% of winter-run populations within an MPG must be viable to achieve MPG viability.
 - b. DIPs containing both winter- and summer-run subpopulations predominantly exhibit the winter-run life-history strategy in Puget Sound and will be considered winter-run for the purpose of estimating 2a.
 - c. A viable MPG must, in addition to the criterion outlined in 2a and 2b, have a geometric mean score of at least 2.2 to be considered viable. This score is the minimum achieved across a range of MPG sizes (with number of DIPs ranging from 8 to 16) with a sufficient fraction of DIPs having viabilities of 85%.

Table 16. Number of viable DIPs required for MPG viability in each of the Puget Sound steelhead MPGs with a requirement of 40% viable DIPs of each major life-history type. Some winter-run DIPs may include some summer-run fish as well, which is most common in the Northern Cascades MPG and along the Strait of Juan de Fuca.

MPG	Life-history type	Number of DIPs	Number viable
Northern Cascades	Summer-run	5	2
	Winter-run	11	5
Central and South Puget Sound	Summer-run	0	0
	Winter-run	8	4
Hood Canal and Strait of Juan de Fuca	Summer-run	0	0
	Winter-run	8	4

DPS Viability

3. A DPS is considered viable only if **all** its component MPGs are viable.

A graphical depiction of representative viability criteria applied to the DPS to depict their relationships is given in Figure 78. This figure emphasizes the hierarchical nature of the criteria across the levels of the components of the DPS. The framework partitions criteria at the DIP level between “persistence” and “sustainability” factors related to VSP components. For example, the framework considers spawner abundance, productivity, occupancy and density of suitable habitat by adults and juveniles, frequency of iteroparity, and sources of human-induced mortality as factors that influence demography primarily and therefore, population, persistence. It considers effective population size, influence of hatchery fish (both genetic and ecological impacts), age variation in spawners, and variation in spawn timing, as factors that influence diversity primarily and, therefore, population sustainability. The framework also conveys the importance of having populations distributed across major habitat types, of having connectivity between resident and anadromous fish where historically they occurred, and of minimizing risk to multiple DIPs due to catastrophic risk. It attempts to include factors considered important to viability, even if current information is inadequate to characterize their influence on viability estimates accurately. Finally, it considers harvest mortality as a factor in the context of other human-induced risk to steelhead such as freshwater habitat loss or climate change).

The TRT applied the criteria to the 32 DIPs in the Puget Sound steelhead DPS to provide a status assessment of the current viability of these units (Figure 79). The hierarchical Bayesian Networks produced the viability values that were used to generate the scores in this figure. Because this figure categorizes the viability scores for each criterion and for each DIP as a whole into 3 bins as described above, one of its primary purposes is to provide a readily visualized

summary of patterns of viability for DIPs across the DPS. Another purpose of this figure is to highlight viability criteria that lack sufficient information, a key first step in outlining a monitoring program for recovery. This assessment is summarized in Figure 79, and it clearly indicates low viability for more than half of the DIPs, all MPGs, and the DPS as a whole. Nearly all DIPs have insufficient current abundance and productivity scores to be considered viable. Most also have low scores for diversity and spatial structure, largely because of extensive hatchery influence, low breeding population sizes, and freshwater habitat fragmentation or loss. In the South Puget Sound and the Hood Canal and Strait of Juan de Fuca MPGs, nearly all DIPs are not viable. The mean score for the 16 DIPs in the Northern Cascades MPG is 11.9, just above the threshold for intermediate viability; however, no summer-run populations are viable using the assessment, so the MPG is not considered to be viable. The mean score for the 8 DIPs in the South Puget Sound MPG is 9.5, and that for the 8 DIPs in the Hood Canal and Strait of Juan de Fuca MPG is 9.9; both scores are below the threshold for intermediate viability.

Under an alternative assessment in which all viability criteria for which data are insufficient are given an intermediate score (2), the outcome of viability changes surprisingly little, even at the level of individual DIPs (Figure 80). Most DIPs still have insufficient current abundance and productivity scores to be considered viable, especially in the South Puget Sound and the Hood Canal and Strait of Juan de Fuca MPGs. Most have intermediate scores for diversity and spatial structure. In the South Puget Sound and the Hood Canal and Strait of Juan de Fuca MPGs, most (11 of 16) DIPs are not viable. The mean score for the 16 DIPs in the Northern Cascades MPG is 11.9, just above the threshold for intermediate viability; however, no summer-run populations are viable using the assessment, so the MPG is still not considered to be viable. The mean score for the 8 DIPs in the South Puget Sound MPG is 10.7, and that for the 8 DIPs in the Hood Canal and Strait of Juan de Fuca MPG is 10.1; both scores are still below the threshold for intermediate viability. Twelve of the 32 DIPs lack sufficient information on the abundance and productivity criteria to be certain about their influences on viability, and all DIPs throughout the DPS have insufficient information on each of the diversity criteria.

Recommended viability criteria

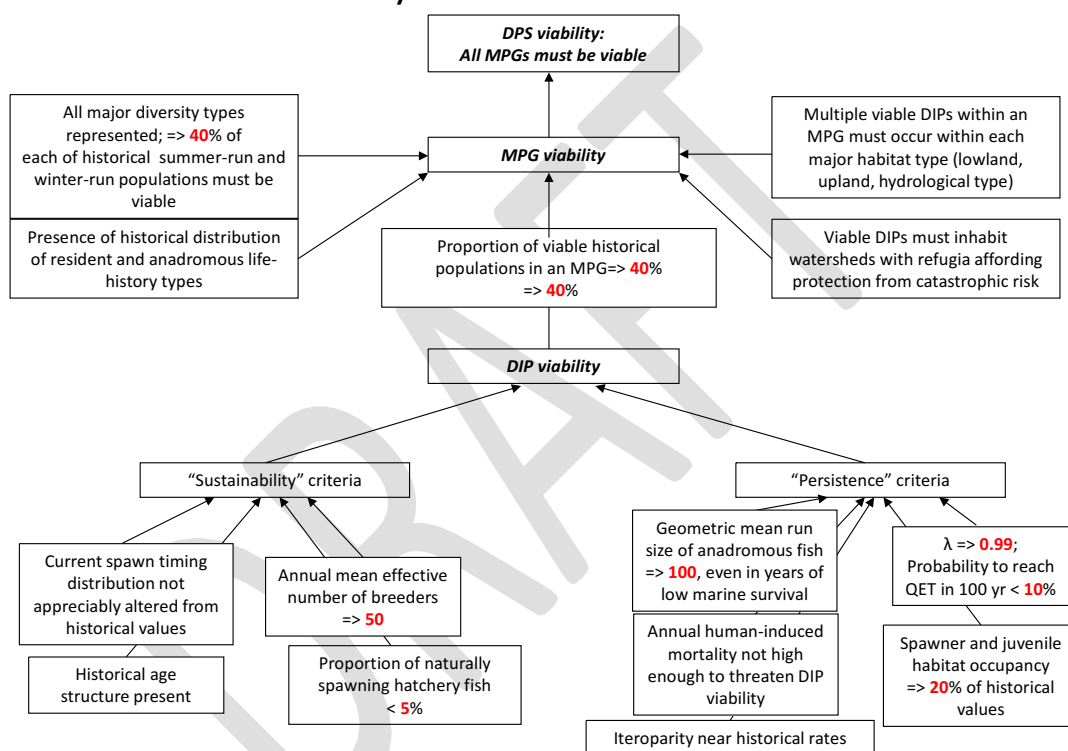


Figure 78. An example set of viability criteria for a Distinct Population Segment (DPS) of steelhead. The chart shows how viability at the scale of the DIP, MPG, and the entire DPS are related. For DIP viability, criteria are divided into those contributing to persistence (i.e., abundance and productivity, extinction risk, and effects of human-induced mortality) and those contributing to sustainability (i.e., spatial structure and diversity, influence of hatchery fish, age structure, and spawn timing). Human-induced mortality includes mortality from fishing, pollution, and habitat loss.

MPG	DIP	VSP Parameter											Viability						
		Abundance			Productivity			Diversity			Spatial structure		DIP	MPG	DPS				
		Adult	Juvenile	OET	Smolts/sp.	Adults/smolt	Lambda	Iteroparity	Hatchery	Spawn timing	Residents	Age				Spawn IP	Rear IP		
N. Cascades	Drayton Harbor trib. (W)	☒	☒	▲	☒	☒	☒	☒	☒	☒	▲	☒	▼	☒	☒	☒	☒		
	Nooksack R. (W)	▼	▼	▲	☒	☒	☒	☒	☒	☒	▲	☒	▼	☒	☒	☒	☒		
	S. Fk. Nooksack R. (S)	▼	▼	▲	☒	☒	☒	☒	☒	☒	▲	☒	▼	☒	☒	☒	☒		
	Samish R./Bellingham (W)	☒	☒	▲	☒	☒	☒	☒	☒	☒	▲	☒	▼	☒	☒	☒	☒		
	Skagit R. (S/W)	▼	▼	▲	☒	☒	☒	☒	☒	☒	▲	▲	▼	☒	☒	☒	☒		
	Nookachamps Cr. (W)	☒	☒	▲	☒	☒	☒	☒	☒	☒	▲	☒	▼	☒	☒	☒	☒		
	Baker R. (S/W)	☒	☒	▲	☒	▼	▼	☒	☒	☒	▲	☒	▼	☒	☒	☒	☒		
	Sauk R. (S/W)	▼	▼	☒	☒	☒	☒	☒	☒	☒	▲	▲	▼	☒	☒	☒	☒	▼	☒
	Stillaguamish R. (W)	▼	▼	☒	▼	▼	▼	☒	☒	☒	☒	☒	▼	☒	☒	☒	☒	▼	☒
	Deer Cr. (S)	☒	☒	▲	☒	☒	☒	☒	☒	☒	▲	☒	▼	☒	☒	☒	☒		
	Canyon Cr. (S)	▲	▲	▲	☒	☒	☒	☒	☒	☒	☒	☒	▼	☒	☒	☒	☒	▲	☒
	Snohomish/Skykomish R. (W)	☒	☒	▲	☒	☒	☒	☒	☒	☒	▼	☒	▼	☒	☒	☒	☒		
	Pilchuck R. (W)	▼	▼	▼	☒	☒	☒	☒	☒	☒	☒	☒	▼	☒	☒	☒	☒	▼	☒
	N. Fk. Skykomish R. (S)	▲	▲	▲	☒	☒	☒	☒	☒	☒	▼	☒	▼	☒	☒	☒	☒		
	Snoqualmie R. (W)	☒	☒	▲	☒	☒	☒	☒	☒	☒	☒	☒	▼	☒	☒	☒	☒		
	Tolt R. (S)	☒	☒	▼	☒	☒	☒	☒	☒	☒	▼	☒	☒	☒	☒	▲	▲	☒	
Central/S. Sound	N. Lk. Washington trib. (W)	▼	▼	☒	▼	▼	▼	☒	☒	☒	☒	☒	▼	☒	☒	☒	☒	▼	☒
	Cedar R. (W)	▼	▼	▼	▼	▼	▼	☒	☒	☒	▲	▲	▼	☒	☒	☒	☒	▼	☒
	Green R. (W)	▼	▼	☒	☒	☒	☒	☒	☒	☒	☒	▲	▼	☒	☒	☒	☒	▼	☒
	Puyallup/Carbon R. (W)	▼	▼	☒	▼	▼	▼	☒	☒	☒	☒	☒	▼	☒	☒	☒	☒	▼	☒
	White R. (W)	▼	▼	☒	☒	☒	☒	☒	☒	☒	▲	☒	▼	☒	☒	☒	☒	▼	☒
	Nisqually R. (W)	▼	▼	☒	▼	▼	▼	☒	☒	☒	▲	☒	▼	☒	☒	☒	☒	▼	☒
	S. Sound trib. (W)	▼	▼	☒	▼	▼	▼	☒	☒	☒	☒	☒	▼	☒	☒	☒	☒	▼	☒
	E. Kitsap Penin. (W)	☒	☒	▼	▼	▼	▼	☒	☒	☒	▲	☒	▼	☒	☒	☒	☒	▼	☒
Hood Canal & SJF	E. Hood Canal (W)	▼	▼	▼	☒	☒	☒	☒	☒	☒	☒	☒	▼	☒	☒	☒	☒	▼	☒
	S. Hood Canal (W)	▼	▼	▼	▼	▼	▼	☒	☒	☒	☒	☒	▼	☒	☒	☒	☒	▼	☒
	Skokomish R. (W)	▼	▼	☒	☒	☒	☒	☒	☒	☒	▲	☒	▼	☒	☒	☒	☒	▼	☒
	W. Hood Canal (W)	▼	▼	☒	☒	▲	▲	☒	☒	☒	☒	☒	▼	☒	☒	☒	☒	▼	☒
	Sequim/Discovery Bay trib. (W)	▼	▼	▼	▼	▼	▼	☒	☒	☒	▲	☒	▼	☒	☒	☒	☒	▼	☒
	Dungeness R. (S/W)	☒	☒	▲	▼	▼	▼	☒	☒	☒	☒	☒	▼	☒	☒	▲	▲	☒	
	Strait of Juan de Fuca indep. (W)	☒	☒	☒	▼	▼	▼	☒	☒	☒	☒	☒	▼	☒	☒	☒	☒	▼	☒
	Elwha R. (S/W)	▼	▼	▼	▼	▼	▼	☒	☒	☒	☒	▲	▼	☒	☒	☒	☒	▼	☒

Key:
 ▼ Low < 40%
 ☒ Moderate 40-85%
 ▲ High > 85%
 ▲ ☒ ▼ Ins. data

Figure 79. Estimates of current viability (low = “not viable”, moderate = “intermediate”, or high = “viable”) for the 32 Demographically Independent Populations (DIPs) of Puget Sound steelhead using the Viable Salmonid Populations (VSP) framework described in the text. Note that many criteria are supported by insufficient data and in most (but not all) of those cases they were given an intermediate value with respect to influence on viability.

MPG	DIP	VSP Parameter											Viability					
		Abundance			Productivity			Diversity			Spatial structure		DIP	MPG	DPS			
		Adult	Juvenile	OET	Smolts/sp.	Adults/smolt	Lambda	Iteroparity	Hatchery	Spawn timing	Residents	Age				Spawn IP	Rear IP	
N. Cascades	Drayton Harbor trib. (W)	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒
	Nooksack R. (W)	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒
	S. Fk. Nooksack R. (S)	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒
	Samish R./Bellingham (W)	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒
	Skagit R. (S/W)	▼	▼	▲	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒
	Nookachamps Cr. (W)	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒
	Baker R. (S/W)	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒
	Sauk R. (S/W)	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒
	Stillaguamish R. (W)	▼	▼	☒	▼	▼	▼	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	▼
	Deer Cr. (S)	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒
	Canyon Cr. (S)	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒
	Snohomish/Skykomish R. (W)	☒	☒	▲	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒
	Pilchuck R. (W)	▼	▼	▼	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	▼
	N. Fk. Skykomish R. (S)	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒
	Snoqualmie R. (W)	☒	☒	▲	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒
	Tolt R. (S)	☒	☒	▼	☒	☒	☒	☒	☒	☒	☒	☒	☒	▲	▲	☒	☒	☒
Central/S. Sound	N. Lk. Washington trib. (W)	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒
	Cedar R. (W)	▼	▼	▼	▼	▼	▼	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	▼
	Green R. (W)	▼	▼	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	▼
	Puyallup/Carbon R. (W)	▼	▼	☒	▼	▼	▼	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	▼
	White R. (W)	▼	▼	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	▼
	Nisqually R. (W)	▼	▼	☒	▼	▼	▼	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	▼
	S. Sound trib. (W)	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒
	E. Kitsap Penin. (W)	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒
Hood Canal & SJF	E. Hood Canal (W)	▼	▼	▼	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	▼
	S. Hood Canal (W)	▼	▼	▼	▼	▼	▼	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	▼
	Skokomish R. (W)	▼	▼	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	▼
	W. Hood Canal (W)	▼	▼	☒	▲	▲	▲	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	▼
	Sequim/Discovery Bay trib. (W)	▼	▼	▼	▼	▼	▼	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	▼
	Dungeness R. (S/W)	☒	☒	▲	▼	▼	▼	☒	☒	☒	☒	☒	☒	▲	▲	☒	☒	☒
	Strait of Juan de Fuca indep. (W)	☒	☒	☒	▼	▼	▼	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	▼
	Elwha R. (S/W)	▼	▼	▼	▼	▼	▼	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	▼

Key:
 ▼ Low < 40%
 ☒ Moderate 40-85%
 ▲ High > 85%
 ☒ Ins. data

Figure 80. Estimates of current viability (low = “not viable”, moderate = “intermediate”, or high = “viable”) for the 32 Demographically Independent Populations (DIPs) of Puget Sound steelhead using the Viable Salmonid Populations (VSP) framework described in the text, but assuming that all viability criteria without quantifiable information are given an intermediate score of 2 (“intermediate”).

Conclusions

Based on a combination of quantitative Population Viability Analyses, collective judgment of qualitative information, and use of habitat-based metrics to estimate intrinsic potential, the Puget Sound Steelhead TRT has developed and applied a framework to evaluate the current biological status of the Puget Sound Steelhead DPS. This framework is based on a series of hierarchical Bayesian Networks intended to integrate the various sources of information that influence viability at the levels of the Demographically Independent Population (DIP), the Major Population Group or biogeographic stratum (MPG), and the entire listed Distinct Population Segment (DPS). This information is biological (e.g., juvenile and adult abundance, population growth rate, freshwater and marine survival, iteroparity, spawn timing), related to habitat characteristics (e.g., habitat use and selection with respect to hydrograph, reach size and gradient, elevation), and related to management (e.g., hatchery influence, harvest effects). The TRT applied the framework to the Puget Sound Steelhead DPS to evaluate its status and with the intent to assist in guiding recovery actions. The framework and the analyses it supports do not set recovery targets at any of the three levels, nor do they explicitly identify specific populations or groups of populations for recovery priority. Rather, the framework and associated analyses are meant to provide a technical foundation for those charged with recovery of listed steelhead in Puget Sound from which they can develop effective recovery plans at the watershed scale (and higher) that are based on biologically meaningful criteria. They are also meant to highlight the data that are needed in future monitoring and evaluation studies to improve these efforts. It should be evident from this report that identifying the best way forward in recovery planning for steelhead would be enhanced considerably by additional information on the demography, diversity, and distribution of steelhead in watersheds throughout Puget Sound.

Consistent with its status as a threatened species under the Endangered Species Act, the Puget Sound Steelhead Distinct Population Segment is not considered to be viable by the TRT. Using a comprehensive set of Bayesian Networks that incorporate factors influencing all four Viable Salmonid Populations criteria (abundance, productivity, diversity, and spatial structure), nearly all of its 32 constituent DIPs, and all 3 of its constituent MPGs are at low viability. Nearly all DIPs in both the South Puget Sound and the Hood Canal and Strait of Juan de Fuca MPGs are not viable. Most of the DIPs score low for all four VSP criteria, and nearly all DIPs have insufficient current abundance and productivity scores to be considered viable. Most DIPs also have low scores for diversity and intermediate scores for spatial structure. The pattern of low viability is widespread throughout Puget Sound, across all three MPGs, and includes both summer- and winter-run populations. The populations with highest viability—and those with highest abundance and diversity—are in northeastern Puget Sound (Northern Cascades MPG).

An analysis incorporating a simpler set of Bayesian Networks that rely only on abundance and productivity criteria produced estimates of steelhead viability that are considerably higher throughout the DPS, but even under this analysis there is substantial uncertainty in the status of at least two of the MPGs and of the entire DPS. Despite the lack of quantitative information for several aspects of diversity and spatial structure, the TRT considers these VSP criteria to be essential for DPS viability into the future, and recommends the use of the more comprehensive networks that encompass all four VSP criteria to evaluate the viability of Puget Sound steelhead.

The TRT's Bayesian Network framework provides a means of evaluating steelhead viability with explicit reference to estimates of historical abundance, productivity, diversity, and spatial distribution steelhead in this region. This framework provides a systematic and transparent mechanism to evaluate viability of the DPS and its component MPGs and DIPs, and lends itself to evaluating alternative recovery scenarios and the effects of specific or alternative recovery actions, especially those operating at the watershed scale.

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Appendix A

State-Space Analyses of Viability of Demographically Independent Populations of Puget Sound Steelhead

For each population, the results of the autoregressive state-space (MARSS) population viability analyses (PVAs) are summarized in up to six subplots. In each group of plots, the top left panel plots the observed counts and the fitted state-space estimate against year, giving the MARSS maximum-likelihood estimate of fit to the abundance data (red curve), the estimated long-term population growth rate (u_{est} , equivalent to $\ln(\lambda)$), and the estimate of process error (Q_{est}). The top right panel plots the probability that the population will reach a particular quasi-extinction threshold (QET) abundance within the next 100 years (with approximate 95% confidence intervals). The QETs for each population applied here (Table 6) are based on an estimate derived from the intrinsic potential metrics described in the main text.

The middle left panel plots the probability density of the time in years to reach QET given that it is reached within 100 years, and the middle right panel depicts the probability of reaching QET in 100 years, given as a function of the number of individuals at the end of the projection. The bottom left panel plots several of the sample population projections estimated by MARSS.

Finally, the bottom right panel depicts the regions of high certainty and uncertainty surrounding the population projections (an extinction risk “envelope”; see Ellner and Holmes 2008). The green region is where the upper 95% CIs of the projections do not exceed $P = 0.05$ —i.e., where the probability of the specified population decline is $< 5\%$. The red region is where the lower 95% CIs of the projections exceed $P = 0.95$ —i.e., where the probability of the specified population decline is $> 95\%$. The grey regions define less certain areas of parameter space between these extremes, with the dark grey region representing the region of highest uncertainty. Note that not all plots and corresponding estimates could be constructed for each population. For example, we were not able to calculate PVA estimates for putative winter-run steelhead DIPs in the Nooksack River or in Southern Puget Sound tributaries, nor were we able to do so for any summer-run steelhead populations in the Puget Sound DPS, except for that in the Tolt River.

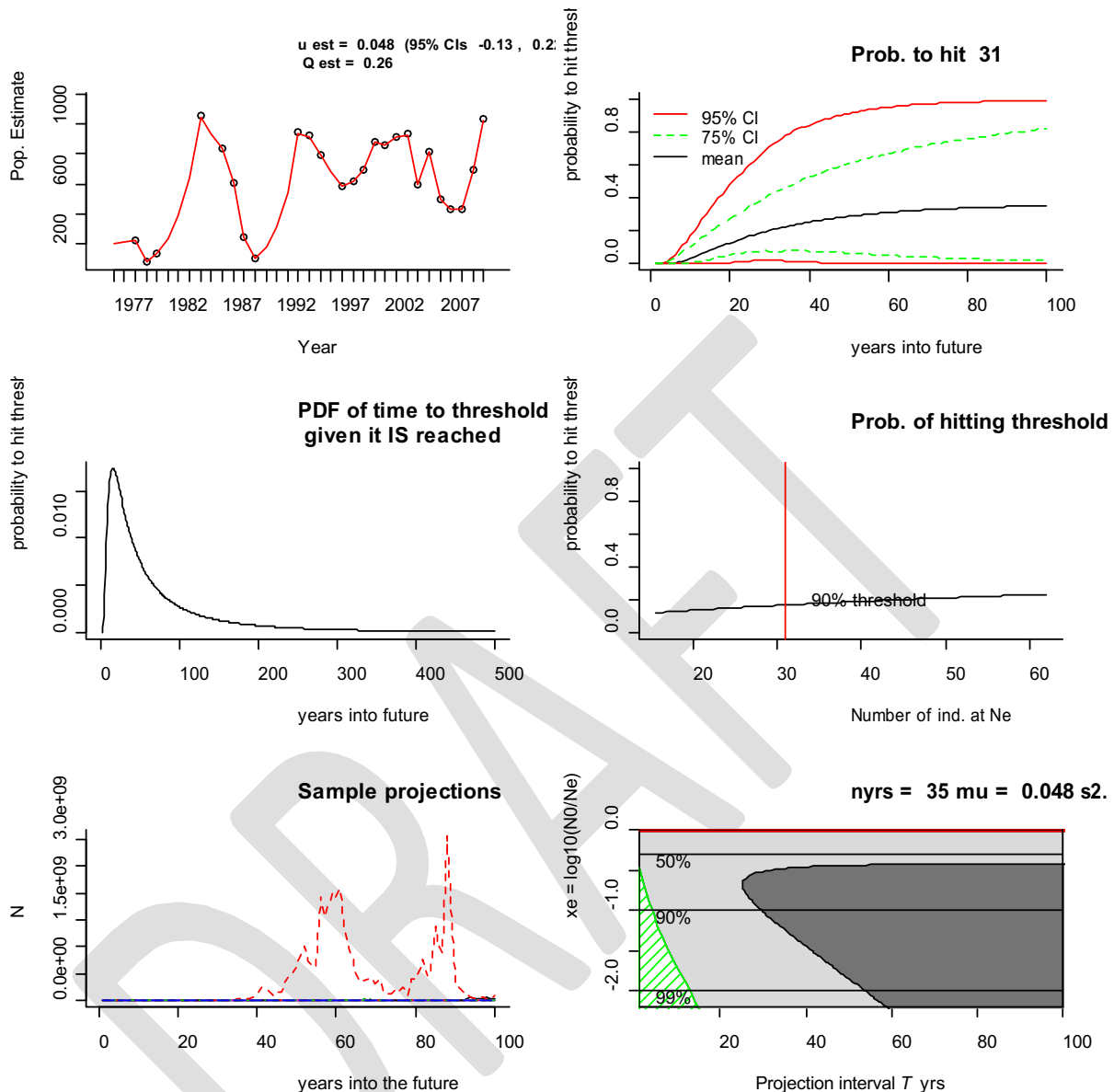


Figure A-1. MARSS-based population viability analysis for Samish River winter-run steelhead. Steelhead counts in the Samish River have varied considerably with a decline over the past decade but have generally declined. The estimated mean population growth rate (u_{est}) is 0.048 ($\lambda = 1.049$) and process error (Q_{est}) is 0.260, with no significant evidence for population trend. Assuming that these counts are a reasonable reflection of spawner abundance, the estimated probability that this steelhead population would decline to a QET of 31 fish is relatively low—about 30% within 100 years. We can be highly confident ($P < 0.05$) that a 90% decline in this population will not occur within the next 5-8 years, and that a 99% decline will not occur within the next 15 years. However, beyond the very near term (i.e., after about 20 years) we are uncertain about the precise level of extinction risk.

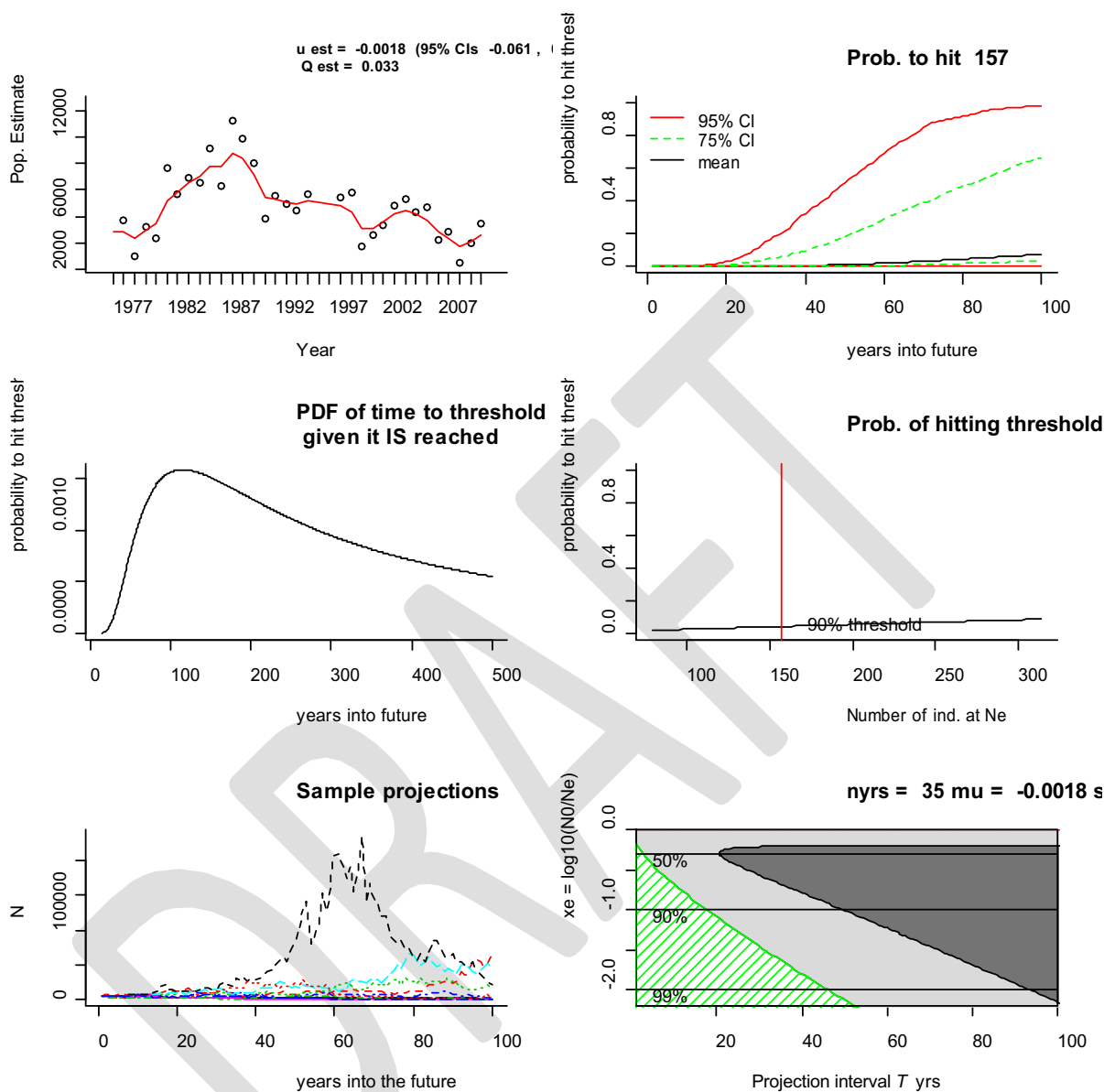


Figure A-2. MARSS-based population viability analysis for Skagit River summer- and winter-run steelhead. Steelhead counts in the Skagit River have been highly variable but have declined since the low 1980s. The estimated mean population growth rate is -0.002 ($\lambda = 0.998$) and process error is 0.033 , with no significant evidence for population trend. The estimated probability that this steelhead population would decline to a QET of 157 fish is very low—less than 10% within 100 years. We can be highly confident ($P < 0.05$) that a 90% decline in this population will not occur within the next 20 years, and that a 99% decline will not occur within the next 45 years. However, beyond the near term (after just a few decades) we are uncertain about the precise level of extinction risk.

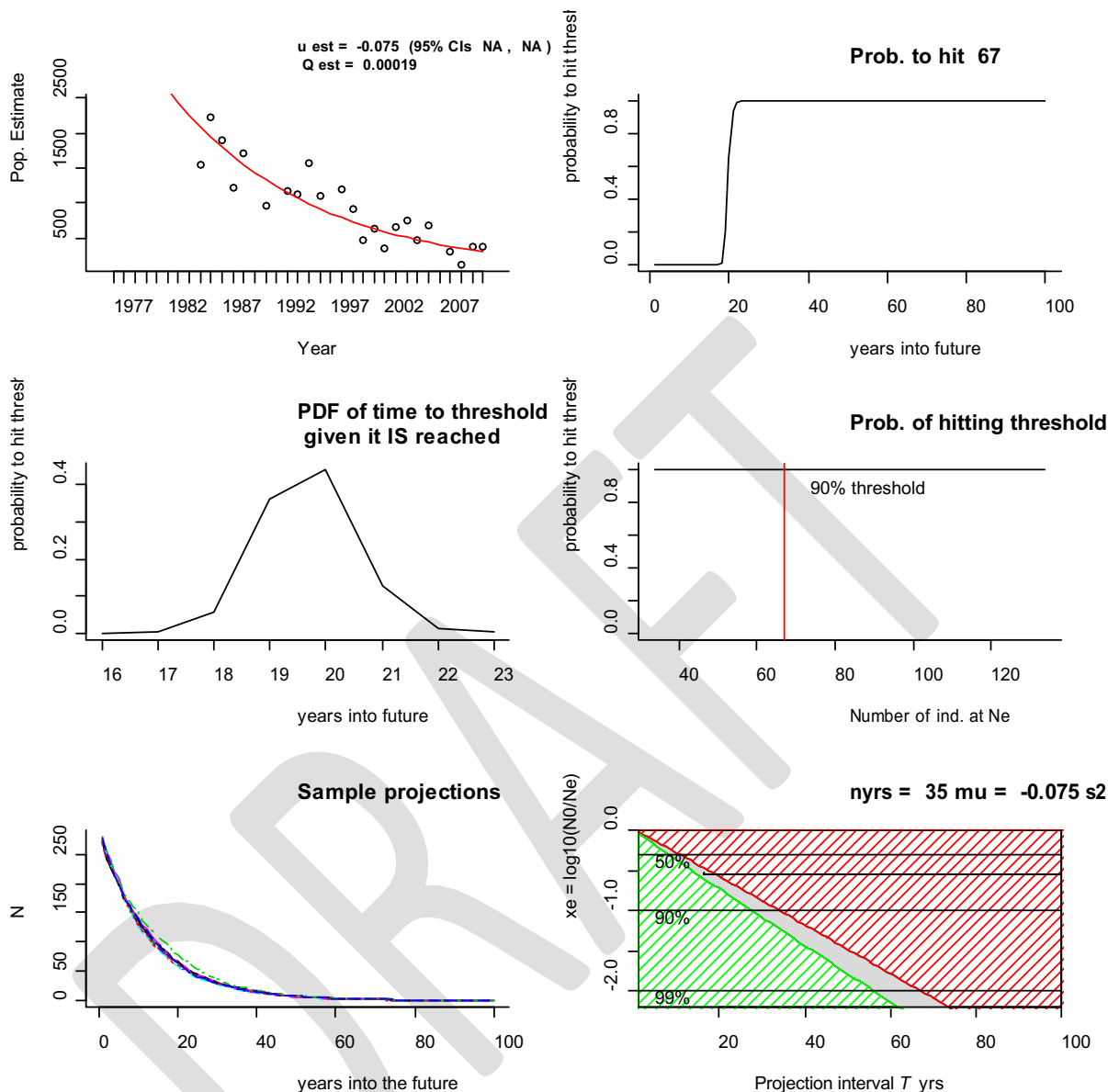


Figure A-3. MARSS-based population viability analysis for Stillaguamish River winter-run steelhead. Steelhead counts in the Stillaguamish River have declined steadily since the early 1980s. The estimated probability that this steelhead population would decline to a QET of 67 fish is high—about 90% within 25 years. With an estimated mean population growth rate of -0.075 ($\lambda = 0.928$) and process error of <0.001 , we can be highly confident ($P < 0.05$) that a 90% decline in this population will not occur within the next 30 years, and that a 99% decline will not occur within the next 55 years. However, a 50% decline is highly likely within 10 years, and a 90% decline within 35 years. There is little uncertainty about a decline in this population if current conditions continue.

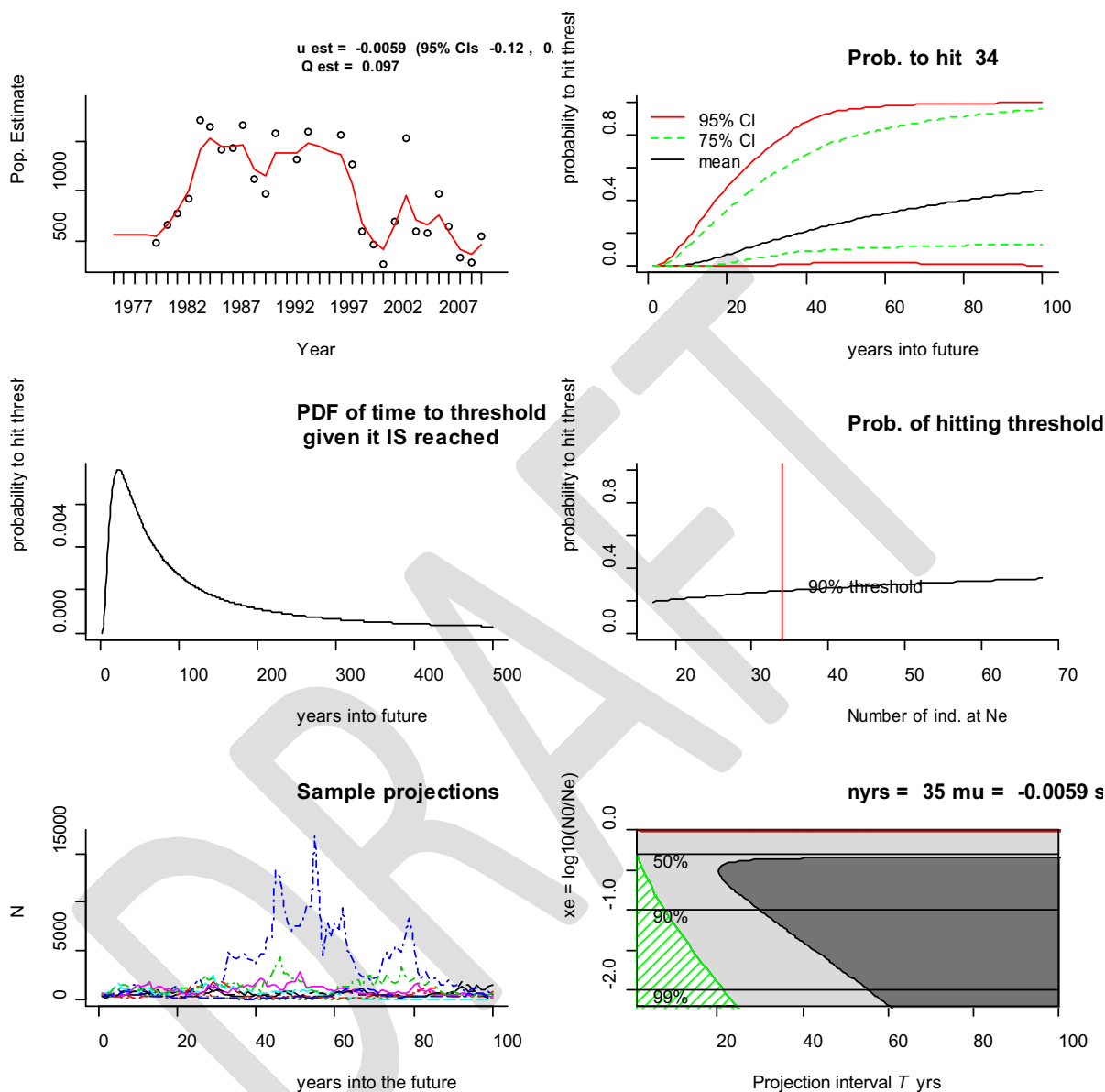


Figure A-4. MARSS-based population viability analysis for Pilchuck River winter-run steelhead. Steelhead counts in the Pilchuck River have declined detectably from levels during the late 1980s and early 1990s, and been relatively low in most years since 2000. The estimated probability that this steelhead population would decline to a QET of 34 fish is relatively low—about 40% within 100 years. With an estimated mean population growth rate of -0.006 ($\lambda = 0.994$) and process error of 0.097 , we can be highly confident ($P < 0.05$) that a 90% decline in this population will not occur within the next 6–8 years, and that a 99% decline will not occur within the next 20 years. . However, beyond the very near term (i.e., after about 20 years) we are uncertain about the precise level of extinction risk.

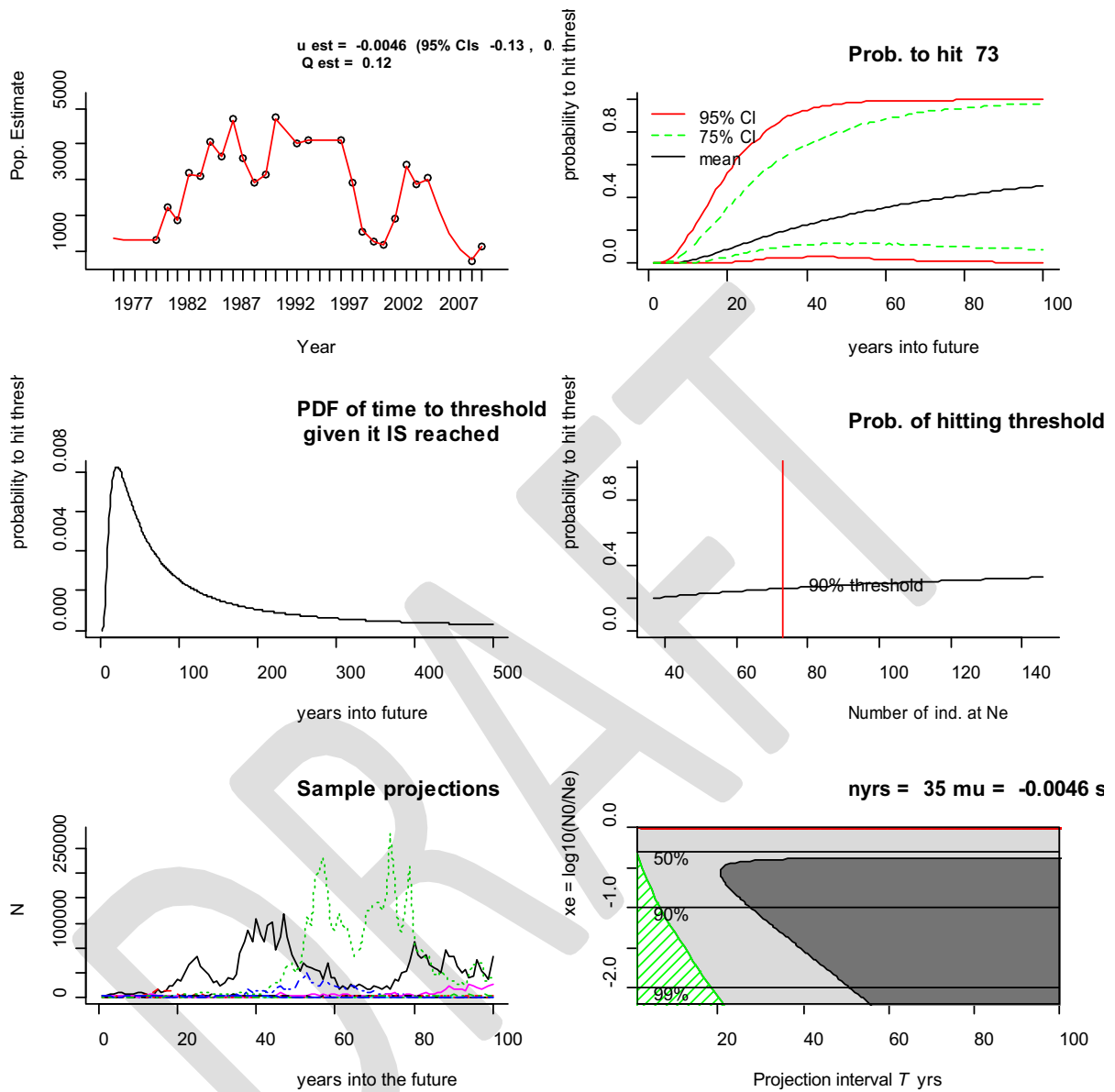


Figure A-5. MARSS-based population viability analysis for Snohomish River winter-run steelhead. Steelhead counts in the Snohomish River have generally declined since the early 1990s but have varied widely. The estimated probability that this steelhead population would decline to a QET of 73 fish is low—about 40% within 100 years. With an estimated mean population growth rate of -0.005 ($\lambda = 0.995$) and process error of 0.120 , we can be highly confident ($P < 0.05$) that a 90% decline in this population will not occur within the next 8-10 years, and that a 99% decline will not occur within the next 20 years. However, beyond the very near term (i.e., after about 20 years) we are uncertain about the precise level of extinction risk.

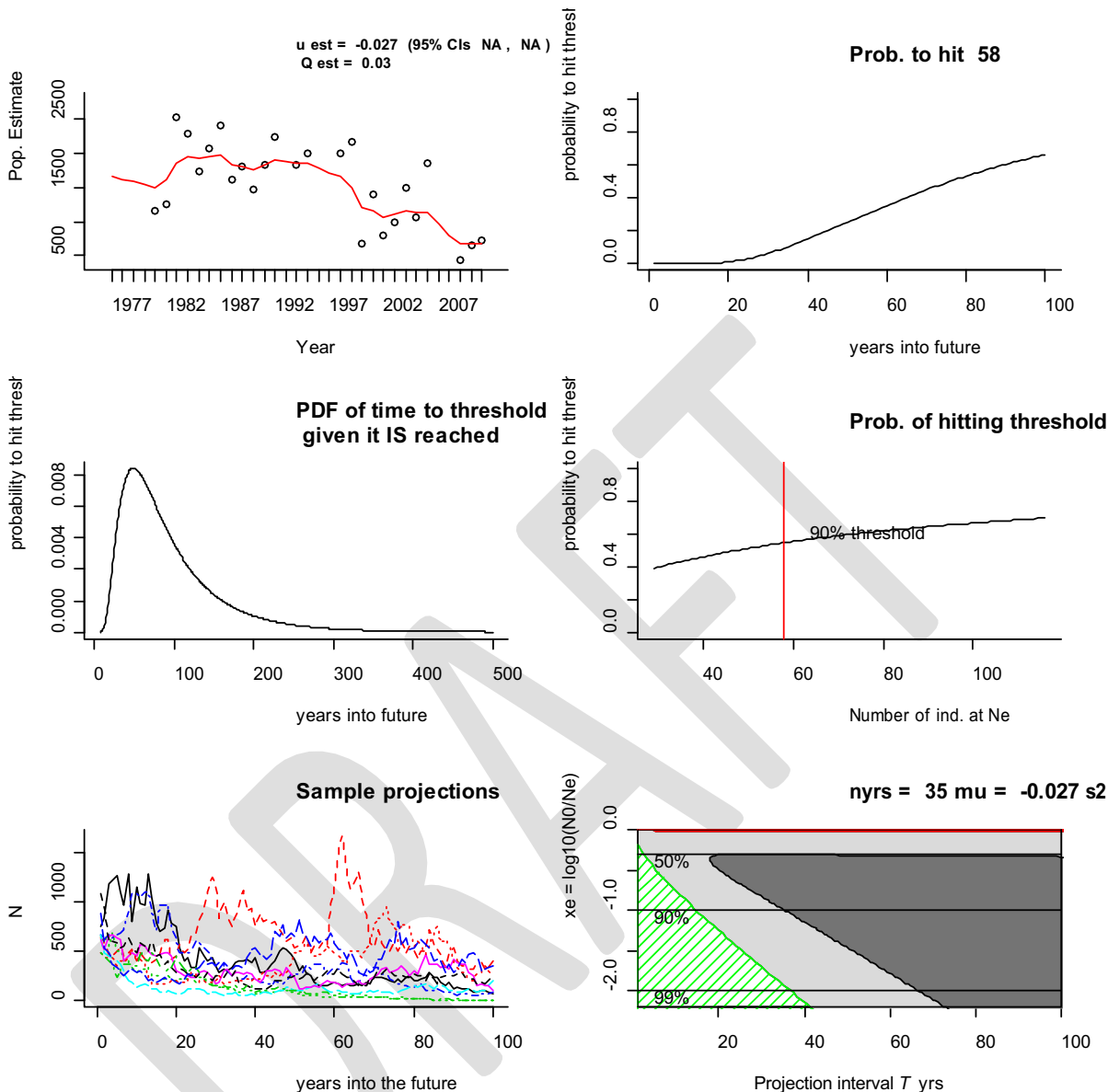


Figure A-6. MARSS-based population viability analysis for Snoqualmie River winter-run steelhead. Steelhead counts in the Snoqualmie River have declined since the early 1990s. The estimated probability that this steelhead population would decline to a QET of 58 fish is relatively high—nearly 70% within 100 years. With an estimated mean population growth rate of -0.027 ($\lambda = 0.973$) and process error of 0.030 , we can be highly confident ($P < 0.05$) that a 90% decline in this population will not occur within the next 15 years, and that a 99% decline will not occur within the next 35 years. However, beyond the next 30-40 years we are uncertain about the precise level of extinction risk.

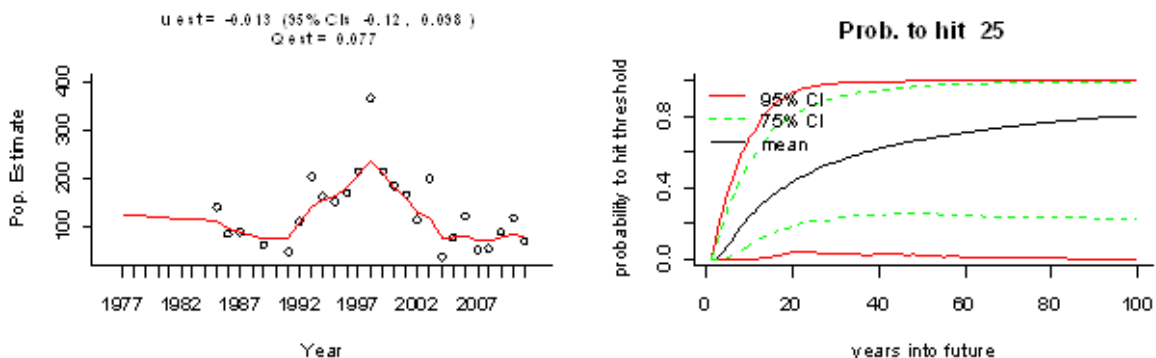


Figure A-7. MARSS-based population viability analysis for Tolt River summer-run steelhead. Steelhead counts in the Tolt River have varied since the 1980s, declining from a modest high in the late 1990s. The estimated probability that this steelhead population would decline to a QET of 25 fish is high—about 80% within 100 years. The estimated mean population growth rate is -0.013 ($\lambda = 0.987$) and the process error is 0.077 . We are highly uncertain about the precise level of extinction risk for this population but it is likely to be high because abundance is typically low but highly variable.

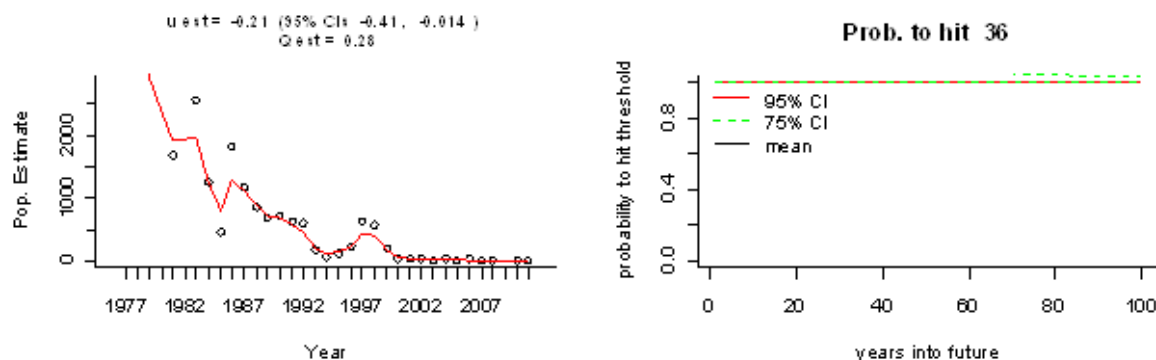


Figure A-8. MARSS-based population viability analysis for Cedar River winter-run steelhead. Steelhead counts in the Lake Washington watershed, including the Cedar River, have declined sharply since the early 1980s and have been very low since the early 1990s. The estimated probability that this steelhead population would decline to a QET of 36 fish is high—at least 90% within the next few years. The estimated mean population growth rate is -0.210 ($\lambda = 0.811$) and process error is 0.280 . We are uncertain about the precise level of extinction risk for this population but it is clear that it is alarmingly high due to very low abundance.

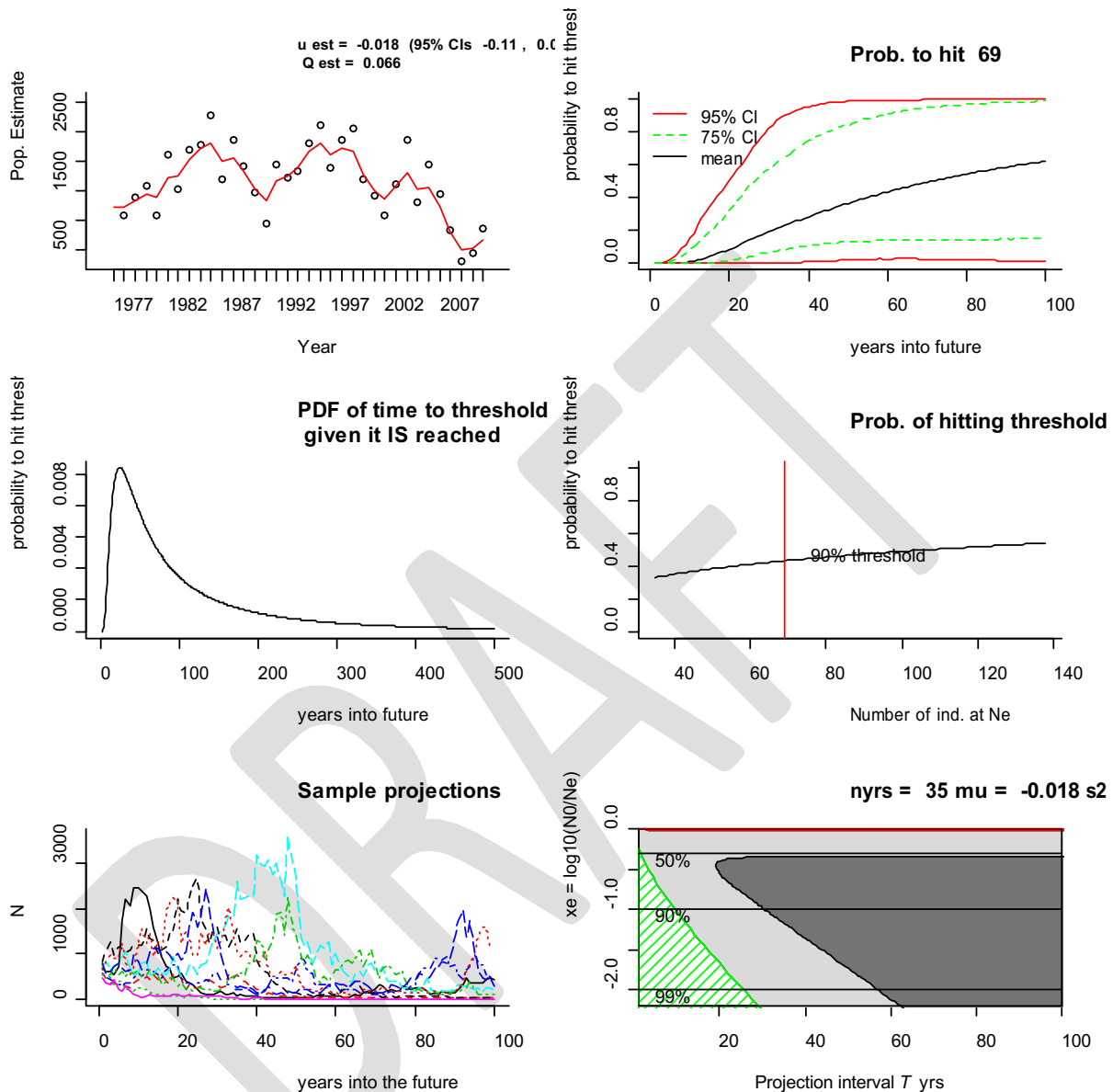


Figure A-9. MARSS-based population viability analysis for Green River summer- and winter-run steelhead. Steelhead counts in the Green River have been variable but have exhibited a clear decline in recent years. The estimated probability that this steelhead population would decline to a QET of 69 fish is moderately high over a VSP time frame—about 50% within 100 years. With an estimated mean population growth rate of -0.018 ($\lambda = 0.982$) and process error of 0.066 , we can be highly confident ($P < 0.05$) that a 90% decline in this population will not occur within the next 10 years, and that a 99% decline will not occur within the next 25 years.

However, beyond the near term (i.e., after about 30 years) we are uncertain about the precise level of extinction risk

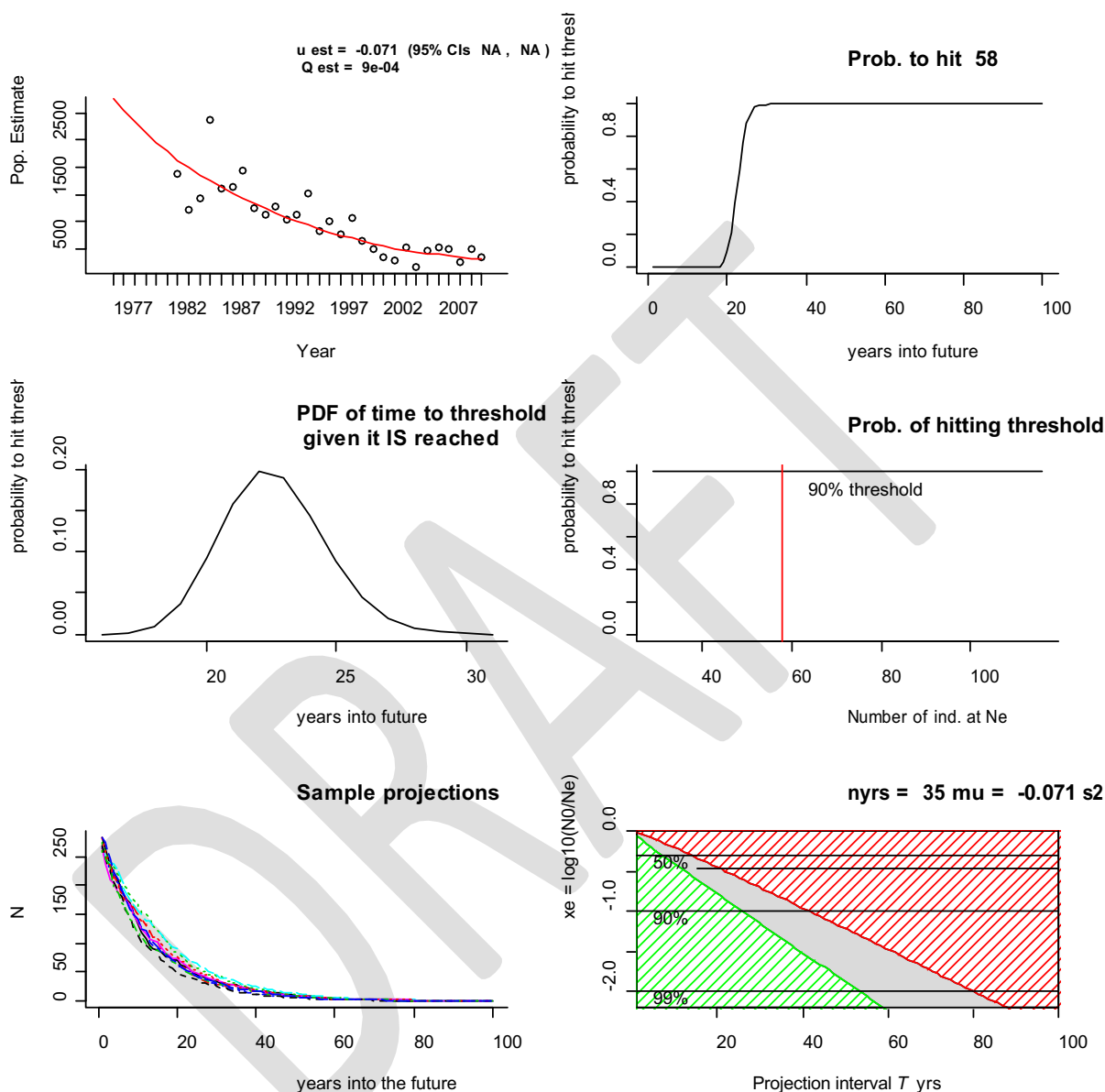


Figure A-10. MARSS-based population viability analysis for Puyallup River winter-run steelhead. Steelhead counts in the Puyallup River have declined steadily since the 1980s. The estimated probability that this steelhead population would decline to a QET of 58 fish is high—about 90% within 30 years. With an estimated mean population growth rate of -0.071 ($\lambda = 0.931$) and process error of <0.001 , we can be highly confident ($P < 0.05$) that a 90% decline in this population will not occur within the next 5-10 years, and that a 99% decline will not occur within the next 25 years. However, a 50% decline is highly likely within 15 years, and a 90% decline

within 40 years. There is little uncertainty that the population will continue to decline within the foreseeable future if current conditions persist.

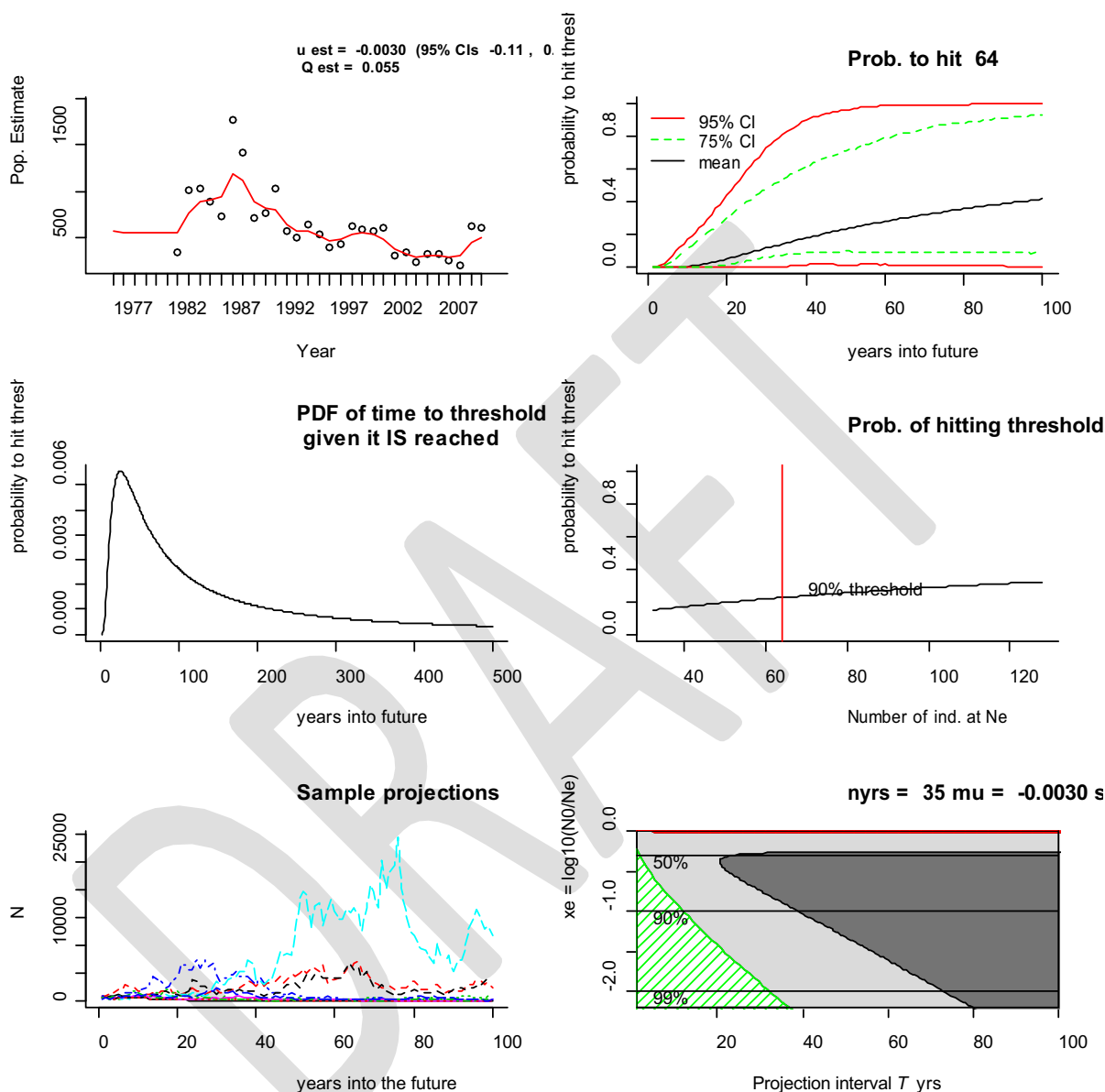


Figure A-11. MARSS-based population viability analysis for White River winter-run steelhead. Steelhead counts in the White River have declined steadily since the 1980s. The estimated probability that this steelhead population would decline to a QET of 64 fish is relatively low—about 40% within 100 years. With an estimated mean population growth rate of -0.003 ($\lambda = 0.997$) and process error of 0.055, we can be highly confident ($P < 0.05$) that a 90% decline in this population will not occur within the next 20-15 years, and that a 99% decline will not occur

within the next 30-35 years. However, beyond the next few decades we are uncertain about the precise level of extinction risk.

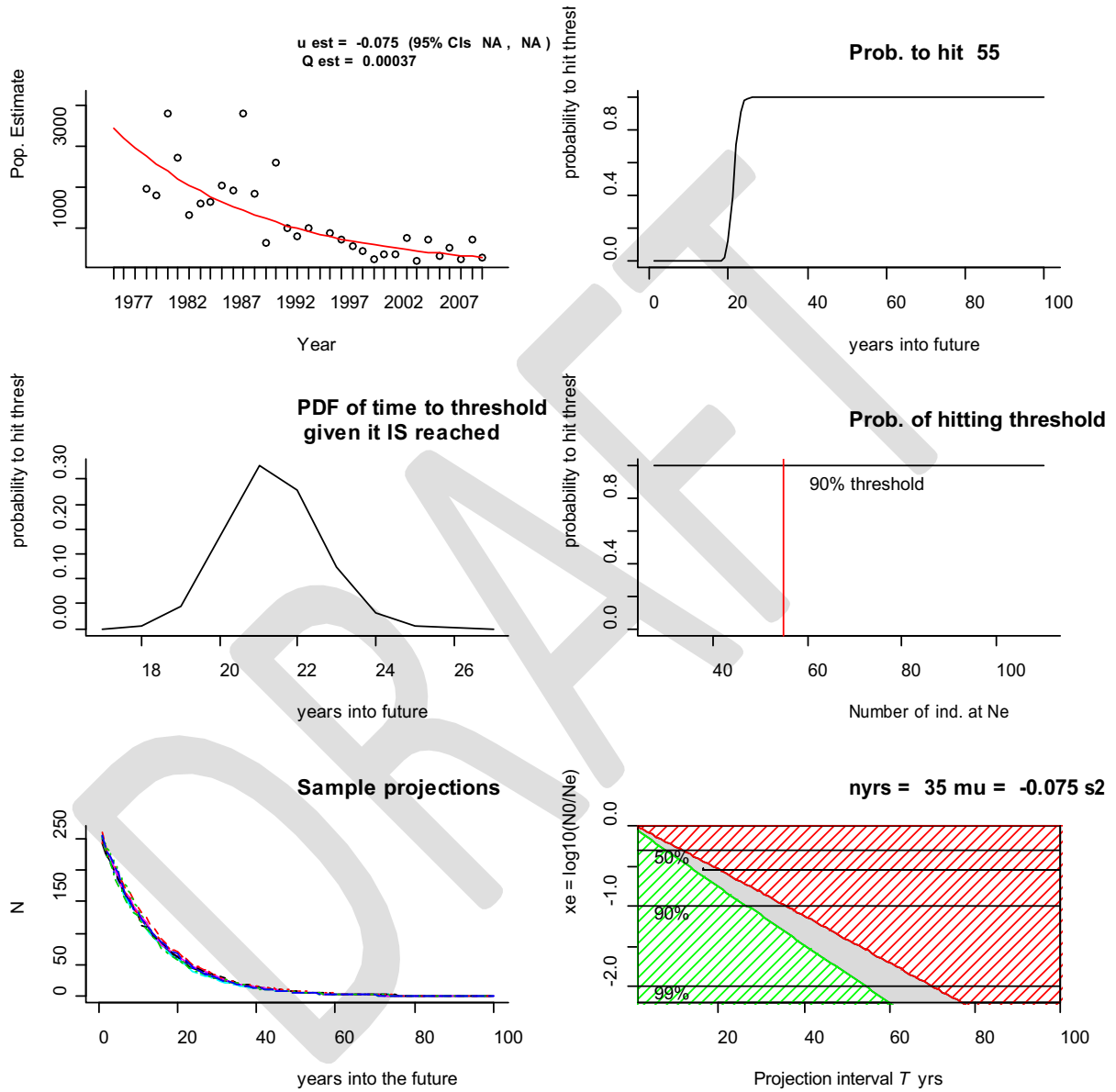


Figure A-12. MARSS-based population viability analysis for Nisqually River winter-run steelhead. Steelhead counts in the Nisqually River declined steadily since about 1990 and have remained low since then. The estimated probability that this steelhead population would decline to a QET of 55 fish is high—about 90% within 25 years. With an estimated mean population growth rate of -0.075 ($\lambda = 0.928$) and process error of <0.001 , we can be highly confident ($P <$

0.05) that a 90% decline in this population will not occur within the next 25-30 years, and that a 99% decline will not occur within the next 55 years. However, a 50% decline is highly likely within 10 years, and a 90% decline within 40 years. There is little uncertainty that the population will continue to decline if current conditions persist.

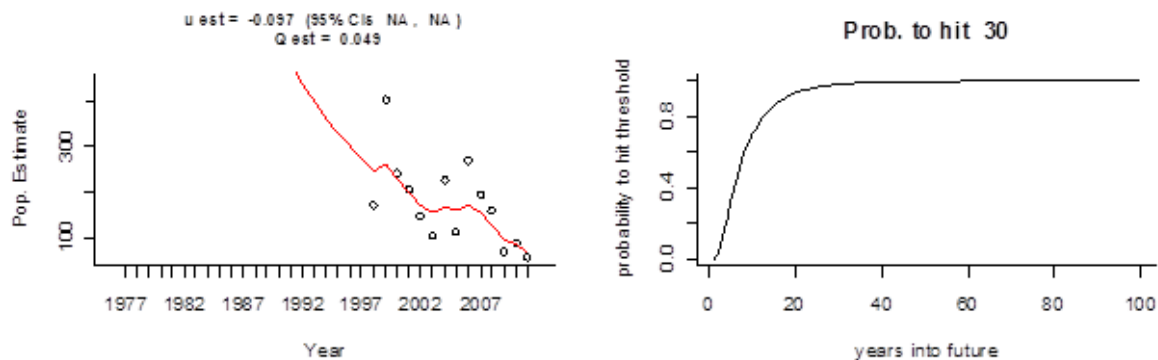


Figure A-13. MARSS-based population viability analysis for South Hood Canal (including the Dewatto and Tahuya rivers) winter-run steelhead. Steelhead counts in South Hood Canal declined steadily since the late 1990s. The estimated probability that this steelhead population would decline to a QET of 30 fish is high—about 90% within 20 years. The estimated mean population growth rate is -0.097 ($\lambda = 0.908$) and process error is 0.049 . We are uncertain about the precise level of extinction risk for this population but it is clear that it is high because of low and steeply declining abundance.

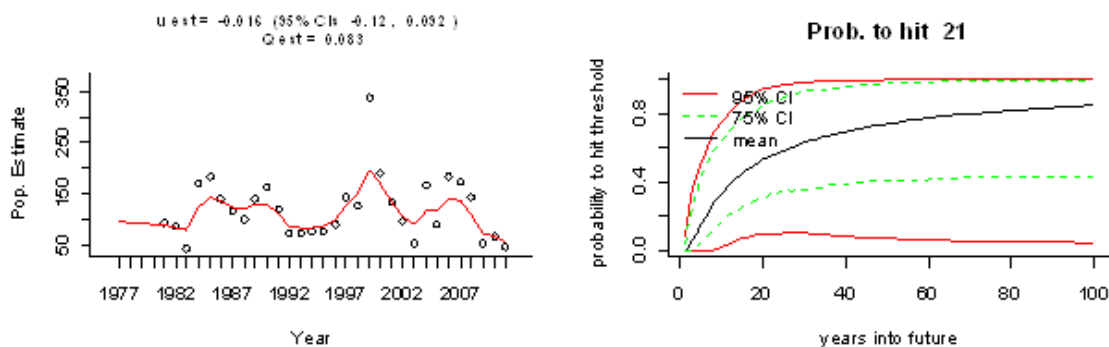


Figure A-14. MARSS-based population viability analysis for Tahuya River winter-run steelhead. Steelhead counts in the Tahuya River have varied and often been quite low but there has been no distinct trend since the 1980s. The estimated probability that this steelhead population would decline to a QET of 21 fish is relatively high—over 80% within 100 years. The estimated mean

population growth rate is -0.016 ($\lambda = 0.984$) and process error is 0.083 . We are uncertain about the precise level of extinction risk for this population but it is clear that it is relatively high because of low abundance.

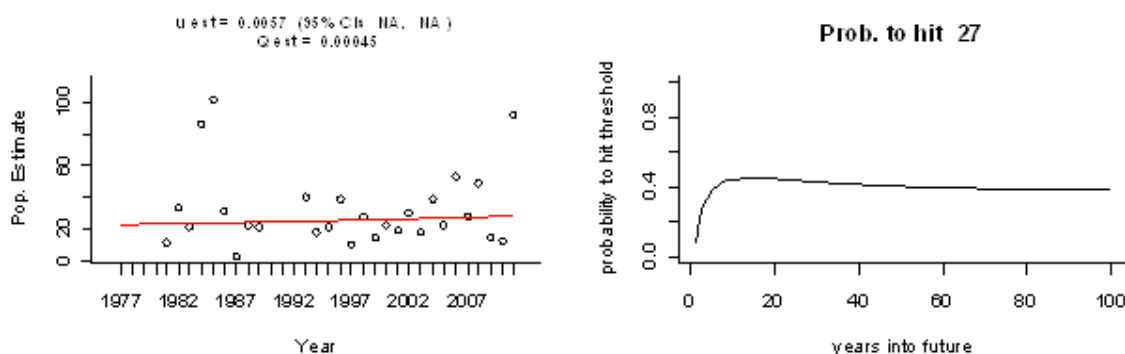


Figure A-15. MARSS-based population viability analysis for East Hood Canal winter-run steelhead. Steelhead counts in East Hood Canal have varied and often been quite low but there has been no distinct trend since the 1980s. The estimated probability that this steelhead population would decline to a QET of 27 fish is relatively low—about 40% within 100 years. The estimated mean population growth rate is 0.006 ($\lambda = 1.006$) and process error is <0.001 . We are uncertain about the precise level of extinction risk for this population but it is clear that it is neither safely low (because of the stable trend) nor very high (because of the very low abundance).

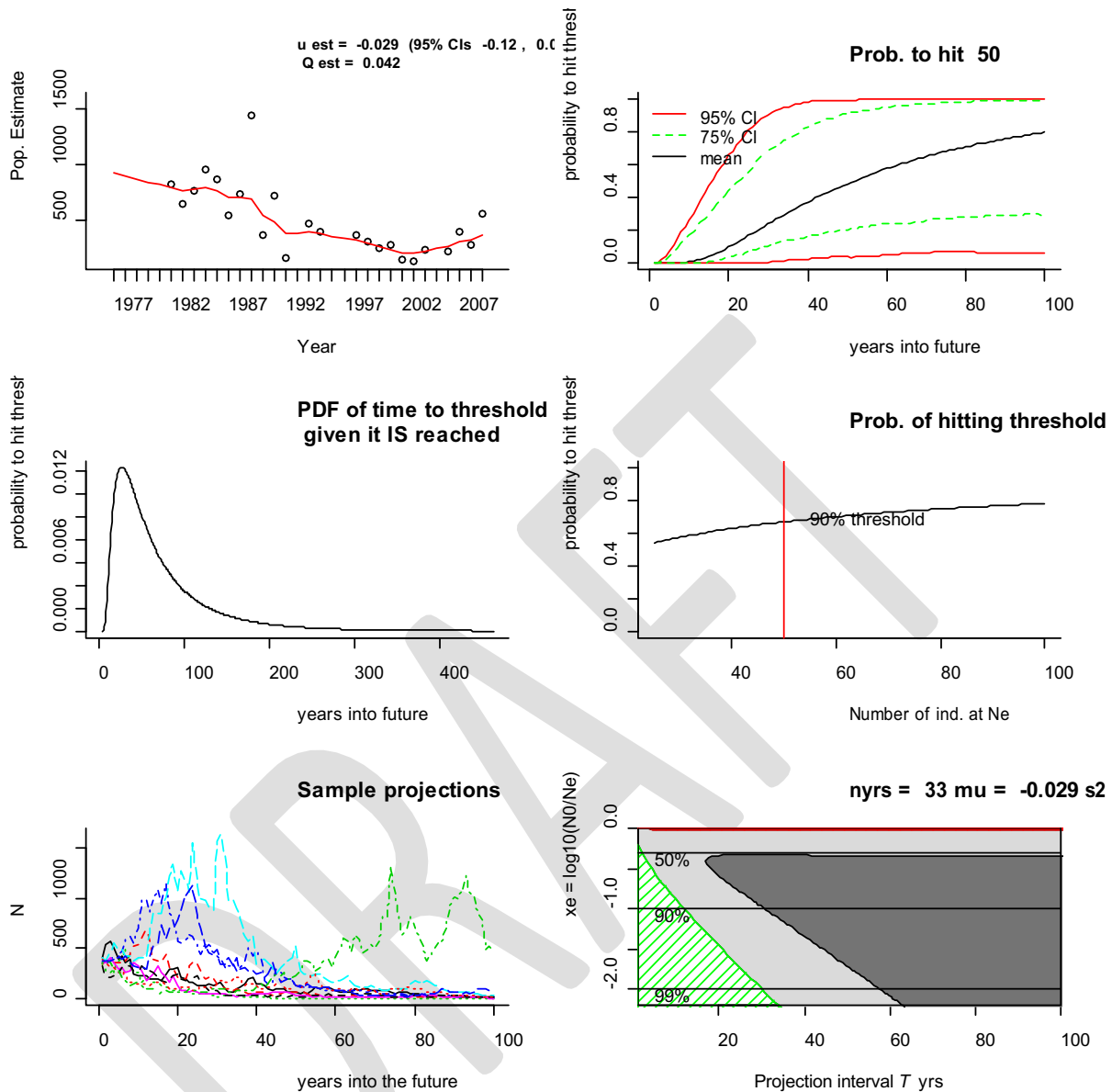


Figure A-16. MARSS-based population viability analysis for Skokomish River winter-run steelhead. Steelhead counts in the Skokomish River have declined since the 1980s. The estimated probability that this steelhead population would decline to a QET of 50 fish is relatively high—over 70% within 100 years. With an estimated mean population growth rate of -0.029 ($\lambda = 0.971$) and process error of 0.042 , we can be highly confident ($P < 0.05$) that a 90% decline in this population will not occur within the next 10 years, and that a 99% decline will not occur within the next 30 years. However, beyond the next two or three decades we are uncertain about the precise level of extinction risk.

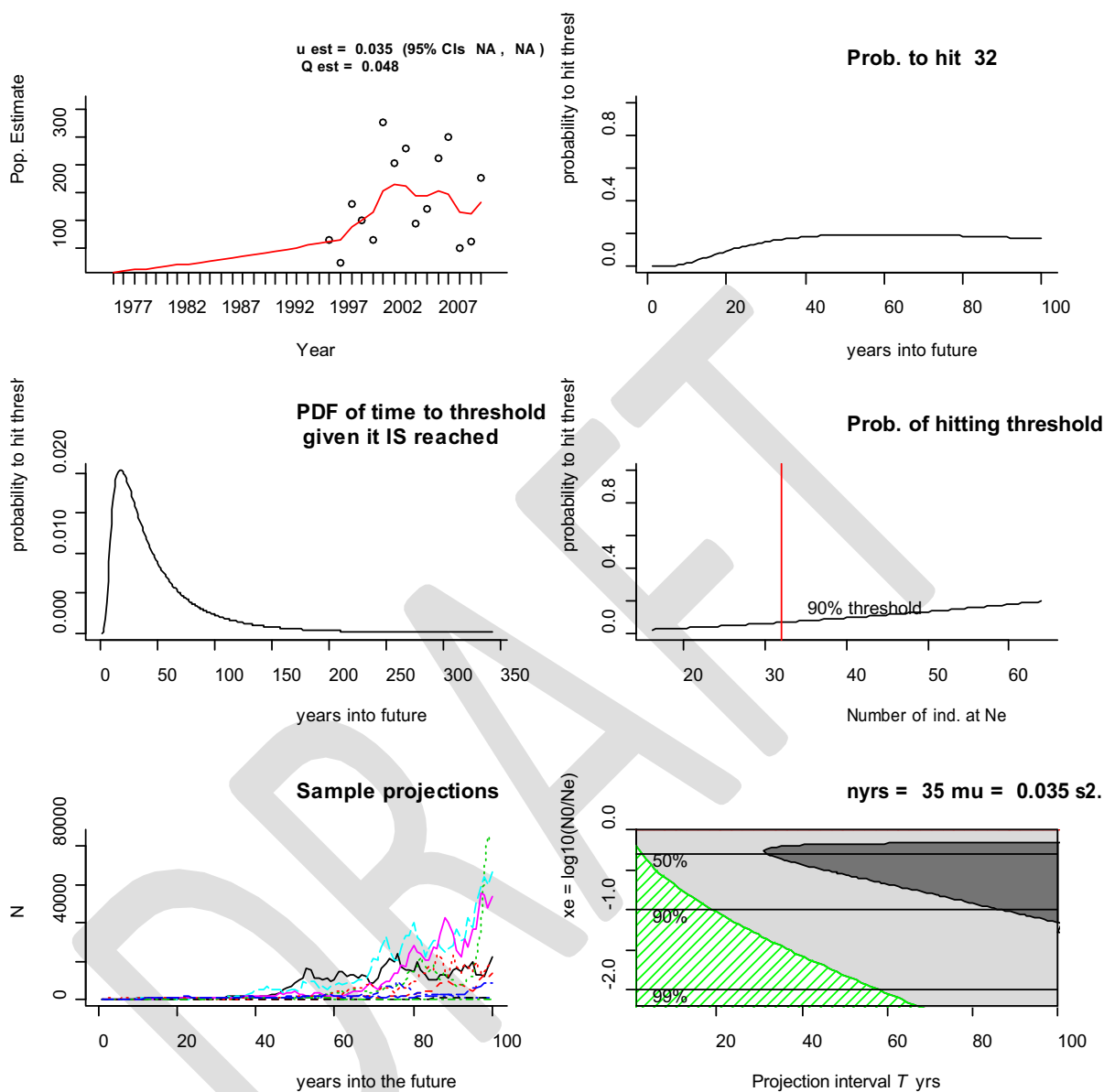


Figure A-17. MARSS-based population viability analysis for West Hood Canal winter-run steelhead. Steelhead counts in West Hood Canal have tended to increase since the mid 1990s but variability in abundance has been high. The estimated probability that this steelhead population would decline to a QET of 32 fish is low—less than 20% within 100 years. With an estimated (positive) mean population growth rate of 0.035 ($\lambda = 1.096$) and process error of 0.048, we can be highly confident ($P < 0.05$) that a 90% decline in this population will not occur within the next 20 years, and that a 99% decline will not occur within the next 60 years. However, beyond the next few decades we are uncertain about the precise level of extinction risk. One issue with this analysis is the inclusion of supplementation fish in the returns for the Hamma Hamma River,

where the contribution of hatchery fish to overall abundance is out of proportion to the stream size.

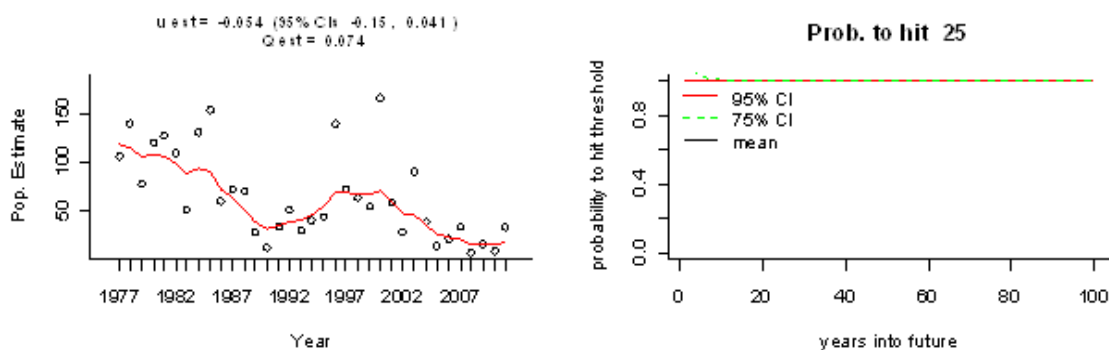


Figure A-18. MARSS-based population viability analysis for Strait of Juan de Fuca lowland tributaries (including Sequim/Discovery Bay, and Snow Creek) winter-run steelhead. Steelhead counts in this area have varied considerably since the 1980s but generally have declined and recently have been very low. The estimated probability that this steelhead population would decline to a QET of 25 fish is high—about 90% within 100 years. The estimated mean population growth rate is -0.054 ($\lambda = 0.947$) and process error is 0.074 . We are uncertain about the precise level of extinction risk for this population but it is clear that it is high due to low abundance.

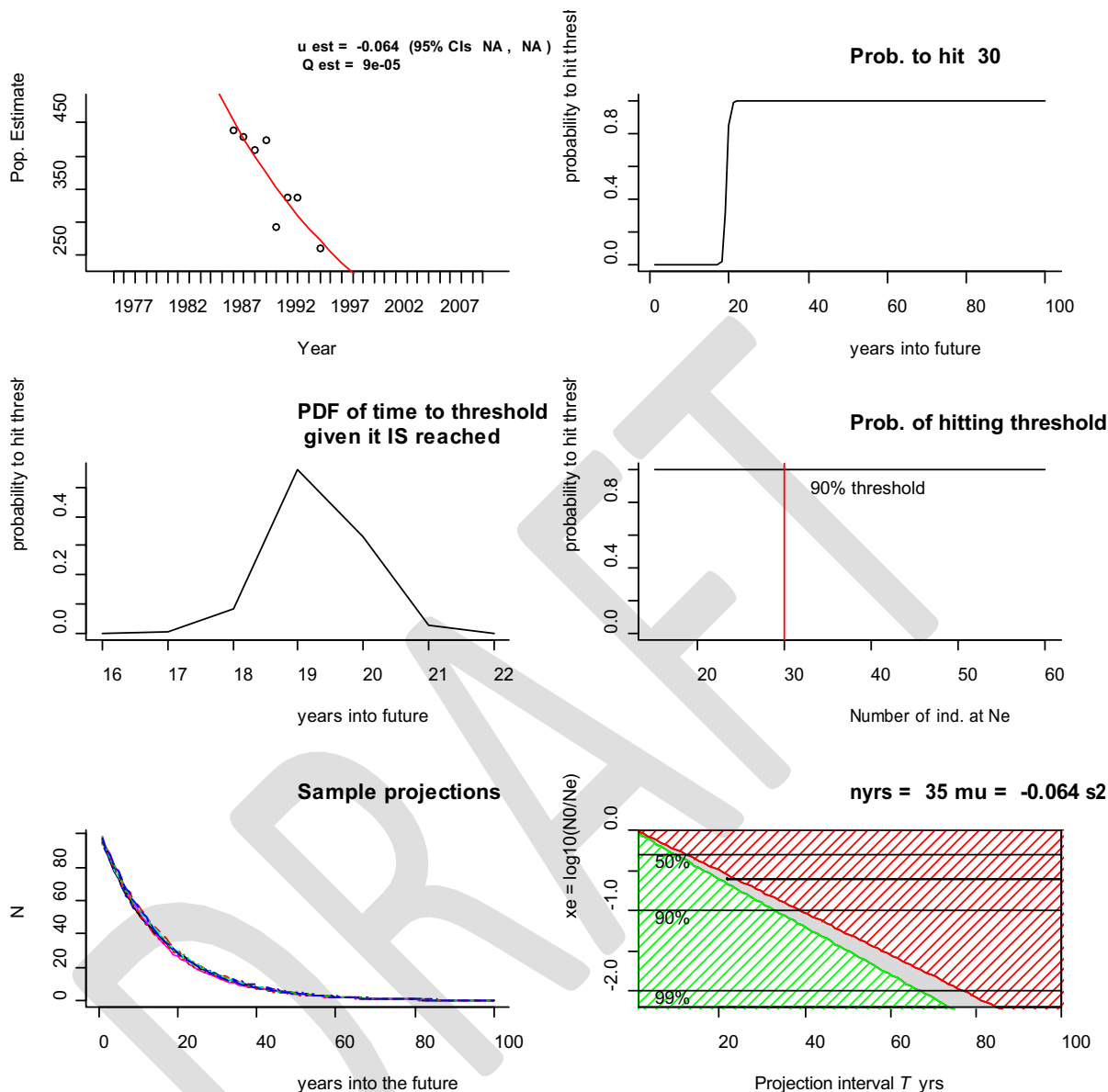


Figure A-19. MARSS-based population viability analysis for Dungeness River summer- and winter-run steelhead. Steelhead counts in the Dungeness River declined steeply between the late 1980s and the late 1990s. Accurate counts in more recent years are not available. The estimated probability that this steelhead population would decline to a QET of 30 fish is high—about 90% within 20 years. With an estimated mean population growth rate of -0.064 ($\lambda = 0.938$) and process error of <0.001 , this analysis indicates that we can be highly confident ($P < 0.05$) that a 90% decline in this population will not occur within the next 35 years, and that a 99% decline will not occur within the next 65 years. However, a 50% decline is highly likely within 12 years, and a 90% decline within 40 years. The analysis indicates that there is little uncertainty that the population would continue to decline if current conditions observed in the 1990s persisted into

the future. However, the lack of data in recent years means that the population's viability is far from certain.

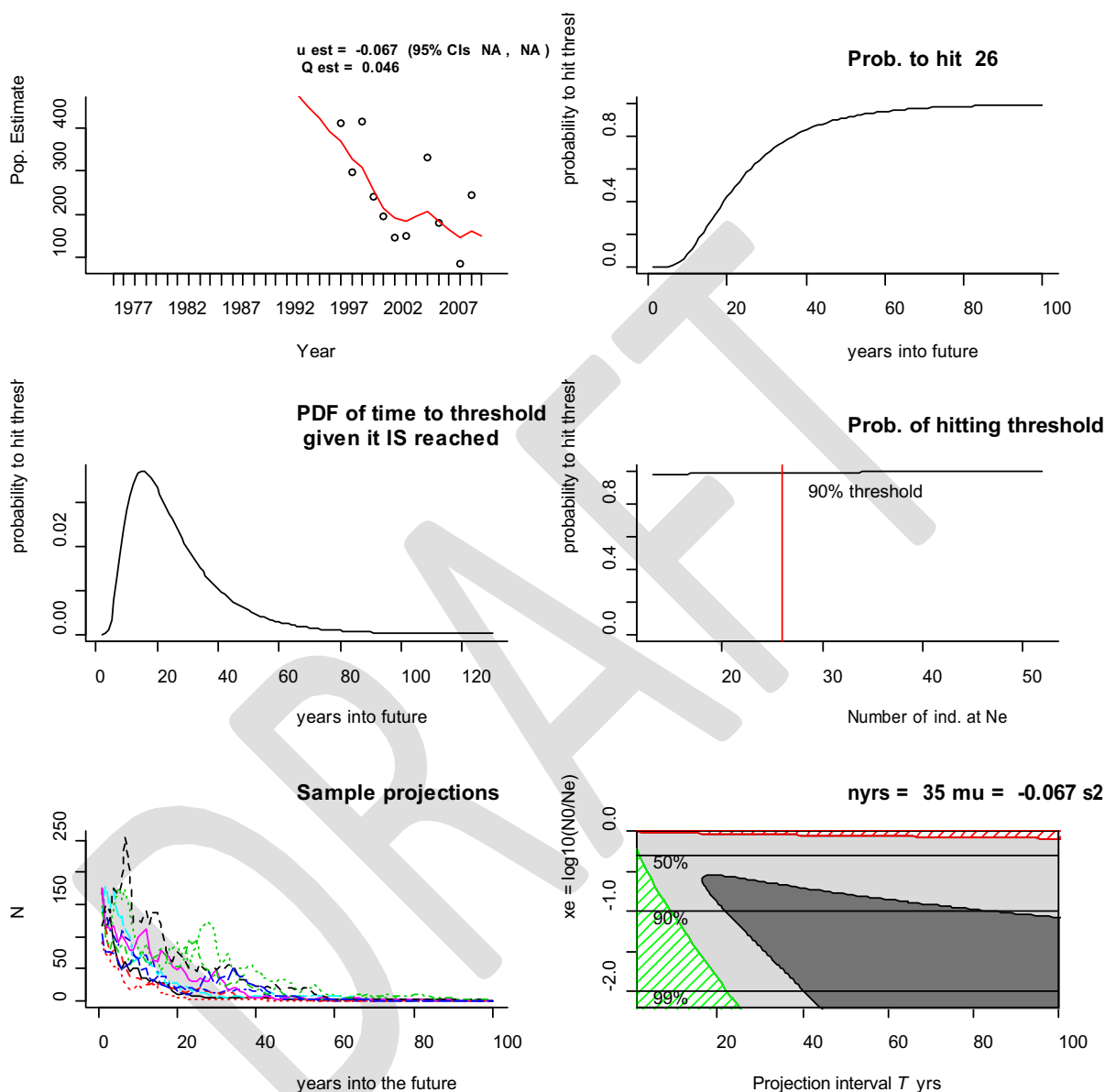


Figure A-20. MARSS-based population viability analysis for Strait of Juan de Fuca Independents (including Morse Creek) winter-run steelhead. Steelhead counts in this area have declined steeply since the late 1990s. Based on the limited count data, the estimated probability that this steelhead population would decline to a QET of 26 fish is high—about 90% within 60 years. With an estimated mean population growth rate of -0.067 ($\lambda = 0.935$) and process error of 0.046 , we can be highly confident ($P < 0.05$) that a 90% decline in this population will not occur within the next 10 years, and that a 99% decline will not occur within the next 25 years. However, we can be confident of a modest decline (perhaps 20%) within 100 years.

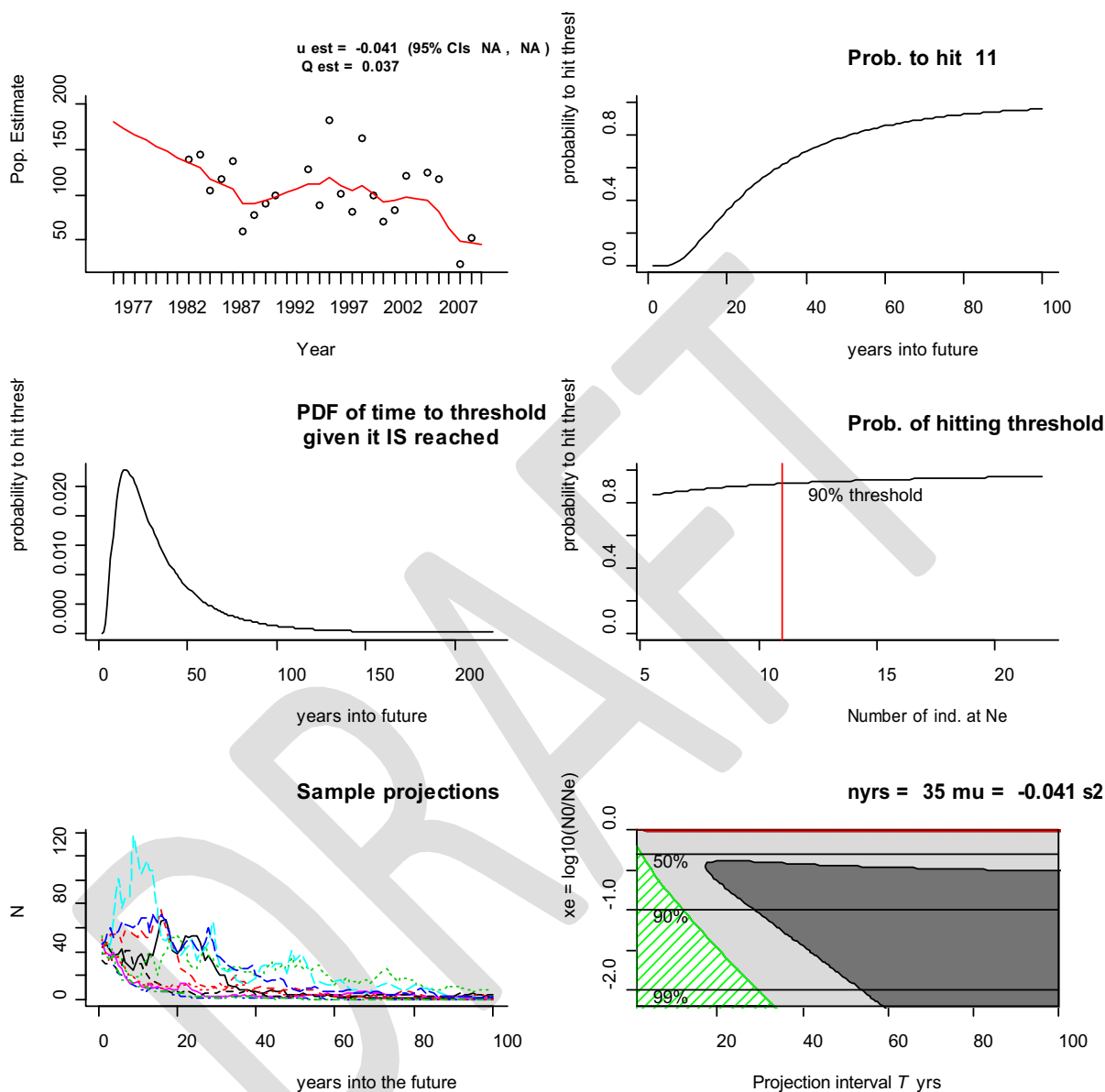


Figure A-21. MARSS-based population viability analysis for Morse Creek winter-run steelhead, part of the Strait of Juan de Fuca Independents winter-run DIP. Steelhead counts in Morse Creek have declined, albeit at a slower rate than Strait of Juan de Fuca Independents steelhead as a whole (Figure A-20), since the mid 1980s. The estimated probability that this steelhead population would decline to a QET of 11 fish is high—almost 90% within 100 years. With an estimated mean population growth rate of -0.041 ($\lambda = 0.960$) and process error of 0.037 , we can be highly confident ($P < 0.05$) that a 90% decline in this population will not occur within the

next 12 years, and that a 99% decline will not occur within the next 30 years. Beyond the next 30 years, however, we are uncertain about the precise level of extinction risk.

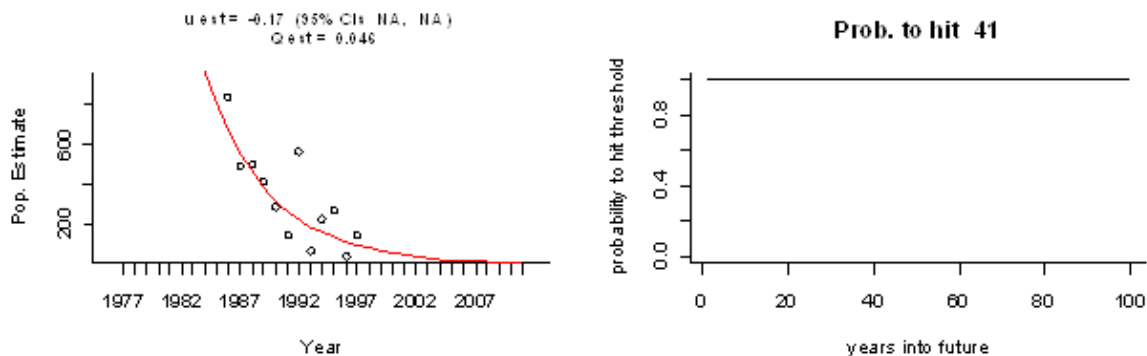


Figure A-22. MARSS-based population viability analysis for Elwha River summer- and winter-run steelhead. Like Dungeness River steelhead counts, steelhead counts in the Elwha River declined steeply between the 1980s and late 1990s, after which data are not available. Based on the limited count data, the estimated probability that this steelhead population would decline to a QET of 41 fish is high—at least 90% currently. The analysis indicates that the estimated mean population growth rate is -0.17 ($\lambda = 0.844$) and the process error 0.046 . The analysis indicates that there is little uncertainty that the population would continue to decline if current conditions observed in the 1990s persisted into the future. However, the lack of data in recent years means that the population's viability, while low, is far from precisely known.

Appendix B

Bayesian Networks Characterizing Viability of Demographically Independent Populations of Puget Sound Steelhead

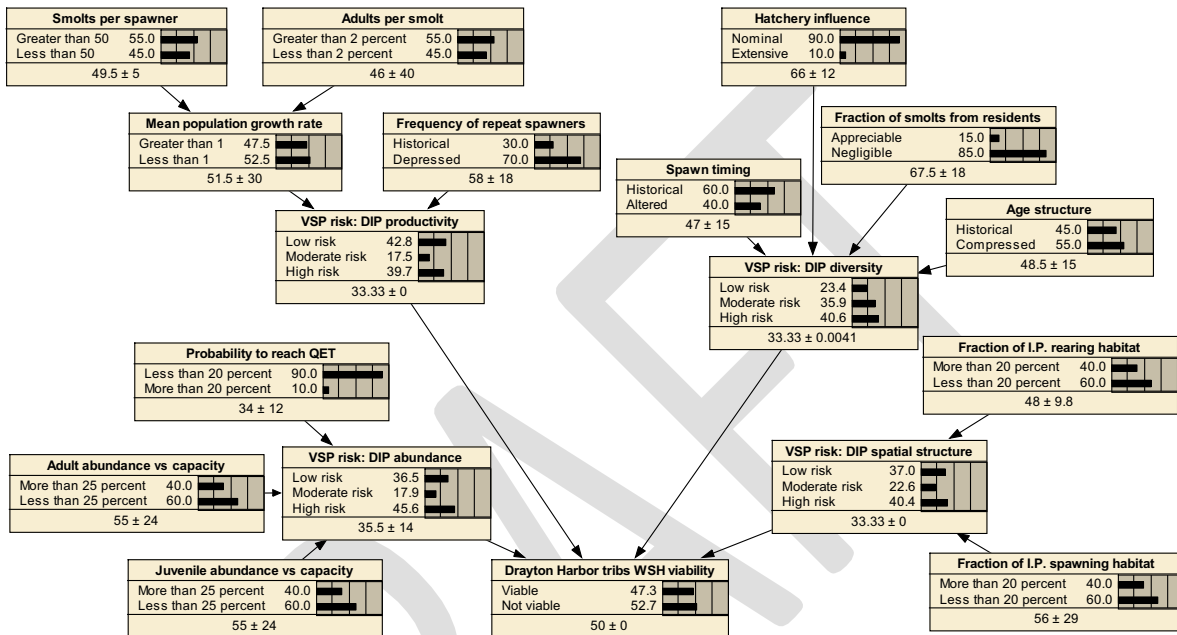


Figure B-1. Bayesian Network for viability of the Drayton Harbor tributaries winter-run steelhead DIP in the Northern Cascades Major Population Group. See main text for a fuller description.

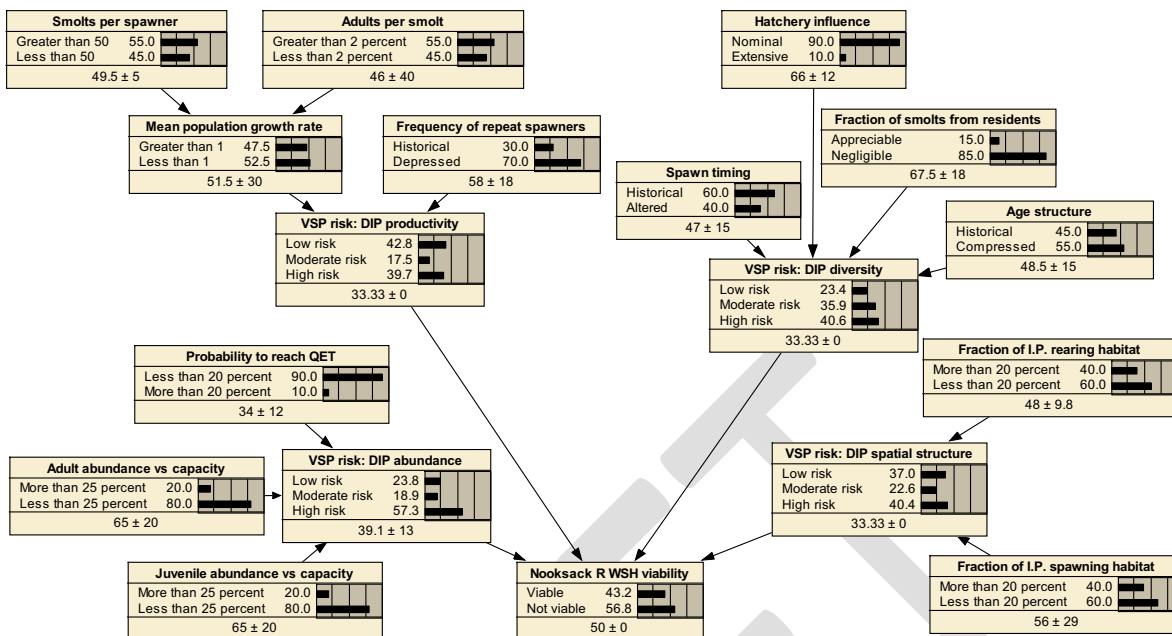


Figure B-2. Bayesian Network for viability of the Nooksack River winter-run steelhead DIP in the Northern Cascades Major Population Group. See main text for a fuller description.

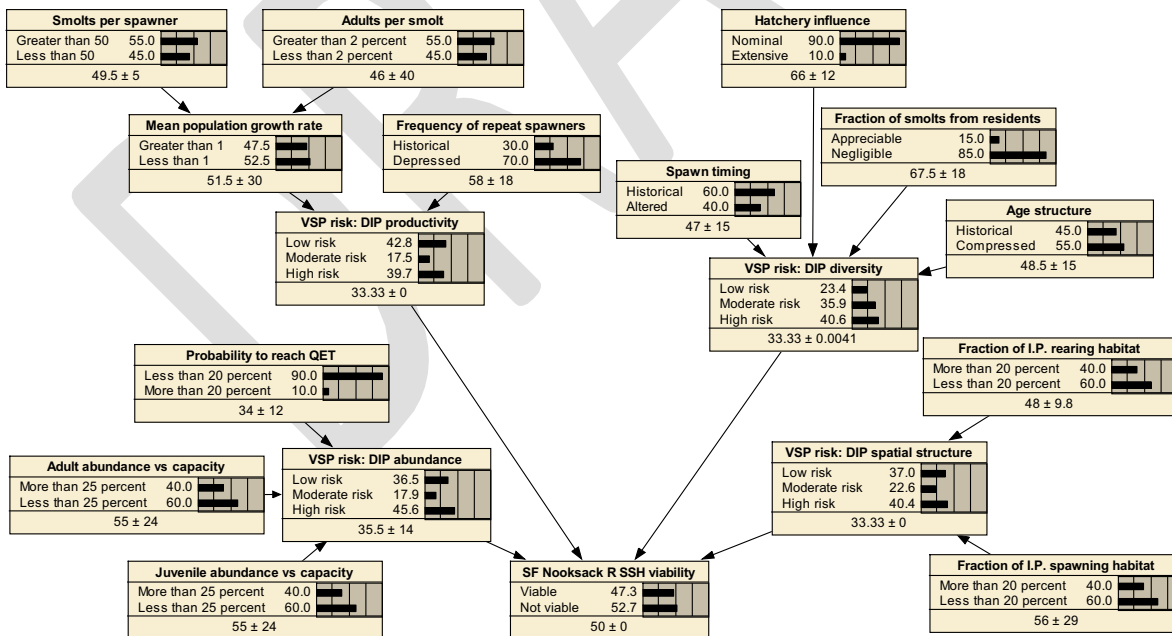


Figure B-3. Bayesian Network for viability of the South Fork Nooksack River summer-run steelhead DIP in the Northern Cascades Major Population Group. See main text for a fuller description.

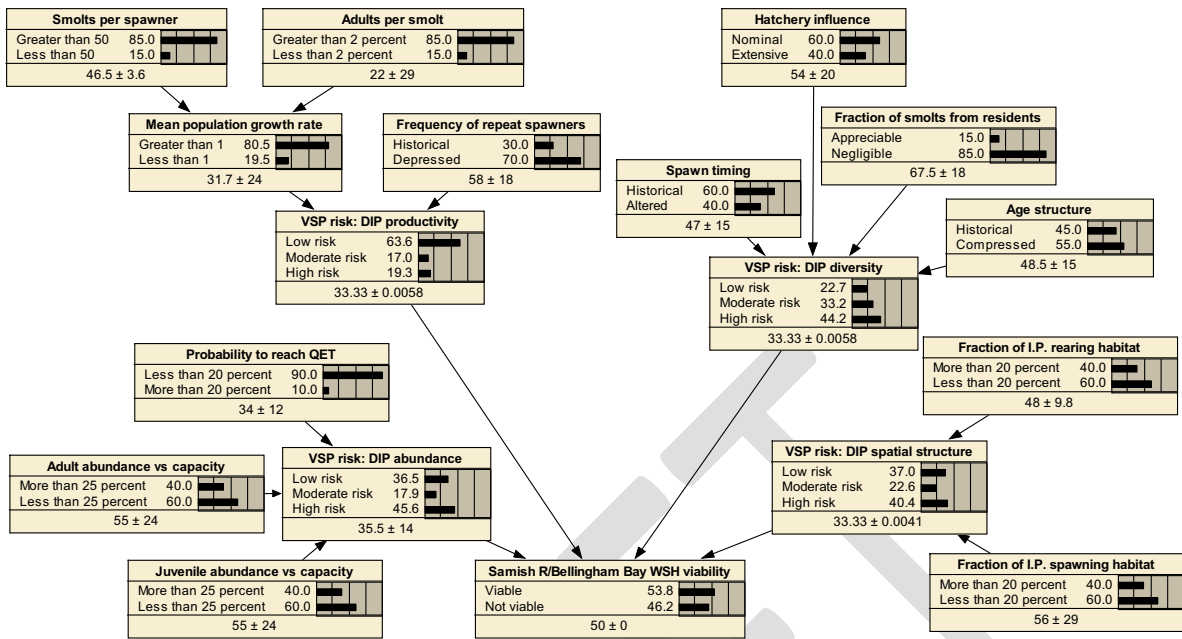


Figure B-4. Bayesian Network for viability of the Samish River/Bellingham Bay winter-run steelhead DIP in the Northern Cascades Major Population Group. See main text for a fuller description.

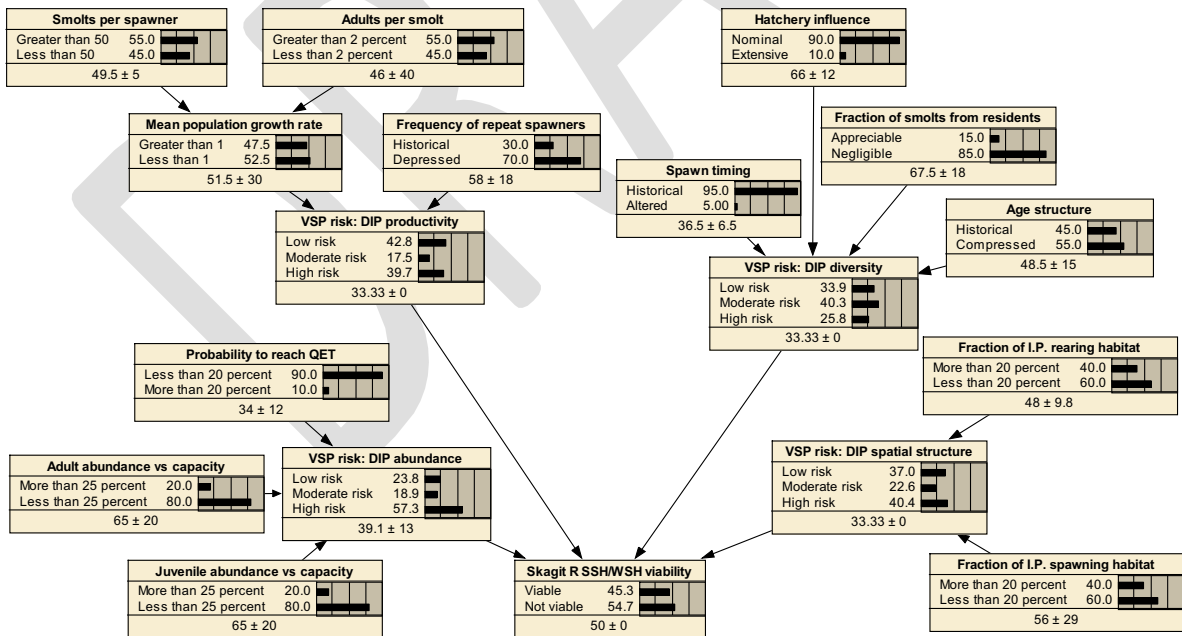


Figure B-5. Bayesian Network for viability of the Skagit River winter- and summer-run steelhead DIP in the Northern Cascades Major Population Group. See main text for a fuller description.

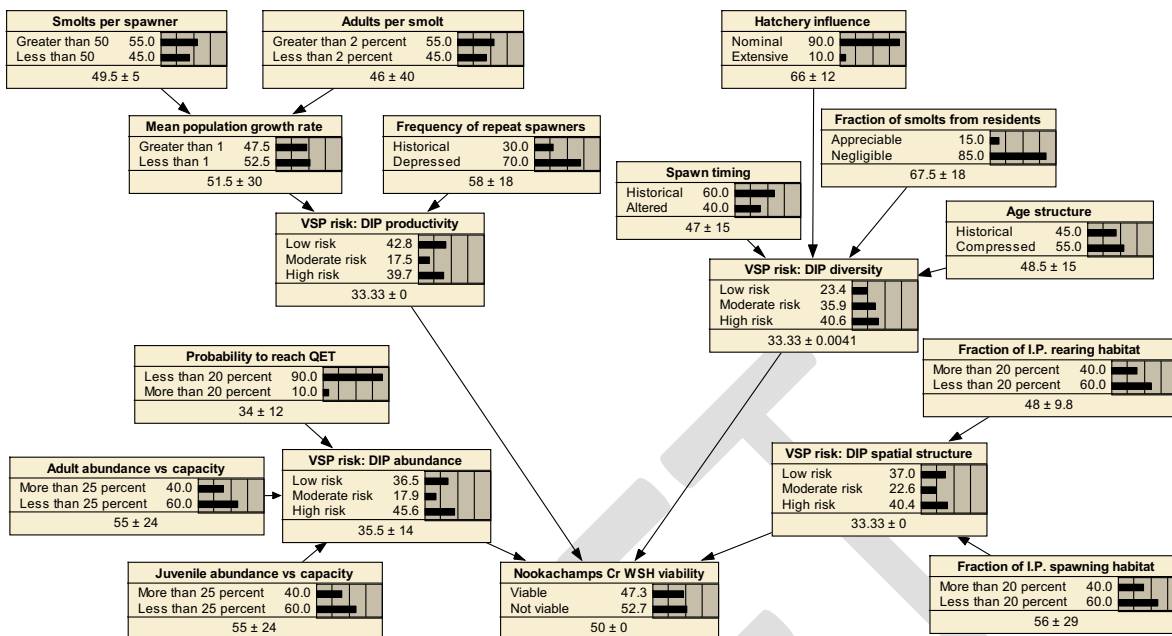


Figure B-6. Bayesian Network for viability of the Nookachamps Creek winter-run steelhead DIP in the Northern Cascades Major Population Group. See main text for a fuller description.

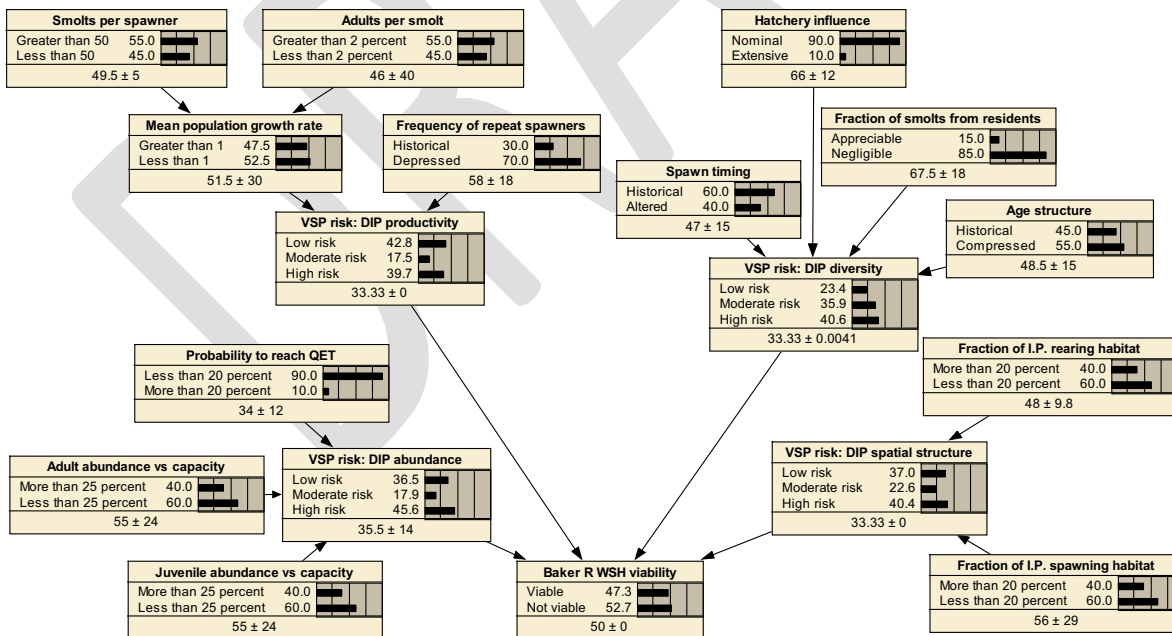


Figure B-7. Bayesian Network for viability of the Baker River winter- and summer-run steelhead DIP in the Northern Cascades Major Population Group. See main text for a fuller description.

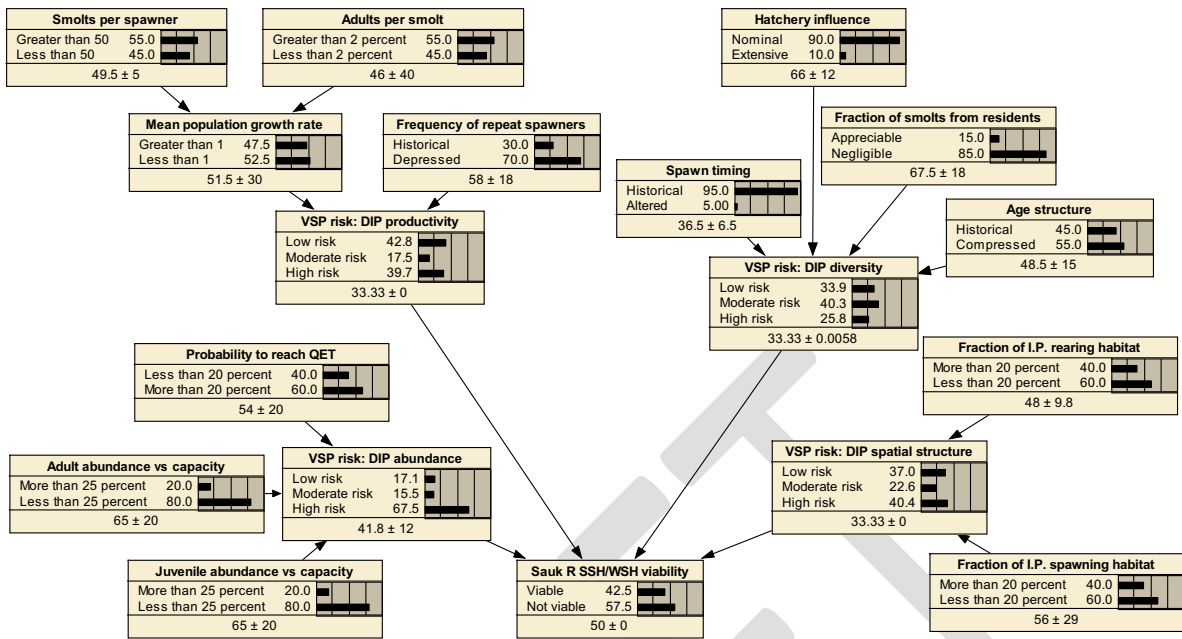


Figure B-8. Bayesian Network for viability of the Sauk River winter- and summer-run steelhead DIP in the Northern Cascades Major Population Group. See main text for a fuller description.

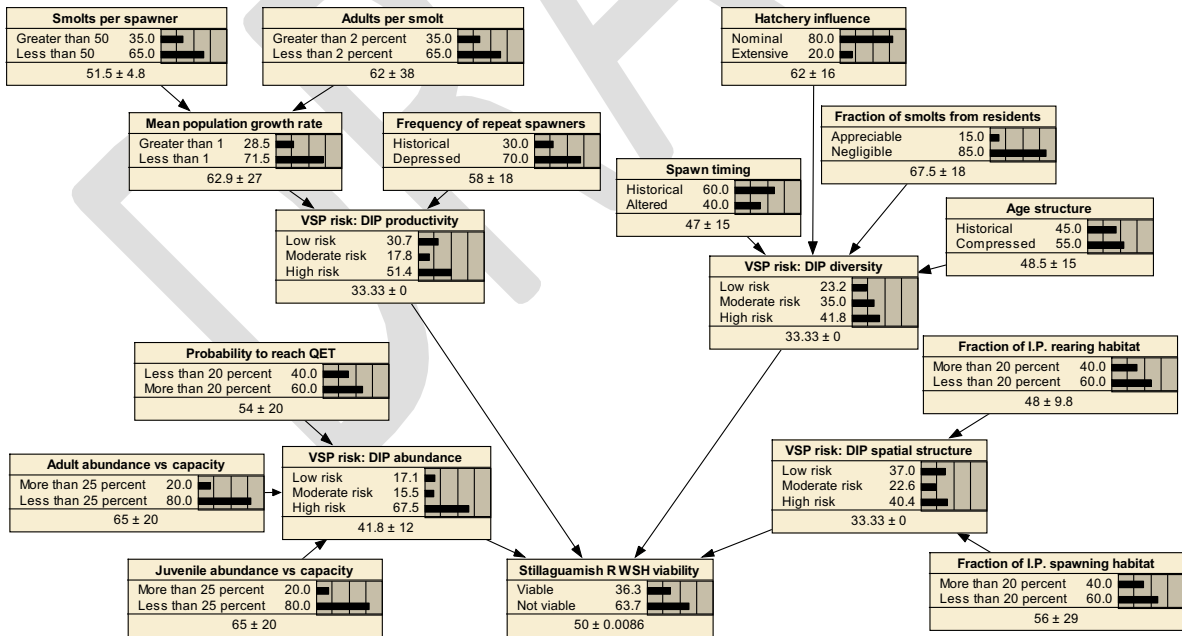


Figure B-9. Bayesian Network for viability of the Stillaguamish River winter-run steelhead DIP in the Northern Cascades Major Population Group. See main text for a fuller description.

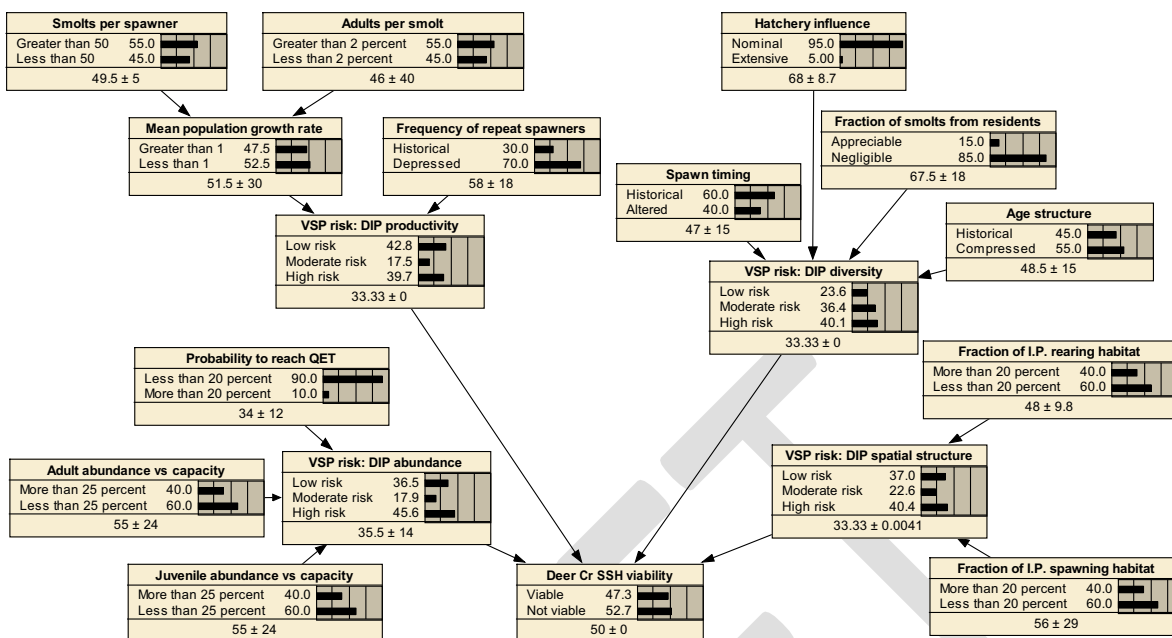


Figure B-10. Bayesian Network for viability of the Deer Creek summer-run steelhead DIP in the Northern Cascades Major Population Group. See main text for a fuller description.

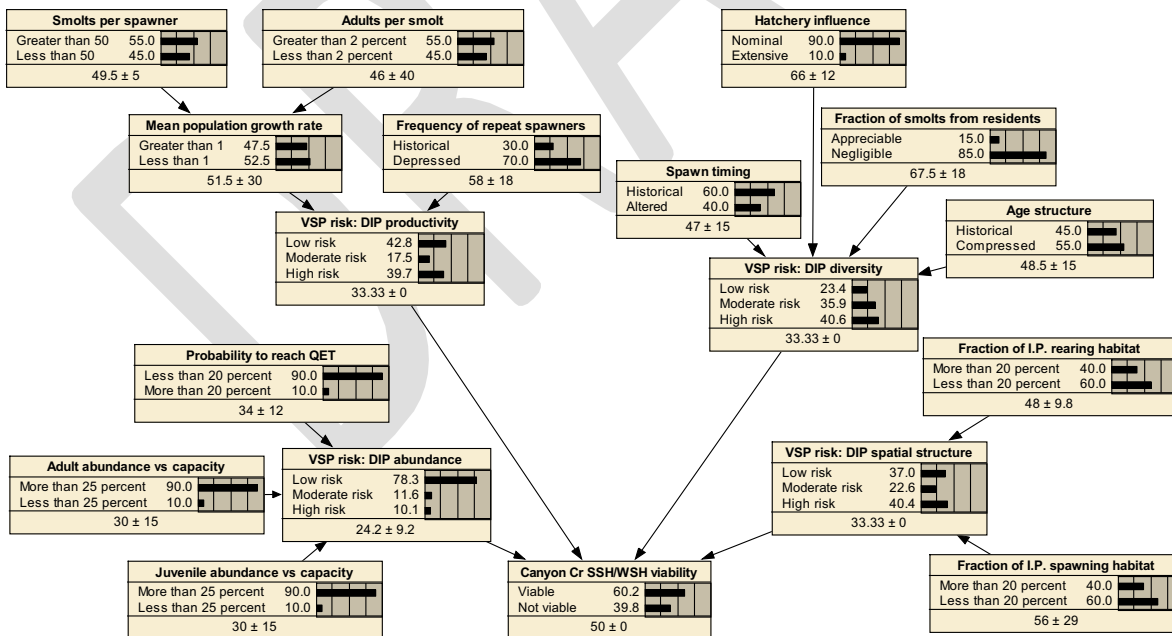


Figure B-11. Bayesian Network for viability of the Canyon Creek summer-run steelhead DIP in the Northern Cascades Major Population Group. See main text for a fuller description.

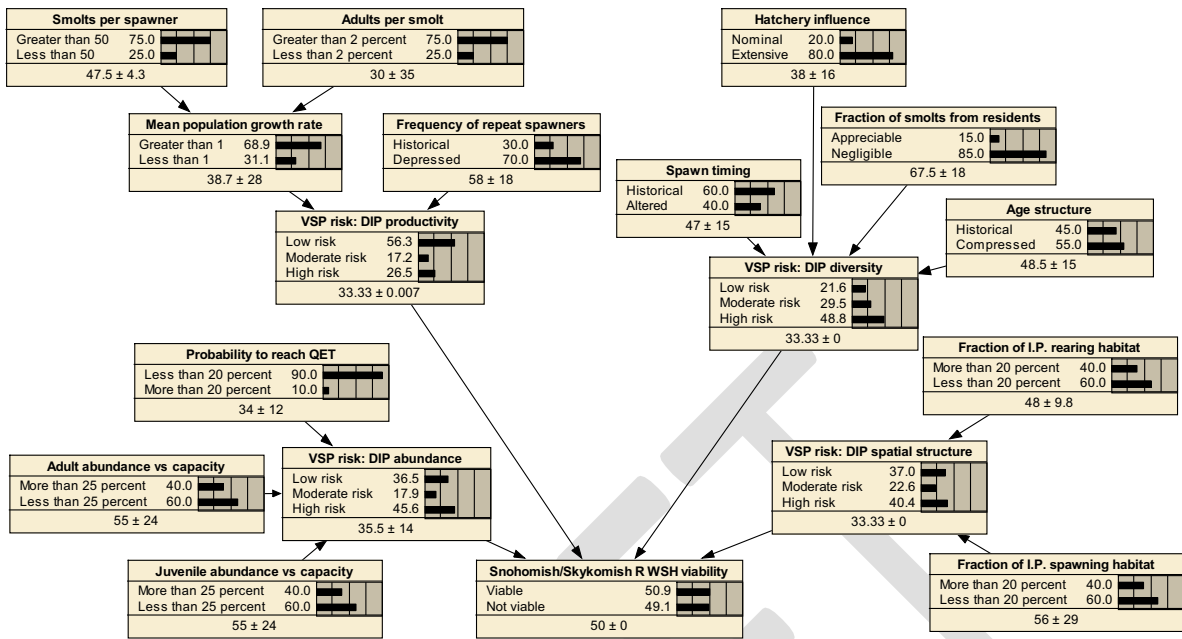


Figure B-12. Bayesian Network for viability of the Snohomish/Skykomish River winter-run steelhead DIP in the Northern Cascades Major Population Group. See main text for a fuller description.

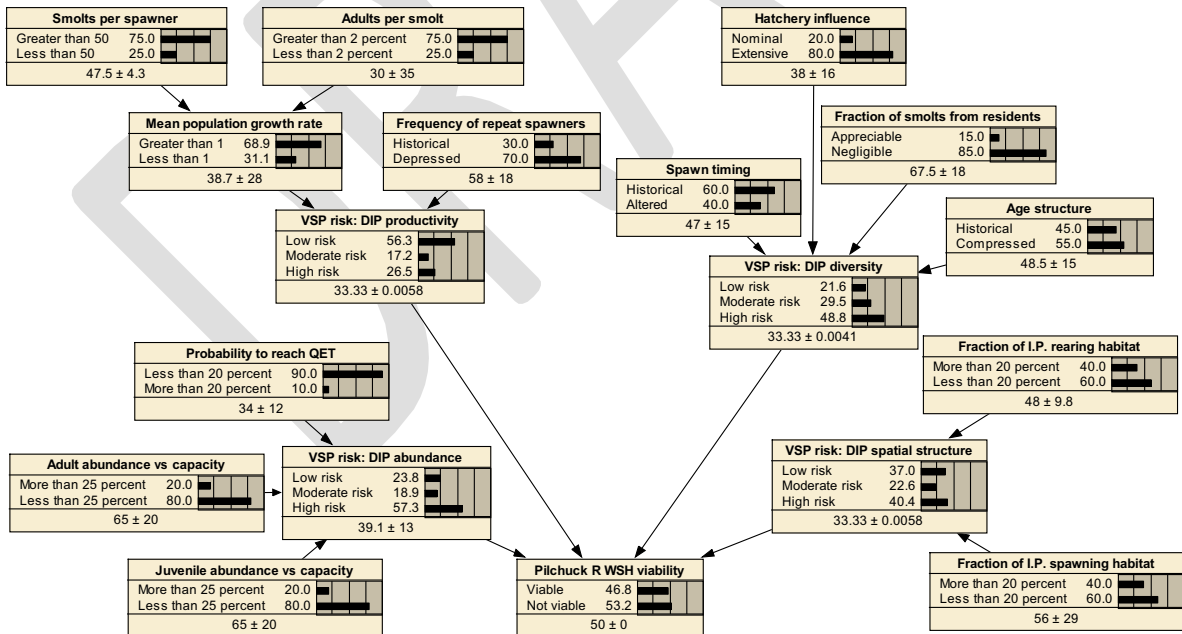


Figure B-13. Bayesian Network for viability of the Pilchuck River winter-run steelhead DIP in the Northern Cascades Major Population Group. See main text for a fuller description.

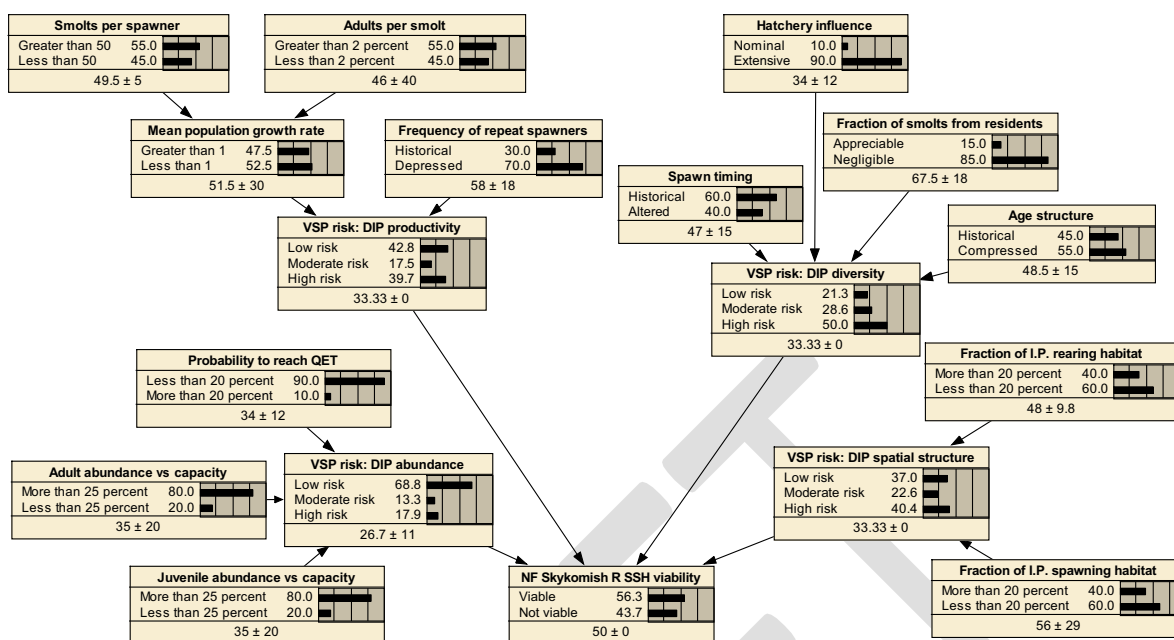


Figure B-14. Bayesian Network for viability of the North Fork Skykomish River summer-run steelhead DIP in the Northern Cascades Major Population Group. See main text for a fuller description.

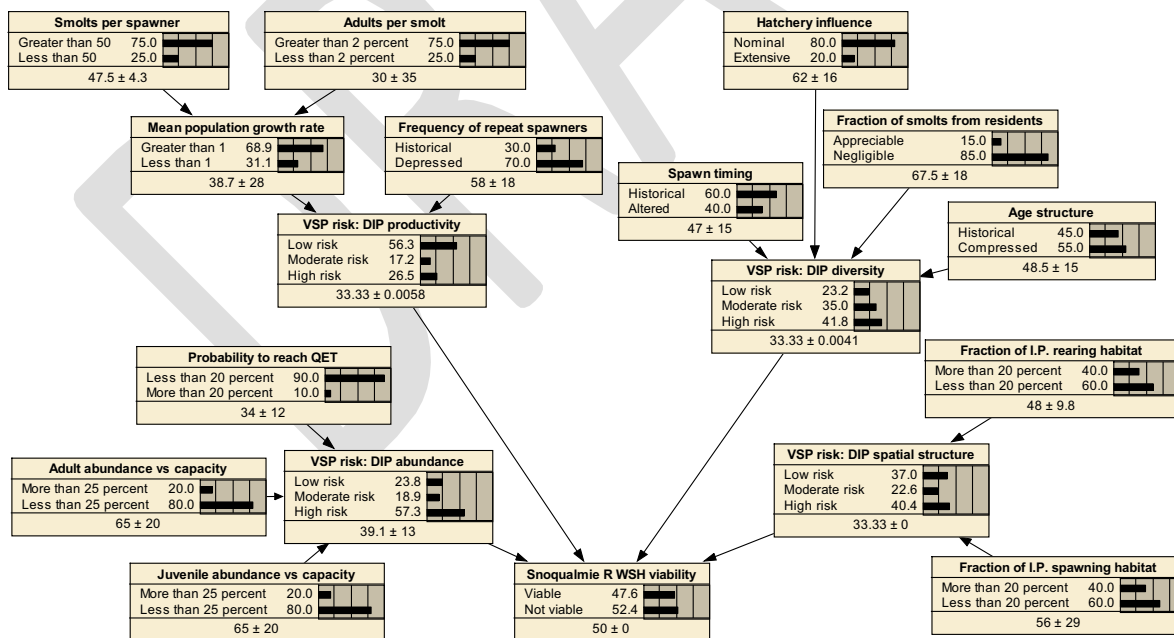


Figure B-15. Bayesian Network for viability of the Snoqualmie River winter-run steelhead DIP in the Northern Cascades Major Population Group. See main text for a fuller description.

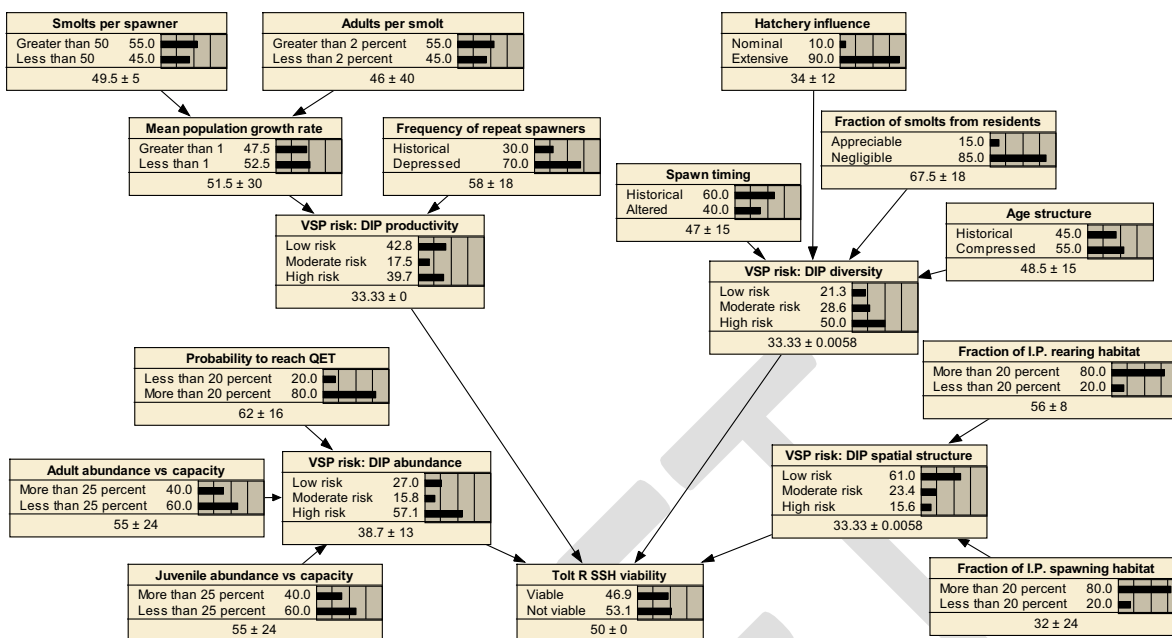


Figure B-16. Bayesian Network for viability of the Tolt River summer-run steelhead DIP in the Northern Cascades Major Population Group. See main text for a fuller description.

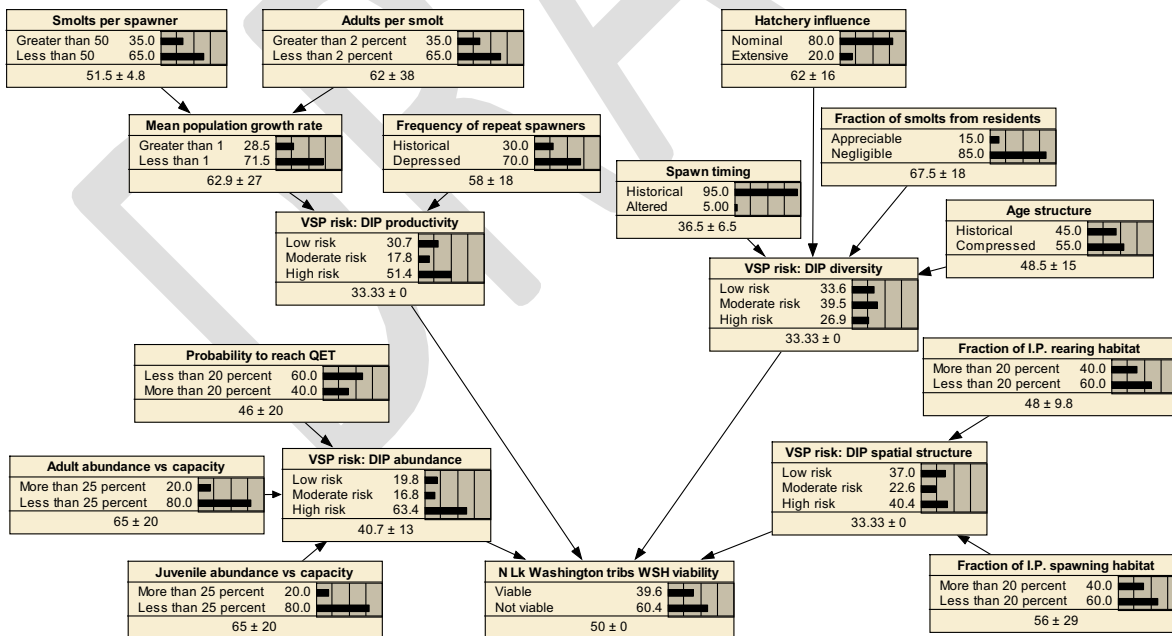


Figure B-17. Bayesian Network for viability of the North Lake Washington tributaries winter-run steelhead DIP in the Central and South Puget Sound Major Population Group. See main text for a fuller description.

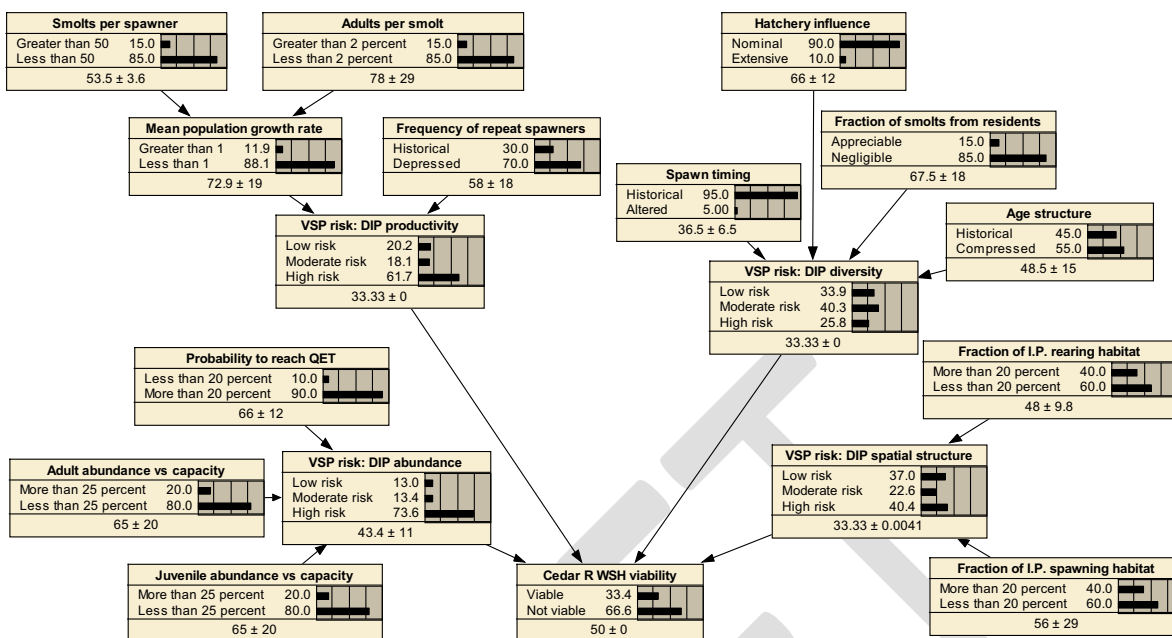


Figure B-18. Bayesian Network for viability of the Cedar River winter-run steelhead DIP in the Central and South Puget Sound Major Population Group. See main text for a fuller description.

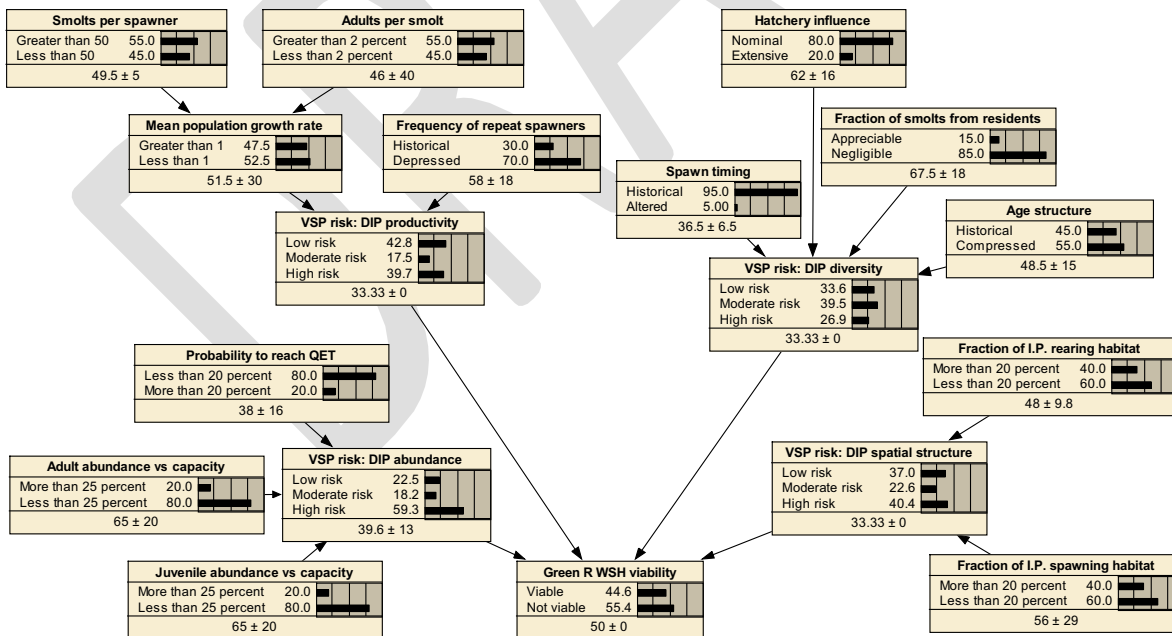


Figure B-19. Bayesian Network for viability of the Green River winter-run steelhead DIP in the Central and South Puget Sound Major Population Group. See main text for a fuller description.

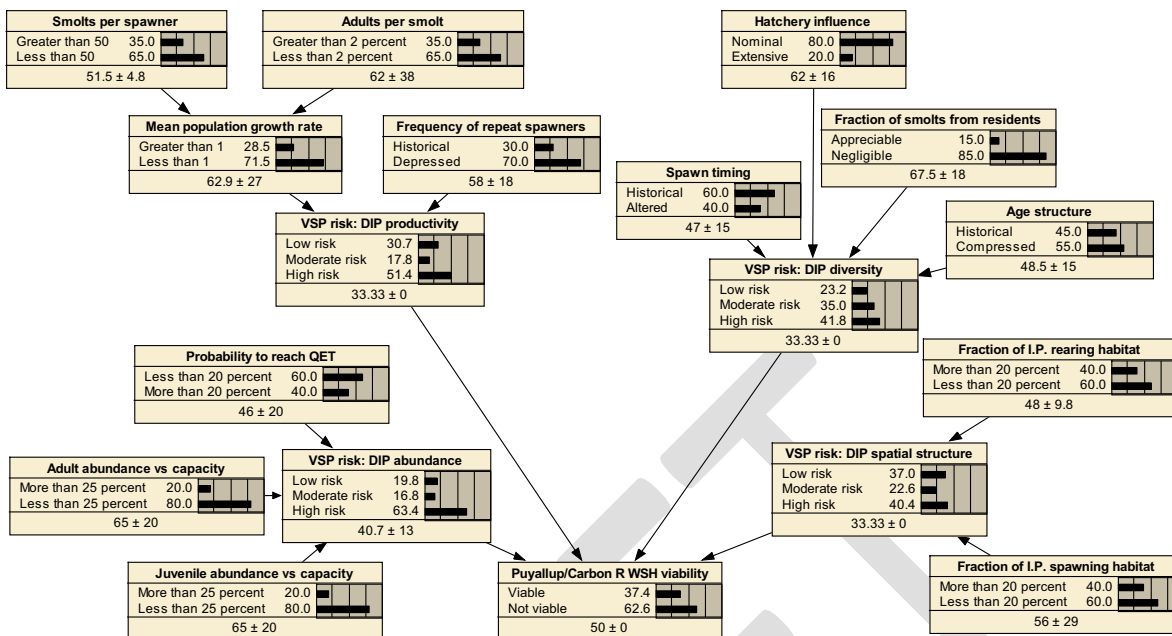


Figure B-20. Bayesian Network for viability of the Puyallup River/Carbon River winter-run steelhead DIP in the Central and South Puget Sound Major Population Group. See main text for a fuller description.

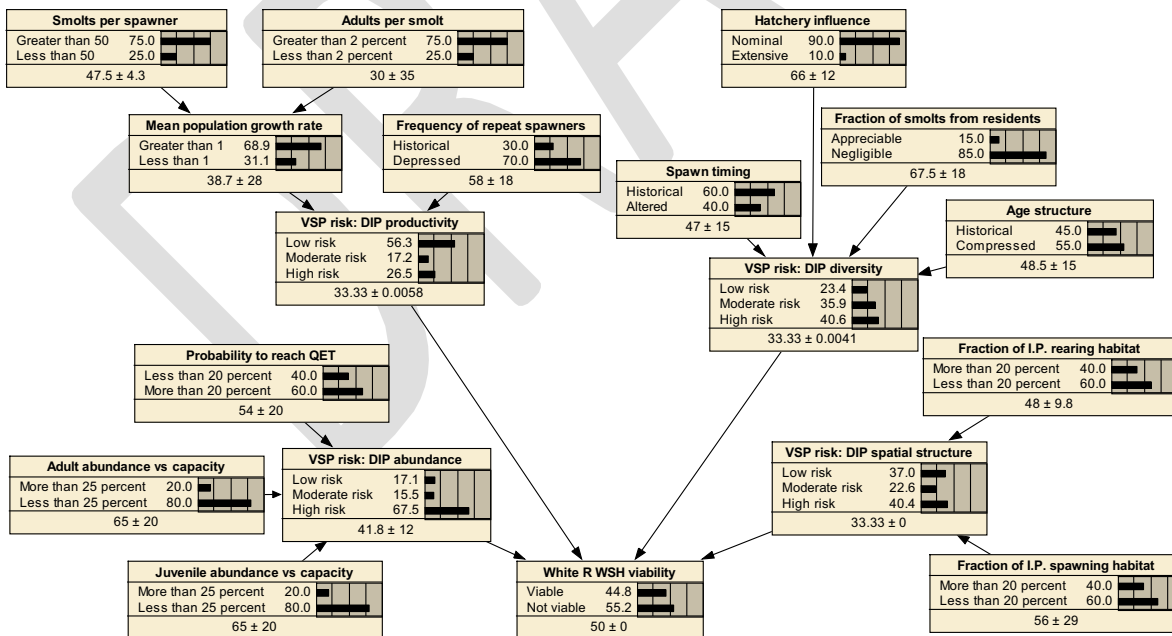


Figure B-21. Bayesian Network for viability of the White River winter-run steelhead DIP in the Central and South Puget Sound Major Population Group. See main text for a fuller description.

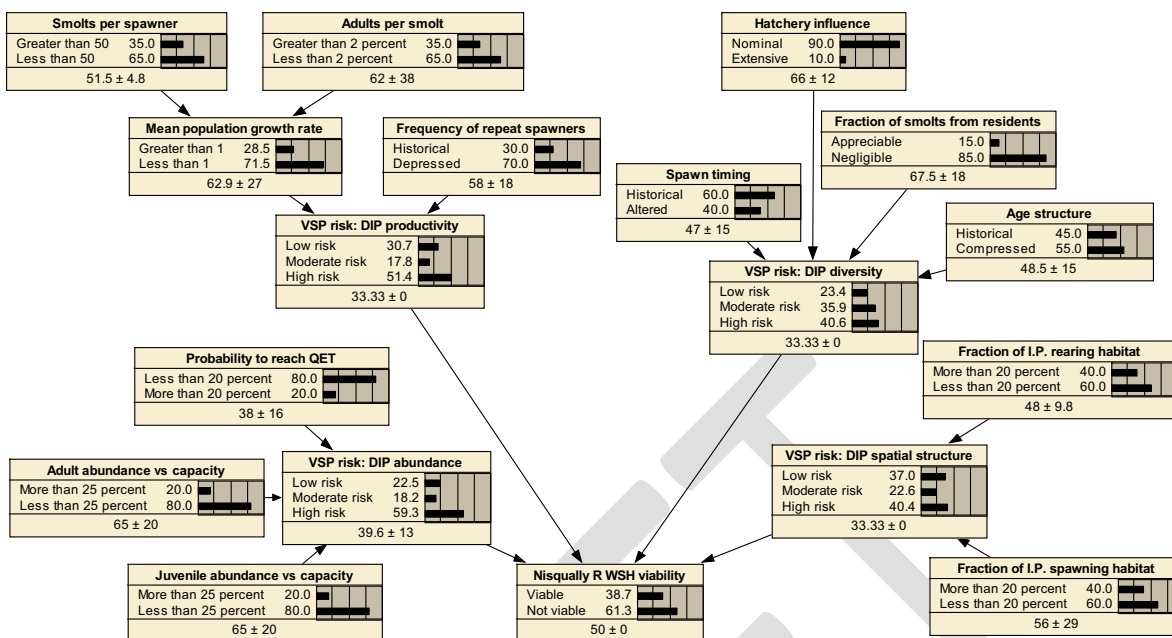


Figure B-22. Bayesian Network for viability of the Nisqually River winter-run steelhead DIP in the Central and South Puget Sound Major Population Group. See main text for a fuller description.

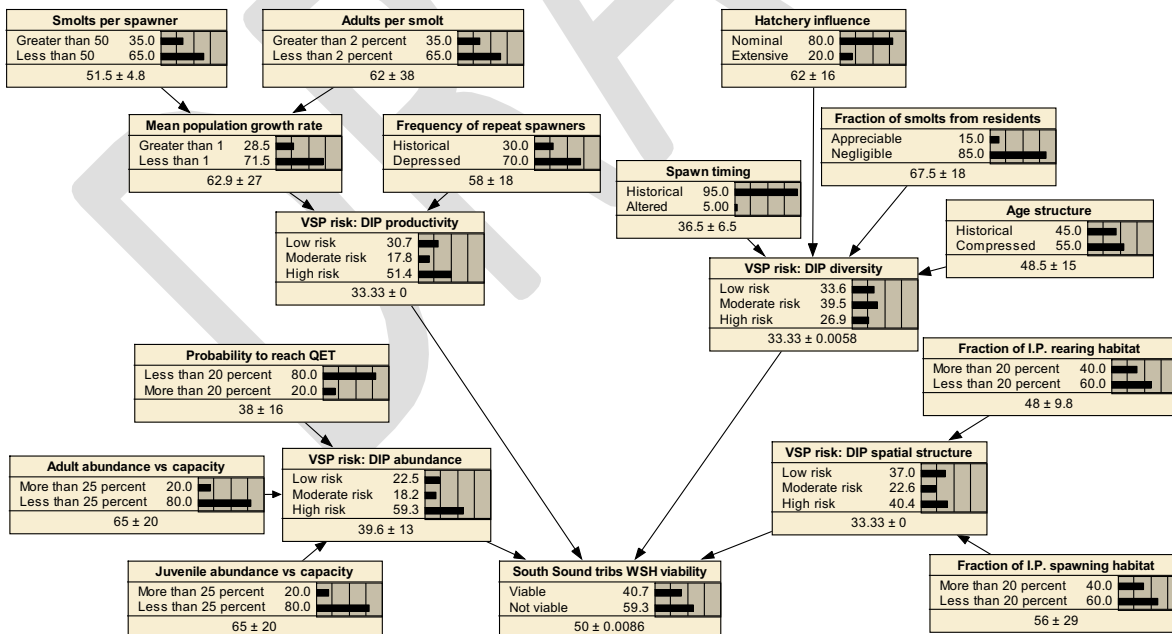


Figure B-23. Bayesian Network for viability of the South Sound tributaries winter-run steelhead DIP in the Central and South Puget Sound Major Population Group. See main text for a fuller description.

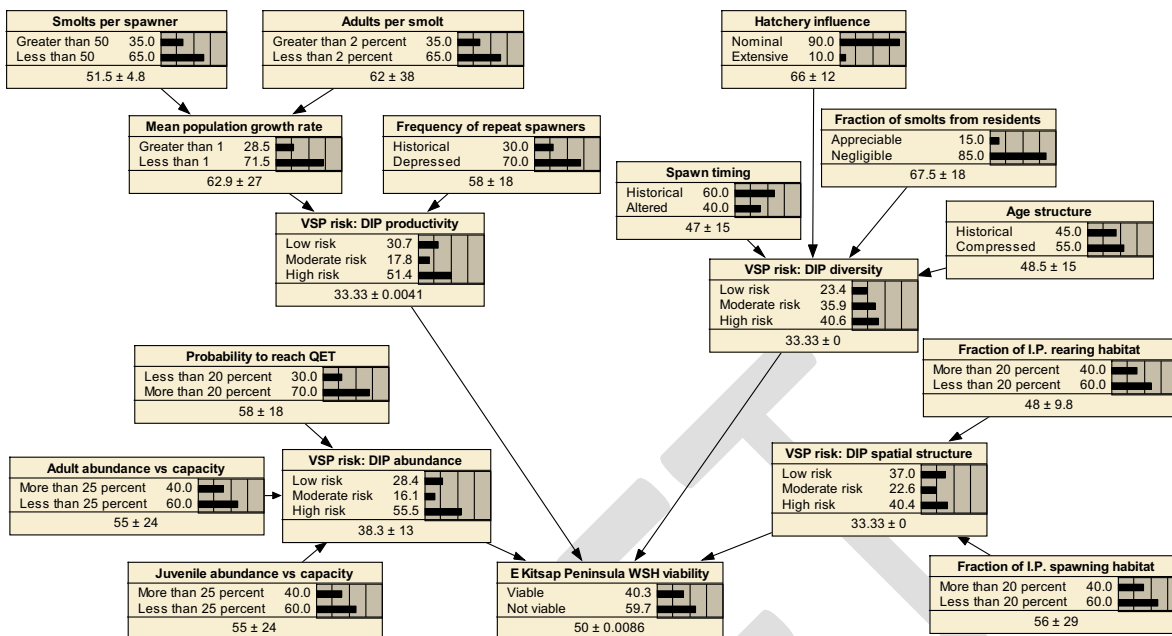


Figure B-24. Bayesian Network for viability of the East Kitsap Peninsula winter-run steelhead DIP in the Central and South Puget Sound Major Population Group. See main text for a fuller description.

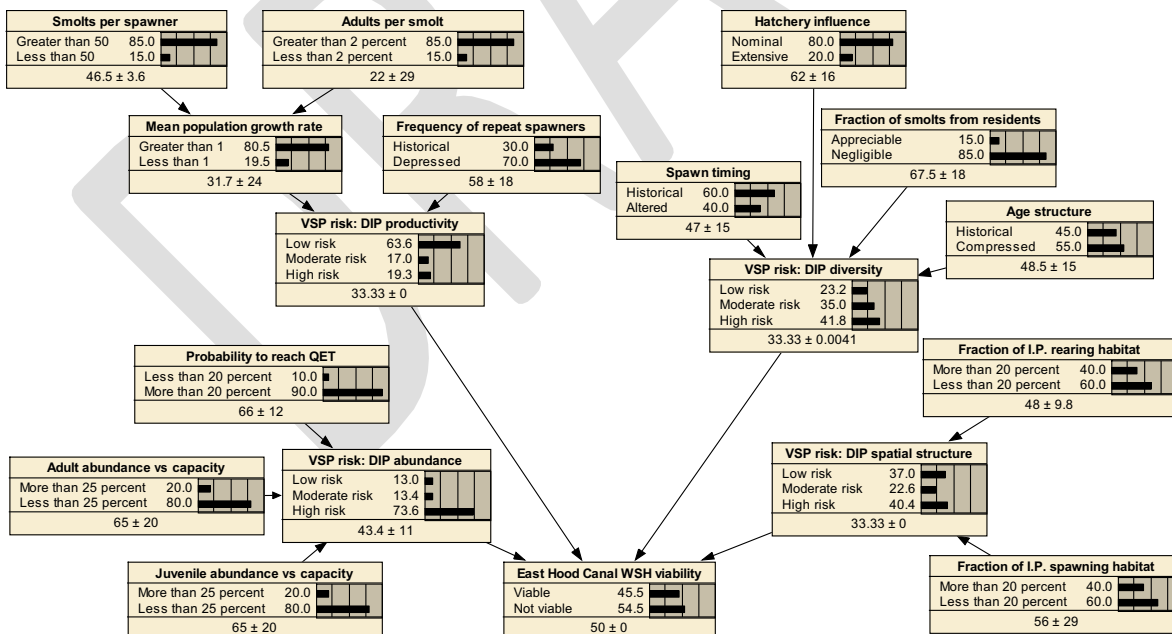


Figure B-25. Bayesian Network for viability of the East Hood Canal winter-run steelhead DIP in the Hood Canal and Strait of Juan de Fuca Major Population Group. See main text for a fuller description.

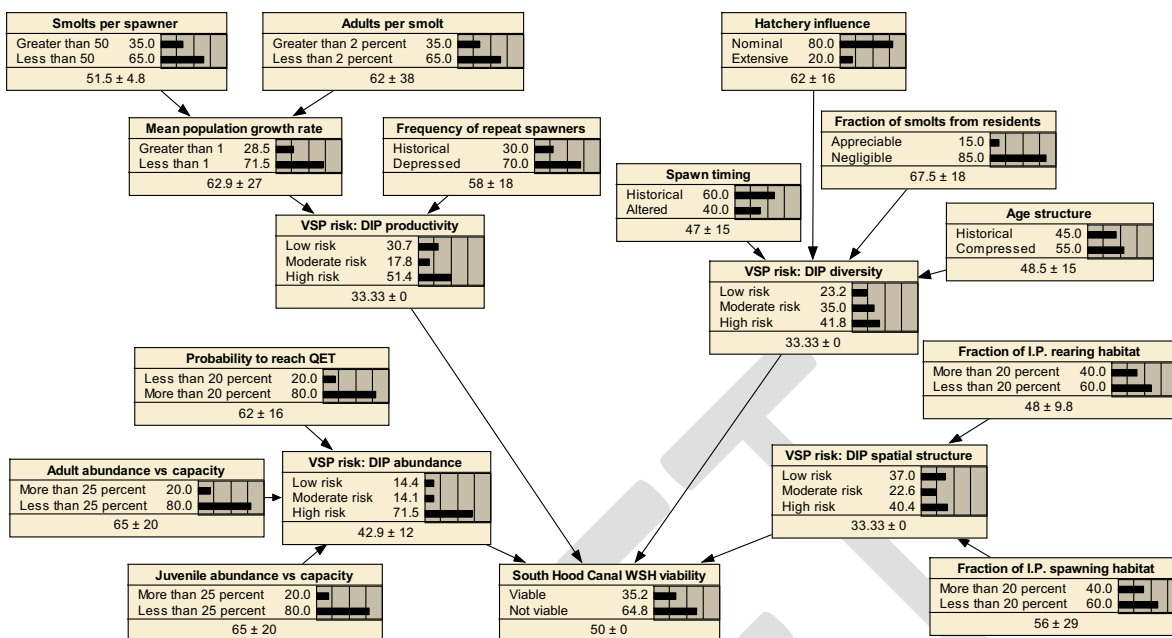


Figure B-26. Bayesian Network for viability of the South Hood Canal winter-run steelhead DIP in the Hood Canal and Strait of Juan de Fuca Major Population Group. See main text for a fuller description.

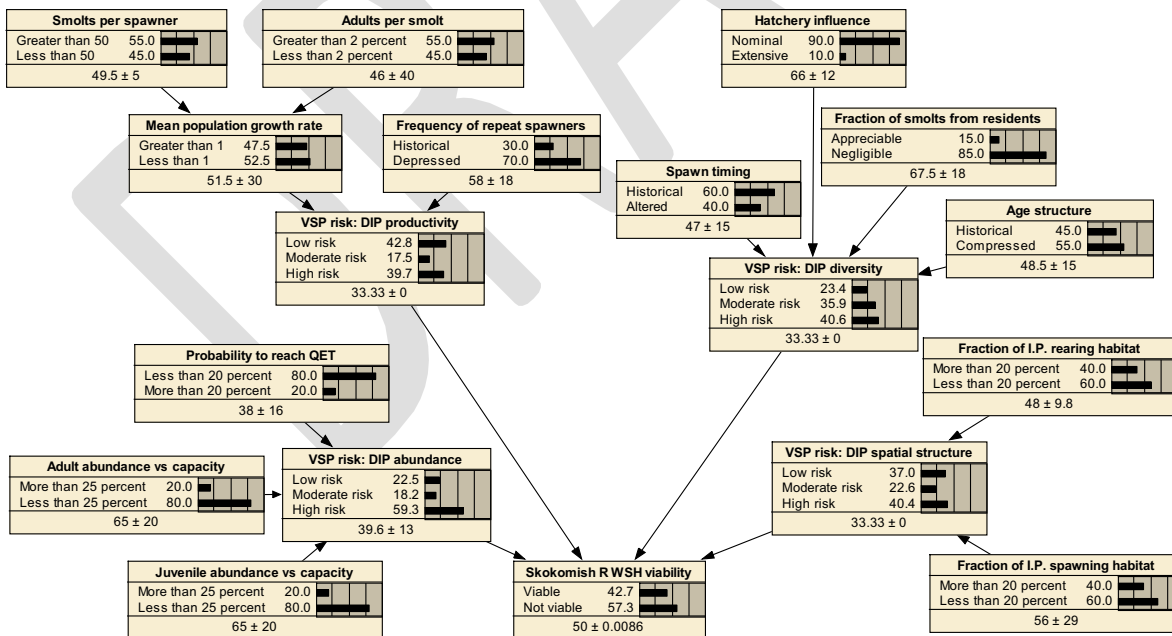


Figure B-27. Bayesian Network for viability of the Skokomish River winter-run steelhead DIP in the Hood Canal and Strait of Juan de Fuca Major Population Group. See main text for a fuller description.

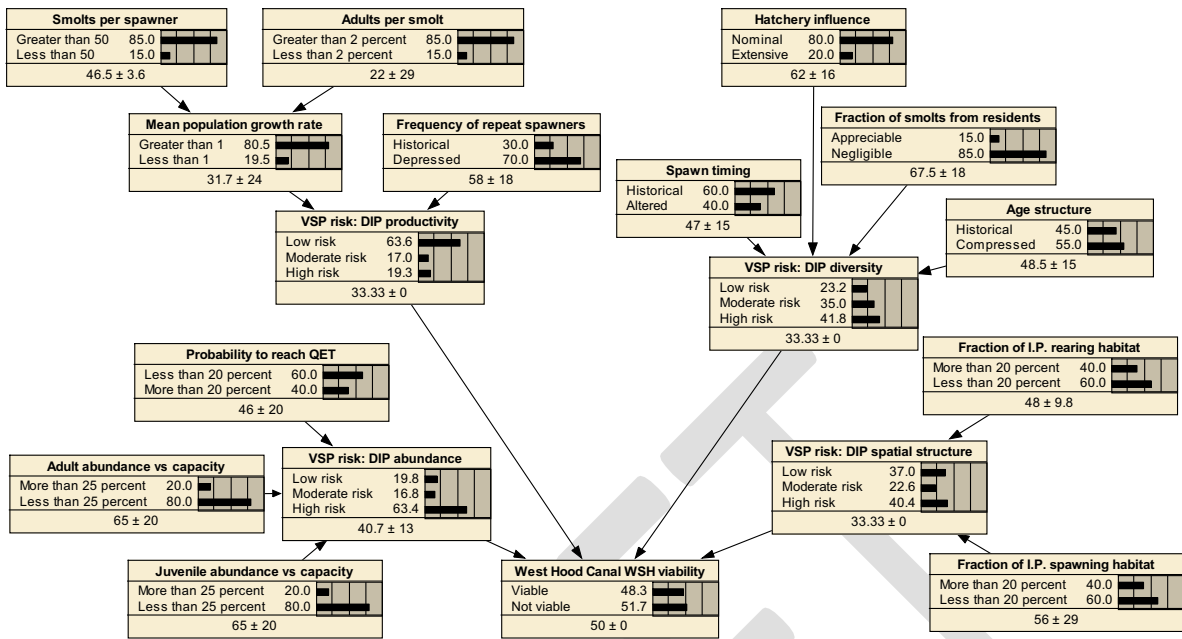


Figure B-28. Bayesian Network for viability of the West Hood Canal winter-run steelhead DIP in the Hood Canal and Strait of Juan de Fuca Major Population Group. See main text for a fuller description.

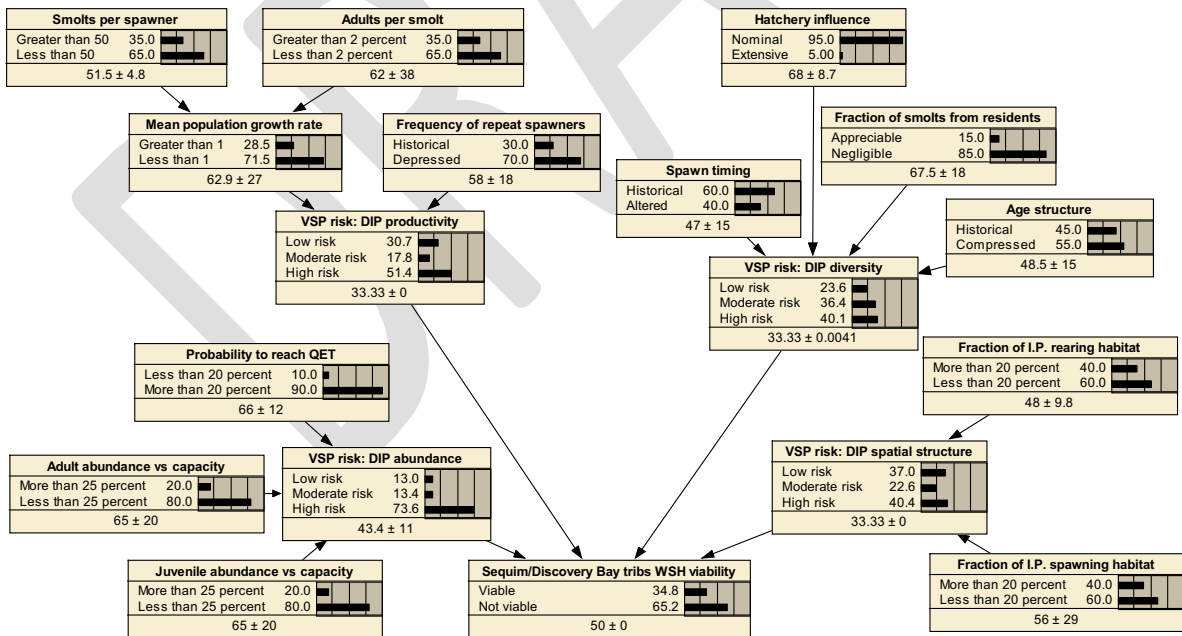


Figure B-29. Bayesian Network for viability of the Sequim/Discovery Bay tributaries winter-run steelhead DIP in the Hood Canal and Strait of Juan de Fuca Major Population Group. See main text for a fuller description.

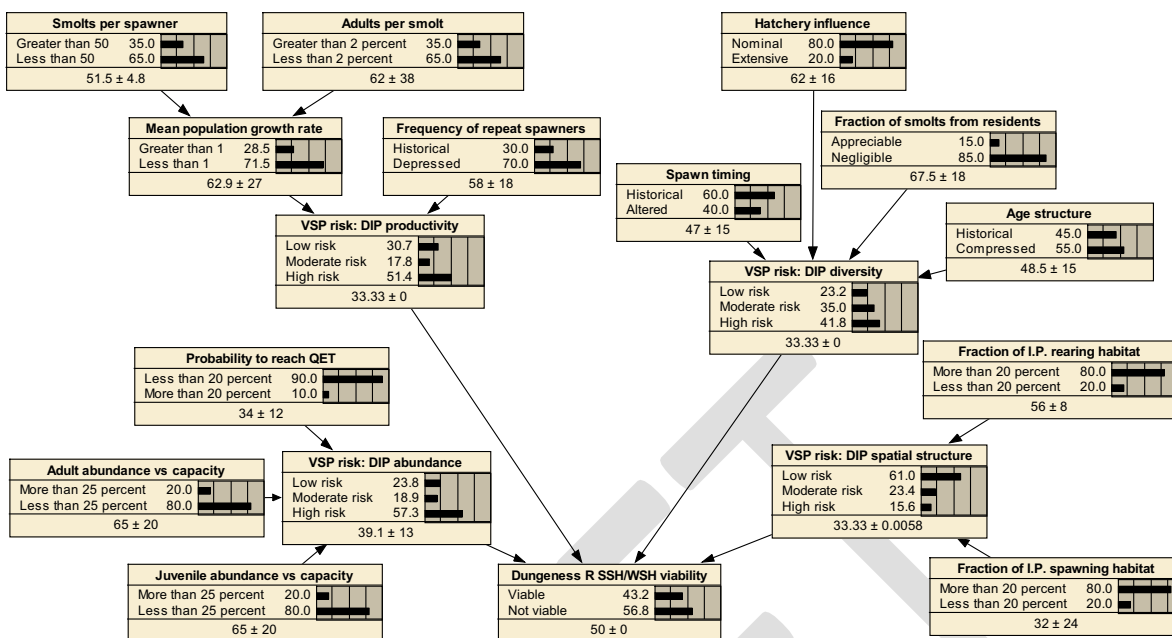


Figure B-30. Bayesian Network for viability of the Dungeness River winter- and summer-run steelhead DIP in the Hood Canal and Strait of Juan de Fuca Major Population Group. See main text for a fuller description.

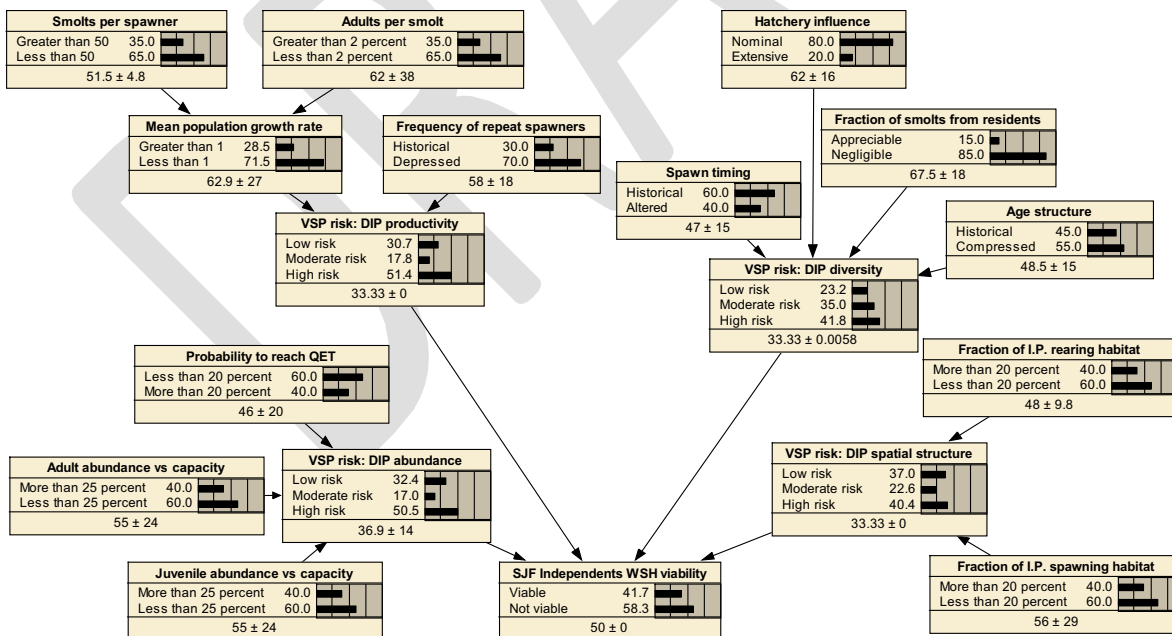


Figure B-31. Bayesian Network for viability of the Strait of Juan de Fuca Independent tributaries winter-run steelhead DIP in the Hood Canal and Strait of Juan de Fuca Major Population Group. See main text for a fuller description.

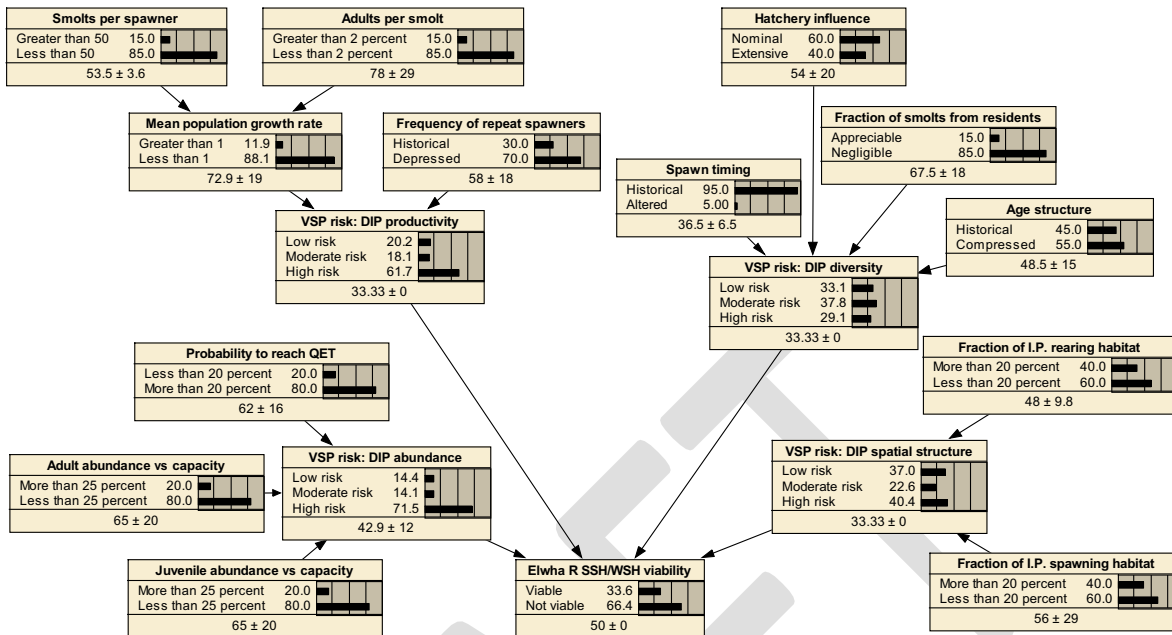


Figure B-32. Bayesian Network for viability of the Elwha River winter- and summer-run steelhead DIP in the Hood Canal and Strait of Juan de Fuca Major Population Group. See main text for a fuller description.

Appendix C

Calculation of Intrinsic Potential Estimates for Demographically Independent Populations of Puget Sound Steelhead

The sustainability of any population is based, in large part, on the maintenance of a minimum numbers of spawners over an extended period. In a simplified life-cycle model of anadromous steelhead, adult abundance is based on freshwater productivity and marine survival. Freshwater productivity, in turn, is based on habitat quality and stream characteristics. In order to estimate freshwater productivity, the TRT generated estimates of stream length, stream area (wetted bankfull area), and stream gradient using GIS-based data layers obtained from the U.S. Geological Survey (the NHD dataset, at a scale of 1:100,000) for 200 m stream reaches. These data were integrated into an intrinsic potential (IP) model to estimate productivity, adapted from data in Gibbons et al. (1985) and the Interior Columbia TRT's steelhead IP model, and based primarily on stream size, gradient (using the USGS 10 m resolution Digital Elevation Model), and hydrograph for reaches below impassable barriers. For Puget Sound steelhead we adopted a model incorporating three stream widths and three stream gradient classes (Table C-1). Stream habitat was initially classified as having low, medium, and high productivity (Table C-1). We then further categorized stream reaches by whether they were mainstem or tributary, and whether the hydrograph was influenced by snowpack or not (intersection of the reach with a 0°C contour in January).

Adult steelhead occupancy of stream reaches was determined from the Washington Department of Fish and Wildlife's Salmonscape database (accessed at the hyperlink <http://wdfw.wa.gov/mapping/salmonscape/>), from steelhead spawning surveys where redd locations were documented, and from the subbasin reports produced by the Washington Conservation Commission.

		Stream Habitat Rating Matrix (below natural barriers)		
		Stream Width (bankfull)		
		0-3 m	3-20 m	> 20 m
Stream Gradient	0.0 – 0.25%	High	Moderate	Low
	0.25 – 4.0%	Moderate	High	Moderate
	> 4.0%	Low	Low	Low

Table C-1. Stream habitat rating for streams for Puget Sound steelhead. Stream size and gradient categories were assigned by TRT members based on consideration of the Interior Columbia TRT's IP model and on expert opinion. The TRT used these basin characteristics to calculate the intrinsic potential (IP) of Puget Sound steelhead basins in order to establish whether a large enough population could be sustained into the foreseeable future.

Steelhead freshwater productivity has been estimated in a number of ways. Chapman (1981) estimated freshwater production under pristine conditions at 0.0877 parr/m² (equivalent to 0.0263 smolts/m²). Gibbons et al. (1985) developed a more complex productivity model, based on observed parr densities categorized according to stream gradient and size, with parr productivity for Puget Sound streams varying from 0.05 to 0.12 parr/m². Gibbons et al. (1985) found that small independent tributaries had some of the highest productivities. On average, western Washington stream productivity was 0.0717 parr/m² with 0.0265 spawners/parr (Gibbons et al. 1985). Similarly, USACE (1988) estimated potential steelhead freshwater productivity at 0.067 parr/m² for streams and 0.041 parr/m² for rivers. We combined an average estimate for parr productivity of 0.0754 parr/m² with the Chapman (1981) parr to smolt survival of 0.30, to establish a 0.023 smolts/m² level of productivity. Low productivity areas were not included in the estimate of potential parr numbers. This is similar to estimates for the Keogh River, 0.032 smolts/m² (Tautz et al. 1992). Smolt to adult survival (SAS) was estimated using Keogh River studies (Ward and Wightman 1989), with a 20% survival rate selected to estimate average pre-European contact productivity.

Using the 20% SAS rate as an estimate of capacity provided a frame of reference for estimating two other abundance thresholds. First, a viability abundance threshold, where a population is sustainable over longer periods, specifically meets the 5% risk of reaching QET over a 100-year period. For planning purposes, IP calculations using a 5% SAS provided a reasonable estimate of the abundance threshold for a viable population. Alternatively, a low abundance threshold provides demographic sustainability over periods less than 100 years and is large enough to prevent the loss of genetic diversity over a similarly short period of time. Using a 1% SAS rate in calculating the IP capacity provided an estimate of this low abundance threshold. Review of the IP calculations suggests that abundance thresholds for populations with higher gradient headwaters were too low; this was especially the case for summer-run populations. For all populations, the low abundance threshold was set at a minimum of 100 adults/yr (4-year average), while the minimum viable abundance threshold was set at 250 adults/yr (4-year average).

Appendix D

Description of Demographically Independent Populations of Puget Sound Steelhead

The purpose of this Appendix is to present, in a condensed form, the Viable Salmonid Population (VSP) attributes (McElhany et al. 2000) of each of the steelhead demographically independent populations (DIPs) that existed historically in the Puget Sound Steelhead DPS.

Abundance and Productivity

Productivity and related trends in abundance reflect conditions that drive a population's dynamics and thus determine its abundance. Changes in environmental conditions, including ecological interactions, can influence a population's intrinsic productivity or the environment's capacity to support a population, or both. Such changes may result from random environmental variation over a wide range of temporal scales (environmental stochasticity). In this section, however, we are most concerned with measures of population growth and related parameters that reflect systematic changes in a population's dynamics (McElhany et al. 2000).

Abundance estimates for each DIP are generally based on expansions of redd counts from index areas. In a few cases, fish passage facilities allow relatively precise counts of returning adults. In other areas, systematic surveys are not available and anecdotal reports alone establish the presence of steelhead. In these cases it may be necessary to use adjacent DIPs as proxies to estimate abundance; however, except where accessibility is limited it is likely that the absence of survey activity is related to low steelhead abundance.

Productivity is generally derived from abundance data series, either as lambda, trend, or spawner/recruit calculations. Given the relatively high uncertainty in abundance estimates (particularly expansions of index redd counts), productivity estimates include considerable uncertainty.

Several historical measures of abundance are included to provide context for present-day abundance estimates. These include a summary of salmon streams conducted in 1930 (WDG 1932). Populations were categorized as being large, medium, scarce, very scarce and absent with no numerical equivalents given. Punch card estimates are derived from Washington Department of Game estimates. These estimates are “corrected” by a factor of 0.60 to account for reporting bias. Peak catch estimates were selected from those return years that were not supplemented, based on data provided in WDG (undated B). Punch card estimates do not include any adjustment for commercial or tribal catch. Finally, habitat based intrinsic potential (IP) estimates were developed to approximate historical production. It should be noted that this system was developed to establish whether or not the basin could support a DIP—it is not considered a precise estimate and likely underestimates potential productivity.

Diversity

In their VSP report, McElhany et al. (2000) identify three general reasons why diversity is important for species and population viability. First, diversity allows a species to use a wider array of environments than it could without it. For example, varying adult run and spawn timing allows several salmonid species to use a greater variety of spawning habitats than would be possible without this diversity. Second, diversity protects a species against short-term spatial and temporal changes in the environment. Fish with different characteristics have different likelihoods of persisting—depending on local environmental conditions. Therefore, the more diverse a population is, the more likely it is that some individuals would survive and reproduce in the face of environmental variation. Third, genetic diversity provides the raw material for surviving long-term environmental changes. Salmonids regularly face cyclic or directional changes in their freshwater, estuarine, and ocean environments due to natural and human causes, and genetic diversity allows them to adapt to these changes.

Two major life history types of steelhead were historically, and are presently, found in Puget Sound: the summer run and winter run. The life histories of summer- and winter-run steelhead have considerable overlap. Both rear in freshwater for 1 to 4 years prior to smoltification, select similar habitats for freshwater rearing, and spend 1 to 4 years in the ocean. However, substantial differences separate these races at the time of adult freshwater entry, degree of sexual maturity at entry, spawning time.

Each year, the majority of naturally produced Puget Sound summer-run steelhead enters freshwater between May and October. These fish are sexually immature upon return to their natal streams. The fish subsequently spawn between January and June, with peak spawning between late February and early April (Leider et al. 1986, WDFW unpublished data). In contrast, wild winter-run steelhead enter freshwater as sexually mature fish between December and May. Spawning occurs between February and June, with peak spawning time in late April and early May, almost two months later than wild summer-run steelhead (Leider et al. 1986 and WDFW unpublished data).

On average, there is a two-month difference in peak spawning time between winter- and summer-run steelhead, although there is probably certainly some temporal overlap in the spawning distribution (Busby et al. 1996). Within the same watershed winter- and summer-run steelhead maintain a high degree of reproductive isolation by spawning in geographically distinct areas, these areas are generally separated by temporal migration windows created by falls or cascades. In a few cases winter- and summer-run steelhead spawn in the same stream reach, but at slightly different times. Hatchery introductions, especially with non-native steelhead, and modifications to barrier falls are a potential source for the breaking down of historical reproductive barriers and the erosion of locally adapted genotypes.

Diversity status is difficult to quantify due to the near absence of information on historical life history characteristics. Any actions that affect basic demographic and evolutionary processes (e.g., patterns of mutation, selection, drift, recombination, migration, and population turnover) have the potential to alter a species' diversity (McElhany et al. 2000). At a minimum, information on hatchery introductions is available for most DIPs. In some cases, genetic

information can substantiate the influence of hatchery fish on the naturally-spawning population. Additionally, habitat diversity (the basis of life history diversity) has been assessed for most populations and there are estimates for the proportion of lost habitat diversity.

Artificial Propagation: Hatchery releases for each DIP have been compiled for the most recent 15 years (3 to 4 generations). Releases of small *O. mykiss* fry (250 fish per pound (fpp)) have been excluded. The contribution of these fish to steelhead abundance is thought to be minimal. Additionally, many fry releases were into lakes and not necessarily intended to enhance the anadromous population. Hatchery broodstock names have been retained, but where Chambers Creek or Skamania River hatchery-derived stocks are used a notation of “CC” or “SK” has been added. Hatchery broodstocks derived from either of these sources are considered as being out-of-DPS stocks.

Spatial Structure

Spatial structure is defined by McElhany et al. (2000) as the geographic distribution of individuals in a population and the processes that create that distribution (i.e., habitat structure or migrational barriers). From a demographic perspective, spatial structure within a DIP prevents the stochastic extirpation of smaller breeding units through migration between units and the reduction in the effects of catastrophic events.

Steelhead within a DIP utilize a variety of habitats for spawning, rearing, and adult holding. Ecological differences among primary streams and their tributaries likely influence the expression of distinct life history strategies. Spatial structure can be viewed on an absolute scale; how much of the historically accessible habitat is still available or usable? Alternatively, the distribution of accessible habitat may also affect spatial structure.

Guidance

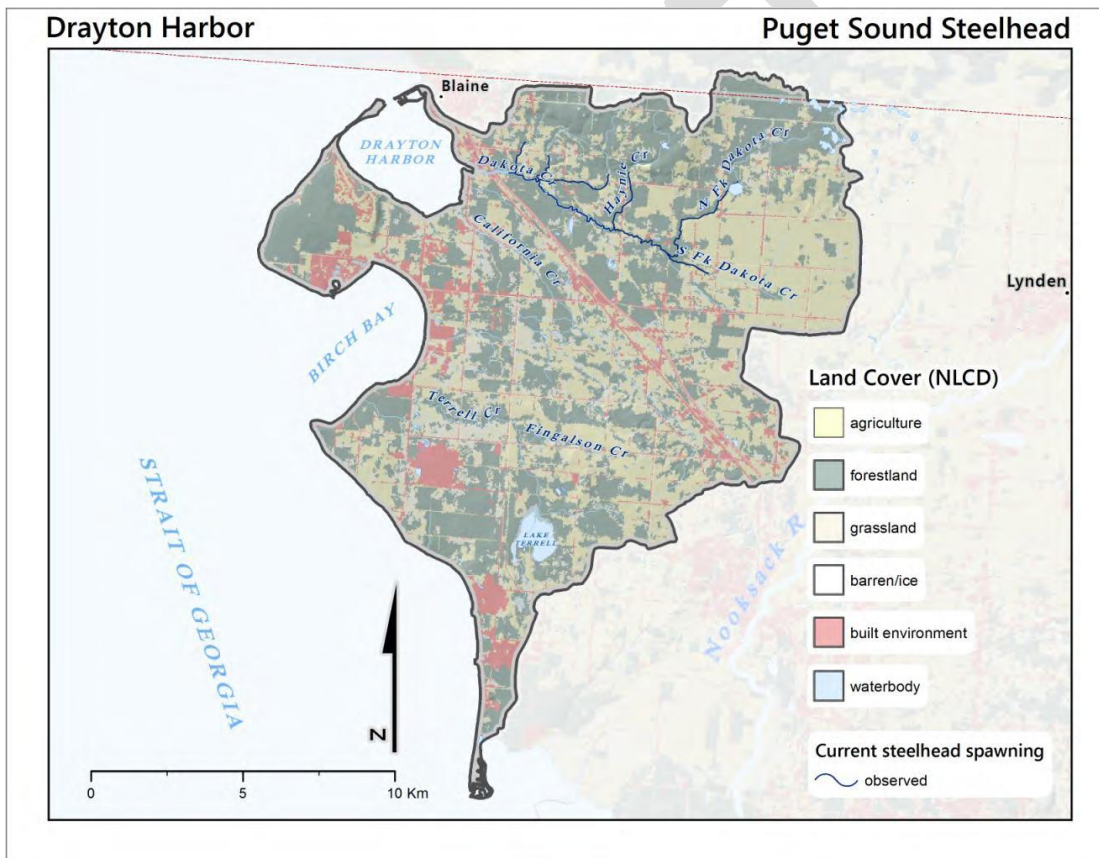
In evaluating the four VSP attributes, some overlap is to be expected; however, one should be mindful to keep “double scoring” effects to a minimum. Each attribute should be considered for its contribution to population viability, or conversely to its contribution to extinction risk. The quantity and quality of the information available will determine, in turn, the accuracy of the estimate of extinction risk. Uncertainty due to data quality should be reflected in VSP scores.

Summaries of Puget Sound Steelhead Demographically Independent Populations

Northern Cascades Steelhead Major Population Group

1. Drayton Harbor Tributaries Winter Run

Overview: This population includes steelhead that spawn in tributaries from the Canadian border to Sandy Point, primarily in Dakota and California creeks (Smith 2002). Although steelhead redds are still reported in this DIP, abundance information is very limited. Spawning habitat is limited.



Abundance and Productivity

	WDF Survey	Punch Card Max	IP Estimate	
Abundance	Medium-sized	67	2,426	4,852
Year	1930	1957	--	

Diversity

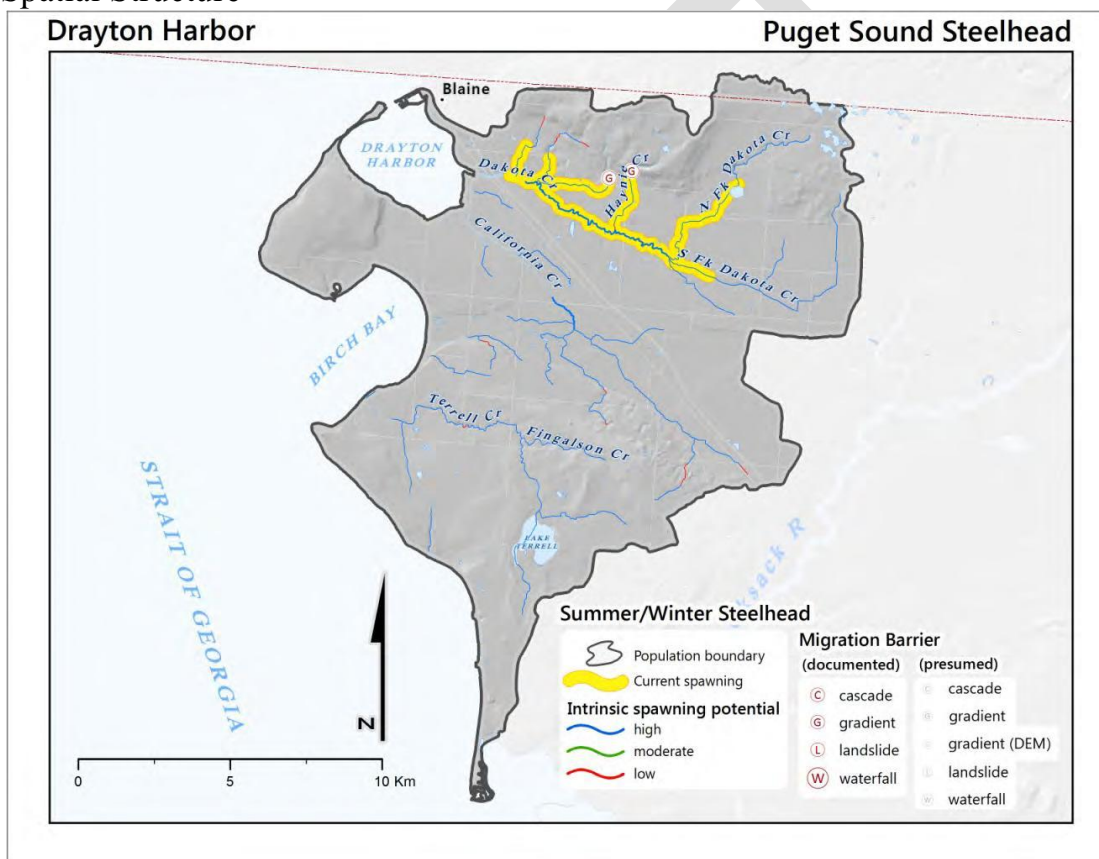
Anecdotal reports suggest the steelhead returning to this DIP are slightly smaller in size and spawn earlier than other nearby populations.

Hatchery Releases

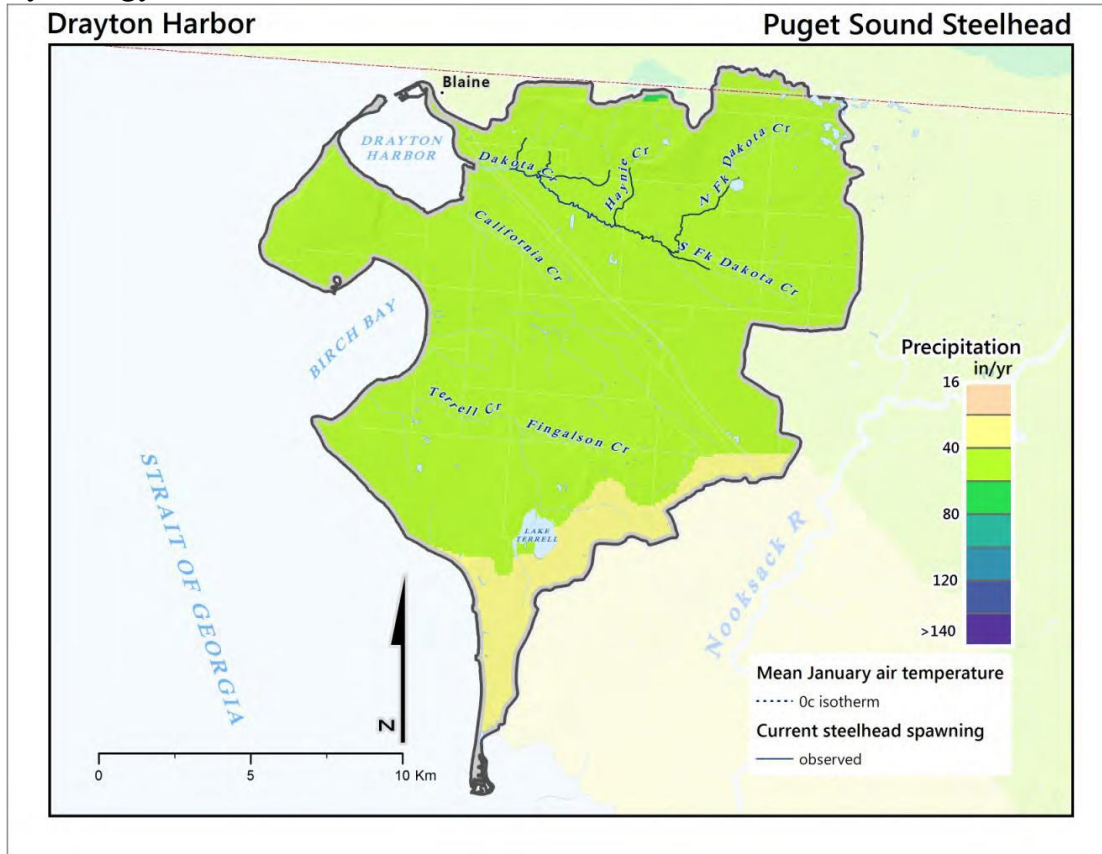
Drayton Harbor Tributaries Winter Run				Total Releases	
Watershed	Duration	Years	Source	(w/i DPS)	(o/s DPS)
			Total	0	0

No known releases since 1995.

Spatial Structure

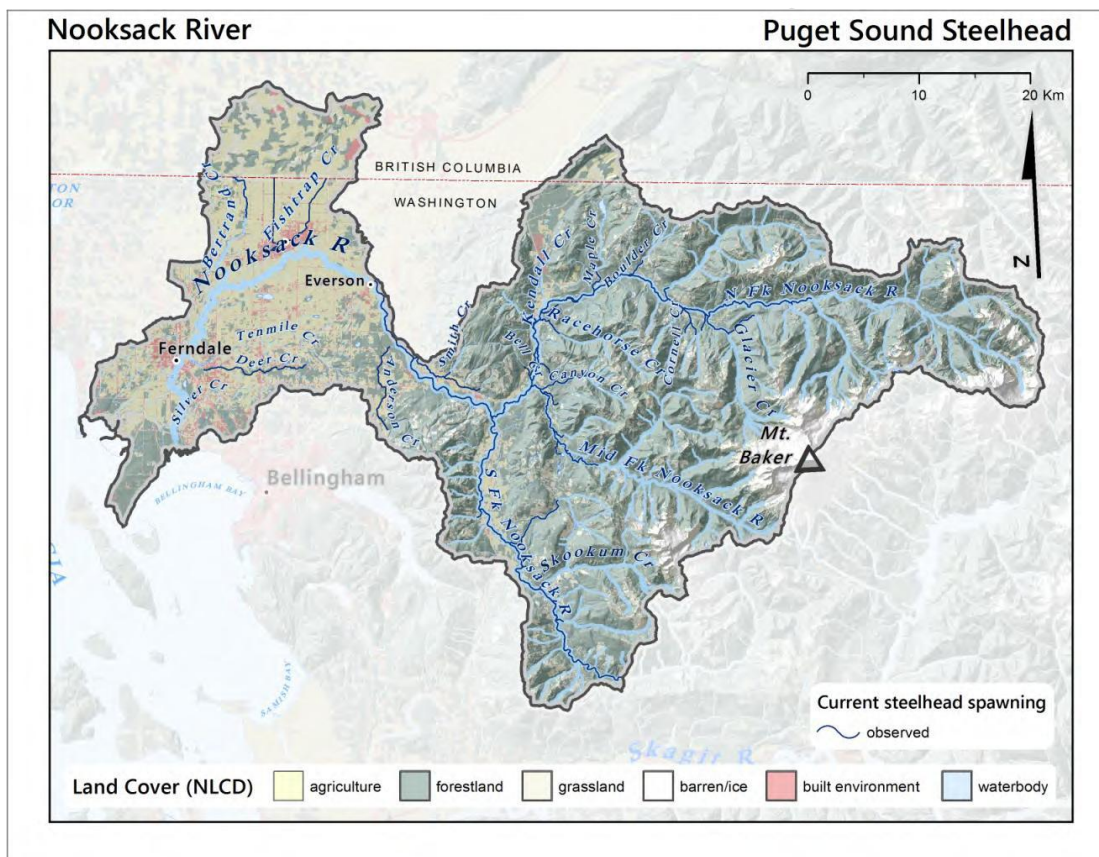


Hydrology



2. Nooksack River Winter Run

Overview: This population includes winter run steelhead in the North Fork, Middle, and South Forks of the Nooksack River. SaSI (WDFW 2005) suggests that the Middle Fork Nooksack River may have supported a summer run of steelhead prior to the construction of the impassable diversion dam at Rkm 11. Glacial conditions limit spawner surveys in the North Fork Nooksack River. Lowland tributaries (Fishtrap and Bertram creeks) presently contribute significantly to overall abundance.



Abundance and Productivity

	WDF Survey	Punch Card Max	Geometric Mean	IP Estimate	
Abundance	Multiple Large and Medium	2114		22,045	44,091
Year	1930	1953		--	

Tributary	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011
Mainstem					1574						1308	1069
North Fork												

Nooksack												
South Fork Nooksack											524	425
Middle Fork Nooksack											69	104

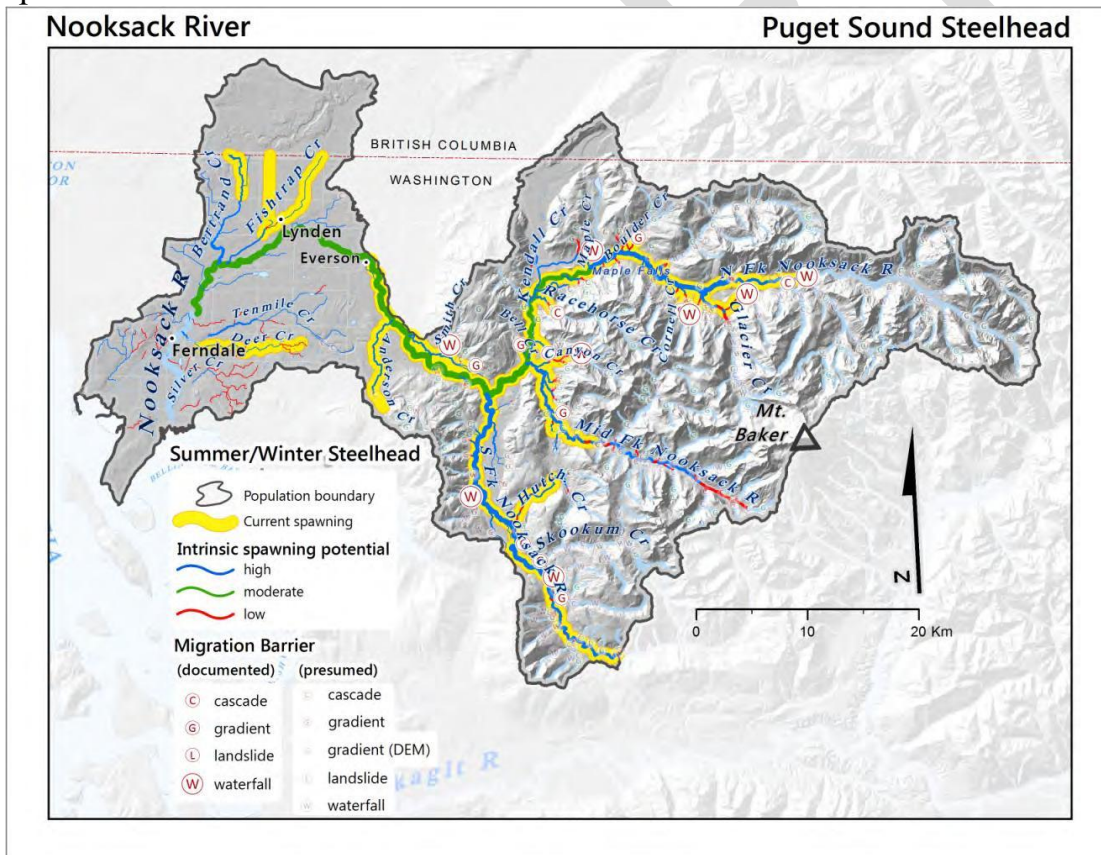
Source: WDFW

Diversity

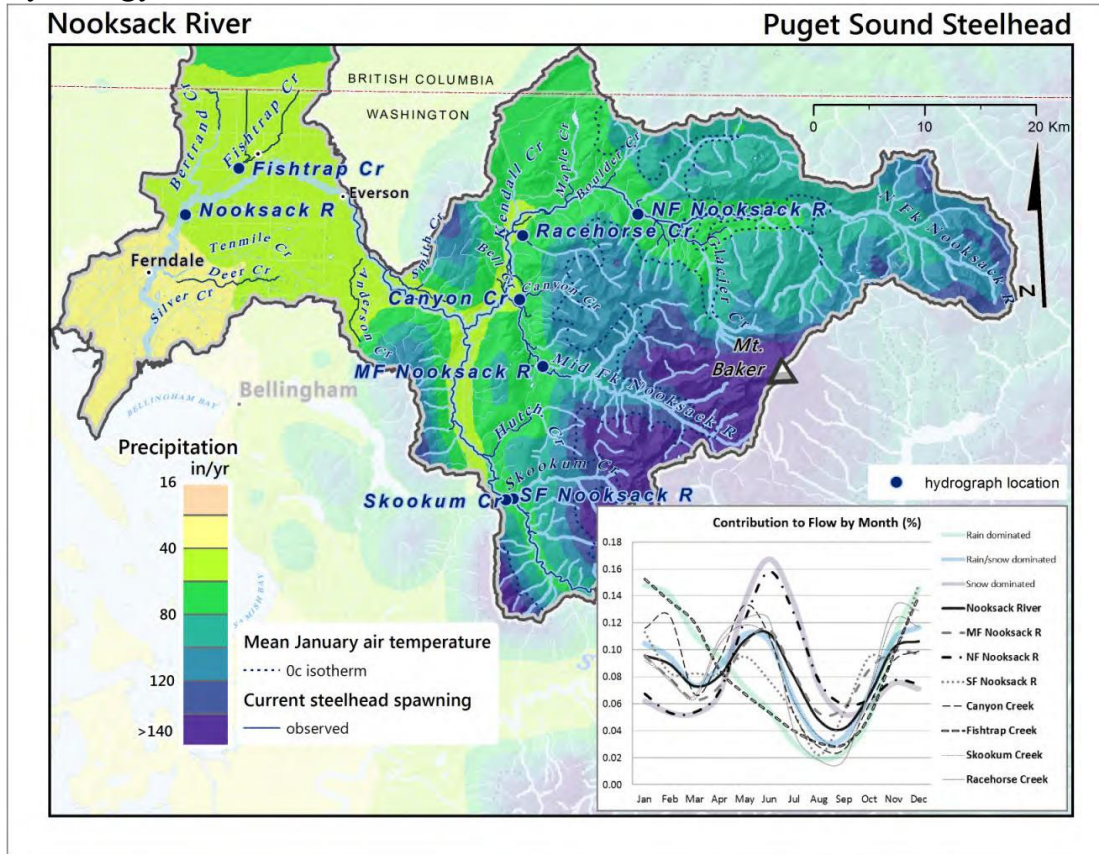
Hatchery Releases

Nooksack River Winter Run				Total Releases	
Watershed	Duration	Years	Source	(w/i DPS)	(o/s DPS)
Kendall Cr.	96-11	14	Tokul/Bogachiel (CC)	0	1,413,238
Nooksack MF	95-98	4	McKinnon Pd (CC)	0	268,215
			Total	0	0

Spatial Structure

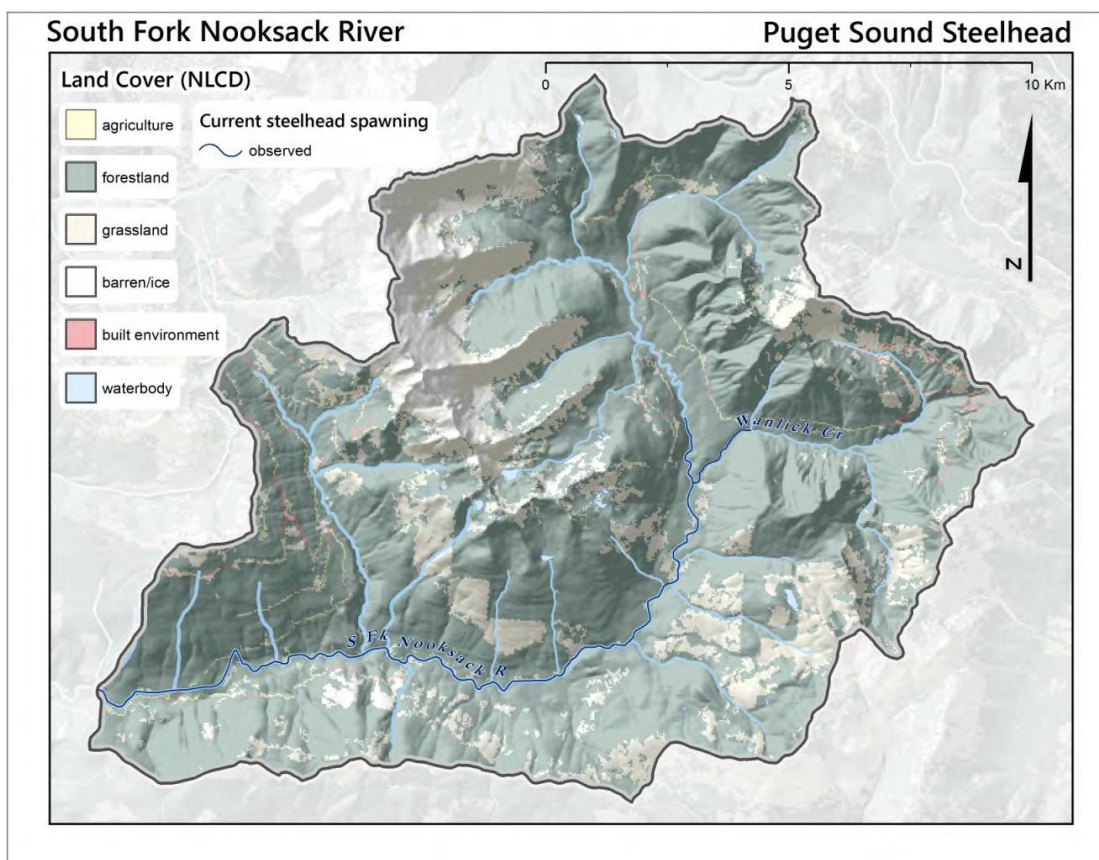


Hydrology



3. South Fork Nooksack River Summer Run

Overview: This population includes steelhead that spawn in tributaries from the headwaters to Sandy Point, primarily in Dakota and California creeks (Smith 2002). Although steelhead redds are still reported in this DIP, abundance information is very limited.



Abundance and Productivity

	WDF Survey	Punch Card Max	Geometric Mean	IP Estimate	
Abundance	Medium Run	31		1,137	2,273
Year	1930	1964			

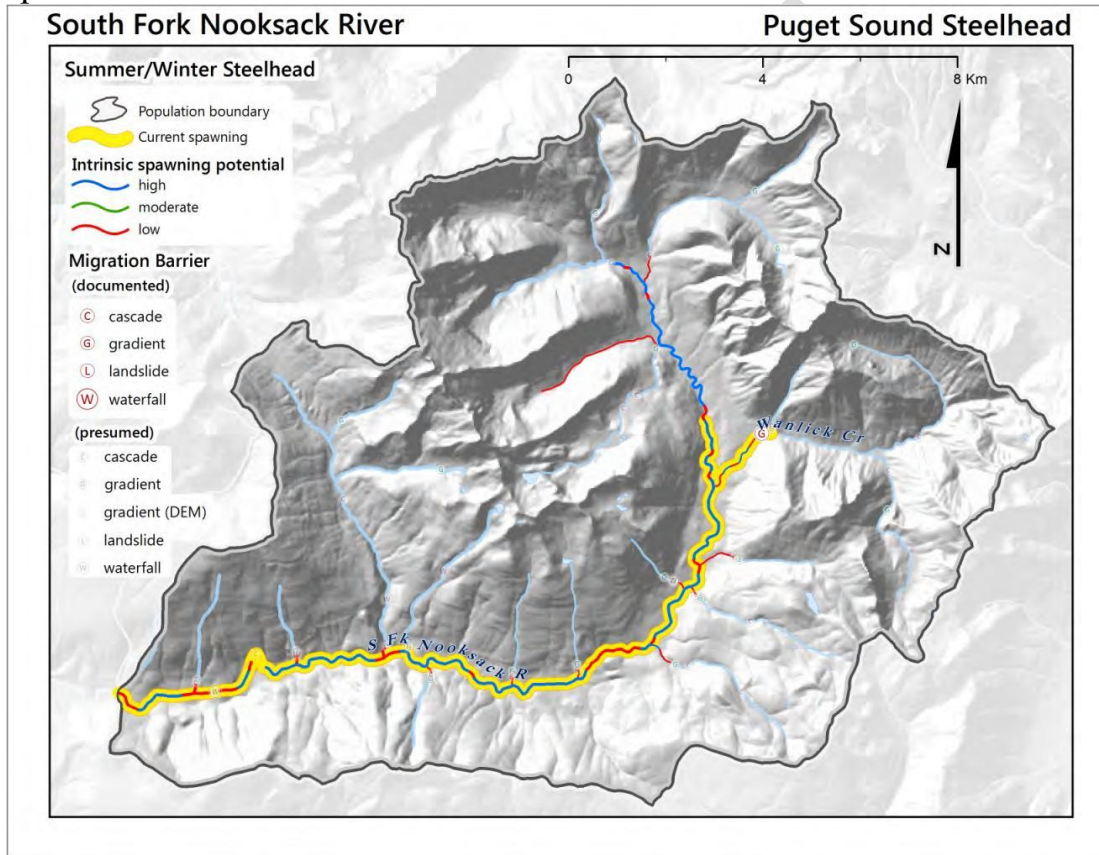
Tributary	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006
South Fork Nooksack										

Diversity

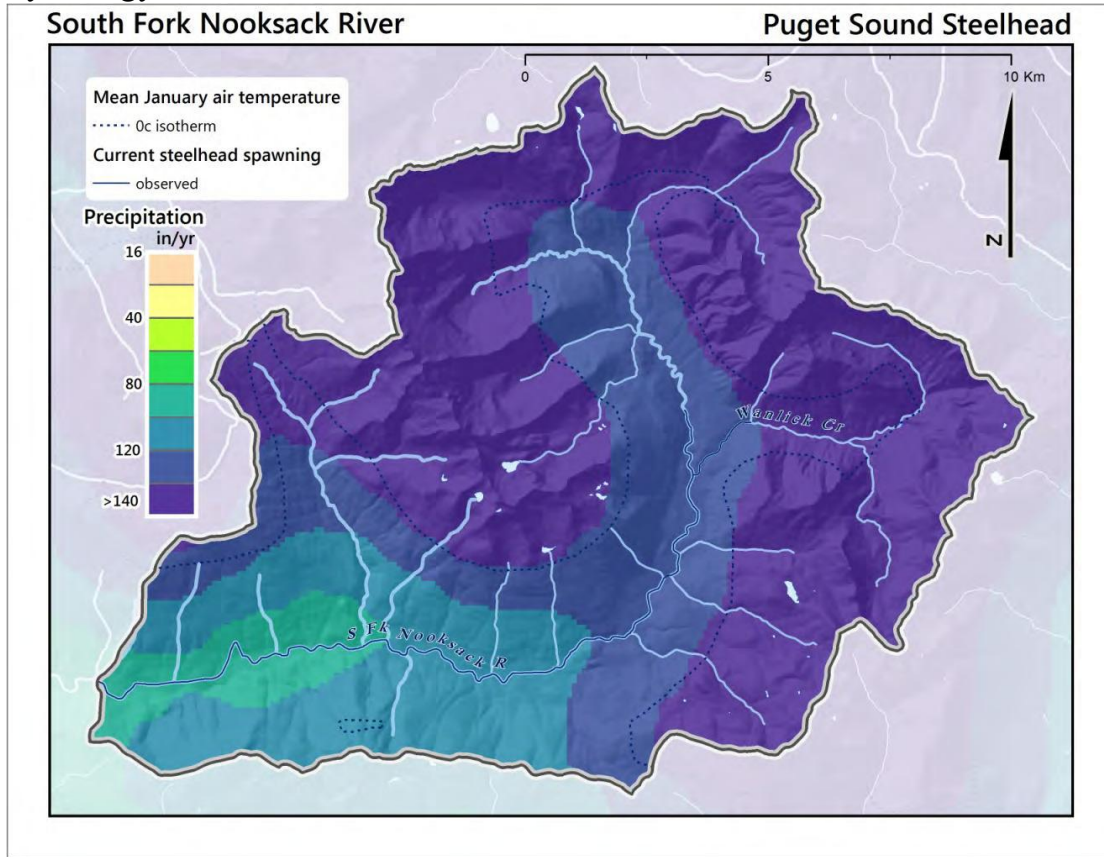
Hatchery Releases

Nooksack River Winter Run				Total Releases	
Watershed	Duration	Years	Source	(w/i DPS)	(o/s DPS)
			Total	0	0

Spatial Structure

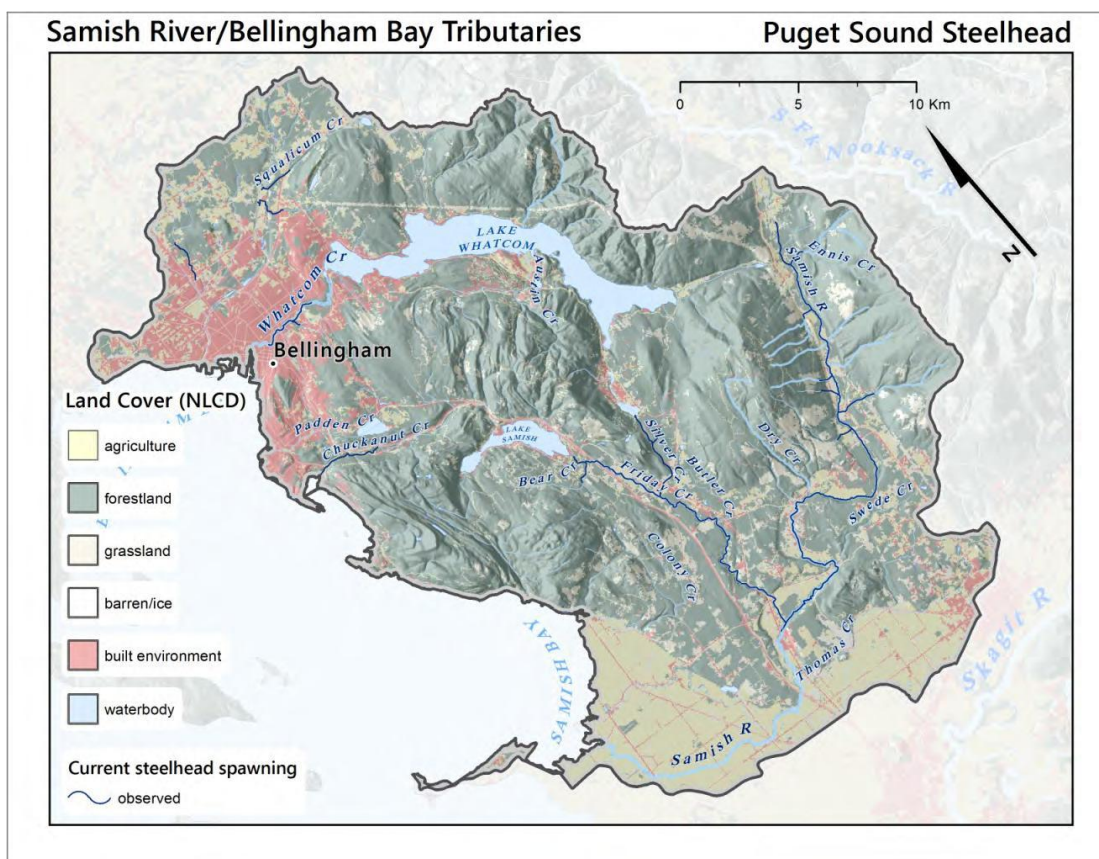


Hydrology



4. Samish River and Bellingham Bay Tributaries Winter Run

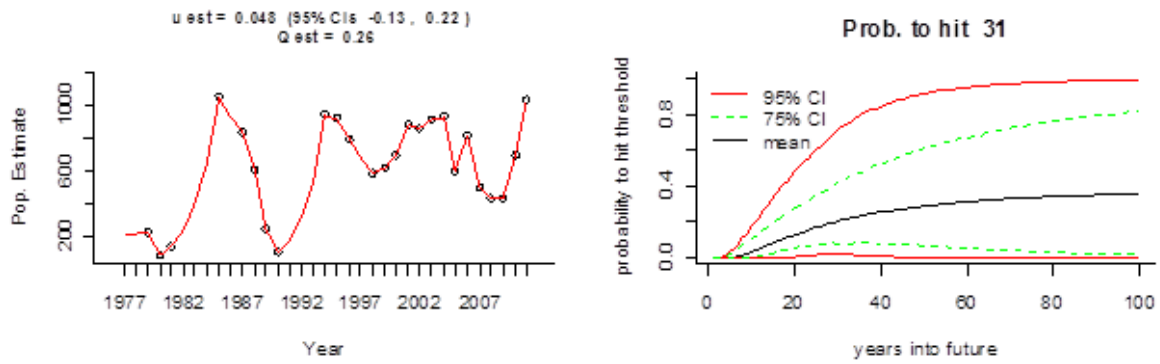
Overview: This population of steelhead exists in an independent tributary to Puget Sound. The Samish Rivers drains into Samish and Bellingham Bays, whereas the headwaters are more closely associated with the Skagit River Basin. The majority of historical and present production is in the Samish Basin, with lesser contribution from the Bellingham Bay tributaries.



Abundance and Productivity

	WDF Survey	Punch Card Max	Geometric Mean	IP Estimate	
Abundance	Not surveyed	1,934	534 (389 - 732)	3,193	6,386
Year	1930	1951	2005-2009	--	

Population	Exp. trend ln(nat. spawners) (95% CI) (1985-2009)
Samish River winter-run	1.008 (0.972 - 1.045)

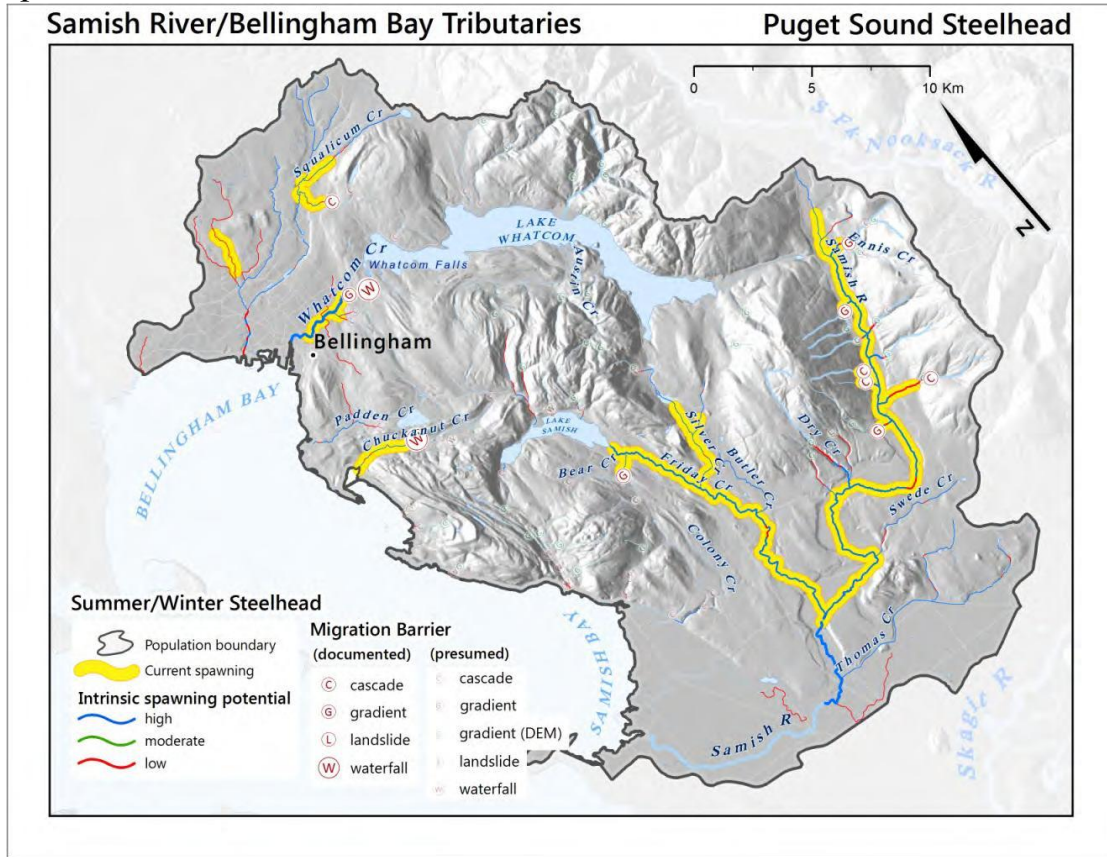


Diversity

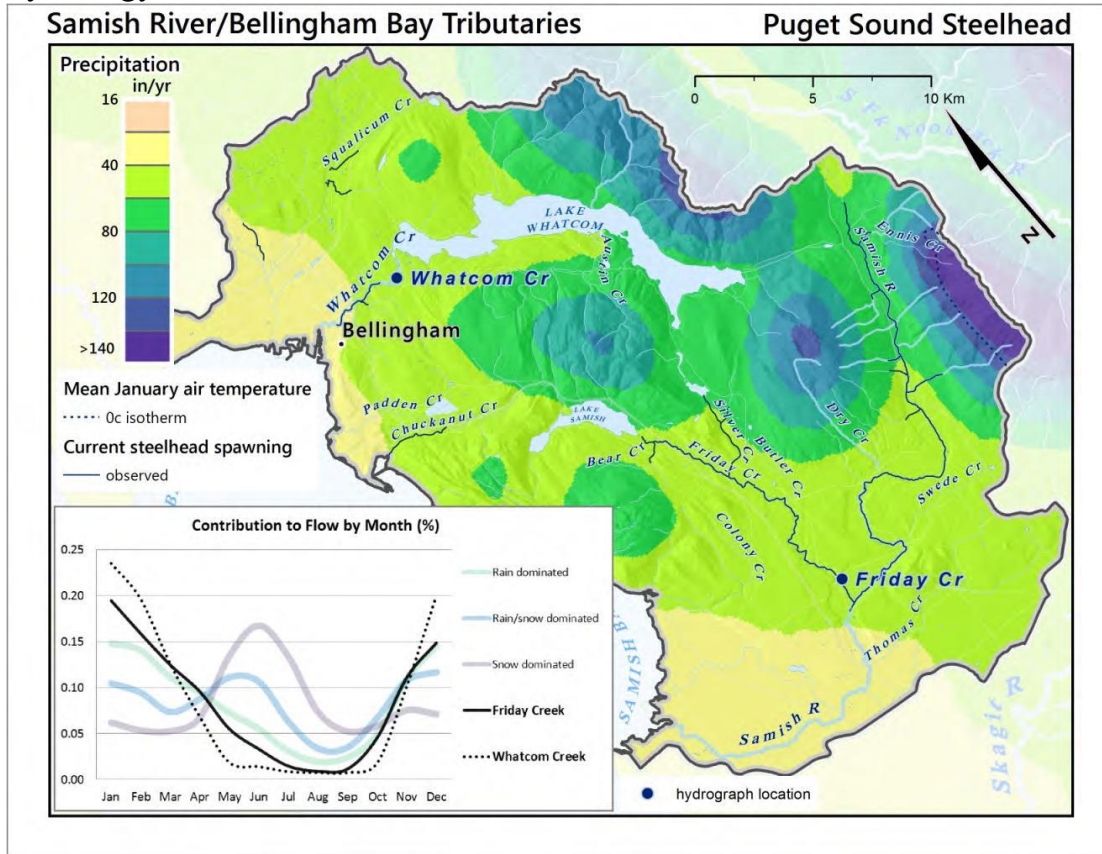
Hatchery Releases

Samish River Winter Run				Total Releases	
Watershed	Duration	Years	Source	(w/i DPS)	(o/s DPS)
Samish R.	95-08	10	Whatcom R/Tokul (CC)	0	324,073
Whatcom Cr.	95-09	12	Whatcom H (CC)	0	170,508
			Total	0	494,581

Spatial Structure

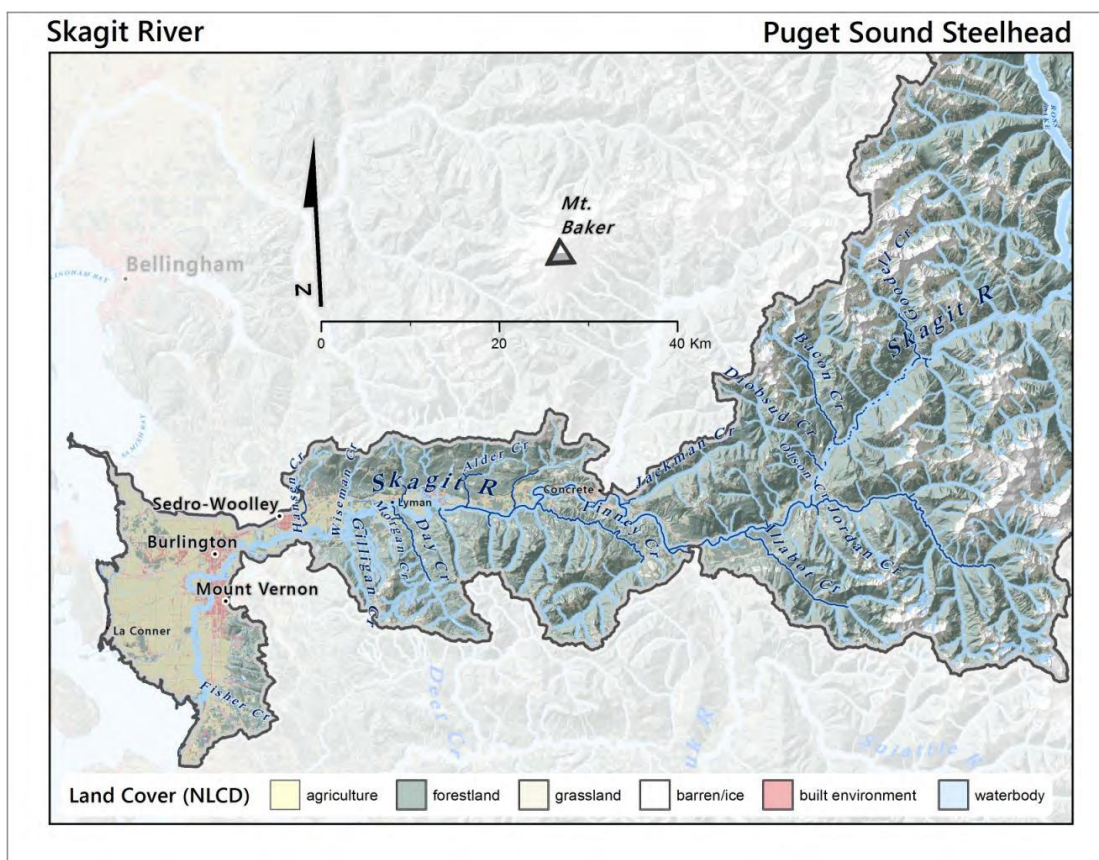


Hydrology



5. Skagit River Winter/Summer Run

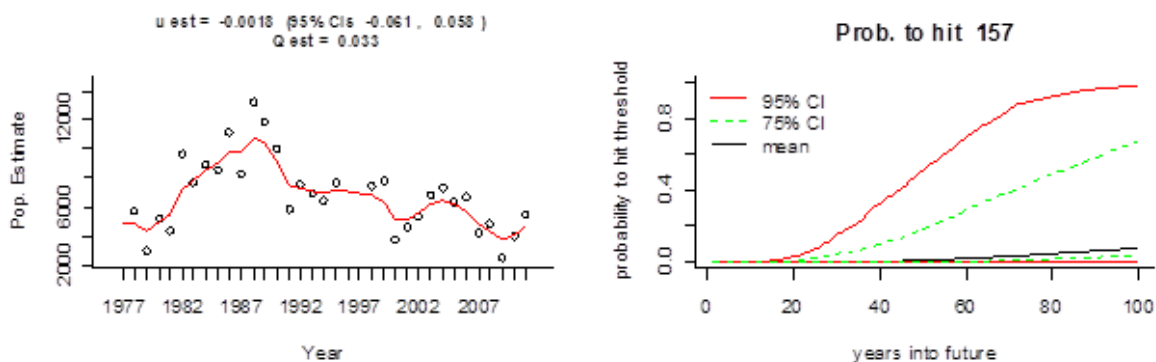
Overview: The population includes both the mainstem Skagit and numerous tributaries. Major tributaries include: Cascade River, Finney Creek, Day Creek, Bacon Creek, and Illabot Creek. Historically, this DIP was likely one of the primary producers of steelhead, both summer and winter run fish, in Puget Sound.



Abundance and Productivity

	WDF Survey	Punch Card Max	Geometric Mean	IP Estimate
Abundance	Multiple Large and Medium	8,022	4648 (2827 - 7642)	64,775 129,551
Year	1930	1950	2005-2009	

Population Skagit River winter-run	Exp. trend ln(nat. spawners) (95% CI) (1985-2009) 0.969 (0.954 - 0.985)
---------------------------------------	--



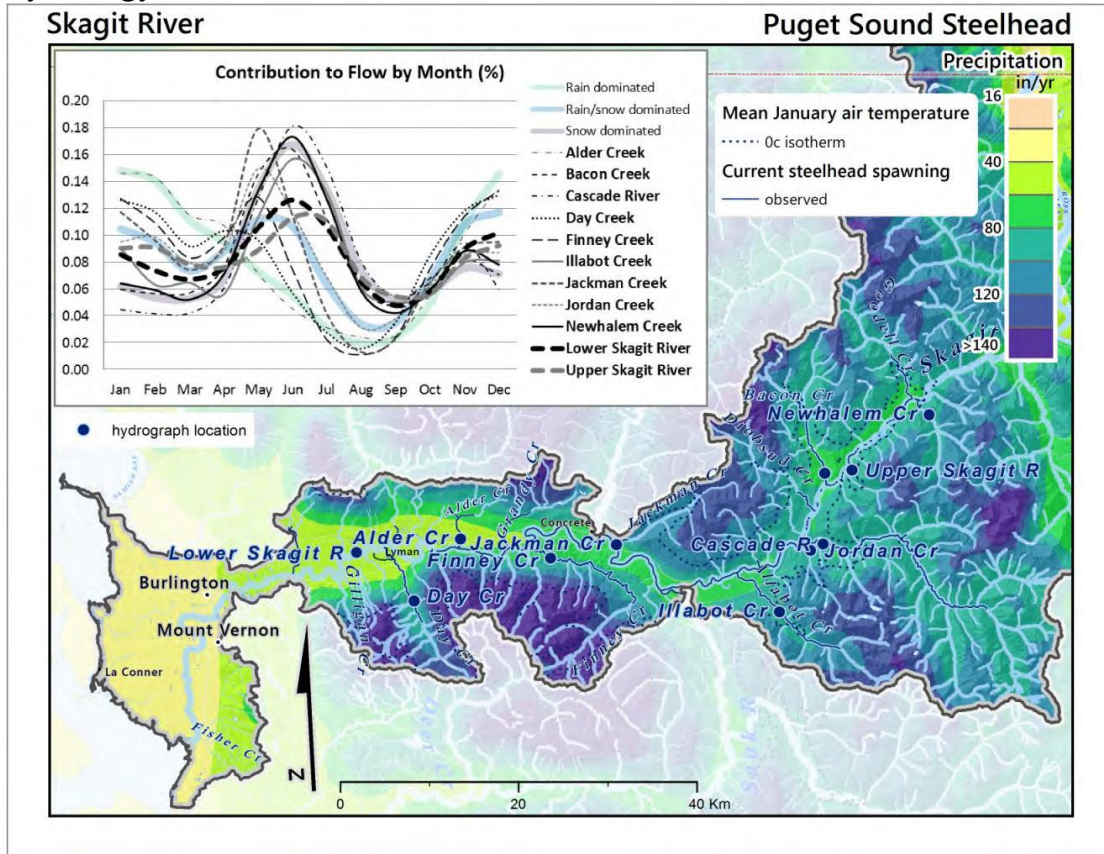
Diversity

Hatchery Releases

Skagit River Winter Run				Total Releases	
Watershed	Duration	Years	Source	(w/i DPS)	(o/s DPS)
Hamilton Slough	97-99	2	Barnaby Slough (CC)		38,350
Barnaby Slough	96-08	12	Barnaby Slough (CC)		1,911,179
Skagit R	95-01	5	Bogachiel/Skagit (CC)		747,392
Cascade R	95-10	16	Marblemount H (CC)		2,576,846
Grandy Cr	96-02	6	Barnaby/Marblemount		324,461
			Total	0	5,598,228

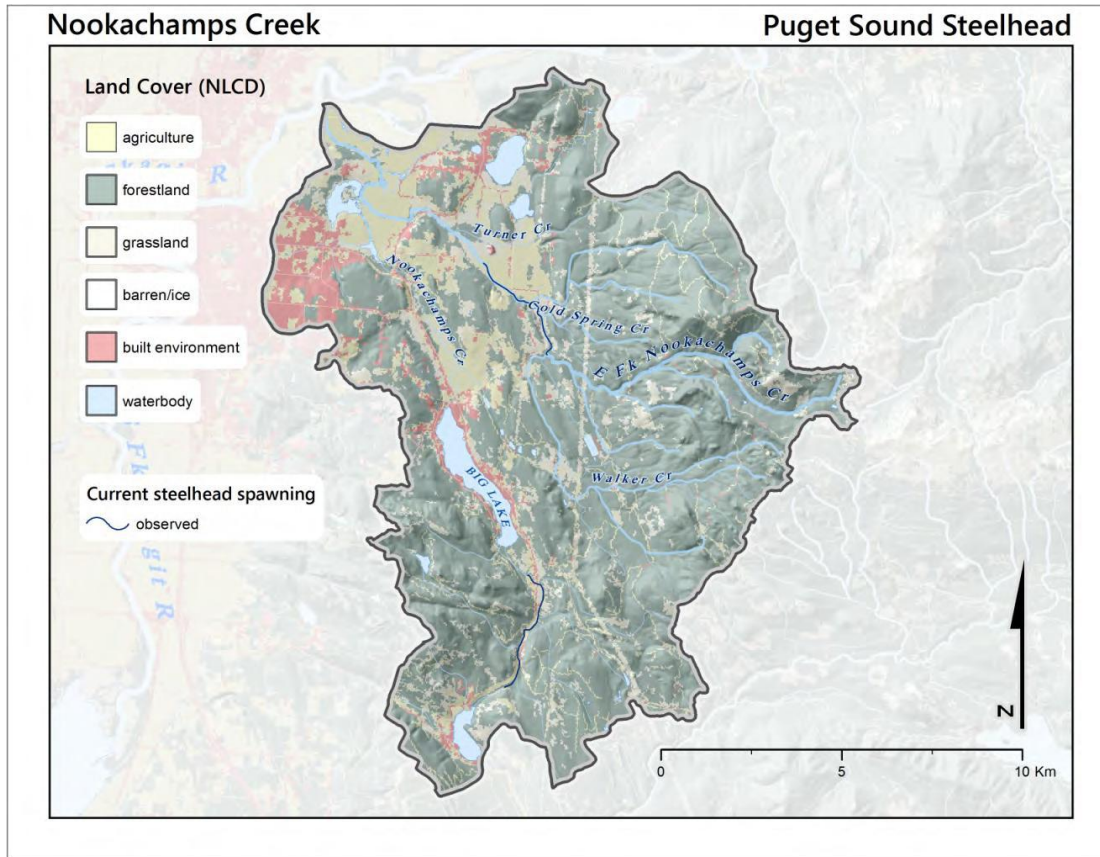
Skagit River Summer Run				Total Releases	
Watershed	Duration	Years	Source	(w/i DPS)	(o/s DPS)
Skagit R	95-98	3	Stillaguamish H		71,256
			Total	0	71,256

Hydrology



6. Nookachamps Creek Winter Run

Overview: Nookachamps Creek was identified as a potential DIP for winter steelhead. This basin met the criteria for basin size and IP production. Very little information is available for this basin other than anecdotal reports of steelhead abundance. Spawning and rearing habitat is primarily in the forks, not the mainstem.



Abundance and Productivity

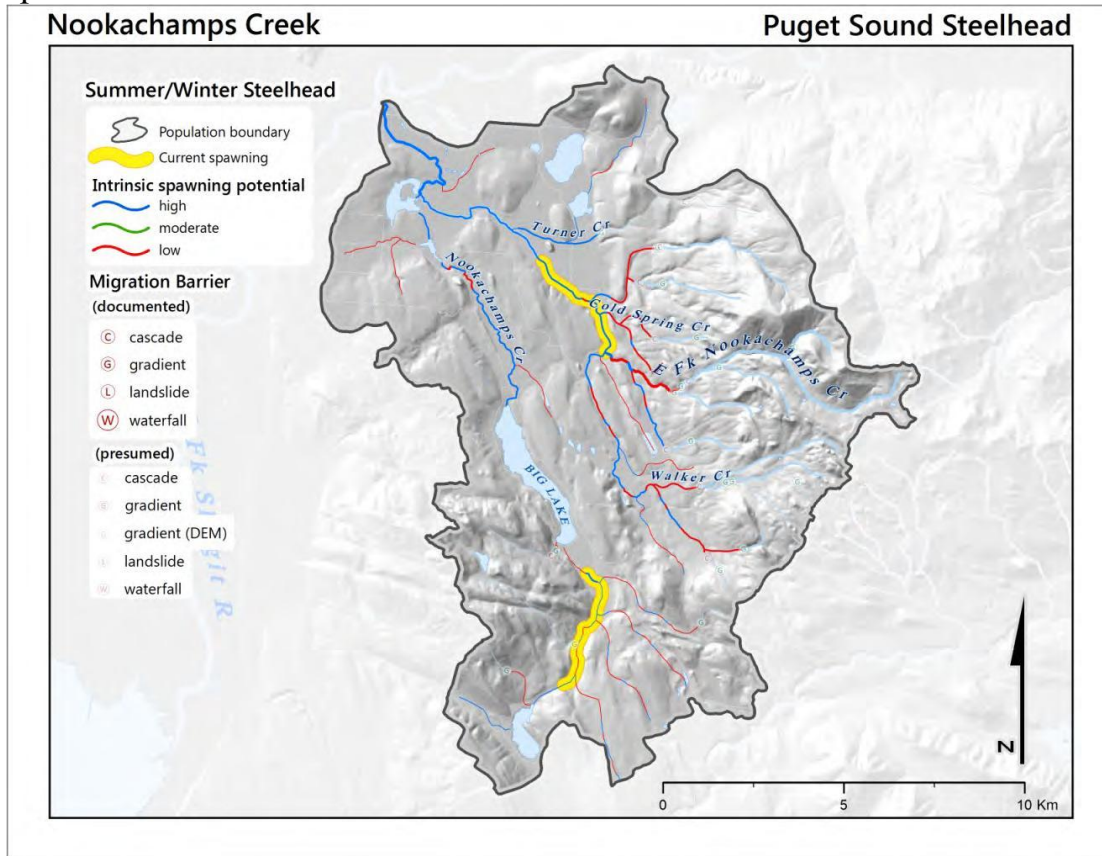
	WDF Survey	Punch Card Max	IP Estimate
Abundance	Scarce	NA	1,231 2,462
Year	1930	NA	

Diversity

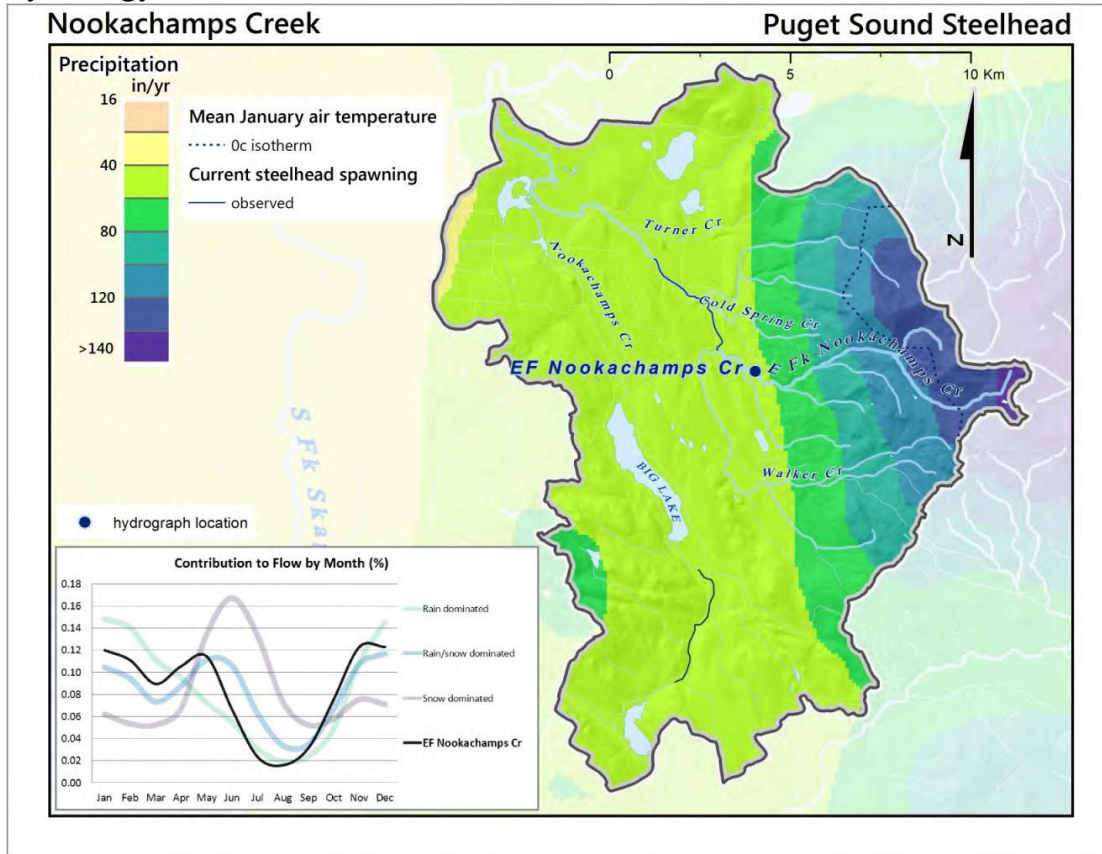
Hatchery Releases

Nookachamps River Winter Run				Total Releases	
Watershed	Duration	Years	Source	(w/i DPS)	(o/s DPS)
			Total	0	0

Spatial Structure

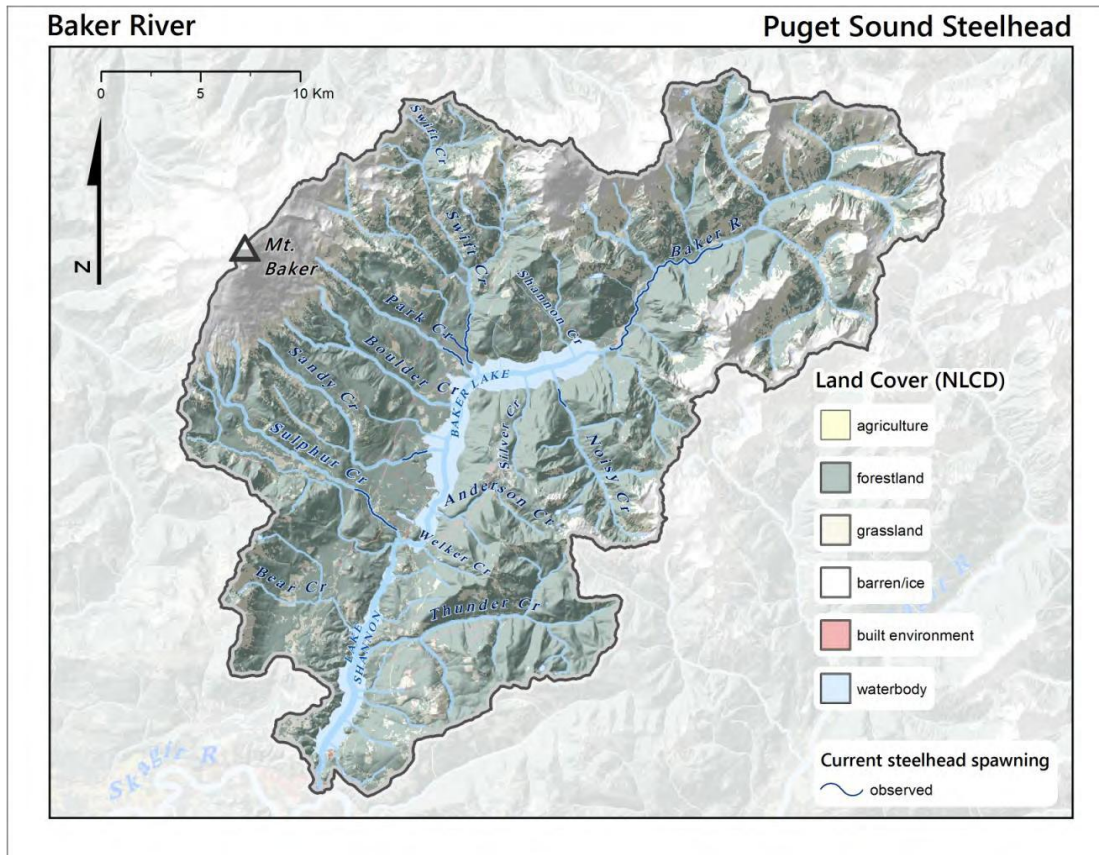


Hydrology



7. Baker River Winter/Summer Run

Overview: Historically, the Baker River was likely a major contributor to Skagit River steelhead runs. The Baker River is the second largest tributary to the Skagit River, with a basin size of 771 km². Access to historical spawning grounds is blocked by the Upper and Lower Baker Dams. Trap and haul operations currently provide the only access to headwater regions.



Abundance and Productivity

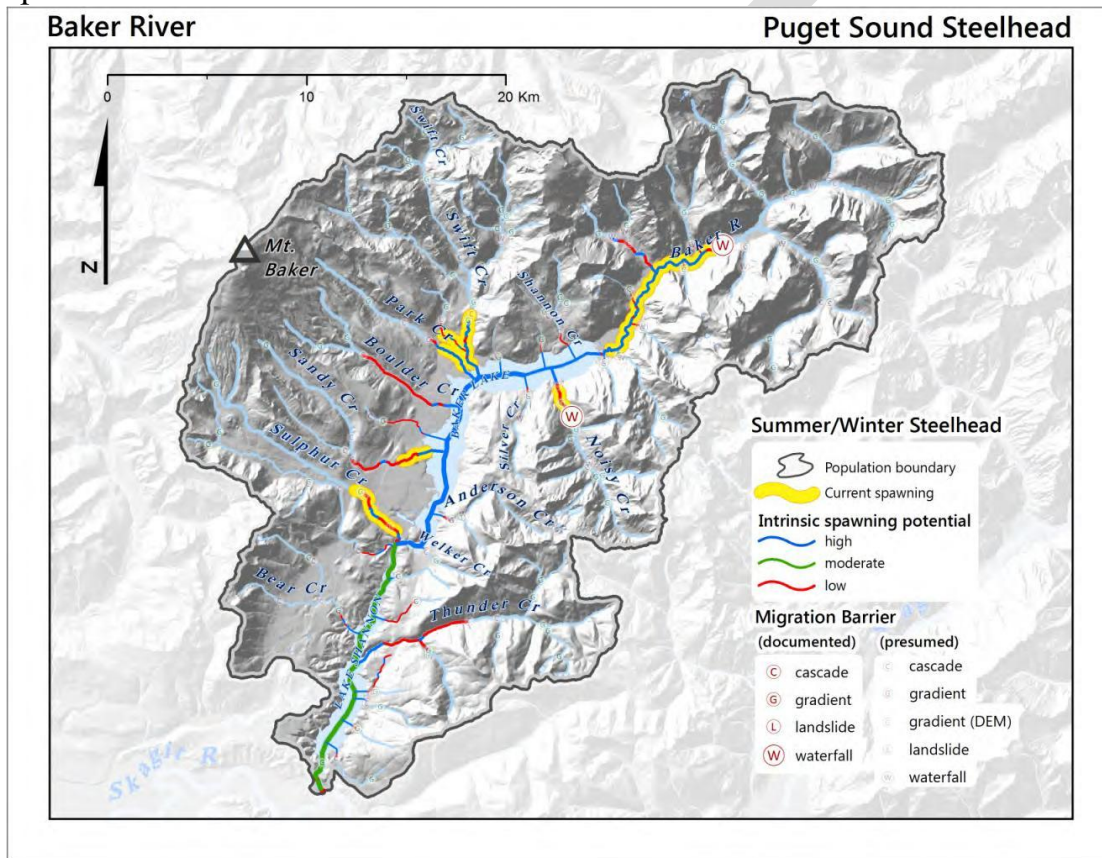
	WDF Survey	Punch Card Max	Geometric Mean	IP Estimate
Abundance	Medium	NA		5,028 10,056
Year	1930			

Diversity

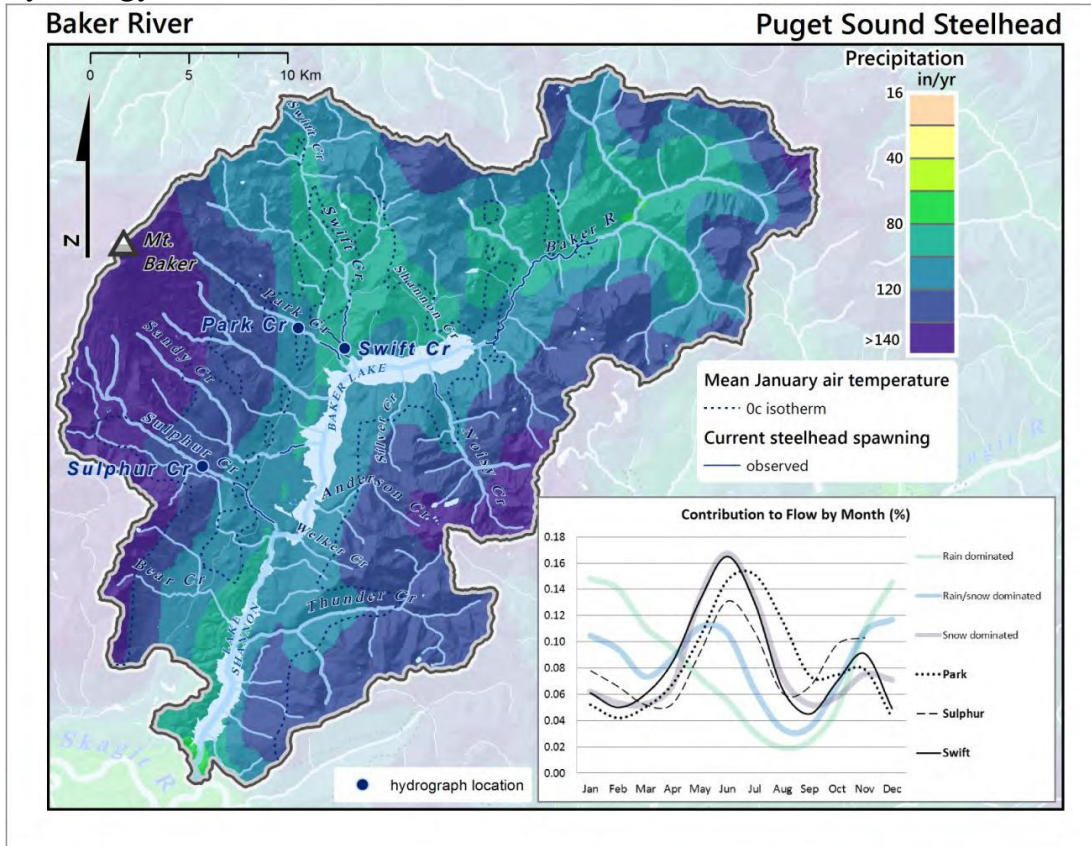
Hatchery Releases

Baker River River Winter Run				Total Releases	
Watershed	Duration	Years	Source	(w/i DPS)	(o/s DPS)
Baker River	95-10	14	Chambers/Baker/Skagit		679,322
			Total	0	0

Spatial Structure

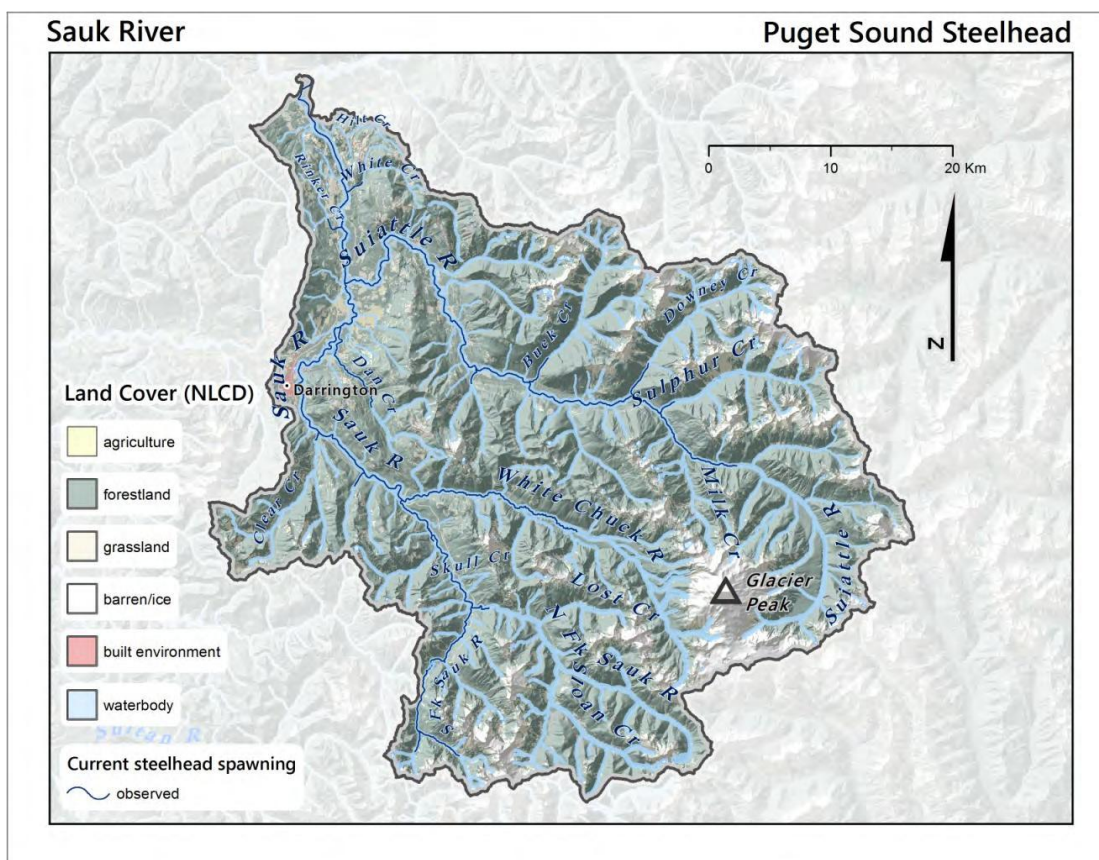


Hydrology



8. Sauk River Winter/Summer Run

Overview: This population includes both winter and summer run steelhead in the Sauk River and its tributaries. Much of the basin consists of higher gradient reaches, and some tributaries are glacially influenced. Historically important, recent returns have been relatively poor.



Abundance and Productivity

	WDF Survey	Punch Card Max	Geometric Mean	IP Estimate
Abundance	Multiple Medium	679	2541	23,230 46,460
Year	1930	1951	2004-2006	

Tributary	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006
Sauk (Sum)										
Sauk (Winter)								2726	1962	3068

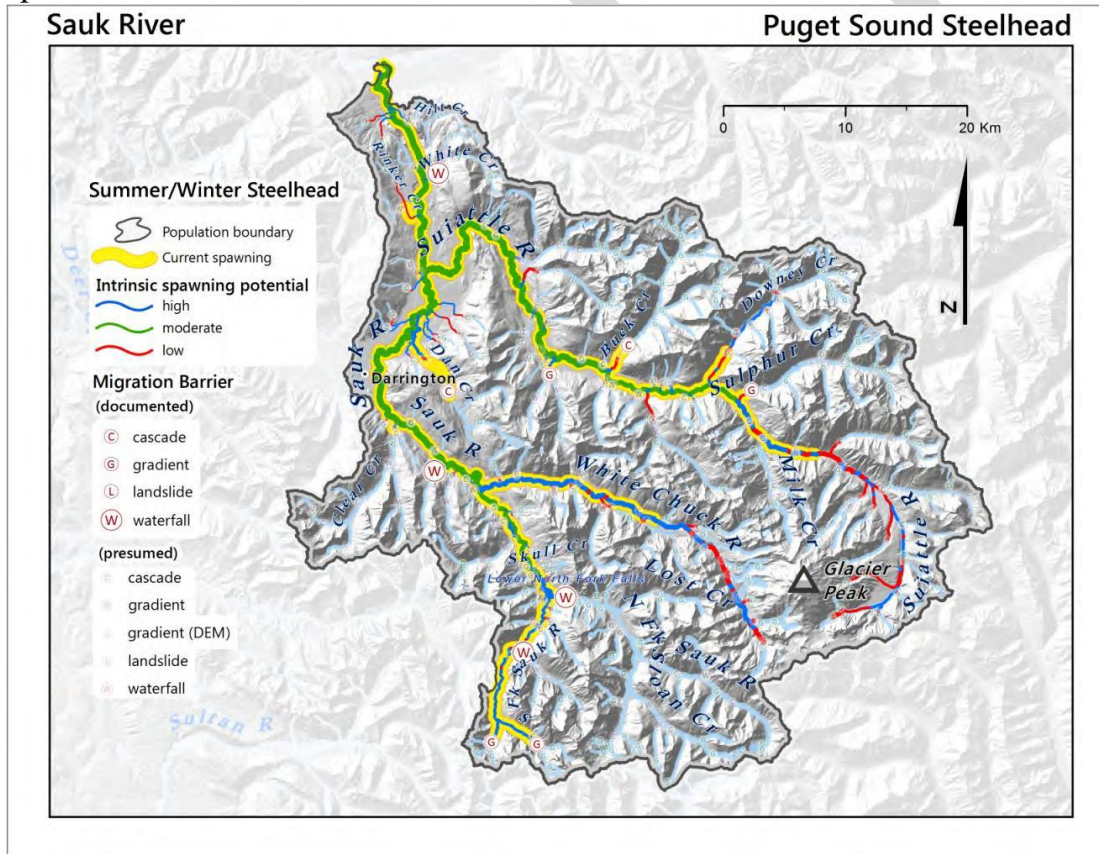
Diversity

Hatchery Releases

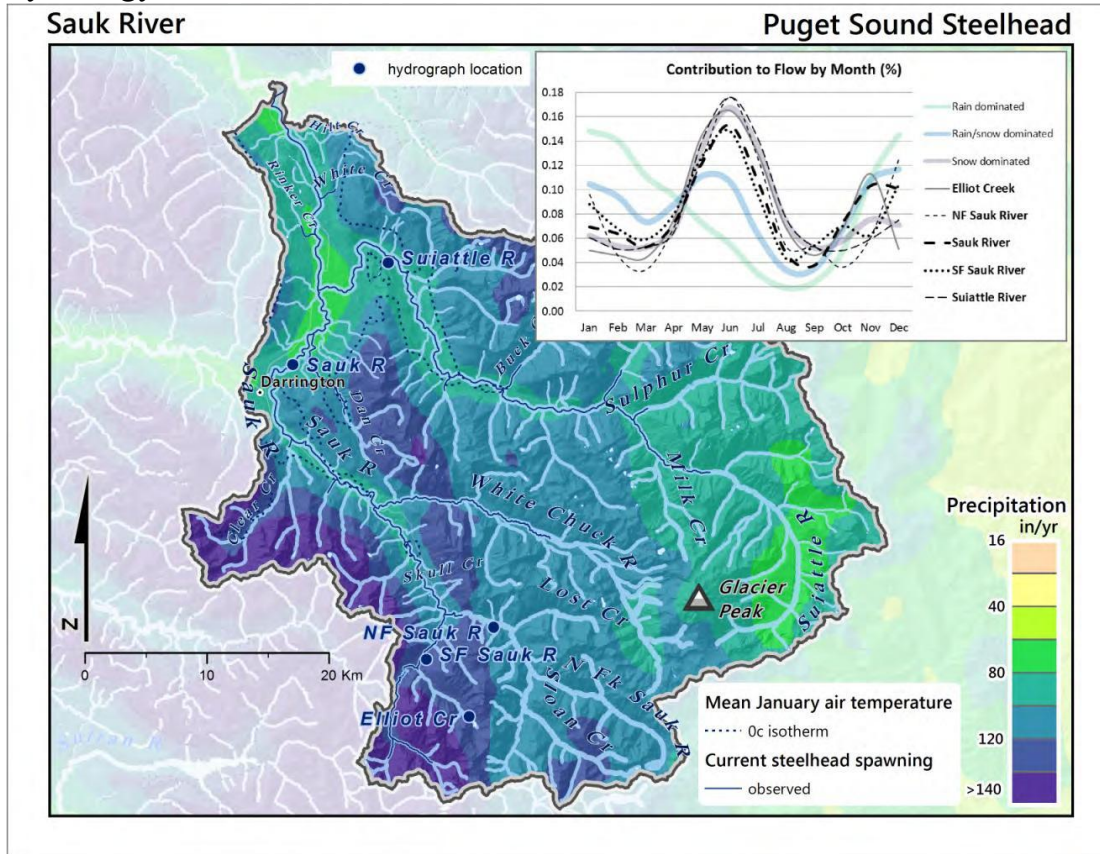
Sauk River Winter Run				Total Releases	
Watershed	Duration	Years	Source	(w/i DPS)	(o/s DPS)
Sauk R	95-08	14	Skagit/Stilli (CC)		323,918
			Total	0	0

Sauk River Summer Run				Total Releases	
Watershed	Duration	Years	Source	(w/i DPS)	(o/s DPS)
			Total	0	0

Spatial Structure

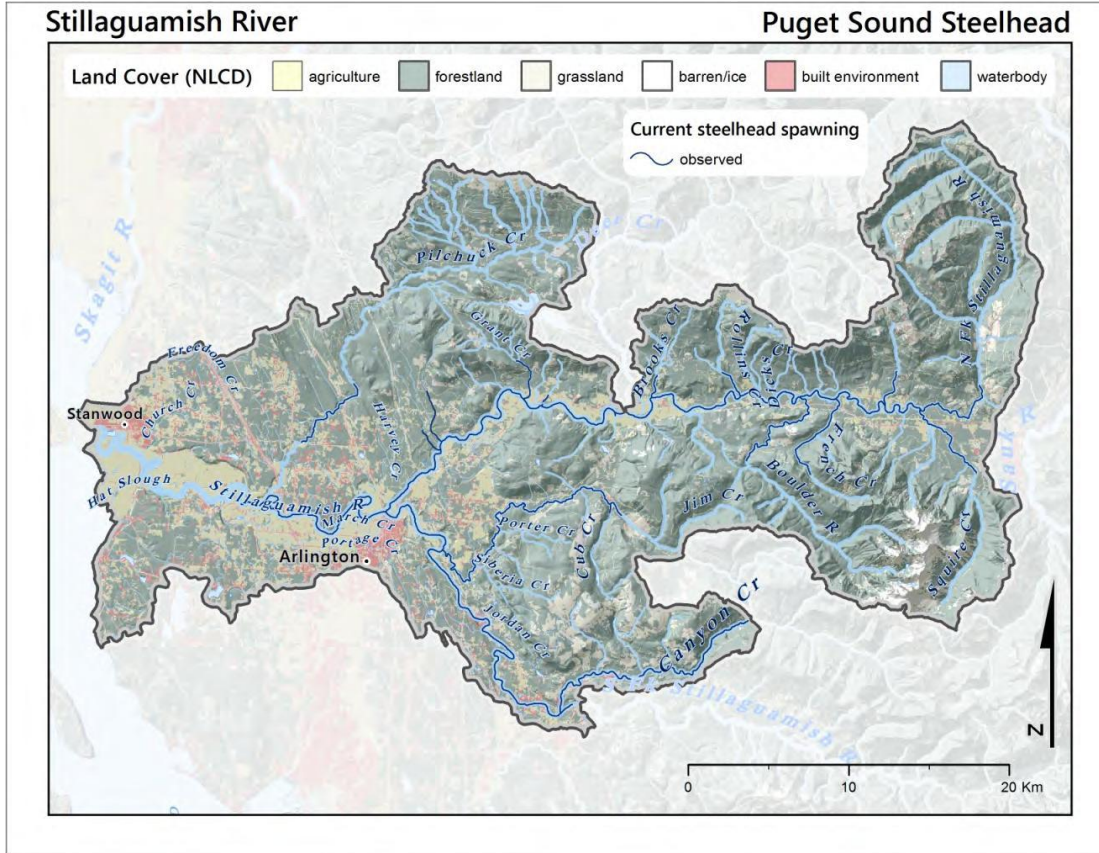


Hydrology



9. Stillaguamish River Winter Run

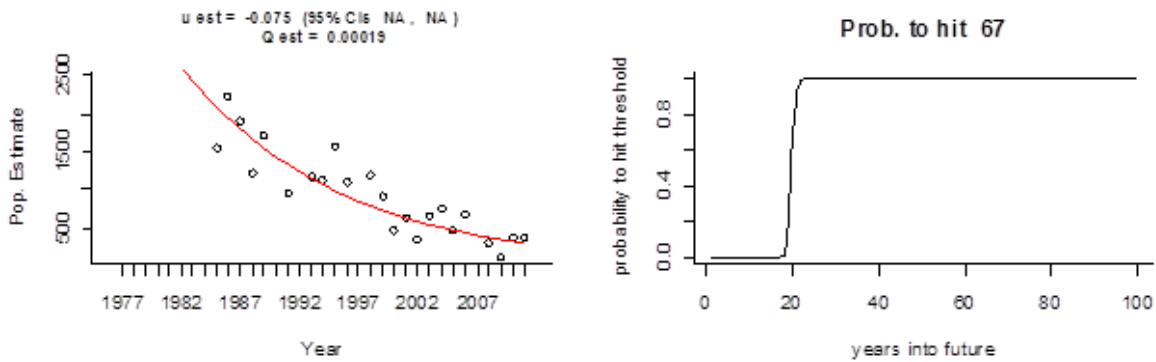
Overview: Winter run steelhead spawn in the mainstem North and South Forks of the Stillaguamish River and in numerous tributaries. Winter run steelhead are considered distinct from the summer run steelhead that spawn in Deer Creek and Canyon Creek above flow barriers because of the likely geographic and temporal separation of spawners.



Abundance and Productivity

	WDF Survey	Punch Card Max	Geometric Mean	IP Estimate
Abundance	Large and Medium	1,564	327 (100 - 1067)	19,118 38,236
Year	1930	1954	2005-2009	

Population	Exp. trend ln(nat. spawners) (95% CI) (1985-2000)
Stillaguamish River winter-run	0.910 (0.887 - 0.934)



Diversity

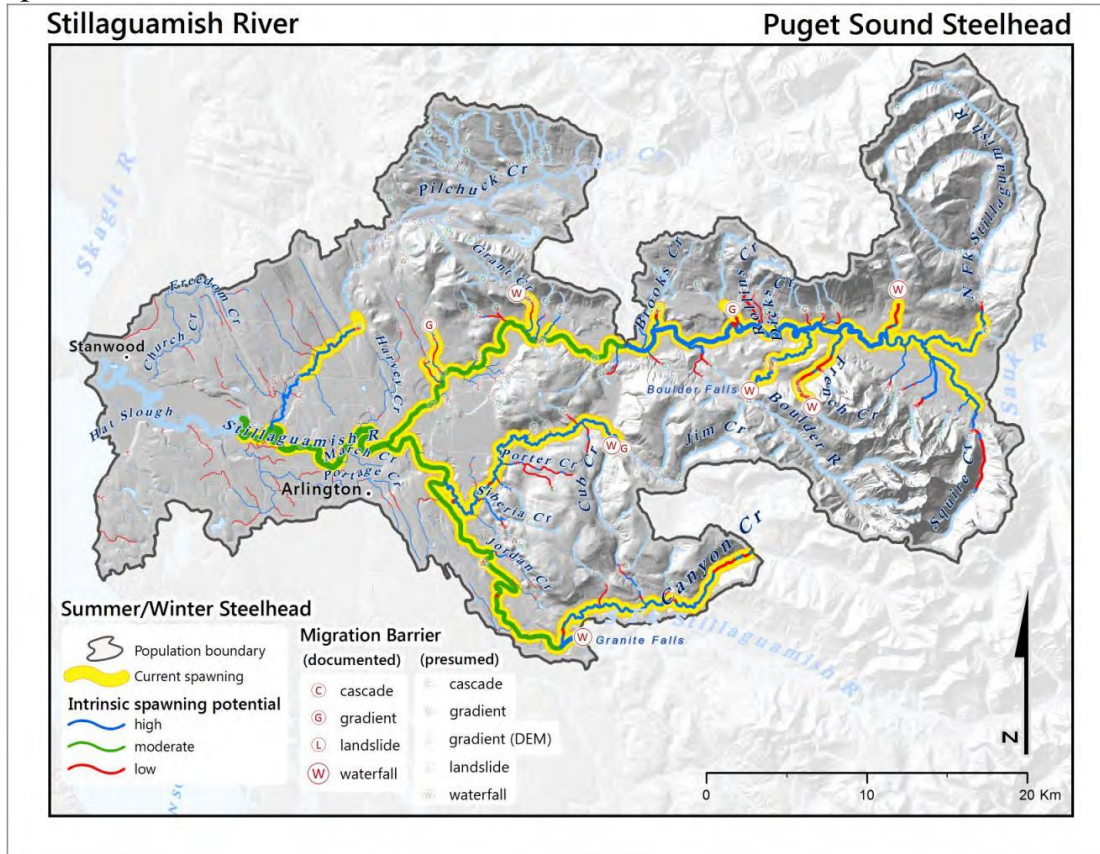
Hatchery Releases – Winter Releases

Stillaguamish River Winter Run				Total Releases	
Watershed	Duration	Years	Source	(w/i DPS)	(o/s DPS)
Canyon Cr	95-03	9	Chambers/Tokul/Sky (CC)		132,365
Johnson Cr	96-01	3	Chambers/Stilli		35,267
Pilchuck Cr	95-09	12	Chamber/Snohomish/ (CC)		117,045
Stillaguamish R	95-11	17	Chambers/Bogachiel/ (CC)		2,048,991
			Total	0	0

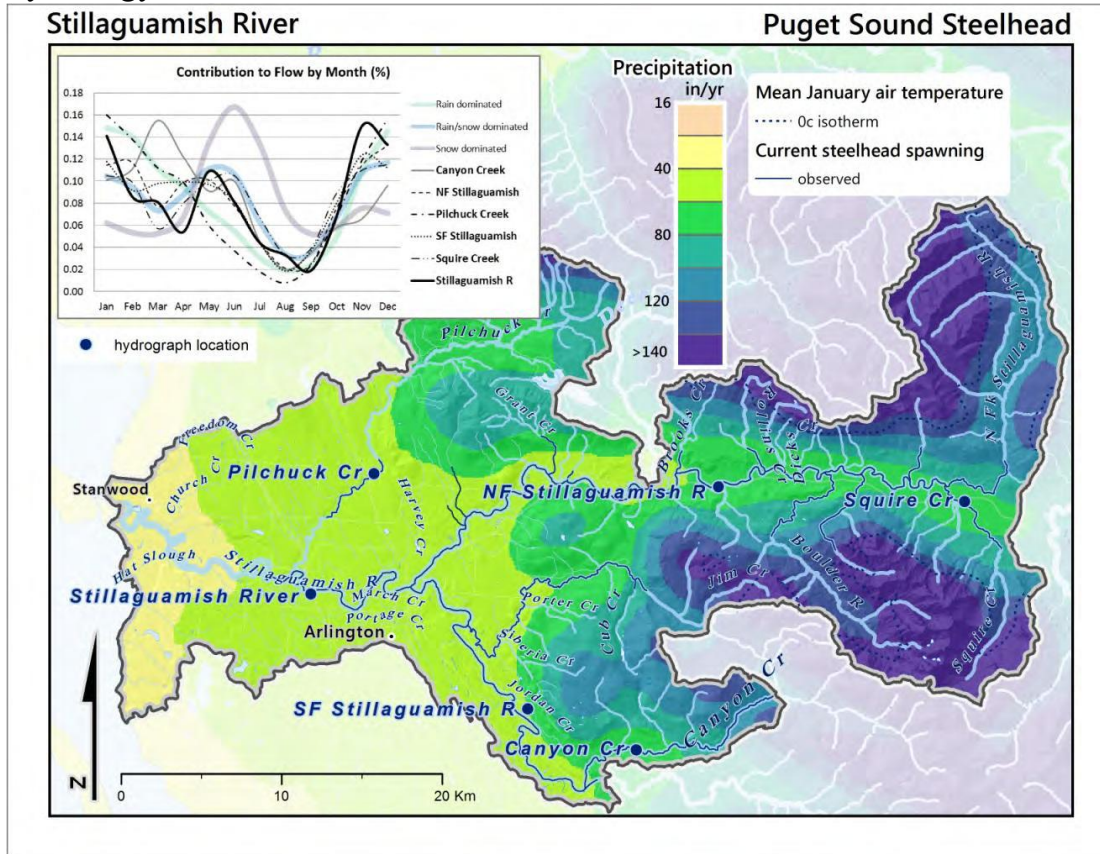
Hatchery Releases – Summer Releases

Stillaguamish River Summer Run				Total Releases	
Watershed	Duration	Years	Source	(w/i DPS)	(o/s DPS)
Stillaguamish R	98-05	5	Snohomish H. (SK)		178,558
NF Stillaguamish R	95-11	16	Stilla/Snohomish H. (SK)		1,077,547
			Total	0	0

Spatial Structure

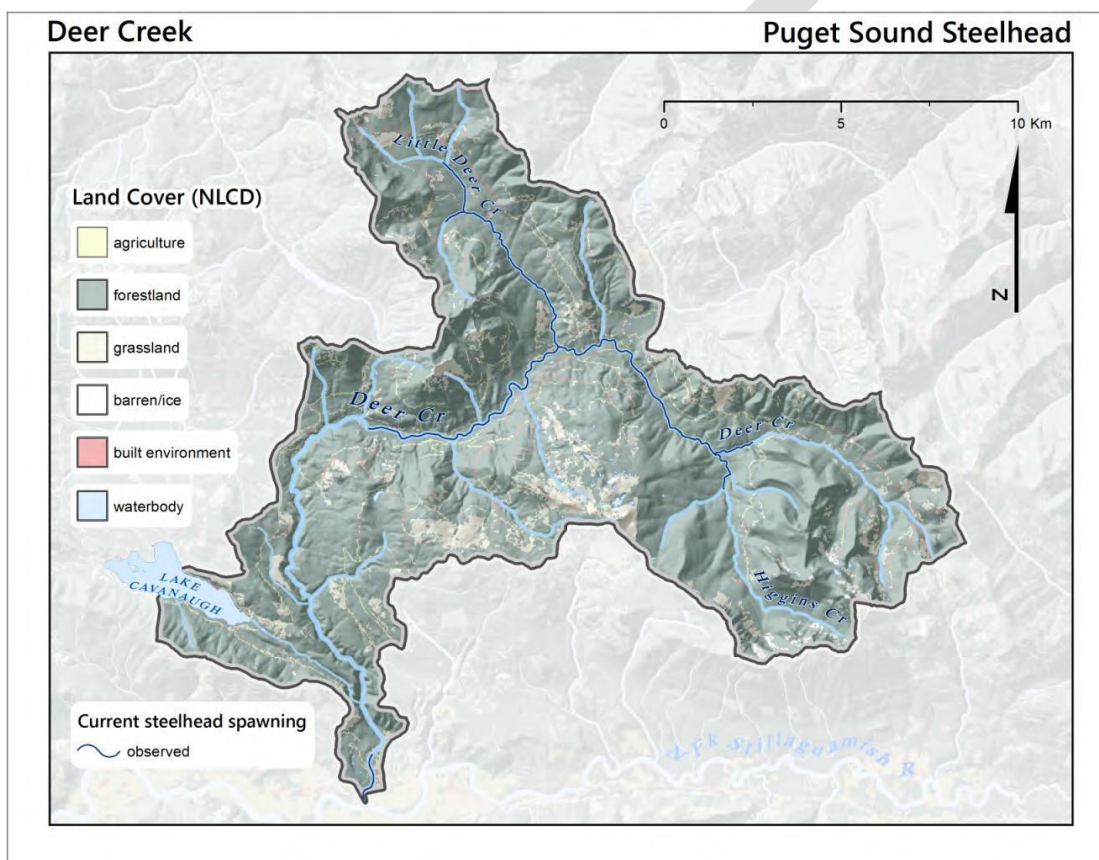


Hydrology



10. Deer Creek Summer Run

Overview: The Deer Creek summer-run steelhead population spawns and rears in the upper portion of Deer Creek. Steep canyons and cascades from Rkm 2.5 to 8 may present a temporal barrier to returning winter-run fish, although Deer Creek is accessible to summer steelhead up to approximately Rkm 32. Even under pristine conditions, the steelhead run into Deer Creek may not have been very large potentially 1,000 to 2,000 adults (WSCC 1999), although the 1929 survey classified Deer Creek as a large population (WDFG 1932).



Abundance and Productivity

	WDF Survey	Punch Card Max	Escapement	IP Estimate	
Abundance	Large	NA	460	1,572	3,144
Year	1930		1994		

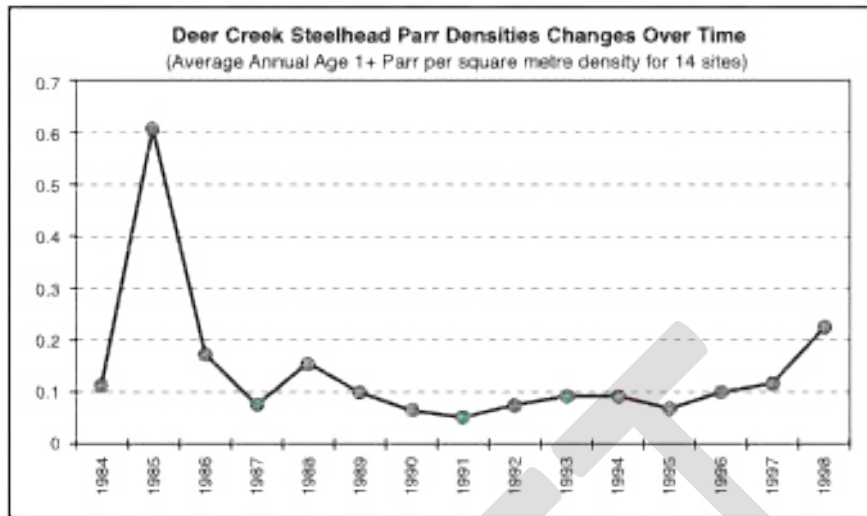


Figure 4. Deer Creek steelhead parr densities.

Kraemer, C. 1999. Management Brief: 1999 Update on the Status of the Deer Creek Summer Steelhead. Draft. Washington Dept. of Fish and Wildlife, Olympia, WA.

Diversity

Hatchery Releases: 1995 - Present

Deer Creek Summer Run				Total Releases	
Watershed	Duration	Years	Source	(w/i DPS)	(o/s DPS)
			Total	0	0

Some Skamania Hatchery summer-run steelhead were released in the 1950-1970s, although there was thought to be little influence on the population.

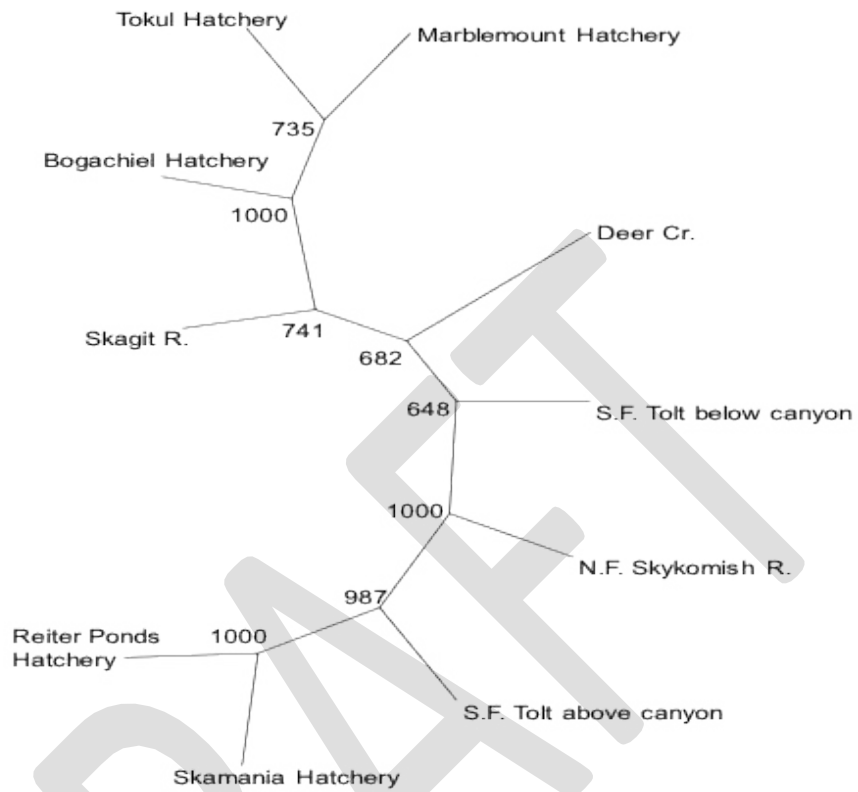
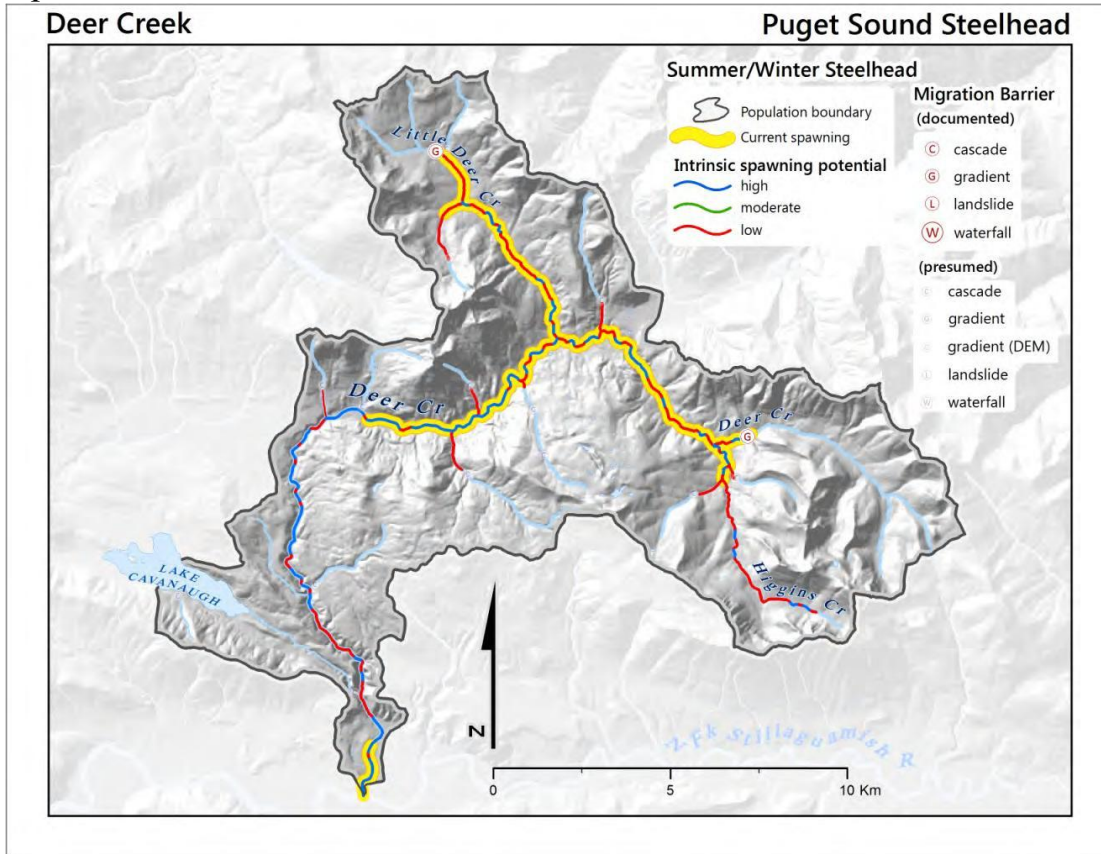


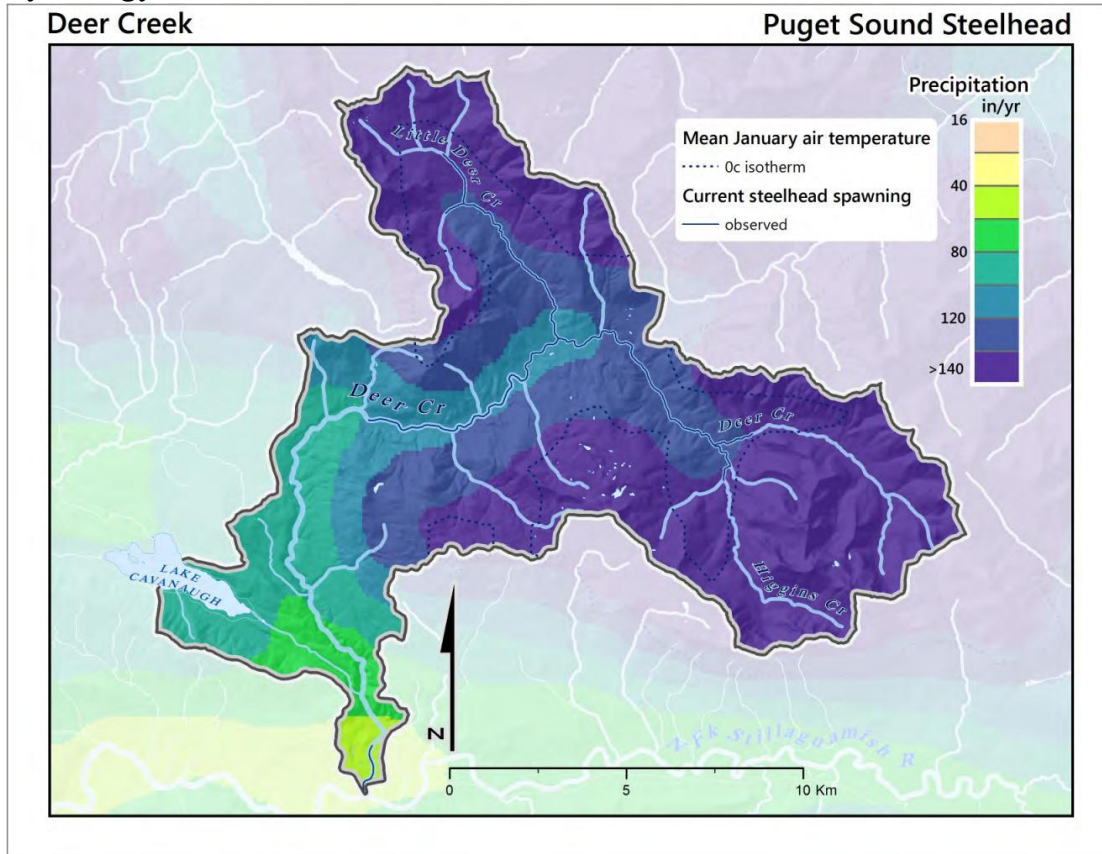
Figure 5. Genetic relationship of steelhead collections from the Snohomish River basin, Puget Sound, and Skamania Hatchery using Cavalli-Sforza and Edwards (1967) chord distance. Bootstrap values are shown at each node.

Figure from Kassler and Bell (2011).

Spatial Structure

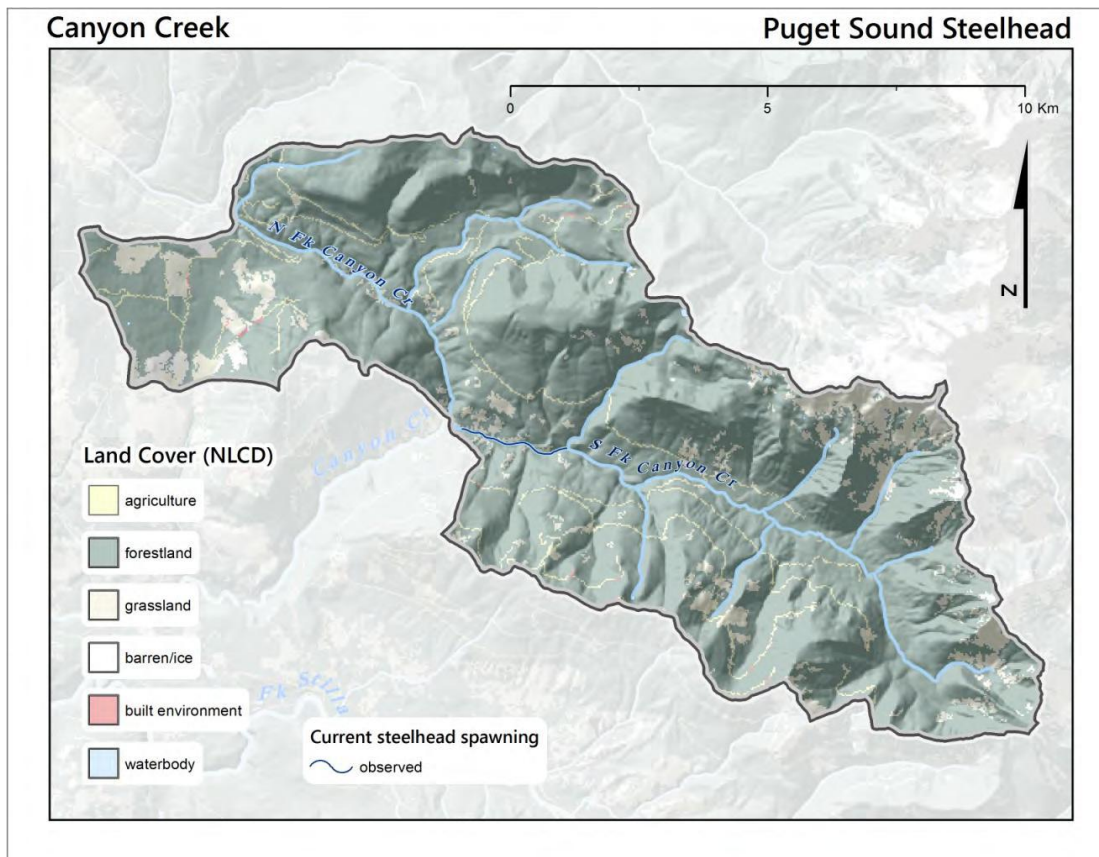


Hydrology



11. Canyon Creek Summer Run

Overview: There is relatively little information available on the existing summer run of steelhead in the Canyon Creek Basin. Information provided by local biologists indicates that a summer-run is still present in the basin. Historically, Canyon Creek was identified as having a relatively good-sized run of steelhead.



Abundance and Productivity

	WDF Survey	Punch Card Max	Geometric Mean	IP Estimate	
Abundance	Large	283*		121	243
Year	1930	1951			

* - Punch card based catch estimates did not differentiate between run times prior to 1960.

Diversity

Hatchery Releases – Winter Releases

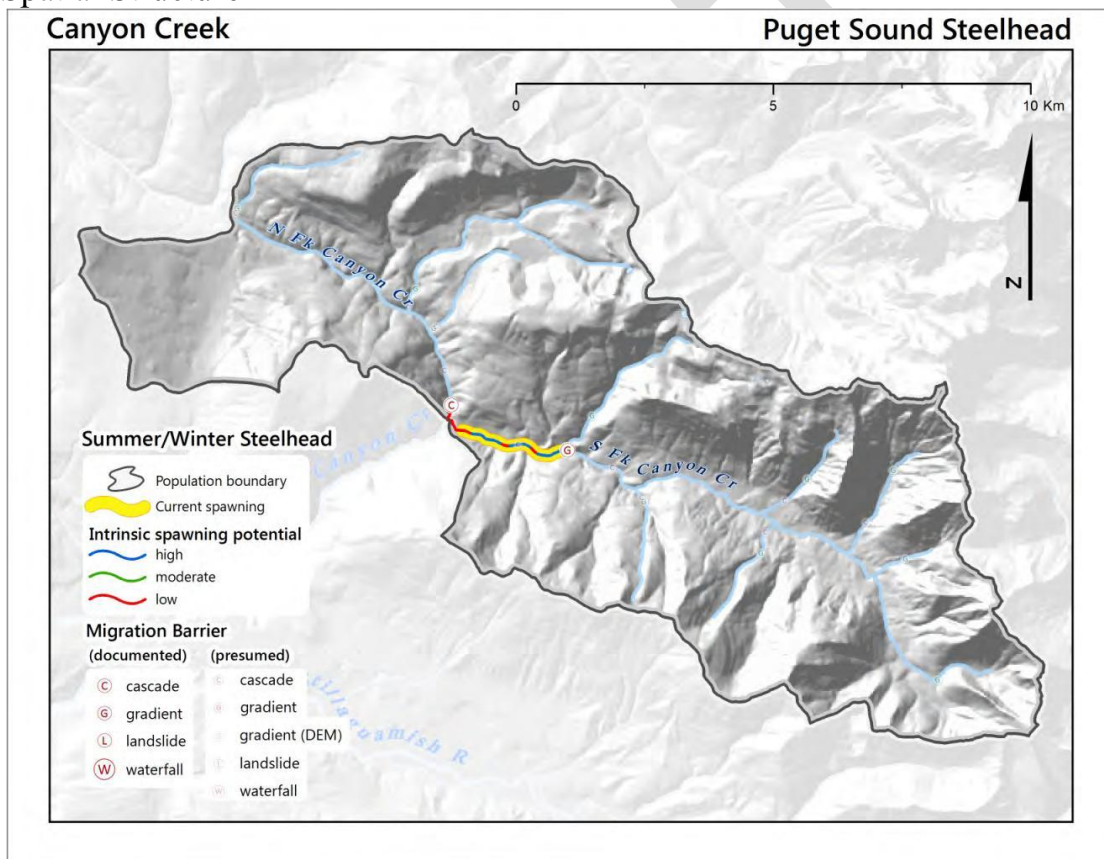
Canyon Creek Summer Run				Total Releases	
Watershed	Duration	Years	Source	(w/i DPS)	(o/s DPS)

			Total	0	0

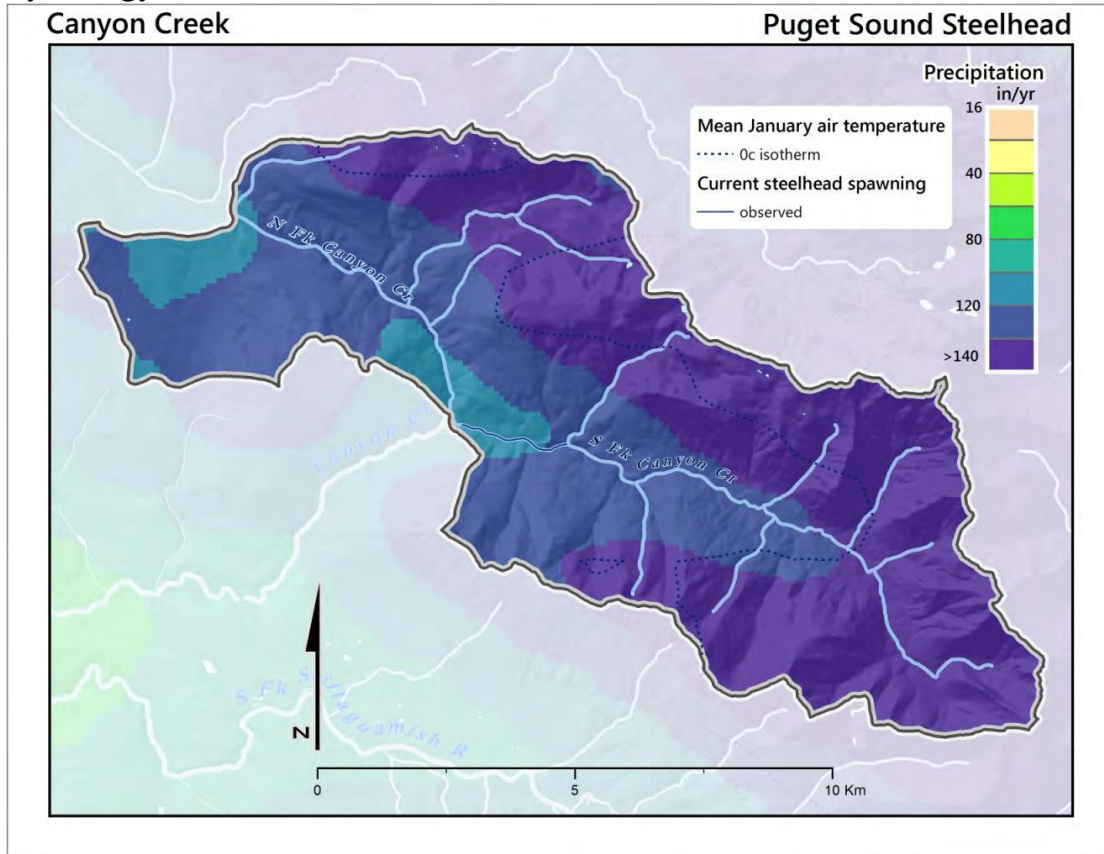
Hatchery Releases – Summer Releases

Canyon Creek Summer Run				Total Releases	
Watershed	Duration	Years	Source	(w/I DPS)	(o/s DPS)
Canyon Cr	95-08	5	Skykomish/Snohomish H. (SK)		40.596
			Total	0	0

Spatial Structure

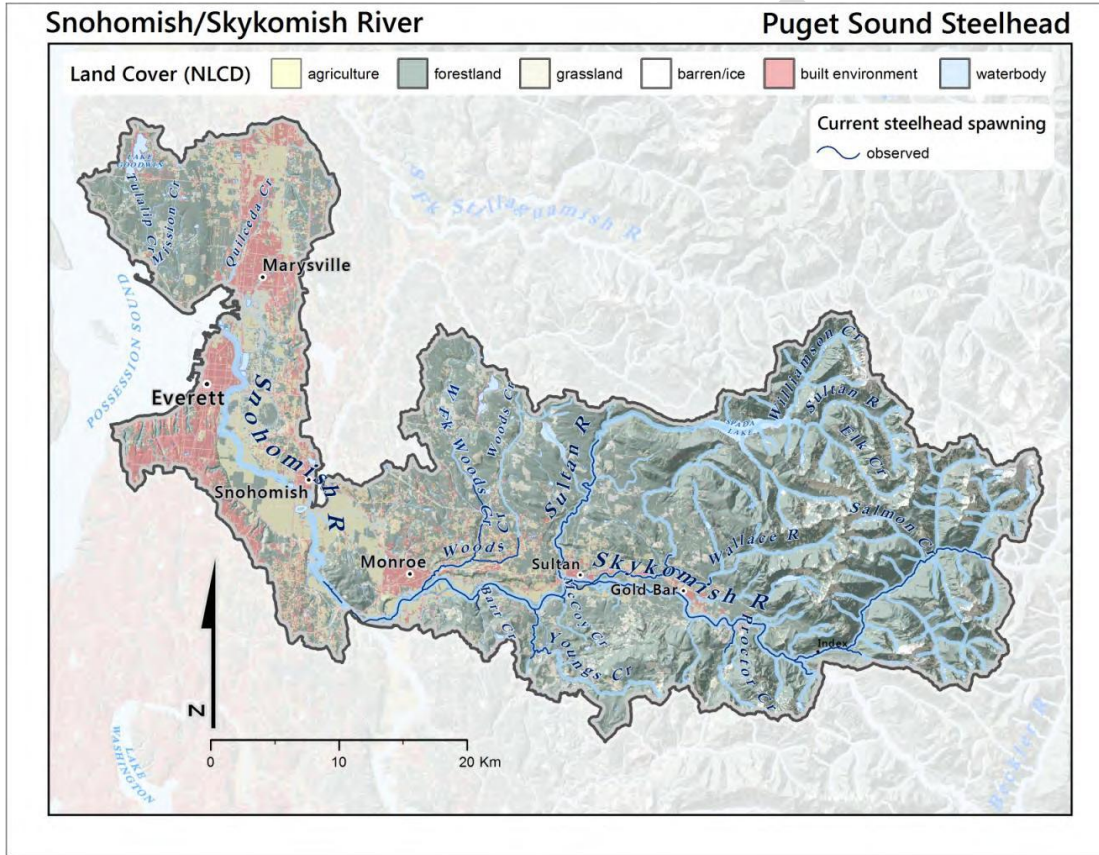


Hydrology



12. Snohomish/Skykomish River Winter Run

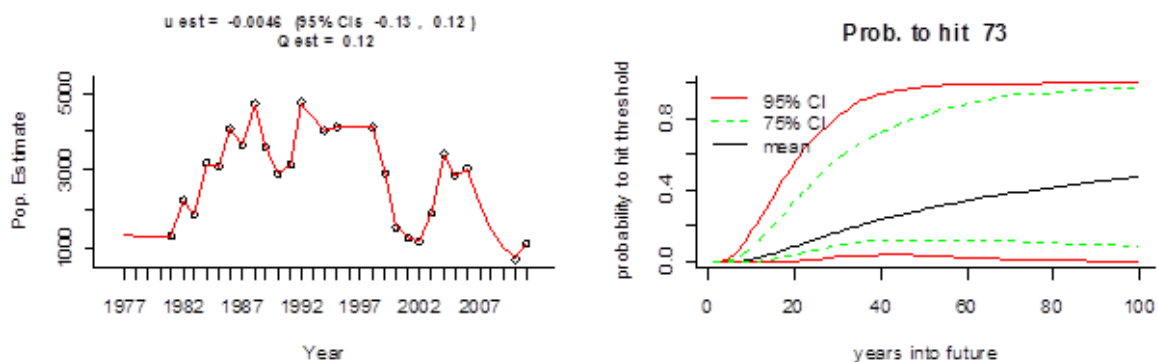
Overview: This population includes winter-run steelhead in the mainstem Snohomish, Skykomish, and Wallace Rivers, in the North Fork Skykomish River below Bear Creek Falls, in the Sultan River, and in several tributaries. WDFW (2003) identified three winter-run populations in the Snohomish Basin based on geographic discreteness. This basin includes both lowland and higher elevation tributaries. Historically, it was one of the primary steelhead producers in Puget Sound.



Abundance and Productivity

	WDF Survey	Punch Card Max	Geometric Mean	IP Estimate
Abundance	Multiple Large and Medium	4,801	4573 (500 - 41865)	21,389 42,779
Year	1930	1951	2005-2009	

Population Snohomish River winter-run	Exp. trend ln(nat. spawners) (95% CI) 1985-2009 0.963 (0.941 - 0.985)
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Diversity

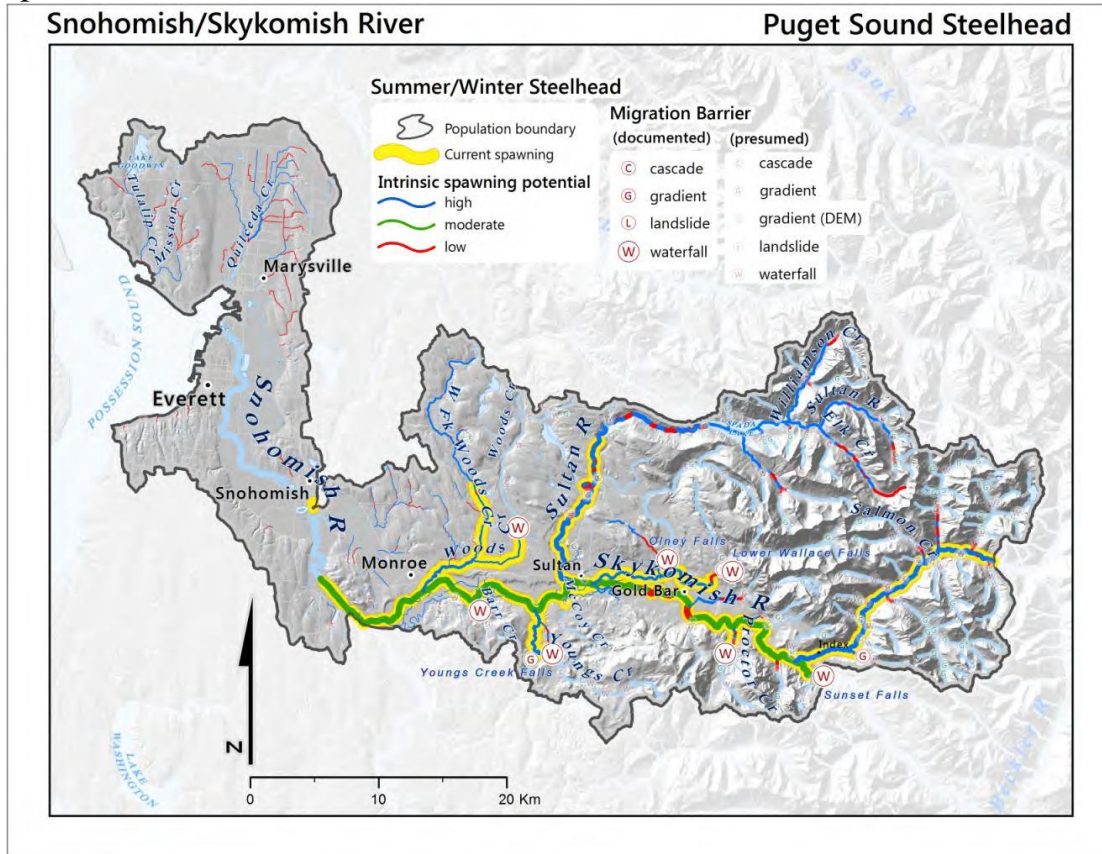
Hatchery Releases

Snohomish Skykomish River Winter Run				Total Releases	
Watershed	Duration	Years	Source	(w/I DPS)	(o/s DPS)
Howard Cr	97-01	6	Tokul/Snohomish (CC)		173,317
Skykomish R	95-11	17	Chambers/Tokul (CC)		2,464,540
Sultan R	95-09	15	Chambers/Tokul (CC)		344,781
Wallace R	95-11	17	Chambers/Tokul (CC)		309,863
			Total	0	0

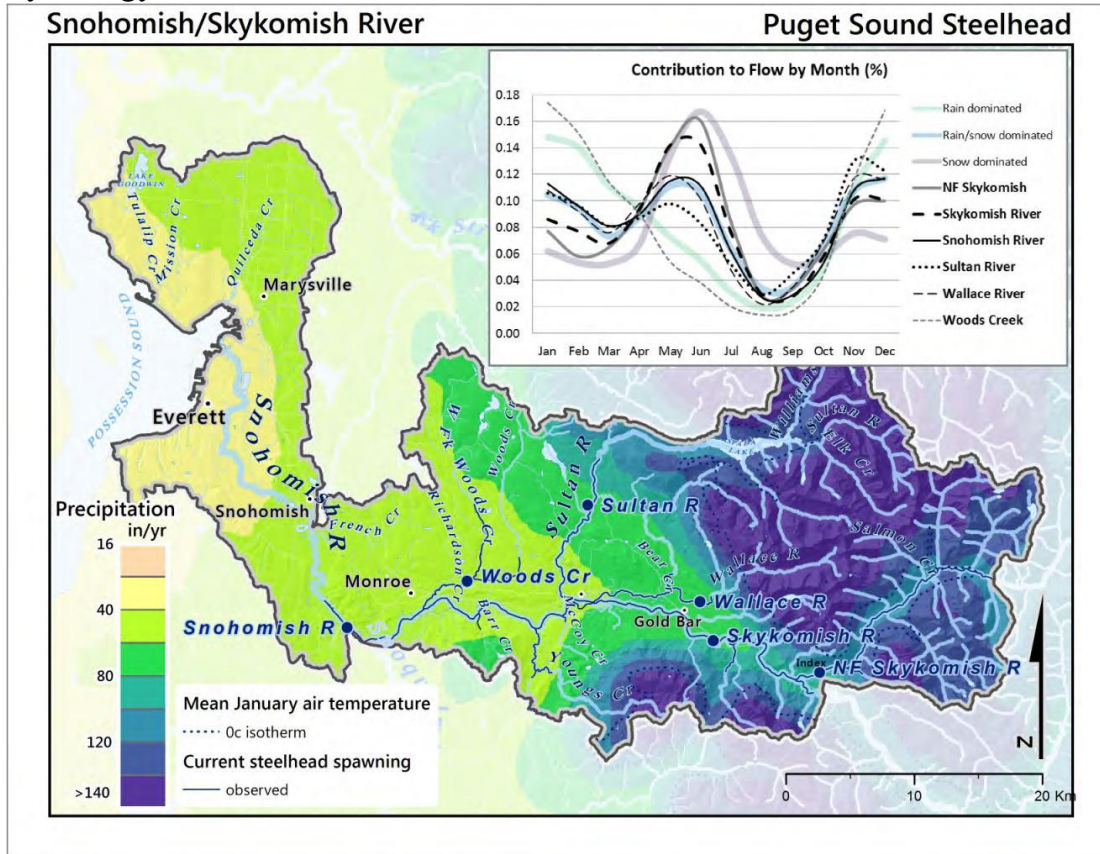
Hatchery Releases – Summer Run

Snohomish Skykomish River Winter Run				Total Releases	
Watershed	Duration	Years	Source	(w/i DPS)	(o/s DPS)
Silver Cr	98-99	2	Snohomish H (SK)		19,334
Index Cr	00	1	Snohomish H (SK)		16,300
Skykomish R	95-11	16	Sky/Snohomish H. (SK)		2,400,055
Sultan R	95-09	15	Sky/Snohomish H (SK)		266,980
			Total	0	0

Spatial Structure

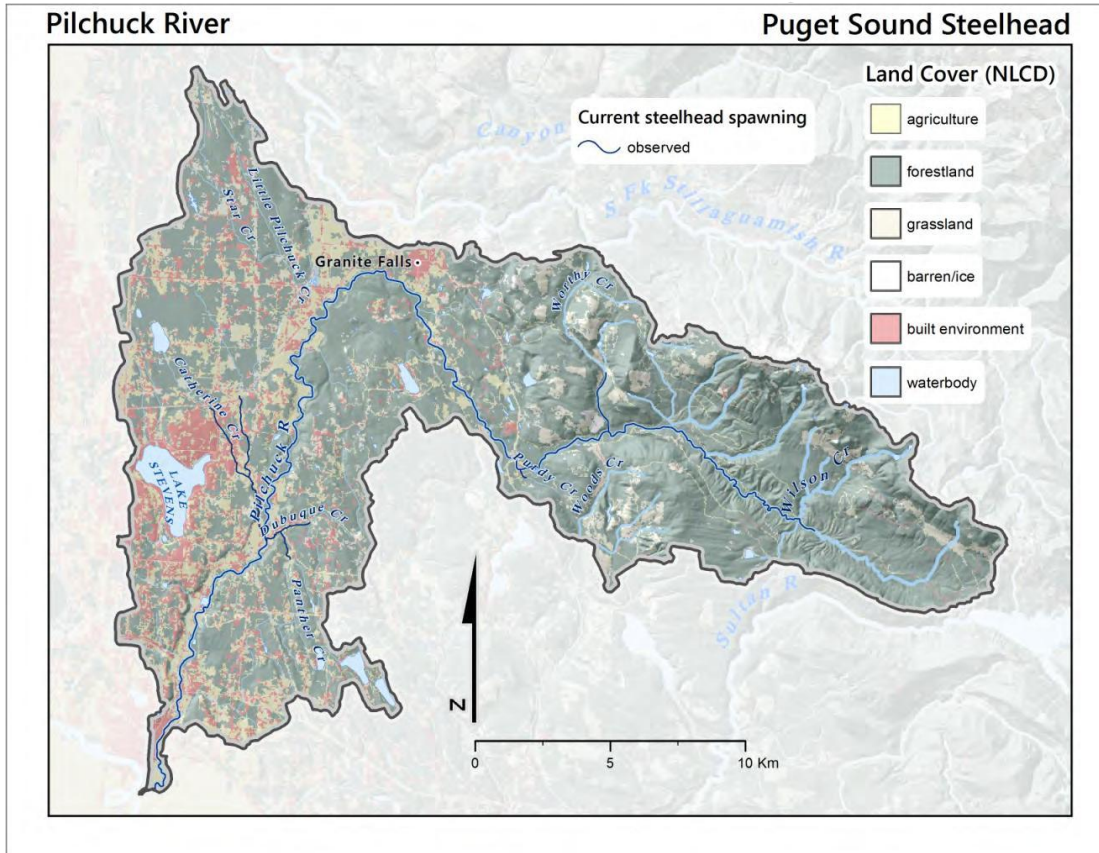


Hydrology



13. Pilchuck River Winter Run

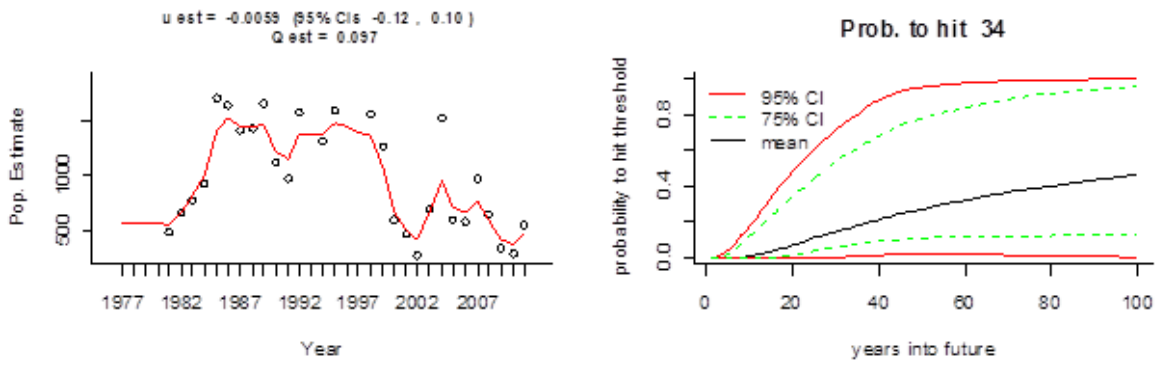
Overview: The Pilchuck River flows through the Northern Cascades and Puget Lowlands Ecoregions. The basin is relatively low gradient and low altitude and exhibits a rainfall dominated flow pattern. There appears to be sufficient habitat (366 km²) to support a sustainable population. The TRT noted that run timing for this DIP was significantly earlier than other populations in the greater Snohomish Basin, providing further confirmation of its DIP status.



Abundance and Productivity

	WDF Survey	Punch Card Max	Geometric Mean	IP Estimate
Abundance	Large	1,583	469.81	5,193 10,386
Year		1952	2006-2010	

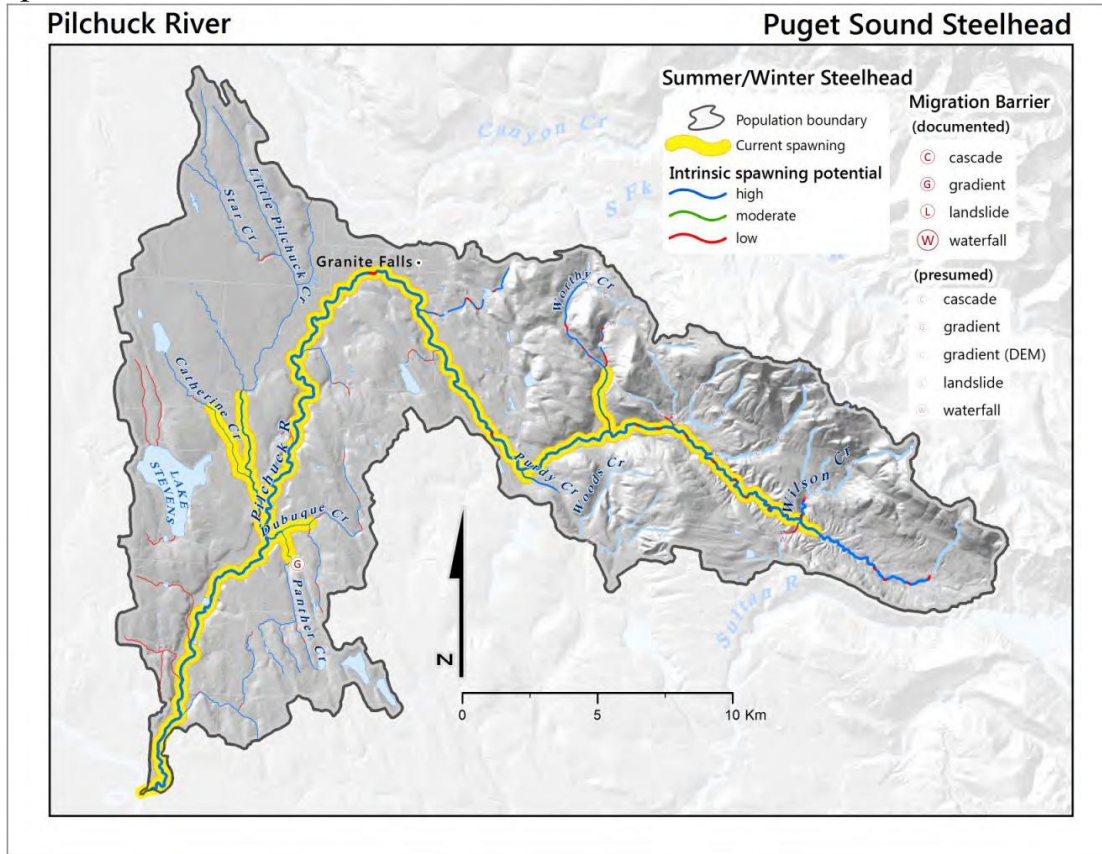
Tributary	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010
Pilchuck	462	279	696	1522	604	580		646	344	294



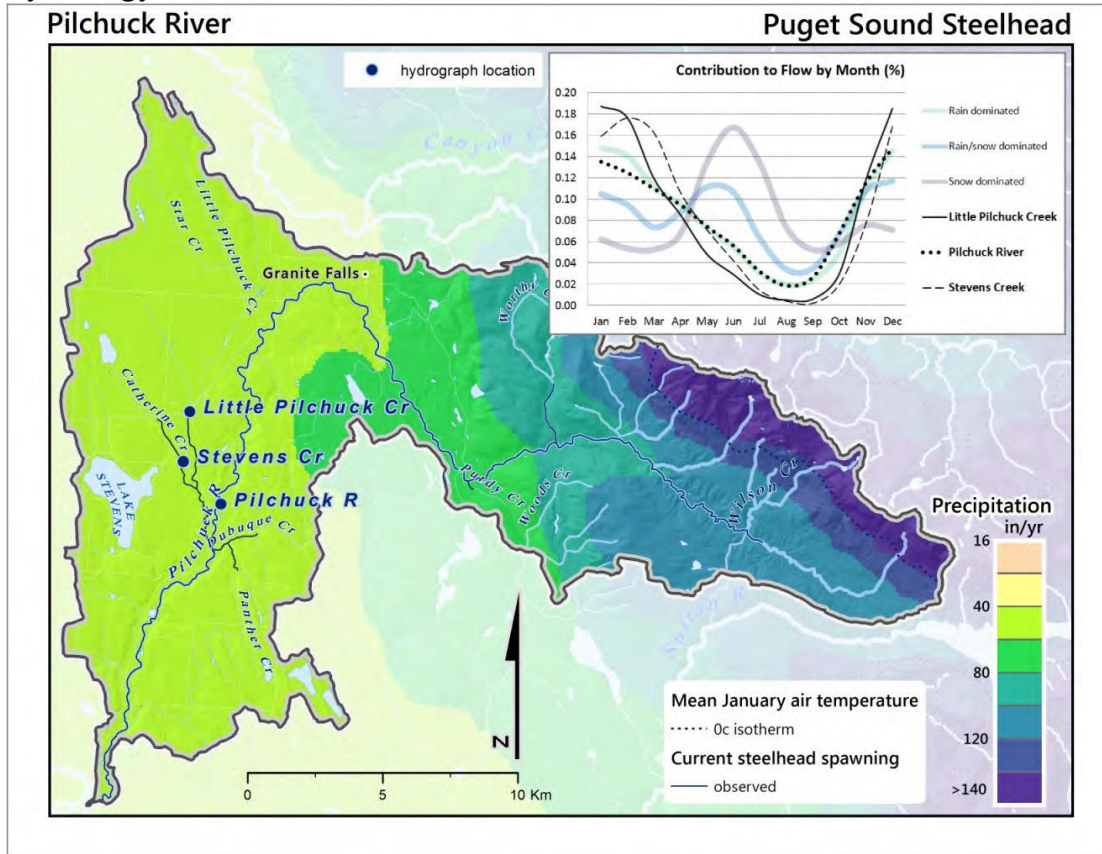
Diversity
Hatchery Releases

Pilchuck River Winter Run				Total Releases	
Watershed	Duration	Years	Source	(w/i DPS)	(o/s DPS)
Pilchuck R	95-09	15	Tokul/Stilli/Skagit (CC)		390,193
			Total	0	0

Spatial Structure

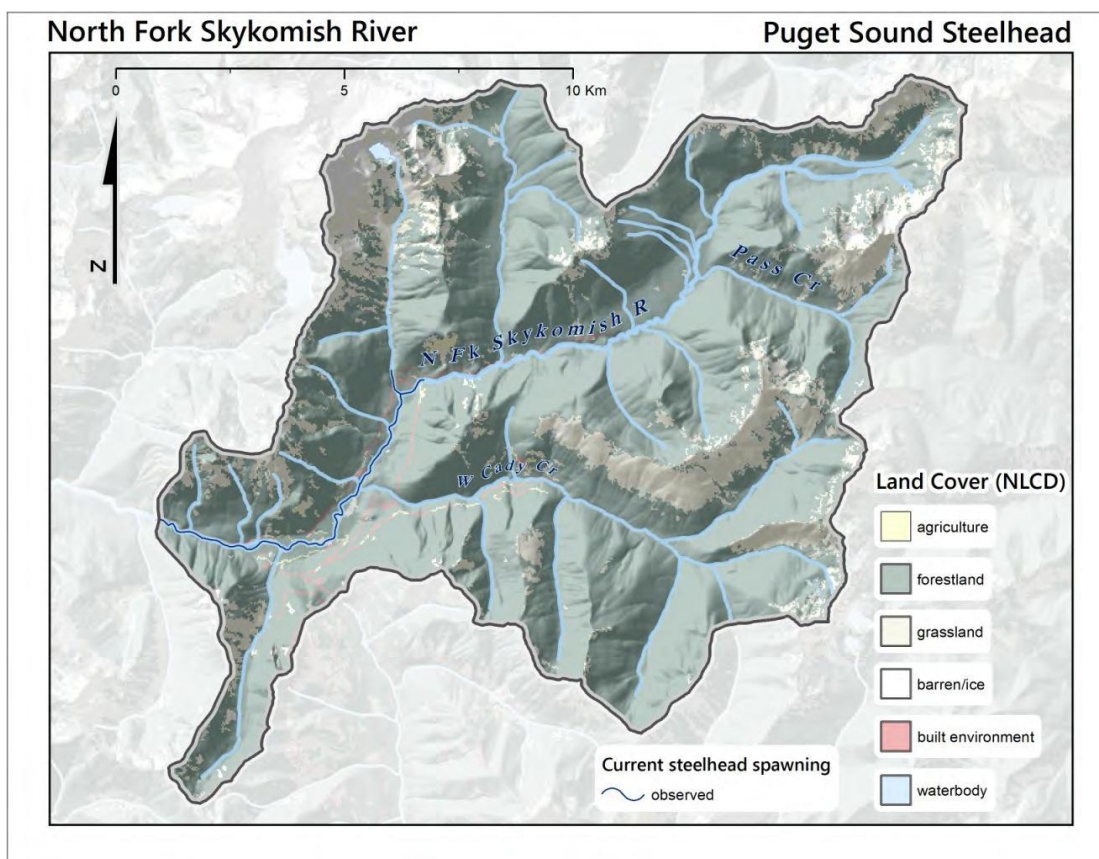


Hydrology



14. North Fork Skykomish River Summer Run

Overview: Summer-run steelhead in the North Fork Skykomish River spawn primarily above Bear Creek Falls (Rkm 21) (WDFW 2005). There is limited spawning habitat above these falls, and accessible habitat may terminate at Rkm 31 (Williams et al. 1975). Falls and cascades may provide some level of reproductive isolation from winter-run steelhead in the Skykomish River, but probably also limit population abundance.



Abundance and Productivity

	WDF Survey	Punch Card Max	IP Estimate
Abundance	Medium	229*	663 1,325
Year	1930	1963	

* Includes only summer-run fish caught in the North Fork and not those caught in the mainstem.

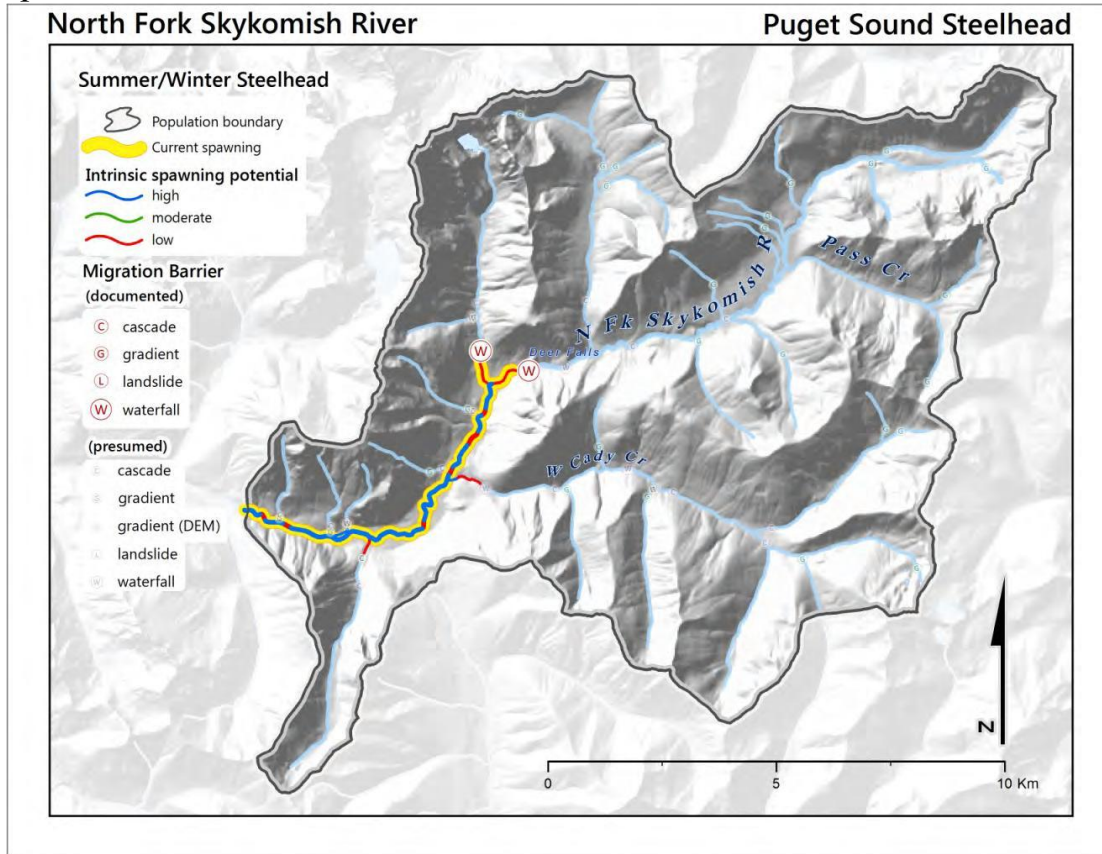
Diversity

Hatchery Releases – Summer Run

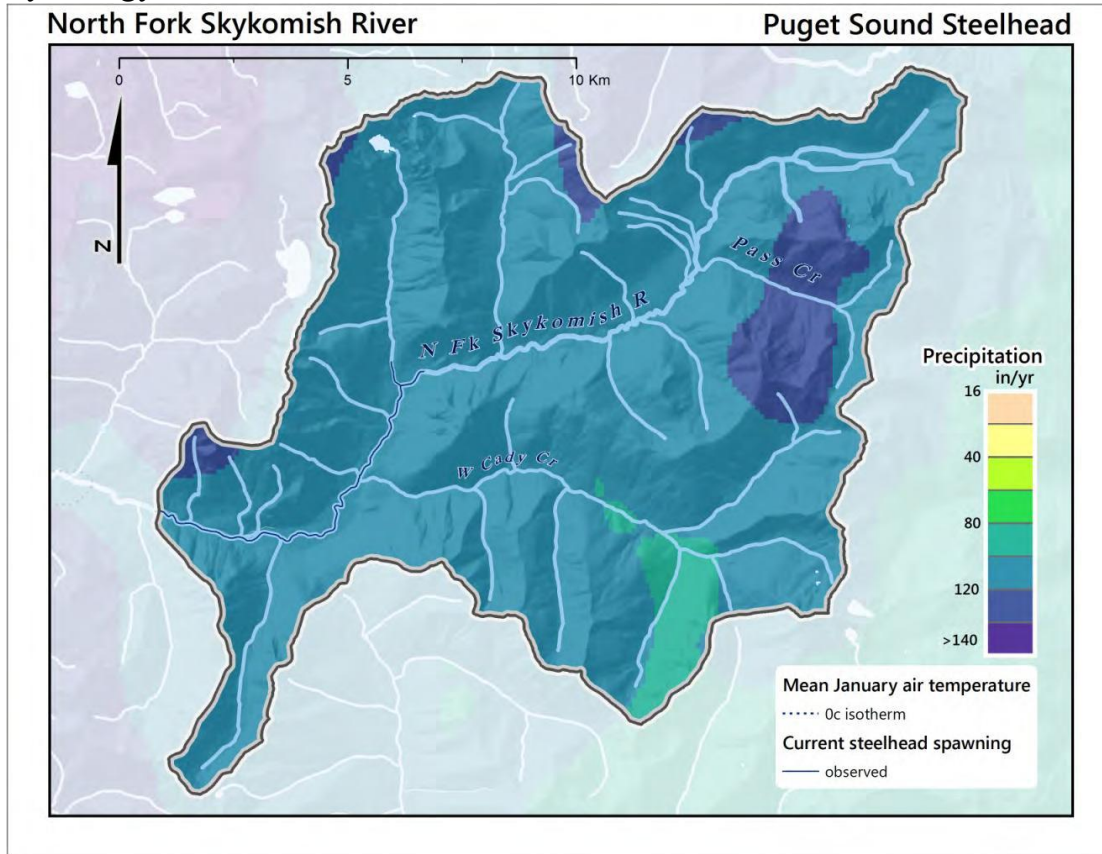
North Fork Skykomish River Summer Run				Total Releases	
Watershed	Duration	Years	Source	(w/i DPS)	(o/s DPS)

NR Skykomish R	96-06	(11)	Sky/Snohomish H (SK)		306,641
			Total		0

Spatial Structure

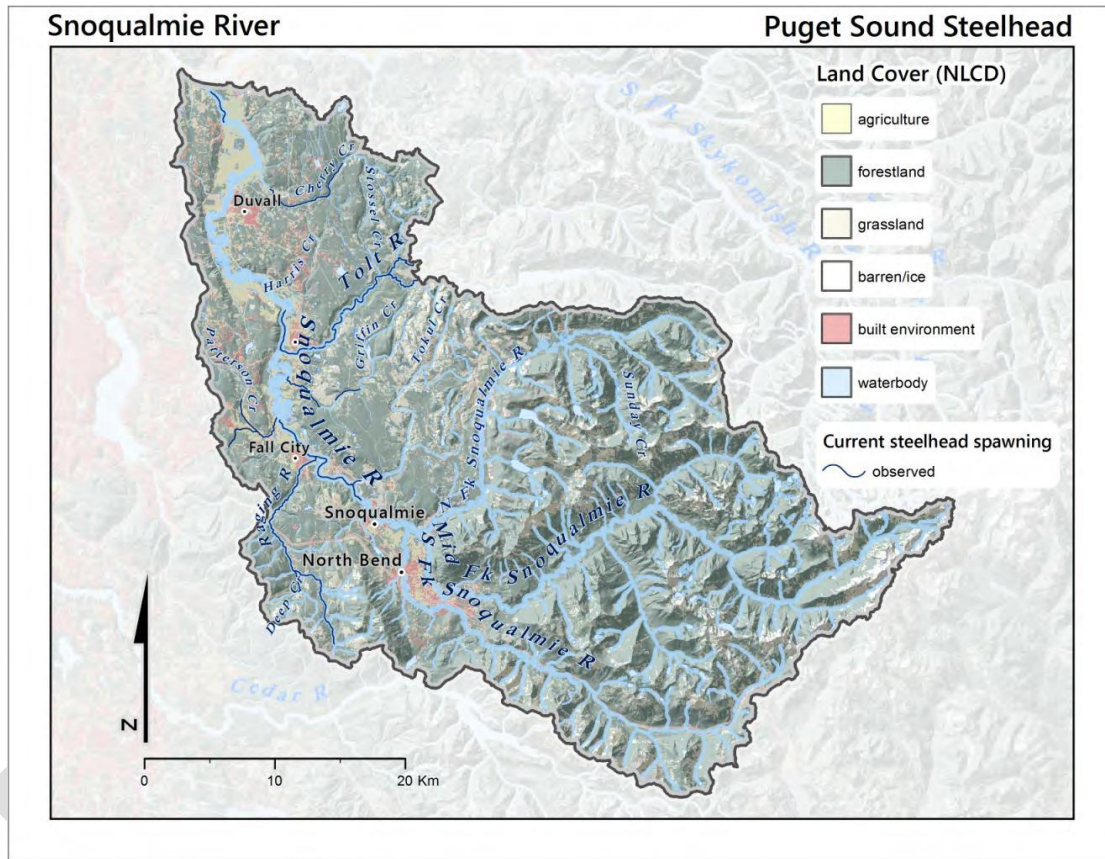


Hydrology



15. Snoqualmie River Winter Run

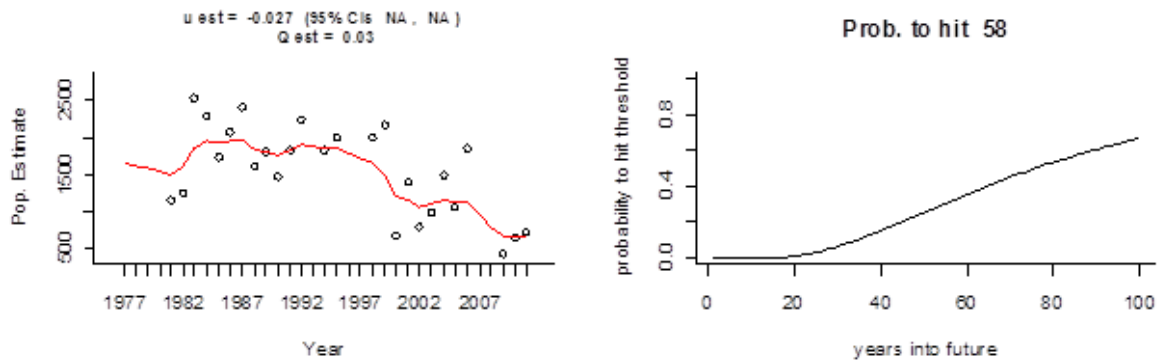
Overview: The Snoqualmie River winter-run steelhead DIP includes fish in the mainstem Snoqualmie River and those in major tributaries: Tolt, Raging, and Tokul creeks. There are numerous historical references indicating that this basin sustained large runs of steelhead.



Abundance and Productivity

	WDF Survey	Punch Card Max	Geometric Mean	IP Estimate
Abundance	Large and Medium	2,791	1092.06	16,740 33,479
Year	1930	1951	2005-2010	

Tributary	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010
Snoqualmie R	1395	789	988	1506	1060	1856				662



Diversity

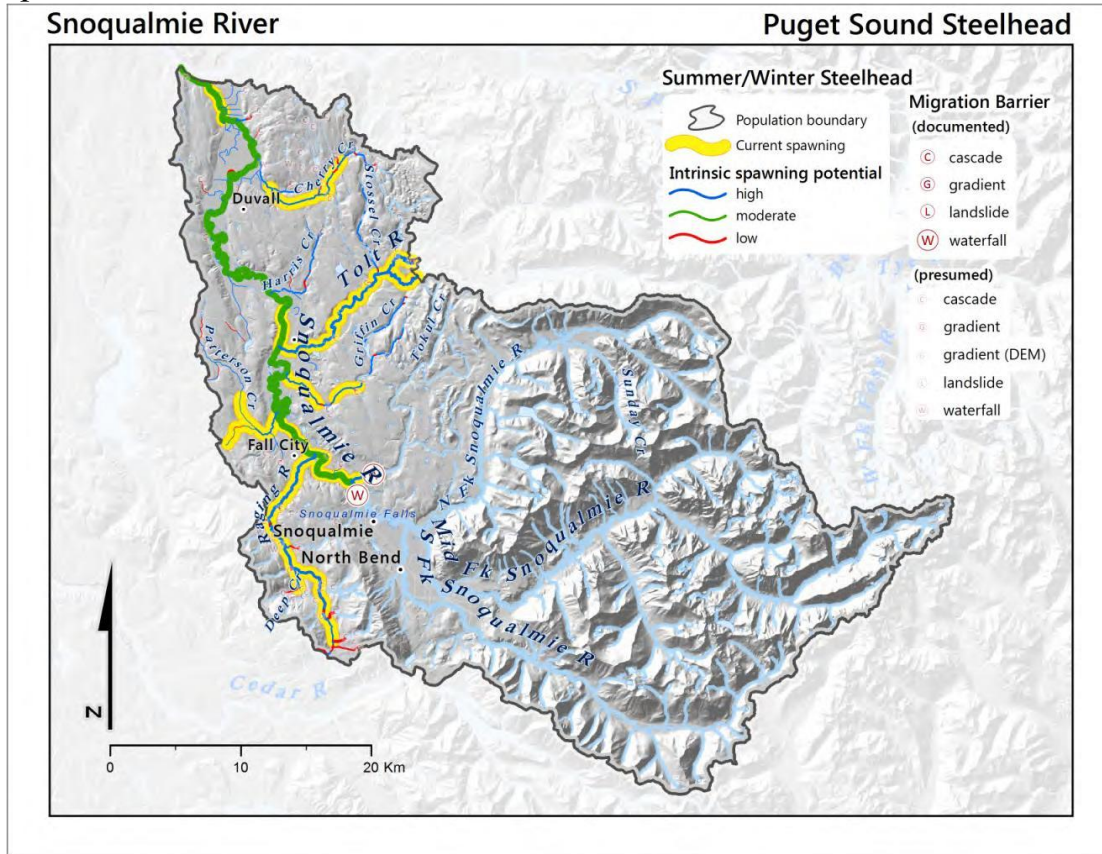
Hatchery Releases

Snoqualmie River Winter Run				Total Releases	
Watershed	Duration	Years	Source	(w/i DPS)	(o/s DPS)
Raging River	95-08	14	Tokul Cr. H. (CC)		206,934
Snoqualmie R	95-09	15	Tokul Cr. H. (CC)		2,290,994
Tokul Cr	09-11	3	Tokul Cr. H. (CC)		329,638
Tolt River	95-08	11	Tokul Cr. H./Reiter (CC)		246,776
			Total	0	0

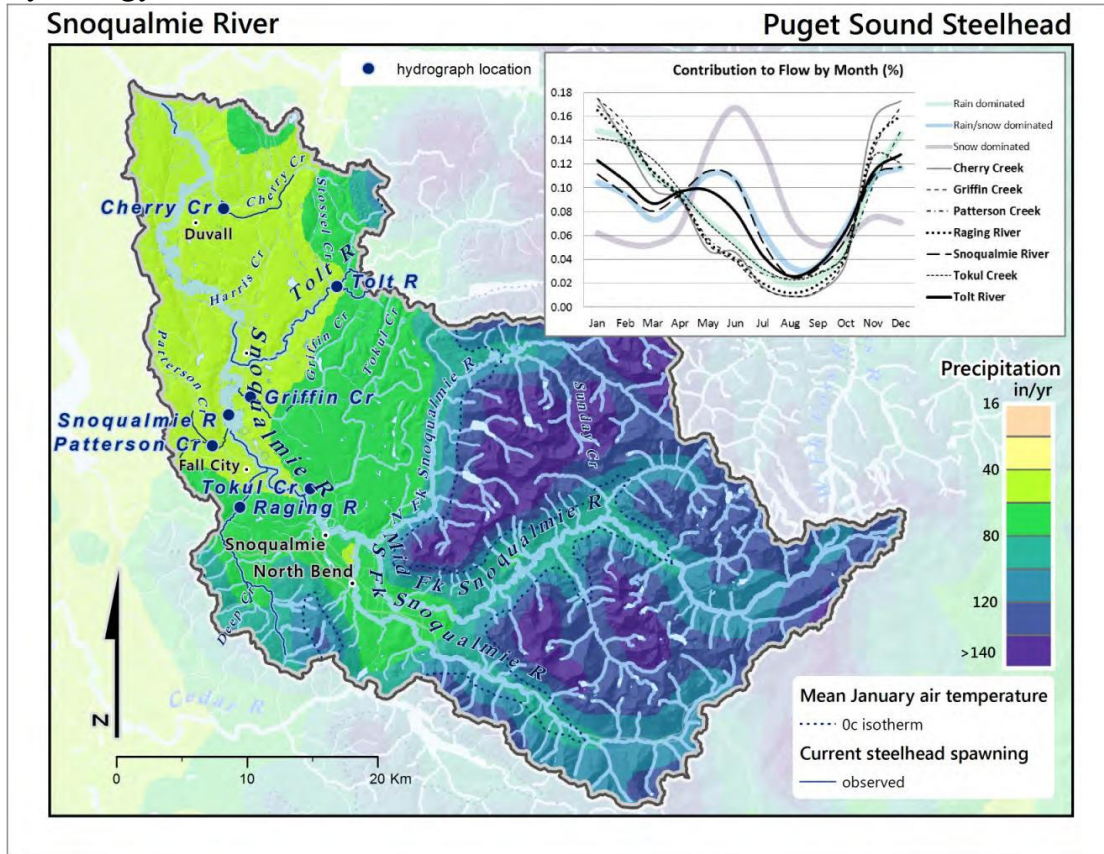
Hatchery Releases – Summer Run

Snoqualmie River Winter Run				Total Releases	
Watershed	Duration	Years	Source	(w/i DPS)	(o/s DPS)
Snoqualmie R	95-08	12	Sky/Snohomish H (SK)		494,660
Tokul Cr	01	1	Snohomish H (SK)		28,330
Raging River	99-07	6	Snohomish H (SK)		177,626
			Total	0	0

Spatial Structure

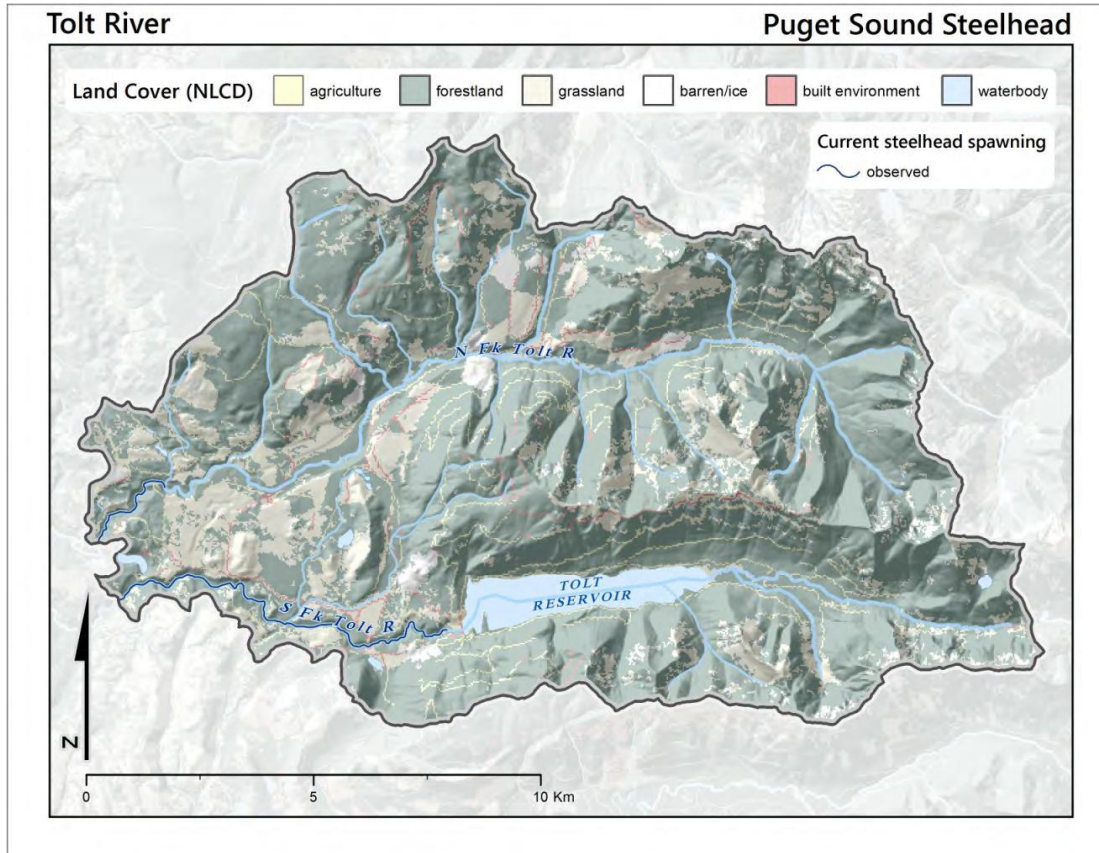


Hydrology



16. Tolt River Summer Run

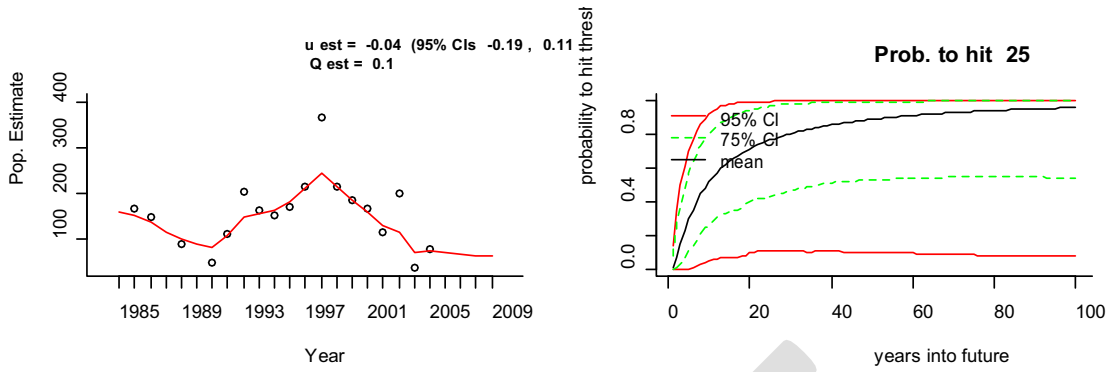
Overview: Summer-run steelhead are found in the North and South Fork Tolt River Basins. Both forks are typical of summer-run steelhead habitat and contain a number of falls and cascades, although the North Fork is higher gradient with steeply sloped canyon walls (Williams et al. 1975). Genetically, Tolt River steelhead are similar to other Snohomish Basin steelhead (Phelps et al. 1997).



Abundance and Productivity

	WDF Survey	Punch Card Max	Geometric Mean	IP Estimate
Abundance	Large and Medium	304*	78.64	321 641
Year	1930	1964	2005-2010	

* Includes only summer-run fish caught in the Tolt River and not those caught in the mainstem Snoqualmie or Snohomish rivers.

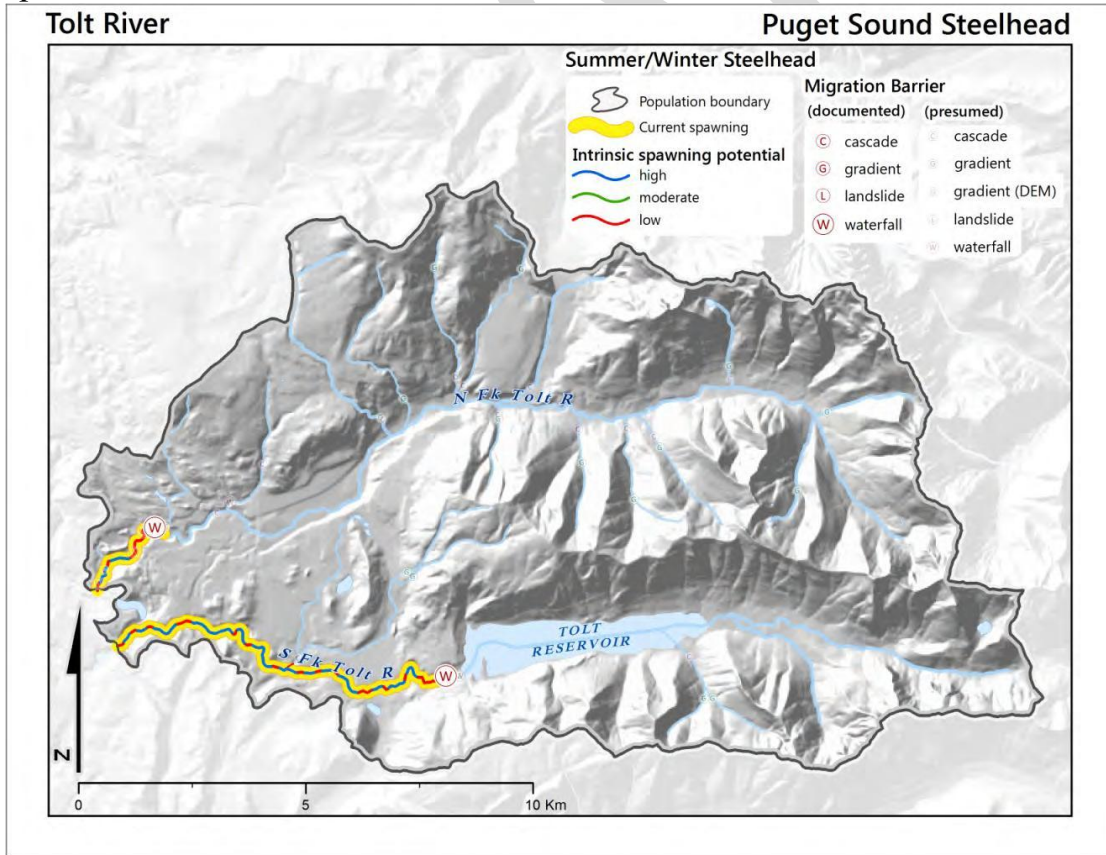


Diversity

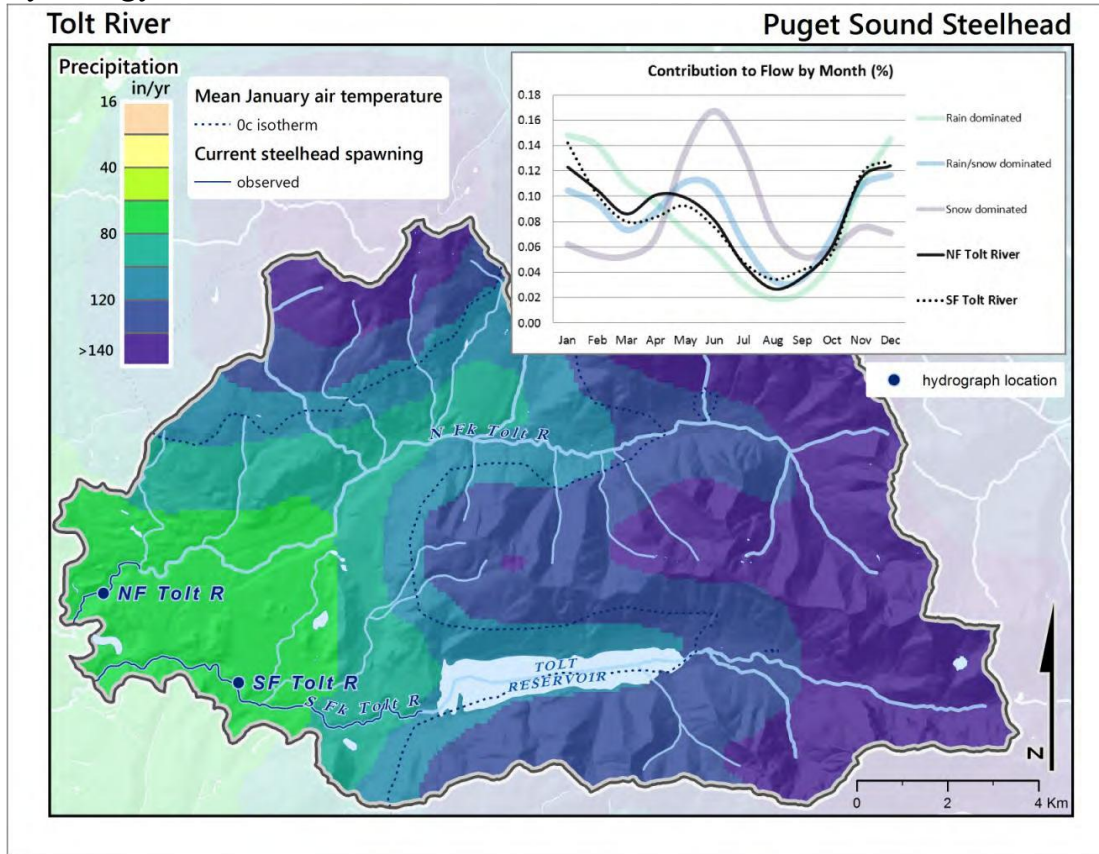
Hatchery Releases – Winter Run

Tolt River Summer Run				Total Releases	
Watershed	Duration	Years	Source	(w/i DPS)	(o/s DPS)
Total				0	0

Spatial Structure



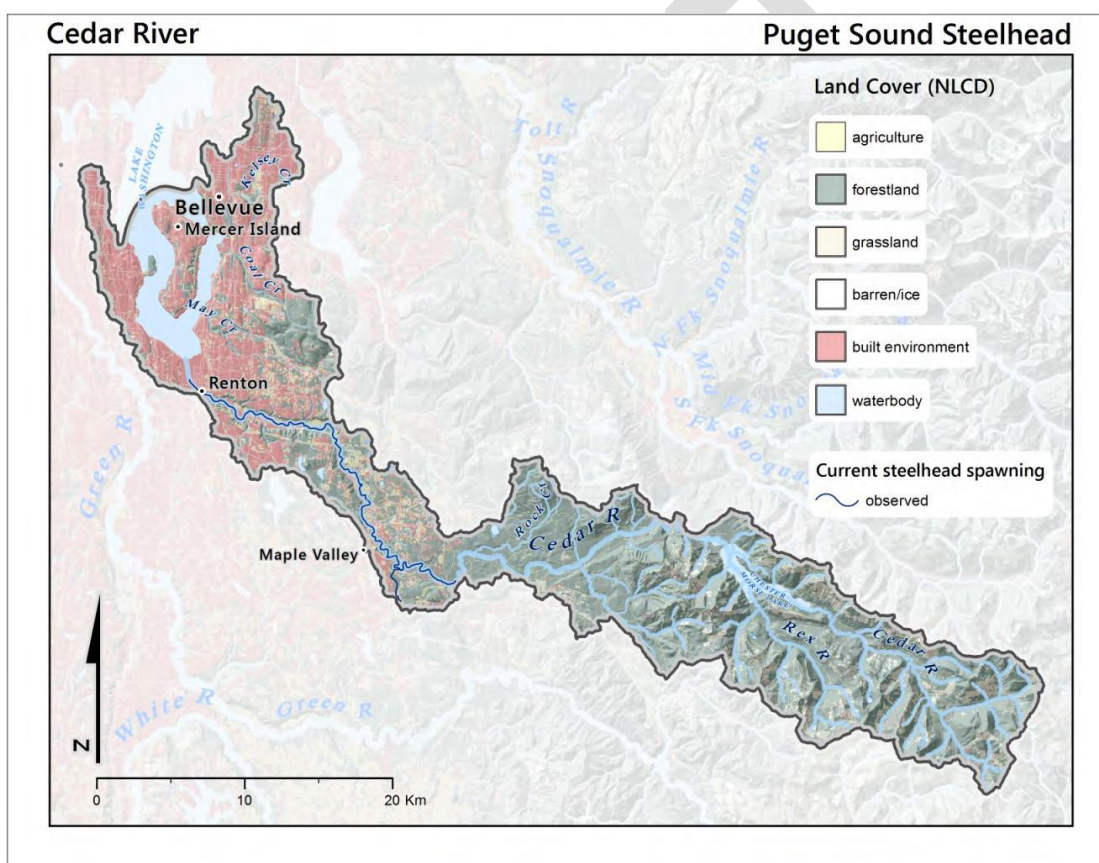
Hydrology



Central and South Puget Sound Major Population Group

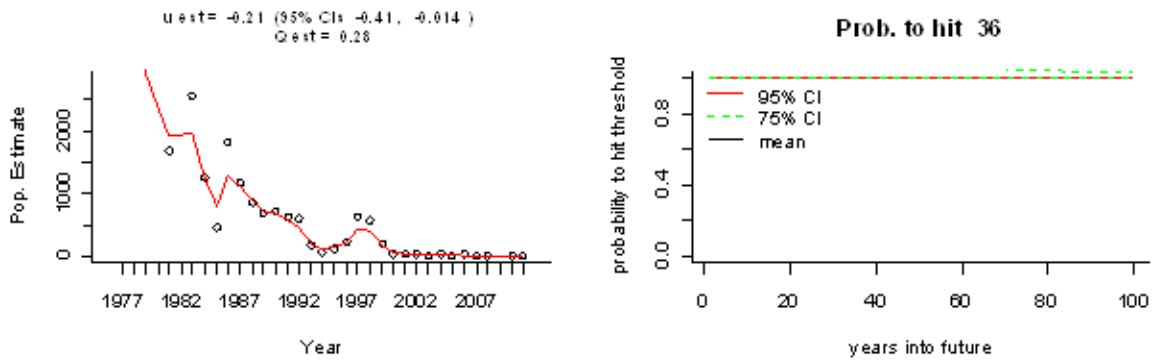
17. Cedar River Winter Run

Overview: This population includes steelhead in the Cedar River and tributaries to the southern end of Lake Washington, primarily May and Coal creeks. Diversion of the Cedar River from its confluence with the Black River to Lake Washington in the early 1900s may have impacted steelhead life-history and abundance. The hydrology of the Cedar River (Rain/Snow) is distinct from other tributaries in the Lake Washington system. Additionally, until recently much of the upper watershed was blocked to anadromous access.



Abundance and Productivity

	WDF Survey	Punch Card Max	IP Estimate	
Abundance	Scarce	353	5,949	11,899
Year	1930	1954		

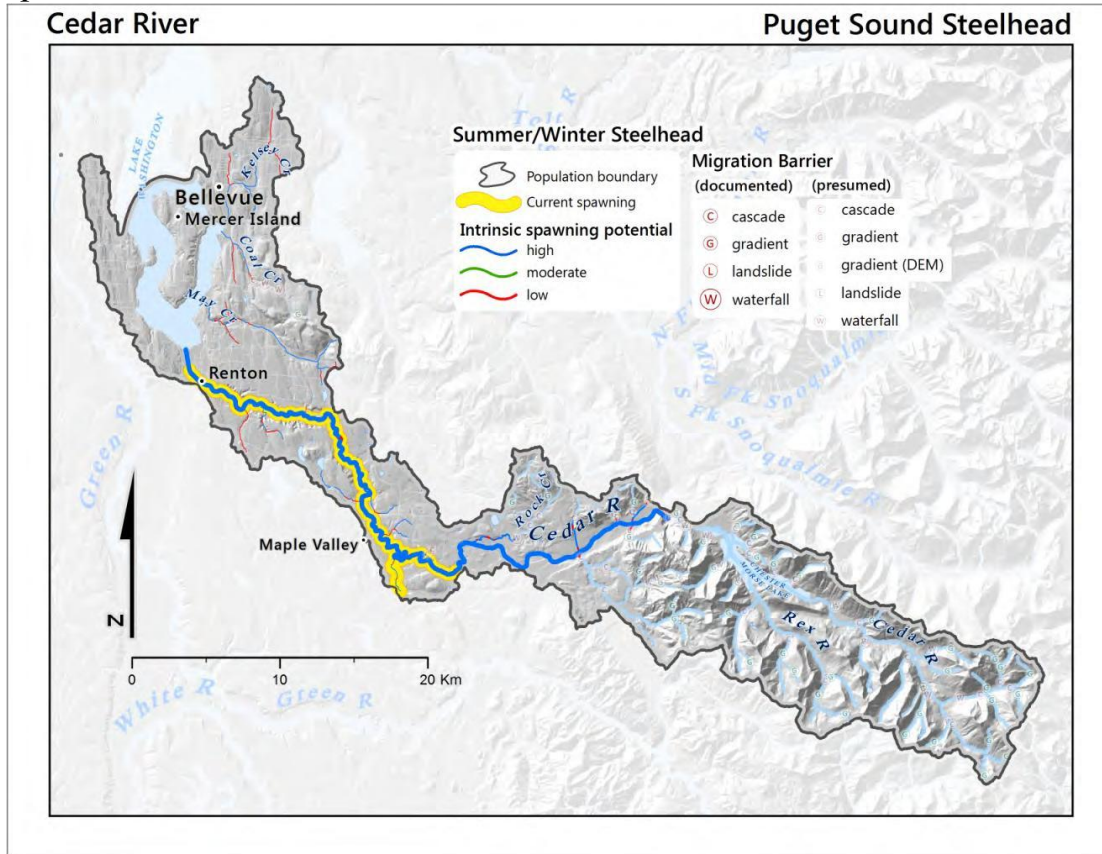


Diversity

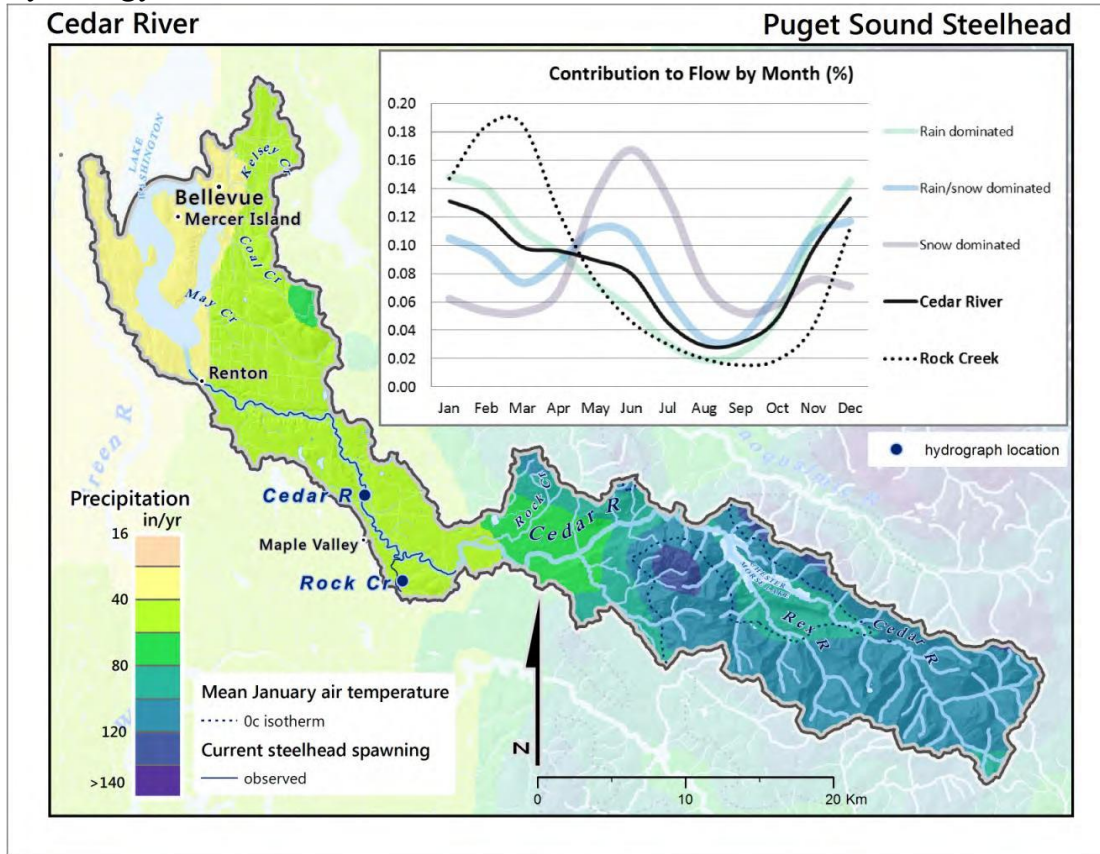
Hatchery Releases – Winter Run

Cedar River Winter Run				Total Releases	
Watershed	Duration	Years	Source	(w/i DPS)	(o/s DPS)
			Total	0	0

Spatial Structure

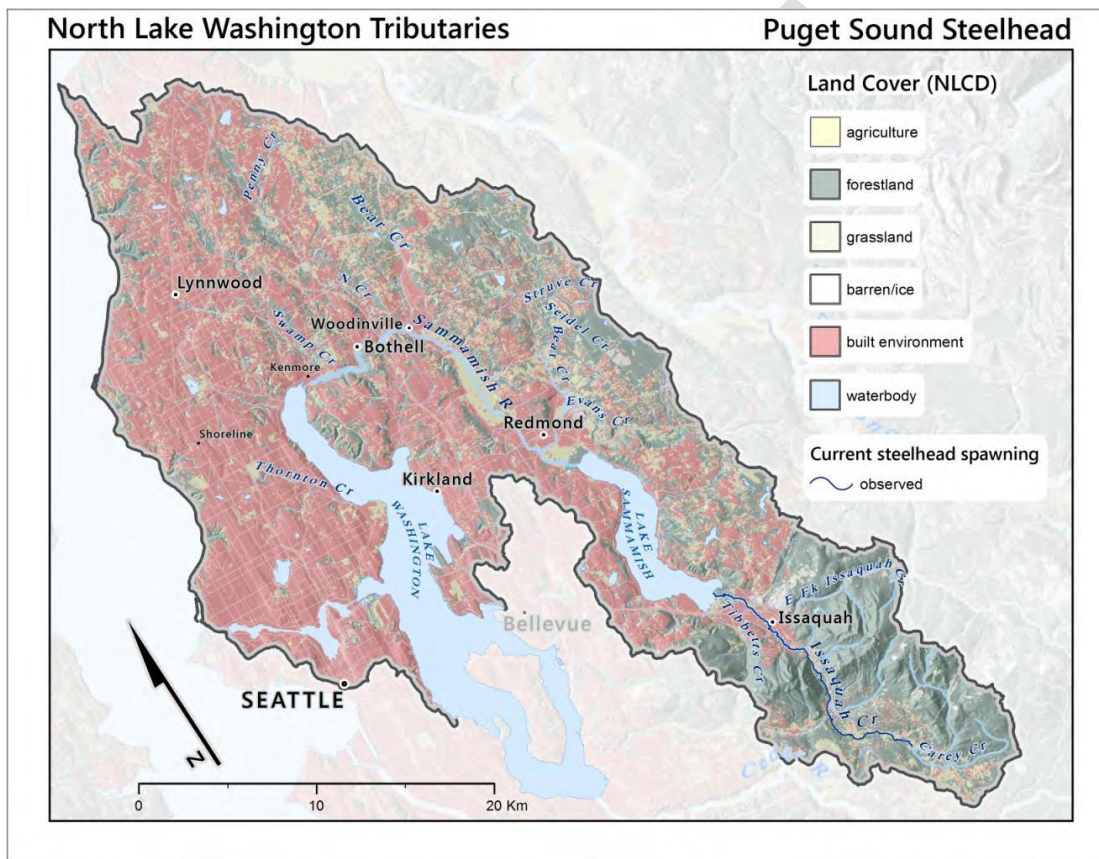


Hydrology



18. Lake Washington and Lake Sammamish Winter Run

Overview: This population includes steelhead that spawn in tributaries to North Lake Washington, the Sammamish River, and Lake Sammamish. The majority of the tributaries drain lowland habitat, with the exception of Issaquah Creek. Given the major modifications in the Lake Washington system, primarily the rerouting of the outlet from the Black River to the Lake Washington Ship Canal and widespread land development, it is difficult to infer historical distribution from current abundance.



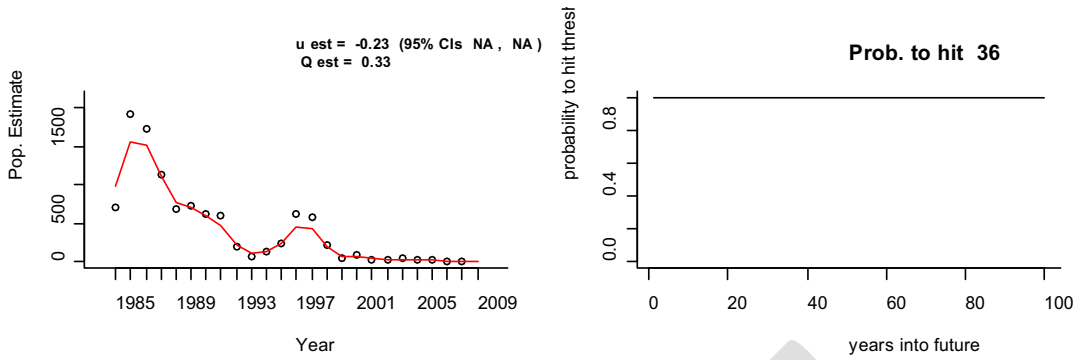
Abundance and Productivity

	WDF Survey	Punch Card Max	Geometric Mean	IP Estimate
Abundance	Absent*	748**	12 (3 - 55)	5,268 10,536
Year	1930	1952	2005-2009	

* Surveys were not conducted in Swamp Creek, North Creek, or Issaquah Creek

** Includes catch from the Lake Washington Ship Canal (which may have been destined for the Cedar River).

Population	Exp. trend ln(nat. spawners) (95% CI) (1985-2009)
Lake Washington winter-run	0.807 (0.770 - 0.845)

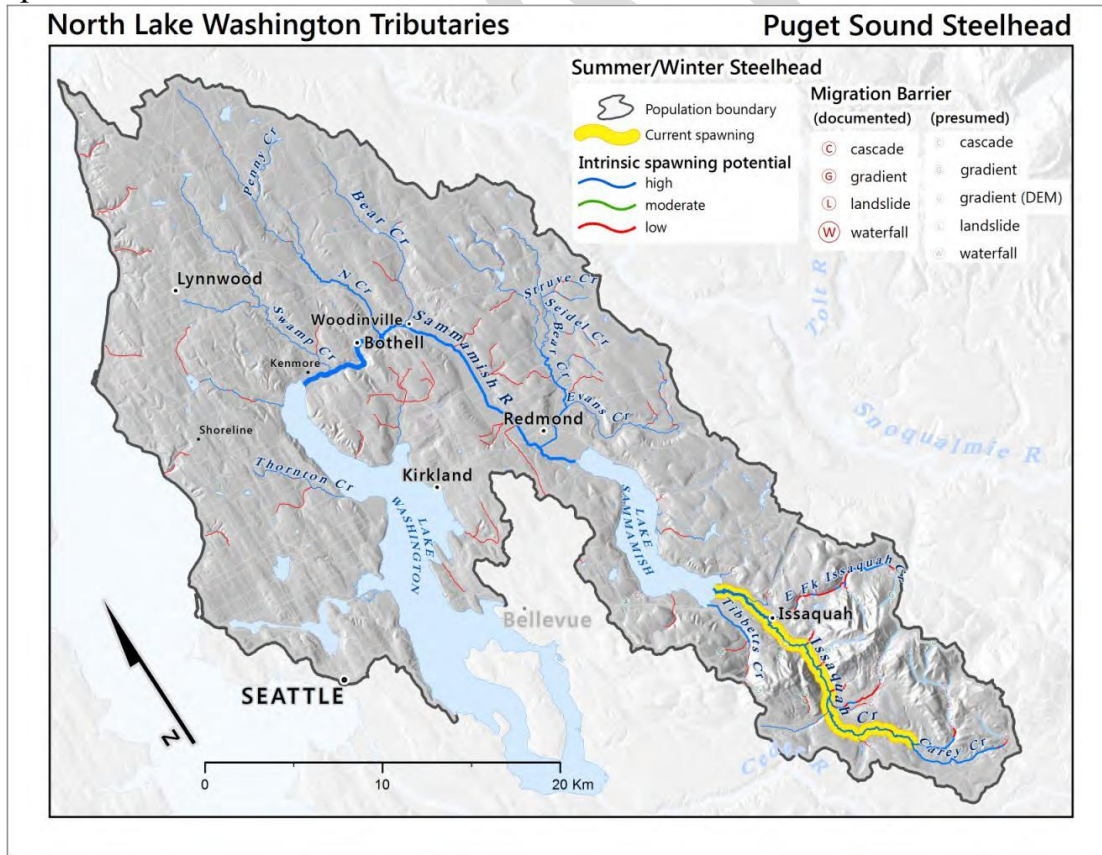


Diversity

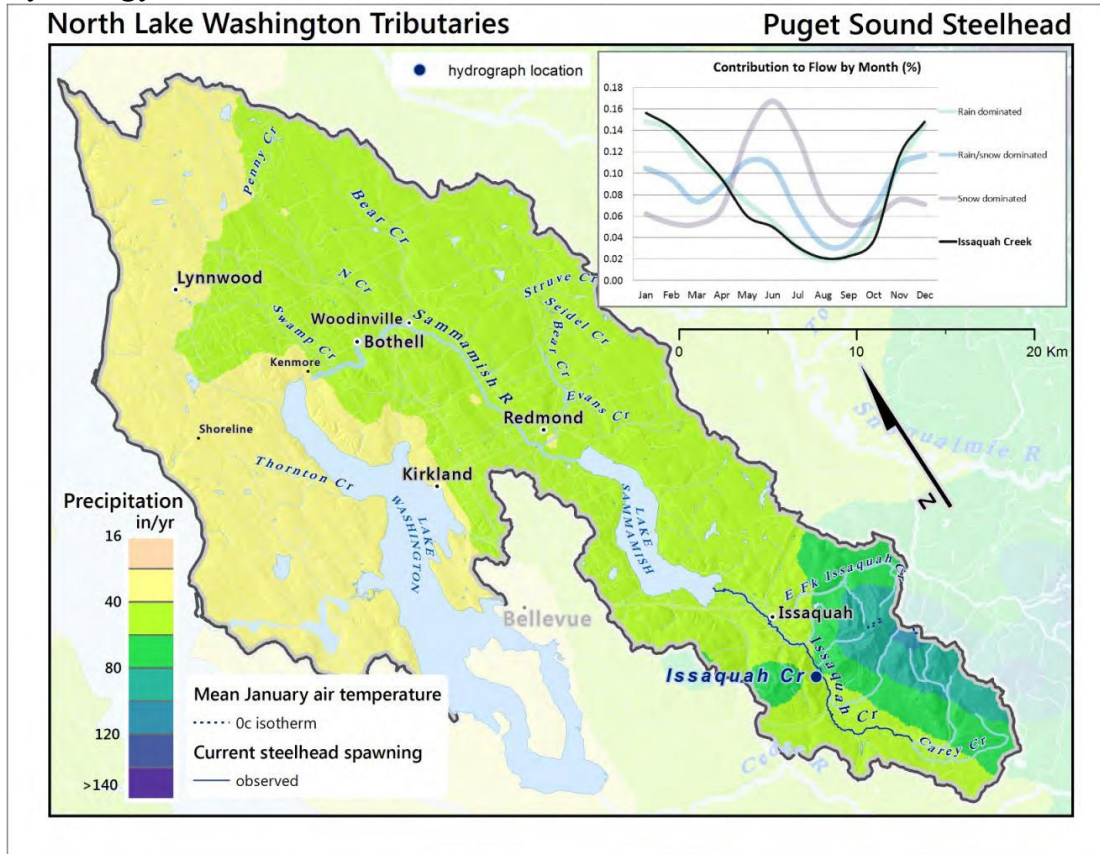
Hatchery Releases – Winter Run

Lake Washington River Winter Run				Total Releases	
Watershed	Duration	Years	Source	(w/i DPS)	(o/s DPS)
Issaquah Cr	98-00	3	Lake Washington	39,516	
			Total	0	0

Spatial Structure

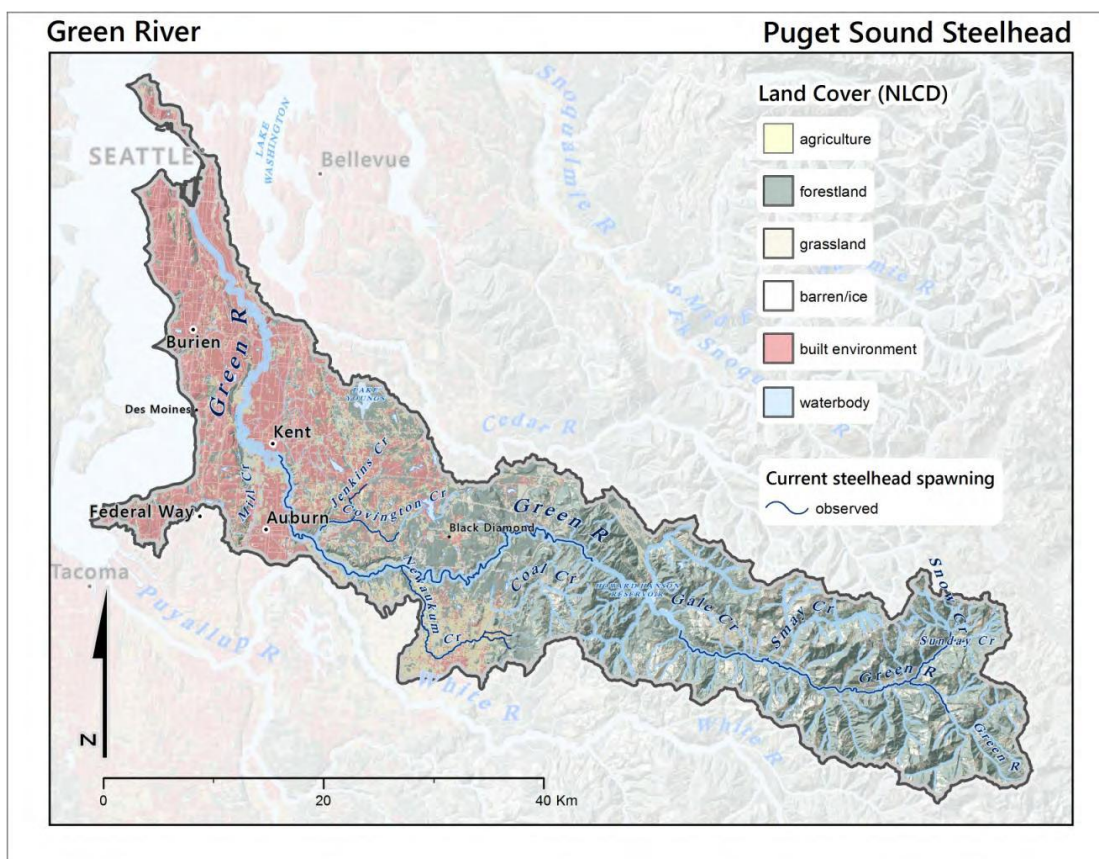


Hydrology



19. Green River Winter Run

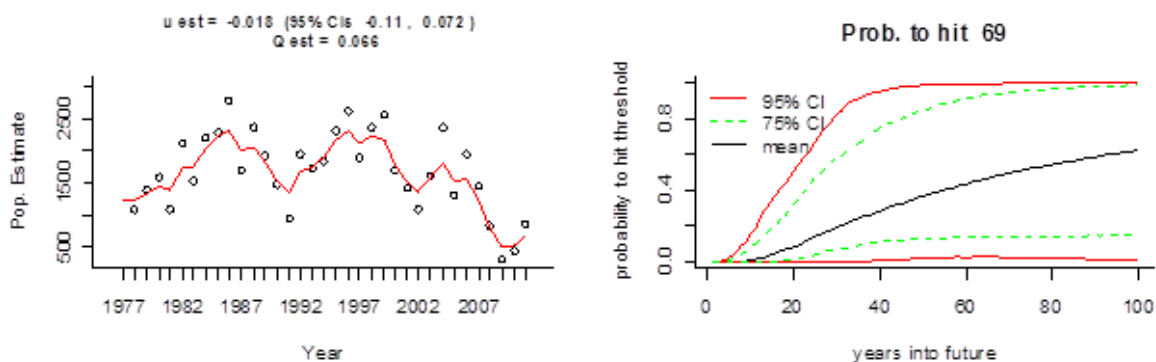
Overview: This population includes steelhead that spawn in the Green River and its tributaries (including the Duwamish River). In the last 150 years the Green River Basin has undergone a number of considerable changes. Connectivity with the Black, Cedar, and White rivers has been lost (although on a geologic time scale these connects were likely transitory), as has access to much of the headwater areas of the Green River.



Abundance and Productivity

	WDF Survey	Punch Card Max	Geometric Mean	IP Estimate
Abundance	Large	4,242	986 (401 - 2428)	19,768 39,537
Year	1930	1950	2005-2009	

Population	Exp. trend ln(nat. spawners) (95% CI) 1985-2009
Green River winter-run	0.992 (0.969 - 1.016)



Diversity

Hatchery Releases – Winter Run

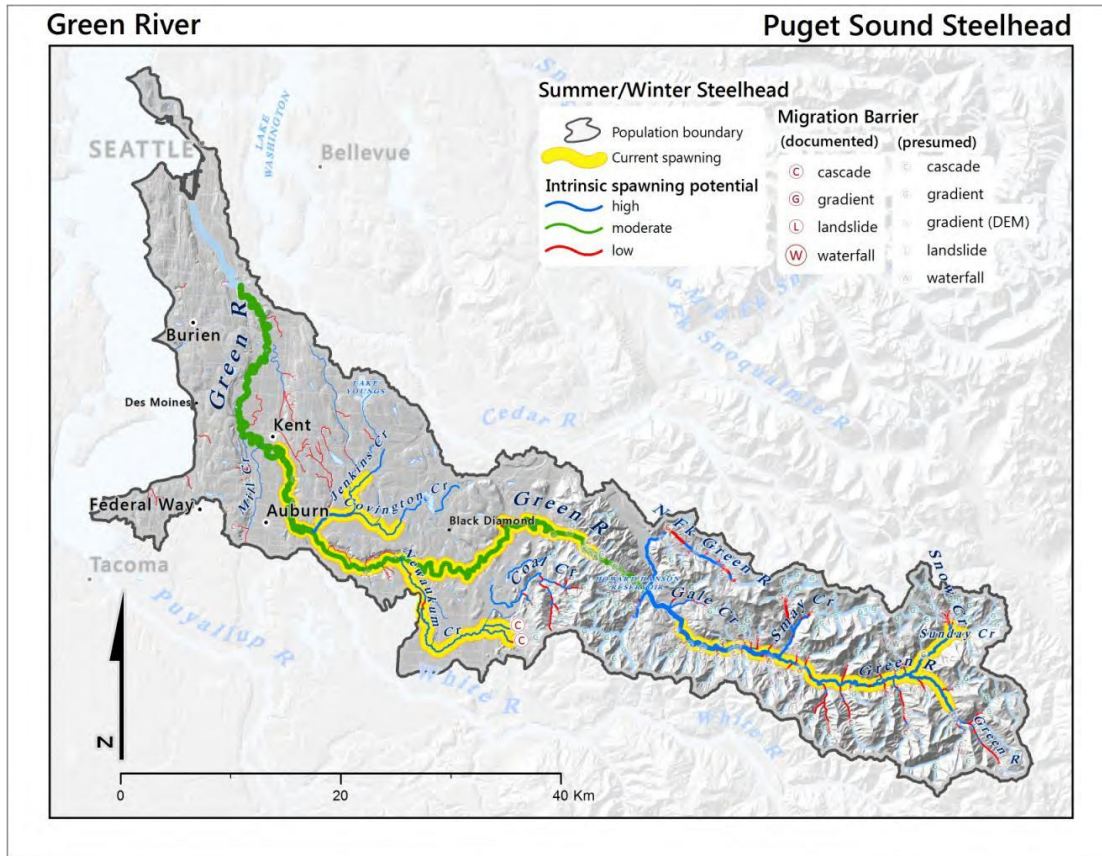
Green River Winter Run				Total Releases	
Watershed	Duration	Years	Source	(w/i DPS)	(o/s DPS)
Big Soos Cr	11	1	Green River (CC)		55,033
Big Soos Cr	03-11	9	Green River Native	461,849	
Crisp Cr	99-02	4	Tokul Cr H (CC)		257,000
Crisp Cr	98-04	3	Green River Native	134,300	
Duamish R	00-01	2	Green River Native	95,269	
Friday Cr	96-97	2	Green River Native	2,262	
Green R	95-11	15	Bogachiel/Tokul (CC)		1,805,397
Green R	95-09	13	Green River Native	1,005,555	
Icy Cr	11	1	Icy Cr (CC)		25,000
Icy Cr	10-11	2	Green River Native	28,964	
Sunday Cr	95-00	4	Green River Native	46,585	
			Total	0	0

Hatchery Releases – Summer Run

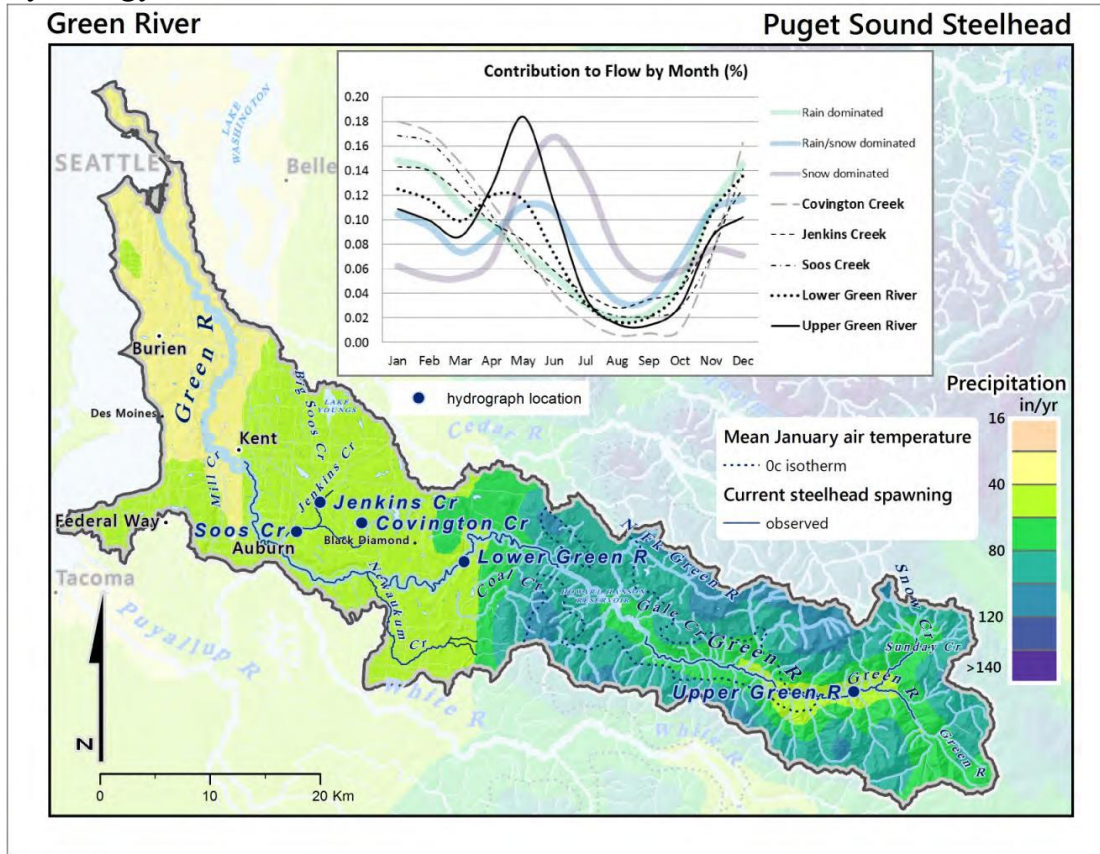
Green River Winter Run				Total Releases	
Watershed	Duration	Years	Source	(w/i DPS)	(o/s DPS)
Big Soos Cr	02-11	10	Green River (SK)		355,017
Green R	95-10	16	Green River (SK)		1,012,567
Icy Cr	10-11	2	Green River (SK)		46,600
			Total	0	0

Spatial Structure

The Headworks Dam (Rkm 98.1) currently blocks anadromous access to the upper watershed. Historically, summer run may have used this now inaccessible habitat.

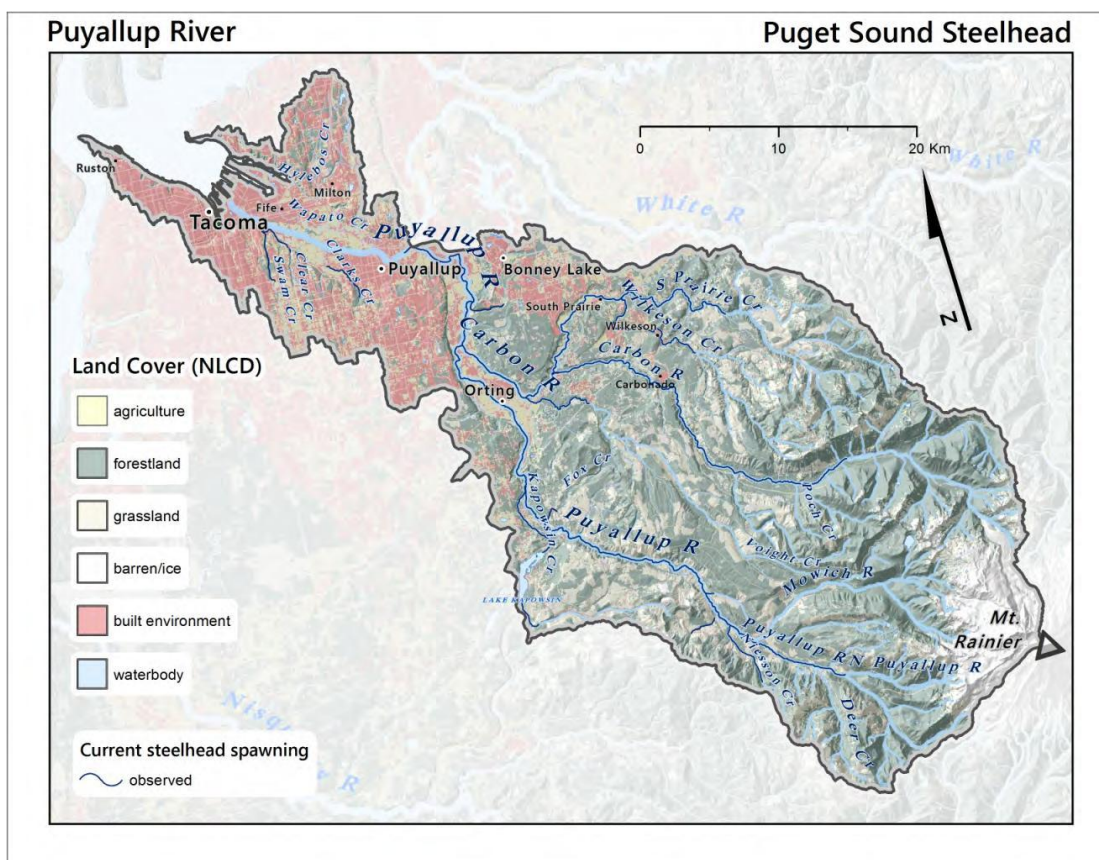


Hydrology



20. Puyallup River (Carbon River) Winter run

Overview: This population includes two SaSI (WDFW 2005) stocks, the Puyallup and Carbon rivers. The TRT determined that the mainstem Puyallup below the confluence of the Puyallup and White Rivers was more closely associated with the Carbon River than the White River.



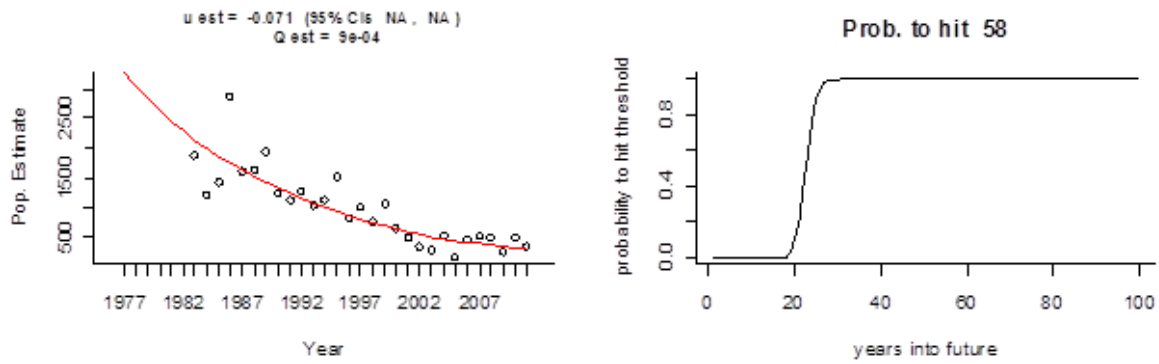
Abundance and Productivity

	WDF Survey	Punch Card Max	Geometric Mean	IP Estimate
Abundance	Multiple Large and Medium	9,190*	326 (178 - 596)	14,716 29,432
Year	1930	1950	2005-2009	

* Catch from the mainstem Puyallup River and Carbon River, which may include White River steelhead.

Population	Exp. trend ln(nat. spawners) (95% CI) 1985-2009
Puyallup River winter-run	0.919 (0.899 - 0.938)

Tributary	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010
Puyallup MS	119	78	52	91	64	139	91	133	51	74
Carbon R	358	248	235	410	98	323	418	367	190	398

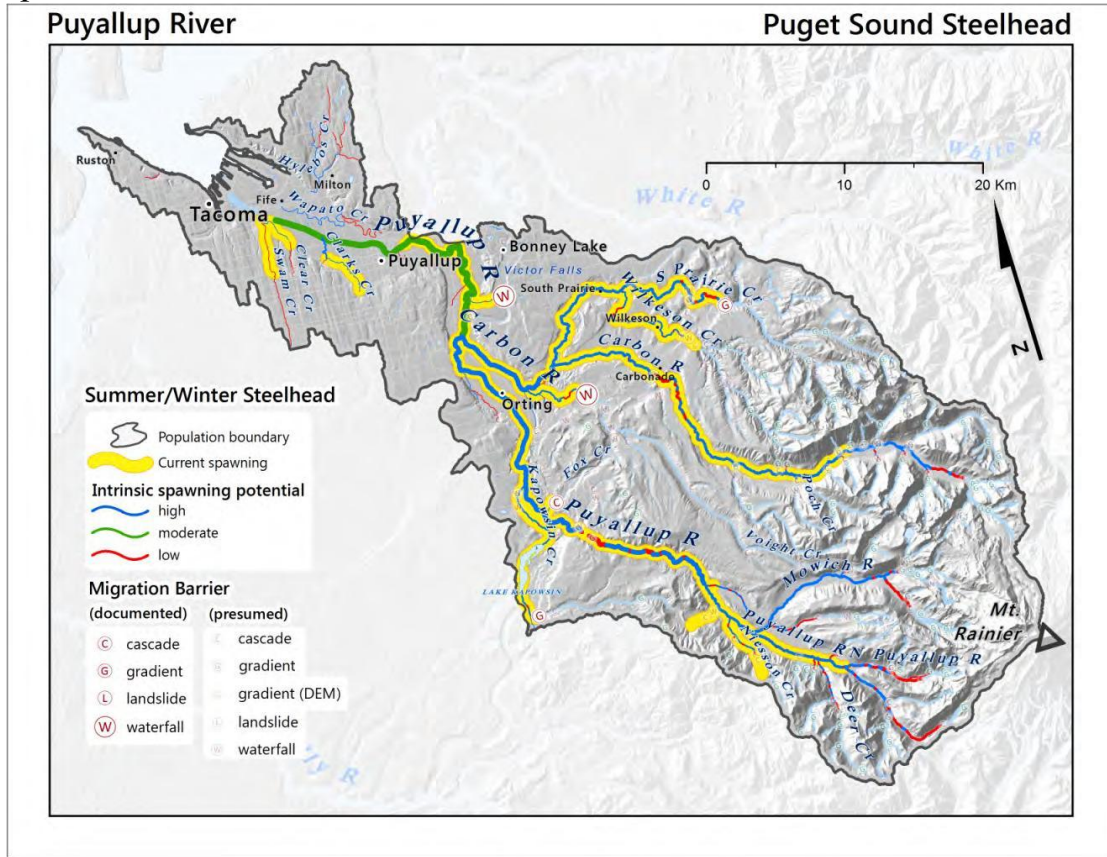


Diversity

Hatchery Releases – Winter Run

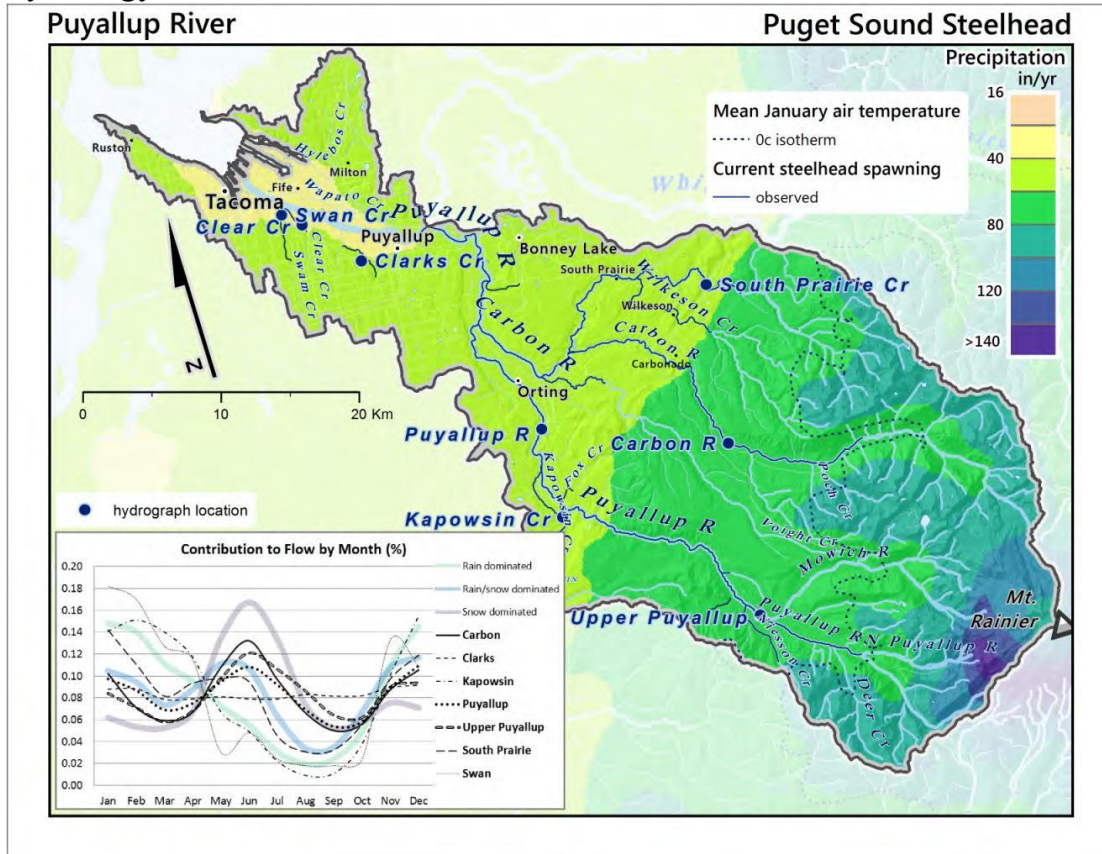
Nooksack River Winter Run				Total Releases	
Watershed	Duration	Years	Source	(w/i DPS)	(o/s DPS)
Clarks Cr	96-09	6	Puyallup H. (CC)		67,550
Diru Cr	95-00	6	Puyallup Tribal H (CC)		592,091
Puyallup R	95-98	4	Tokul Cr H (CC)		369,761
Viola Cr	09	1	Voights Cr H (CC)		187,550
Voight Cr	95-09	15	Voights Cr H. (CC)		2,214,396
			Total	0	3,431,348

Spatial Structure



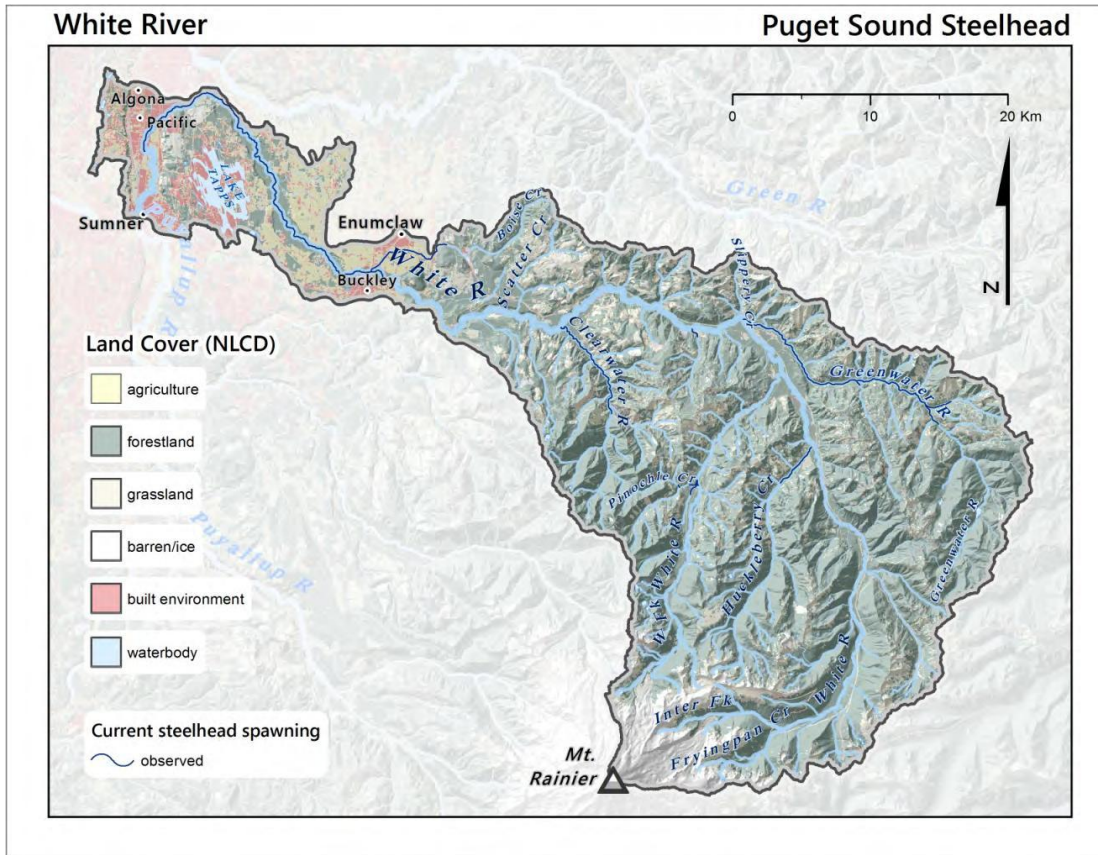
DRAFT

Hydrology



21. White River Winter Run

Overview: This population includes one SaSI (WDFW 2005) stock, the White River. The TRT determined this population begins at the confluence of the White and Puyallup Rivers. This DIP includes a number of glacially influenced tributaries.

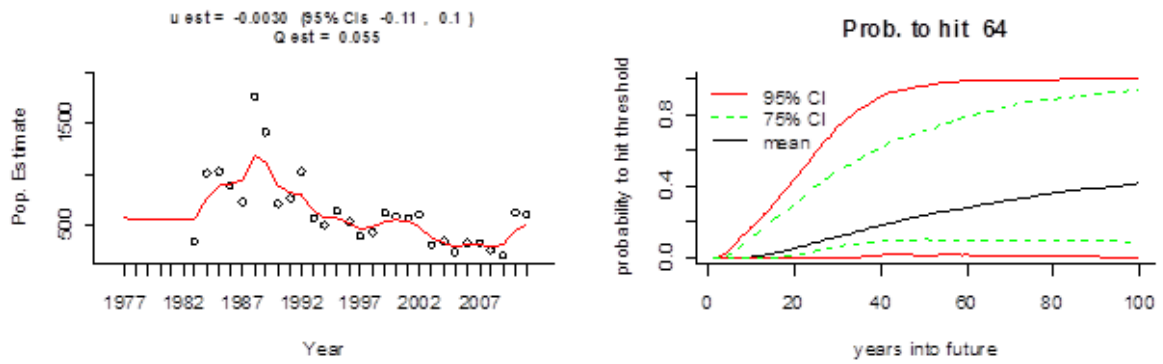


Abundance and Productivity

	WDF Survey	Punch Card Max	Geometric Mean	IP Estimate
Abundance	Medium	827*	265 (206 - 342)	17,490 34,981
Year	1930	1952	2005-2009	

* Does not include White River steelhead caught in the mainstem Puyallup River

Population	Exp. trend ln(nat. spawners) (95% CI) 1985-2009
White River winter-run	0.938 (0.923 - 0.952)



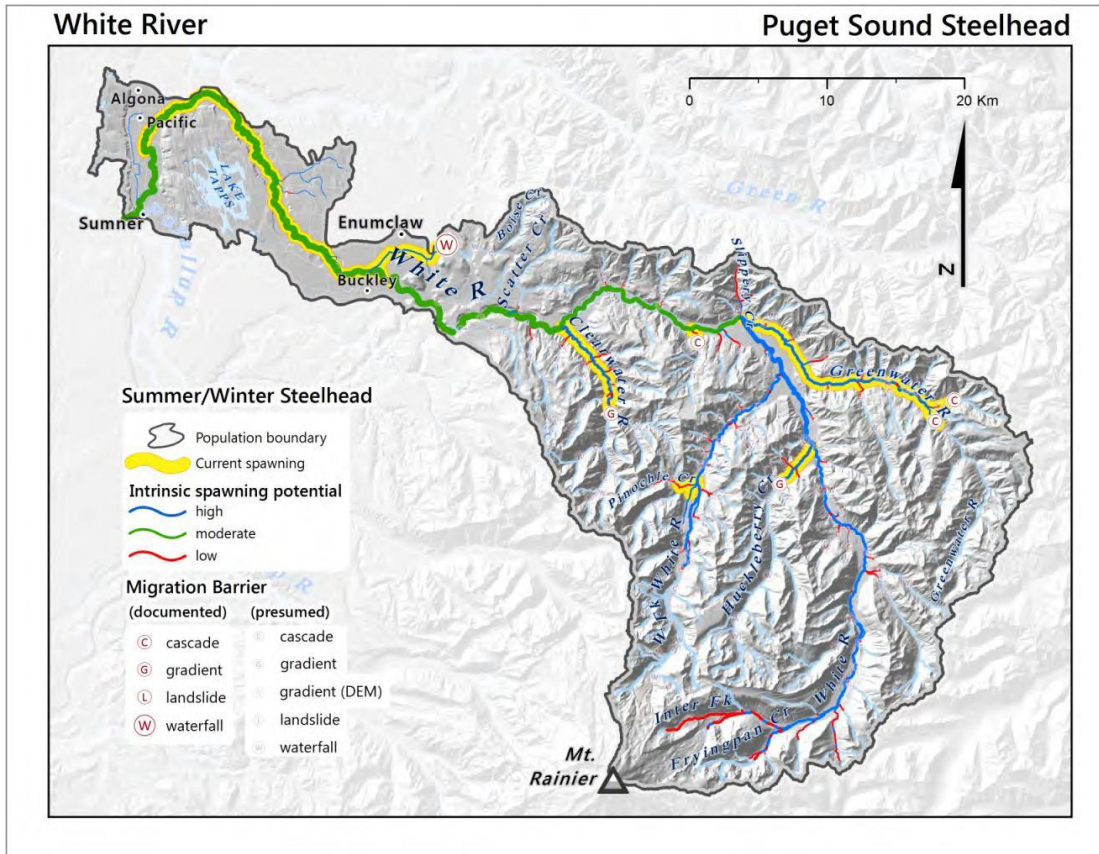
Diversity

Hatchery Releases – Winter Run

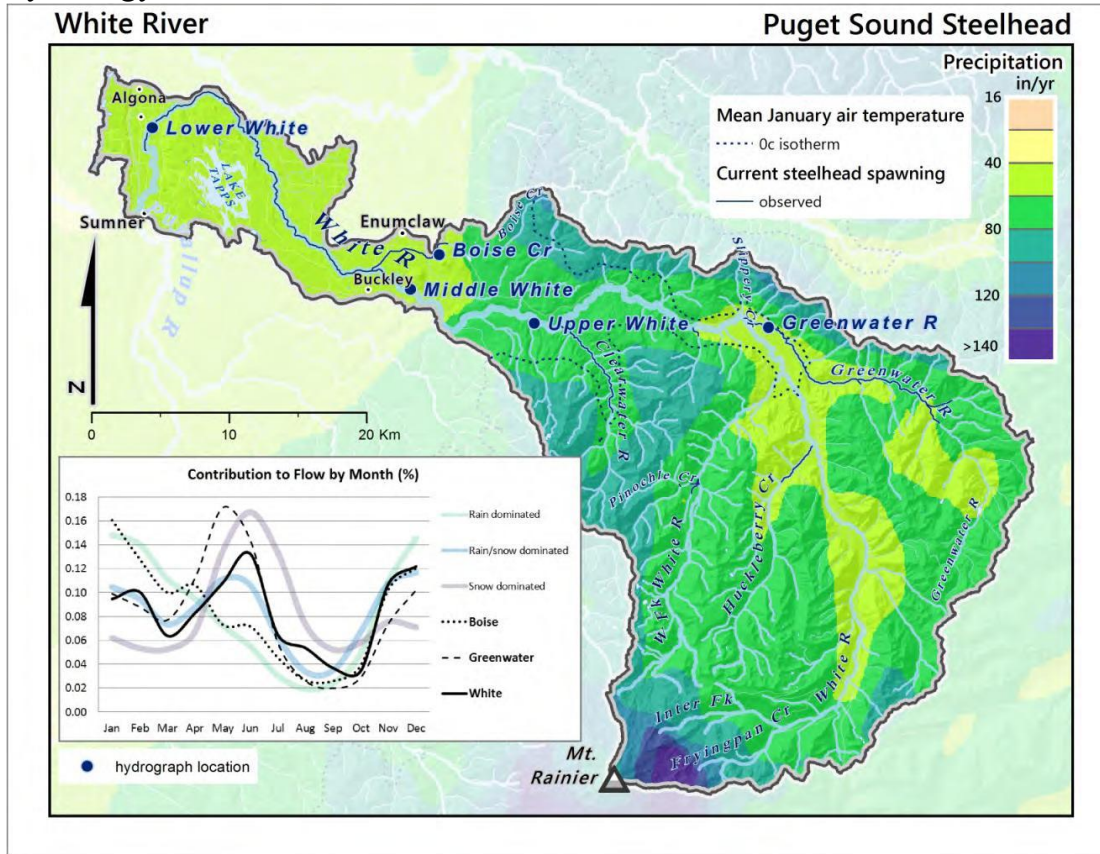
White River River Winter Run				Total Releases	
Watershed	Duration	Years	Source	(w/i DPS)	(o/s DPS)
White R	95-10	9	Puyallup H. (CC)		205,979
			Total	0	0

Spatial Structure

Much of the White River basin is accessible, although passage past Mud Mountain Dam is only possible via the trap and haul program that has been operated by the USACE since the 1940s.

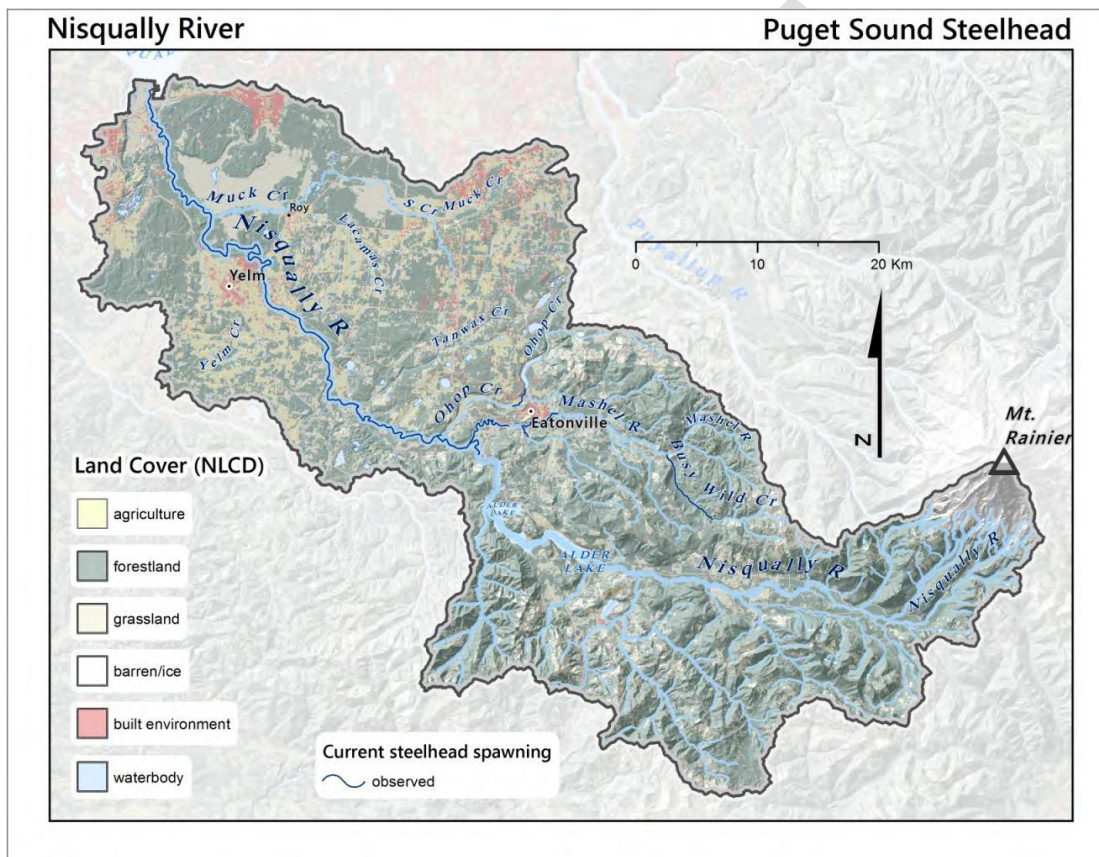


Hydrology



22. Nisqually River Winter Run

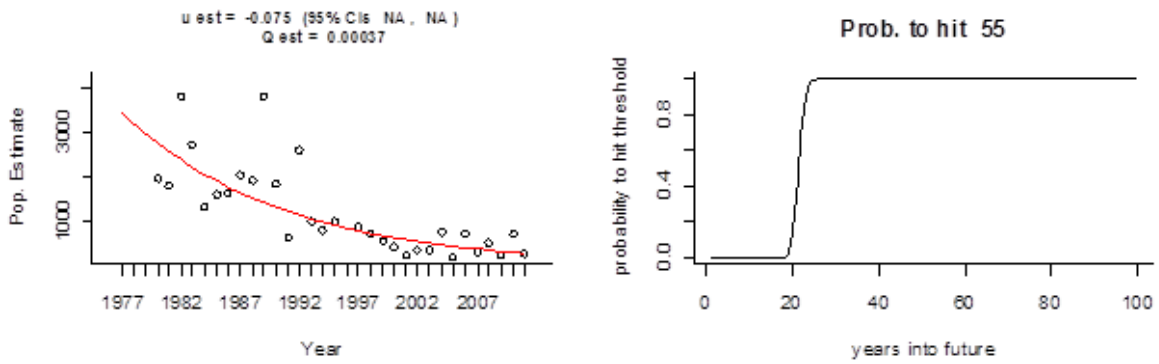
Overview: In contrast to the rest of the Southern Puget Sound region, which is predominantly lowland stream habitat, the Nisqually River drains the glacial slopes of Mt. Rainier. The TRT considered that ecological differences between the Nisqually River and surrounding South Sound tributaries are sufficient to rDPSIt in life history and reproductive differentiation. Anecdotal information suggests that the Nisqually River steelhead population was quite large.



Abundance and Productivity

	WDF Survey	Punch Card Max	Geometric Mean	IP Estimate
Abundance	Multiple Medium	2,769	402 (178 - 908)	15,330 30,660
Year	1930	1952	2005-2009	

Population	Exp. trend ln(nat. spawners) (95% CI) 1985-2009
Nisqually River winter-run	0.914 (0.890 - 0.940)



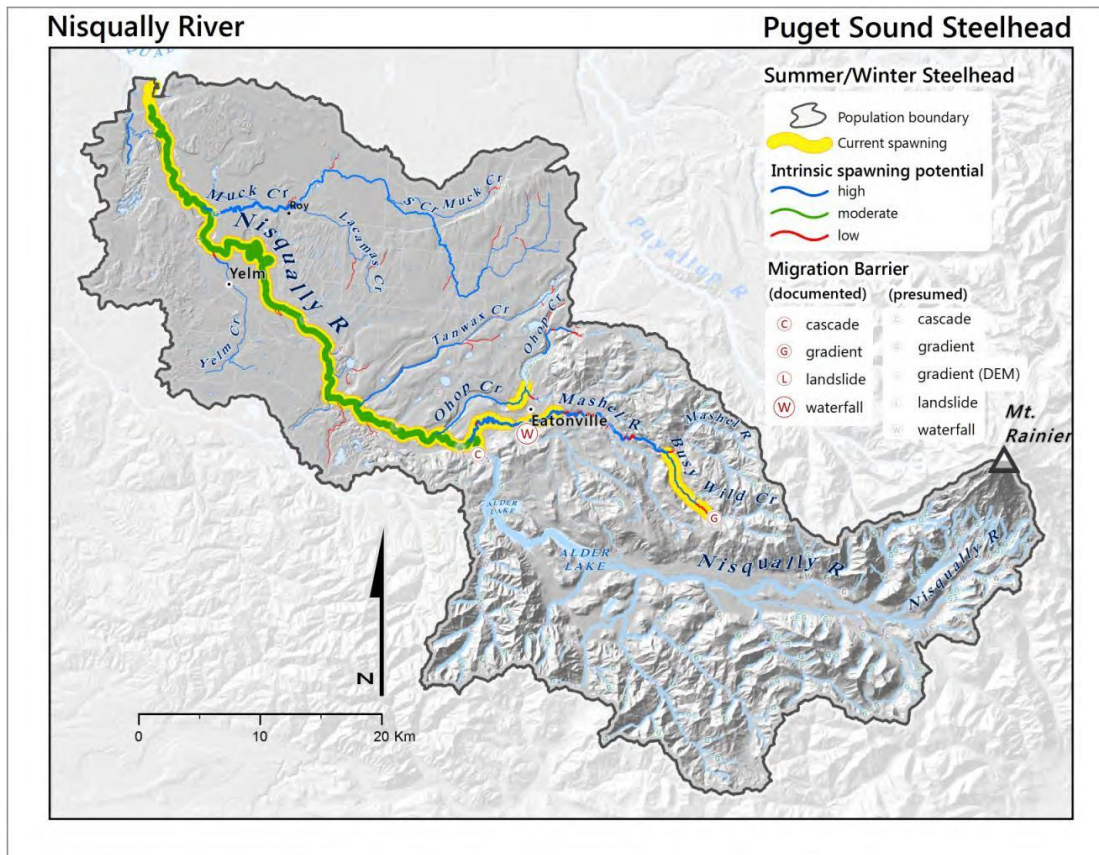
Diversity

Hatchery Releases – Winter Run

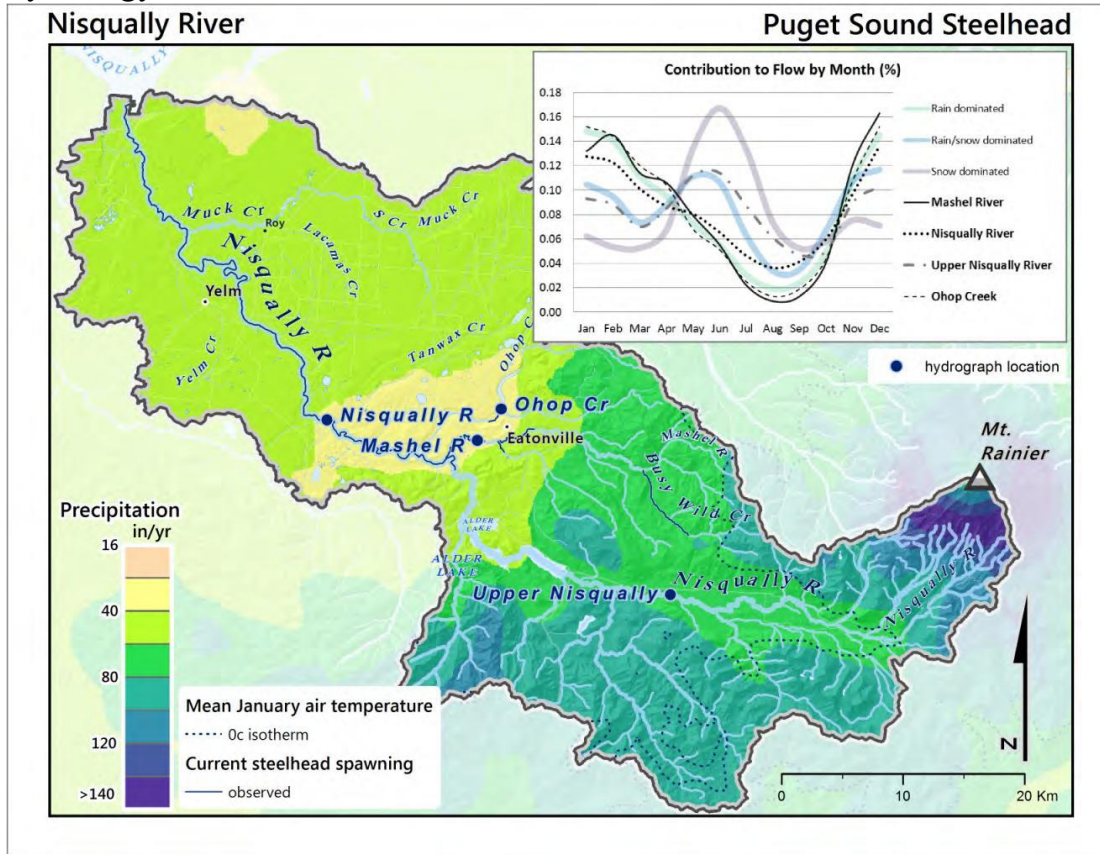
Nisqually River Winter Run				Total Releases	
Watershed	Duration	Years	Source	(w/i DPS)	(o/s DPS)
Lake St Clair	98	1	Skykomish H.		11,494
			Total	0	0

Spatial Structure

Historically a series of cascades near the present site of the La Grande and Alder dams may have been a seasonal barrier, but they also could have posed a complete barrier to fish passage.

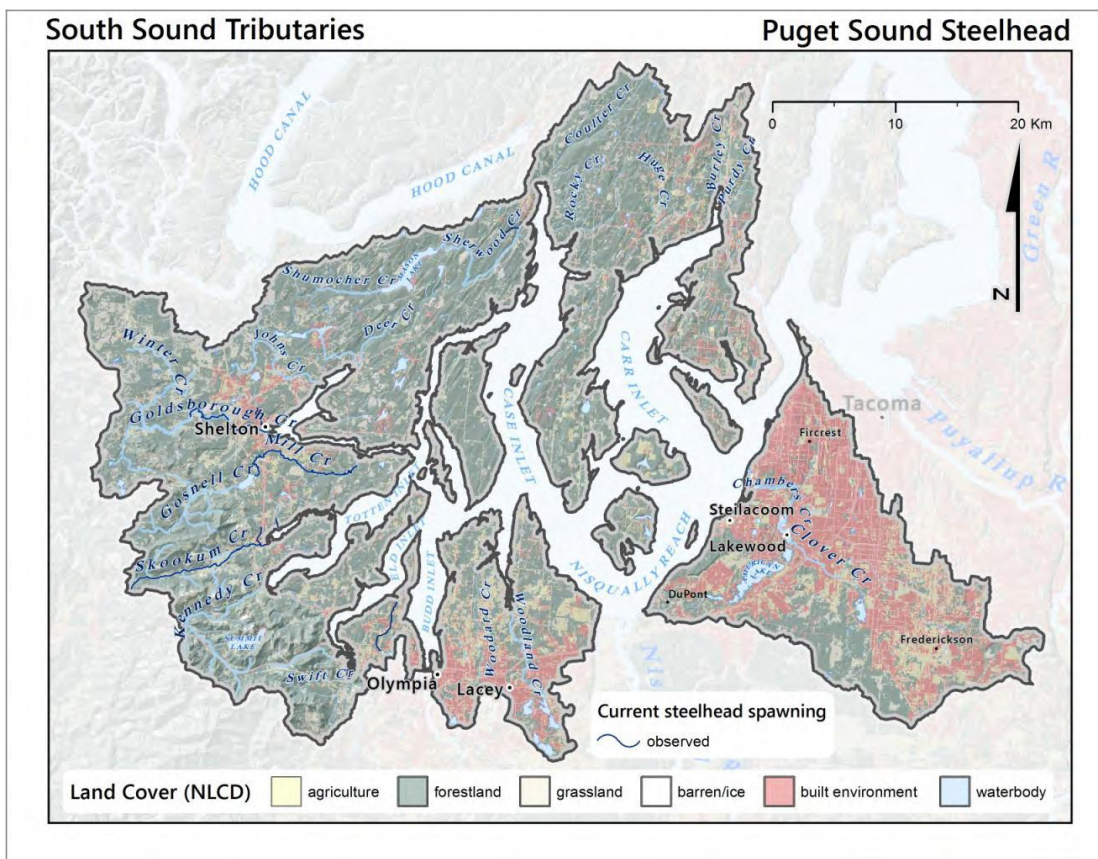


Hydrology



23. South Sound Tributaries Winter Run

Overview: This population includes four SaSI winter steelhead stocks (WDFW 2005): Chambers Creek, Eld Inlet, Totten Inlet, Hammersley Inlet and Case/Carr Inlet—effectively all of the lowland tributaries entering into Southern Puget Sound. Little current or historical information is available on abundance or life history characteristics for this population.



Abundance and Productivity

	WDF Survey	Punch Card Max	IP Estimate
Abundance	NA	85*	9,854 19,709
Year			

* Compiled from a number of different streams draining to South Puget Sound: Coulter Creek, Goldsborough Creek, Kennedy Creek, Mill Creek, Percival Creek, and Sherwood Creek

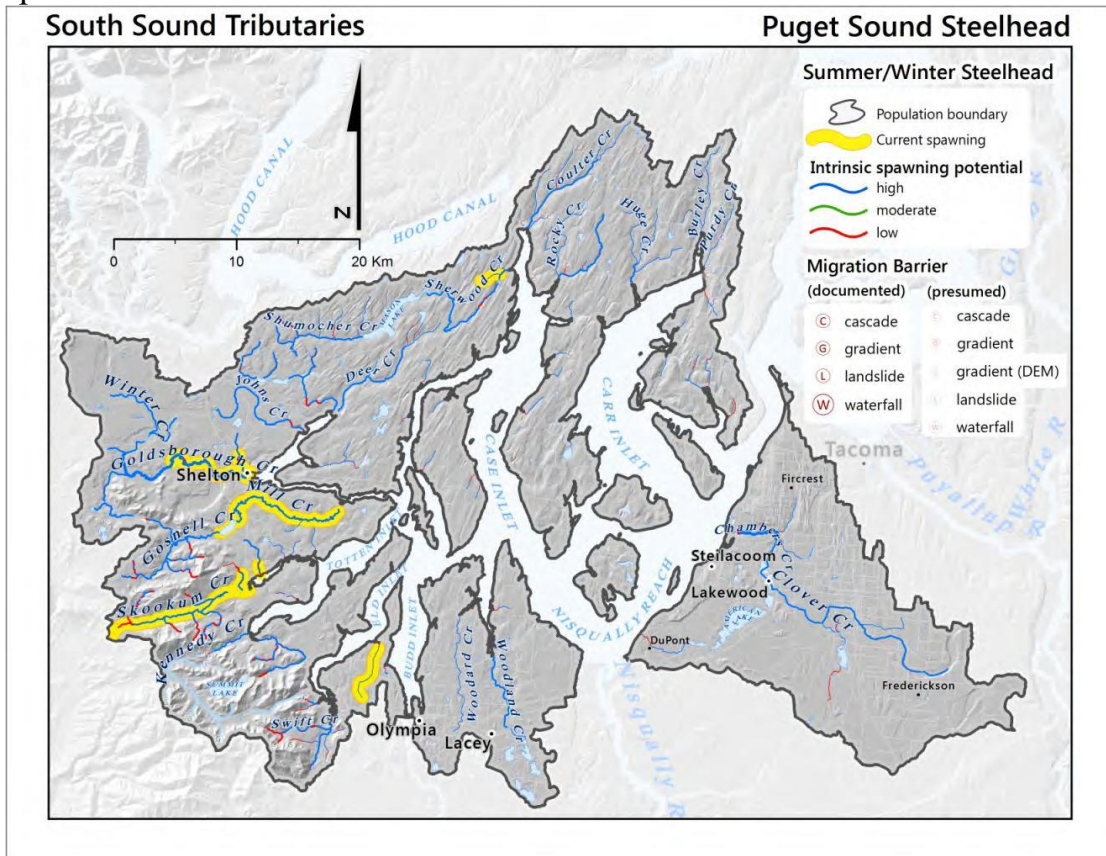
Diversity

Hatchery Releases – Winter Run

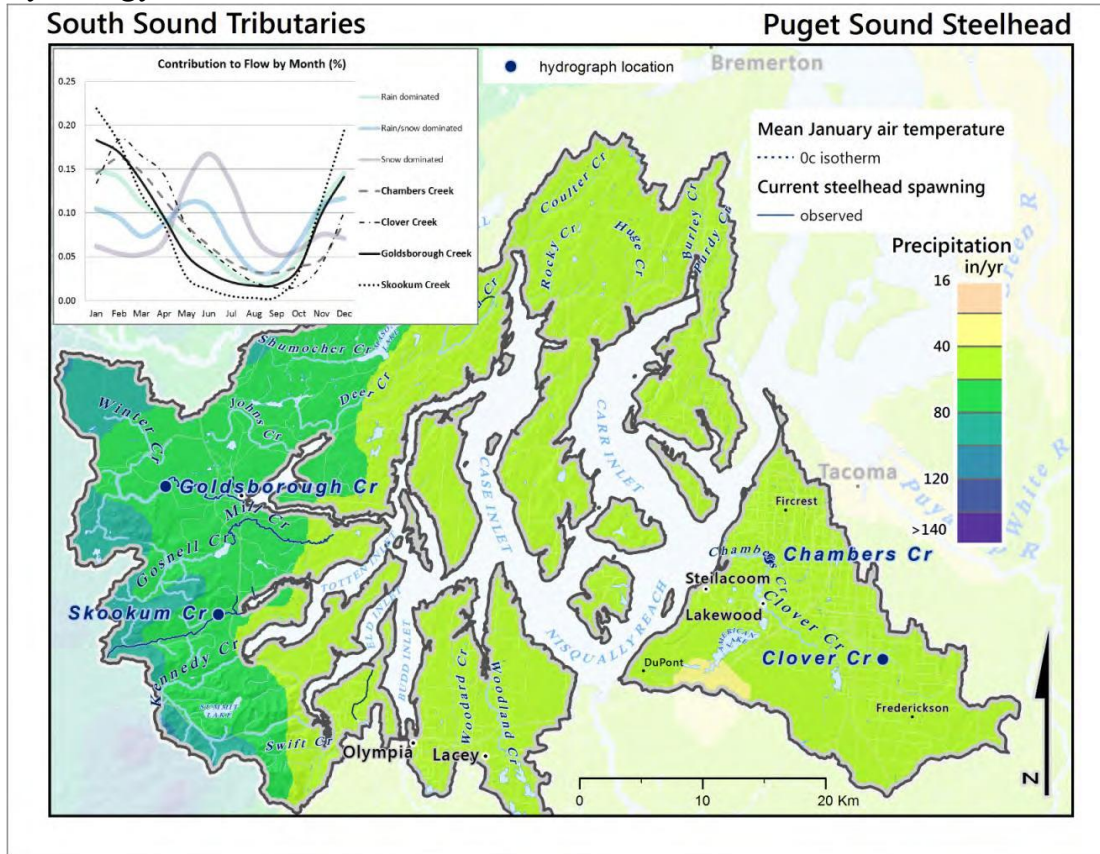
South Sound Winter Run	Total Releases
------------------------	----------------

Watershed	Duration	Years	Source	(w/i DPS)	(o/s DPS)
Kennedy Cr	96	1	Bogachiel H. (CC)		9,996
Deschutes R	96-05	9	Bogachiel/Tokul (CC)		290,654
Chambers Cr	95-96	2	Chambers Cr H		90,887
			Total	0	0

Spatial Structure

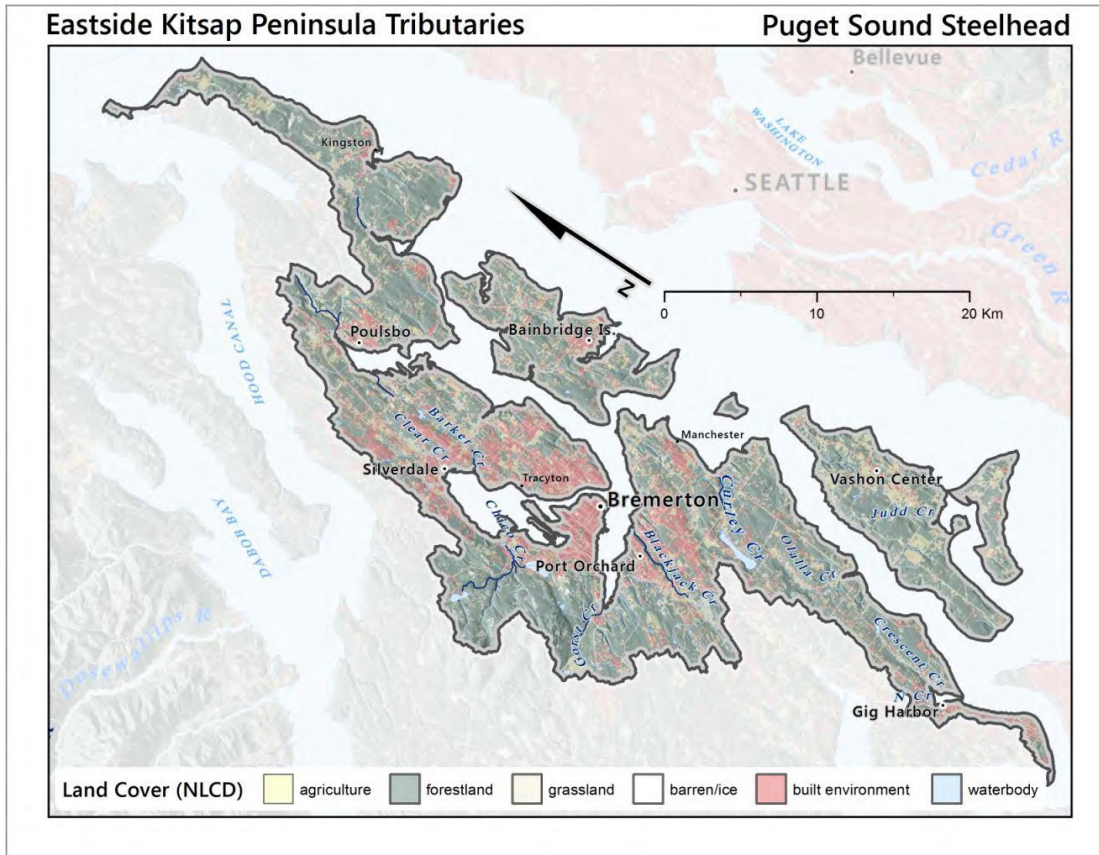


Hydrology



24. East Kitsap Peninsula Winter Run

Overview: This population includes small lowland independent tributaries on the east side of the Kitsap Peninsula. There is limited information, other than presence, for the east side of the Kitsap Peninsula, with the exception of Curley Creek.



Abundance and Productivity

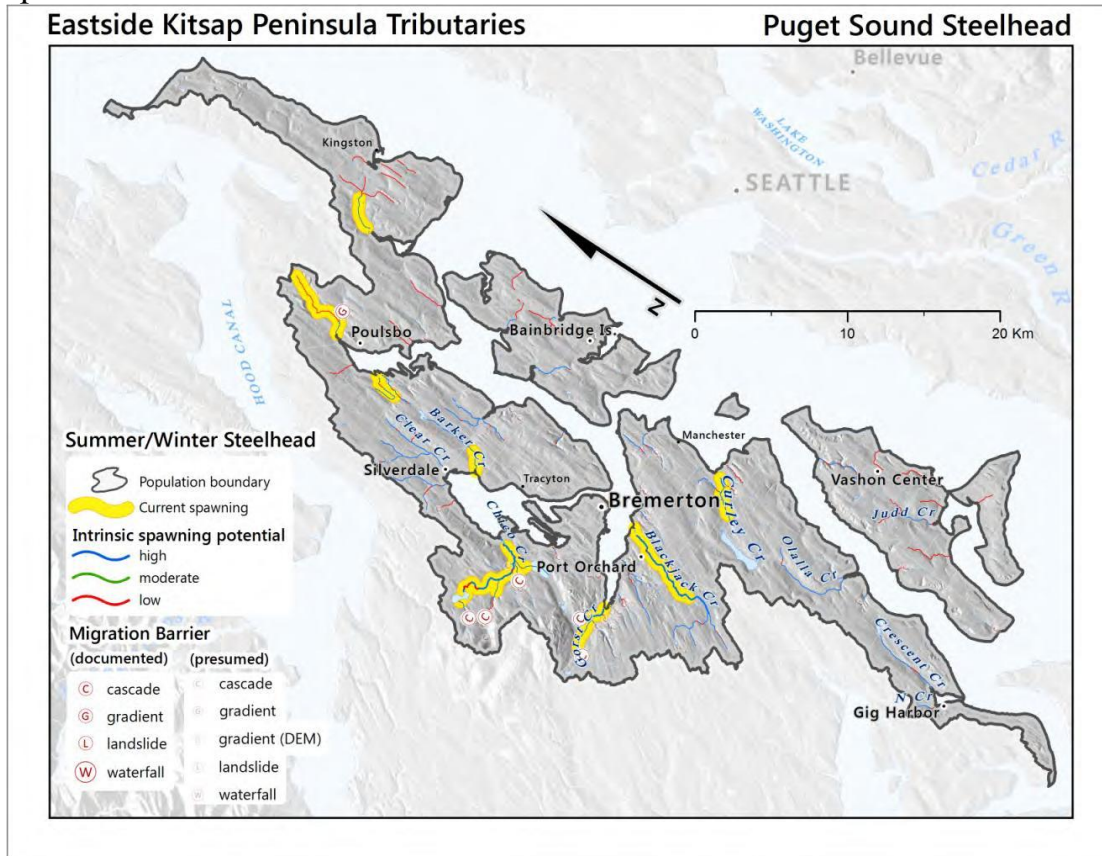
	WDF Survey	Punch Card Max	IP Estimate	
Abundance	NA	53	1,557	3,115
Year		1963		

Diversity

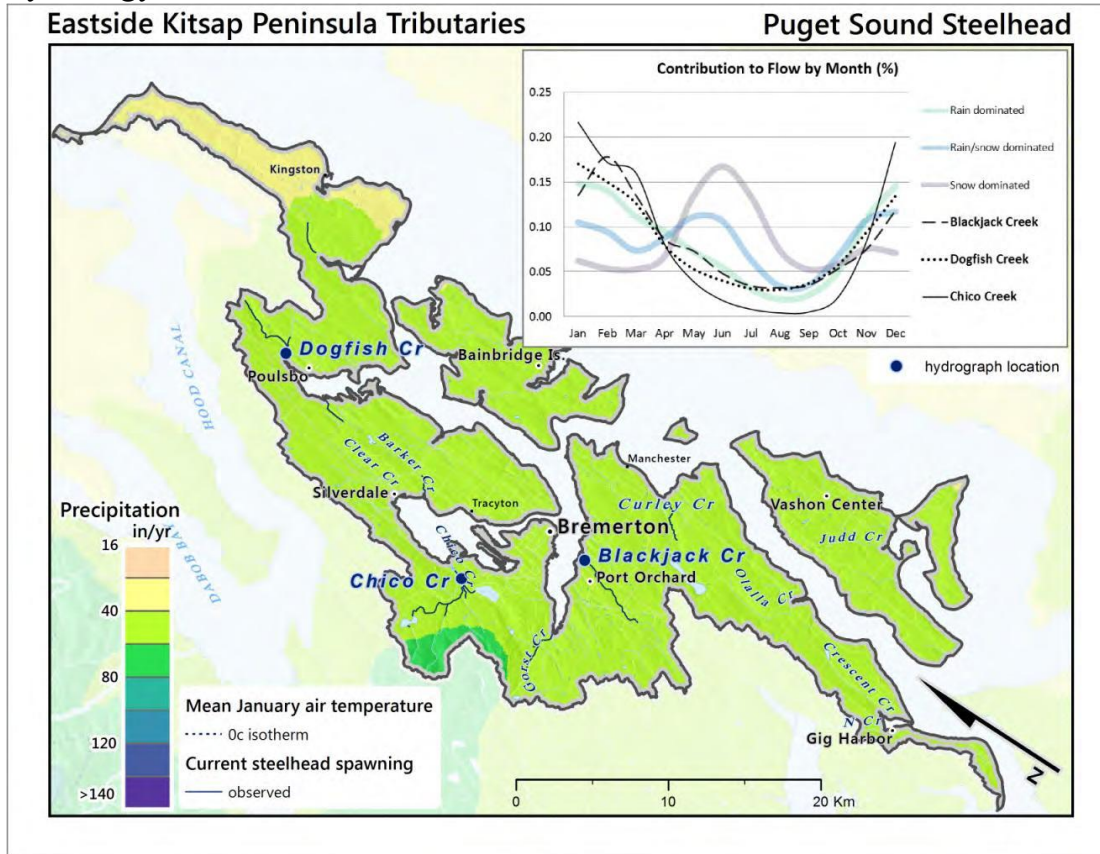
Hatchery Releases – Winter Run

East Kitsap Winter Run				Total Releases	
Watershed	Duration	Years	Source	(w/i DPS)	(o/s DPS)
			Total	0	0

Spatial Structure



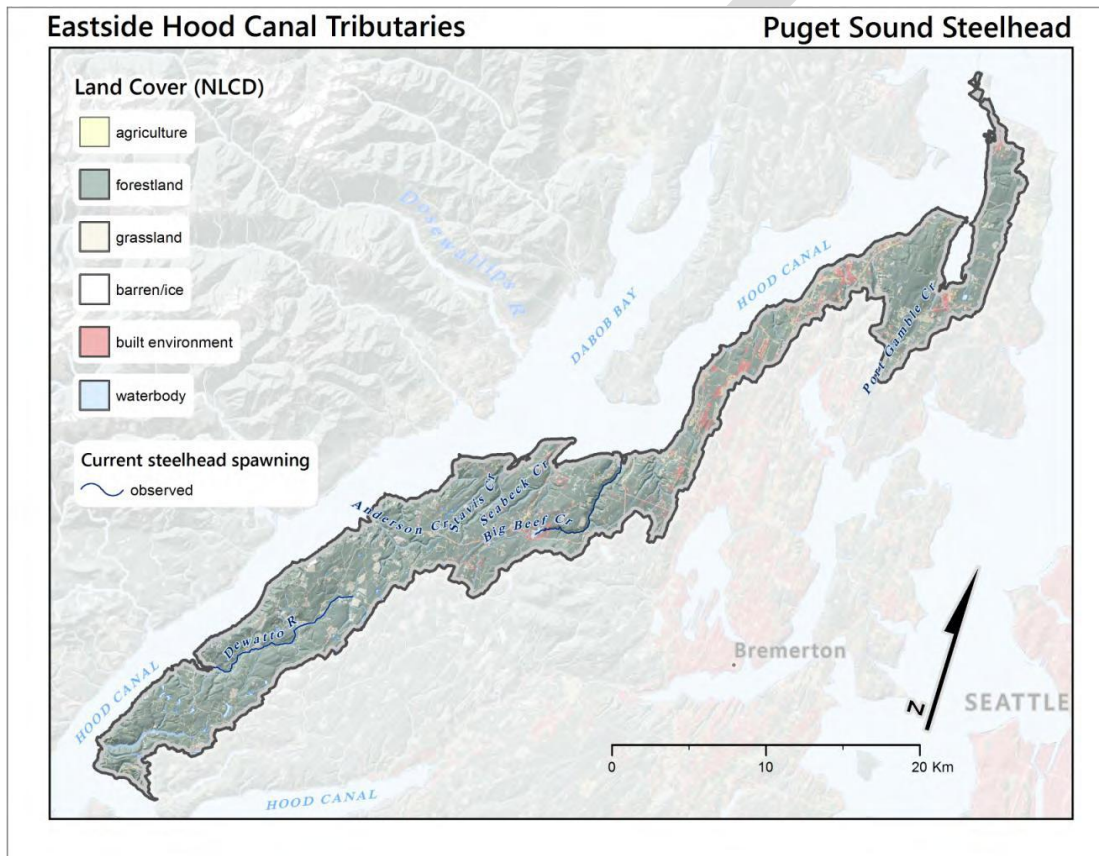
Hydrology



Hood Canal and Strait of Juan de Fuca Major Population Group

25. East Hood Canal Winter Run

Overview: This population includes winter steelhead spawning in small lowland independent tributaries on the west side of the Kitsap Peninsula (eastern shore of Hood Canal) from Point No Point to the southern end of Hood Canal (Alderbrook and Twanoh creeks). The primary streams in this DIP include Big Beef Creek, Anderson Creek, and the Dewatto River.



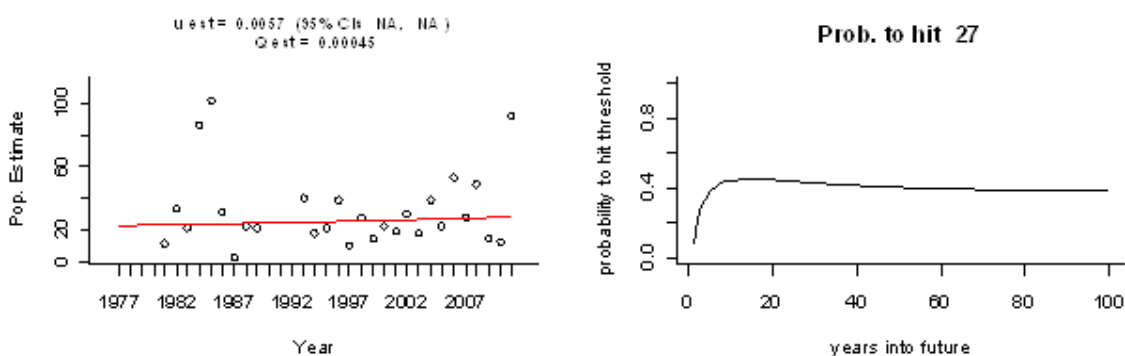
Abundance and Productivity

	WDF Survey	Punch Card Max	Geometric Mean	IP Estimate
Abundance	NA	327*	213 (122 - 372)	1,270 2,540
Year		1958	2005-2009	

* Includes estimates from Big Beef Creek and Dewatto River.

Population	Exp. trend ln(nat. spawners) (95% CI) 1985-2009
East Hood Canal winter-run	1.022 (0.997 - 1.048)

Tributary	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011
Dewatto R	30	18	39	23	53	28	49	15	13	92

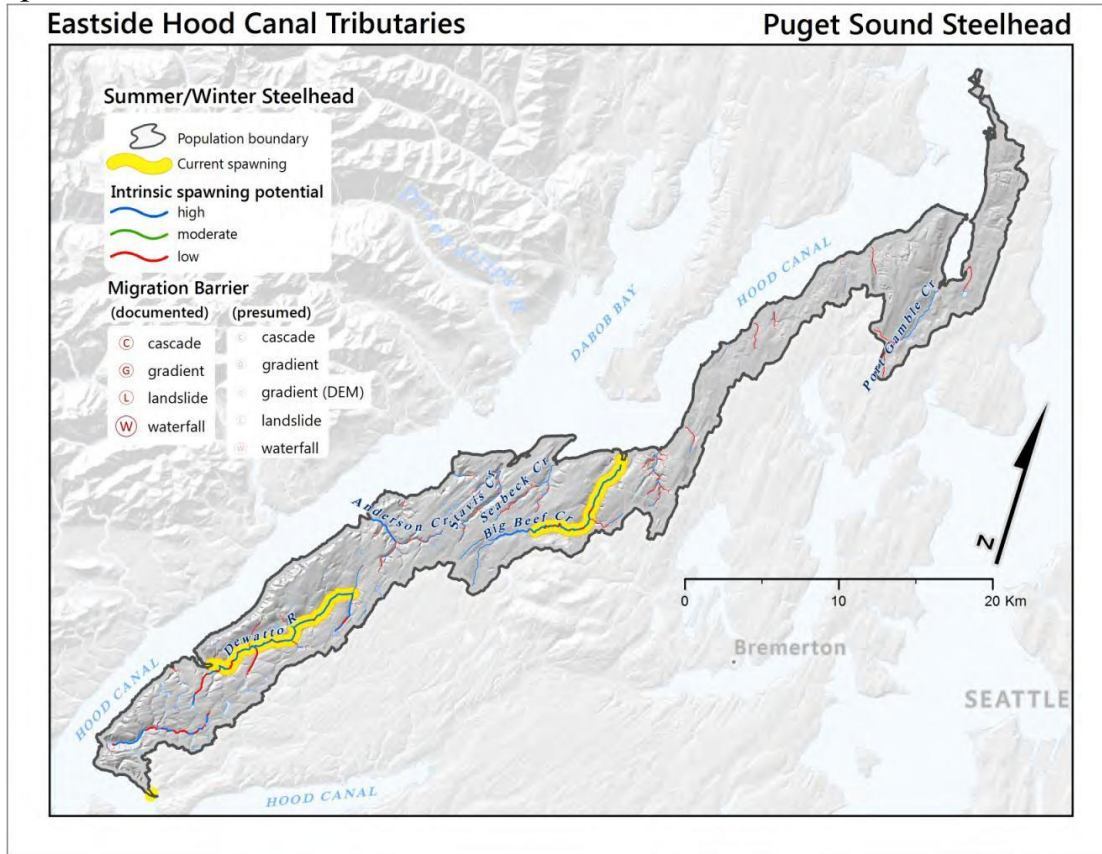


Diversity

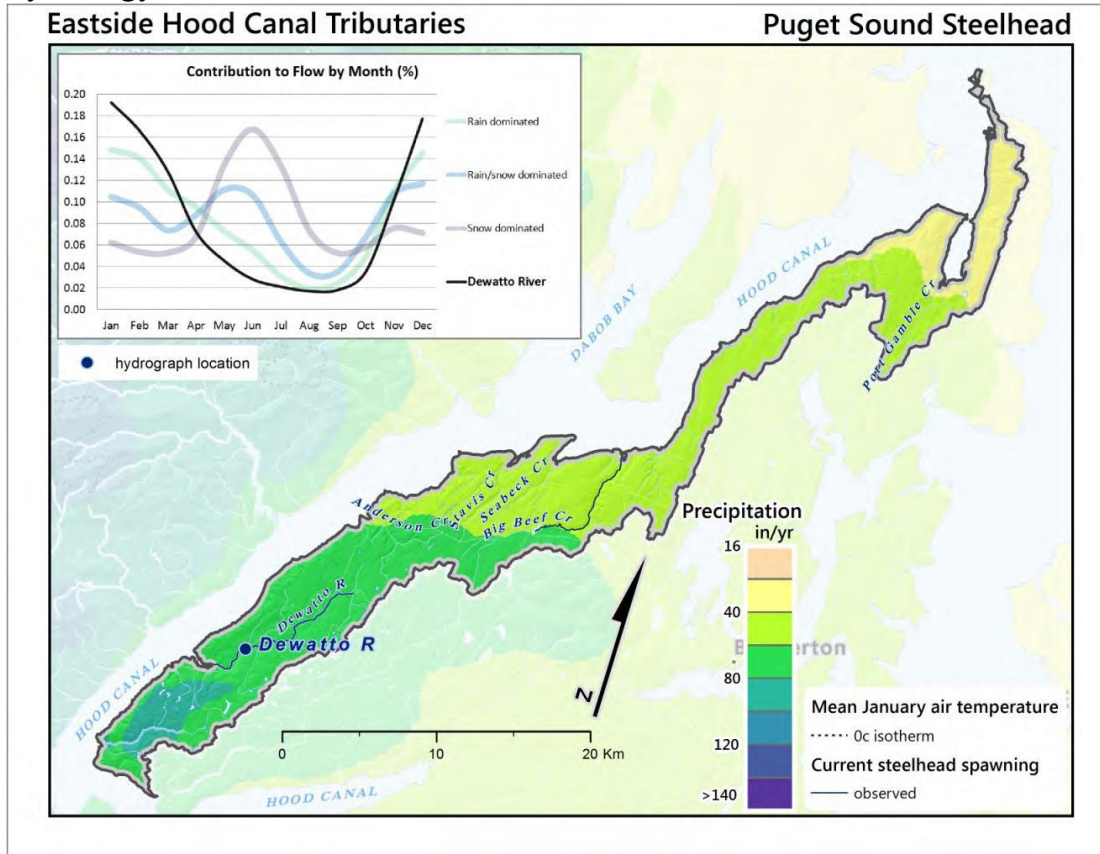
Hatchery Releases – Winter Run

East Hood Canal River Winter Run				Total Releases	
Watershed	Duration	Years	Source	(w/i DPS)	(o/s DPS)
Dewatto R	09-10	2	Native	14,183	
			Total	0	0

Spatial Structure

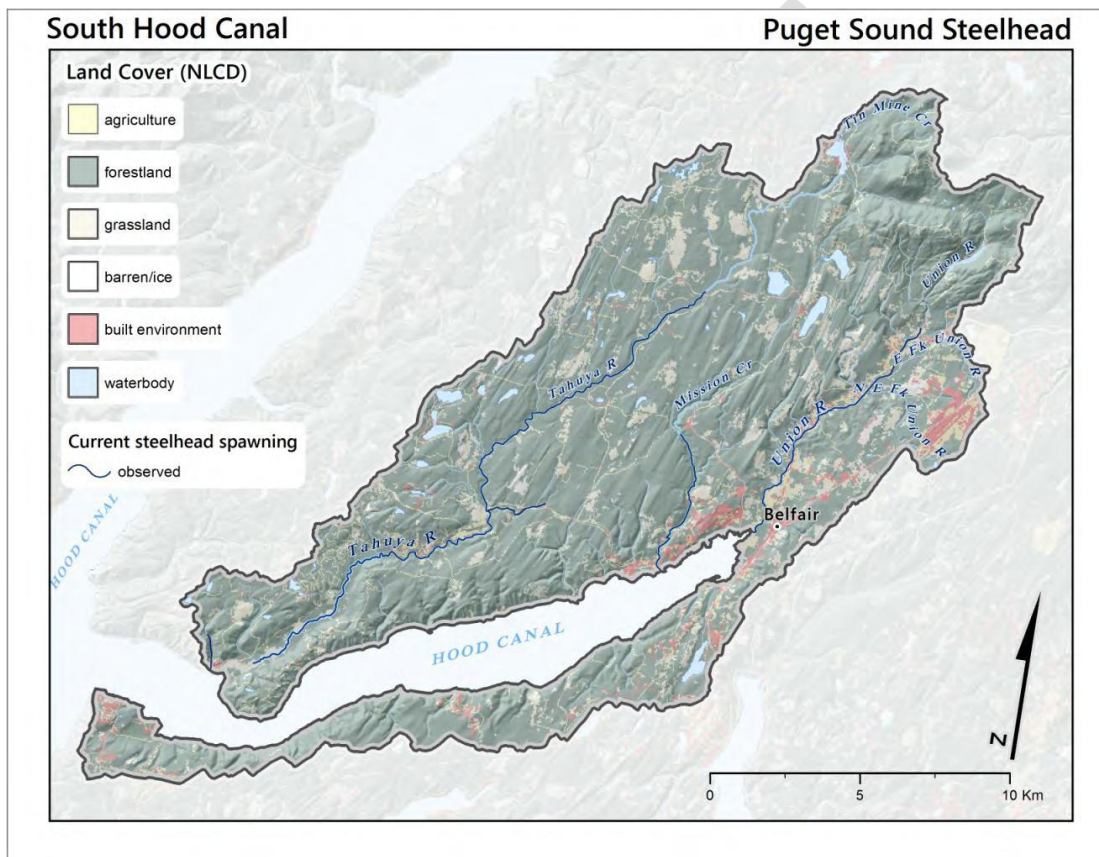


Hydrology



26. South Hood Canal (Tahuya and Union Rivers) Winter Run

Overview: This population includes winter steelhead spawning in independent tributaries on the southwest side of the Kitsap Peninsula (eastern shore of Hood Canal) including the Tahuya and Union rivers to the southern end of Hood Canal (Alderbrook and Twanoh creeks). The primary streams in this DIP include the Tahuya and Union rivers. Stream surveys conducted in 1932 give very general estimates of abundance with larger runs of steelhead in the Tahuya and Union rivers (WDG 1932).

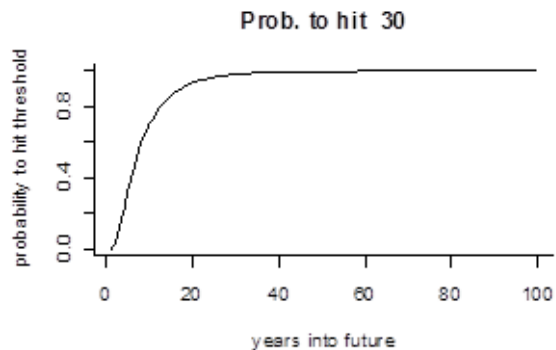
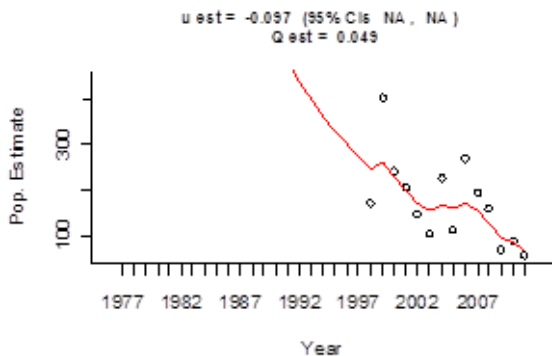


Abundance and Productivity

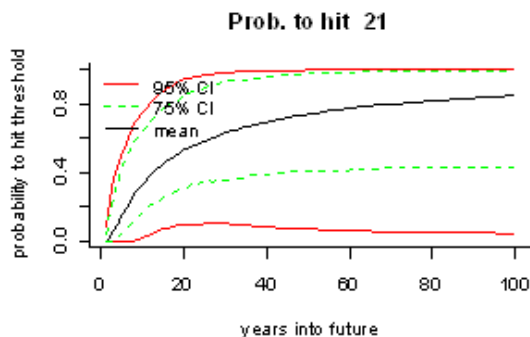
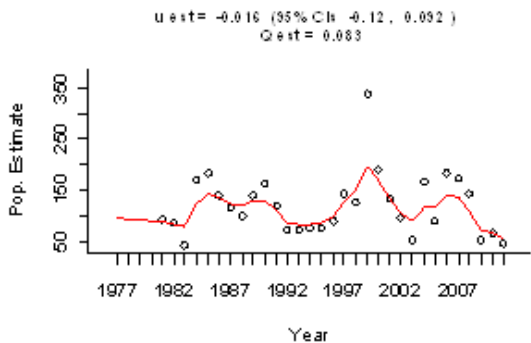
	WDF Survey	Punch Card Max	IP Estimate	
Abundance	NA	640	2,985	5,970
Year		1952		

Tributary	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011
Tahuya R	97	53	168	91	183	175	144	53	68	47
Union R	49	50	58	23	86	21	15	15	21	11

South Hood Canal:



Tahuya River:

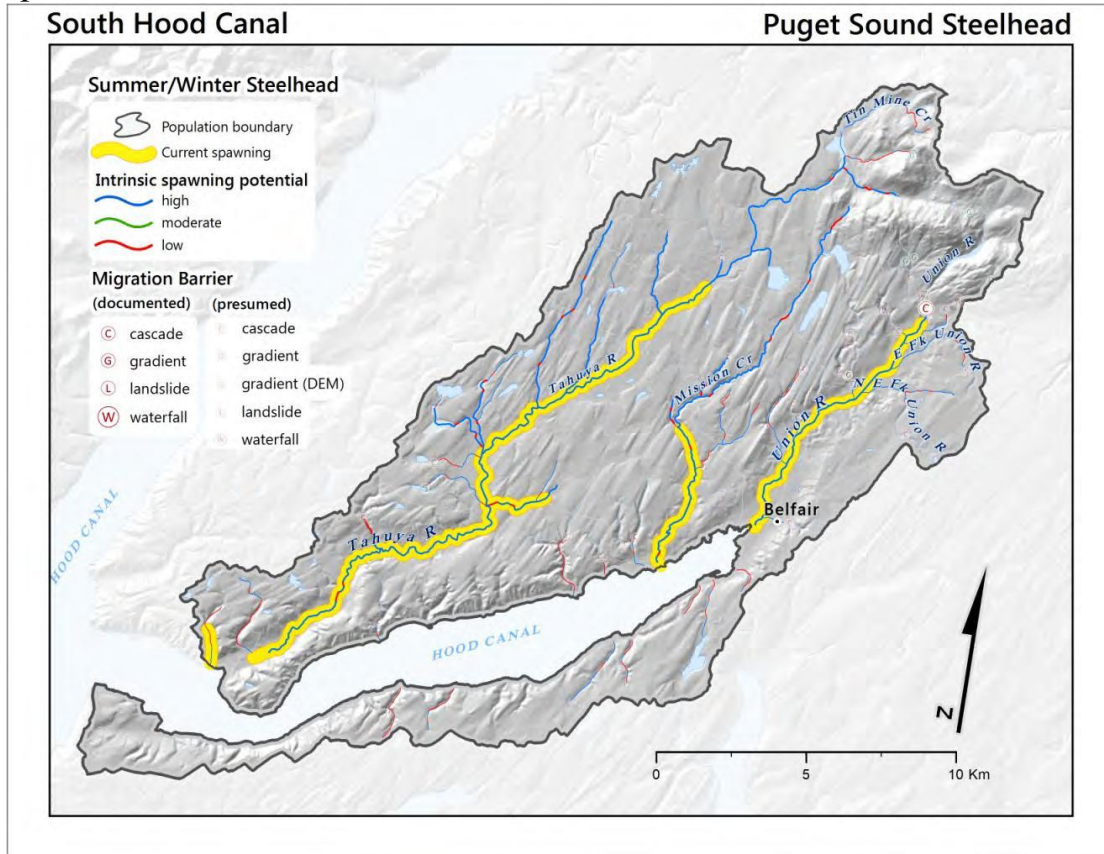


Diversity

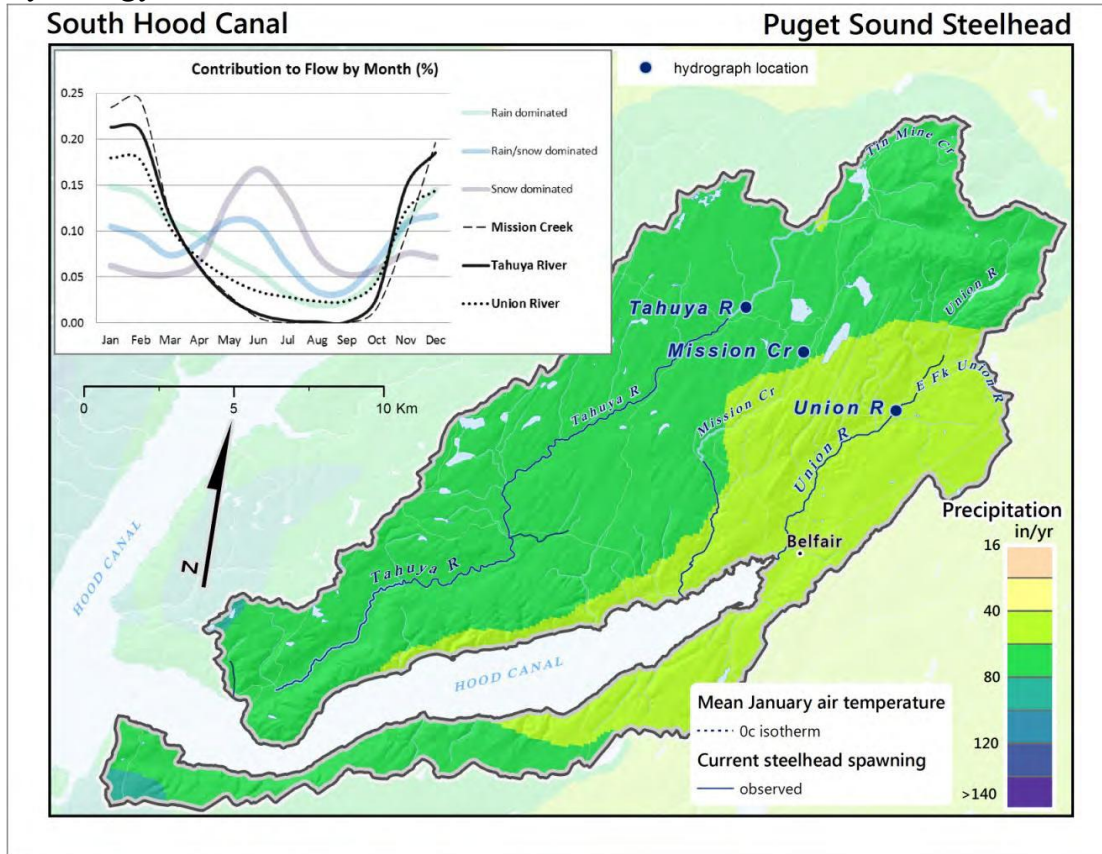
Hatchery Releases – Winter Run

South Hood Canal Winter Run				Total Releases	
Watershed	Duration	Years	Source	(w/i DPS)	(o/s DPS)
			Total	0	0

Spatial Structure

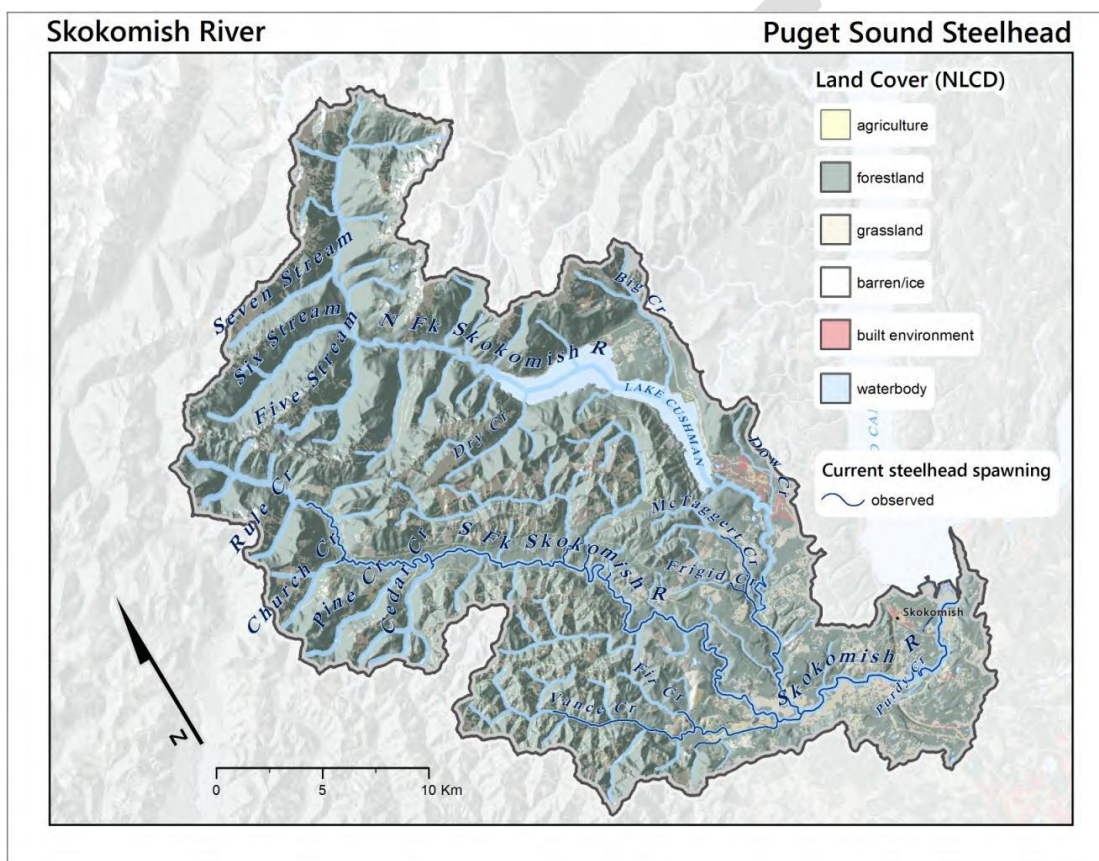


Hydrology



27. Skokomish River Winter Run

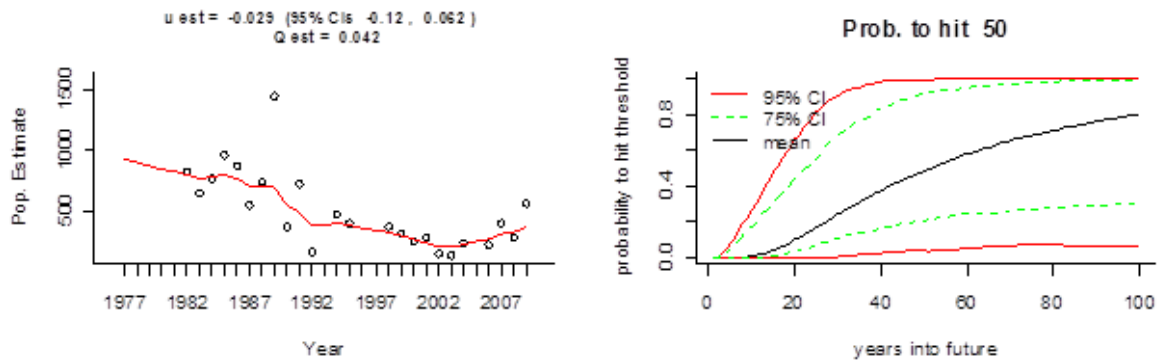
Overview: This population contains native winter-run steelhead in the North and South Forks of the Skokomish River. Much of the North Fork Skokomish River is currently inaccessible beyond Cushman Dam No. 2 (Rkm 27.8). Steelhead currently utilize both lowland tributaries (for example Vance Creek) and headwater areas of the South Fork Skokomish. There has been considerable debate as to whether winter run steelhead had access beyond the series of falls in the lower North Fork Skokomish River; steelhead may have had access at least to the Staircase Rapids at Rkm 48.1 (Williams et al. 1975).



Abundance and Productivity

	WDF Survey	Punch Card Max	Geometric Mean	IP Estimate	
Abundance	NA	693	355 (183 - 686)	10,030	20,060
Year		1952	2005-2009		

Population Skokomish River winter-run	Exp. trend ln(nat. spawners) (95% CI) 1985-2009 0.956 (0.932 - 0.979)
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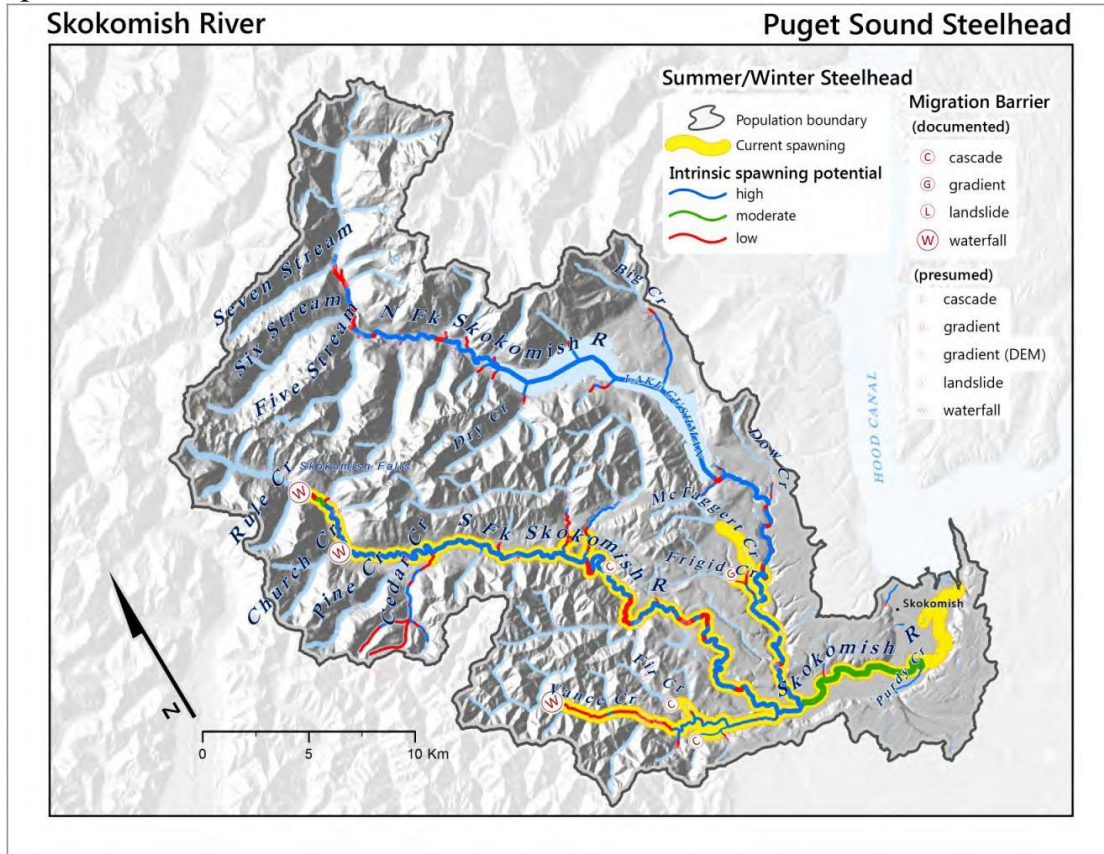


Diversity

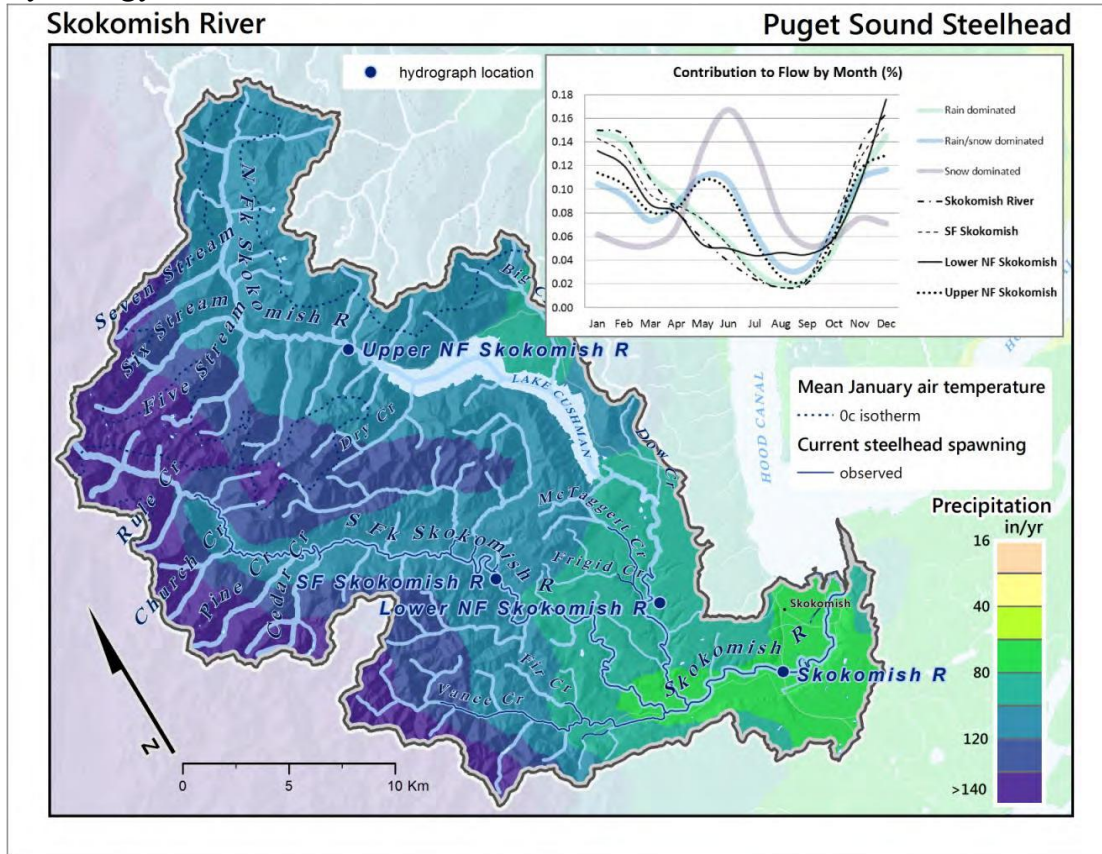
Hatchery Releases – Winter Run

Nooksack River Winter Run				Total Releases	
Watershed	Duration	Years	Source	(w/i DPS)	(o/s DPS)
SF Skokomish R	95-11	11	Eells Springs (CC)		450,198
Hunter Cr	96-97	2	Bogachiel H (CC)		43,351
			Total	0	0

Spatial Structure

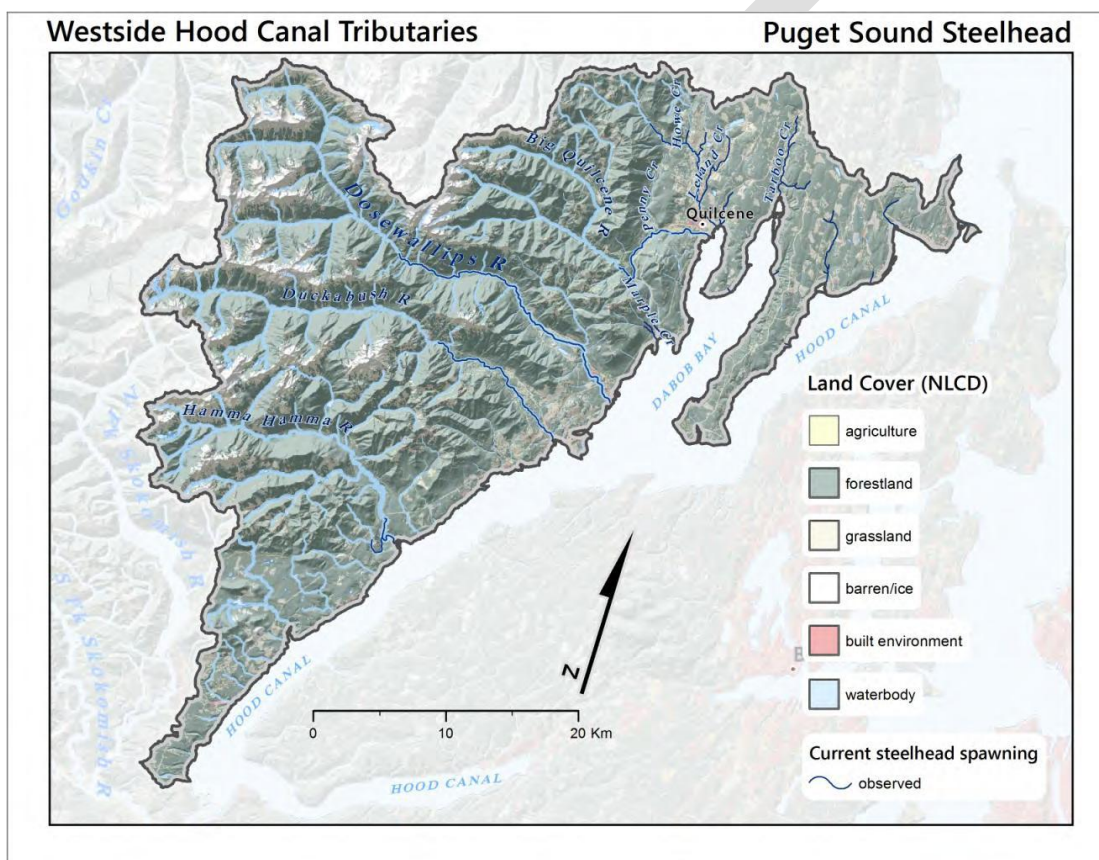


Hydrology



28. West Hood Canal Winter Run

Overview: This population combines winter-run steelhead from four SaSI stocks (WDFW 2005: Hamma Hamma, Duckabush, and Dosewallips rivers, and Quilcene/Dabob Bay. WDFW (2005) identified these as distinct stocks based on their geographic separation; however, genetically, resident, parr, and smolt *O. mykiss* from the Duckabush and Dosewallips cluster together relative to steelhead populations on the east side of the Hood Canal. All of these rivers drain the east slope of the Olympic Mountains, with falls or cascades blocking access to most of the higher elevation habitat.



Abundance and Productivity

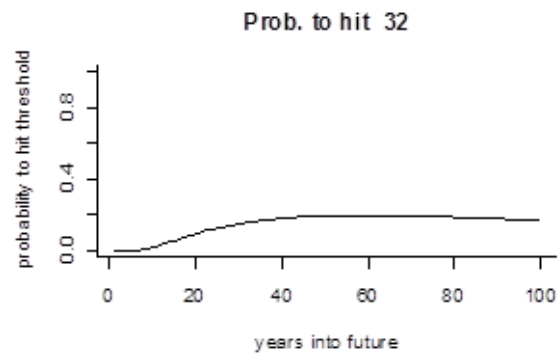
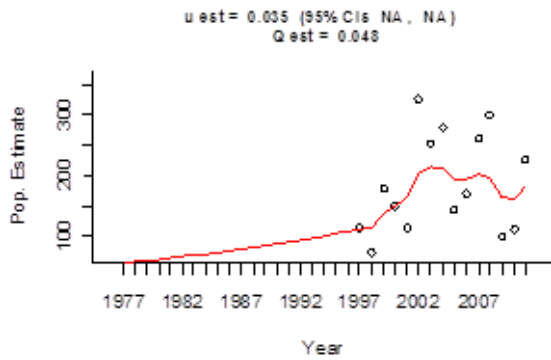
	WDF Survey	Punch Card Max	Geometric Mean	IP Estimate	
Abundance	Large	982*	208 (118 - 366)	3,608	7,217
Year	1932	1952	2005-2009		

*Hamma Hamma, Duckabush, Dosewallips, and Quilcene rivers. This year includes some hatchery returns.

Population	Exp. trend ln(nat. spawners) (95% CI) 1985-2009
West Hood Canal winter-run	1.022 (0.997 - 1.048)

Tributary	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011

Hamma Hamma R	230	134	214	123	73	193	198	81	42	45
Duckabush R	16	8	29	10	21	16	18	12	29	120
Dosewallips R	52	96				15	42			31
Quilcene R	30	16	36	9	76	39	41	6	41	31

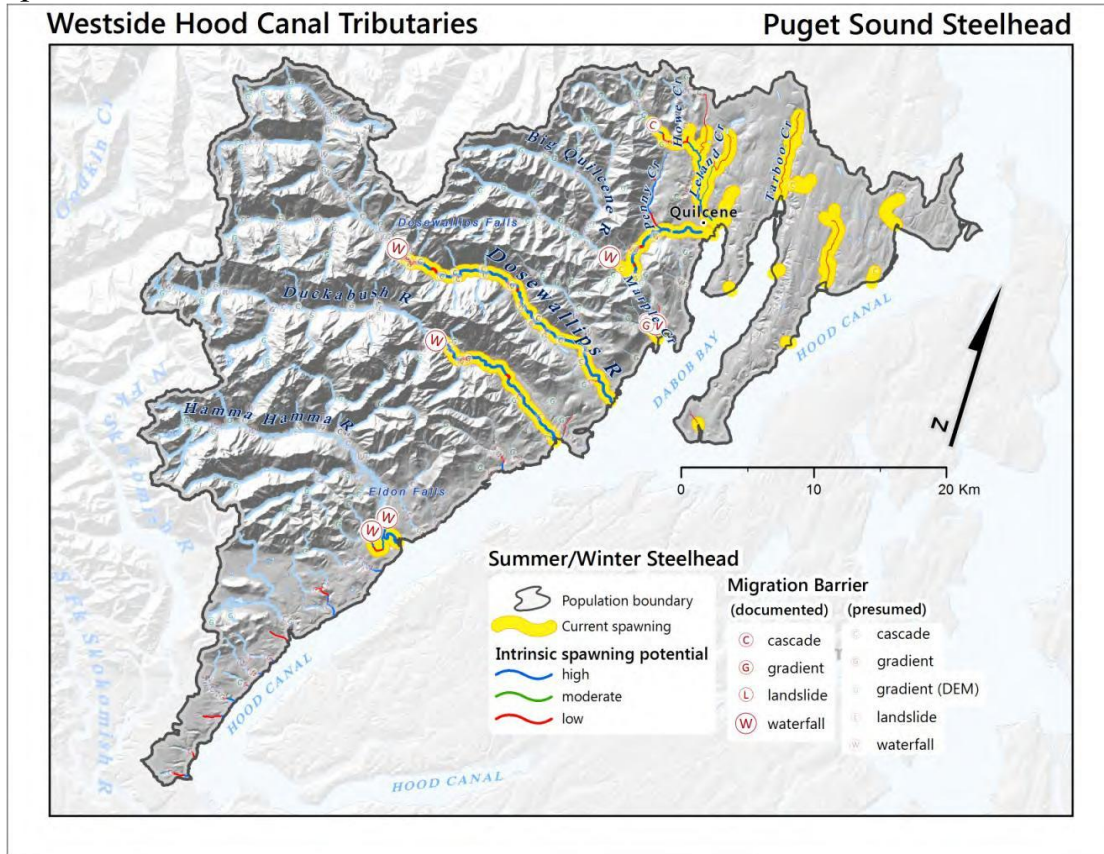


Diversity

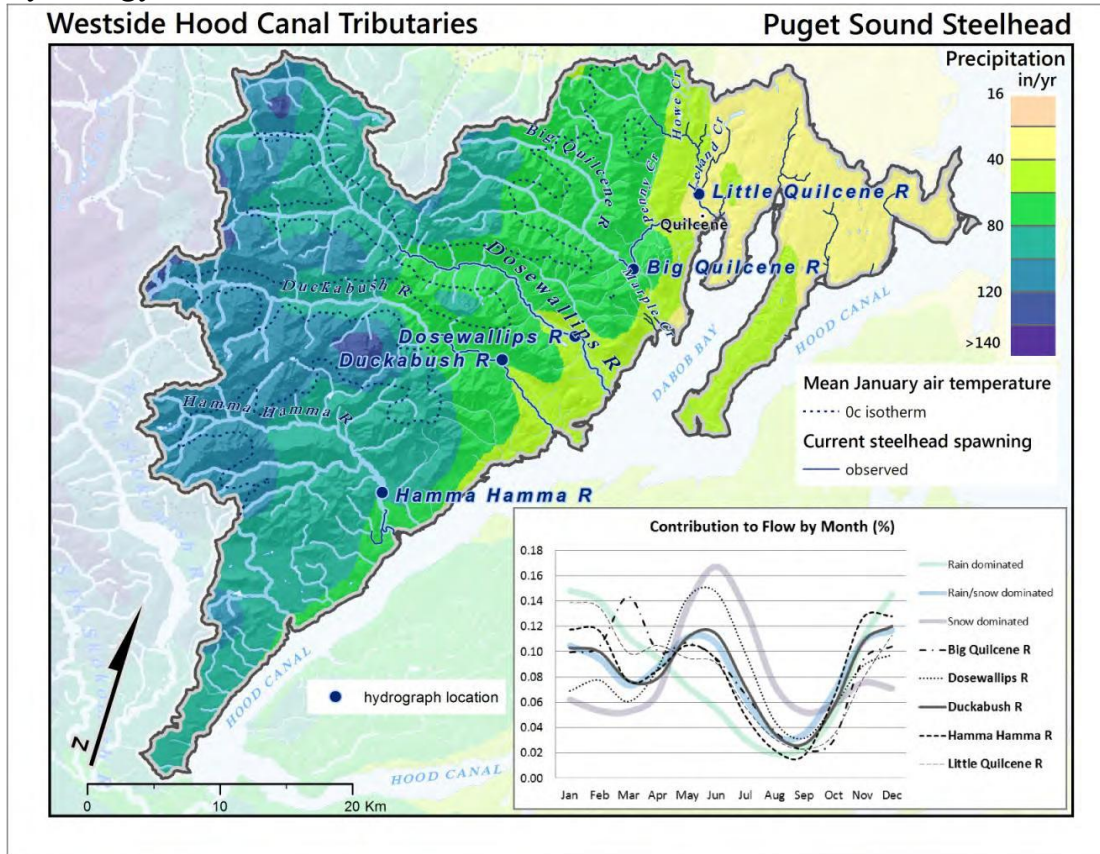
Hatchery Releases – Winter Run

West Hood Canal Winter Run				Total Releases	
Watershed	Duration	Years	Source	(w/i DPS)	(o/s DPS)
Dosewallips R	95-03	7	Bogachiel H		80,142
Duckabush R	95-03	7	Bogachiel H		65,860
Duckabush R	09-10	2	Native	6,595	
Hamma Hamma	00-05	5	Native	7,306	
John Cr (HH)	00-05	4	Native	2,837	
			Total	0	0

Spatial Structure

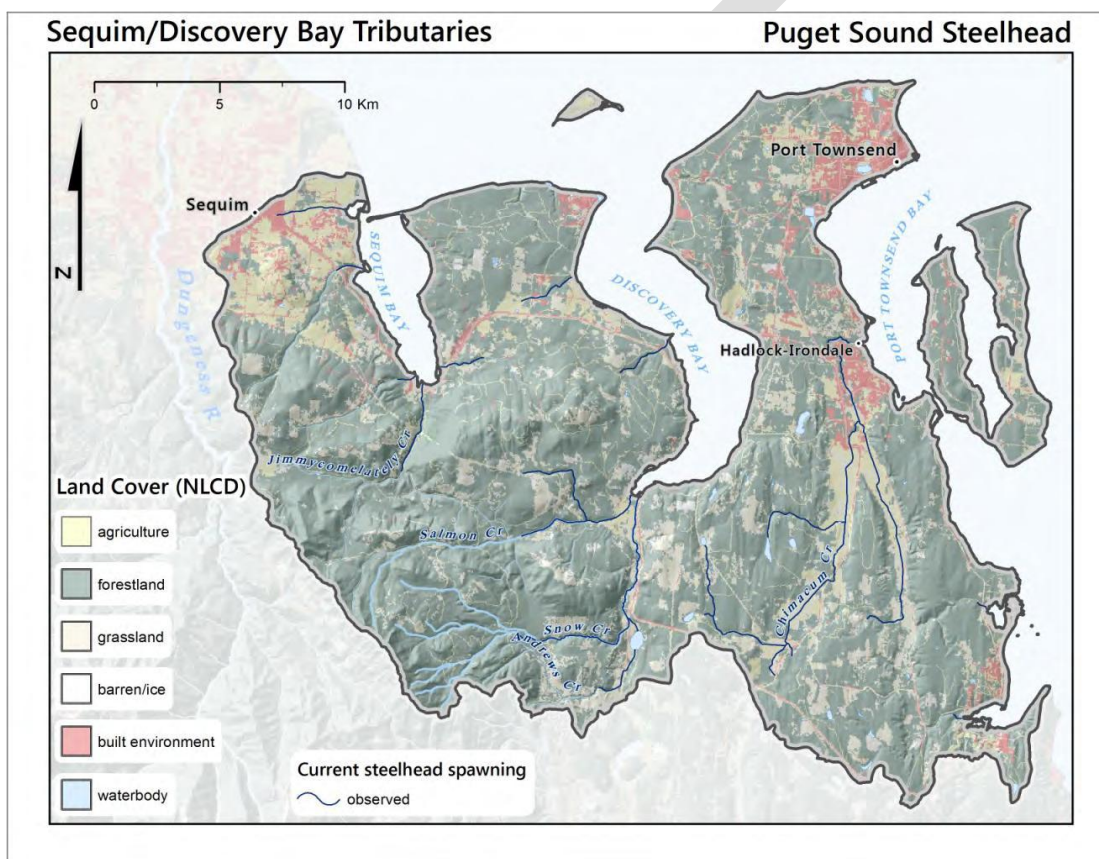


Hydrology



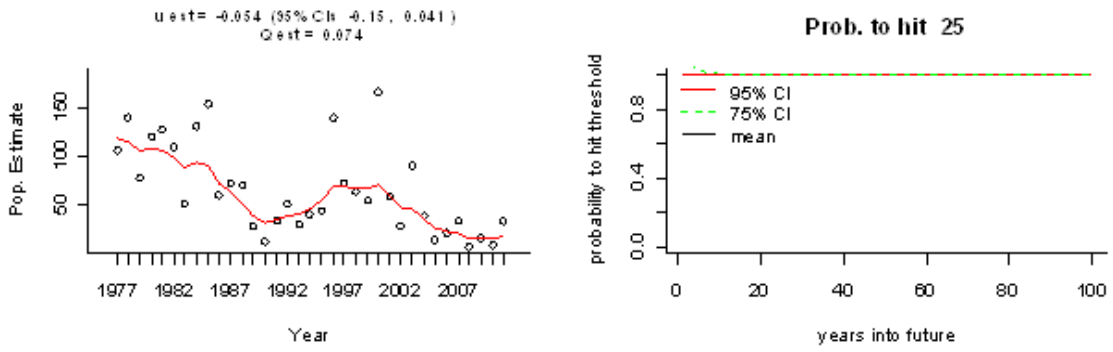
29. Strait of Juan de Fuca Lowland Tributaries (Sequim Bay and Discovery Bay) Winter Run

Overview: This population combines two SaSI stocks, Sequim Bay and Discovery Bay, and includes winter-run steelhead that occupy streams in the Quimper Peninsula (Pt. Townsend) that were not included in the WDFW (2005) stock list. The entire population is located within the Puget Lowland Ecoregion and stream flows are rain-dominated with many streams lacking surface flow during summer. Although the basin size for this DIP, 802 km², is well above the minimum, the majority of the area contains relatively small independent streams.



Abundance and Productivity

	WDF Survey	Punch Card Max	Geometric Mean	IP Estimate
Abundance	NA	200		512 1,024
Year		1962		

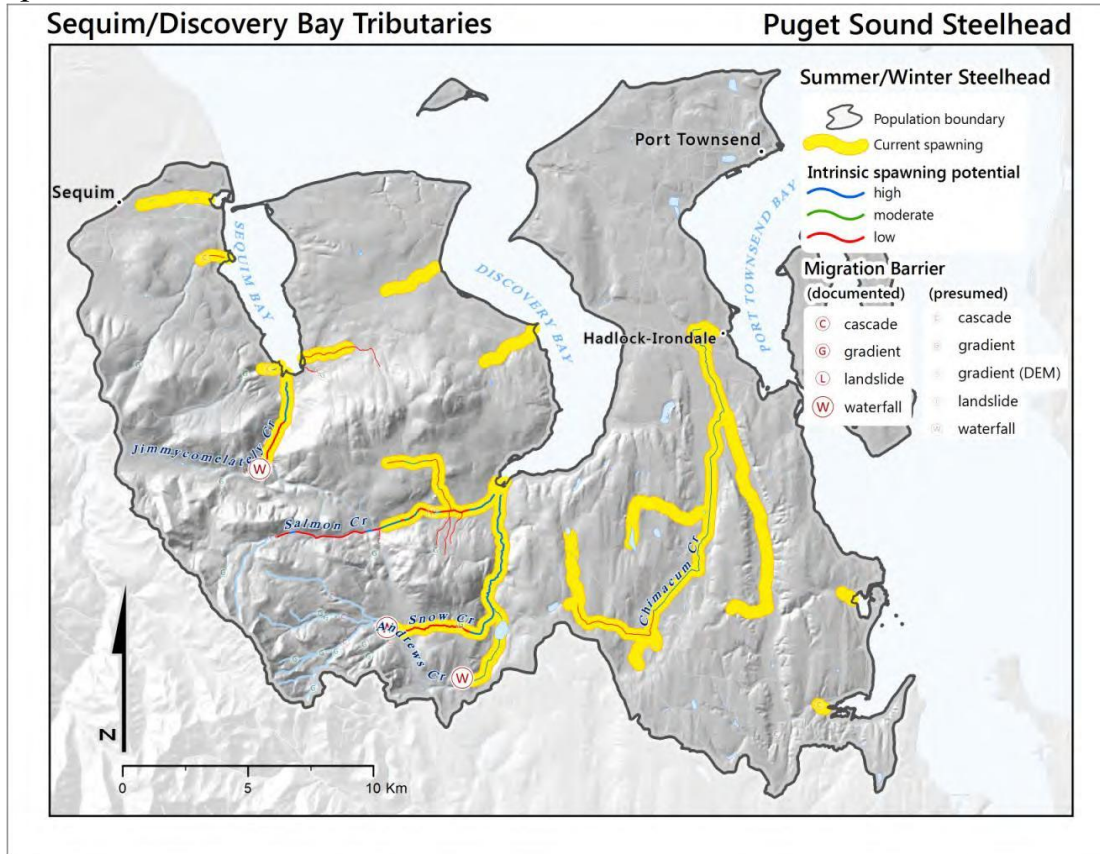


Diversity

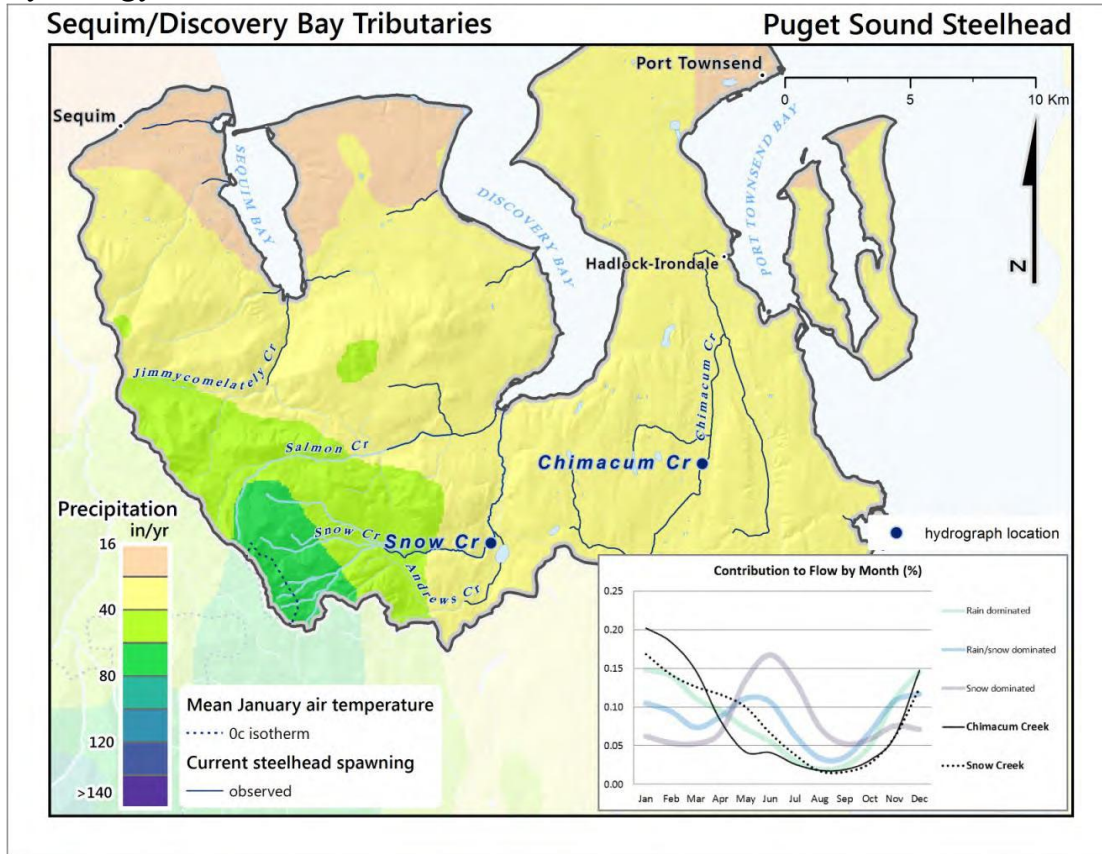
Hatchery Releases – Winter Run

Sequim & Discovery Bay River Winter Run				Total Releases	
Watershed	Duration	Years	Source	(w/i DPS)	(o/s DPS)
			Total	0	0

Spatial Structure

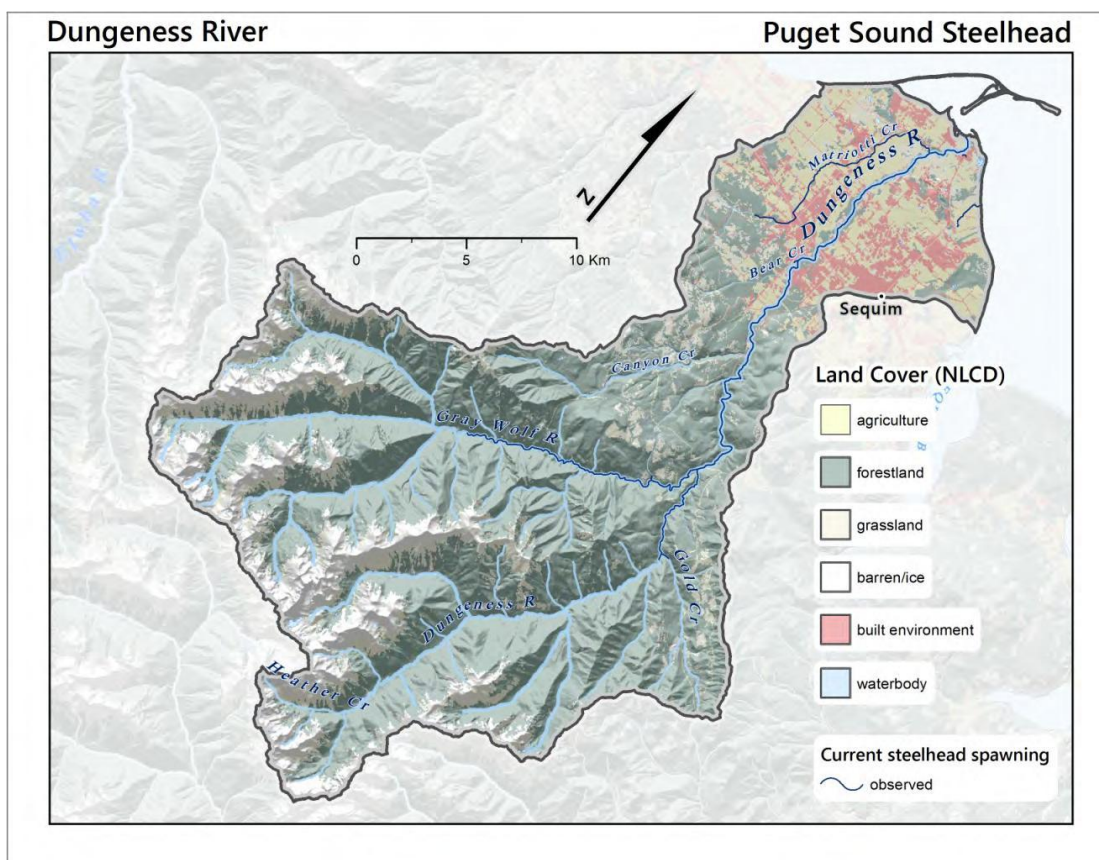


Hydrology



30. Dungeness River Winter Run

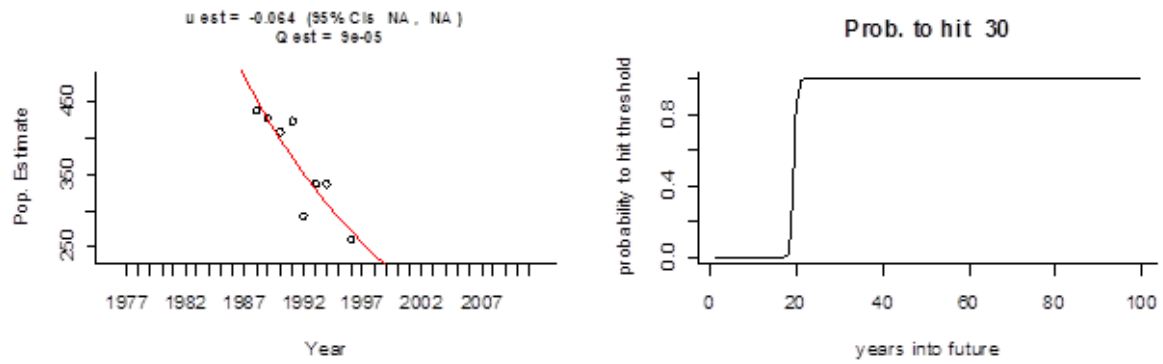
Overview: This population includes steelhead spawning in the mainstem Dungeness and Grey Wolf rivers. Much of the mainstem and upper headwaters are glacially influenced. Anecdotal information indicates that this population was historically quite abundant.



Abundance and Productivity

	WDF Survey	Punch Card Max	Geometric mean	IP Estimate
Abundance	NA	348		2,039
Year		1946	2005-2009	

Population	Exp. trend ln(nat. spawners) (95% CI) 1985-2009
Dungeness River winter-run	0.926 (0.909 - 0.943)

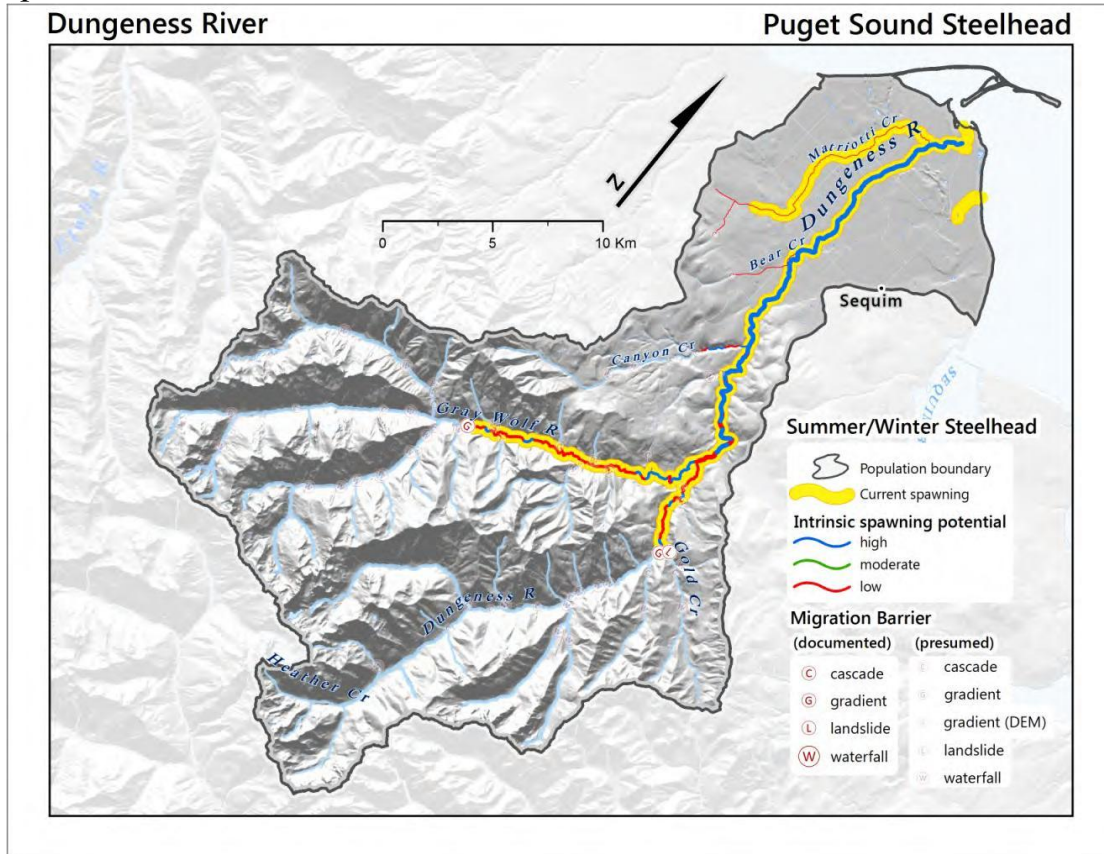


Diversity

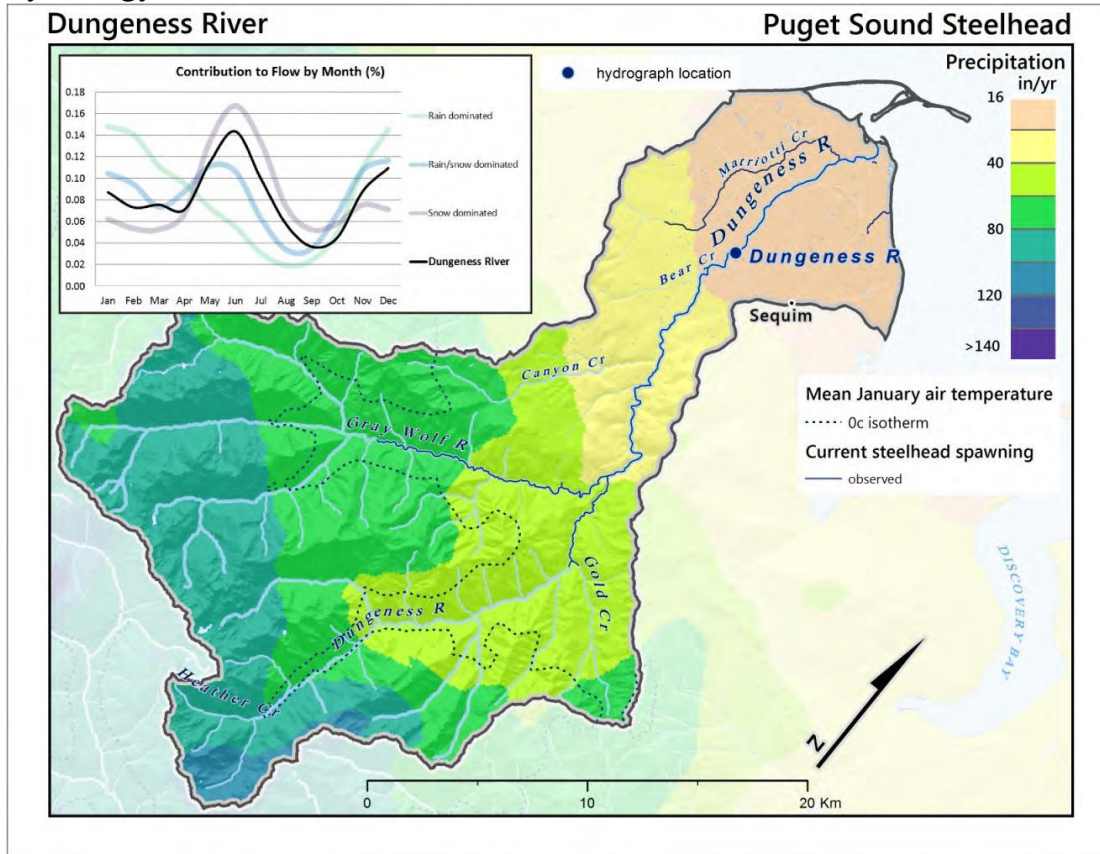
Hatchery Releases – Winter Run

Dungeness River Winter Run				Total Releases	
Watershed	Duration	Years	Source	(w/i DPS)	(o/s DPS)
Dungeness	95-10	16	Bogachiel/Dungeness (CC)		158,427
			Total	0	0

Spatial Structure

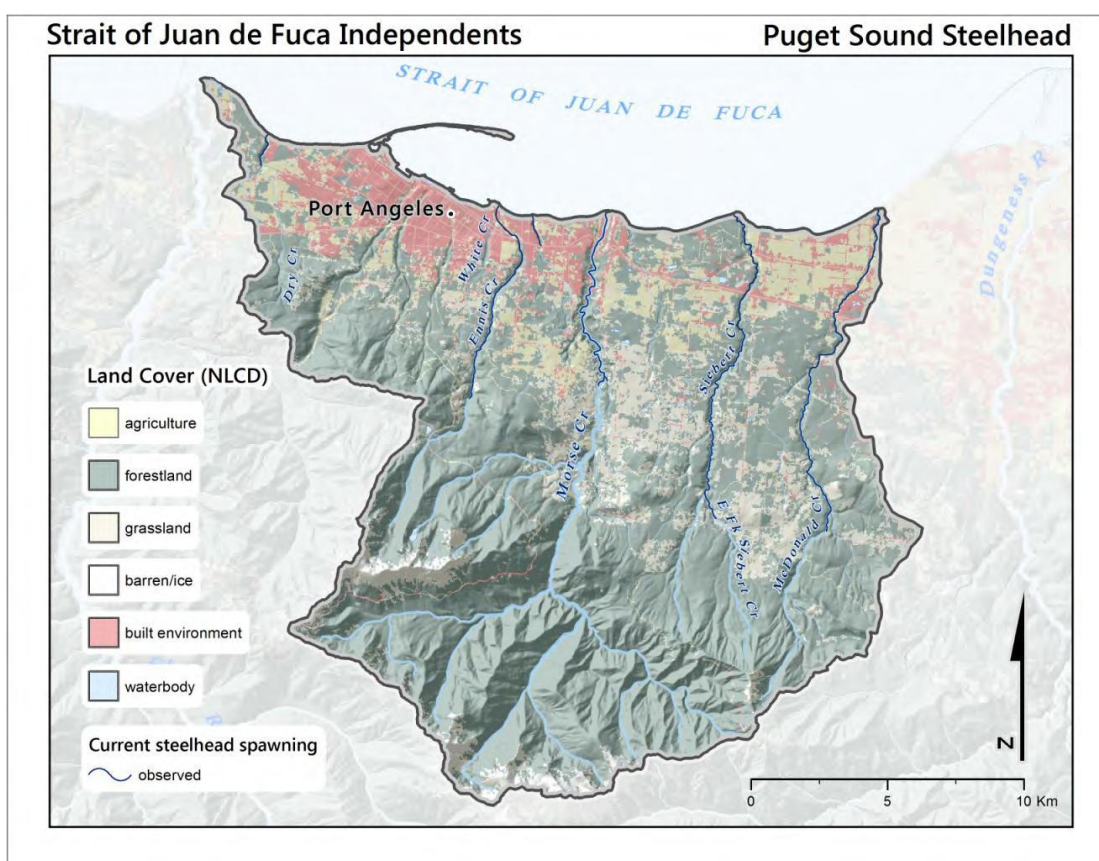


Hydrology



31. Strait of Juan de Fuca Independent Tributaries Winter Run

Overview: This population consists of steelhead spawning in small independent tributaries to the Strait of Juan de Fuca between the Dungeness and Elwha rivers, including Ennis, White, Morse, Siebert, and McDonald creeks. While each of the tributaries is relatively small, collectively, the creeks cover a 410 km² watershed.



Abundance and Productivity

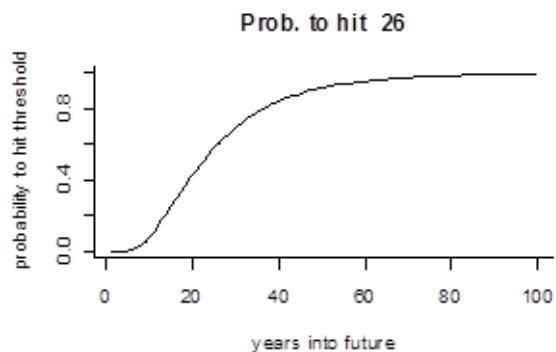
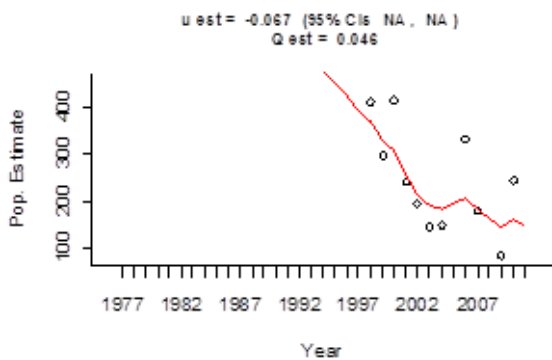
	WDF Survey	Punch Card Max	Geometric Mean	IP Estimate	
Abundance	NA	258*	147 (53 - 405)	728	1,456
Year		1958	2005-2009		

*Includes Morse and McDonald creeks only.

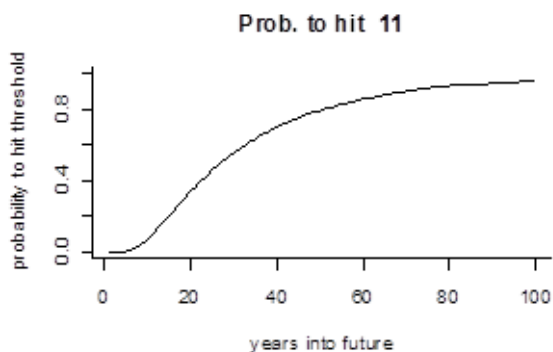
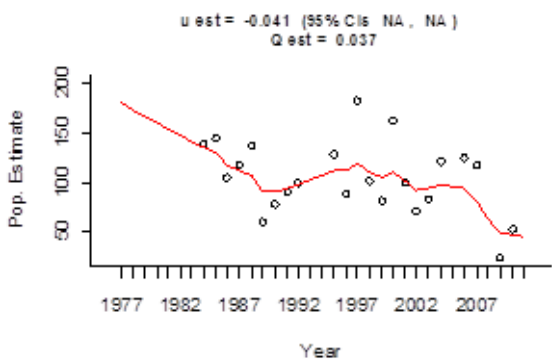
Population	Exp. trend ln(nat. spawners) (95% CI)
SJF winter-run	0.964 (0.899 - 1.031)

Tributary	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011
Morse Creeks	71	84	121		124	118		24		
McDonald Cr	125	63	29	89	206	63	49	63	193	

Strait of Juan de Fuca Independents:



Morse Creek:

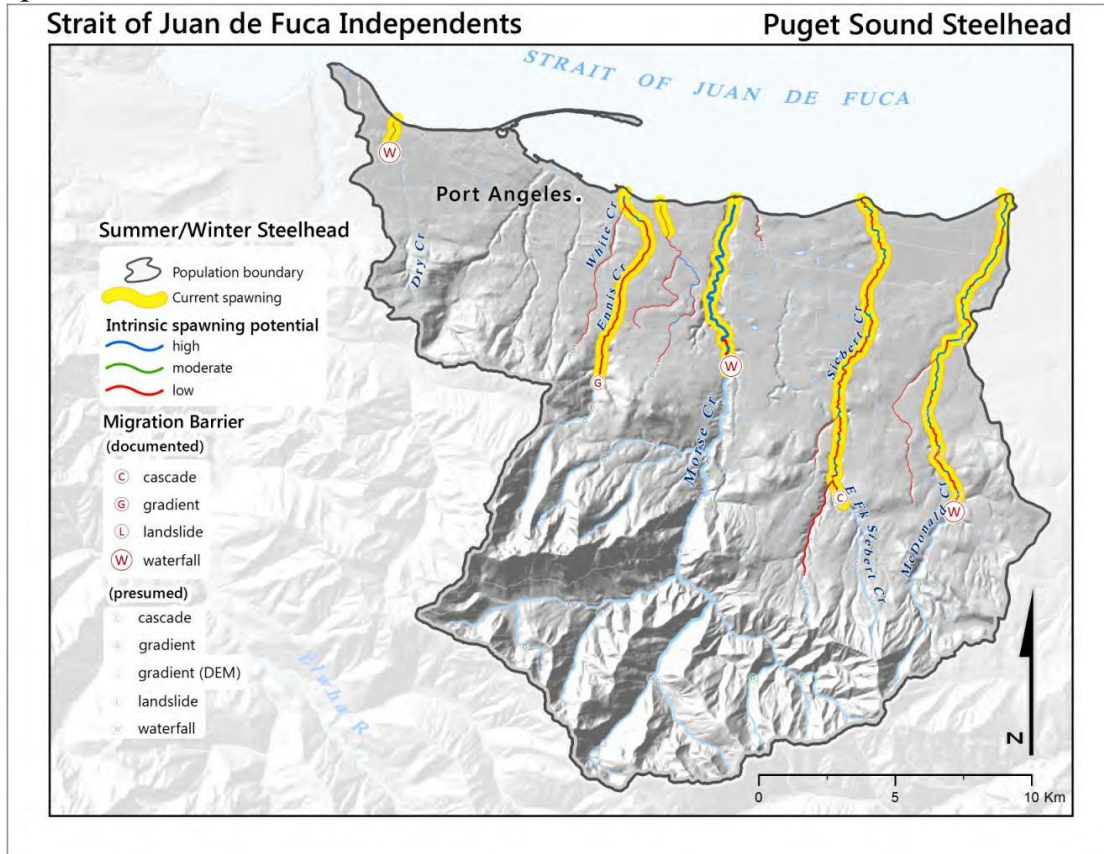


Diversity

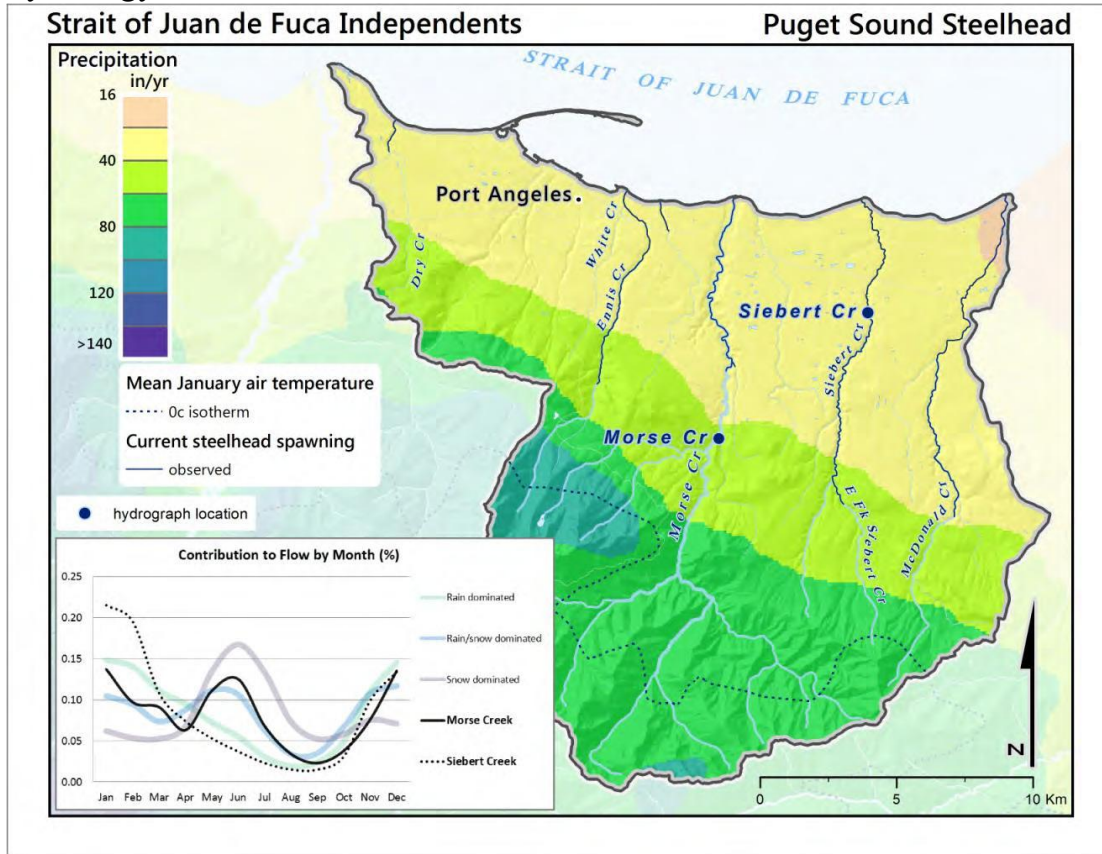
Hatchery Releases – Winter Run

Strait of Juan de Fuca River Winter Run				Total Releases	
Watershed	Duration	Years	Source	(w/i DPS)	(o/s DPS)
Morse Cr.	95-04	10	Bogachiel H.		60,115
			Total	0	0

Spatial Structure

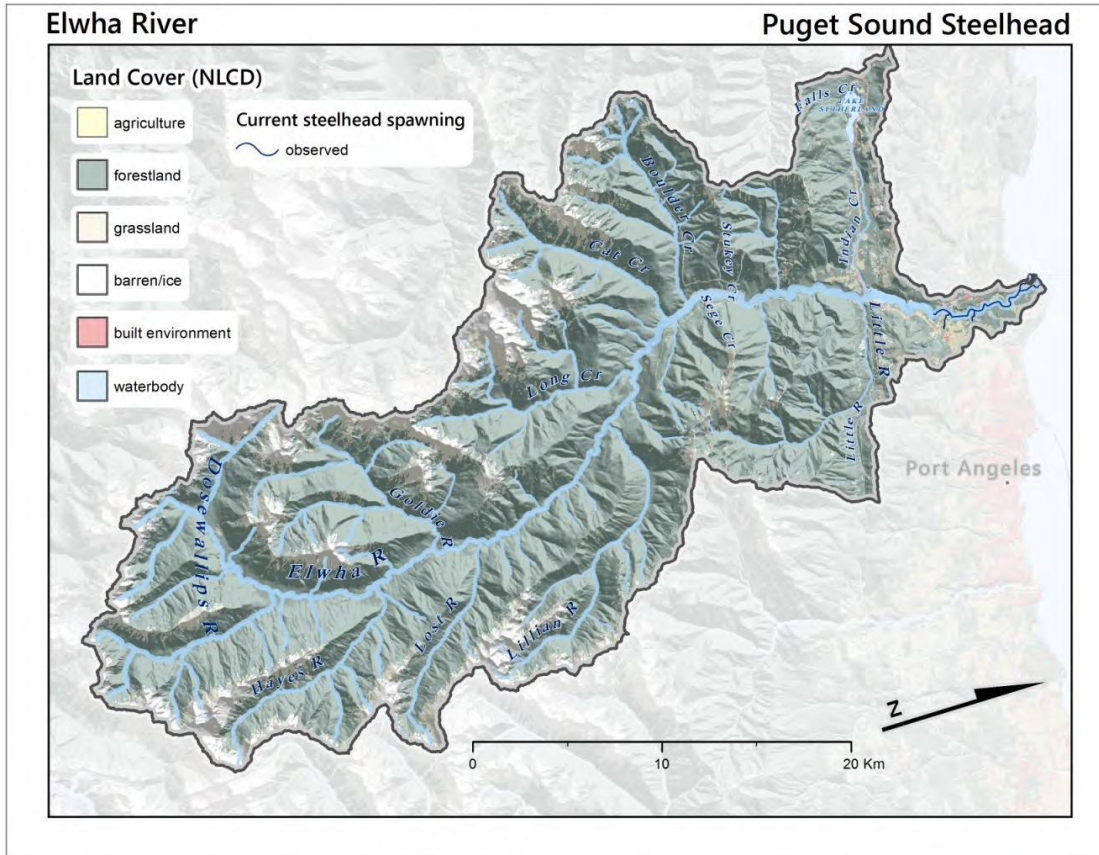


Hydrology



32. Elwha River Winter Run

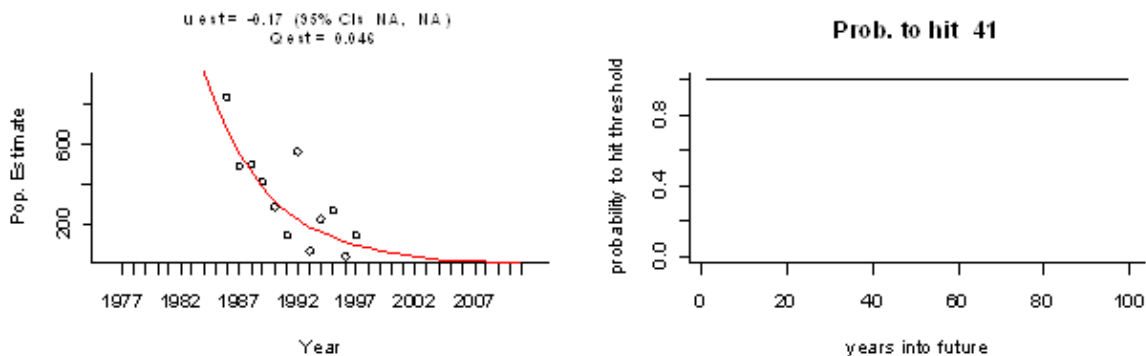
Overview: Winter run steelhead were historically present in the Elwha River Basin, although little is known of their distribution of life history diversity prior to the construction of the two Elwha River Dams in the early 1900s. Currently only 8 Km of lowland mainstem habitat is accessible in the lower Elwha River. Ongoing dam removal activities will allow access to the entire basin in the near future.



Abundance and Productivity

	WDF Survey	Punch Card Max	Geometric Mean	IP Estimate
Abundance		746		7,116 14,231
Year		1952		

Population	Exp. trend ln(nat. spawners) (95% CI) 2005-2009
Elwha River winter-run	0.840 (0.749 - 0.943)



Diversity

Hatchery Releases – Winter Run

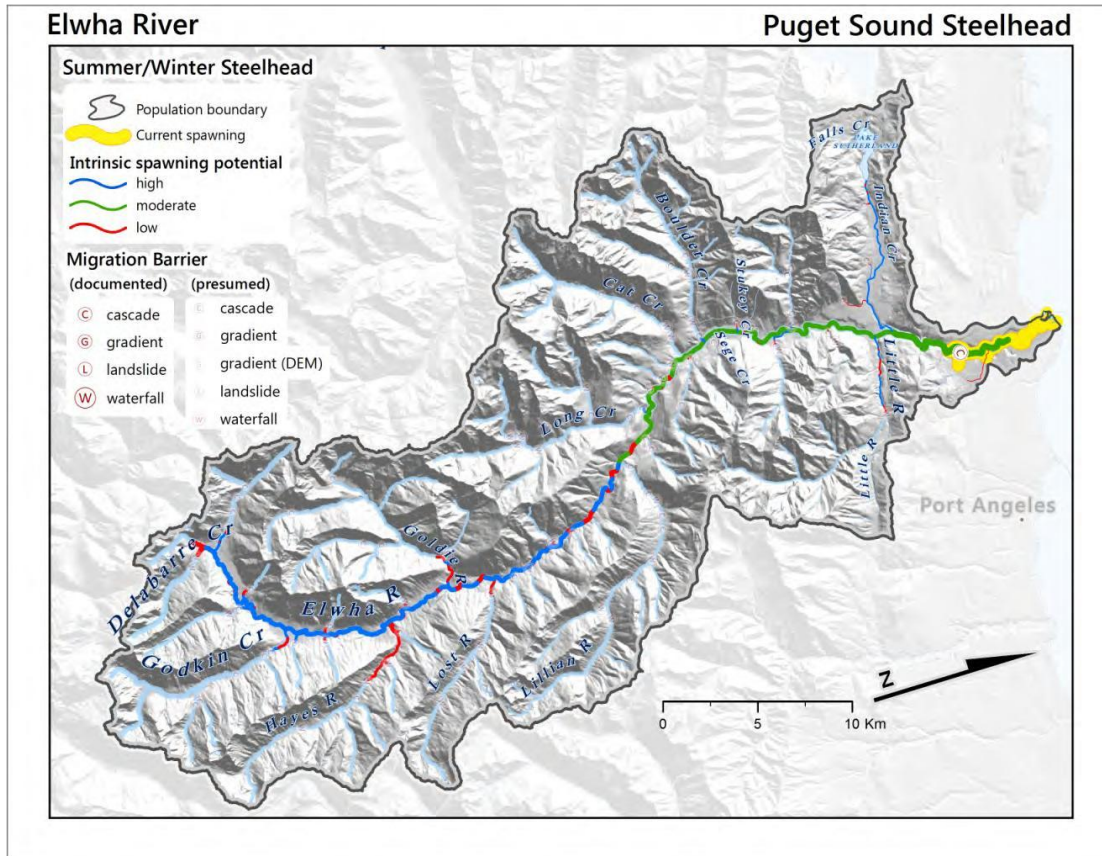
Elwha River Winter Run				Total Releases	
Watershed	Duration	Years	Source	(w/i DPS)	(o/s DPS)
Elwha R.	95-10	16	Elwha/Bogachiel (CC)	0	2,036,243
			Total	0	0

Hatchery Releases – Summer Run

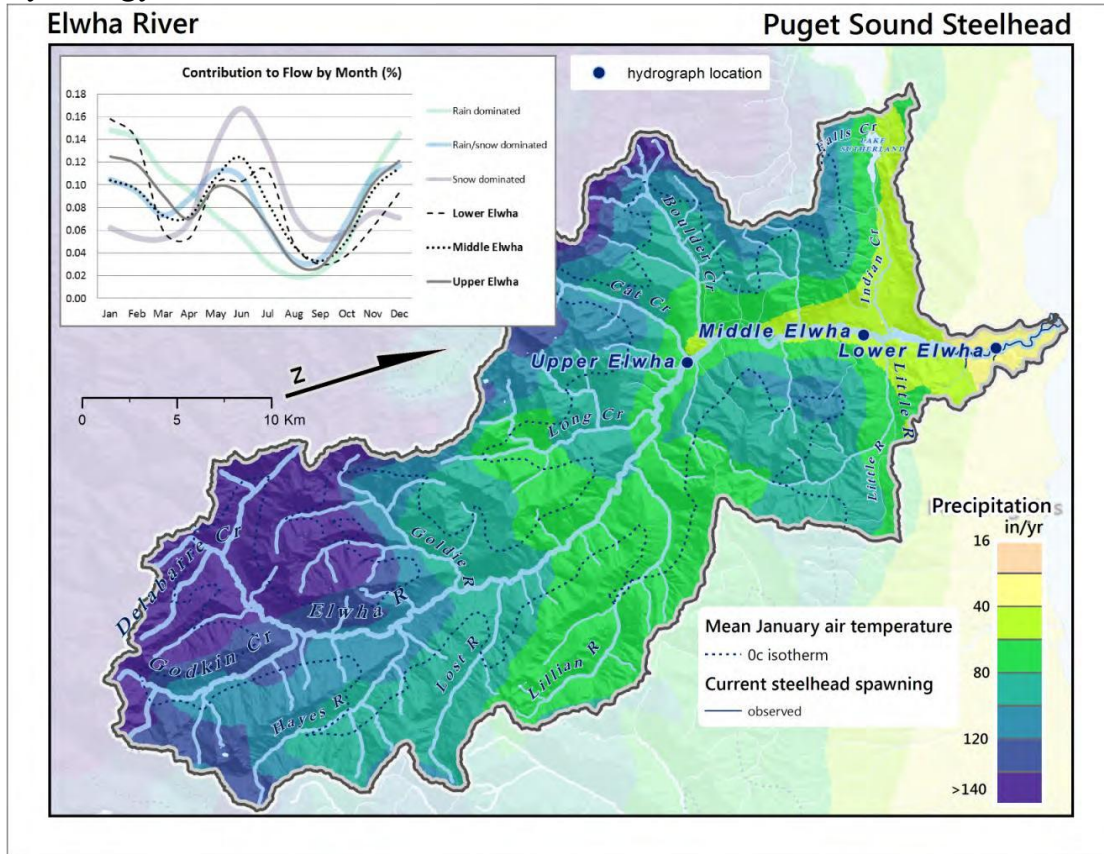
Elwha River Winter Run				Total Releases	
Watershed	Duration	Years	Source	(w/i DPS)	(o/s DPS)
Elwha R.	95-00	16	Bogachiel (SK)	0	85,445
			Total	0	0

Spatial Structure

The two Elwha River dams constructed in the early 1900s at Rkm 7.9 and Rkm 21.6 are presently being removed.



Hydrology



Appendix E

Interim Abundance-Based Viability Guidelines for Puget Sound Steelhead

Assessment of DPS viability is rooted in the evaluation of demographically independent population VSP parameters. From a recovery planning standpoint, however, viability criteria for Puget Sound steelhead are more easily understood from a DPS to DIP—i.e., a top down—perspective. In part this reflects the nature of the challenge the TRT faces in identifying population-specific viability criteria for Puget Sound steelhead. In contrast to Chinook salmon, *O. tshawytscha*, the quality and quantity of data on steelhead abundance and life history are much more limited. Although there have been a number of recent efforts by the co-managing agencies to consolidate existing databases and to expand sampling (especially genetic sampling), the TRT is only able to assess VSP status for roughly 50-70% of the 32 DIPs in the DPS. In developing DIP-level viability criteria the TRT had to compare the metrics that are most biologically relevant to viability with those that are available, or may become available in the foreseeable future. While this process continues, there is a desire by public, governmental, and tribal entities to begin recovery efforts. As an interim measure, the TRT recommends the use of DIP abundance goals to support initial recovery planning. Existing DPS and MPG level viability criteria (described below) provide the framework for developing recovery scenarios. Interim abundance criteria were estimated using the Intrinsic Potential (IP) model and correspond to different levels of sustainability (see Appendix C).

1. Those DIPs selected for achieving “viable” status should maintain a four-year average spawner abundance specified by a 5% smolt-to-adult survival rate (SAS, see Table E-1).
2. Of the remaining populations in each MPG, at least 75% of the populations should maintain four-year average spawner abundances specified by a 1% SAS rate (Table E-1).
3. Finally, the remaining 25% of the populations in each MPG should not be allowed to degrade below their current level of abundance.
4. Spawner counts will consider “naturally produced” adults only, not including those naturally produced fish that are known to be descended from out-of-DPS lineages.

In addition to these abundance thresholds, the TRT recommends the following actions to address information needs while recovery planning is pursued:

1. Juvenile and adult monitoring efforts should be expanded into DIPs with little or no current monitoring.
2. Genetics samples should be acquired in those DIPs that are currently not represented.
3. Selected DIPs (or subbasins within DIPs) should be intensively monitored for life stage survivals.
4. Selected DIPs (or subbasins within DIPs) should be monitored to estimate the contribution of resident *O. mykiss* to anadromous escapement.
5. Selected DIPs (or subbasins within DIPs) should be monitored to estimate the influence of hatchery introductions.

Given the current status of most DIPs in the Puget Sound Steelhead DPS, these abundance levels are well above current abundance estimates. It falls upon the recovery planning entities to determine which populations are to be recovered to full viability. Under any potential scenario it is likely that considerable time and effort will be required to reach the viability criteria. Under these circumstances there appears to be little risk to establishing interim abundance goals.

DRAFT

Final Review Draft—May Be Circulated With Authors' Consent

Table E-1. Interim DIP abundance goals for steelhead in Puget Sound, based on a four-year average. Abundance goals for summer-run fish (red) are still under review. QET, quasi extinction threshold; SAS, smolt to adult survival. Minimum abundance = 100 (Low Abundance), 250 (Viable).

POPULATION BASIN				QET	Low Abundance	Viabile	Capacity
Population Name	Area KM2	Mean Elev. (m)	Total Stream Len. (m)		1 % SAS	5 % SAS	20 % SAS
Baker River	771	999	421,859	36	503	2,514	10,056
Canyon Creek	100	864	47,716	24	100 (12)	250 (60)	243
Cedar River	650	461	402,349	35	595	2,975	11,899
Deer Creek	180	761	105,313	31	157	786	3,144
Drayton Harbor	223	37	206,057	26	243	1,213	4,852
Dungeness River	564	978	306,740	30	246	1,232	4,930
Eastside Hood Canal Tributaries	342	99	174,736	27	127	635	2,540
Eastside Kitsap Peninsula Tributaries	703	75	259,413	25	156	779	3,115
Elwha River	833	1,021	472,871	41	712	3,558	14,231
Green River	1,444	463	834,472	69	1,977	9,884	39,537
Nisqually River	1,991	524	1,030,771	55	1,533	7,665	30,660
Nookachamps Creek	183	252	159,503	27	123	616	2,462
Nooksack River	1,982	619	1,257,480	73	2,205	11,023	44,091
North Fork Skykomish River	156	1,195	117,602	25	100 (66)	331	1,325
North Lake Washington Tributaries	978	119	441,887	36	527	2,634	10,536
Pilchuck River	356	253	242,383	34	519	2,597	10,386
Puyallup River	1,395	672	803,817	58	1,472	7,358	29,432
Samish River/Bellingham Bay Tributaries	661	203	453,694	31	319	1,596	6,386
Sauk River	1,897	1,132	1,079,263	103	2,323	11,615	46,460
Sequim/Discovery Bay Tributaries	557	197	234,042	25	100 (51)	256	1,024
Skagit River	5,543	1,098	2,815,113	157	6,478	32,388	129,551
Skokomish River	634	570	411,699	50	1,003	5,015	20,060
Snohomish/Skykomish River	1,595	420	1,021,690	73	2,139	10,695	42,779
Snoqualmie River	1,615	620	1,134,038	58	1,674	8,370	33,479
South Fork Nooksack River	172	926	99,347	27	114	568	2,273
South Hood Canal	295	126	216,935	30	299	1,493	5,970
South Sound Tributaries	1,860	84	582,451	42	985	4,927	19,709
Stillaguamish River	1,230	398	927,234	67	1,912	9,559	38,236
Strait of Juan de Fuca Independents	403	611	246,441	26	100 (73)	364	1,456
Tolt River	182	784	117,732	25	100 (32)	250 (160)	641
Westside Hood Canal Tributaries	1,433	715	842,382	32	361	1,804	7,217
White River	1,285	1,061	863,251	64	1,749	8,745	34,981
				1,462	30,449	153,194	613,662

Appendix F

Identifying Key Factors Influencing the Population Dynamics and Productivity of Steelhead

The intrinsic and extrinsic factors that influence the abundance and demographic dynamics of coastal steelhead populations, which are often small and variable, are typically difficult to identify. Fish survival, growth, age, and fertility all affect individual fitness and, consequently, population productivity, but it is usually difficult to determine which of these factors is more important than another for a particular population. Although demographic trends can be estimated from time series of periodic (e.g., annual) census data, determining the mechanisms underlying these trends requires at a minimum estimating the basic vital rates of survival, growth, and fertility. Ascertaining these factors can help to illuminate particular aspects of the life history that are contributing to population decline or increasing the risk to viability. Determining whether a population is stable or declining is a primary objective of conservation, but uncovering the mechanisms underlying these states is critical to identifying sustainable conservation and recovery strategies.

In an attempt to provide some insight into the factors that might constrain viability or enhance productivity in coastal steelhead populations, in this section we apply a population viability analysis (PVA) to a population of wild steelhead to assess trend, dynamics, and extinction risk. We follow this with an analysis of these dynamics in combination with information on individual survival, size and estimated growth, and fertility. Recent theoretical advances in understanding how demography and adaptation affect population dynamics, combined with powerful genetic approaches to identify relationships among individuals, provide a much more powerful set of tools for achieving these aims than has previously been available. When coupled with careful, regular monitoring of population abundance and key characteristics of potential breeders, such as size, age, fecundity, and timing of breeding, the ability to effectively reconstruct molecular pedigrees for wild populations using DNA markers allows unprecedented opportunities to dissect the components of population dynamics.

To this end we analyze demographic and genetic data collected from a small wild population of steelhead from Sashin Creek, Baranof Island, Alaska (see Thrower and Joyce 2004; Thrower and Hard 2009). The population is enumerated annually as the individuals pass through a monitoring weir which permits collection of all migrating adults and juveniles. The data collected include size (length in mm), adult sex, and stream entry and exit timing. We estimated age and fecundity (number of returning adult offspring) from a molecular pedigree we reconstructed for the anadromous adults in the creek during this period from a set of 13 polymorphic DNA microsatellite markers using the software FRANz 0.99 (Riester et al. 2009). FRANz uses a full Bayesian probability model to assign parentage; for these data we set the threshold for parentage assignment at 95%.

The temporal trend in the size of the anadromous population between 1986 and 2011 is shown in the upper left panel of Figure F-1. A PVA applied to this time series with the 'MARSS' package (v. 2.3, Holmes and Ward 2011) in R (R Development Core Team 2012) indicates that, over this period, the population is declining at a rate of 3.4% annually, corresponding to a

population growth rate of 0.967; the process variance (variance thought to arise from genetic or demographic stochasticity or from random environmental variation), σ_p^2 , is estimated at 0.00019. The MARSS model, which is described more fully in the main text of this report, uses a state-space framework to project the population's dynamics 100 years into the future. What this PVA indicates is that, based on the observed trend, the population is likely to reach a minimum threshold size of 10 adults within 20-25 years (upper right and lower left panels); over the next 17-27 years, the population is expected to decline by up to 50% if current conditions persist (lower right panel).

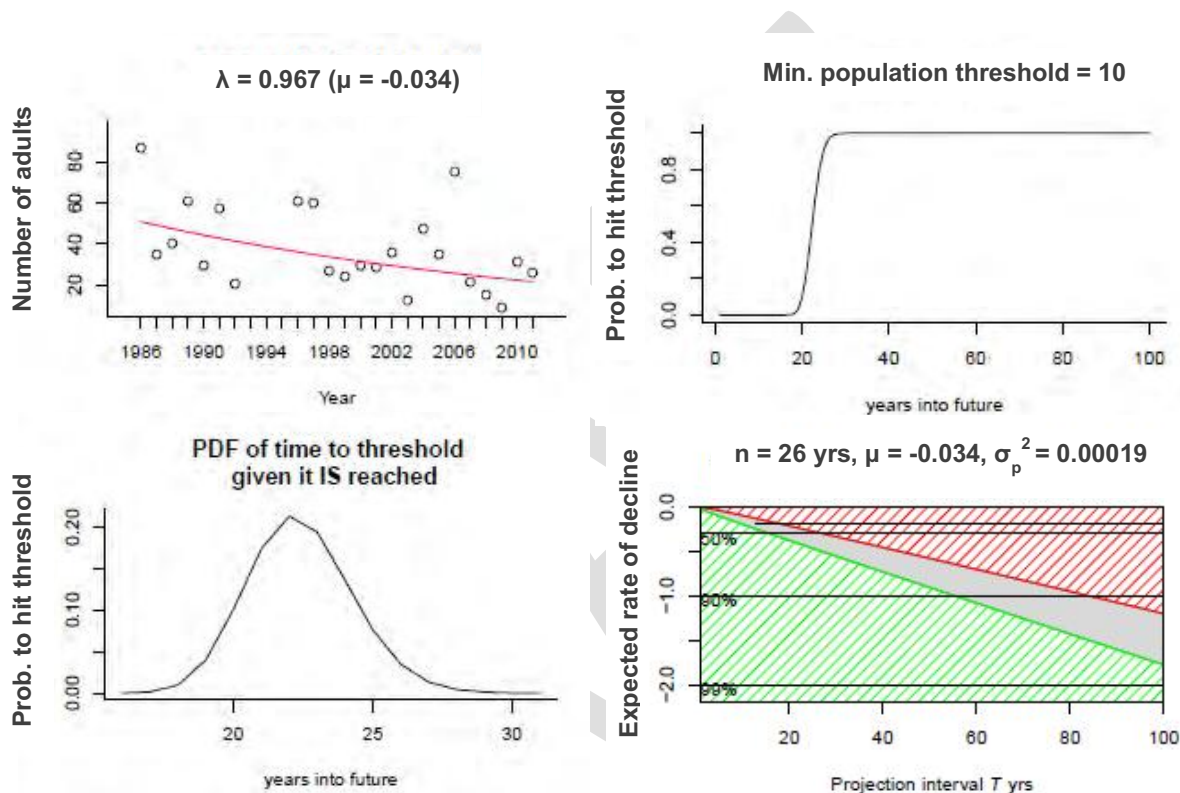


Figure F-1. Population viability analysis of wild Sashin Creek (Alaska) steelhead, based on a time series of adult escapement between 1986 and 2011. The PVA was conducted with the ‘MARSS’ package (v. 2.3, Holmes and Ward 2011) in R (R Development Core Team 2012; see text).

What the PVA alone does not—and cannot—tell us is what is driving these dynamics. To aid this effort, we need additional information, and another approach. One approach is to examine how particular phenotypes contribute directly to population productivity. Coulson et al. (2006) and Pelletier et al. (2007) developed a method they called “de-lifing,” which essentially estimates how population growth rate varies when individuals are removed sequentially from the population with replacement. The method is akin to the jackknifing procedure common in statistical practice. De-lifing fits linear models that estimate the relationships between fitness, measured here as lifetime reproductive success, and phenotypic variation, and then examines

how population productivity changes with these variables. The analysis indicates that males residing longer in the stream make significantly higher contributions to population productivity ($P < 0.05$); there is a tendency for larger females to contribute more to productivity but these results are not significant ($P > 0.05$). The analysis is summarized graphically in Figure F-2. In this figure, contour plots of relative fitness for males and females sampled from the pedigree suggest that large females tend to have higher fitness; stream entry and residence time information obtained from the molecular pedigree suggests further that larger males that remain in the stream longer have higher fitness, while the large females that spawn and then return to the ocean within 2-3 weeks tend to have higher fitness.

Contribution to population growth rate

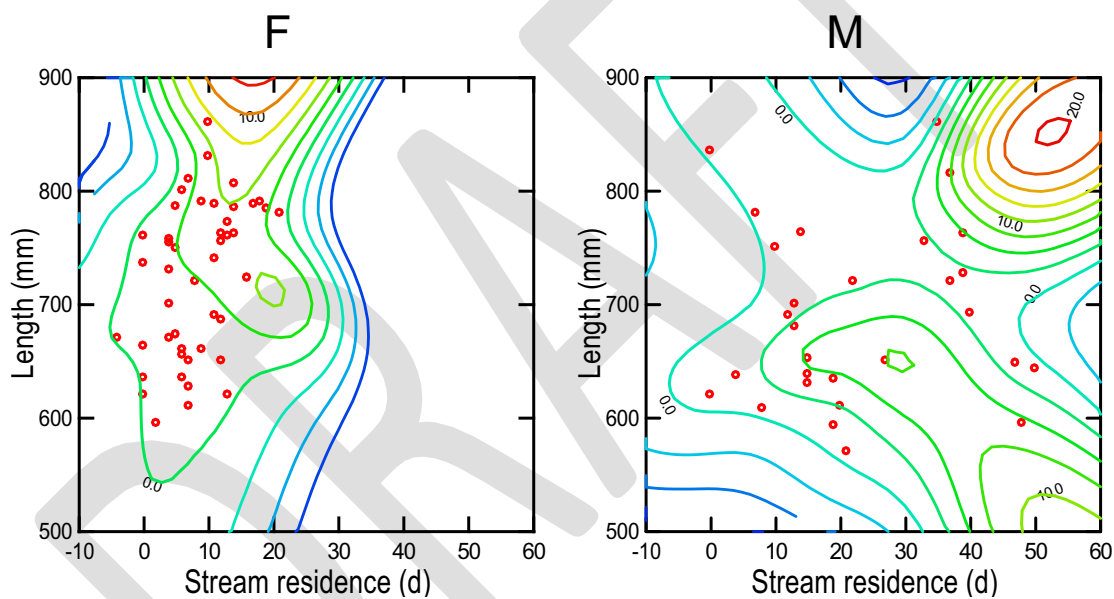


Figure F-2. Contour plots summarizing for adult females (left) and males (right) the relationship between relative fitness, estimated as individual contribution to population growth rate (z-axis), and size (y-axis) and stream residence time (x-axis). The data are given by the open red circles and the contour lines represent contours of individual fitness (X 1000). The highest fitness values are represented by the red peaks on the plots, with blues lines representing the valleys of lowest values of fitness, and green lines slopes of intermediate values. The contributions to population productivity were estimated according to the formulas in Coulson et al. (2006).

Another approach that is gaining traction in the ecological literature, called an Integral Projection Model (IPM), is appealing because it can help to determine the direct influences of individual survival, growth and reproduction on population productivity. An IPM is an

innovative analytical tool designed to estimate the temporal dynamics of a population when the fates of its members depend on characteristics that are continuous or reflect a combination of discrete and continuous characteristics. These characteristics, or states, include traits such as size (length, weight), age, survival, fecundity, and distribution of offspring sizes. In much the same way that an analysis of function-valued traits related to an analysis of discrete traits (Kingsolver et al. 2001), an IPM is analogous to a matrix population model (Leslie 1945, 1948; Lefkovich 1965; Caswell 2001), the classical approach to estimating vital rates that affect population productivity and persistence from demographic data on stage or age transitions. A key difference between an IPM and a matrix population model is that the IPM does not discretize state variables *a priori*, and its approach is pertinent to the study of population dynamics of species where an individual's state (e.g., sexual maturity or reproductive lifespan) depends directly on its growth, size, or age. This is important because assuming that continuous underlying states are discrete can lead to bias in estimating population dynamic parameters (Metcalf et al. 2013). An IPM evaluates the distribution of individuals across these state variables between census times (typically annually) by projecting from models that estimate the underlying vital rates as a function of the continuous or quasi-continuous state variables (Easterling et al. 2000; Ellner and Rees 2006). When combined with a pedigree or marking methods that identify individuals and their relatives, an IPM can provide this information.

Why should we consider such approaches as the IPM? The answer is simple: when we cannot conduct robust, replicated experiments to ascertain how aspects of life history affect population dynamics, the best alternative is to apply appropriate models to the available information and then analyze these models with suitable quantitative methods that can identify these relationships. Indeed, if one could simply rely on correlations between demographic trends and changes in key life history parameters to confirm hypotheses about the factors that limit viability in natural populations, then methods such as IPMs and evolutionary models would be unnecessary in inferring causality. Unfortunately, this fact and the inability to conduct the relevant experiments that might answer these questions for natural populations in particular environments make such methods essential. The IPM is one rigorous and systematic way to try to uncover the relationships between these key demographic and evolutionary patterns. In essence, it is a formal framework for analyzing the dynamics of a system, such as a natural population, that is structured by a mix of discrete and continuous characters that can be measured. The study of the dynamics of these character distributions has the potential to afford insight into ecological dynamics across a range of levels of organization, including communities as well as populations (Coulson 2012).

The data we considered for the demographic analysis constituted a subset of 144 individuals from five consecutive broods and representing two complete generations (parents and their adult offspring) collected between 1997 and 2008. We applied the IPM to these data using the 'IPMpack' package (v. 1.6; Metcalf et al. 2013) in R v. 2.15.2 (R Development Core Team 2012). We built a survival function for the IPM around a polynomial logistic regression relating size in year t to survival from year t to year $t+1$, and we built a growth function around a polynomial regression relating size in year t to survival from year t to year $t+1$.

An IPM is characterized by a kernel, or function, \mathbf{K} that represents the probabilities of growth and survival between stages, and the production of offspring and their recruitment:

$$n(y, t + 1) = \int_L^U \mathbf{K}(y, x)n(x, t)dx$$

where $n(y, t + 1)$ is the distribution across size y of n individuals at census $t + 1$, $n(x, t)$ is the distribution across size x of n individuals at census t , and L is the lower and U the upper size limit represented in the IPM (Metcalf et al. 2013).

\mathbf{K} is itself composed of one kernel that defines survival and growth (the \mathbf{P} kernel) and another kernel that defines reproduction (the \mathbf{F} kernel):

$$\int_L^U \mathbf{K}(y, x)n(x, t)dx = \int_L^U [\mathbf{P}(y, x) + \mathbf{F}(y, x)]n(x, t)dx$$

where the \mathbf{P} kernel is given by

$$\int_L^U \mathbf{P}(y, x)n(x, t)dx = \int_L^U survival(x)growth(y, x)dx$$

and the \mathbf{F} kernel is given by

$$\int_L^U \mathbf{F}(y, x)n(x, t)dx = \int_L^U c_1 c_2 c_z \dots fecundity_1(x)fecundity_2(x) \dots fecundity_z(y, x) dx$$

where c_i are constants for the functions relating size and fecundity and z indicates the stages or years (Metcalf et al. 2013).

Using the average and SD of adult length estimated from the data (706.54 and 67.68 mm, respectively), we first constructed survival and growth elements of the IPM. We did not have longitudinal size estimates for most (123) of the individuals, only estimates of average growth in length between years estimated from the pedigree. We fitted a polynomial regression to the longitudinal size data available for 22 adults to estimate the size in year $t + 1$ (e.g., a 6-year-old adult) from the size in year t (e.g., a 5-year-old adult) for all adults, based on a mean of approximately 9.3% annual growth in length and with normally distributed random error based on the variation observed in size in year t . The fitted regression was $y_{t+1} = 533.2 - 0.0872 y_t + 0.0006 y_t^2$ ($r = 0.778$). Mean generation time was 6 years. We defined the survival component of the \mathbf{P} kernel as a polynomial logistic regression relating size and size² in year t to survival from year t to year $t + 1$ (y_{surv}), and the corresponding growth component as a polynomial regression relating size and size² in year t to size in year $t + 1$ (y_{growth}). The models provided the following fits:

$$y_{surv} = -13.52 + 0.00297 * size - 0.00001633 * size^2$$

$$y_{growth} = 0.005988 - 0.02961 * size + 0.0007527 * size^2$$

These data are plotted in Figure F-3, with curves representing expected values (Eq. F-5 and F-6) fitted to the points. The annual growth relationship to initial size was nonlinear. There was no evidence that adults returning earlier or later than average had lower or greater growth or

survival. The plot of survival on size suggests that the increase in annual survival with size is appreciable, perhaps 30-40% for fish > 800 mm vs 10% for smaller fish.

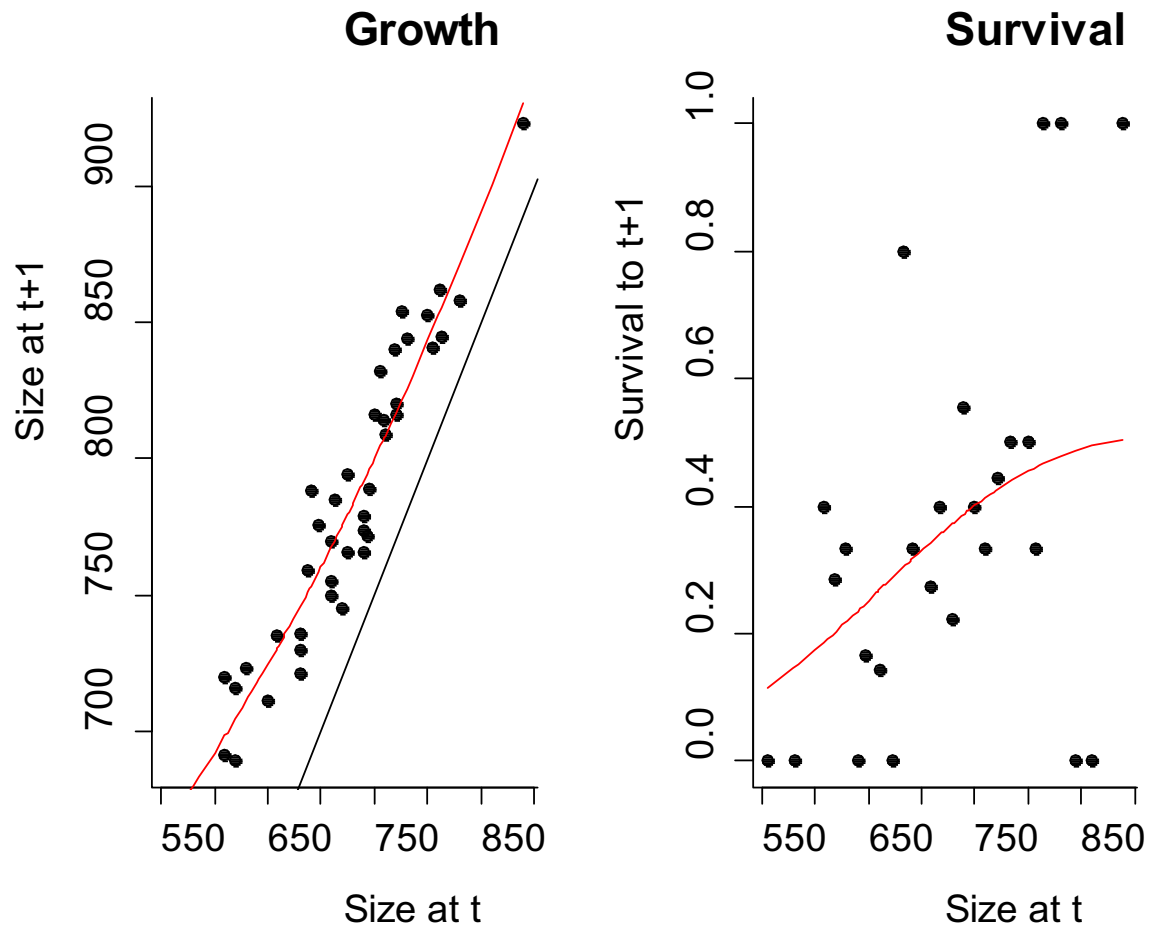


Figure F-3. Estimated growth and survival functions for Sashin Creek, AK steelhead (see text). The corresponding red curves are the fitted expected values (see Equations F-5 and F-6). The black line indicates the 1:1 relationship of sizes in subsequent years.

Diagnostics applied to the estimated \mathbf{P} matrix, using a starting size of 550 mm and a target size of 750 mm, showed no evidence of outliers or that the size range or that the number of size bins selected was insufficient (Figure F-4). These diagnostics do not indicate any serious problems in fitting vital rate functions to the data or estimating IPM components.

Numerical resolution and growth

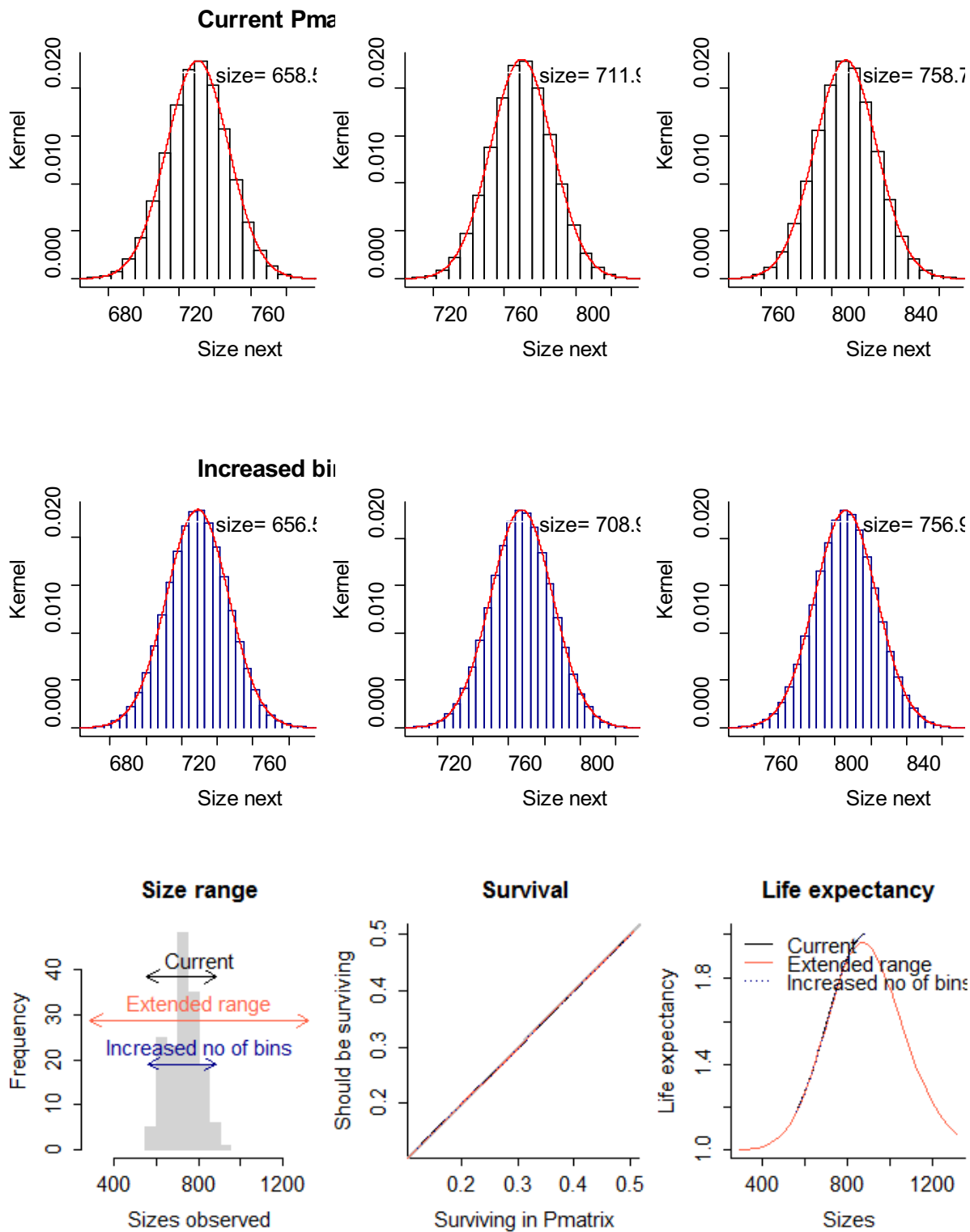


Figure F-4. IPM diagnostics applied to the steelhead survival and growth data, indicating an appropriate size range and resolution in number of size bins to estimate IPM matrices. There is no mismatch between the observed sizes and the range fitted in the \mathbf{P} matrix. The red lines and blue bars indicate the results of increasing the size range and bin resolution, respectively, on the model fitting. The correspondence of the black and red lines in the ‘Survival’ and ‘Life expectancy’ plots indicate that the predictions of the discretized matrix do not depart appreciably from the fitted survival model over the range of observed values.

We then defined a normally distributed fertility kernel \mathbf{F} representing adult offspring production based on parental size in year t (y_{fec}), using the observed data to define the parameters of that distribution. The general linear model estimate was:

$$y_{fec} = 0.224535 + 0.001198 * size$$

Figure F-5 indicates no consistent pattern in adult progeny produced as a function of adult size. There is also no consistent pattern with adult run timing (data not shown). The maximum number of adult offspring produced by a spawning adult was four over the time series, produced by adults as small as 610 mm and as large as 750 mm.

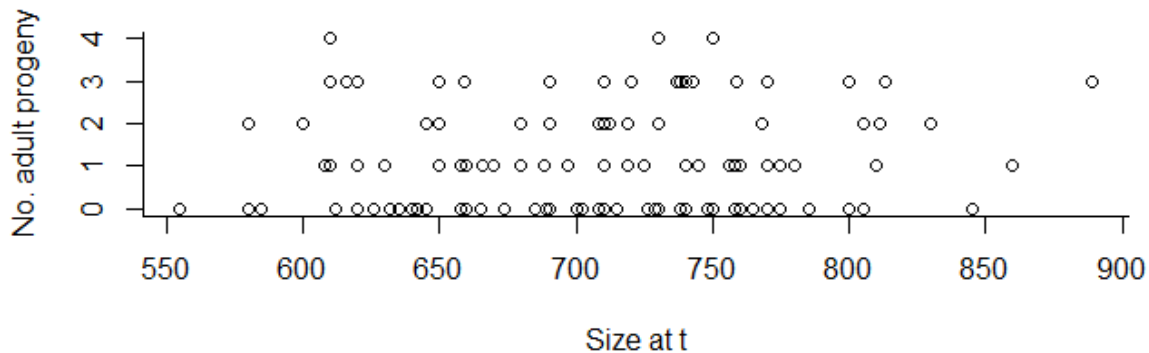


Figure F-5. Estimated number of adult offspring as a function of adult size in Sashin Creek, Alaska steelhead.

The following pair of plots (Figure F-6) depict the survival-growth transition kernel \mathbf{P} that accounts for survival and growth transitions only (i.e., no covariates), between size in year t and size in year $t + 1$, using 70 meshpoints. The transition kernel estimates a weak curvilinear fit of survival and growth transitions to the size data, with the highest (and much higher) probability of surviving and growing to return the following year for the largest adults. From this transition kernel the estimates of mean life expectancy and time to reach the target size across the

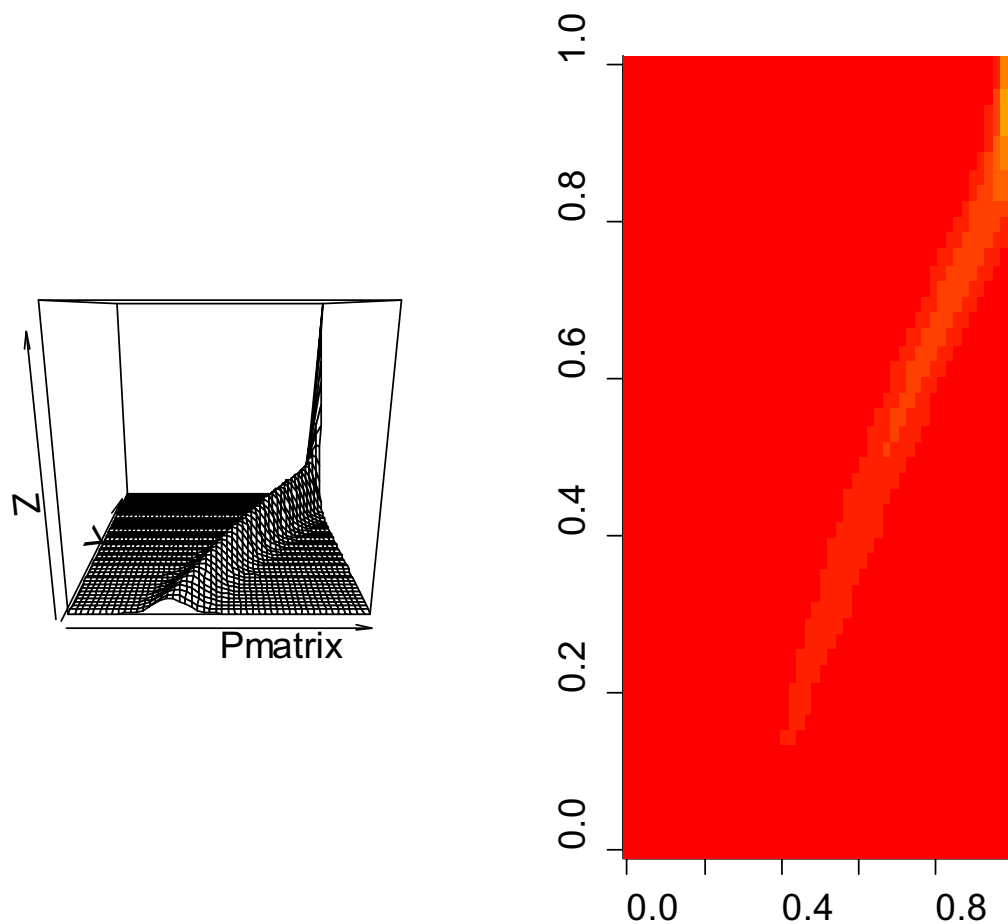


Figure F-6. (Left) A graphical depiction of the survival-growth transition kernel P indicating the probability of a survival and growth transition (z-axis) as a function of sizes in adjacent annual censuses, showing a weak curvilinear fit to the size data. (Right) A view of the kernel from above, with the red regions indicating low probabilities and yellow regions higher probabilities of a transition.

range of meshpoints in the survival-growth transition kernel P are shown in Figure F-7. The plot at left predicts a survival advantage for larger adults, as expected from the relationship observed in Figure F-3; the predicted life expectancy rises from about 1 year for adults <600 mm long to about 1.75 years for fish 750 mm long. The plot of passage time at right estimates that surviving steelhead take two years to grow to a target size of 750 mm from a length of 650 and three years

if smaller than that. Growth at sea between successive spawning events has a clear influence on future survival and fertility.

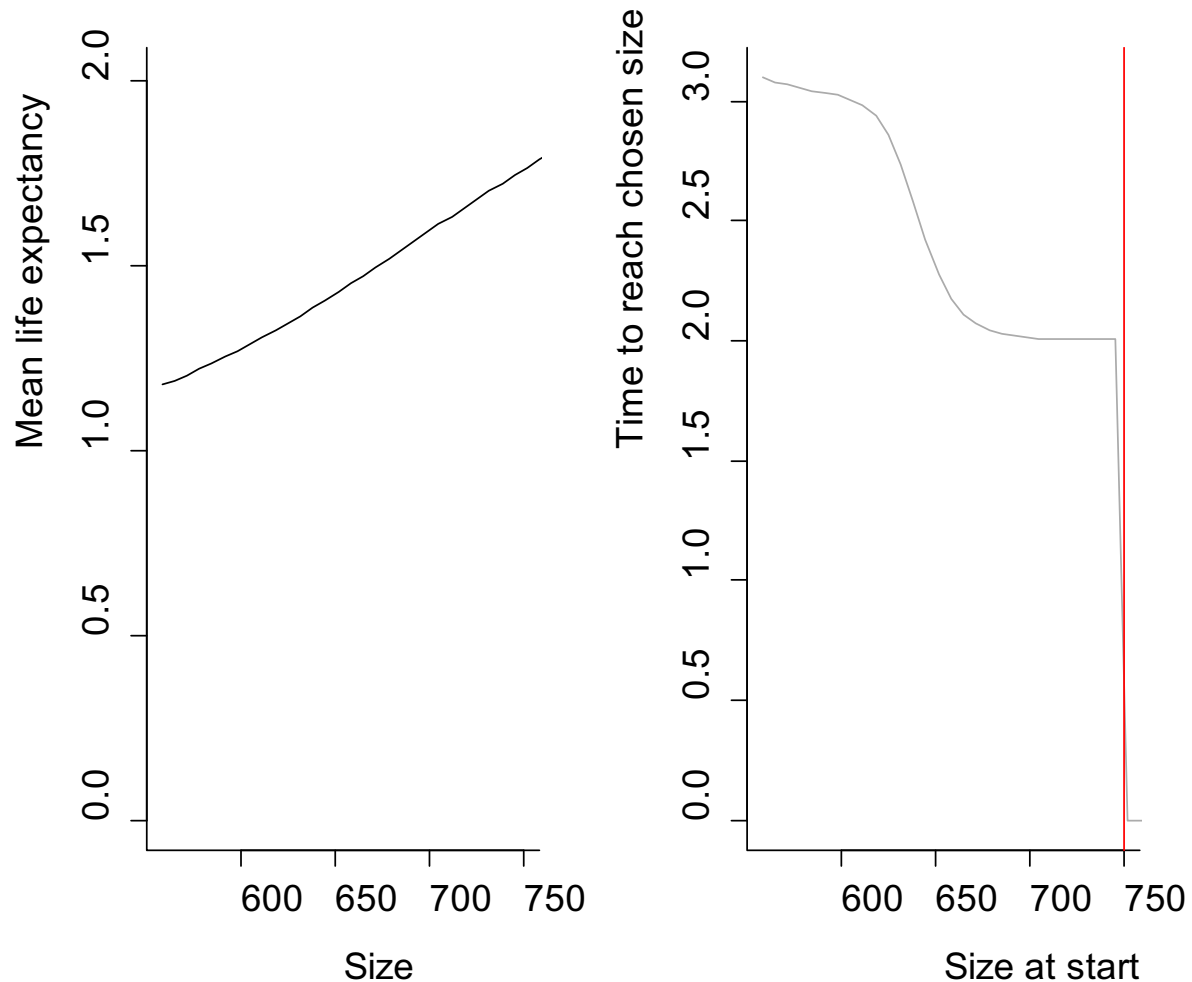


Figure F-7. Estimated mean life expectancy and passage time to reach a target size of 750 mm as a function of size in year t .

An IPM constructed from the data, assuming a target size of 750 mm and using a logistic model of survival and a simple linear model of growth with no covariates except for size, produced the following results for survival, growth, life expectancy, and passage time as functions of size (Figure F-8). Given the estimates of survival and growth, the IPM predicts that mean life expectancy increases from 1.0 ± 0.5 years for adults <550 mm to nearly 2.0 ± 1.0 years for fish >850 mm long. The IPM predicts passage times to 750 mm of 2 years for adults >600 mm long and up to 4 years for adults smaller than 450 mm. The P kernel at lower left indicates

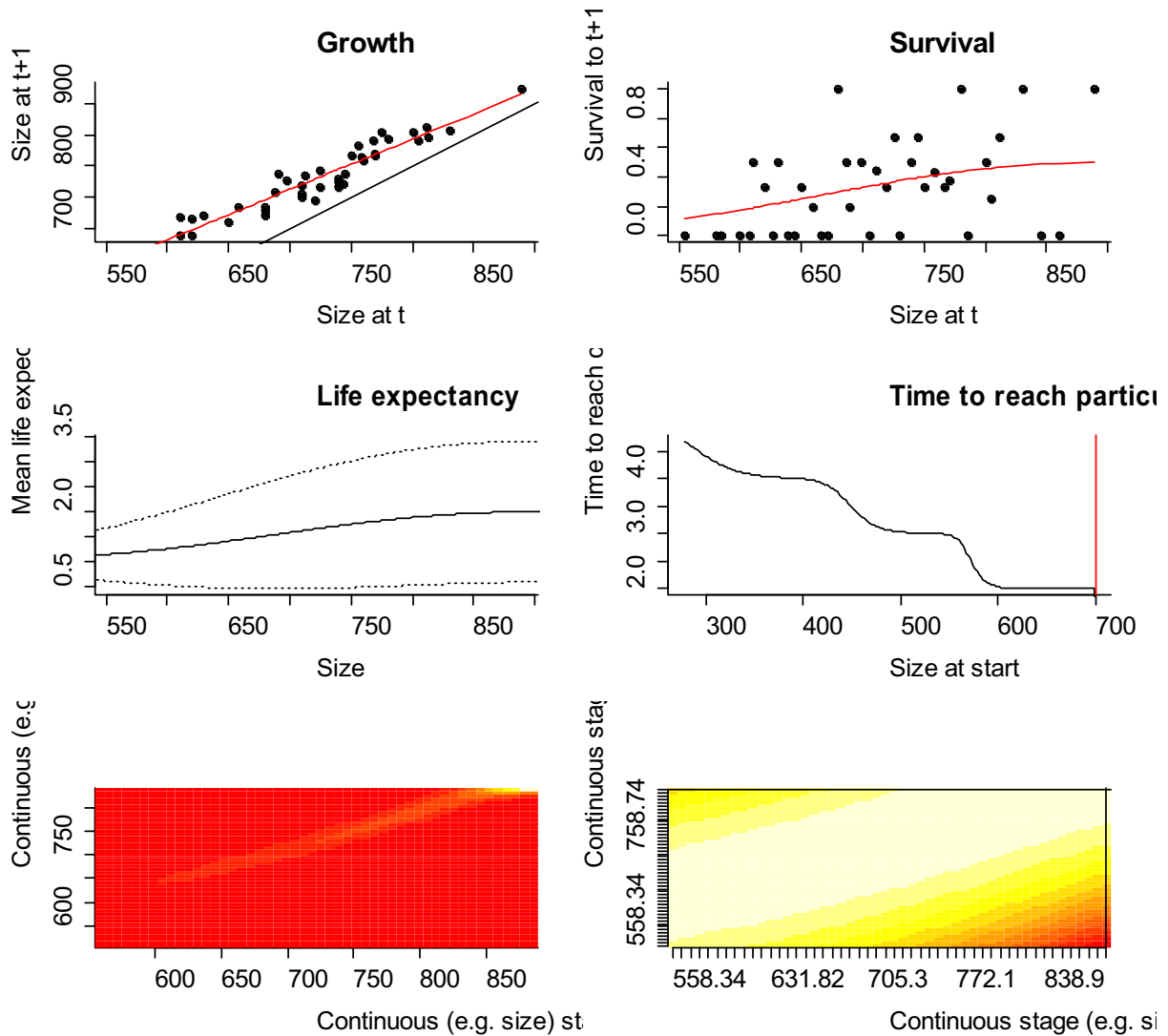


Figure F-8. Summary of some key results from integral projection model (IPM) incorporating a simple logistic function describing survival and a simple polynomial function describing growth, with no covariates. The top four plots indicate predicted patterns of growth, survival, life expectancy, and passage time as functions of size. Fitted functions are given by the red curves for the first two plots. 95% confidence intervals for life expectancy bracket the predicted values along the solid curve. The bottom left plot illustrates the probability of a survival-growth transition (on the z-axis) and sizes at two successive censuses (year t on the x-axis and year $t + 1$ on the y-axis). The bottom right plot illustrates the probability of a reproductive transition (on the z-axis) and sizes at two successive censuses (year t on the x-axis and year $t + 1$ on the y-axis). In both of these plots, low values of transition probability are represented by red regions and high values by yellow regions. The predicted transition for individual survival and growth is more closely linked to size; that for reproduction (production of adult offspring) is not closely linked to size.

the probabilities of a survival-growth transition as a function of sizes at successive censuses (year t on the x-axis and year $t + 1$ on the y-axis). The F kernel at lower right indicates the probabilities of a reproduction transition as a function of those sizes. In both of these plots, low values of the transition are represented by red regions and higher values by bright yellow regions. The probabilities of individual survival and growth transitions are relatively closely associated with size, but they are high only for very large fish (ca. 850 mm long). The probabilities of reproduction for surviving adults (production of adult offspring) are not closely linked to size and indeed can be high for fish of various sizes, but these probabilities tend to be lower for fish that grow less between spawning events.

Combining the P and F kernels to construct a full IPM that integrates growth, survival, and fecundity and is fitted iteratively to the 1997-2008 data estimates the population's net reproductive rate per generation, R_0 , at 1.80. This represents the mean number of adult females produced by a female over her lifetime. With a mean generation time of 6 years, this estimate of R_0 corresponds to an estimate of the per capita growth rate or finite rate of increase, λ , of 1.10, and an estimate of the instantaneous rate of change, r , of 9.8% increase per year. The population is, on average, showing positive population growth over the 1997-2008 period. The overall weak declining trend of the population between 1986 and present (Figure F-1) is driven largely by a population decline between the 1980s and the late 1990s.

Figure F-9 summarizes some projections of the integral projection model (IPM). The results indicate that population growth rate is sensitive to both growth and survival, but depends heavily on the reproductive success of larger adults, especially those larger than 750 mm. Sensitivity analysis, which measures how small changes in population growth rate are affected by small changes in survival-growth and reproduction transitions, indicates that population growth rate is most sensitive to the survival and growth of fish that are between 700 and 750 mm in one year, and grow to larger than 750 mm by the next year. When proportional changes in population growth rate relative to proportional changes in these transitions are examined through elasticity analysis, which standardizes sensitivities to minimize bias due to trait scale effects, the IPM indicates that population growth rate is most sensitive to the performance of fish that are between 700 and 750 mm in one year and are about 750 mm in the following year.

Figure F-10 supports this pattern, showing how sensitive population growth rate is to the nonlinear component of the relationship between survival and growth, which implies that the survival of fast-growing fish is key to high population productivity. The elasticity analysis indicates that the most influential factors for high population productivity appear to be the linear component of the relationship between survival and growth and the average production of adult offspring. The factors that tend to depress population productivity are low survival between years and the nonlinear component of the relationship between survival and growth that indicates disproportionately higher survival of larger adults, implying that poor marine survival and limited annual growth in some years could threaten population viability.

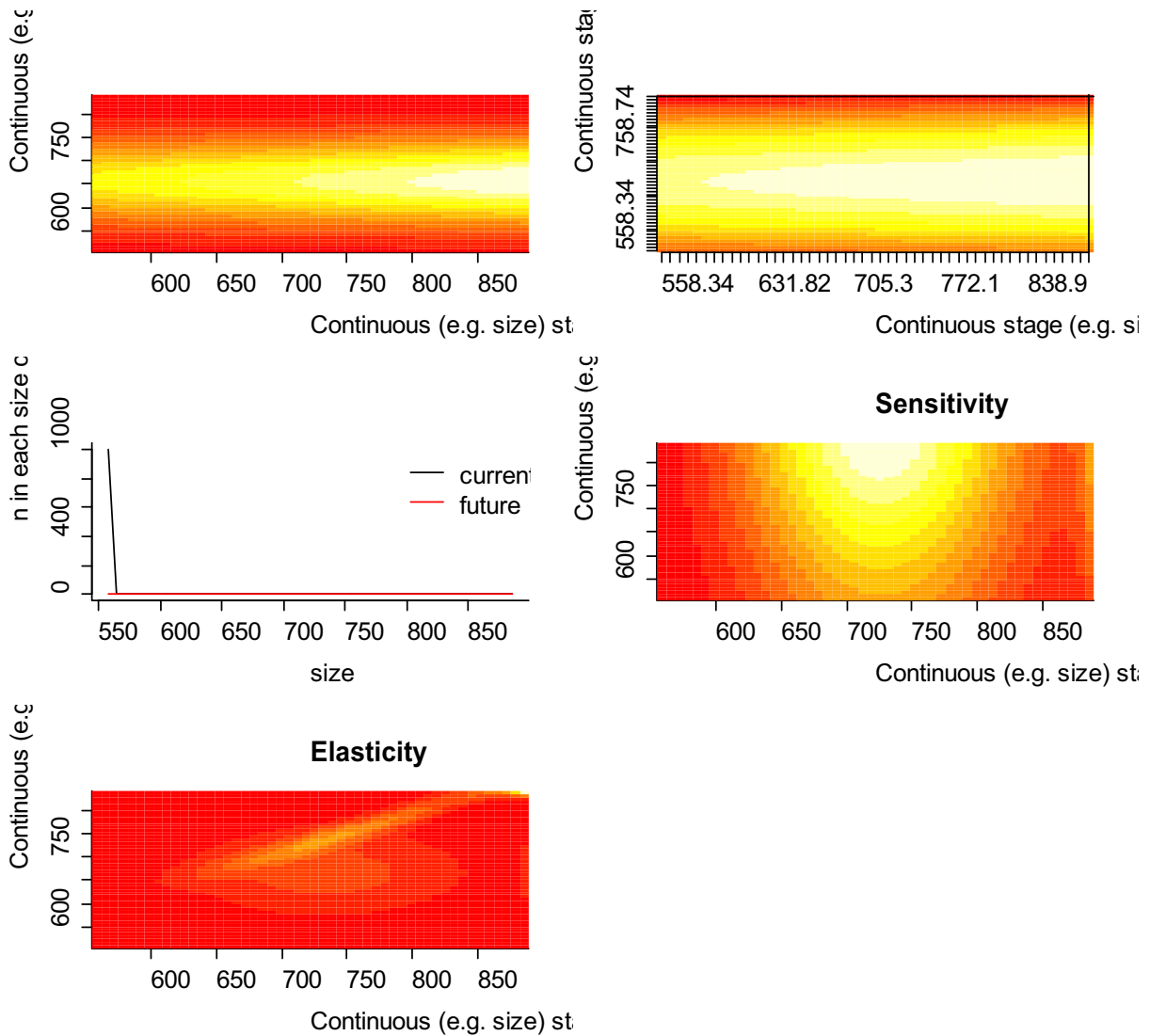


Figure F-9. A few projections from the integral projection model (IPM) described in Figure F-8. The top two plots plot the projected distributions of individual survival and growth (left) and fecundity (right) in the population over 10 years against the meshpoints of size in the \mathbf{P} kernel. The middle left plot projects that a size structure dominated by smaller (~ 550 mm) adults will produce few larger adults in the future. The sensitivity plot at middle right illustrates the predicted relationship between population growth rate (on the z-axis) and sizes at two successive censuses (year t on the x-axis and year $t + 1$ on the y-axis), showing that it is most sensitive to the reproductive success of adults initially between about 700 and 750 mm and subsequently >750 mm, suggesting that population growth rate is sensitive to annual growth of breeders as well as iteroparity. The corresponding elasticity plot at lower right, for which sensitivities are standardized to minimize bias due to trait scale effects, suggests that population growth rate is most influenced by the reproductive success of adults between 700 and 750 mm. In these two latter plots, low sensitivities and elasticities are represented by red regions and high values by yellow regions.

Taken together, the results of this analysis quantify an expected pattern: that survival, growth, and lifetime reproductive success of relatively large breeding adults are critical to higher productivity of this wild steelhead population. It appears that sufficiently high interannual survival of steelhead in the marine environment is essential to high productivity, implying the importance of iteroparity. It is also evident that rapid marine growth of adults can have substantial benefits for the survival as well as the fecundity of both first-time spawners and repeat spawners.

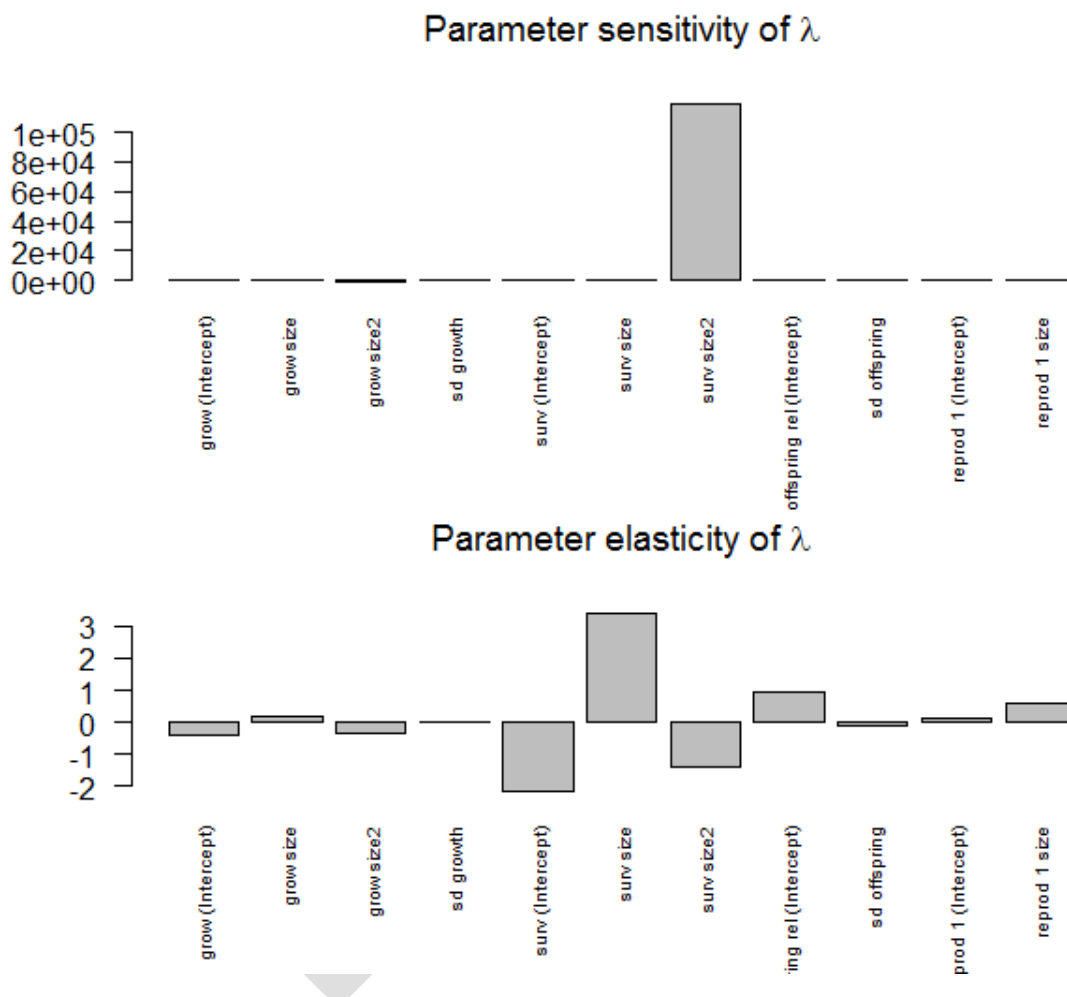


Figure F-10. Graphical summary of the sensitivity and elasticity analyses of the estimate of finite rate of population increase (λ). The sensitivity plot indicates the large effect that the relationship between survival and the nonlinear growth component has on λ , suggesting that the survival of fast-growing fish is key to higher productivity. The corresponding elasticity plot, for which sensitivities are standardized to minimize bias due to trait scale effects, indicates that the most influential factors for high productivity are the linear component of the relationship between survival and growth and the average production of adult offspring. The factors that tend to depress population productivity are low survival between years and the nonlinear component of the relationship between survival and growth.

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