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ESTIMATION OF HISTORIC SALMON POPULATIONS AND ITS
APPLICATION TO CONTEMPORARY SALMON CONSERVATION

By

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Dissertation

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for the degree of

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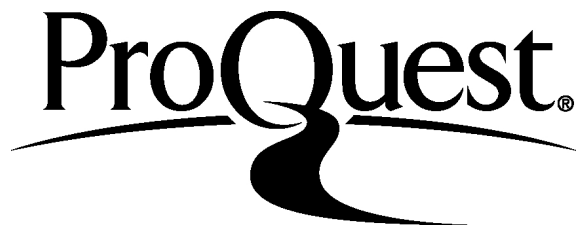
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CHAPTER ONE

Introduction

Populations of wild Pacific salmon and steelhead (*Oncorhynchus sp.*) in the eastern Pacific Rim have experienced significant declines in abundance and associated genetic and life history diversity over the course of the twentieth century (Nehlsen et al 1991, Slaney et al 1996, Myers et al 1998, Lichatowich 1999). In the Pacific Northwest of the United States, declines in the abundance of most populations accelerated in the last two decades of the century and have continued into the first two decades of the twenty-first (Busby et al 1996, Myers et al. 1998, Good et al.2005, Hard et al. 2007, Ford et al. 2011). These declines have resulted in the listing of numerous population aggregates referred to as either ‘distinct population segments’ (DPSs) or ‘evolutionarily significant units (ESUs) as ‘threatened’ or ‘endangered’ under the U.S. Endangered Species Act (ESA, section 50 Code of Federal Regulations, §17.11-.12). In British Columbia (BC), although no salmon populations have yet been listed under Canada’s Species At Risk Act (SARA) concerns over declining populations led to the adoption in 2005 of a federal Wild Salmon Policy (WSP). The WSP requires that population aggregates of all species of Pacific salmon in BC, termed ‘conservation units’ (CUs), be identified and that target levels of abundance, genetic diversity, spatial structure, and life-history diversity¹, termed “benchmarks” be identified to guide the management of CUs and their component populations so as to insure their long-term persistence (see, e.g., Holtby&Ciruna, 2007).

The overarching conservation purpose of these federal laws and policies is to preserve and, where necessary, rebuild the abundance and diversity of extant salmon populations so as to

¹ In the remainder of this chapter and in subsequent chapters I will use the term ‘diversity’ without qualification to refer broadly to genetic, life-history, and spatial diversity of a population or conservation unit. Where a narrower concept is required or intended I will use the term with the appropriate qualifier such as, for example, ‘genetic diversity’.

assure their long-term persistence and adaptability. This is no small task in view of multiple stressors that have caused the decline of salmon populations (Nehlsen et al 1991 and Slaney et al. 1996, Lichatowich 1999). These stressors include; 1) the considerable loss, modification, and destruction of freshwater and estuarine habitats that are essential to salmon throughout several critical stages of their life histories, 2) interactions with salmon produced by large-scale artificial production (hatchery) programs intended variously to augment harvest opportunities and mitigate for loss of habitat, 3) artificial production programs intended to assist in rebuilding wild salmon populations, and 4) overharvest in numerous commercial fisheries along the Pacific coast and in rivers during the salmon's migration to its natal river to spawn (Busby et al., 1996, Myers et al. 1998, Good et al. 2005, Hard et al 2007, Ford 2011).

A considerable amount of information regarding the biology of salmon and steelhead exists today (see, for example, Groot & Margolis 1991, Groot, Margolis, and Clarke 1995, and Quinn 2005, Hard et al. 2007, Ford et al. 2011, Kendall et al. 2014). This is complemented by a considerable amount of data on the abundance of specific salmon populations during the past 20 to 50 years -- primarily adult run size or spawning escapement numbers (see, for example, DFO 2011, PacFIN 2013) -- and by a battery of robust statistical techniques for analyzing that data (Gelman et al 1995, Quinn & Deriso 1999, Gelman and Hill 2007, Bolker 2008, Kery & Schaub 2012).

Populations of wild salmon and steelhead in what I will refer to as the historic period, that encompasses the late nineteenth and early twentieth centuries from approximately 1890 to 1930, several decades prior to the majority of the recent declines, were considerably larger than their current levels (Myers et al. 1998, Yoshiyama et al. 1998, Lichatowich 1999, Meengs and Lackey 2005, Gayeski et al. 2011, Price et al. 2013). What is often uncertain is just how large they were relative to current population levels. But while we may be confident that most salmon and steelhead populations during the historic period were larger than today, the knowledge of the levels of abundance that we do possess is lacking in the detail that typifies the current state of our knowledge of salmon biology. It is rare to know how abundant salmon populations of current conservation concern were at the time when major anthropogenic stressors first began to impact their abundance in the late nineteenth and early twentieth centuries. Lastly, we have little idea of

how these populations managed to attain and maintain the greater levels of abundance that were characteristic of them at this time.

Under these circumstances there is a risk that management actions intended to recover or preserve current wild salmon populations will aim too low and fail to establish levels of abundance and diversity great enough to assure the long-term persistence of wild salmon and their ecosystems. This risk is related to the more general concern with how natural resource management agencies choose, if not identify, management reference points that has been aptly characterized by Daniel Pauly as the “shifting baseline syndrome” (Pauly 1995). As Pauly describes it “...this syndrome has arisen because each generation of fisheries scientists accepts as a baseline the stock size and species composition that occurred at the beginning of their careers, and uses this to evaluate changes. When the next generation starts its career, the stocks have further declined, but it is the stocks at that time that serve as a new baseline. The result obviously is a gradual shift of the baseline, a gradual accommodation of the creeping disappearance of resource species, and inappropriate reference points for evaluating economic losses resulting from overfishing, or for identifying targets for rehabilitation measures.”

I hypothesize that the task of recovering wild salmon and steelhead populations is hampered by the absence of a more detailed understanding of the abundance of wild populations in the not-too-distant past. In particular, we need to achieve a better understanding of the capacity of freshwater habitat for producing juvenile, pre-migrant salmon and steelhead that characterized wild populations during the historic period. I hypothesize that achieving robust estimates of the juvenile rearing capacity of the freshwater habitats of historic wild salmon and steelhead populations will increase the probability of identifying more robust and effective management targets for the recovery of currently at-risk wild populations.

While attaining the greater abundance levels that characterized the few decades immediately preceding the recent declines is likely to prove valuable, even essential, to preserving wild salmon populations in the short run, it is less clear that they will secure persistence and resilience for the long-term, especially in the face of foreseeable rapid changes in the fresh- and salt-water environments of salmon due to climate change (see, for example, Hare & Francis 1995, Crozier

et al. 2008, Schindler et al. 2008, Mantua et al. 2010, Wade et al. 2014). Salmon populations in the late nineteenth and the early decades of the twentieth centuries appear to have been significantly larger than those that immediately preceded the recent declines yet they are still recent enough that some quantitative biological and physical habitat data is available to permit reasonable estimates of abundance to be made (Argue & Shepard 2005, Meengs & Lackey 2005, Gayeski et al 2011, Price et al. 2013). Populations during the historic period were not pristine and many had already experienced significant loss or impairment of freshwater rearing habitat (Lichatowich 1989, Beechie et al, 1994, Yoshiyama et al. 1998, Gottesfeld & Rabnett, 2008). Nonetheless, most populations from large (sixth-order and higher²) tributary rivers along the coast of the Pacific Northwest (PNW) from the Central Valley of California to Southeast Alaska, remained two to twenty times larger than the majority of those populations today (see, for example, Price et al. 2013, Gayeski et al. 2011, Myers et a. 1998, Hard et al. 2007, Lichatowich 1989, 1999, Slaney et al. 1996, Nehlsen et al 1991, Yoshiyama et al 1998, Meengs & Lackey 2005).

Importantly, salmon populations during this period were the focus of numerous commercial fisheries whose catch records provide insight into the levels of population abundance extant at this time. These catch records can be analyzed in ways that permit estimates of the unfished, equilibrium, abundance of many large salmon and steelhead populations to be robustly estimated. Estimates of the equilibrium abundance of the wild adult population may then be combined with life history information to estimate the levels of juvenile production that produced and maintained the equilibrium adult abundance. In turn, the estimated levels of juvenile production can be combined with estimates of the amount of then-available juvenile rearing habitat to estimate the productivity of historic populations as per-unit rearing area capacity (number of juveniles-per-square meter rearing habitat).

In the following chapters I show how this may be done for two representative salmon populations and one steelhead population. I present and illustrate two general methods for estimating the abundance of historical salmon population run sizes from commercial fishery catch record data. I apply one method to Skeena River chum salmon circa 1920 and to

² For definitions of stream order, see Leopold 1994.

Stillaguamish River steelhead circa 1895. I apply the second method to Skeena River sockeye salmon for the period 1888 to 1919. These three cases have a sufficient amount of the kinds of data that are required for the successful application of the methods and thus provide robust illustrations of the utility of the methods when sufficient data for their application is available.

For Skeena River chum and Stillaguamish River steelhead I provide estimates of the juvenile production that produced the estimated adult abundance and estimates of the historically available juvenile rearing habitat from which I derive estimates of the capacity of rearing habitat area of the each population as numbers-per-square-meter. I then provide estimates of the amount juvenile rearing habitat area currently available in each of the river systems and show how these may be combined with the historic capacity estimates to identify habitat based recovery targets for chum salmon and steelhead populations and to direct monitoring of recovery efforts³. Finally, using the examples of Skeena chum salmon and Stillaguamish steelhead, I explain how this approach will avoid the shifting baseline syndrome in the identification of conservation targets.

Addressing the problem: integrating historical run-size estimation, life-cycle modeling, and estimates of historically available habitat.

Commercial catches of wild salmon and steelhead during the historical period that were large by contemporary standards contributed significantly to the declines that PNW salmon populations experienced during the first half of the twentieth century, but they also provide quantitative evidence that many populations were still considerably larger than they had become by the ending decades of the twentieth century. Levels of abundance during the historical period are, therefore, likely to provide useful information about the levels of abundance that PNW salmon populations and conservation units need to attain in order to secure their long-term persistence (see also, Rosenberg 2005), provided these levels could be estimated with reasonable accuracy and precision. At a minimum obtaining serviceable, reasonably robust estimates of salmon

abundance during the historical period will provide a counterbalance to the shifting baseline that may threaten contemporary conservation planning initiatives.

Estimating the size of historical salmon populations has recently been of interest to salmon biologists, whether out of general scientific curiosity or a belief that such knowledge has applicability to contemporary conservation. Recent noteworthy endeavors include Price et al. 2013, Gayeski et al., 2011; Meegs & Lackey 2005; Schick et al 2005; Titus et al. 2010; Yoshiyama et al. 1998, 2001; and Yoshiyama & Moyle 2010. All of these have in common the use of commercial catch data to varying degrees and some discussion of habitat loss and impairment since the early commercial catches. Meegs & Lackey (2005) and Gayeski et al. (2011) are particularly noteworthy in attempting to estimate current recovery potential based on their estimates of historical abundance. But while providing important insight into past levels of abundance, most analyses do not go beyond noting the discrepancy between the estimated historical abundance and current abundance levels. And with the exception of Gayeski et al (2011) and Price et al (2013) the analyses rely on point estimates of harvest rates or their range and point estimates of average fish weight to translate commercial catch data from pounds to numbers of fish. While these approaches do acknowledge the uncertainty of the abundance estimates in a general way and generally provide reasonable ranges for the estimates, they fail to fully incorporate the uncertainties into the abundance estimations themselves and so provide no way of estimating how probable the estimates are. It is desirable to remedy this shortcoming in estimates of historical salmon abundance so as to better delimit the confidence that can be accorded such estimates.

It would be of further value to know how much of the abundance estimated for a population during the historical period may be attainable by the remaining representatives of the population in the near future. This requires obtaining an estimate of the historical capacity and productivity of the freshwater spawning and/or juvenile rearing habitat of a population and an estimate of how much of that capacity and productivity exists today or could be achieved in the near future (due, for example, to salmon recovery planning efforts). This, in turn, requires information about

³ Sockeye salmon rear in lake systems and funding was not sufficient to acquire the data needed to estimate lake rearing habitat for the numerous sockeye populations in the Skeena. So I do not provide an estimate of the historic

historical and current freshwater habitat conditions and some autecological information about how the salmon species in question utilizes those environments.

In the following chapters I show how this may be accomplished. In broad outline, it is a five-step process:

1. Acquire historical commercial catch data for the focal period of interest and obtain an estimate of the size of the adult salmon population from which the catch was obtained (the focal population).
2. Build a life-cycle model of the salmon species of interest and parameterize it so as to achieve the commercial catch from a population of the total size estimated in step 1. This will yield an estimate of the total number of juveniles at an appropriate key life stage (e.g., smolts) that had to have been produced in order to produce the total adult population from which the historical catch was obtained.
3. Estimate the amount of freshwater juvenile salmon rearing habitat available to the focal population at the time of the focal period and the amount of that habitat remaining currently.
4. Estimate the average capacity of freshwater rearing habitat in the focal period as number of rearing juveniles per square meter ($\# \text{juveniles}/\text{m}^2$) by dividing the estimated total number of juveniles by the estimated total amount of rearing habitat area.
5. Estimate the current production potential of current habitat by multiplying the amount of currently available rearing habitat by the estimated historical per-unit-rearing-area capacity of that habitat, then estimate adult production potential by multiplying the estimated juvenile numbers by an appropriate value of juvenile-to-adult survival.

juvenile sockeye production associated with the estimate of adult abundance using Method II.

I show how credible estimates of historical adult salmon population sizes may be obtained from commercial catch data (step 1) and how to translate the estimated population numbers into estimates of juvenile rearing habitat capacity (step 2). I then show how the estimates of historic juvenile rearing habitat capacity can aid in understanding ways to help conserve salmon populations (steps 3 – 5).

In a recent publication (Gayeski et al. 2011) I presented a general method for estimating the abundance of historical salmon populations using commercial fishery catch data combined with qualitative and quantitative historical information about the salmon species affected and the nature of the commercial fishery. The method was applied to estimate the abundance of several large steelhead populations in Puget Sound, in 1895 near the beginning of large commercial fisheries directed at steelhead. This publication provided a part of the basis for the present Ph.D. project, which provides the foundation for the method and extends the method to include the estimation of the juvenile rearing capacity associated with the estimated historic adult population. The present project was initiated with a related application (Price et al. 2013) in which I refined the general method and applied it to estimate the abundance of chum salmon in the Skeena River in British Columbia in the second half of the second decade of the twentieth century.

In Chapter 2 I describe the mathematical foundation of the general method (Method I) and in Chapter 3 I illustrate its application to the case of Skeena chum salmon described in Price et al. (2013). The application of Method I to the case of Skeena chum salmon differs from the application to Puget Sound steelhead in the kinds of data available and required different strategies for achieving the estimate of historical abundance from which the historical commercial catch was obtained that was of interest in each case. In Chapter 4, therefore, I first briefly review the application of the method to Puget Sound steelhead. I then compare and discuss the different issues involved in estimating the historic abundance in the two cases.

In Chapter 5 I illustrate an alternative and complementary method (Method II) for estimating historical salmon abundance based in traditional stock-recruitment theory that can be employed when there is a multi-generation, quasi-long-term record of large commercial catches. I illustrate

this by estimating the equilibrium, unfished, abundance of the Skeena River sockeye salmon population during the period from 1888 to 1913 that spans the development of a large non-native commercial fishery in the lower Skeena River dominated by salmon canneries (Pritchard 1948, Shepard and Withler 1958, Ricker and Smith 1975, Harris 2001). I compare this approach to the approach illustrated in the two cases in Chapters 3 and 4.

In Chapters 6 and 7, I develop age-structured life cycle models of Skeena river chum salmon and Stillaguamish River steelhead, respectively, and employ them to estimate the juvenile production that produced the historical adult abundance estimated in Chapters 3 and 4. Each of these chapters also provides estimates of the amounts of juvenile rearing habitats for each species available during the historical period and under contemporary conditions. The historical habitat data are used to provide estimates of the historic capacity⁴ of freshwater rearing habitat available to each species. Capacity is measured as the number of juvenile salmon or steelhead at a particular life stage per square meter of available rearing habitat at the unfished, equilibrium adult abundance of the population. These two cases involve juvenile life histories that differ significantly in the duration of freshwater residence and rearing prior to migration to the ocean that motivate different approaches to the estimation of historic juvenile rearing densities. For each species, I describe how the rearing densities estimated for the historic periods may be applied to estimate the recovery potential of the two populations under current conditions.

Chapter 8 concludes the Dissertation by providing a synthesis of the methods of estimating historic adult abundance and the method of estimating juvenile rearing capacity of populations using habitat data and life-cycle modeling. I describe how the rearing densities estimated for the historic period may be applied to current conditions to provide estimates of the recovery potential of current salmon and steelhead populations and provide interim targets or thresholds

⁴ Throughout I use the term ‘capacity’ to refer to the abundance of either a juvenile or adult life stage under equilibrium (unfished) conditions. Occasionally I will use the term ‘productivity’ to refer to the same phenomena, where the context makes it clear that I am referring to the ability of the population to fill either freshwater rearing or spawning habitat under unfished, equilibrium conditions. I consider the freshwater rearing or spawning capacity of a salmon or steelhead population under equilibrium conditions an index of the productivity of the population, the ability of the population to fill rearing or spawning habitat. The term ‘productivity’ normally refers to the ability of the population to increase in numbers, typically adults, when abundance has been reduced to “low” numbers. The term is probably best reserved for use in this context. But unless otherwise indicated, use of the term ‘productivity’ in this document will be equivalent to ‘capacity’ as defined above.

for monitoring the progress of population recovery as well as assist in developing recovery-based research and monitoring plans that address critical data gaps relevant to the development and modification of robust recovery plans.

By connecting the estimation of historic salmon and steelhead abundance to contemporary population recovery and management concerns by employing life-cycle modeling and historic and current freshwater habitat data to estimate historic and current juvenile rearing capacity, the abundance of historic populations may be seen to be directly relevant for developing recovery targets for currently at-risk salmon and steelhead populations.

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CHAPTER TWO

A Bayesian Approach to Estimate Salmon Run Size from Short Time Series Catch Data

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ABSTRACT.

The abundance of salmon populations early in the history of large in-river commercial fisheries may be estimated from the total seasonal commercial catch when enough information exists with which to estimate the harvest rate, provided that the clumped distribution typical of seasonal runs of salmon and within-season catches do not nullify the expected operation of the law of large numbers when catches are aggregated over the entire season. Simulated data with varying degrees of within-season clumping is used to evaluate the accuracy of the binomial likelihood and the negative binomial likelihood in the Gamma-Poisson parameterization for estimating the terminal run size of salmon populations. The fishery is modeled as a terminal in-river fishery in which returning adult salmon encounter the gear as they migrate upstream during a daily period of ten hours over a ten week season, for a total season consisting of 700 hourly runs. Both the run of fish and the daily fishery are modeled on an hourly basis with the hourly run of fish simulated to exhibit various degrees of clumping at daily and weekly scales. Binomial and Gamma-Poisson likelihoods are employed in a Bayesian framework to estimate the total return from the aggregate catch for the entire modeled season. Results are evaluated by comparing principal moments of the estimated seasonal run to the true simulated value. Catch data at a finer scale of one week is also analyzed using both the total weekly catch and all of the hourly data for the week to further evaluate the reduction in precision and the increase in bias when the estimate of the total run is based on the aggregate catch instead of the individual hourly catches. Results show that the accuracy of the results with either likelihood depend on how informative the prior on the average harvest rate can be parameterized. When a moderately informative unimodal prior is defensible both likelihoods perform reasonably well with similar bias and precision. When a

non-informative, uniform prior must be used the Gamma-Poisson performs marginally better and provides a more conservative abundance estimate than the binomial. Results confirm the expectation that the operation of the law of large numbers is sufficiently strong that the aggregate catch data will generally provide a robust estimate of historical salmon abundance under a reasonable range of conditions that can be expected to be encountered using historical commercial catch data.

INTRODUCTION.

Salmon catch data spanning a single generation or a single year can be employed to estimate the abundance of salmon runs during the early history of large scale commercial fisheries in rivers of the west coast of the United States. Salmon populations during this period, extending from the latter half of the nineteenth century to approximately 1930, will be referred to as 'historic' to distinguish them from more recent populations that have been subject to a legacy of freshwater habitat damage, hatchery production, and/or mixed stock fisheries along the continental shelf of the eastern Pacific. Recent examples of the estimation of the abundance of historic salmon populations from short time series of commercial catch data are Gayeski et al. (2011) and Price et al. (2013). Gayeski et al. (2011) estimated the abundance of Puget Sound steelhead near the turn of the twentieth century using commercial catch data for 1895, the year of the single largest catch in the record and which occurred within the first six years of the development of the commercial steelhead fishery in Puget Sound. Price et al. (2013) estimated the abundance of Skeena River chum salmon during the period in which large in-river commercial catches of chum salmon first occurred using the geometric mean of the catches for years 1916 – 1919.

Catch data selected from early in the history of a fishery can provide a means to estimate the unfished, equilibrium, abundance of a salmon or steelhead population. Such data will reflect the unfished size of the population before the population has had time to respond to potential selective pressures arising from the imposition of harvest mortality and/or selection on key life history characteristics, particularly the size or age structure. Analysis of such catch data can, therefore, provide important insight into the abundance of salmon populations prior to the losses of habitat and stock diversity that have contributed to the declines of many Pacific Northwest salmon and steelhead populations over the final decades of the twentieth and first two decades of the twenty-first centuries (Slaney et al. 1996, Myers et al. 1998, Lichatowich 1999, Good et al. 2005, Hard et al 2007, Ford 2011).

Under such circumstances, the estimation of the annual run size from the catch data will depend critically on two issues, the estimation of the harvest rate applied to the run that is represented by the catch data and the appropriate probability distribution (or likelihood) to employ for estimating the run from the catch plus the harvest rate. Estimation of harvest rates will depend on information about the fisheries and the gear(s) employed that result in the catch data. The likelihood used will depend in large part on the amount of information about the fishery that is available, particularly the finest temporal and spatial scales at which the catch data can be partitioned. For much of the historical catch data of interest, the scale will be very broad, typically only the aggregate, season total, catch itself. This was the case for the estimates of Gayeski et al. (2011) and Price et al. (2013).

At such large scales a reasonable likelihood to employ would seem to be the binomial (Eq. [1]):

$$C \sim \text{Binom}(N, R), \tag{1}$$

where C is the total catch, N is the total run (the quantity of interest to be estimated), and R the harvest rate (the probability of success of the catch). This was the likelihood employed by Gayeski et al (2011).

However, the binomial likelihood applies most straightforwardly to series of independent Bernoulli trials (Casella & Berger 2001, Gelman et al. 1995, Feller 1971, Vol. 1, Chpt. VI), and it may be objected that the catch of fish in salmon fisheries is not well represented as a series of Bernoulli trials. Terminal, in-river salmon harvests generally consist of a series of hourly and daily catches that extend over a period of several weeks or months during which the number of fish available fluctuates in both time and space (fishing areas). Consequently, catches are more likely to be clumped as is the distribution of salmon in a run of fish encountering the fishing gear during the course of the seasonal return of the fish.

Clumped distributions of animal populations commonly give rise to negative binomial distributions of samples of data from such populations. This suggests that a reasonable alternative to the binomial for estimating the total abundance of an aggregate from samples that may have come from a clumped distribution is a Gamma-Poisson distribution, which well represents the process most likely to underlie and generate samples having a negative binomial distribution (Casella and Berger 2001, Gelman et al. 1995, Hilborn and Mangel 1997). A Gamma-Poisson likelihood was employed by Price et al. (2013).

The negative binomial (Gamma-Poisson) likelihood for catch data, C , is (Eq. [2]):

$$C \sim \text{Poisson}(\text{Gamma}(N,R)), \quad (2)$$

where N and R have the same interpretation as in the binomial (Eq. [1]).

Samples from a population that exhibits a clumped, negative binomial, distribution arising from a Gamma-Poisson process thus result from a two-stage process, as follows: in the first stage, the Poisson rate parameter, λ , governing the random sampling (harvest) from the population is drawn (sampled) from a Gamma distribution with shape parameter, α , and scale parameter, β , where the mean of the Gamma distribution = $\alpha*\beta$. In this context, α = the total abundance of the population being sampled (the total run encountering the fishing gear during a specific time interval), and β = the average harvest rate to which the sampled population is subject:

$$\lambda \sim \text{Gamma}(\alpha = N, \beta = R). \quad (3)$$

Then in the second stage, the catch is derived as a Poisson random variate with rate parameter, λ :

$$C \sim \text{Poisson}(\lambda).$$

(4)

Neither Gayeski et al. (2011) nor Price et al. (2013) provided a formal demonstration of the appropriateness of employing either likelihood for estimating the annual return of salmon/steelhead populations from aggregate catch data spanning an entire fishing season, relying instead on heuristic arguments of the expected appropriateness of each likelihood based on the law of large numbers (Casella & Berger 2001). In order to rely on analysis of aggregate catch data for estimating the unfished abundance of historic populations of interest, it is necessary to determine whether or not there is any bias in such estimation using the binomial likelihood, and if so, how great such bias is likely to be. It is also necessary to determine if reliance on the negative binomial may be more accurate, having less bias; and if so, how much additional complexity to the analysis is required if the negative binomial is to be preferred. A formal analysis of the application of the two likelihoods in the context of estimating the annual return of a salmon/steelhead population from aggregate catch data is required in order for the general approach to have a secure foundation. I provide that foundation by applying the Bayesian analysis framework used by Gayeski et al. (2011) and Price et al. (2013) to simulated run size and catch data that are representative of the context of terminal in-river fisheries typical of early commercial salmon and steelhead fisheries in the Pacific Northwest in the late nineteenth and early twentieth centuries. I simulate several series of hourly salmon run and catch data spanning periods of weeks or months that display varying degrees of clumping and that represent typical terminal salmon fishing scenarios. I then estimate the aggregate run size from the aggregate of the simulated catches using both binomial and negative binomial likelihoods in a Bayesian estimation framework to generate a posterior distribution of estimated run sizes. Results are evaluated in terms of how close several summary quantities from the posterior distributions of the estimated runs are to the true value used to simulate the data.

The results show that for large catches that are the sum of tens to hundreds of hourly or daily catches, the mean of the estimation of the total return using the binomial likelihood is generally

within plus or minus 1% of the true value with coefficients of variation (standard deviation/mean) less than 9% when moderately informative prior distributions on the harvest rate are employed. When uninformative, uniform priors on the harvest rate are used, the mean of the estimated total return is between 5% and 14% of the true value with coefficients of variation of 18%. Estimation using the Gamma-Poisson likelihood is marginally less biased (mean of the estimated run closer to the true value) over the range of prior distributions on the harvest rate evaluated, but the difference is generally not significant except when a uniform prior on the harvest rate must be relied on. For most applications, use of either likelihood under these conditions is a matter of choice. Results for estimation of temporal segments of simulated catches at the scale of one week were similar. The application of the Gamma-Poisson involves only a minor additional complication in the calculation of the posterior distribution at practically no additional computation time. On grounds of general precision, therefore, the Gamma-Poisson is recommended. However, use of the binomial is unlikely to involve much additional bias or imprecision in most applications whose purpose is to achieve a reasonable estimate of the abundance of large salmon and steelhead populations or aggregates of numerous smaller populations.

METHODS.

To evaluate the accuracy of each of the two likelihoods for estimating total population size from aggregate catch data, several data sets were simulated using a Gamma-Poisson distribution, parameterized to result in differing degrees of clumping at a range of temporal scales from hours to days to weeks. The simulated data sets represent the kind of temporal variation in numbers of fish susceptible to the fishing gear that might be expected in common terminal in-river gauntlet-type salmon fisheries employing gears like gillnets, purse seines, and fish traps. All simulations were conducted in Matlab® 7.10 using custom scripts.

Catch data simulated as the outcome of a Gamma-Poisson process will be overdispersed or clumped. The overdispersion can be viewed as arising from the following two processes: first, given a common harvest rate (β), the average catch rate for each hour's fishing effort is

dependent on the size of the hourly run of fish that pass the fishing gear which results in the mean rate realized in that hour for that run size; second, application of the resulting mean catch rate to the hourly run takes the form of a random, Poisson process. It is this kind of fine-scale detail that is absent when only aggregate, end-of-season, catch data are available as will typically be the case when historical, commercial catch data are employed to estimate the size of the run of fish that yielded the aggregate catch. Aggregating catches from multiple temporal catches governed by a Gamma-Poisson process and estimating the total run from which the aggregate catch was obtained using each of the two likelihoods provides a robust test of the accuracy and relative merits of each likelihood.

Simulation Scenarios.

Simulation scenarios were developed that represent a terminal gauntlet fishery in which discrete blocks (runs) of fish encounter a fishery for a specific length of time (one hour) as they migrate through the terminal area enroute to the spawning grounds. I considered three simulation scenarios for this type of fishery.

Scenario 1.

The fishery occurs daily for 10 hours for a period of 10 consecutive weeks (total 700 hours and 700 hourly catches). First, the total run N for the season is chosen. For the results discussed here I chose 500,000. This would be the primary quantity of interest in an estimation of historical run size from aggregate catch data.

Second, the total season's run is randomly divided into 10 weekly runs N_k ($k = 1$ to 10) as follows. A series of ten uniform random numbers on $[0,1]$ are chosen and summed. Then each of the 10 is rescaled by dividing by the sum of the 10 to produce the proportion p_k ($k = 1$ to 10) of the seasonal run to be assigned to each week: $N_k = N * p_k$. Each of the N_k is then rounded down to the nearest integer.

Third, each weekly run total N_k is similarly divided into 7 daily runs N_{jk} ($j = 1$ to 7 , $k = 1$ to 10). Fourth, each daily run N_{jk} is randomly divided into hourly runs N_{ijk} ($i = 1$ to 10 , $j = 1$ to 7 , $k = 1$ to 10). The rounding processes result in the actual run size for the season being slightly (as much as 700) smaller than 500,000 so the actual seasonal run size to be estimated will be this marginally smaller number.

Last, each of the 700 hourly runs N_{ijk} is fished according to a Gamma-Poisson process to yield each hourly catch C_{ijk} , as follows. For each hour a Poisson rate parameter, λ_{ijk} , was drawn randomly from a Gamma distribution with shape parameter α equal to the run size for that hour (N_{ijk}), and scale parameter β equal to the average harvest rate over the entire season (Eq. [5]), where the mean of the Gamma = $\alpha*\beta$, and the variance = $\alpha*\beta^2$:

$$\lambda_{ijk} \sim \text{Gamma}(N_{ijk}, \beta) \tag{5}$$

For scenario 1, β was set to 0.60.

The catch for that hour, C_{ijk} was then drawn as a Poisson random variable with rate λ_{ijk} (Eq. [6]):

$$C_{ijk} \sim \text{Poisson}(\lambda_{ijk}). \tag{6}$$

This procedure will produce catches C_{ijk} from a negative binomial process that will, therefore, be overdispersed relative to having been drawn randomly from a binomial (Bernoulli) process.

Scenario 2.

Scenario 2 was identical to scenario 1 except that the beta parameter of the Gamma distribution from which the Poisson rate parameter (λ_{ijk}) was sampled each hour was drawn randomly from a Beta distribution with mean equal to 0.6 that spanned a range between approximately ± 0.15 of the mean. The specific parameters used were Beta parameter $\text{Beta}_\alpha = 60.0$ and $\text{Beta}_\beta = 40.0$, which has a mean of 0.6 and central 99% between 0.47 and 0.72. Thus, each λ_{ijk} was drawn according to equation 5':

$$\lambda_{ijk} \sim \text{Gamma}(N_{ijk}, \beta_{ijk}), \quad (5')$$

where $\beta_{ijk} \sim \text{Beta}(\text{Beta}_\alpha, \text{Beta}_\beta)$.

For both scenarios 1 and 2, the hourly run sizes, N_{ijk} , lambdas, λ_{ijk} , and catches, C_{ijk} , were recorded and daily, weekly and seasonal totals cumulated and recorded together with the harvest rate (catch/run) for each hour, day, and week, in addition to the totals for the entire season.

The purpose of scenarios 1 and 2 was to evaluate the amount of variability in the total seasonal catch introduced by the Gamma-Poisson process that generated the catches at the fine (hourly) scale, and to evaluate the performance of binomial and negative binomial likelihoods to estimate the total seasonal run size from the aggregate catch data plus estimates of the harvest rate.

Scenario 3.

Scenario 3 simulated harvest for one week (7 days of 10 hours fishing each) . A value of 10,000 was chosen for the total weekly run and partitioned randomly among each of the seven days

following the approach of scenario 1. The hourly runs N_{ij} ($i = 1$ to 10 , $j = 1$ to 7) for each day were then set deterministically by multiplying the daily run N_j by the following proportions: 0.04, 0.04, 0.08, 0.10, 0.12, 0.16, 0.20, 0.14, 0.08, 0.04. Hourly catches, C_{ij} , were determined as in scenario 1 using equations 3 and 4.

The purpose of this scenario is to produce a smaller data set to which estimation algorithms could be applied and to include additional information that may be available in some circumstances that could be included in a Bayesian estimation of the total daily or weekly run. For example, the size of the hourly runs passing a lower river terminal fishery may be determined by environmental conditions such as tidal stage and direction, moon phase, light intensity, water temperature and visibility, knowledge of which could in principle enable estimates to be made of the proportion of each daily run that is expected to enter during each hour of the fishery. Scenario 3 provides for perfect knowledge of these conditions.

Likelihoods evaluated to estimate run sizes from catches.

I estimated the total weekly run size from the aggregate weekly catch (the sum of the 70 hourly catches; scenario 3) and for the entire season (sum of the 700 hourly catches; scenarios 1 and 2) using the two likelihoods, the binomial (Eq. [L1]), and the Gamma-Poisson (Eq. [L2]).

$$P(N|C,R) = [N!/(C!*(N-C)!)]*R^C*(1-R)^{(N-C)}, \quad (L1)$$

where the exclamation sign (!) represents the factorial.

$$P(N|C,R) = P(\lambda|GA = N, GB = R)*P(C|\lambda), \quad (L2)$$

where GA is the shape parameter (alpha) of the Gamma distribution and GB is the scale parameter (beta).

All estimates were produced using Bayesian inference and a program that sampled the posterior probability distribution of the likelihood using a Metropolis-within-Gibbs sampling routine. This required placing prior distributions on run size N, harvest rate R, and (for L2) the Poisson rate parameter λ . For each likelihood, three sets of priors on the harvest rate R were used to examine the impact of uncertainty about R on the accuracy of the different likelihoods : a uniform on [0.4, 0.75] achieved using a Beta(1.001, 1.001), (mean = 0.575); a Beta(61.9, 41.27), (mean = 0.60, stdev = 0.048, central 99% = [0.47, 0.72]); and a Beta(150, 100) (mean = 0.60, stdev = 0.031, central 99% = [0.52, 0.68]). The prior distributions on N and λ for each data set were specified as uniform distributions with upper and lower bounds set to span the entire range of possible values given the range of the harvest rate R and the value of the catch data, C..

In order to better evaluate the accuracy of the two likelihoods when applied to the aggregate weekly catch data for Scenario 3, a third likelihood (L3) was evaluated. L3 is simply the concatenation of L2 applied to each of the 70 hourly catches to estimate each of the hourly runs and the common harvest rate, deriving summary parameters for the seven daily runs (DN_j, j = 1 to 7) and the total weekly run (DNW). This required estimating 141 independent parameters (the common harvest rate parameter R (= the Gamma beta parameter), the 70 hourly runs (FN_{ij}, i = 1 to 10, j = 1 to 7), and the 70 lambdas (λ_{ij}) from which each random value of the hourly catch, C_{ij}, was drawn). Even though the number of parameters to be estimated exceeded the number of independent data points (the 70 hourly catches) it is still to be expected that using all of the fine scale (hourly) catch data will permit the common harvest rate, R, to be estimated more precisely than using the single aggregate catch data point alone, and this in turn should permit the

individual run sizes to be estimated with less variability than the total run using the aggregate catch alone, resulting in a narrower posterior distribution for the total run DNW.

RESULTS.

Results of the data simulations.

Scenarios 1 and 2.

Across 1000 replicate simulations of 700 hourly harvests under scenario 1 the total seasonal run averaged 499,616 and ranged from 499,590 to 499,700. Harvest averaged 299,731 and ranged from 297,351 to 302,033; the aggregate harvest rate averaged 0.5999 and ranged from 0.5952 to 0.6045. Under scenario 2, total seasonal run averaged 499,616 and ranged from 499,590 to 499,710. Harvest averaged 299,752 and ranged from 295,007 to 304,702; the aggregate harvest rate averaged 0.6000 and ranged from 0.5905 to 0.6099. Harvest rates for individual hours (C_{ijk}/N_{ijk}) under scenario 1 spanned a considerably broader range between 0.40 and 0.80, as expected from the Gamma-Poisson process governing hourly harvest, but the central 90% of values spanned the range [0.53, 0.64]. Hourly harvest rates under scenario 2 spanned an even broader range as expected from the combination of random variation in the scale parameter (the harvest rate, R) that added additional variability to the Gamma-Poisson process governing hourly harvests. Still, the central 90% of the distribution of simulated hourly harvest rates spanned the relatively narrow range [0.52, 0.65].

Scenario 3.

Data from a single run of the scenario were used to evaluate the relative abilities of the binomial and Gamma-Poisson likelihoods to estimate hourly, daily and weekly run sizes from the simulated catches. The size of the total weekly run was 9,966. Daily runs ranged from 1031 to 1950 and daily catches ranged from 617 to 1172. Hourly runs ranged from 41 to 390 and hourly catches ranged from 18 to 231. Of the 70 hourly catches 69 were within plus or minus 18 of the value of the Poisson lambda from which the hourly catch was randomly chosen. The remaining

catch was within 29 of the value of lambda from which it was drawn. Of the 70 hourly catch values, 63 were within plus or minus 20% of the corresponding lambda values; the other 7 ranged from plus or minus 22% to 36% of corresponding lambda values.

Hourly harvest rates ranged from 0.39 to 0.83, and averaged 0.61 with a standard deviation of 0.087. Daily harvest rates ranged from 0.42 to 0.87 and averaged 0.61 with standard deviation 0.09. These harvest rate data well illustrate the dispersion that can result from a Gamma-Poisson process and the simulated data should provide an appropriate challenge for the estimation algorithms (likelihoods).

Results from the run size estimations.

Scenario 1.

The results for scenarios 1 and 2 were essentially identical, so I report results only for scenario 1.

Table 1 show summary results for the estimations of the run size N from one of the representative simulations, where the catch data $C = 299,762$ and the total run $N = 499,608$.

Figures 1 and 2 show the posterior estimates of harvest rate and run size from L1 and L2 for the entire season from one replicate simulation of scenario 1 using a uniform prior on the seasonal run size and a mildly informative Beta(61.9, 41.27) prior on the harvest rate, spanning the range [0.45, 0.75] and centered on the true value of 0.6. Figures 3 and 4 show the results from the application of L1 and L2 to the same data but with a highly informative Beta(150,100) prior placed on the harvest rate. Figures 5 and 6 show the results with a broad uniform prior on the harvest rate spanning the interval [0.4, 0.75]. In all cases the true run size is 499,608 and the catch is 299,762.

Scenario 3.

Figures 7 and 8 show the posterior distributions of the common harvest rate (Beta) and weekly run size, DNW, for likelihood L3 overlaid on that for likelihood L2. The true run size was 9,966 and the total catch 6,034. The true average harvest rate was 0.60, as described above.

For these estimates a broad uniform prior was placed on the weekly run size, DNW, and a mildly informative Beta prior (Beta(61.9, 41.27)) was placed on the harvest rate that had a mean = 0.60, and over 99% of the probability mass on the interval [0.45, 0.75]. 300,000 samples from the posteriors were retained using a thinning interval of 50. Consistent with expectations, the posteriors of L3 for both parameters are noticeably narrower (more precise) than those from L2. For the harvest rate, R, the posterior mean (standard deviation) of L3 is 0.60 (0.026) and the mode is 0.60. The central 90% of the posterior distribution lies between 0.55 and 0.64. For L2, the values are 0.6 (0.048) and 0.59, with central 90% on the interval [0.52, 0.68]. For the run size, DNW, the posterior mean (standard deviation) of L3 is 10,247 (448) and the mode is 10,203. The central 90% of the posterior distribution lies between 9,500 and 11,000. For L2, the values are 10,103 (840), 9,835, and [8,840, 11,550]. Non-zero probabilities under L2 range as low as 7800 and as high as 15100; under L3 the range is from 8700 to 12100.

The posteriors from L3 thus provide something of a gold standard against which to compare the posteriors for L1 and L2. Figures 9 and 10 show the posterior distributions of L2 overlaid on those of L1 for harvest rate, R, and run size, DNW using the same set of priors. Figures 11 and 12 show the posterior distributions for the same pairs of likelihoods but using a less informative uniform prior on harvest rate R (Beta) on the interval [0.40, 0.75].

With an informative prior on the harvest rate (Figures 9 and 10), there is little difference in the estimation of the harvest rate, though there appears to be a slight tendency for the Gamma-Poisson to place more of the posterior mass above the true value than does the binomial (Figure 9). This results in a corresponding tendency for the Gamma-Poisson to place more of the posterior mass of the run (DNW) below the true value (Figure 10), though the difference is

extremely small and the proportions of the posteriors above and below the true value are identical for all practical purposes.

The tendency for the binomial to under-estimate R when information is weak relative to the Gamma-Poisson is more apparent when a uniform prior is placed on R (Figure 11). Even so, the shapes of the posteriors of the run size are similar with modes lying below the true value, though the mode of the Gamma-Poisson has modestly larger posterior mass (Figure 12).

DISCUSSION.

The fact that the mean harvest rates on the season runs of ~500,000 were all essentially equal to the average value of R (0.60) under all replicate simulations for both scenarios when informative priors are employed (Figures 1 and 3) is encouraging for the prospect of employing the binomial likelihood to estimate the seasonal run from aggregate catches. When the catch data is this large (~300,000), there is no meaningful difference in the performance of the two likelihoods in estimating either the harvest rate or the run size when there is enough information on the harvest rate to restrict it within some minimal bounds and provide a reasonable indication of the mode of the distribution, as appears to be the case for the Beta (61.9, 41.27) prior (Figures 1 and 2, Table 1, rows 2 and 3).

The mean value of the estimated run N is estimated marginally more accurately by the Gamma-Poisson, L2 (within - 700, compared to + 3900 for the binomial, L1). But the coefficient of variation (standard deviation/mean) is practically identical for each (8.1% and 8.4%, respectively), indicating reasonable precision for both estimations. This is significant and encouraging with respect to the legitimacy of using the binomial likelihood to estimate run sizes associated with large historical commercial catches of salmon. The aggregate catch from scenario 1 is the sum of 700 independent hourly catches each generated from a Gamma-Poisson process with common mean rate parameter. Similar results are obtained from data generated under scenario 2 (not shown) in which the rate (scale) parameter of the Gamma distribution is a

Beta random variate centered on the same average rate (0.60) used in scenario 1. Figures 3 and 4 reinforce this conclusion, showing that when a highly informative prior on the harvest rate is available there no noticeable difference between the estimates of the run achieved using either of the two likelihoods.

These results for the estimation of total seasonal run size from the aggregate of catches over a season, when the individual catches during the season follow an over-dispersed pattern arising from a random Gamma-Poisson process, show that the effects of over-dispersion at the fine, sub-season, scales, are washed out as it were when summed over the season. In fact, a noticeable and significant process of averaging occurs even at subseason scales, such as the weekly catch (compare figures 2 and 10) when a weakly informative prior is placed on the harvest rate. This is a vivid illustration of the operation of the law of large numbers.

When an uninformative, uniform, prior on the harvest rate must be employed, the estimates of both the harvest rate and the total run are much more uncertain (Figures 5 and 6 and Table 1, rows 6 and 7). In this case, the choice of likelihood is more important. Not only does the precision of the estimate of the run depend strongly on the shape and the breadth of this prior, but the choice of likelihood can have an effect on the shape of the posterior distribution of the run and, thereby, on the bias of the estimate, measured in Table 1 as the difference between the true value of N and the posterior mean. In this case the Gamma-Poisson-likelihood performs better than the binomial, placing more of the posterior probability near the true mean, resulting in less bias. Given very weak information, if any, about the harvest rate that produced a given historical aggregate catch, it will clearly be prudent to employ the Gamma-Poisson likelihood (L2) in preference to the binomial (L1), to insure an element of conservatism that may be absent from the binomial in a particular case.

In general, use of L2 will not involve any significant complexity not presented by use of L1. In the context of a Bayesian estimation procedure, as here, L2 requires a prior for a third parameter,

the mean λ for the Poisson process governing the aggregate catch. As shown by simulation as well as inspection of the probability mass of the distribution of λ (not shown), for any choice of rate parameter λ , the posterior distribution of this parameter will invariably lie within plus or minus 40% of the value of the mean (the catch) for small catch values less than 50, with the range above and below the value of the catch decreasing with increasing values of the catch. For large aggregate catches, such as 300,000 in scenarios 1 and 2, for example, the standard deviation of the Poisson is less than 550, and plus or minus 2000 which has nearly zero probability is plus or minus 0.1% of the mean. So a uniform prior on λ is easily included.

The ability of the Gamma-Poisson to provide robust estimates of the total run from the aggregate of fine-scale catches that are generated by Gamma-Poisson-like processes results from the additive property of the shape parameter of the Gamma and of the rate parameter of the Poisson. The sum of the distributions of two Gamma distributions with common scale parameter β and shape parameters θ_1 and θ_2 (Gamma(θ_1 , β), Gamma(θ_2 , β)) will have the same distribution as a Gamma($(\theta_1+\theta_2)$, β). Similarly, the sum of the distributions of Poisson(λ_1) and Poisson(λ_2) will have the same distribution as a Poisson($\lambda_1+\lambda_2$) (see, e.g., Gelman et al 1995, Appendix 1). It is further encouraging that the operation of the law of large number alone appears to confer similar robustness on the binomial (L1) when the data for the aggregate catch is reasonably large and some information on the harvest rate can be obtained.

At finer temporal scales, such as the aggregate catch for one week as illustrated by the results for scenario 3 (Figures 7 – 12), the results are fundamentally similar to those for the aggregate catch for the entire season. Where a moderately informative prior on the harvest rate is justifiable, the posterior distribution of estimates for both the harvest rate and the total run are nearly identical between the binomial (L1) and Gamma-Poisson (L2) likelihoods (Figures 9 and 10). When an uninformative prior must be employed posterior distributions of both are uncertain, spanning the range of the priors, with the Gamma-Poisson providing slightly more conservative estimates of the run, as indicated by the modes in Figure 12.

The results using L3, the conjunction of L2 for each individual catch, show the increase in precision and reduction in bias that can be achieved when most (in this case all) of the fine scale catch data is available. This, of course, will not be the case for large aggregate historical catch data, but merely serves to help appreciate how having to rely on the aggregate catch data contributes to the increase in the uncertainty of the estimate of the true run size, indicated by the addition spread of the posterior distribution relative to L3 (Figure 8). Importantly, even in this case the posterior mean of the estimate using the Gamma-Poisson on the aggregate catch data (L2) is very close to that obtained using all of the data (L3).

The results of these analyses of catch data simulated as the outcome of a random Gamma-Poisson process on temporal components of the total seasonal run show that the binomial likelihood may generally be relied upon to estimate the aggregate, total run from which an total season's catch was obtained when modest information is available for parameterizing the prior on the harvest rate. When this is the case, the estimates obtained from the binomial will be nearly as accurate as estimates obtained using the Gamma-Poisson. When an uninformative prior must be placed on the harvest rate, estimates using the binomial can be expected to be more biased, on the order of 8% to 10%, compared to the bias in estimates obtained using the Gamma-Poisson. Since little additional computational complexity is involved in using the Gamma-Poisson in preference to the binomial, the Gamma-Poisson should be preferred, at least for the case where an uninformative prior on the harvest rate must be used.

Despite these caveats, the results of the simulations show that the mean of the posterior distribution of the total run can be expected to be reasonable close to the true value for estimates using the Gamma-Poisson in all cases and for estimates using the binomial when some information is available to support the use of an informative unimodal prior on the harvest rate. Estimates of the total run using the mean of the posterior under these conditions will generally be within 5% or less of the true value. Estimates with this level of accuracy will be reliable for the principal purpose of estimating to a close approximation the unfished abundance of returning

adult salmon and steelhead populations that were harvested early in the development of terminal in-river fisheries of the late nineteenth and early twentieth centuries.

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TABLES.

Table 1. Values from the posterior distributions of the Bayes estimate of the total run from simulated data under Scenario 1 for the binomial likelihood (model L1) and Gamma-Poisson likelihood (model L2) for each of three prior parameterizations of the harvest rate R. The simulated catch = 299,762. Model codes correspond to the labels in Figures 1 – 6.

Model Code	Likelihood	Prior on R	Mean N	Std N	C.V. N	Mode N	True N	True N - Mean N
L1XM	Binomial	Beta(61.9, 41.27)	503,470	42,434	0.084	493,340	499,608	3,862
L2M	Gamma-Poisson	Beta(61.9, 41.27)	498,910	40,372	0.081	497,260	499,608	-698
L1XN	Binomial	Beta(150, 100)	501,720	26,148	0.052	497,660	499,608	2,112
L2N	Gamma-Poisson	Beta(150, 100)	500,540	26,219	0.052	498,730	499,608	932
L1XU	Binomial	Beta(1.001, 1.001)	566,890	103,840	0.183	682,350	499,608	67,282
L2U	Gamma-Poisson	Beta(1.001, 1.001)	526,390	94,955	0.180	400,780	499,608	26,782

FIGURES.

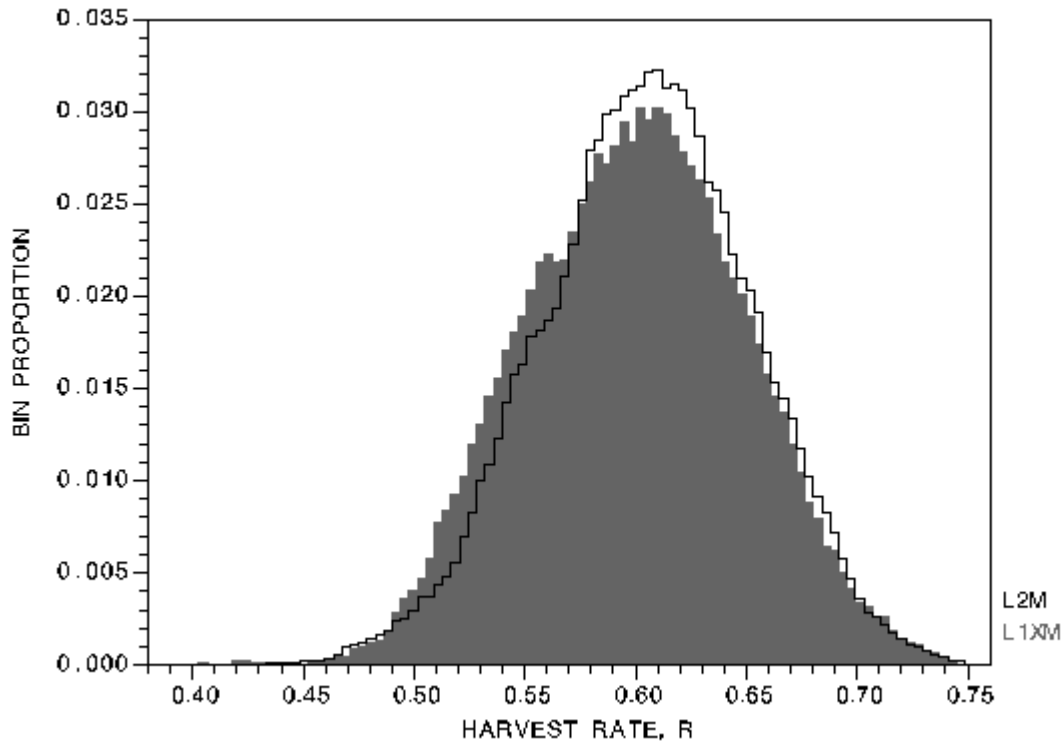


Figure 1. Posterior estimates of common harvest rate, R from L1 (binomial likelihood, solid grey) and L2 (Gamma-Poisson likelihood, black outline) applied to data from one replicate simulation from Scenario 1. True run size is 499,608 and catch is 299,762. Moderately informative prior on R: Beta (61.9, 41.27) prior on R. True harvest rate = 0.60.

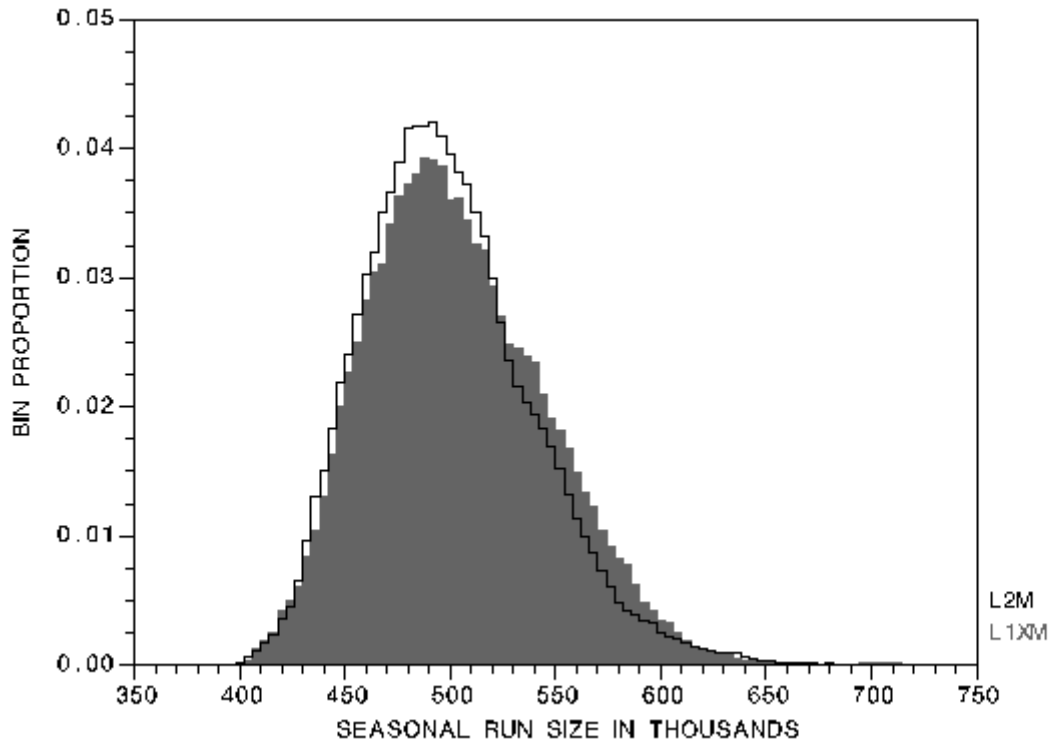


Figure 2. Posterior estimates of seasonal run size from L1 (binomial likelihood, solid grey) and L2 (Gamma-Poisson likelihood, black outline) applied to data from one replicate simulation from Scenario 1. True run size is 499,608 and catch is 299,762. Moderately informative Beta (61.9, 41.27) prior on R. True harvest rate = 0.60. L1: mean $N = 555,512$; standard deviation of $N = 99,361$; coefficient of variation = 0.084. L2: mean $N = 537,667$; standard deviation = 97,735; coefficient of variation = 0.081.

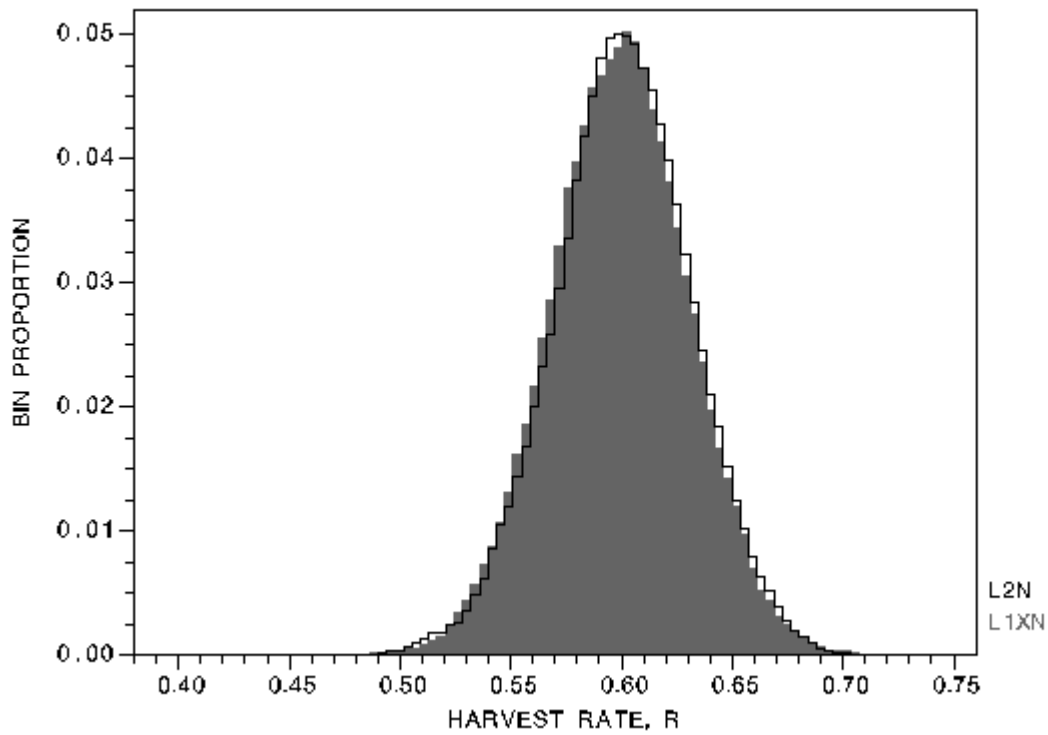


Figure 3. Posterior estimates of common harvest rate, R from L1 (binomial likelihood, solid grey) and L2 (Gamma-Poisson likelihood, black outline) applied to data from one replicate simulation from Scenario 1. True run size is 499,608 and catch is 299,762. Highly informative prior on R : Beta (150, 100) prior on R . True harvest rate = 0.60.

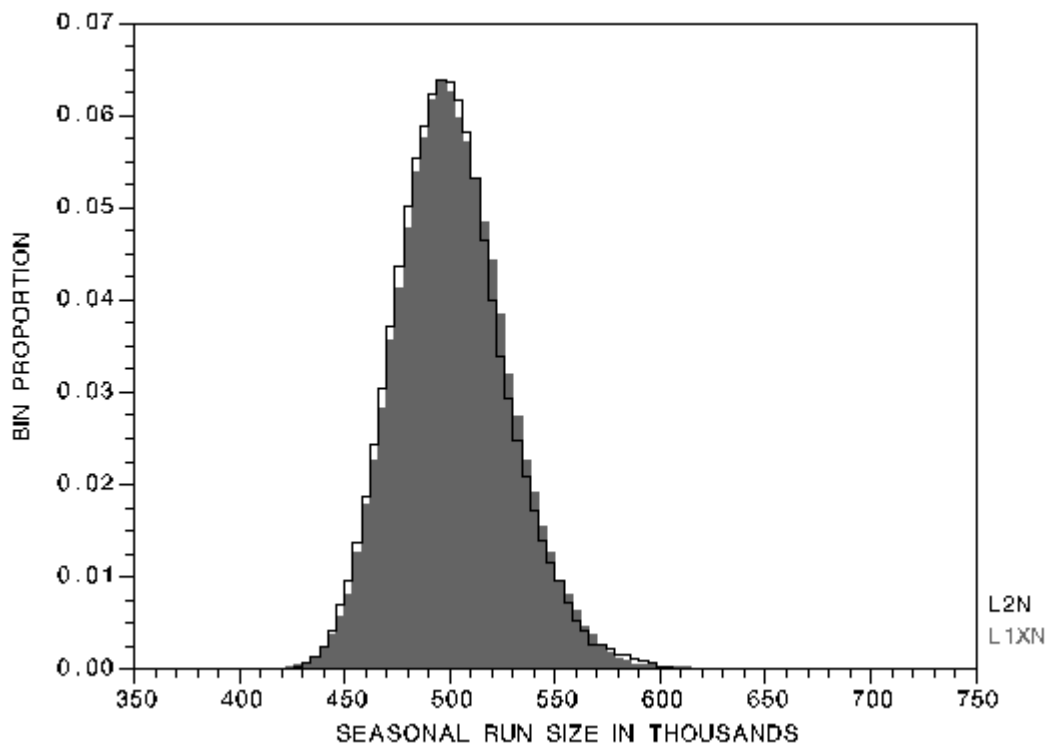


Figure 4. Posterior estimates of seasonal run size from L1 (solid grey) and L2 (black outline) applied to data from one replicate simulation from Scenario 1. True run size is 499,608 and catch is 299,762. Highly informative prior on R: Beta (150, 100) prior on R. True harvest rate = 0.60. L1: mean $N = 501,720$; standard deviation of $N = 26,148$; coefficient of variation = 0.052. L2: mean $N = 500,540$; standard deviation = 26,219; coefficient of variation = 0.052.

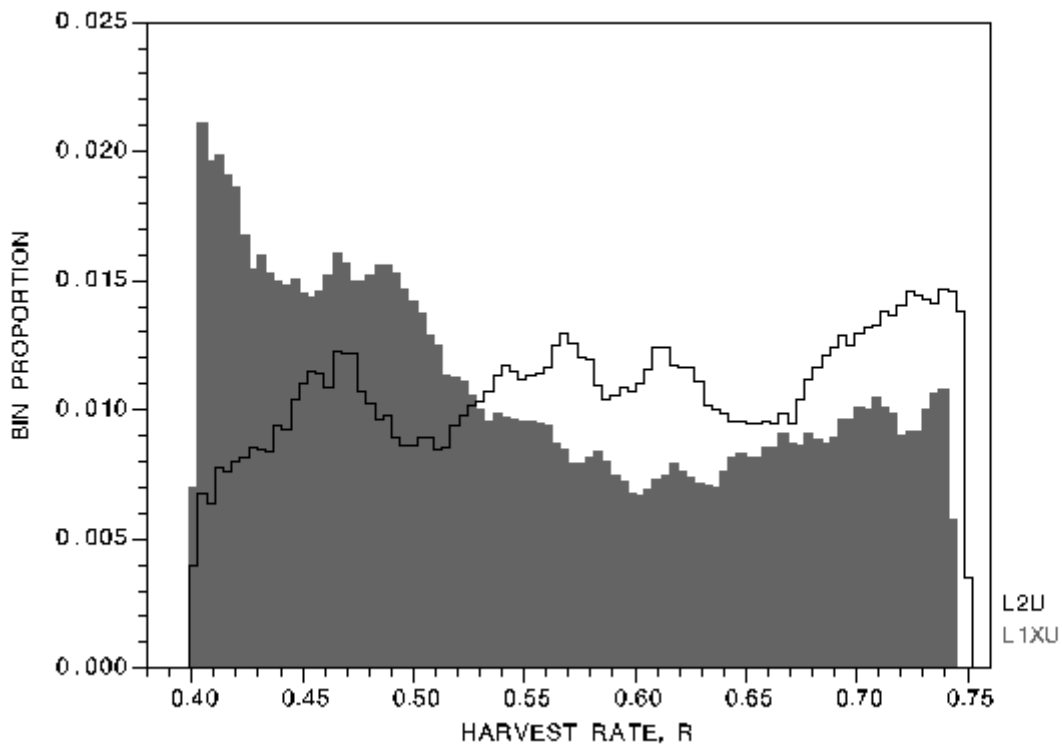


Figure 5. Posterior estimates of common harvest rate, R from L1 (solid grey) and L2 (black outline) applied to data from one replicate simulation from Scenario 1. True run size is 499,608 and catch is 299,762. Uniform prior on R : Beta (1.001, 1.001). True harvest rate = 0.60.

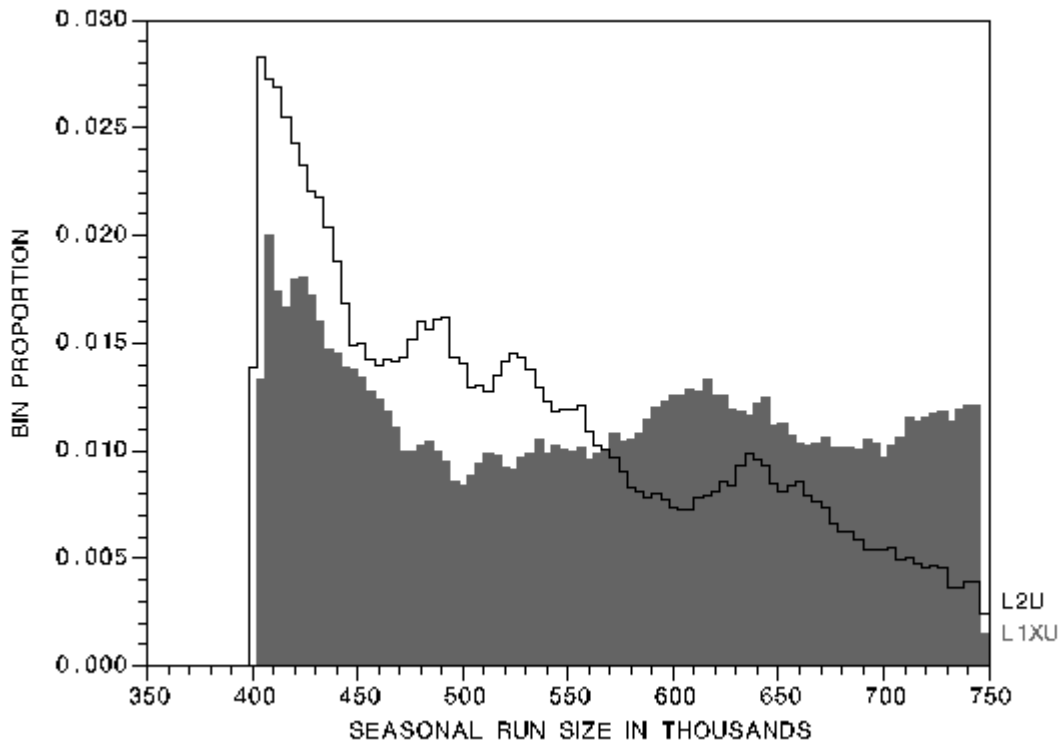


Figure 6. Posterior estimates of seasonal run size from L1 (binomial likelihood, solid grey) and L2 (Gamma-Poisson likelihood, black outline) applied to data from one replicate simulation from Scenario 1. True run size is 499,608 and catch is 299,762. Uniform prior on R: Beta (1.001, 1.001) . True harvest rate = 0.60. L1: mean $N = 566,890$; standard deviation of $N = 103,840$; coefficient of variation = 0.183. L2: mean $N = 526,390$; standard deviation = 94,955; coefficient of variation = 0.18.

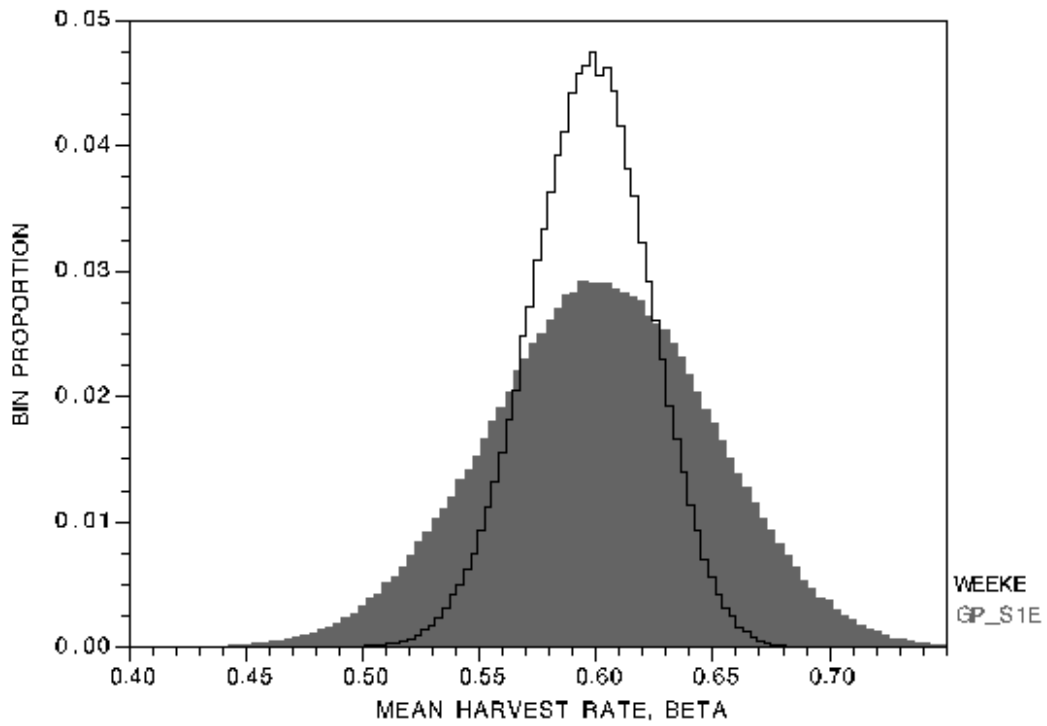


Figure 7. Posterior estimates of common harvest rate, R (Beta), from L2 (“GP_S1E”, solid grey) and L3 (“WeekE”, black outline) using an informative $\text{Beta}(61.9, 41.27)$ prior on R . True harvest rate = 0.60.

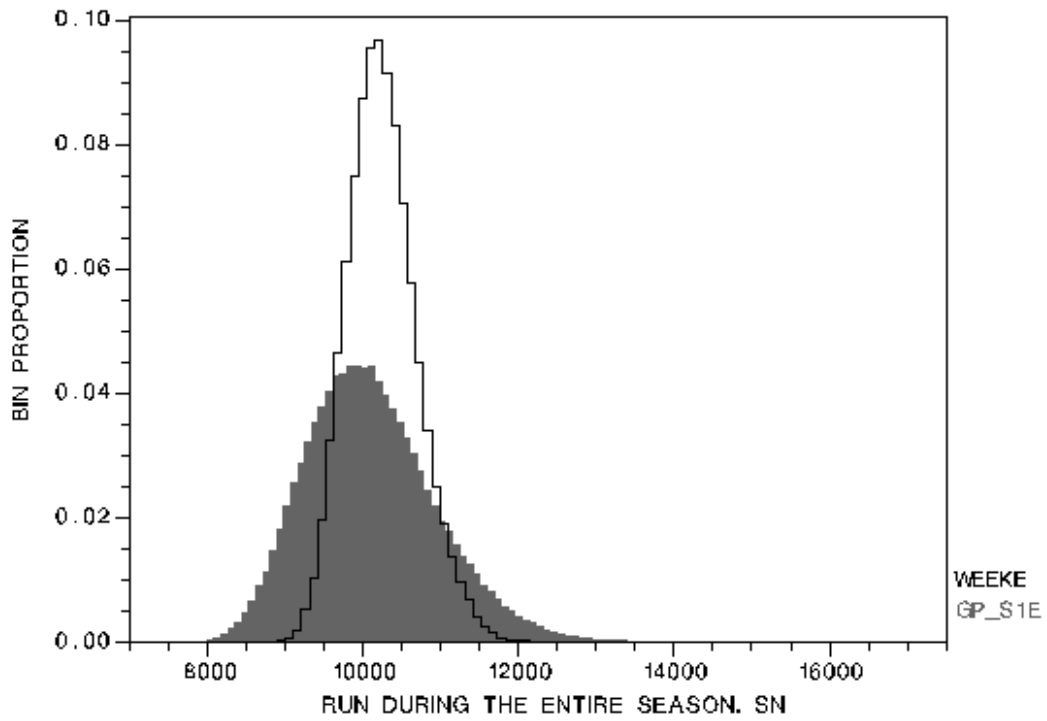


Figure 8. Posterior estimates of aggregate run size for the week, SN, from L2 (“GP_S1E”, solid grey) and L3 (“WeekE”, black outline) using an informative Beta(61.9, 41.27) prior on R.. True run size = 9966.

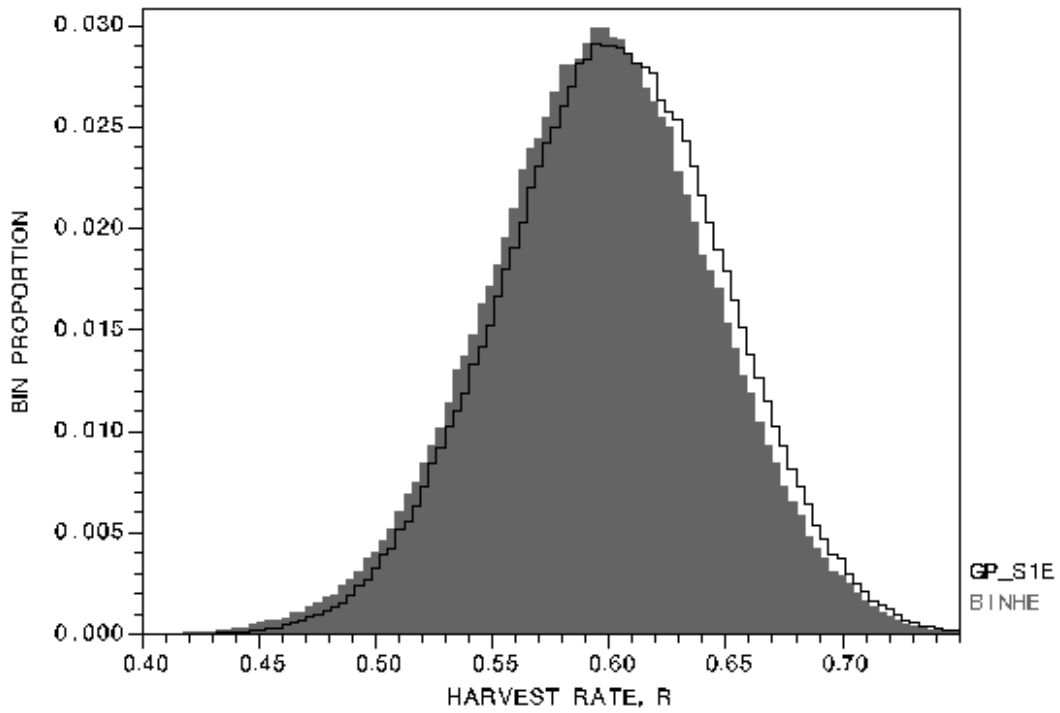


Figure 9. Posterior estimates of common harvest rate, R (Beta), from L1 (“BINH2E”, solid grey) and L2 (“GP_S1E”, black outline) using an informative Beta(61.9, 41.27) prior on R. True harvest rate = 0.60.

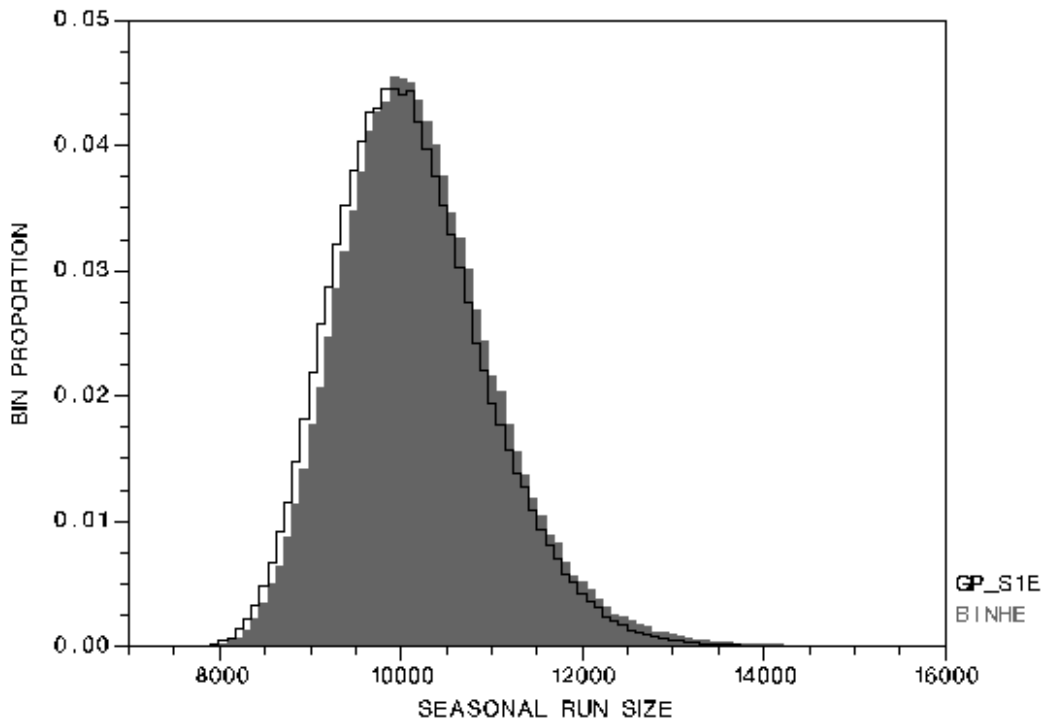


Figure 10. Posterior estimates of aggregate run size for the week, DNW, from L1 (“BINH2E”, solid grey) and L2 (“GP_S1E”, black outline) using an informative $\text{Beta}(61.9, 41.27)$ prior on R . True run size = 9966

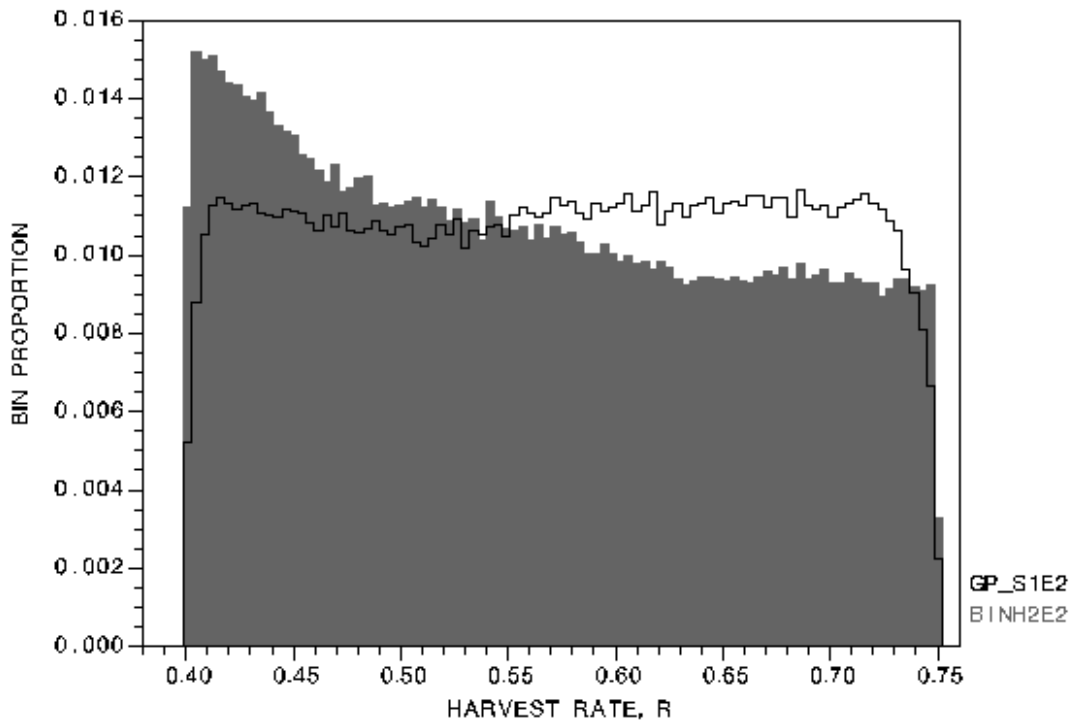


Figure 11. Posterior estimates of common harvest rate, R (Beta), from L1 (“BINH2E2”, solid grey) and L2 (“GP_S1E2”, black outline) using a uniform prior on R on the intervals $[0.40, 0.75]$. True harvest rate = 0.60.

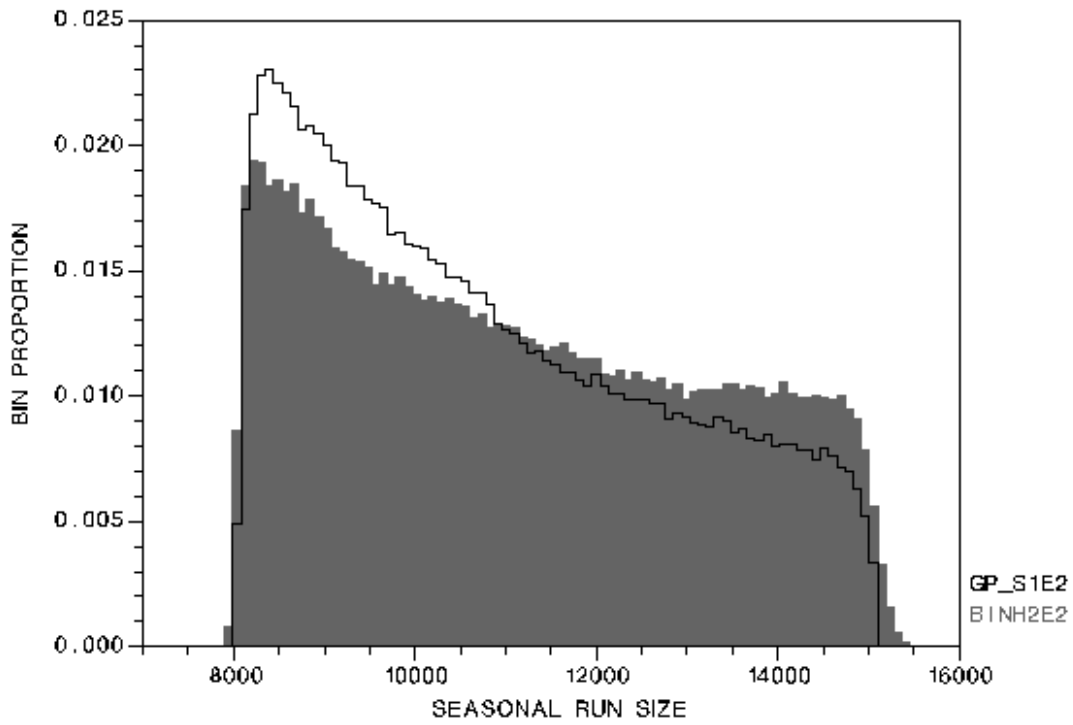


Figure 12. Posterior estimates of aggregate run size for the week, DNW, from L1 (“BINH2E2”, solid grey) and L2 (“GP_S1E2”, black outline) using a uniform prior on R on the intervals $[0.40, 0.75]$. True run size = 9966

CHAPTER THREE

Estimation of the Abundance of Skeena River chum salmon (*Oncorhynchus keta*) during the early rise of commercial fishing 1916 – 1919

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December 21, 2015

ABSTRACT.

Reported commercial catch data and historical information were used to estimate the abundance of Skeena River chum salmon *Oncorhynchus keta*, during the early rise in the commercial fishery of 1916-1919, to provide an historical perspective for recovery plans. A Bayesian analysis was applied to address the uncertainties associated with the estimation process. Based on the historical catch of 204,000 in 1919, and an estimated harvest rate of 0.32 to 0.58, the estimated return of Skeena chum salmon ranged from 355,000 to 619,000, with the most probable single estimate of 431,000. The estimated return of chum salmon based on the 1916-1919 geometric mean catch of 154,000 ranged from 268,000 to 471,000, with the most probable single estimate of 325,000. The posterior modal historical estimates are 36 to 48 times larger than the most contemporary period of 2007-2010. Whereas intense harvest pressure is the single most probable factor to explain the initial decline in chum salmon abundance, other factors such as natural variation in survival, loss of spawning and rearing habitat, and interaction with hatchery fish in the ocean also likely conspire to inhibit their recovery. Nonetheless the Skeena catchment is largely pristine today, and the robust estimates of historical abundance provided by the analysis should be of value to contemporary management and conservation agencies for rebuilding such severely diminished populations.

INTRODUCTION.

This chapter is based on Price et al. (2013) of which I was a co-author and responsible for all of the technical analysis of the historical harvest data and the Bayesian estimation of historical abundance that constitutes the core of the paper. This chapter is written to emphasize the technical analysis to a greater extent than the published version of Price et al (2013).

In this chapter, I present the first case-study, Skeena river chum salmon (*Oncorhynchus keta*) at the beginning of the period when they first became subject to intense commercial fishing. This occurred during the latter half of the second decade of the twentieth century. Chum salmon are currently the most depressed of all Skeena salmon populations and are identified as a conservation concern by Canada's Department of Fisheries and Oceans (DFO) (English et al 2012). Pursuant to Canada's 2005 Wild Salmon Policy (WSP), DFO is currently in the process of identifying management units, known as Conservation Units (CUs), for Skeena River chum salmon and benchmarks of abundance, productivity, and diversity by which to manage each CU so as to secure its long-term existence (Holtby and Ciruna 2007).

I first provide some ecological and biological background to the Skeena River catchment and its salmon and steelhead populations to provide context for the estimations of the historical (1916 to 1919) abundance of Skeena chum salmon. Following this, I provide the details of the estimation of that abundance using Method I. The value of the estimation to contemporary conservation concerns such as the determination of appropriate benchmarks for Skeena chum salmon CUs will be taken up in chapters 6 and 8.

The Skeena River, located in the northwestern portion of British Columbia, is the second-largest watershed in British Columbia, and home to a rich diversity of populations of steelhead and all five Pacific salmon species (Figure 1) The Skeena is over 550 kilometers (nearly 350 miles) long and enters the Pacific Ocean at Prince Rupert, just south of the Alaska panhandle, draining an area of 54,432 square kilometers (21,000 square miles; Gottesfeld and Rabnett 2008). The Skeena catchment is geologically complex, encompassing numerous biogeographic regions and ecosystem types from coastal lowlands to the temperate forest uplands of the interior Nechako

Plateau and is home to multiple local populations of all five Pacific salmon species and steelhead. Its headwaters include the headwaters of the upper Skeena in the Slamgeesh range of north-central BC, which is part of the Sacred Headwaters⁵, the headwaters of the upper Bulkley River on the Necahko Plateau in west-central BC, and the headwaters of the Morice River, the major tributary to the Bulkley, in the glacier fields of the Coast Range. As a result the Skeena and its numerous tributary rivers contain numerous types of river ecosystems and high degrees of habitat complexity, with correspondingly high levels of diversity of populations and life histories for each of the salmon species.

Habitat complexity encompasses the number and variety of different types of riverine and floodplain aquatic habitat structures and their hydraulic connectivity to the main river channel. A basic typology of floodplain habitats important for juvenile salmonid rearing and adult spawning is provided by Stanford et al, 2005, who identify three principal types: shallow shorelines (SS), parafluvial (PF) springbrooks, and orthofluvial (OF) springbrooks. The shallow shoreline is the area of the main river channel adjacent to the bank and extending out to a depth of 0.5 m with current velocities equal to or less than 0.5 m/s, the parafluvial is the area of the floodplain that is annually scoured by flooding and inundated frequently by bankfull or higher flows, and the orthofluvial is the older, more stable, and primarily depositional area of the floodplain that is inundated infrequently by large floods with long (multi-decadal) recurrence intervals. Parafluvial springbrooks occur in flood-scoured channels in the PF zone and are fed by river-derived groundwater discharged from the alluvial aquifer; they are connected to the main river channel at their downstream end at less than overbank flows, become side channels at moderate overbank discharges, and may become completely inundated during large flood-level discharges. Orthofluvial springbrooks are located further from the main channel bank, and often are adjacent to or within floodplain benches with older-growth vegetation. Like PF springbrooks, OF springbrooks are connected to the main channel at their downstream ends, but are fed by aquifer discharge via longer groundwater flow paths.

⁵ The Sacred Headwaters refers to the subalpine area that contains the headwaters of the Skeena, Nass, and Stikine rivers.

By comparison with most rivers on the west coast of the US, the Skeena remains remarkably intact and holds great promise as a stronghold of salmon and steelhead biodiversity. But the river is not free of threats to that diversity, both past and present. Railroad construction on the north bank of the Skeena downstream of the town of Terrace began as early as 1910. Highway construction began in the 1920s and resulted in restricted channel migration and restriction or elimination of access of fish to off-channel spawning and rearing habitats (Pritchard 1948, Gottesfeld & Rabnett 2008). For the most part, until the 1970s little major habitat damage to tributary watersheds had occurred. During the thirty-year period from the 1970s to 2000s, logging occurred in most of the major tributaries, especially those close to the major roadways on and near the lower and middle Skeena River (up to the Kispiox) and the Bulkley River. Much of the damage that was caused by the logging of the 1970s and early 1980s has begun to heal.

Historical information, including efforts by government scientists to rebuild the stocks (cf. Pritchard 1948) indicates that the major impacts on the health and diversity of the Skeena's salmon and steelhead populations have been due to overfishing (Walters et al. 2008, Wood 2008, Hooton 2011). Overfishing started well before any impacts to riverine ecosystems. Major commercial fisheries developed in the lower Skeena by the mid-1880s focused primarily on sockeye and to a lesser extent on coho salmon and Chinook salmon. The landed catch of sockeye salmon exceeded one million for the first time in 1899. In the same year the commercial catch of Chinook exceeded 100,000. By 1911, catches of both sockeye and pink salmon each regularly exceeded one million, and catches of coho and Chinook regularly exceed 200,000 (Pritchard 1948, Argue and Shepard 2005). Steelhead were primarily by-catch in these fisheries, particularly the sockeye fishery which was always by far the most lucrative of all of the fisheries. Steelhead by-catch in excess of 20,000 annually became a regular occurrence after 1914. Catches of chum salmon numbered between one and thirty thousand between the turn of the century and 1913 before dramatically increasing to between one and two hundred thousand in the last half of the second decade (Argue and Shepard 2005).

Before 1950, overfishing had clearly occurred and resulted in major declines of total abundance of all species, as well as loss of diversity as numerous small populations of all species succumbed to the intense harvest pressure of the mixed stock fishery in the lower Skeena. That

fishery primarily targeted sockeye originating from Babine Lake, which historically had contributed 70% or more of the Skeena's total sockeye production (Walters et al. 2008). The 2008 Report of the Skeena Independent Science Review Panel (Walters et al. 2008) noted that by 1950, roughly one-third of Skeena salmonid populations had disappeared.

The decline in diversity and the attendant reduction in the abundance of the remaining populations have, more or less, continued since 1950 with one major exception. By the 1930s overfishing had resulted in a considerable decline in the annual catch of the mainstay of the commercial fishery, Skeena sockeye. Between 1932 and 1950, the sockeye catch failed to exceed 800,000 in 13 of the 19 years. Catches remained depressed through the 1960s. By the early 1960s studies by Canada's Department of Fisheries and Oceans (DFO) had concluded that sockeye production from Babine Lake was limited by lack of available spawning habitat, and plans were made to enhance the amount of available spawning habitat in Babine Lake by building artificial spawning channels in several major tributaries of the Lake.⁶ What became known as the Babine Lake Development Project (BLDP) began in 1965, and by 1976 artificial spawning channels on the Fulton River and Pinkut Creek had a capacity for nearly 800,000 sockeye spawners (Gottesfield and Rabnett 2008). Sockeye harvest in the lower Skeena began to rise above one million by the mid-1970s and by the 1980s and 1990s regularly exceeded two million (Wood 2008).

The artificial increase in Babine sockeye production during this entire period had significant impacts on the abundance and diversity of most other salmon as well as steelhead populations in the Skeena, because the timing of their river entry overlapped with the targeted Babine sockeye. Steelhead, chum and sockeye populations from outside the Babine have been particularly affected.

⁶ Babine Lake in which the majority of juvenile Babine River sockeye rear before becoming smolts is the largest natural lake in British Columbia, covering a total area of 191 square miles. Because of its size, it generally has significantly more rearing habitat area than the available sockeye spawning habitat, considerable though it is, can fill. What simpler way to "solve" this "problem" than by building more spawning habitat? There is now some reasonable doubt as to whether or not there really is a free lunch here, but that is an important story for another day (Cf. Walters et al 2008).

As noted above, chum have been identified as having a high conservation concern. The average annual run size of chum salmon returning to all four CUs during the contemporary period of 1982-2010 was 39,758. For the most recent four-year period of 2007-2010, the average annual run size of Skeena-bound chum salmon was 8,972 (English et al 2012). This is considerably smaller than the geometric mean commercial catch for 1916-1919 of 154,000 or the largest annual catch in this period of 204,000.

METHODS.

Estimation of the Historical Abundance of Skeena River Chum Salmon.

The fishery and catch data of 1916 to 1919.

In the case of the Skeena chum salmon, the catch data available is from a recent DFO document in the Canadian Technical Reports in Fisheries and Aquatic Sciences series (Argue & Shepard 2005) which provides the most thorough and official tabulation of commercial catch data of British Columbia salmon species and steelhead from 1825 to 1950. These authors estimated the catch numbers from the total reported weight of the catch using an average weight for Skeena chum salmon estimated from sampling of northern British Columbia commercial catches for the years 1951 to 1954 and companion analyses to determine that these average weights were likely to differ little from average weights during the periods for which the catch data was obtained.

Prior to 1914 annual commercial catches of Skeena River chum salmon were less than 30,000. They exceeded 50,000 for the first time in 1914 and 100,000 for the first time in 1916. Between 1916 and 1919, catches remained above 100,000 and steadily increased from 115,000 to a peak catch in 1919 of 204,000. The geometric mean catch in this four year period was 154,000. Importantly, this catch occurred prior to the use of gas-powered boats in 1924 that enabled fishers to fish in nearshore areas away from the mouth of the Skeena where non-Skeena stocks had a higher probability of entering the catch. The catch of Skeena chum declined below 100,000 in 1920 and remained below 130,000 for six years until the largest catch on record of 328,000 in

1926 (Argue & Shepard 2005, Table 46). Catches declined thereafter, and following a catch of 181,000 in 1932, never again approached 100,000.

Estimating the abundance of the adult return of Skeena chum salmon from the catch data.

Four years is approximately one generation of Skeena chum salmon (Ricker 1980, Salo 1991). This makes it appropriate to focus the estimation of the historic run size of Skeena chum on the period from 1916 to 1919 and the geometric mean (mean of the natural log catch numbers) for that period. An alternative point of focus would be the large catch of 204,000 of 1919, but the geometric mean catch of the four year period will result in a more conservative estimate. So here I consider just the 1916 – 1919 geometric mean catch. Price et al. (2013) provides estimates for both the 1916 – 1919 geometric mean and the 1919 catch and is attached as an Appendix.

In a more contemporary, data rich, situation it would be preferable to reconstruct a series of annual run sizes (spawner escapements plus harvest) from a time series of annual catch and escapement numbers. If the time series of annual spawner and total numbers of returning adults were stationary, this would also permit the estimation of a spawner-to-adult recruit relationship that would provide an estimate of the average productivity of the stock (cf., Hilborn and Walters 1992, Quinn and Deriso 1999). That is not generally the case, however, with the historical period.

Instead, one must settle for estimating the run for one or a short series of years from harvest data. The period chosen needs to be early in the development of a commercial fishery yielding relatively large catches of the focal stock before the stock shows a population response to the imposition of high harvest mortality. The closer to the period of no or very low levels of fishing-induced mortality, the nearer the estimated run size will be to the unfished equilibrium size of the stock, a common measure of the stock's capacity. If suitable catch data of this kind is not available, the method can not be employed. For example, if catches were known to have been large or harvest otherwise intensive for several generations or decades before reliable quantitative catch data became available the stock would most probably have responded to lower

spawning escapements and would be producing run sizes well below those of the unfished population.

The Skeena chum catch data for the period between 1916 and 1919 satisfy this criterion. Prior to 1916 the commercial catch of Skeena chum was relatively low, so the catches during this period are likely to reflect production from large spawning escapements that may have been typical for much of the history of the stock in the several generations preceding the imposition of harvest mortality. The first commercial harvest records for chum salmon date from 1901, yet the catch remained negligible until 1914 compared to all other commercially caught Skeena salmonids (Argue and Shepard 2005). Annual chum salmon catch steadily increased from 1914 (64,000) to 1919 (204,000), declined and varied for several years, but peaked in 1926 (328,000). Before gasoline-powered vessels were introduced on the Skeena River in 1924, an oar and sail gill-net fishery prevailed (Milne 1955; Price et al. 2013, Figure 2). The limited range of the row-boats confined the commercial fishery during this early period primarily to the Skeena River (Milne 1955; Wood 2008), which provides strong evidence that the vast majority of chum salmon caught were of Skeena origin.

Despite the growing trend in catch during 1914-1919, there was not a directed fishery for chum salmon; chum salmon were incidentally caught in the sockeye and coho salmon (*O. kisutch*) fisheries (Milne 1955; Lyons 1969). Sockeye salmon were harvested annually between mid-June and the end of August predominantly within the Skeena River (Milne 1955; Wood 2008). Some form of an “outside” fishery also existed, whereby a portion of fishing effort occurred within the Skeena estuary during the first three weeks of the sockeye salmon fishery (Ross 1967; Wicks 1975; Blyth 1991). The resulting catch abundance of the outside fishery was reportedly much smaller than the later “inside” fishery when sockeye salmon concentrated within the established fishing boundaries (Ross 1967; Wicks 1975; Figure 1). The coho salmon fishery occurred from the end of August to mid-September (Carothers 1941; Milne 1955). Today, as I assume occurred in the past, the annual return of Skeena chum salmon peaks by the third week of August, and the run continues into September (see Tyee Test Fishery 2012 for data).

The estimation of the harvest rate is the critical element in applying Method I to historic catch data to estimate the total adult return. Given the details on the conduct of the sockeye and coho fisheries, estimating the harvest rate that was applied to the chum run requires estimating the following parameters:

SHR, the sockeye harvest rate,

SHCh, the proportion of the sockeye harvest rate that would apply to chum (since chum have a larger body size and were less vulnerable to the gear specifically designed to catch sockeye),

ChRS, the proportion of the total chum run that would encounter (and thus be vulnerable) to the sockeye fishery (since the chum run started sometime after the sockeye run and extended beyond the end of the sockeye fishing season),

CoHR, the coho harvest rate,

CoHCh, the proportion of the coho harvest rate that would apply to chum,

(1-ChRS), the proportion of the total chum run that would encounter the coho fishery (equal to 1 minus the proportion that would encounter the sockeye fishery).

The total harvest rate on chum salmon is then derived as a function of the five independent quantities in equation [1]:

$$ChHR = (ChRS * SHCh * SHR) + [(1 - ChRS) * CoHCh * CoHR]. \quad (1)$$

Importantly, there is a considerable amount of data available for the sockeye fishery and there are robust estimates of the sockeye harvest rate (SHR) spanning the period of interest by Canadian fishery scientists (e.g., Shepard and Withler 1958; Ricker 1973; Ricker and Smith 1975; Wood 2008). This provides an anchor for estimating the harvest rate.

The estimate of focal population abundance is then carried out as a Bayesian inference by placing prior distributions on the five independent parameters required to derive an estimate of the harvest rate on the focal chum population (ChHR), and the remaining parameters of the

likelihood employed to derive the estimate of the focal populations size. For this case, I employ the Gamma-Poisson likelihood (Chapter 2, Equation [2] and equation [2] below), and so derive estimates of the posterior distributions of the main parameter of interest, the run size N , and for λ , the Poisson rate parameter for the 1916 – 1919 geometric mean catch, C , of 154,000.

The Gamma-Poisson likelihood for this case is:

$$P(C|\lambda, N, ChHR) = P(C|\lambda) * P(\lambda|N, ChHR), \quad (2)$$

which is the joint probability of obtaining the catch, C , given a Poisson distribution with rate parameter, λ , and obtaining λ from a gamma distribution with parameters N , and $ChHR$. In this parameterization, the expected value of the gamma is $\alpha * \beta$ (in this case, $N * ChHR$), which will also be the expected value of λ . Since the expected value of a Poisson-distributed random variable is also λ , the expected value of the Poisson-distributed catch, C , will also be equal to λ , which will be the mean of the gamma-Poisson. But unlike the Poisson distribution, the variance of the gamma-Poisson will be greater than the mean, and equal to $\alpha * \beta * (1 + \beta)$. Thus, the variance of the catch, C , will be: $N * ChHR * (1 + ChHR)$. In our situation, C (catch data) is a constant, and λ , $ChHR$, and N are the parameters to be estimated.

There is little uncertainty in the estimation of λ , since the coefficient of variation (c.v. = standard deviation/mean) for large values of λ (as is the case here) is very small (e.g., for $\lambda = 200,000$, the standard deviation will be $\sqrt{200,000} = 447$, and c.v. = $447/200,000 = 0.00224$). However, considerable uncertainty is involved in estimating N , $ChHR$, and each of the five independent parameters in equation 1 ($ChRS$, $SHCh$, SHR , $CoHR$, $CoHCh$), from which the aggregate chum salmon harvest rate, $ChHR$, is derived. These uncertainties are addressed by employing a Bayesian approach, placing prior distributions on all unknown parameters, and using a Metropolis-within-Gibbs Markov Chain Monte Carlo (MCMC) algorithm to sample the posterior distribution (equation 3) corresponding to the Gamma-Poisson likelihood (equation 2):

$$P(\lambda, N, ChHR|C) = P(\lambda|C) * P(N, ChHR|\lambda). \quad (3)$$

The Bayes estimate of the terminal run size was conducted using the Fortran shell program Metropolis-within-Gibbs (MTG), written by the late Dr. Daniel Goodman (Environmental Statistics Group, Department of Biology, Montana State University, Bozeman, Montana). MTG implements the Metropolis-within-Gibbs algorithm, sampling a joint distribution specified by a joint log proportional density function (which for the Bayes analysis, is the joint posterior coded to a proportionality as the product of the joint prior and joint likelihood). The posterior distribution of the unknown parameters in equation (3) (N , and $ChHR$) was sampled with the catch, C , set to 154,000. For each estimate, 500,000 samples were retained using a thinning interval of 50 (i.e., every 50th sample was retained) to reduce the autocorrelation among parameter values which results from the MCMC sampling of the posterior distribution, and to insure thorough sampling of the entire posterior probability space. The priors and posteriors of parameters selected for histogram display were binned into 100 equal-size bins on the x-axis to produce smooth histograms, and to provide reasonably fine-scale resolution of the posterior probability densities. Histograms of the posterior distributions for the parameters contributing to the chum salmon harvest rate (i.e., $ChRS$, $SHCh$, SHR , $1 - ChRS$, $CoHCh$, and $CoHR$) were examined together with summary statistics for the MCMC samples to verify that the entire posterior parameter space had been properly sampled.

Justification of the prior distributions.

The parameterizations of the prior distributions were based on available data regarding the conduct of the fisheries and associated gear-type, the known and estimated run-timings of each species, and the relative and absolute body size of chum salmon. The prior distributions and their parameters are listed in Table 1. To be conservative, I chose values that tended to give smaller estimates of the total chum salmon population size for the following priors.

The Poisson rate parameter for the distribution of the chum catch, PLAM

Given the assumption that the total catch of chum salmon is a Poisson random variable, I placed upper and lower limits on a uniform distribution of the rate parameter, $PLAM$, which spanned all

possible values that could yield the numerical catch, C . For values of C as large as those for the two time periods whose catch I evaluate, values of $PLAM$ will lie well within plus or minus 10% of C , so we set the lower boundary at $0.9 * C$ and the upper boundary at $1.1 * C$. This guaranteed that all possible values of the posterior probabilities of $PLAM$ would be found.

The proportion of the total chum salmon run that encountered the sockeye salmon fishery, ChRS.

The commercial Skeena sockeye salmon fishery historically closed by the end of August each year (Milne 1955). The majority of chum salmon are thought to return to the Skeena River before the end of August, but the exact proportion remains unknown. Data from the Tyee test fishery, which dates to 1956, suggests that this proportion may be somewhere between 67% and 75% of the entire annual return of Skeena chum salmon (Tyee Test Fishery 2012). As noted above, I assume that this range also applies to the period of interest herein (1916-1919); thus, I placed a uniform distribution on the parameter between these two boundaries, 0.67 and 0.75.

The proportion of the annual sockeye salmon harvest rate to which chum salmon were vulnerable, SHCh.

Although chum salmon were targeted by the Skeena fishery to some extent, it is improbable that harvest rates were higher than on sockeye salmon during the years of the evaluation because chum salmon had inferior market value compared to sockeye salmon (Milne 1955; Lyons 1969). Furthermore, chum salmon were substantially larger on average than sockeye salmon (i.e., 6.4 kg compared to 2.9 kg; Argue and Shepard 2005), which made chum salmon less susceptible to capture in sockeye salmon specific gill-nets (i.e., $5^{3/4}$ mesh; Milne 1955) that retain fish within a narrow size range (Hamley 1975; Muir et al. 1994). Thus, the actual harvest rate on chum salmon likely was some fraction of the estimated sockeye salmon harvest rate, perhaps 50% to 60%, and certainly not more than 90%. Therefore, a uniform distribution was placed on $SHCh$ bounded between 0.60 and 0.90.

The total annual harvest rate on the sockeye run, SHR.

The harvest rate on Skeena sockeye salmon during the period 1915-1919 has been estimated at 0.62 (Ricker 1958, 1973; Ricker and Smith 1975), and substantiated by Wood (2008). However, good as this estimate may be, it is likely that there is some degree of uncertainty surrounding these estimates when applied to any single year; accordingly, I placed a uniform distribution on the parameter between 0.58 and 0.66 to account for some uncertainty.

The proportion of the total chum salmon run that encountered (and were potentially subject to harvest during) the post-sockeye salmon season coho salmon fishery, 1-ChRS.

The sampling of this parameter was calculated deterministically by subtracting each value sampled from the prior of *ChRS* from 1. This is because we are estimating the proportion of the chum salmon run that remained after the sockeye salmon fishery, but were also vulnerable to the late-season coho salmon fishery (i.e., we assume that all chum salmon were either exposed to the sockeye salmon or coho salmon fishery).

The proportion of the total harvest rate on the post-sockeye salmon season coho run to which the overlapping proportion of the chum salmon run (1-ChRS) were vulnerable, CoHCh.

Chum salmon were substantially larger on average than coho salmon (i.e., 6.4 kg compared to 4.4 kg; Argue and Shepard 2005), and may have been less likely than coho salmon to be caught in the late-season gill-net fishery. Additionally, chum salmon were unlikely to be caught in the hook-and-line fishery that targeted coho salmon during our period of interest. But to be conservative and given the paucity of information, I placed the same distribution and limits on the harvest rate on the late-season chum salmon run as I did for chum salmon subject to the sockeye salmon fishery. That is, I felt that chum salmon were as vulnerable to the coho salmon fishery as they were to the sockeye salmon fishery (i.e., 0.60 and 0.90).

The harvest rate on the post-sockeye salmon season coho salmon fishery, CoHR.

Harvest rates on coho salmon were not likely higher than the harvest rates on sockeye salmon because sockeye salmon had superior market value (Milne 1955); canneries, and fishermen, made the majority of their money on sockeye salmon (Ross 1967; Lyons 1969; Wicks 1975). And although some fishermen only participated in the sockeye salmon fishery (Knight and Koizumi 1976), others were involved in an additional hook-and-line fishery that targeted coho salmon (Blyth 1991). To account for the uncertainties in fishing effort conservatively, I placed a uniform distribution on the *CoHR* parameter between 0.45 and 0.60.

The informative character of the prior distribution of the chum salmon harvest rate, ChHR.

Despite having to employ uniform priors for five independent parameters to obtain the prior distribution for the aggregate harvest rate on Skeena chum salmon (*ChHR*), the resulting prior had a unimodal bell shape centered around the mid-point of 0.45. This resulted from a common property of the multiplication of several uniform distributions, and yielded a considerable reduction in the uncertainty surrounding this parameter. The critical information lies in the upper and lower limits of the contributing uniforms, which I delimited as best I could given the available historical information as explained above. Thus, even with little or no information on the shape of the component parameters of this prior, the aggregation of multiple uniforms yielded a prior that contained considerably more information than if I had placed a uniform prior directly on *ChHR*.

Sensitivity of the prior for the chum salmon harvest rate, ChHR, to the limits of the component parameter distributions.

I examined the sensitivity of the distribution of *ChHR* to the lower and upper limits of the parameter components to determine how influential each limit of each component is to the distribution of *ChHR*; methods and results are presented in the Appendix. Essentially, the prior on *ChHR* was moderately sensitive to increases of 0.1 to 0.2 in the upper limits of *SHR* and *CoHR* (Appendix, Tables A1-A2), values for the sockeye salmon and coho salmon harvest rates that are well above any estimates made for these fisheries. The prior on *ChHR* was insensitive to

changes of 0.1 to 0.2 to the lower or upper limits of *ChRS*, *SHCh*, and *CoHCh* (Appendix, Tables A3-A5).

The terminal chum salmon run size, N.

The only information on historical chum salmon abundance is the company records of canned packs and other products, which were converted to catch in pieces by Argue and Shepard (2005). Accordingly, I simply bounded the prior distribution of *N* broadly between the minimum and maximum values possible, given the values of the prior distributions contributing to *ChHR*. Given the values of the priors, the minimum value of $ChHR = (0.67 * 0.60 * 0.58) + (0.33 * 0.60 * 0.45) = 0.32$. The maximum value of $ChHR = (0.75 * 0.90 * 0.66) + (0.25 * 0.90 * 0.60) = 0.58$. Given a value for the catch, *C*, the lower bound on $N = C / 0.58$, and the upper bound on $N = C / 0.32$. The posterior distribution of *N* then will be bound within these limits; this permits the sampling of the posterior of *N* to examine only possible values of *N*, and thereby increases the efficiency of the MCMC algorithm.

Comparison of historical and contemporary Skeena chum salmon run sizes.

I used run-reconstruction estimates of chum salmon returning to the Skeena River during 1982-2010 (see English et al. 2012) to compare the results of historical (1916-1919) run sizes with recent abundance. Because chum salmon in Canada are managed within the context of Conservation Units (CU; Wild Salmon Policy 2005), I apportioned our historical chum salmon abundance estimate into respective CUs for the Skeena; these include: Skeena estuary, Lower Skeena, Middle Skeena, and Upper Skeena (Holtby and Ciruna 2007). I used DFO's management target escapement goals assigned for each CU to approximate the historical proportion of chum salmon that likely returned to each CU. The assigned goals and proportions are: Skeena estuary (2,775; 4%), Lower Skeena (43,975; 76%), and Middle Skeena (11,000; 19%; DeMarco 1991). Given the absence of target goal data for the Upper Skeena CU, which currently consists of only a single small spawning population (Gottesfeld and Rabnett 2008), I assume this CU historically represented 1% of the combined Skeena chum salmon abundance.

RESULTS.

The prior distribution of the aggregate harvest rate on chum salmon (*ChHR*) during 1916-1919 ranged from 0.32 to 0.58, with the most probable value centered on 0.45 (Figure 2). Because the catch data fail to provide independent information on the harvest rate, the posterior distributions of *ChHR* are identical to the priors. Based on the geometric mean catch for 1916 – 1919 of 154,000 the estimated return of chum salmon ranged from a minimum of 268,000, to a maximum of 471,000, with the most probable single estimate of 325,000 (Figure 3, Table 2.). There is a 95% probability that the run was greater than 296,000, and a 5% probability that it exceeded 408,000.

The average annual run size of chum salmon returning to the Skeena estuary and watershed during the contemporary period of 1982-2010 was 39,758. For the most recent four-year period of 2007-2010, the average annual run size of Skeena-bound chum salmon was 8,972. The posterior modal historical estimates of the total run size of chum salmon returning to the Skeena during the period of 1916-1919 is times larger than the contemporary period of 1982-2010, and 36 times larger than the most recent period estimate of 2007-2010. Apportioning our historical modal chum salmon run size estimate for the period 1916-1919 into separate Skeena CUs, results in a 38- to 43-fold difference with the most recent contemporary period (Table 3).

DISCUSSION.

The results show that a credible estimate of the historic abundance of Skeena chum salmon can be obtained from catch data spanning a chum salmon single generation while fully accounting for the important uncertainties that are involved in producing an estimate from sparse historical data. The Bayes inference approach using a Gamma-Poisson likelihood provides a robust basis for estimating total run size from aggregate, full-season, catch data while propagating all uncertainties through the inference.

The results reveal a large discrepancy between the return of 94 years ago, and returns of today. At least four potential explanations for the discrepancy exist: marine survival differences between periods, loss of spawning and rearing habitat, over-exploitation, and poor data quality. I discuss each in turn.

Differences in marine survival between periods.

Marine climate variability at basin-wide and regional scales has a well-known influence on Pacific salmon productivity (Mantua et al. 1997; Meuter et al. 2002). Ocean survival of Alaska and south-coast British Columbia salmon populations appears to exhibit a strong and consistent correlation with indices of ocean productivity, such as the Pacific Decadal Oscillation (PDO; Mantua et al. 1997; Beamish et al. 2000). Similarly, consistent effects of regional sea surface temperatures (SST) on the survival of Pacific salmon have been observed (Meuter et al. 2002, 2005; Connors et al. 2012). For example, the relatively recent 20- to 30-year time period associated with warmer ocean temperatures on British Columbia's south coast are thought to have contributed to the four-fold decline in the marine survival of steelhead trout *O. mykiss* (Ward 2000). Furthermore, the large and consistent decreases in sockeye salmon productivity in many areas along the west coast of North America since the late 1990s may be due to similar processes (Peterman and Dorner 2012).

However, it seems unlikely that the large difference in abundance between historical and contemporary periods that I have estimated for Skeena chum salmon could be accounted for by differences in ocean productivity, for three reasons. First, salmon populations in northern British Columbia do not appear to respond to productivity indices, such as the PDO, as strongly as populations further south or north (Hare et al. 1999; Hill et al. 2009). Second, even if Skeena chum salmon responded strongly to such indices, ocean conditions in the decade leading up to the large run of 1919, as indexed by the PDO, were not distinctly favorable or vastly different from those experienced in recent years (Hare et al. 1999; Biondi et al. 2001). Finally, coastal ocean conditions (as measured by PDO or SST, both admittedly indirect and statistically noisy indices) explain a relatively small proportion of the variability in salmon productivity (i.e., recruitments per spawner) compared to other factors (Meuter et al. 2005; Connors et al. 2012).

Salmon share a common resource pool in the north Pacific; as such, large increases in salmon abundance can reduce survival rates (Peterman 1984; Ruggerone and Neilson 2004; Helle et al. 2007). For example, the dramatic increase in abundance of artificially-produced (hatchery) salmon likely have increased competition in oceanic feeding grounds for wild salmon populations, leading to reduced productivity (Cooney and Brodeur 1998; Heard 1998; Zaporozhets and Zaporozhets 2004). Pink salmon abundance in the north Pacific, which has more than doubled since the 1950s owing to hatchery supplementation (Ruggerone et al. 2010), is suspected to have had a strong negative influence on the productivity of numerous British Columbia sockeye salmon populations (Connors et al. 2012). Moreover, the large release of hatchery-produced chum salmon in Alaska since the late 1980s is considered a likely factor in the steep and recent decline of wild chum salmon north of Southeast Alaska (Ruggerone et al. 2010). The annual release of 2 billion Japanese hatchery-produced chum salmon could potentially affect the growth of wild chum salmon from Alaska and British Columbia because these enhanced fish are broadly distributed throughout much of the north Pacific (Myers et al. 2004). Russia also releases 360 million hatchery chum salmon annually (Ruggerone et al. 2010), and combined with the annual release of Alaskan and Japanese hatchery chum salmon and pink salmon, could negatively affect the survival of wild chum salmon from the Skeena River.

Might competitive effects from the increased abundance of hatchery fish be the primary driver of abundance decline in Skeena chum salmon over the last century? Again, this seems unlikely for two reasons. First, although the annual release of billions of Japanese and Russian hatchery-produced chum salmon is thought to be inhibiting the recovery of wild chum salmon populations in Russia (Radchenko 1998; Kaeriyama et al. 2007), over-harvest and perhaps freshwater habitat degradation in the southern area of the Russian Far East are considered the key factors that have affected the overall decline in Russian wild chum salmon (Ruggerone et al. 2010). Second, Skeena chum salmon populations were already significantly reduced by the 1930s, and remained low until at least 1950 (Argue and Shepard 2005), long before large-scale hatchery production commenced. It is certainly true, however, that the substantial increase in hatchery fish now utilizing the north Pacific may account for the large decline of Skeena chum salmon over the contemporary period of 1982-2010.

Loss of spawning and rearing habitat.

The Skeena River is currently one of North America's most important salmon producers (Gottesfeld and Rabnett 2008). Chum salmon spawn mostly in the coastal portion of the watershed, and commonly utilize back-channels and spring-brooks in the lower Skeena River and adjacent tributaries. Emergent fry may hold for several weeks in floodplain spring brooks as pre-smolts (J. Stanford, unpublished data). While industrial development in the watershed remains in its infancy, some habitat degradation has occurred. With relevance to chum salmon, several back-channel habitats in the lower Skeena River have been altered or cut-off by railroad and highway construction, and logging has been extensive (Gottesfeld and Rabnett 2008). Unfortunately, the extent of spawning habitat loss or degradation for Skeena chum salmon has not been quantified. But data deficiency aside, we believe that the difference between our historical abundance estimate and contemporary period far exceeds even the most exaggerated estimate of spawning habitat loss. For example, habitat loss for steelhead trout returning to Puget Sound (a region of high-density urban and industrial development) was recently estimated to be no more than 33% (Gayeski et al. 2011). Notably, this estimated loss in habitat was deemed negligible in the context of a 25-fold reduction in steelhead trout abundance. The Skeena River by comparison is essentially in pristine condition. Although reductions in marine productivity, owing to warmer sea temperatures or oceanic competition from hatchery fish, likely far outweigh freshwater habitat loss for Skeena chum salmon, further work is needed to assess the current levels of spawning habitat abundance, and to evaluate the current potential of these habitats to produce juveniles.

Overexploitation during the rise of industrial fishing.

Declines in marine productivity and available spawning habitat have undoubtedly contributed somewhat to the current low numbers of chum salmon returning to the Skeena watershed. However, intense harvest pressure is the single most probable factor to explain the initial decline in chum salmon abundance. Severe over-harvest of most species of salmon is believed to have occurred during the rise of industrial fishing on the Skeena (Gottesfeld and Rabnett 2008), and

an evaluation of the historical catch data lends support to this hypothesis. With regards to chum salmon, the peak catch years of 1919 and 1926 coincided with heights in fishing effort. The number of canneries reached a maximum during the years 1917-1919 and 1926 (Ross 1967; Lyons 1969), and the number of gill-net licenses exceeded 1,000 for the first time in 1919 (Milne 1955), which surpassed the previous maximum in 1915 by ~ 200 licenses. Despite advances in fishing technology after 1924 (e.g., gasoline-powered vessels and mechanical net-drums, which substantially increased catch efficiency), and the perpetuation of intense fishing effort (annual gill-net licenses exceeded 1,100 until 1935; Milne 1955), overall chum salmon catch has generally declined since 1926 (Argue and Shepard 2005). Thus, perhaps analogous to wild chum salmon in Russia south of the Amur River and in Japan, fishing pressure likely significantly reduced the historical abundance of Skeena River chum salmon, and other interactive anthropogenic influences discussed above may now inhibit recovery.

An additional factor perhaps further inhibiting the recovery of Skeena chum salmon, and exacerbated by previous fishing-induced declines in spawner abundance, is the resulting loss in marine-derived nutrient subsidies. Some evidence suggests that spawning salmon influence juvenile salmonid growth rates, and the perpetuation of future generations through carcass deposition and nutrient cycling (Gende et al. 2002). Estuaries can receive a large proportion of post-spawning salmon nutrients (Cak et al. 2008), which is of particular importance for chum salmon that rear as juveniles in estuaries. It is plausible that the fertility of the Skeena River and estuary has declined considerably, related to more than 100 years of intense exploitation of most Skeena salmonids, and the subsequent reduction in returning salmon nutrients. A nutrient shortage may constrain population sizes far below historical levels as a result of density-dependent mortality in juveniles (Larkin and Slaney 1997; Gresh et al. 2000), and impede the recovery of diminished populations (Achord et al. 2003).

Data quality.

One concern regarding the catch data used for our historical estimate is that perhaps a portion of chum salmon caught during 1916-1919 originated in systems other than the Skeena. It is generally understood that chum salmon were incidentally harvested in the more lucrative

sockeye salmon fishery during the period of our evaluation (Milne 1955; Lyons 1969). Some fishing effort may have occurred beyond the river and within the Skeena estuary between mid-June and the first week of July (Ross 1967; Wicks 1975; Blyth 1991). Because chum salmon generally do not enter the Skeena River until after the second week of July (but may have historically returned earlier), it is plausible that a proportion of chum salmon caught during the outside fishery originated elsewhere. Recent gill-net catch data (1970-2009) for DFO's statistical area 4 (a vast area that extends far beyond the mouth of the Skeena River), suggests that up to 12% of chum salmon with unknown origin are caught before the second week of July (Pacific Salmon Commission 2011). Historical and contemporary run-timings of chum salmon being equal, these data suggest that up to 12% of the total catch calculated by Argue and Shepard (2005) may not have originated in the Skeena. For the year 1919, this would amount to a maximum of 25,000 non-Skeena chum salmon. Importantly, this proportion was probably offset by Skeena-bound chum salmon caught in the Nass and Alaska fisheries that are not included in Argue and Shepard's (2005) catch reconstructions. Catch data from the southern Southeast Alaska management area show that a total of 4.1 million chum salmon were caught in 1919, with an average of 3.3 million chum salmon caught annually during 1916-1919; more than 57 million chum salmon were caught during 1919 in the combined Alaska fisheries (Byerly et al. 1999). If only 0.05% of chum salmon caught in the Alaska fisheries of 1919 were of Skeena origin, the number would exceed the estimated proportion of non-Skeena chum salmon. This provides further evidence that the historical run size estimates are conservative, and are more likely to under-estimate, than to over-estimate, the true historical run size of Skeena chum salmon.

Contemporary estimates of chum salmon abundance are based on poor data quality. Chum salmon returning to the largest chum salmon spawning area in the Skeena catchment, the Ecstall River, have not been enumerated since 2002; in fact, only five out of 59 known spawning areas have spawner counts in the previous decade (see English et al. 2011). Additionally, the contemporary run-reconstruction estimates that I examined are based on numerous assumptions of limited catch, run-timing, and escapement data; all of which have inherent uncertainties (English et al. 2012). Furthermore, a significant portion of the chum salmon run may spawn in the mainstem Skeena, which very often is turbid and would make detection of spawners and redds difficult. Given these data uncertainties, and because hatchery-produced chum salmon

constitute a portion of the aforementioned contemporary estimates, the number of wild chum salmon annually returning to the Skeena could be either lower or higher.

Relevance for conservation.

The principal value of an estimation of the terminal run size of an historical salmon population of current conservation concern is that it provides an index of the historical capacity and potential of the system to produce chum salmon, provided of course that the ecosystem still remains largely intact, or capable of benefiting from remedial actions. Based on the geometric mean run estimate of 325,000 during 1916-1919, of which 154,000 were harvested, the Skeena River had the capacity to support at least 171,000 chum salmon spawners annually. This historical escapement should be of value to contemporary management, particularly in the context of the order of magnitude lower abundance of chum salmon returning to the Skeena River in the most recent period. Admittedly, I cannot say anything about how this decline relates to the natural variability in chum salmon abundance over time, which may have varied widely, as exemplified recently for western Alaskan sockeye salmon (Rogers et al. 2013).

Canada's modern conservation policy for Pacific salmon attempts to protect distinct populations (Wild Salmon Policy 2005). Four CUs have been identified for Skeena chum salmon (Holtby and Ciruna 2007), and the present analysis suggests that, currently, these CUs are severely diminished compared to a century ago. Although two separate investigations have shown that Skeena chum salmon may represent a single large population (e.g., Beacham et al. 1987; Kondzela et al. 1994), other data suggest that at least two separate races may exist in addition to the four CUs. For example, there appears to be an early run of chum salmon that spawn in downwelling areas of main river channels, and a late run that spawn in upwelling groundwater of back-channels (J. Stanford unpublished data), as has been described for chum salmon in Russia (Kuzishchin et al. 2010) and Alaska (Gilk et al. 2005). Given the disproportionately large harvest pressure on the early chum salmon run during the ~ 40-year Skeena sockeye salmon fishery leading up to 1916, this type of life-history diversity for Skeena-bound chum salmon may be significantly reduced compared to 150 years ago. Indeed, as Gottesfeld and Rabnett (2008)

suggest, "...chum are probably the Skeena watershed salmon species in greatest danger of significant loss of spawning stocks and genetic diversity".

Conservation initiatives and recovery plans for Skeena River chum salmon will require an evaluation of credible hypotheses about the decline in historical abundance that the estimate of historical abundance suggests. An assessment of this loss is necessary to identify appropriate abundance targets for recovery that will ensure the persistence of Skeena chum salmon.

Competitive interactions with hatchery fish, loss in genetic diversity and spawning habitat, by-catch in mixed-stock fisheries, possible changes in the magnitude of marine productivity, and loss of marine-derived nutrient subsidies, are all likely contributors to the historical decline in Skeena chum salmon.

It is imperative that monitoring efforts for wild chum salmon returning to the Skeena watershed be vastly improved, as the continued erosion of monitoring effort handicaps informed fishery and conservation decisions (Price et al. 2008). Notably, "The available data are not adequate to assess current [chum salmon] status..." (Walters et al. 2008). While there is evidence that a portion of chum salmon spawning groups have been lost, and others are at very low abundance, some optimism is warranted. The Skeena watershed remains a relatively intact salmon producing system, and as such, recovering substantially larger wild chum salmon populations is a foreseeable possibility; but only if conservation measures aimed at reducing the factors inhibiting their recovery are immediately initiated.

In Chapter 6, I present a life-cycle model for Skeena chum salmon and apply it to the estimate of historic adult abundance of this chapter to estimate the number of juvenile chum salmon that the Skeena would need to have been produced in order to sustain such adult abundance. I apply the estimate of juvenile production to estimates of the amount of historical (circa 1920) and current rearing habitat and scale the estimated historical juvenile chum production to historical area to obtain estimates of the historic per-unit floodplain area juvenile chum capacity of the Skeena and discuss the relevance of the estimate to contemporary conservation of Skeena chum salmon.

Related issues for conservation of Skeena chum in light of the estimate of historic abundance in this chapter will be taken up then.

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TABLES.

Table 1. Lower and upper limits of the uniform prior distributions for the parameters used in the Bayesian estimation of the terminal run size of the Skeena River chum salmon.

<i>Parameter</i>	<i>Lower Bound</i>	<i>Upper Bound</i>
<i>PLAM (λ)</i>	<i>0.9*C</i>	<i>1.1*C</i>
<i>ChRS</i>	<i>0.67</i>	<i>0.75</i>
<i>SHCh</i>	<i>0.60</i>	<i>0.90</i>
<i>SHR</i>	<i>0.58</i>	<i>0.66</i>
<i>1-ChRS</i>	<i>0.25</i>	<i>0.33</i>
<i>CoHR</i>	<i>0.45</i>	<i>0.60</i>
<i>CoHCh</i>	<i>0.45</i>	<i>0.60</i>
<i>N</i>	<i>C/max(ChHR)</i>	<i>C/min(ChHR)</i>

Table 2. Commercial catch (C) of Skeena River chum salmon as estimated by Argue and Shepard (2005) and the posterior marginals of the estimated terminal run size (N) in thousands.

<u>Year</u>	<u>C</u>	<u>Mode N</u>	<u>Median N</u>	<u>Mean N</u>	<u>SD N</u>	<u>Central 90%</u>
1916 – 1919	154	325	344	348	34.6	297 - 408

Table 3. Comparison of historical (1916 – 1919) and contemporary (1982 – 2010) skeena River chum salmon abundance by conservation unit (CU). NA: No estimate provided.

CU	1916 – 1919	1982 – 2010	2007 - 2010
Skeena Estuary	13,012	800	308
Lower Skeena	247,228	34,372	6,531
Middle Skeena	61,807	5,268	1,432
Upper Skeena	3,253	NA	NA

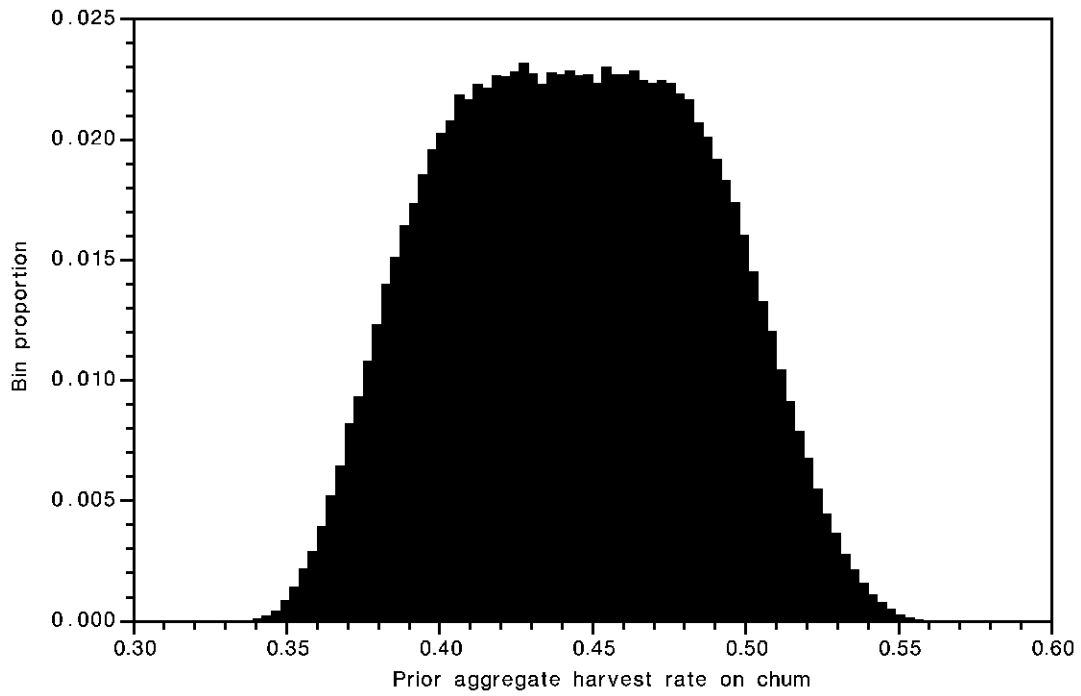


Figure 2. Histogram of the prior distribution of the aggregate harvest rate on skeena chum for the period 1916 – 1919.

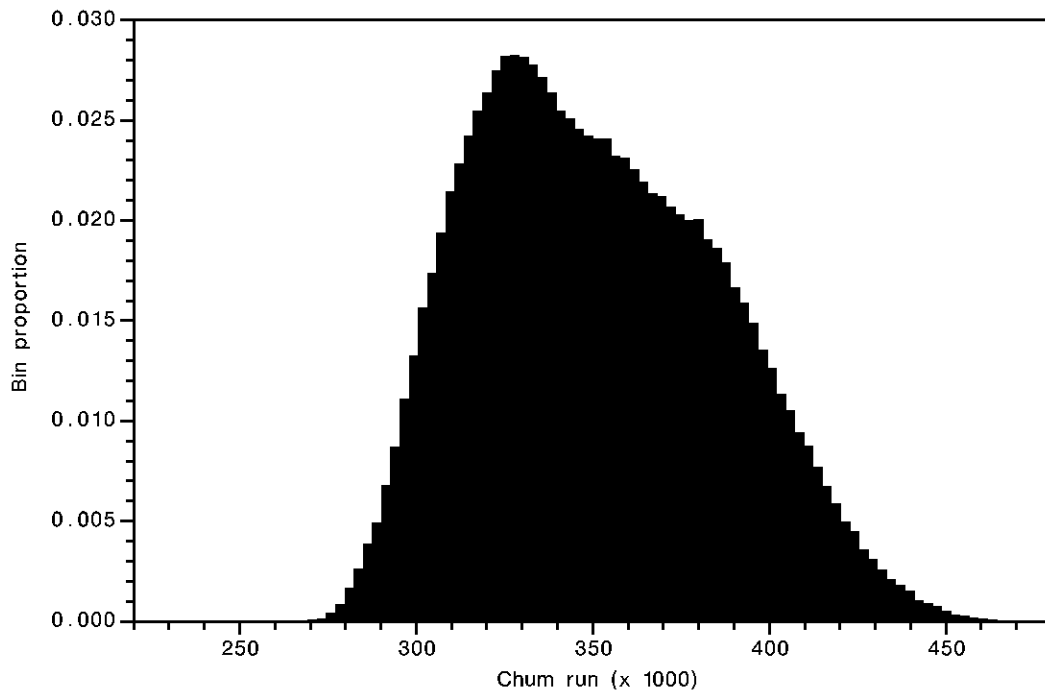


Figure 3. Histogram of the posterior distribution of the terminal Skeena River chum salmon run for the period 1916 – 1919 based on the geometric mean commercial catch of 154,000 reported by Argue and Shepard (2005).

APPENDIX.

Sensitivity of the prior on the chum harvest rate, ChHR, to the limits of the component uniform prior distributions.

To evaluate the sensitivity of *ChHR* to the lower and upper limits of the uniform distributions of the component prior distributions from which *ChHR* is derived, we created 21 samples (each consisting of 1,000,000 random values) of *ChHR* generated by randomly sampling the uniform distributions of the five underlying component uniform distributions, and calculating *ChHR* using equation (1).

$$(1) \text{ ChHR} = (\text{ChRS} * \text{SHCh} * \text{SHR}) + [(1 - \text{ChRS}) * \text{CoHCh} * \text{CoHR}].$$

The 21 samples included the default parameterizations of the five component distributions. Each of the remaining 20 samples was created by changing the lower or upper limits of one of the component distributions as shown in Tables 1-5. The quintile values (minimum, 20th, 40th, 60th, 80th percentiles, and maximum) of the cumulative distribution of each sample of 1,000,000 were calculated for comparison to the quintiles of the default parameterization. This is a limited sensitivity analysis, in which the upper or lower limit of a single component was changed while keeping all other limits at their default values. As noted in the manuscript, the results of the evaluation of the individual limits show that interactions among the component parameters under multiple changes to the upper and lower limits would be unlikely to have a large impact on the range and shape of the distribution of *ChHR*.

The header of each table shows the lower and upper limits of the default parameterization of the uniform distribution of the component parameter analyzed. The first row of each table contains the column labels, and the second row displays the quintile values of *ChHR* under the default parameterization of all five component distributions. Rows 3 to 6 display the quintile values of *ChHR* when the lower or upper limit of the uniform distribution of the component parameter is changed from the default value to the value indicated in the first column of the row. For

example, row 3 of Table A1 shows the change in *ChHR* when the lower limit on the uniform distribution of the sockeye salmon harvest rate, *SHR*, is set to 0.50 instead of the default 0.58, and the default upper limit of 0.66 is retained together with the default lower and upper limits of the remaining four independent parameters.

Table A1 shows results of when the lower limit on *SHR* is reduced from the default value of 0.58, to 0.50 and 0.40 (reductions of 14% and 31%, respectively), and when the upper limit is raised from the default 0.66, to 0.75 and 0.85 (increases of 14% and 29%, respectively). The lowered limits have a negligible impact on the maximum value of the posterior of *ChHR*, and produce a negligible increase in the range of the central 20% of the distribution when the lower limit is reduced 31% to 0.40 (i.e., the range changes from [0.431, 0.457] to [0.379, 0.408]). The range of the entire distribution is increased from [0.325, 0.574] to [0.253, 0.574] for the 31% reduction in the lower limit. Any such reduction in the lower limit on *SHR* would, of course, increase the upper limit of the posterior distribution of the terminal run.

Increasing the upper limit of the uniform on *SHR* from the default value of 0.66 (the maximum harvest rate estimate made by Ricker (1975) and substantiated by Wood (2008) for Skeena sockeye throughout the period of record) to 0.75 and 0.85 (increases of 14% and 29%, respectively), has a negligible effect on the minimum value of *ChHR*, but a noticeable and biologically significant effect on the maximum value of *ChHR*. For example, increasing the upper limit of *SHR* to 0.75 and 0.85, increases the maximum value of *ChHR* to 0.64 and 0.70, respectively, which would produce a reduction in the lower tail of the posterior distribution of the chum salmon terminal run size, lowering the minimum run size from 268,000 to 220,000 for the 1916-1919 geometric mean catch of 154,000, and from 355,000 to 291,000 for the 1919 catch of 204,000. The effect of either increase on the central 20% of the distribution of *ChHR* is much less dramatic. For example, increasing the upper limit to 0.85, increases the central 20th percentile range from [0.431, 0.457] to [0.475, 0.508].

Results of similar changes in the lower and upper limits of the component prior for the coho harvest rate, *CoHR*, are similar but smaller in magnitude than for *SHR* (Table A2). Increasing the upper limit from the default of 0.60, to 0.75, increases the maximum value of *ChHR* to 0.616

(from 0.574), which has only a small impact on the central 20%, increasing the range from [0.431, 0.457] to [447, 473]. This would produce a small reduction in the posterior of the terminal run size. Increasing the upper limit on *CoHR* to 0.90 from 0.60, increases the maximum of *ChHR* to 0.653, and the central 20th percentile to [0.462, 0.490]. This would produce a further modest reduction in the posterior of the run size.

The changes to *ChHR* resulting from alterations of similar magnitudes to the limits of the remaining three independent component priors shown in Tables A3-A5, are noticeably smaller. Because the upper limits of both *SHCh* and *CoHCh* (the proportions of the total harvest rates on sockeye salmon and coho salmon to which chum salmon were vulnerable) in the default parameterization were very large (i.e., 0.90), only reductions of 0.10 and 0.20 in the upper limit were evaluated, and these only contribute to lowering the *ChHR* upper limit. Overall, the changes in the upper and lower limits evaluated in Tables A3-A5 produced negligible changes in the magnitude and range of the central 20% of the distribution of *ChHR*. Notably, increasing the upper limit on the proportion of the chum salmon run encountering the sockeye salmon fishery, *ChRS*, from the default of 0.75 to 0.95 (Table A3, bottom row) increases the maximum value of *ChHR* to 0.587 from 0.574, and produces an even smaller increase in the location and magnitude of the central 20th percentile [0.431, 0.457] compared to [0.436, 0.465]. All other alterations of lower limits of course serve to further reduce the values of *ChHR* across the entire distribution, which would result in increases of the posterior distribution of the terminal chum run size.

Table A1. Results of the sensitivity analysis from changes made to the lower and upper limits of *SHR*, the total annual harvest rate on the sockeye salmon run, from the default uniform distribution (0.58, 0.66).

Parameter/ percentile	Minimum	20th percentile	40th percentile	60th percentile	80th percentile	Maximum
<i>SHR</i> - default	0.325	0.403	0.431	0.457	0.485	0.574
<i>SHR</i> - low 0.4	0.253	0.348	0.379	0.408	0.445	0.574
<i>SHR</i> - low 0.5	0.295	0.381	0.409	0.434	0.464	0.574
<i>SHR</i> - high 0.75	0.330	0.422	0.452	0.481	0.514	0.635
<i>SHR</i> - high 0.85	0.328	0.439	0.475	0.508	0.551	0.699

Table A2. Results of the sensitivity analysis from changes made to the lower and upper limits of *CoHR*, the total annual harvest rate on the coho salmon run, from the default uniform distribution (0.45, 0.60).

Parameter/ percentile	Minimum	20th percentile	40th percentile	60th percentile	80th percentile	Maximum
<i>CoHR</i> - default	0.325	0.403	0.431	0.457	0.485	0.574
<i>CoHR</i> - low 0.25	0.288	0.379	0.409	0.435	0.465	0.574
<i>CoHR</i> - low 0.35	0.309	0.392	0.420	0.446	0.475	0.572
<i>CoHR</i> - high 0.75	0.327	0.417	0.447	0.473	0.503	0.616
<i>CoHR</i> - high 0.90	0.328	0.430	0.462	0.490	0.523	0.653

Table A3. Results of the sensitivity analysis from changes made to the lower and upper limits of *ChRS*, the proportion of the total chum salmon run that encountered the sockeye salmon fishery, from the default uniform distribution (0.67, 0.75).

Parameter/ percentile	Minimum	20th percentile	40th percentile	60th percentile	80th percentile	Maximum
<i>ChRS</i> - default	0.325	0.403	0.431	0.457	0.485	0.574
<i>ChRS</i> - low 0.50	0.315	0.400	0.425	0.449	0.476	0.572
<i>ChRS</i> - low 0.60	0.323	0.402	0.429	0.454	0.481	0.573
<i>ChRS</i> - high 0.85	0.329	0.405	0.433	0.461	0.491	0.581
<i>ChRS</i> - high 0.95	0.328	0.405	0.436	0.465	0.497	0.587

Table A4. Results of the sensitivity analysis from changes made to the lower and upper limits of *SHCh*, the proportion of the annual sockeye salmon harvest rate to which chum salmon were vulnerable, from the default uniform distribution (0.60, 0.90).

Parameter/ percentile	Minimum	20th percentile	40th percentile	60th percentile	80th percentile	Maximum
<i>SHCh</i> - default	0.325	0.403	0.431	0.457	0.485	0.574
<i>SHCh</i> - low 0.40	0.247	0.334	0.378	0.422	0.466	0.572
<i>SHCh</i> - low 0.50	0.287	0.369	0.404	0.440	0.475	0.574
<i>SHCh</i> - high 0.70	0.325	0.380	0.394	0.406	0.420	0.484
<i>SHCh</i> - high 0.80	0.326	0.393	0.413	0.431	0.451	0.527

Table A5. Results of the sensitivity analysis from changes made to the lower and upper limits of *CoHCh*, the proportion of the total harvest rate on the post-sockeye salmon season coho salmon run to which the overlapping proportion of the chum salmon run were vulnerable, from the default

Parameter/ percentile	Minimum	20th percentile	40th percentile	60th percentile	80th percentile	Maximum
<i>CoHCh</i> - default	0.325	0.403	0.431	0.457	0.485	0.574
<i>CoHCh</i> - low 0.40	0.296	0.386	0.415	0.442	0.471	0.575
<i>CoHCh</i> - low 0.50	0.315	0.395	0.423	0.450	0.478	0.576
<i>CoHCh</i> - high 0.70	0.327	0.389	0.415	0.442	0.469	0.546
<i>CoHCh</i> - high 0.80	0.327	0.396	0.423	0.449	0.476	0.560

CHAPTER FOUR
Comparison of the Application of Method I to Skeena chum salmon 1916 - 1919
and Puget Sound steelhead 1895

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December 21, 2015

ABSTRACT.

The application of Method I to two case studies are compared. The two cases, Stillaguamish River (Puget Sound) steelhead in 1895 and Skeena River chum salmon at the end of the second decade of the twentieth century (1916 to 1919) differ in the amount and kind of data available for estimating the total numeric catch and the average harvest rate applied to the total returning adult run from which the catch was derived. The estimation of the 1895 return of Stillaguamish steelhead relied on qualitative and quantitative historical information regarding agricultural settlement of the river basin and unreported harvest of steelhead by settlers and tribal people, in addition to information about the commercial steelhead fishery. The estimation of the return of Skeena chum 1916 to 1919 was able to rely on more detailed information regarding the commercial fishery on sockeye and coho salmon as well as chum salmon. The use of a Bayesian estimation framework enabled prior distributions for the key uncertain parameters (including the harvest rate, run size, and in the case of steelhead the average fish weight) to be developed that appropriately captured the uncertainties in the available data and propagated them through to the estimation of the total adult return. The relative precision of the estimates in the two cases are evaluated and compared. The results suggest that the estimation of Stillaguamish steelhead likely represents a limiting case of the use of sparse quantitative and qualitative data that are sufficiently informative to support a useful estimate of historical salmon/steelhead abundance. The comparison of the details of the application of Method I in the two cases shows that the method can be fruitfully applied to a broad range of historical cases that have varying kinds and degrees of information available with which to estimate prior distributions for the harvest rate.

INTRODUCTION.

Method I (cf. Chapter 2) was initially developed to estimate the abundance of Puget Sound steelhead (*Oncorhynchus mykiss*) at the end of the nineteenth century based on commercial steelhead harvest data for 1895. Full details of this analysis were published by Gayeski et al. (2011) which is included in the Appendix. Gayeski et al. (2011) analyzed the commercial harvest data available for four large rivers in northern Puget Sound and the remaining aggregate of rivers in Puget Sound from which steelhead were commercially harvested and for which harvest data was available following Washington statehood in 1889. The year 1895 produced the single largest commercial catch of steelhead. Because this catch occurred early in the rise of the Puget Sound commercial fishery for steelhead Gayeski et al. (2011) argue the 1895 data “is likely to reflect the abundance of Puget Sound steelhead populations in the late-nineteenth century immediately preceding the buildup of a directed commercial fishery and, therefore, provides the best quantitative data from which to estimate the abundance of these populations.”

In this Chapter, I restrict my focus to the details of the estimation of the historical (1895) abundance of the Stillaguamish River, one of the four large north Puget Sound rivers for which Gayeski et al. (2011) provided estimates of the total adult steelhead return in 1895. My purpose here is to describe the details of the application of Method I to the Stillaguamish data and to compare it to the application to the case of Skeena River chum salmon that was described in Chapter 3. The comparison will illustrate the primary issues that arise in applying Method I to historical salmon harvest data and demonstrate the flexibility of the Method when a Bayesian inference approach is employed.

In Chapter 7 I develop a life-cycle model for this steelhead population in order to estimate the historic steelhead parr capacity of the Stillaguamish in 1895 based on estimates of the abundance of historically available steelhead rearing habitat. This will complement the estimate of the historic chum salmon habitat capacity of the Skeena River that is the subject of Chapter 6.

METHODS.

Estimation of the 1895 steelhead return to the Stillaguamish River.

Gayeski et al. (2011) used the commercial catch data for the Stillaguamish River in 1895 provided in the report of the U.S. Commission of Fish and Fisheries of 1898 (Wilcox 1898). The reported catch was 180,000 pounds. Importantly, Wilcox and others reporting Puget Sound fisheries data during the end of the nineteenth and the first several decades of the twentieth noted that tribal subsistence harvest and catch by settlers in the river valleys were also likely to have been significant and, according to Wilcox (1898) were probably equal to the commercial harvest. My co-authors, Bill McMillan and Pat Trotter, therefore, conducted extensive review of historical literature regarding the settlement of Puget Sound lowland river basins and the development of agriculture on the floodplains during the latter half of the nineteenth century to estimate the extent and range of these non-commercial catches. These estimates were employed to expand the reported commercial catch data, as described below.

In addition to the reported commercial catch data, estimation of the total run required estimation of three unknown parameters: 1) the total steelhead catch that was unreported or otherwise not included in the reported commercial catch; 2) the average weight of the steelhead caught; and 3) the harvest rate on the total run that produced the total catch. These unknown parameters were treated as prior parameters in the Bayesian estimation process, which required the specification of appropriate distributions and associated parameters. As in the case of Skeena chum circa 1920 (Chapter 3), no information existed that would permit informative priors with unimodal parametric distributions to be identified. Consequently, uninformative uniform distributions were employed and reasonable limits specified within which their true values were most likely to lie.

In this initial application of Method I, I chose to employ a binomial likelihood to estimate the total adult run, N , where the total catch $T \sim \text{Binomial}(N, R)$:

$$P(T|N, R) = \binom{N}{T} * T^R * (N - T)^{(1-R)}, \quad (1)$$

where T = total catch in numbers of fish, N = total size of the run, and R = harvest rate.

Thus, catch (T) is viewed as resulting from a binomial sampling of the total run, N , at an average harvest rate, R .

In order to employ this approach, however, the reported commercial catch, C (in pounds), has to be expanded to account for the unreported catch and the expanded total catch weight transformed to numbers of fish to arrive at an estimate of the total catch in numbers of fish, T . This was done as follows. The reported commercial catch C was multiplied by a quantity U that represents the ratio of unreported catch to reported commercial catch to arrive at a figure for the unreported catch (in pounds). This number was then added to the reported catch to derive a number for the total catch (in pounds). Next, the total catch was divided by the average weight (in pounds) of the steelhead caught, W , to attain a figure for the total numbers of steelhead caught, T . Thus:

$$T = (C + C*U)/W \text{ or equivalently, } T = C*(1+ U)/W , \quad (2)$$

where T = total numbers caught, C = the reported commercial catch, U = the ratio of unreported catch to reported commercial catch, and W = the average weight of steelhead caught (in pounds).

However, the only firm figure in equation (2) is C , the total commercial catch. Uncertainty surrounds the ratio of unreported-to-reported commercial catch (U), and the average weight of the steelhead entering the catch (W). These uncertainties required that prior distributions be placed on both U and W and the algorithm for deriving total catch numbers from catch weight repeatedly applied to arrive at total catch of fish, T (equation 2) by drawing different values of U and W from the respective distributions. Consequently, a distribution of values of T is generated for the single value of C reported. Thus, the Bayesian analysis in this case is somewhat atypical in that the inference on N is conducted on values of T that are themselves uncertain and consequently are represented by a distribution (the distribution of T).

In Gayeski et al. (2011), the Bayes inference on N was programmed and carried out using the Fortran shell program SWL (Sampling Weighted Likelihood) written by the late Dr. Daniel

Goodman, Environmental Statistics Group, Department of Biology, Montana State University, Bozeman. SWL samples the prior distributions by direct simulation with calls to random number generators, and then weights each sampled set of values of parameters by their likelihood, cumulating histograms and posterior summaries of the sampled parameter values weighted accordingly. This contrasts with sampling or re-sampling the joint posterior as Markov Chain Monte Carlo approaches do (and which I used for the Skeena chum salmon analysis in Chapter 3). This is extremely efficient for calculations of low dimension (four or fewer parameters) as is the case here with four unknown parameters, N , R , U , and W . This efficiency enabled the estimation to employ ten million (10,000,000) samples from all prior distributions and to calculate the posterior distributions of all quantities of interest from these samples using little computer time.

Uniform distributions for the unknown parameters N , R , U , and W , were chosen with upper and lower limits selected on biological and historical grounds to bracket the most likely range within which the true parameter values lie. These are listed in Table 1. Random values of N , R , U , and W were drawn from the respective prior distributions, and equation (2) applied to the values of U , W and the population-specific value of catch-in-pounds, C , of 180,000 to generate a sample value of T . A posterior value of N was then obtained by calculating the likelihood of N (equation (1)) from the values of N , R and the derived sample value of T . By sampling 10,000,000 random combinations of N , R , U , and W adequate sampling the joint parameter space was assured.

Full details on the justification of the values of the prior parameters are provided in Gayeski et al. (2011). Briefly, I and my two co-authors considered the available historical information on the average weight of steelhead and the information relevant to the unreported catch and placed upper and lower limits on the uniform prior distributions that we believed spanned the appropriate range. The lower limit placed on the run size, N , was chosen based on the smallest possible value for the numerical catch T given the value of C , the upper limit of M (average fish weight), and the lower limit on U , since the total run can be no smaller than the numbers caught. The upper limit on N was placed just above the largest possible value of N given the largest possible value of T and the smallest possible value of the harvest rate R (0.40). In this way the

data and the likelihood determined the entire posterior distribution. The limits on the harvest rate, R , were chosen based on the judgement of myself and my two co-authors on how large or small a proportion of the total run the minimum and maximum catch T was likely to be given the size of the Stillaguamish River basin.

RESULTS.

The posterior distributions of the N , T , and R are shown in Figures 1 –3, respectively, and listed in Table 2.

The posterior distribution of run size N and the distribution of total catch T are essentially normal with modes (peaks) at or close to the center of the distributions. This is expected given the uniform priors employed. The shape of the distribution of the catch data, T , results from the uniform distributions for U and M employed in equation (2), as did the distribution of the prior of the harvest rate on Skeena chum salmon (ChHR) described in Chapter 3. This is an illustration of the central limit theorem which states that a large number of random samples from a finite distribution, such as the uniform distribution, is expected to have a normal distribution regardless of the distribution chosen (Casella and Berger 2001, Chapter 5). Given normal distribution of the data, the near-normality of binomial distributions for large sample size and appropriately broad uniform priors on R and N , near-normality in the posterior of N is expected.

Importantly, the posterior of N is shrunk considerably away from the lower and upper limits of the uniform prior. This shows that the data are informative, given the priors, although there is still considerable uncertainty remaining as to the actual value of N , as shown by the full distribution.

One might expect the shape of the posterior distribution of R to be uniform and thus not noticeably different from the prior distribution. However, it is slightly left-skewed, with slightly more of the probability mass at lower values of R than at intermediate or large values (Figure 3). This results from the interaction of the near-normal shapes of the distributions of T and N and

the binomial likelihood. The likelihood values (weights) assigned to each value of R in the posterior are the sum of calculations involving that value of R and the pairs of values of N and T drawn randomly from their priors that produce non-zero probabilities. Values of R near the upper end of the prior distribution will have high likelihood values only for values of T that are large and values of N that are low, and these combinations constitute only a very small proportion of the sampled joint parameter space. There are relatively more ways to combine random values of T with random values of N that will yield non-zero probabilities for low values of R than there are for high values of R . The slight left skew of the posterior of R also accounts for the slightly non-normal, right skew of the posterior of N . Large posterior values of N occur for any given value of the total catch T only if the harvest rate R is “small”.

Although the prior distributions of M , R , and U are uniform, assigning equal probability to any value within the upper and lower limits, and in this sense are uninformative, the range chosen is informative. If higher or lower limits were chosen, different posterior distributions, at least at the upper and lower ends of the posterior distributions, would occur. So, although uniform distributions capture lack of information and uncertainty about the shape of the distribution of parameter values of interest they do contain a degree of limited information regarding how small or large the value of a parameter can be.

When, as here and in the case of Skeena chum salmon in Chapter 3, the principal parameter of interest in applying Method I is the terminal run size, the prior for the harvest rate, R , is critical. Conservatism (guarding against over-estimating the size of the run) is enforced by (reasonably) large values of R . From this perspective caution urges guarding against under-estimating R . Conversely, to guard against failing to account for possibly larger than expected historical run size, caution urges against over-estimating R . At a minimum, as in the case of the applications of Method I here and in chapter 3, a reasonable balance will be struck by identifying the most reasonable upper and lower limits given both historical information on the conditions of the actual harvest and more general knowledge about salmon fisheries and the levels of mortality that salmon populations of each species are capable of sustaining.

As in the case of Skeena chum salmon the estimated abundance of the terminal run of steelhead in the Stillaguamish in 1895 is considerably larger than recent estimates. Tables 2a and 2b show summary data for recent estimates of the adult wild steelhead population of the Stillaguamish and the estimate for 1895 from Gayeski et al. (2011), respectively. In addition to the run size estimates, Tables 3a and 3b show the estimated length of stream accessible to adult steelhead currently and in 1895. These were used by Gayeski et al. (2011) to scale the run size estimates to returning adults per-linear-kilometer of accessible stream length so as to obtain a rough habitat-based index of adult abundance. These metrics are discussed in detail in Gayeski et al. (2011).

The tables show that accessible stream length in the Stillaguamish currently is 67% that of 1895. This contrasts with a 50-fold reduction in run size between the 5th percentile of the posterior distribution of the 1895 estimate and the 25 year average for 1980 - 2004 and a 67-fold reduction from the posterior mode of the 1895 estimate. This provides evidence that loss of habitat alone is unlikely to explain the reduction in population abundance since 1895.

Table 4 shows summary data for recent estimates of the adult Skeena River chum salmon run and for the 1916 – 1919 estimate from Price et al. (2013), showing an 8-fold reduction in the abundance of Skeena chum measured from the 1982 – 2010 average annual run and a 39-fold reduction measured from the 2007 – 2010 annual average.

Comparison of the application of Method I to Skeena chum salmon circa 1920 and Stillaguamish steelhead in 1895.

Table 5 shows the catch and estimated run size data from both the Skeena chum and Stillaguamish steelhead historical abundance estimates. Despite the inevitable broad posterior distributions of the estimated run sizes, both estimates indicate dramatic reductions in adult population numbers between the focal periods of interest and current conditions. Both estimates are reasonably precise. The coefficients of variation (standard deviation/mean) are 0.2 for the steelhead estimate and 0.1 for the chum estimate. So, the combination of the data and the priors proves relatively informative regarding the possible size of the runs. This is also shown by the

absolute magnitude of the range of the two estimates as measured by the central 90% of the posterior distributions. For Skeena chum, the difference between the 95th percentile and the 5th percentile is 111,000. The relative magnitude of the two percentile estimates is 1.37, meaning that the 95th percentile abundance is 1.37 times larger than the 5th percentile. For the Stillaguamish, the difference is 48,300. The relative magnitude of the Stillaguamish estimate is 1.93, showing that it is the more uncertain of the two estimates.

The significantly lower coefficient of variation. of the Skeena chum estimate is due to two factors, the relatively precise independent estimate of the harvest rate on Skeena sockeye salmon (SHR, cf. Chapter 3) and the slightly more precise estimates of the remaining component priors on the aggregate harvest rate on chum salmon, ChHR (Chapter 3). These latter involved estimates of the coho harvest rate, the proportions of the sockeye and coho salmon fisheries to which Skeena chum were vulnerable, and the proportion of the sockeye and coho harvest rates that applied to the larger body size chum. The existence of a significant amount of detail regarding the conduct of the sockeye fishery permitted a narrow range to be imposed on the uniform prior distributions of these parameters. In sum this resulted in high confidence that the aggregate harvest rate on chum had to have been lower than the harvest rate on sockeye during the 1916 – 1919 period. The combination of five independent component prior parameters with uniform distributions contributing to the prior distribution of the aggregate chum harvest rate, ChHR, produced a moderately informative, bell-shape prior distribution for this prior. This in turn produced a unimodal posterior distribution of the run size. In addition, the total catch numbers were obtained from Argue & Shepard (2005) as described in Chapter 3 and so did not involve any of the uncertainty that attended the estimation of the total numbers caught that was involved in the case of Stillaguamish River steelhead.

DISCUSSION.

These two cases illustrate the flexibility that is available for constructing a reasonable prior distribution for the harvest rate, R , that is central to the application of Method I to historic salmon harvest data. The issue that often confronts researchers interested in developing an

estimation of historical salmon runs is the scarcity of data regarding the conduct of the fishery and the structure of the adult populations, particularly age and sex ratio data and a credible estimate of the annual spawning escapement. Generally, all that may be available is the commercial catch data, as in the two cases examined here. In these situations, the choice is stark: provide an estimate from the catch data using an estimate of the harvest rate, or do not provide any estimate.

In order to obtain an estimate of the run size under these circumstances, two conditions should be met. First, as described in Chapter 3, the harvest data should come from a relatively large single commercial catch or a series of annual catches of one or two generations length early in the history of the commercial fishery, so that the population is unlikely to have been changing in response to the sudden addition of harvest mortality. Second, enough information about the fishery and the harvesting of the population in question must exist to support the development of a credible prior distribution for the harvest rate, R . The easiest way to test this second condition is to develop a prior for R , apply Method I and evaluate whether the posterior distribution of the run, N is credible and informative. If insufficient information exists to restrict the prior for R to a sufficiently narrow range, there will be no value to providing an estimate of N that has an extremely broad posterior distribution. Conversely, a prior on R that has a very narrow range will be very informative and result in a narrow posterior distribution of N . Such precision will be very suspicious if the available data on the conduct of the fishery is not clearly strong enough to secure the credibility of the prior. But this can be expected to be discovered by any credible peer review process or reviewer.

When the available series of commercial catch data spans three or more generations, it may be worthwhile or even preferable to conduct a stock-recruit analysis (Method II, c.f. Chapter 5). This will, however, usually be challenging due to the lack of sufficient (or any) annual spawning data. In Chapter 5, I illustrate Method II by conducting a stock-recruit analysis of Skeena River sockeye salmon early in the development of the commercial fishery. I show the value of doing this when circumstances permit, even in the absence of spawning survey data, and I compare the results to analyses employing Method I.

Chapter 2 showed that the binomial and Gamma-Poisson likelihoods will provide credible estimates of total adult abundance from aggregate catch data, assuming the availability of a minimal amount of information about the harvest rate. The results in the present chapter show that embedding either likelihood in a Bayesian estimation framework provides considerable flexibility for incorporating a variety of kinds of information in order to specify a prior distribution for the harvest rate that will be informative enough to achieve a reasonably informative posterior distribution of the historic population size of interest. The two cases examined required rather different approaches to identifying the prior for the harvest that each reflected the different kinds of information available.

In the case of the Stillaguamish the prior was a uniform distribution whose upper and lower limits were based on judgements about the likely intensity of the harvest on the population in light of the estimated total catch (reported commercial catch plus estimated unreported catch), the size of the Stillaguamish catchment and the amount of stream kilometers accessible to adult steelhead. The addition to the total reported commercial catch of the estimated unreported catch of steelhead increased the total estimated numeric catch to a large enough magnitude to support the specification of a credible lower limit on the harvest rate (40%, Table 1), while the numeric catch in conjunction with knowledge of the development of the early Puget Sound commercial steelhead fishery and the extent of the commercial fishery in the Stillaguamish at the time of interest provided information to support a credible upper limit (70%, Gayeski et al. 2011). This case represents the least information for a fishery that is still capable of providing enough information for the prior on the harvest rate to achieve a minimally informative posterior distribution for the total run. Under these circumstances, the posterior distribution of the run, N , was surprisingly narrow, with a coefficient of variation of 0.20 (Table 5).

The case of Skeena River chum salmon shows how the prior for the harvest rate may be defined so as to be moderately informative by incorporating data from another well-studied historic population within the basin (Skeena sockeye) and related information regarding run time of chum, sockeye, and coho salmon, together with information about the timing and conduct of the fishery (described in Chapter 3, and in Price et al. 2013). The information content of this prior compared to that for Stillaguamish River steelhead resulted in the posterior distribution of the

total run, N, that was much narrower than for the Stillaguamish (Table 5), though significant uncertainty remained regarding the absolute size of the run.

In both cases, the results were informative for the important comparison to the contemporary condition of Skeena chum salmon and Stillaguamish River steelhead. In each case, the estimated range of abundance shows that the total abundance of the historic populations was considerably greater than current populations to an extent that appears unlikely to be accounted for by the quantitative losses of freshwater spawning or rearing habitat alone. This result alone is relevant to the determination of targets and measures for recovering currently at-risk salmon and steelhead populations, which will be discussed in detail in Chapters 6 – 8. The important point here is that this is achieved despite the presence of non-trivial uncertainties in the data available for estimating the abundance of historic salmon populations in a manner that is relevant to contemporary conservation concerns.

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TABLES.

Table 1. 1895 Reported commercial catch and prior distributions. C and M are in pounds, RLO and RHI are rates, NLO and NHI are numbers of fish.

Population	C	M-Lo	M-Hi	U-Lo	U-Hi	R-Lo	R-Hi	N-Lo	N-Hi
Stillaguamish	180,000	7.0	9.5	0.5	1.0	0.4	0.7	40,000	130,000

Table 2. 1895 Posterior distributions of total run N and harvest rate R and distribution of the total numerical catch for steelhead in the Stillaguamish River in 1895.

Parameter	Mean	Mode	Standard deviation	Central 90%
Run size, N	73,700	69,200	14,900	51,700 – 100,000
Total catch, T	38,500	37,700	4,700	31,100 – 64,600
Harvest rate, R	0.54	0.42	0.09	0.41 – 0.68

Table 3a. Stillaguamish steelhead run size from NOAA fisheries 2005 Status Review. SC is the number of stream kilometers in the Stillaguamish River basin currently accessible to adult steelhead. FKM is fish-per-accessible stream kilometer.

Population	N, 1980-2004	N, 2000-04	SC	FKM, All Years	FKM, 5 years
Stillaguamish	1027.7	550.2	445	2.31	1.24

Table 3b. estimated Stillaguamish steelhead run size in 1895. SH is the estimated number of stream kilometers in the Stillaguamish River basin accessible to adult steelhead in 1895. FKM is fish-per-accessible stream kilometer.

Population	Posterior Mode N	Posterior 5 th %ile N	SH	FKM, Mode N	FKM, 5%ile N
Stillaguamish	69,200	51,700	668	104	77

Table 4. Comparison of historical (1916 – 1919) and contemporary (1982 – 2010) Skeena River chum salmon abundance.

Population	1916 – 1919	1982 – 2010	2007 - 2010
Skeena chum	325,000	40,450	8,271

Table 5. Catch and posterior distributions of the size of the terminal runs, N, of Skeena chum 1916 – 1919 and Stillaguamish steelhead 1985. Catch and Run numbers, N, in thousands. Stillaguamish catch is in thousands of pounds. Skeena catch is numbers of fish.

Population	Catch	Mean N	Mode N	SD N	C.V. N	Central 90%
Skeena	154	348	325	34.6	0.1	297 - 408
Stillaguamish	180	73.7	69.2	14.9	0.2	51.7 - 100

FIGURES.

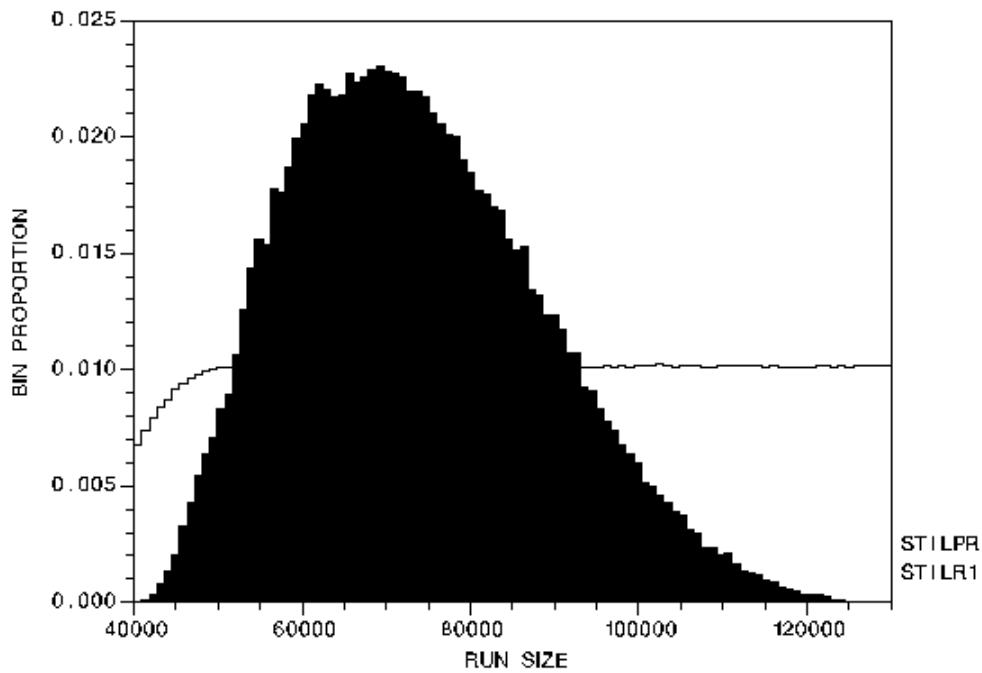


Figure 1. Prior distribution (thin line) overlaid on the posterior distribution (black fill) of the total steelhead run for the Stillaguamish River in 1895. (Mean = 73,700; mode = 69,200; standard deviation = 14,900; central 90% of the posterior distribution:51,700 – 100,000) The thin black line is the prior distribution.

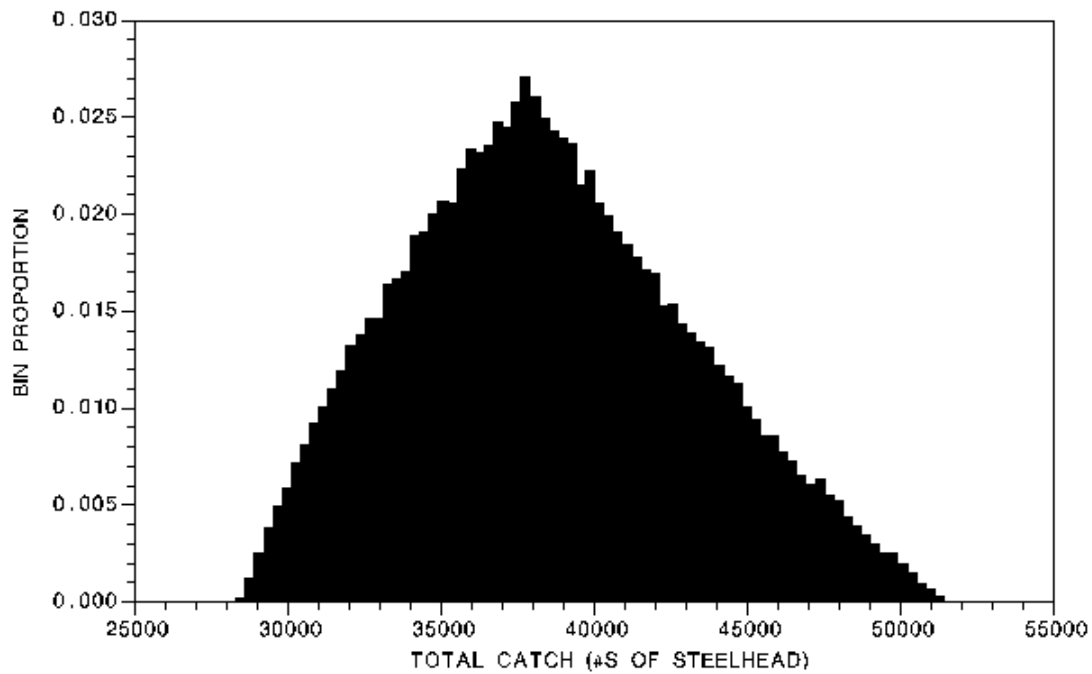


Figure 2. Distribution of the total numerical catch of steelhead, T, for the Stillaguamish River in 1895. (Mean = 38,500; mode = 37,700; standard deviation = 4,700; central 90% of the posterior distribution: 31,100 – 46,600).

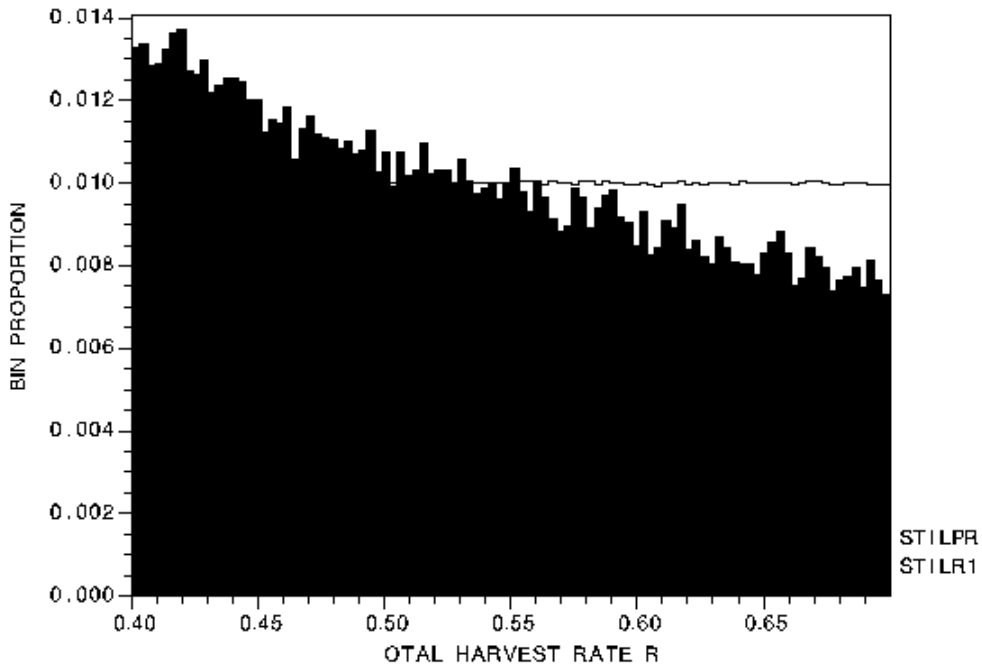


Figure 3. Prior distribution (thin line) overlaid on the posterior distribution (black fill) of the total harvest rate, R, for the Stillaguamish River in 1895. (Mean = ;0.54 mode = 0.42; standard deviation = 0.09; central 90% of the posterior distribution: 0.41 – 0.68).

CHAPTER FIVE
Stock-Recruit Analysis of Skeena River Sockeye Salmon During
the First Three Decades of Major Commercial Fishing, 1888 – 1919.

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ABSTRACT.

A stock-recruit analysis is employed to estimate the abundance of Skeena River sockeye salmon for brood years 1888 to 1913, that encompasses the period of the build-up of the commercial sockeye fishery on the lower Skeena River up to the period immediately preceding the use of gasoline motors by the commercial fleet. A stock-recruit analysis of the historic catch data series was made possible by estimates of historic escapement of Skeena sockeye and adult age data from samples of the commercial catch at canneries extending from 1912 to 1954. The age data were used to create six stock-recruit data sets for brood years 1888 to 1913 that accounted for uncertainty in the age composition of the brood year returns for brood years 1888 to 1911 that lacked age data. Bayesian estimation was used to fit both the Ricker and the Schnute-Kronlund models to each data set. The resulting estimates are compared to point estimates derived by applying Method I (chapter 2) to six five-year geometric mean catches from within the period using point estimates of the harvest rate for each period. The stock-recruit parameter estimates for both models were equally accurate and precise, with coefficients of variation for the regression error averaged over all six data sets of 0.16 and coefficients of variation for the equilibrium abundance ranging from 0.06 to 0.12. The posterior mode of the equilibrium abundance for the entire period averaged over the six data sets was 2,000,000 for each of the two stock-recruit models compared to an average estimate of 2,350,000 for the six Method I point estimates. The central 90% of the posterior distributions, however, encompassed the Method I estimates for all six data sets. The results show that where multi-generation catch and harvest rate data are available for a historic salmon stock Method I can provide a rough approximation of the capacity of the stock for the years chosen. The stock-recruit analysis will make more use of all available data and provide a more integrative analysis that more fully accounts for the

uncertainties in the data, and is to be preferred where the available data permits the more detailed analysis.

INTRODUCTION.

Chapters 3 and 4 described the application of Method I of estimating the historical abundance of salmon and steelhead populations using commercial catch data complemented by auxiliary information about the fishery. This method will typically be the one that must be employed in most contexts where fisheries on specific stocks built up rapidly (within one to three generations) before declining, indicating that the stocks had responded to the imposition of high levels of fishing mortality. In a few other cases, significant catches may have built up more slowly and/or fisheries may have sustained high catches for three or more generations before exhibiting pronounced declines indicative of overfishing. A clear example of this situation occurs with Skeena River sockeye salmon (*Oncorhynchus nerka*).

The commercial catch of Skeena sockeye from 1877 to 1950 from Table 46 of Argue and Shepard (2005) is listed in Table 1 and graphed in Figure 1. This catch occurred in the lower Skeena River (see Figure 1 of Chapter 3) and so captured returning adult sockeye bound for all spawning tributaries of the Skeena. The catch first exceeded one million in 1899 and averaged nearly 1,300,000 from 1899 to 1931. The catch dropped sharply in 1932 and averaged 750,000 from 1932 to 1950. The commercial catch first rose over 500,000 in 1884 and began to sustain catches above 600,000 beginning in 1888. The largest catch in the record, 2,452,000 occurred in 1910 and was nearly equaled in 1919 by a catch of 2,422,000 (Table 1). The catch never approached two million after this year.

The increasing catch from the mid-1800s to the turn of the century and the sustained high catch levels between one and two million from 1889 to 1919 render the application of Method I less clear than in the cases of Skeena chum salmon (1916 – 1919) and Puget Sound steelhead in 1895. Method I could be applied to any relevant period within the period from roughly 1890 to 1919, such as a single sockeye generation or two, or a single year. Results from such an approach will likely be somewhat informative. The long period of sustained high catches suggests that a

stock-recruit analysis is likely to be more informative, if spawner age data and spawner numbers were available. Such data is typically lacking for salmon populations in the nineteenth and early twentieth centuries as previously noted in Chapter 3 and 4.

In the case of Skeena sockeye, however, it is possible to undertake a stock-recruit analysis due to the availability of age-data from samples of the commercial catch that were obtained regularly beginning in 1912. These data are available in Shepard and Withler (1958). Using these data together with auxilliary data from publications by other fisheries scientists from the Pacific Biological Station in British Columbia I was able to create a series of stock-recruit data sets for Skeena sockeye salmon for spawning years 1888 to 1913. The Methods section describes why it was necessary to create and analyze more than one data set and how the data sets were created.

METHODS.

Creating stock-recruit data sets for the 1888 – 1913 brood years.

I chose the year 1888 as the first brood year for which to develop a stock-recruit analysis. I chose 1913 as the last brood year because recruits will consist of returning adults of ages 4, 5, and 6. Consequently, the 1913 spawning year is the last for which I can construct a complete set of recruits (from age 4 returns in 1917, age 5 returns in 1918, and age 6 returns in 1919). I chose the year 1888 somewhat arbitrarily because it is the first year with a catch greater than 600,000 and except for the following year (1889) the catch never declined significantly below 600,000 for the entire period of interest. Consequently, the catch data should be highly informative of the productivity of the Skeena sockeye stock as a whole during this period, provided the brood year recruits can be reasonably reconstructed.

Next, I estimated the annual return (catch plus escapement) for each year 1888 to 1919. Ricker (1973) and Ricker and Smith (1975) estimated five-year average harvest rates for Skeena sockeye from estimated commercial catches following the approach of Milne (1955) and Shepard and Withler (1958) of estimating the harvest rate from the number of commercial

licenses and average catch per boat per day for the different classes of fishers in the commercial fishery (white, Indian, Japanese). I accepted the reported harvest rates at face value and applied the estimated harvest rate for each year to the reported commercial catch from Argue and Shepard (2005) for that year (Table 1), so $Run_X = Harvest_X / HarvestRate_X$, where Run_X is the total return, $Harvest_X$ the total harvest, and $HarvestRate_X$, the harvest rate in year X. The resulting data are listed in Table 2.

In order to apply the estimated returns I needed to estimate the proportions of adults in each age class in the total estimated return for each return year. Skeena River sockeye salmon return at ages 4, 5, and 6 (Milne 1955, Shepard and Withler 1958), with ages 4 and 5 constituting approximately 90% of the total run on average during the period of interest. The largest stock of all Skeena sockeye is the Babine River stock that spawns in the mainstem of the Babine river and several smaller rivers and streams tributary to Babine Lake, accounting for an estimated 70% of all Skeena sockeye in 1946 and 1947 (Brett 1952) and it is generally considered that this value was characteristic of the Babine's contribution to the total Skeena sockeye escapement previous to this time. The Babine stock is considered to consist of age 4 and 5 adults only. Age 6 adults comprised significant proportions of the Morice Lake stock in the Morice/Bulkley river catchment and Alastair Lake in the Gitdoix River catchment, tributary to the lower Skeena River, which Brett (1952) reported to constitute 13% of the average escapement in 1946 and 1947 (cf. also Clemens 1938). These two stocks consisted primarily of age 5 and 6 adults, so age 6 sockeye made some smaller proportion of the average escapement. It is suspected that Skeena salmon abundance was considerably reduced by the 1920s and it is estimated that by 1950 roughly one-third of the original biodiversity of Skeena salmon had disappeared (Walters et al. 2008). Based on the likelihood of substantial loss of the less numerous non-Babine sockeye stocks at the time the estimates of the proportion of stocks with substantial 6-year olds in the annual returns reported by Clemens (1938) and Brett (1952) were made, I assumed that age 6 sockeye were likely to have composed 9 - 10% of the average annual return of Skeena river sockeye.

Sampling of the commercial sockeye catch in the lower Skeena began in 1912 and the numbers of age 4 and age 5 sockeye in the catch were estimated from scale sampling of catch samples at

selected canneries (Shepard and Withler 1958). I used the age 4 and age 5 data for catch years 1912 to 1954 from Table I of Shepard and Withler (1958) to estimate the proportion of age 4 sockeye in the total catch of four and five year old sockeye during this period. In order to make use of this age 4 proportion data to reconstruct recruits for brood years 1888 to 1913, I first had to estimate the proportions of age 4 and age 5 sockeye in catch/brood years 1888 to 1912. Second, I have to estimate the proportion of age 6 sockeye in the aggregate adult return for all years 1888 to 1919 from which brood year recruits for 1888 to 1913 need to be reconstructed and adjust the age 4 and age 5 proportions for these years accordingly so that the proportions of ages 4, 5, and 6 sum to 1.0.

A common approach to stock recruit analysis when the age composition of annual adult returns is missing or otherwise unavailable is to apply the average age composition to the annual adult return numbers. The average age composition may be specific to a population and available from a proportion of past adult returns or general age composition for the species from stocks thought to be similar in age structure to the stock of interest. It is known that this will generally result in an upward bias in the estimate of the stock productivity parameter, alpha (Zabel and Levin 2002). To address this issue, I created five stock-recruit data sets from simulated age composition data as described in the following paragraphs and a sixth data set from the average age composition data for years 1912 to 1954 plus the incorporation of an estimate of the average proportion of age-6 sockeye for this period. This enabled me to compare the relative bias of using simulated age data instead of average age data.

To estimate the proportion of age 4 sockeye in the returns for 1888 to 1911, I first performed a time series analysis of the 1912 – 1954 data. I employed the time series analysis program ITSM version 6.0 Student Edition (ITSM2000; Brockwell, P. J. and R. A. Davis 1996) for this purpose. The time series analysis showed that the series was an autoregressive (AR4) series with stationary mean of 0.527, normally distributed white noise with zero mean and finite standard deviation σ of 0.175, and significant autocorrelations up to lag 4. The autocorrelation coefficients, R, were: R1: 0.2629, R2: -0.0893, R3: -0.1607, R4: 0.4609. Since the time series was stationary during the period 1912 to 1954 I assumed that it had remained stationary since at least 1888. This permitted me to simulate age 4 proportions backwards in time to 1888 starting from 1915 (to

account for the four significant lag correlation coefficients). I simulated 1000 random age 4 proportions for years 1888 to 1911 using a custom Matlab script I wrote for this purpose. Age 5 proportions from the simulated series are equal to 1-minus-the age 4 proportion.

Next I simulated 1000 series of age 6 proportions for years 1888 to 1919 to incorporate with the simulated age 4 and age 5 proportions for 1888 to 1911 and the actual age 4 and age 5 proportions for 1912 to 1919. I assumed that the mean proportion of Age-6 was between 9 and 10 percent (0.09 – 0.10). I simulated 1000 random age 6 proportions for years 1888 to 1919 from a Beta distribution with parameters $\alpha = 17.0$ and $\beta = 153.0$ using a custom Matlab script. This will produce simulated values with a mean = 0.10 and standard deviation = 0.023, and highest central 95% density interval [0.057, 0.146]. When added to the age 4 and age 5 proportions, this will result in average proportions age 4: 0.479, age 5: 0.43, and age 6: 0.091. These proportions were applied to obtain recruits from estimated total returns for return years 1912 to 1919 for all six data sets and for return years 1888 to 1919 to obtain recruits for all return years for the data set using the average age composition.

I then randomly chose five of the 1000 simulated age 4/5 proportions to employ together with the actual age 4/5 proportions for 1912 to 1919 to construct a recruitment series for brood years 1888 to 1913. I randomly chose five of the simulated series of age 6 proportions and randomly paired them with one of the five randomly chosen series of simulated age 4/5 proportions, re-adjusting the proportions for each simulated year to sum to 1.0. This produced five random series of proportions of age 4, 5, and 6 for years 1888 to 1919 that were then used to create five recruitment series for brood years 1888 to 1913 for further analysis.

The five series of age proportions were applied to the estimated annual runs for 1888 to 1919 to obtain five series of recruits for brood years 1888 to 1913. The escapement was then estimated by subtracting the commercial catch from the estimated annual run. The escapement values represent the escapement from the lower Skeena commercial fishery that was then subject to First Nations' subsistence and commercial catch. This catch was estimated to be significant in the Babine River and of lesser magnitude in other rivers of the Bulkely and the lower, middle and upper Skeena (Shepard and Withler 1958). Shepard and Withler (1958) report data for 1935

to 1948 and estimated the First Nations catch during this period to have been 9.2% of the total escapement. This period occurred more than three decades after the First Nations upriver fishery had been severely curtailed, most importantly at the Babine Weir on the Babine River following the 1904 sockeye season (Harris 2001, Chapter 2). Accordingly, I estimated the First Nations' catch from the escapement for 1905 to 1919 to be 10% of the estimated escapement, and 13% for the period from 1888 to 1904. The First Nations fishery was further reported to have been directed almost exclusively at stocks composed nearly entirely of age 4 and age 5 fish (Shepard and Withler (1958), so the two percentages (10% and 13%) were applied to the sum of age 4 and age 5 returns in the escapement. The figure of 13% is an arbitrary estimate and is intended to account for some modest amount of additional First Nations' catch before the restriction of the Babine weir fishery following 1904. Note that the more the escapement is reduced, the smaller the estimate of the actual spawning stock will be and the greater the estimated productivity of the stock will be. So caution is necessary in adjusting the escapement in this way. However, as I discuss in the Results, erring on the side of under-estimating the spawning escapement will most likely result in underestimating the equilibrium abundance, which is the ultimate quantity of interest of the stock-recruit analysis in this application.

The estimated run, harvest, harvest rate, escapement, First Nations catch, and Spawner numbers resulting from this approach is shown in Table 2. Five sets of spawner and recruit data for brood years 1888 to 1913 are then created by applying each of the sets of age proportions to the estimates runs (Table 2, column 2). Each of the five data sets is shown in Tables 3 – 7. Note that the number of spawners in a given year is slightly different between the five data sets. This is due to the First Nations catch being calculated from the proportion of the escapement comprised of only four- and five-year old fish and this proportion varies each year due to the random variation in the proportion of six-year old fish in each annual run. The data set created by applying the average age composition to all return years is shown in Table 8.

Analysis of the stock-recruit data sets.

I evaluated each of the six data sets by first applying the Beverton-Holt and Ricker stock-recruit models to each. The Beverton-Holt model is of the form

$$R = \alpha * S / (1 + S/\beta), \quad (1)$$

where S is the number of spawners producing a particular brood, R is the number of resulting adult recruits, including harvest removals, α is the productivity parameter, and β is the density-dependence parameter, here interpreted as the number of spawners at which recruitment is half of the asymptotic maximum, $\alpha * \beta$. The equilibrium abundance (EQ) at which the number of recruits is equal to the number of parent brood year spawners is

$$EQ = (\alpha - 1) * \beta. \quad (2)$$

The Ricker model is of the form

$$R = \alpha * S * \exp(-S/\beta), \quad (3)$$

where α , R and S have the same interpretation as in the Beverton-Holt, \exp is the base of the natural logarithm, and β is the spawner abundance that produces the maximum number of recruits. The equilibrium abundance for this model is

$$EQ = \text{Ln}(\alpha) * \beta. \quad (4)$$

The Ricker model typically produces a curve that peaks at spawner abundance levels in the middle of the spawner data and descends after the peak, rather than leveling off as it approaches an asymptote. The Beverton-Holt model can produce unrealistically large estimates of the productivity parameter (α) for data sets that lack data for recruitment from low spawner abundance levels (Hilborn and Walters 1992, Goodman 2004). The Ricker model does not suffer from this problem because there is an analytic relationship between α , the productivity of the stock at low spawner abundance, and the slope of the descending limb of the stock-recruit curve at levels of spawner abundance greater than the level of maximum recruitment, β . The steepest part of the curve occurs at a spawner level equal to $2 * \beta$, where the slope is $-\alpha * \exp(-2)$ (Goodman 2004). This permits the Ricker model to obtain information on the value of α from

spawner-recruit data points greater than β which prevents it from producing unrealistically large values of α from data sets lacking points at low spawner abundance.

This phenomenon occurs with the Skeena stock-recruit data sets, as illustrated in Figure 2. Both models are fit using maximum likelihood (MLE) regression. The fits to the regressions are both good and similar as judged by the regression errors, σ .

Figure 2 well illustrates the problem the Beverton-Holt model has in estimating the productivity parameter α . Despite this the two fits to the data, as indicated by the regression errors, are practically identical. But note the two EQ values. There is a difference of more than 300,000 spawners and recruits, the Beverton-Holt being the larger. Since this is the principal parameter of interest in applying Method II it is important to attempt to determine the most appropriate model form, if possible. This can be accomplished by employing the Schnute-Kronlund (S-K) stock-recruit model (Schnute and Kronlund 1996). The S-K model has the form

$$R = \alpha * S / (1 + \gamma S / \beta)^{1/\gamma}, \quad (5)$$

where all terms have the same interpretation as for the Beverton-Holt and the third parameter (γ) controls the shape of the curve, ranging from Ricker, when $\gamma = 0$ to Beverton-Holt when $\gamma = 1$. At intermediate values of γ the shapes of the curves are intermediate.

For the S-K model

$$EQ = ((\alpha^\gamma - 1) / \gamma) * \beta. \quad (6)$$

I address the problem of stock-recruit data sets that produce equally good fits to Ricker and Beverton-Holt models but where the value of the productivity parameter (α) is poorly estimated and unrealistically large following the approach employed by Goodman (2004). I conduct a Bayesian analysis of the 1888 to 1913 Skeena sockeye stock-recruit data sets using the Ricker model and fit a parametric distribution to the posterior distribution of the widest productivity parameter (α). I then use this parametric distribution as an informative prior for α in a stock-

recruit analysis of the six data sets using the S-K model to determine the most reasonable stock-recruit model on which to base the final estimates of the equilibrium abundance for brood years 1888 to 1913 for each data set.

RESULTS.

Figures 3 – 8 show the proportions of ages 4, 5, and 6 sockeye in the estimated annual runs for the five simulated data sets and for the data set using the average ages for brood years 1888 to 1911 and the actual proportions of ages 4 and 5 for brood years 1912 to 1919 adjusted for the inclusion of the estimated average proportion of age 6 sockeye of 0.091. The proportions from the five simulations show a wide range of proportions for each return year. Note that the proportions of ages 4 and 5 for return years 1913 to 1919 are slightly different between the five data sets due to the inclusion of random proportions for age 6. But the relative proportions of age 4 to age 5 are constant for all five sets. The estimated number of spawners, ages 4 – 6, and recruits for brood years 1888 to 1913 for each of the six data sets are shown in Tables 3 to 8.

Bayes estimates of the parameters of the Ricker and Schnute-Kronlund stock-recruit models.

Data set #2 (Table 4) yielded the largest modal value of the productivity parameter (α) with the broadest posterior distribution of the six fits to the Ricker model. I therefore chose this distribution to provide an informative prior distribution for the productivity parameter of the Schnute-Kronlund model. A Gamma distribution was fit in Matlab to the posterior alpha data from the Ricker fit to data set # 2 and produced a very close fit with shape parameter = 24.1664 and scale parameter = 0.3092 (Figure 9). The S-K model with an informative Gamma (24.1664, 0.3092) prior distribution on alpha was then fit to each of the six data sets. The gamma parameter (γ) of the S-K model was examined to evaluate whether or not there was a clear preference for either the Ricker (γ close to zero) or the Beverton-Holt (γ close to 1.0) for each of the six data sets.

The posterior values of the parameters of the Ricker and Schnute-Kronlund models at the joint mode for model fits to all six data sets are shown in Table 10. The joint posterior mode is the most probable set of values of all parameters, in contrast to the marginal mode of a single parameter which is the most probable value of the parameter measured over all sampled values of all other parameters. The joint mode is, in effect, the maximum likelihood estimate (MLE) for the conjunction of all parameters and will have the smallest regression error (best fit) compared to the marginal modes of the parameters considered individually. All six fits of the Ricker model were reasonable with regression errors (sigma) ranging from 0.22 to 0.33.

Inspection of the values of the S-K gamma parameter at the joint mode for each data set reveals no clear preference for either model except for data set # 2, which clearly favors the Ricker model ($\gamma = 0.002$). For the remaining five data sets the S-K joint modal value of gamma ranges from 0.25 and 0.37, which doesn't favor the Beverton-Holt and weakly favors the Ricker. However, inspection of the marginal posterior distributions of the fits to these five data sets shows that all have non-trivial probability masses over the entire width of the distribution, and the posterior marginal of the fit to data set #2 shows significant mass for values of gamma as large as 0.5. The posterior distribution of gamma for data set #2 is shown overlaid on the posterior distribution for data set #4, the set for which the mode of gamma was largest in Figure 10. The shape of the gamma posterior for data set #4 is representative of the fit to the other four data sets.

The fit of the Ricker to data sets #2 and #4 show that the Ricker is a reasonable fit to the data. Figures 11, 12, and 13 show the posterior distributions of data set #2 overlaid on those of data set #4 for α , β , and σ , respectively. Figures 14, 15 and 16 show the corresponding distributions for the S-K model.

The informative Gamma prior on the S-K productivity parameter (α) achieved the objective of restricting the posterior distribution of parameter values to within a realistic range, and also showed the data to be mildly informative as well as can be seen in Figures 14 – 16. In Figures 17 and 18 the alpha posteriors for two of the six data sets, data sets #4 and #6, the set derived from the average age composition, are shown overlaid on the prior. The posterior for data set #4 shows

the data to have very little, if any, information about the value of alpha and so is driven almost entirely by the prior. The posterior for data set #6 is shrunken toward the middle of the prior distribution and centered very near but lower than the mode of the prior showing that the data is somewhat informative (in addition to the information extracted from data set #2 by the fit of the Ricker model from which the prior on alpha was derived). This is also shown in the joint posterior modes for data set #6 for “SK alpha” and for data set #2 for Ricker (R alpha) which is the prior for the SK model (Table 10).

The main parameter of interest, the equilibrium abundance, is reasonably well-estimated by both models and all six data sets. With the exception of data set #2 for which the Ricker model is clearly the appropriate one, there is some uncertainty regarding the best model to fit to the other five data sets (Table 10, Figure 10). In particular the Beverton-Holt model cannot be entirely excluded for any of the five data sets. However, the most probable model is an intermediate one closer to the Ricker than to the Beverton-Holt, with Schnute-Kronlund model shape parameter (γ) approximately 0.3. This indicates that there is some degree of over-compensatory density dependence in the data but not as severe as for a pure Ricker.

On balance, however, there is no clear choice between the Ricker and the intermediate S-K. This is shown in part by the data for the joint posterior modes of the parameters of both models (Table 10). Table 11 lists the coefficients of variation (standard deviation/mean) of parameters alpha, beta, sigma (regression error), and equilibrium for both models for data sets #2 and #4, which are representative of the values for the fits to the remaining four data sets. The C.V.'s of two of the four parameters for both models and both data sets are particularly revealing, those for the regression error (sigma) and for the equilibrium abundance. The C.V.'s for sigma are essentially identical (0.15, 0.16) for both models, showing that both models explain the data equally well.

The C.V.'s for the equilibrium are noticeable smaller than those for the productivity and capacity parameters (α and β , respectively) with values ranging from 0.06 to 0.12. The values for the Ricker model are smaller than for the S-K but not significantly so (0.06 vs. 0.09, and 0.09 vs. 0.12). This reflects the strong negative correlation between alpha and beta in both models, which ranges between -0.85 and -0.9 . Figures 13 and 16 show the posteriors of the equilibrium for the

two model fits to data sets #2 and #4. Both posteriors for the fits to data set #2 are precise with narrow modes at or near 1,900,000. Both posteriors for data set #4 (the set with the widest, least precise Ricker alpha posterior) are equally less precise with modes near 2,000,000 (Ricker) and 2,100,000 (S-K), (Table 10).

Comparison of the posteriors for the equilibrium for data set #6 that resulted from application of the average age data to obtain brood year recruits and data set #2 shows similar results (Figures 19 and 20). Both models estimate a larger mode for the average age-based data set (#6), in the neighborhood of 2,100,000 (Ricker) and 2,200,000 (S-K), and the posteriors for both data sets are equally precise for both models as judged by the spread of the posterior distributions.

Run estimation using a simple application of Method I to geometric mean catch data.

The alternative approach of estimating the equilibrium abundance of Skeena sockeye by applying Method I to geometric means of the harvest and estimates of the harvest rate is illustrated in Table 9. For this exercise I used five-year geometric means of the commercial catch for years 1890 to 1919 (Table 1). The harvest rates during this period are reasonably narrowly estimated by Ricker (1973), as described in Methods, so there is little point to conducting a Bayesian estimation using a narrow informative or uninformative uniform prior distribution on the harvest rate centered on the Ricker (1973) five year average point estimates. The uncertainty can be more simply bracketed by point estimates at values above and below the point estimates. This contrasts with the situation for Skeena chum salmon described in Chapter 3 and 4 where significant uncertainties had to be addressed in order to estimate the harvest rate on chum salmon.

To bracket the small uncertainty in the estimated harvest rates, I chose values 5% above and 5% below the five year averages of Ricker (1973) and simply estimated the run for each five-year interval by dividing the five-year geometric mean catch by $0.95*HR$, HR , and $1.05*HR$, where HR equals the five-year average harvest rate for the period from Ricker (1973) (Tables 2 and 9). For the five year mean of the harvest rate for 1915 – 1919 of 0.62, this approach bracketed the harvest rate between 0.59 and 0.65, which is just inside the limits of 0.58 and 0.66 of the uniform

prior distribution placed on the sockeye harvest rate for 1916 to 1919 in the Bayes estimate of the chum run for this period described in Chapter 3 and employed by Price et al. (2013), so I consider this approach to bracket the central 95% of the likely range of the harvest rates.

The mean estimated run size ranges from 2,138,000 for the period 1915 – 1919 to 2,495,000 for the period 1890 – 1894. The range for the 1915 – 1919 period is 2,037,000 to 2,251,000. The range for the 1890 – 1894 period is 2,376,000 to 2,626,000 (Table 9).

DISCUSSION.

The contrast between the six stock-recruit data sets.

Proportions of age 4 and 5 adult sockeye in the annual returns of Skeena sockeye for years 1888 to 1911 were simulated from time series data of proportions in return years 1912 to 1954 derived from sampling of the lower Skeena commercial catch. These simulated proportions were supplemented by random samples of the proportion of age 6 adults in the annual returns based on estimates of the average proportion of age 6 sockeye from the literature on the history of Skeena sockeye harvest. Simulated proportions of age 6 sockeye were also added to the actual sampled proportions of ages 4 and 5 in the returns for years 1912 to 1919. The simulated proportions of ages 4 to 6 for return years 1888 to 1919 were used to create stock-recruit data sets for brood years 1888 to 1913 from estimates of the annual returns calculated from reported commercial catch data and estimates of the corresponding annual harvest rate. Five such data sets were randomly chosen for stock recruit analysis in addition to a sixth data set based on the average proportions of age 4 and 5 sockeye in the annual returns for 1912 to 1954.

The five data sets created from random distributions of the proportions of adults age 4 to 6 in the annual returns for 1888 to 1911 and random proportions of age 6 added to the sampled proportions of age 4 and 5 in the returns for 1912 to 1919 contained strongly contrasting proportions between one another and thus provided a broad range of possible age proportions in the corresponding stock-recruit data (Figures 3 – 7; Tables 3 – 7). These data sets provided a

sound basis for evaluating the possible bias of using stock-recruit data sets for Skeena sockeye during the period of interest derived from average age data noted by Zabel and Levin (2002).

Comparison of the Ricker and Schnute-Kronlund stock-recruit analyses.

A preliminary evaluation of the application of the Beverton-Holt model to the stock-recruit data revealed the inability of the model to provide reasonable estimates of the productivity parameter (α), but the regression error indicated the overall fit was as good as the fit of the Ricker model (Figure 2). To better determine the most appropriate model structure for estimating the stock-recruit parameters of each data set, the three-parameter Schnute-Kronlund model was employed in a Bayesian analysis in which the alpha parameter was constrained by an informative prior parameter with a Gamma distribution fit to the posterior distribution from the Bayesian analysis of the Ricker model for the data set (#4) that produced the broadest, least informative, posterior distribution. This prevented the S-K model from selecting fits that required unrealistically large alpha values.

The results from fitting the S-K model to each of the six data sets produced posterior distributions of the productivity parameter, alpha, and the primary parameter of interest, the equilibrium abundance (EQ) that were very similar to those of the Ricker model. However, the fits to five of the six data sets indicated that the most probable form of the model was an intermediate that was weakly Ricker-like with regard to the presence of over-compensation, as indicated by posterior modes of the S-K model shape parameter gamma (γ) between 0.25 and 0.38 (Table 10, Figure 10). Data set #2 was an exception in strongly fitting the Ricker model (gamma = 0.002, Table 10, Figure 10).

The analyses of all six data sets from both models were strongly concordant with respect to the estimation of the equilibrium abundance, as evidenced by the posterior joint mode of all parameters (Table 10) and by the marginal posterior distributions of the equilibrium (EQ) (Table 11, Figures 13, 16, 19 and 20). The lowest estimated posterior modal value was 1,817,000 for the Ricker model estimate of data set #2. The highest was 2,084,000 for the S-K model estimate of

data set #3. These results demonstrated the expected result that the equilibrium would be the most precisely estimated of all parameters as a result of the negative correlation between the alpha and beta (productivity and capacity) parameters of the stock-recruit models, which ranged between -0.85 and -0.90 .

This supports the conclusion that the equilibrium abundance has a high probability of being reasonably well-estimated when modest uncertainty surrounds the estimation of the productivity and capacity parameters, as indicated by the standard deviations of the respective posterior distributions. This also validates the use of multiple simulated stock-recruit data sets, based on historical age data, that incorporate a broad range of historically possible age proportions in the annual returns to evaluate the range of influence that differing age proportions may have on the estimated values of the stock-recruit parameters. It is to be expected from this approach that a) the productivity, capacity, and (in the case of the S-K model) model shape parameters may differ significantly from one another in both the values of the posterior modes and in the precision of the estimate (the spread of the posterior distributions), and b) the equilibrium abundance will be relatively precisely estimated and the estimates for most if not all of the data sets will broadly overlap one another.

Comparison of the estimates of stock-recruit parameters between the five random age proportion data sets (1 – 5) and the data set (6) derived from the application of the average age proportions.

The estimation of the parameters of the Ricker and S-K models using the data set created using the average age data showed no significant upward bias in the estimate of the productivity of the stock (Table 10). The mode of the productivity parameter (α) at the posterior joint mode for the Ricker model for the average-age data set was slightly larger than four of the five data sets created from random age simulations (6.14 compared to 5.68 for the random age data set having the smallest estimated alpha) and significantly lower than the value of 7.47 for the set with the largest estimated alpha (Table 10). For the S-K model the value of alpha at the posterior joint mode was very similar for all six models (range 7.0 to 7.49) and smallest for the average age data set (Table 10). Significantly, the value of the main parameter of interest, the equilibrium abundance (EQ) for the average data set (#6), was intermediate in value at the posterior joint

mode among the six data sets for both the Ricker and S-K models (Table 10) and, as noted above, all six values of the posterior modes for both models were very close to one another.

In this particular application, therefore, there would have been no bias in relying solely on a stock-recruit analysis based on the average age data set. However, this was only revealed by the comparison to five data sets created by simulating different random age proportions using data derived from the historically available age proportion data. Since this requires little additional effort, it is recommended that the use of average age data be employed together with simulated age proportion data, preferably based on stock-specific data whenever possible.

Comparison of the estimates of equilibrium abundance from the stock-recruit analyses to the estimates using the simple application of Method I.

Compared to the simple application of Method I to geometric mean catch and harvest rate data, the stock-recruit analyses provide more conservative estimates of the historical equilibrium abundance and a more complete account of the uncertainty of the estimates. The posterior joint modes of EQ for both the Ricker and S-K model estimates of all stock-recruit six data sets are up to 700,000 smaller than estimates from the simple application of Method I (compare Tables 9 and 10). The mean values of the Method I estimate range from 2.1 to 2.5 million. The values of the posterior joint modes of the Ricker and S-K estimates range from 1.8 to 2.1 million.

Despite having to rely on simulated adult return data and estimates of spawner numbers derived from estimates of First Nations' catch of age 4 and 5 fish from the escapement, the stock-recruit analyses employ much more information about the size of the stock over the entire period than the simple application of Method I to geometric mean catches and harvest rates over five year periods. The wider range of the point estimates of abundance in the Method I analysis also show the difficulty of identifying any particular period of time from 1890 to 1919 to choose on which to base the estimate. As explained in Chapters 2 and 3, Method I will be most accurate and will be most clearly applicable when applied to an series of relatively large catches of one to three generations length that occur early in the history of the commercial fishery and when data is

lacking from which to conduct a stock-recruit analysis. Chapter 4 shows that it can fruitfully be applied to a single year's catch under these circumstances.

The commercial catch data for Skeena sockeye starts in 1877 with small catches relative to the size of the stock. Estimated harvest rates did not exceed a rate of 35% until the start of the 20th century (Tables 1 and 2). Equally important, over the entire period of interest (through return year 1919), the catch tended to increase as the harvest rate continually increased. As a consequence the Method I estimate of the equilibrium run size did not decline until the last five-year period (1915 – 1919) and even then the decline was modest at best. This was a classic case of increasing harvest of a stock composed of multiple populations of varying sizes and inherent productivities occurring during the early history of a commercial fishery (cf., Ricker 1958, 1973). Over-fishing in the sense of fishing at harvest rates in excess of the maximum sustainable yield (MSY) of which the stock may have been capable under constant environmental conditions, had probably been exceeded by the estimated harvest rate of 59% for the 1910 – 1914 period (Ricker 1973, Ricker & Smith 1975). Nonetheless, for several reasons discussed by Ricker (1958, 1973), it would still require several more generations for the overharvest to manifest itself as a marked and prolonged decline in both the catch and the stock (Table 1, Figure 1), as actually occurred by the 1930s.

Although one might make a case for accepting the simple Method I estimates of 2.4 to 2.6 or 2.2 to 2.5 million for the first or second periods (1890 – 1894, 1895 - 1899), respectively, as the best estimates of the historic equilibrium abundance of Skeena sockeye, the more conservative estimates of 1.8 to 2.1 million at the posterior joint modes are more defensible. In addition, the posterior marginal distributions of EQ for all of the data sets under the Ricker and S-K models include the mean and range values from Method I (Table 9), so the Bayes estimates do not exclude values several hundred thousand larger than the modes reported in Table 10 (e.g., Figures 13, 16, 19, 20), but rather properly include them within the marginal posterior distributions of the Bayes stock-recruit analysis, thereby reflecting the uncertainty.

To provide a conservative range for the uncertainty of the Bayes estimate of equilibrium for the stock-recruit analysis, the best approach is to pick the Schnute-Kronlund model estimate that has

the smallest regression error. This is the estimate for data set #6, the average age data set for which the regression error is 0.218 (Table 10). For this data set the 5th percentile of the posterior distribution of the equilibrium abundance, EQ, is 1,880,000 and the 95% percentile is 2,500,000 (Figure 20). From this perspective the results from the simple application of Method I are coherent with the more informative stock-recruit analysis.

It is important to recognize that during the period from 1890 to 1919 when harvest rates were steadily increasing to rates in excess of later estimates of MSY, stocks of lower productivity were likely being over-harvest and eliminated from the aggregate population. As noted by Ricker (1958, 1973) and others (e.g., Hilborn and Walters 1992), this will have the effect of making the aggregate of remaining stocks appear more productive than the original aggregate. Evidence of this effect is the fact that the estimates of the annual runs using the estimated harvest rates (Table 2) show the largest runs occurring during the period from 1910 to 1920 (Table 2, Figure 1). Neither Method I nor the stock-recruit analysis (Method II) are able to parse this out given the absence of detailed information on the annual stock composition of the aggregate stock during this period. But the stock-recruit analysis provides a much more integrative estimate of the average performance of the aggregate stock over the entire period which still sustained high overall abundance throughout. So, it is reasonable to conclude that the estimated equilibrium abundance levels from the stock recruit analysis of any one of the six data sets provides a robust estimate, the estimate from the S-K model estimate of data set #6 providing the single most conservative estimate.

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TABLES.

Table 1. Skeena River commercial sockeye salmon landings from Table 46 of argue & Shepard (2005).

Year	Commercial Catch (thousands)
1877	30
1878	84
1879	105
1880	209
1881	222
1882	312
1883	402
1884	641
1885	133
1886	464
1887	581
1888	694
1889	573
1890	914
1891	760
1892	901
1893	591
1894	635
1895	682
1896	969
1897	615
1898	792
1899	1123
1900	1375
1901	1075
1902	1560
1903	677
1904	1231
1905	1116
1906	1131
1907	1423
1908	1831
1909	1151
1910	2452
1911	1716
1912	1211
1913	693
1914	1704
1915	1524

1916	798
1917	861
1918	1615
1919	2422
1920	1132
1921	536
1922	1067
1923	1729
1924	1975
1925	1018
1926	1078
1927	1100
1928	453
1929	1018
1930	1714
1931	1217
1932	699
1933	363
1934	716
1935	693
1936	1084
1937	538
1938	617
1939	857
1940	1454
1941	1013
1942	374
1943	322
1944	796
1945	1217
1946	618
1947	380
1948	1185
1949	766
1950	526

Table 2. Estimated Skeena sockeye run, harvest, and spawner data for brood years 1888 to 1913. Run = adult return to the lower Skeena. Harvest = the commercial catch in the lower Skeena commercial fishery. H Rate = the harvest rate on the run estimated by Ricker (1973). Escapement = Run-minus-Harvest, FN Catch = the estimated First Nations' catch of age 4 and age 5 sockeye from the Escapement for simulated data set #1 (see Table 3 and text for a detailed explanation). Spawners = Escapement-minus-FN Catch.

Year	Run	Harvest	H Rate	Escapemen t	FN Catch	Spawners
1888	2776	694	0.25	2082	245	1837
1889	2294	573	0.25	1720	203	1518
1890	3047	914	0.30	2133	257	1876
1891	2532	760	0.30	1772	211	1561
1892	3005	901	0.30	2103	242	1861
1893	1972	591	0.30	1380	160	1221
1894	2115	635	0.30	1481	177	1303
1895	1948	682	0.35	1266	145	1121
1896	2768	969	0.35	1799	213	1586
1897	1758	615	0.35	1143	139	1003
1898	2264	792	0.35	1471	173	1299
1899	3207	1123	0.35	2085	248	1836
1900	2865	1375	0.48	1490	175	1314
1901	2240	1075	0.48	1165	132	1032
1902	3250	1560	0.48	1690	197	1493
1903	1410	677	0.48	733	86	648
1904	2565	1231	0.48	1334	156	1178
1905	1993	1116	0.56	877	102	775
1906	2020	1131	0.56	889	83	806
1907	2541	1423	0.56	1118	100	1018
1908	3270	1831	0.56	1439	130	1309
1909	2055	1151	0.56	904	82	822
1910	4156	2452	0.59	1704	158	1546
1911	2908	1716	0.59	1192	109	1084
1912	2053	1211	0.59	842	78	764
1913	1175	693	0.59	482	43	439
1914	2888	1704	0.59	1184	107	1077
1915	2458	1524	0.62	934	86	848
1916	1287	798	0.62	489	43	446
1917	1389	861	0.62	528	48	479
1918	2605	1615	0.62	990	90	899
1919	3906	2422	0.62	1484	137	1347

Table 3. Spawners and recruits for data set #1.

Year	Spawners	Age 4	Age 5	Age 6	Total Recruits
1888	1837	975	816	168	1958
1889	1518	938	628	236	1802
1890	1876	1319	753	246	2318
1891	1561	959	1174	109	2242
1892	1861	1348	844	220	2412
1893	1221	805	1050	270	2125
1894	1303	993	1032	274	2298
1895	1121	1905	1000	280	3186
1896	1586	1591	459	329	2380
1897	1003	1500	1424	143	3067
1898	1299	1496	779	261	2536
1899	1836	488	1202	205	1895
1900	1314	1102	773	144	2019
1901	1032	1015	903	261	2179
1902	1493	973	1982	326	3281
1903	648	298	1415	190	1903
1904	1178	1529	1345	300	3174
1905	775	520	2150	251	2922
1906	806	1706	1887	153	3745
1907	1018	771	755	128	1654
1908	1309	1145	497	270	1912
1909	822	549	1955	194	2698
1910	1546	663	1417	146	2227
1911	1084	846	554	113	1513
1912	764	587	337	226	1149
1913	439	939	655	289	1884

Table 4. Spawners and recruits for data set #2.

Year	Spawners	Age 4	Age 5	Age 6	Total Recruits
1888	1834	549	585	223	1356
1889	1511	1221	875	193	2289
1890	1879	1017	1151	315	2483
1891	1562	604	1633	124	2362
1892	1861	820	558	130	1507
1893	1216	1076	927	351	2354
1894	1308	1207	1629	301	3137
1895	1118	1227	1696	185	3108
1896	1592	867	878	256	2002
1897	1005	1176	2141	164	3481
1898	1291	852	345	232	1430
1899	1843	902	783	193	1877
1900	1316	1550	599	147	2296
1901	1026	1202	928	174	2304
1902	1488	944	516	322	1782
1903	649	1851	529	201	2581
1904	1176	2418	1213	316	3947
1905	774	642	2723	309	3674
1906	806	1117	1290	194	2601
1907	1014	1309	739	96	2144
1908	1309	1120	512	233	1865
1909	823	566	1983	190	2739
1910	1547	673	1420	115	2208
1911	1086	848	569	106	1524
1912	765	603	339	325	1266
1913	437	944	628	372	1944

Table 5. Spawners and recruits for data set #3.

Year	Spawners	Age 4	Age 5	Age 6	Total Recruits
1888	1840	1208	700	204	2113
1889	1510	1116	537	87	1741
1890	1878	1374	544	249	2167
1891	1569	1316	926	121	2364
1892	1860	1593	460	203	2256
1893	1215	1177	1140	309	2626
1894	1307	921	1449	248	2618
1895	1109	1449	1764	229	3442
1896	1586	852	1033	370	2255
1897	1004	978	991	125	2094
1898	1297	1889	516	191	2596
1899	1840	769	1466	194	2430
1900	1313	908	966	235	2110
1901	1029	832	1150	178	2160
1902	1495	634	1303	261	2199
1903	647	1060	1074	186	2321
1904	1173	1934	1305	346	3586
1905	774	564	3340	207	4111
1906	810	469	1096	115	1681
1907	1014	1605	770	127	2501
1908	1306	1167	498	327	1992
1909	822	550	1912	205	2667
1910	1548	649	1411	111	2171
1911	1082	843	571	125	1539
1912	762	605	334	250	1188
1913	439	930	649	372	1950

Table 6. Spawners and recruits for data set #4.

Year	Spawners	Age 4	Age 5	Age 6	Total Recruits
1888	1830	2064	618	280	2962
1889	1516	1227	400	149	1776
1890	1882	1436	1605	250	3290
1891	1559	194	822	236	1252
1892	1853	1696	1014	179	2889
1893	1212	508	1515	258	2281
1894	1314	570	1947	343	2860
1895	1114	1003	1214	209	2426
1896	1586	1307	944	312	2563
1897	1014	1086	2414	138	3638
1898	1295	524	685	229	1438
1899	1835	587	754	212	1554
1900	1319	1581	677	135	2393
1901	1027	1104	1378	218	2700
1902	1491	507	991	273	1770
1903	647	1332	1462	219	3013
1904	1176	1535	1111	502	3148
1905	775	725	2669	329	3724
1906	806	985	690	157	1832
1907	1016	1889	754	115	2757
1908	1307	1142	504	271	1917
1909	824	556	1954	200	2710
1910	1554	663	1414	137	2214
1911	1087	844	558	125	1527
1912	764	592	334	210	1136
1913	438	930	660	396	1987

Table 7. Spawners and recruits for data set #5.

Year	Spawners	Age 4	Age 5	Age 6	Total Recruits
1888	1835	875	1106	175	2157
1889	1512	612	766	154	1532
1890	1879	1174	1399	360	2933
1891	1570	394	1660	156	2210
1892	1856	748	1047	266	2060
1893	1224	555	700	338	1594
1894	1304	1298	1161	210	2669
1895	1114	1708	1101	157	2966
1896	1596	1553	778	217	2548
1897	1007	1305	756	110	2170
1898	1303	2277	553	209	3039
1899	1842	748	342	139	1229
1900	1310	2014	1299	171	3484
1901	1024	555	871	215	1640
1902	1485	978	1035	279	2292
1903	646	1291	675	214	2181
1904	1174	2315	1431	375	4121
1905	771	410	2748	165	3324
1906	807	1033	2008	161	3201
1907	1016	735	752	94	1581
1908	1307	1140	514	221	1875
1909	823	567	1991	126	2685
1910	1549	676	1460	122	2258
1911	1080	872	566	102	1539
1912	764	599	340	185	1124
1913	437	947	667	431	2044

Table 8. Spawners and recruits for data set #6 using average age compositions for brood years 1888 to 1911

Year	Spawners	Age 4	Age 5	Age 6	Total Recruits
1888	1836	1440	848	192	2480
1889	1517	945	910	177	2031
1890	1881	1013	837	252	2102
1891	1563	933	1190	160	2283
1892	1855	1326	756	206	2288
1893	1217	842	973	292	2107
1894	1306	1085	1379	260	2724
1895	1116	1537	1232	204	2972
1896	1586	1372	963	295	2631
1897	1008	1073	1398	128	2599
1898	1298	1557	606	233	2397
1899	1838	676	1103	181	1960
1900	1314	1229	857	184	2269
1901	1027	955	868	231	2054
1902	1490	968	1093	297	2357
1903	647	1217	1406	187	2810
1904	1176	1566	884	378	2828
1905	773	985	1787	264	3036
1906	808	1991	1251	187	3428
1907	1016	1393	742	107	2242
1908	1308	1124	507	263	1894
1909	822	561	1960	223	2744
1910	1549	665	1399	117	2181
1911	1084	835	568	126	1530
1912	765	602	333	237	1172
1913	438	929	652	355	1937

Table 9. Simple Method I estimates of the run/equilibrium abundance of Skeena sockeye for the 1890 to 1919 return years.

Period	G.M.Catch	HR	Mean Run	95% HR Run	105% HR Run
1890-94	748	0.3	2495	2626	2376
1895-99	816	0.35	2331	2454	2220
1900-04	1140	0.48	2374	2499	2261
1905-09	1305	0.56	2330	2453	2219
1910-14	1432	0.59	2427	2554	2311
1915-19	1326	0.62	2138	2251	2037

Table 10. Parameter estimates at the joint posterior mode for the Ricker and Schnute-Kronlund models for the six stock-recruit data sets for Skeena sockeye brood years 1888 to 1913. R stands for Ricker; SK for Schnute-Kronlund. See text for the meaning of the parameters. Beta and EQ parameters are in thousands.

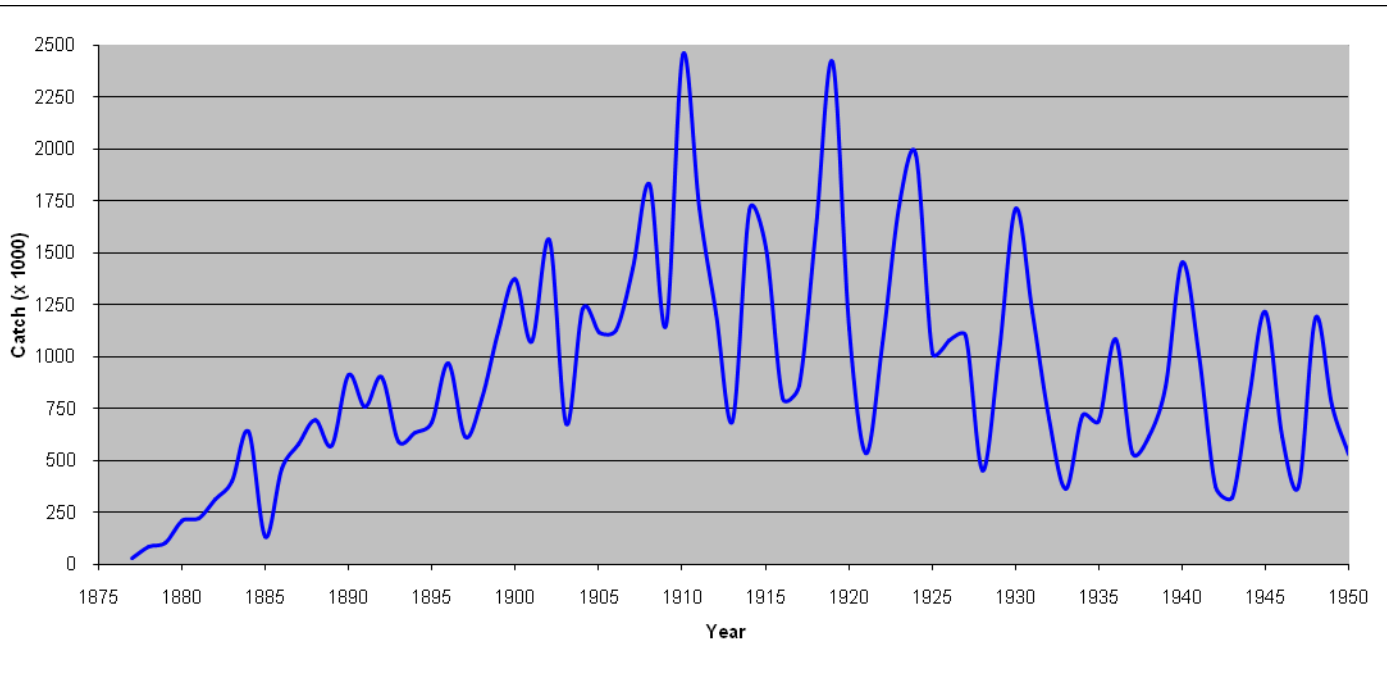
Model Parameters	Data Set 1	Data Set 2	Data Set 3	Data Set 4	Data Set 5	Data Set 6
R alpha	5.68	7.47	5.69	5.97	5.9	6.14
R beta	1143	904	1151	1099	1088	1086
R sigma	0.257	0.274	0.249	0.328	0.321	0.222
R EQ	1986	1817	2000	1962	1932	1972
SK alpha	7.18	7.31	7.24	7.49	7.25	7
SK beta	737	916	718	686	734	814
SK sigma	0.256	0.276	0.248	0.322	0.319	0.218
SK gamma	0.35	0.002	0.365	0.375	0.302	0.249
SK EQ	2064	1826	2084	2062	1989	2038

Table 11. Coefficients of variation (c.v., standard deviation/mean) of the posterior distributions of parameters alpha, beta, regression error sigma, and equilibrium abundance for Ricker and Schnute-Kronlund model fits to data sets #2 and #4.

Data Set & Parameter	Ricker	Schnute-Kronlund
D2 alpha	0.2	0.16
D4 alpha	0.24	0.19
D2 beta	0.16	0.22
D4 beta	0.24	0.31
D2 sigma	0.16	0.16
D4 sigma	0.16	0.15
D2 equilibrium	0.06	0.09
D4 equilibrium	0.09	0.12

FIGURES.

Figure 1. Commercial catch of Skeena River sockeye salmon 1877 to 1950.



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Figure 2. Ricker and Beverton-Holt stock recruit curves fit to data set #1. Beverton-Holt (blue curve). Ricker (red curve). Replacement (1:1) line (black line). Beverton-Holt MLE $\alpha = 47.0$, regression error $\sigma = 0.26$. Ricker MLE $\alpha = 5.7$, regression error $\sigma = 0.26$.

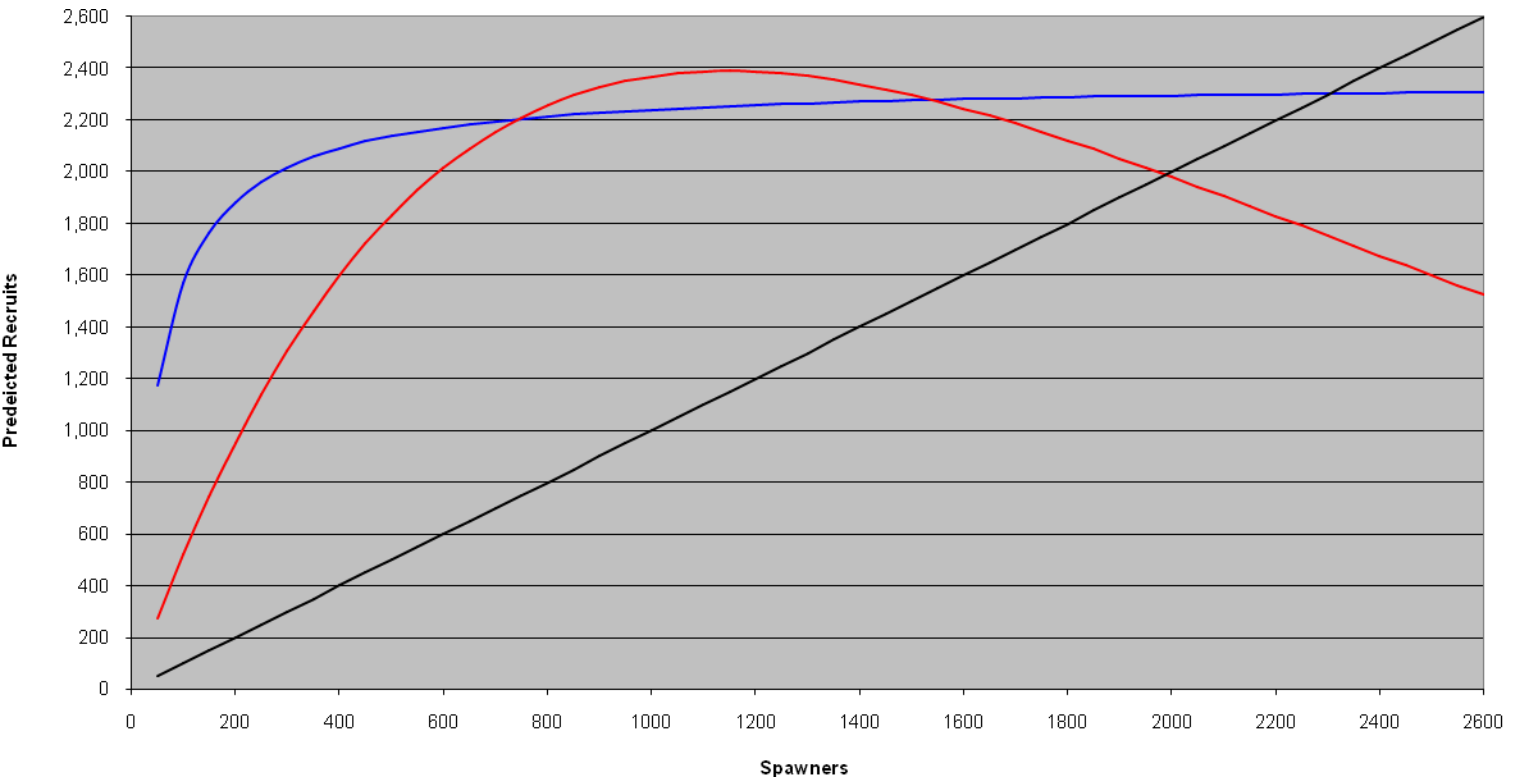


Figure 3. Proportions of 4, 5, and 6 year old sockeye in the estimated annual returns of Skeena sockeye for return years 1888 to 1919. Age 4 (blue), Age 5 (magenta), Age 6 (yellow). Age 6 proportions are on the right y axis.

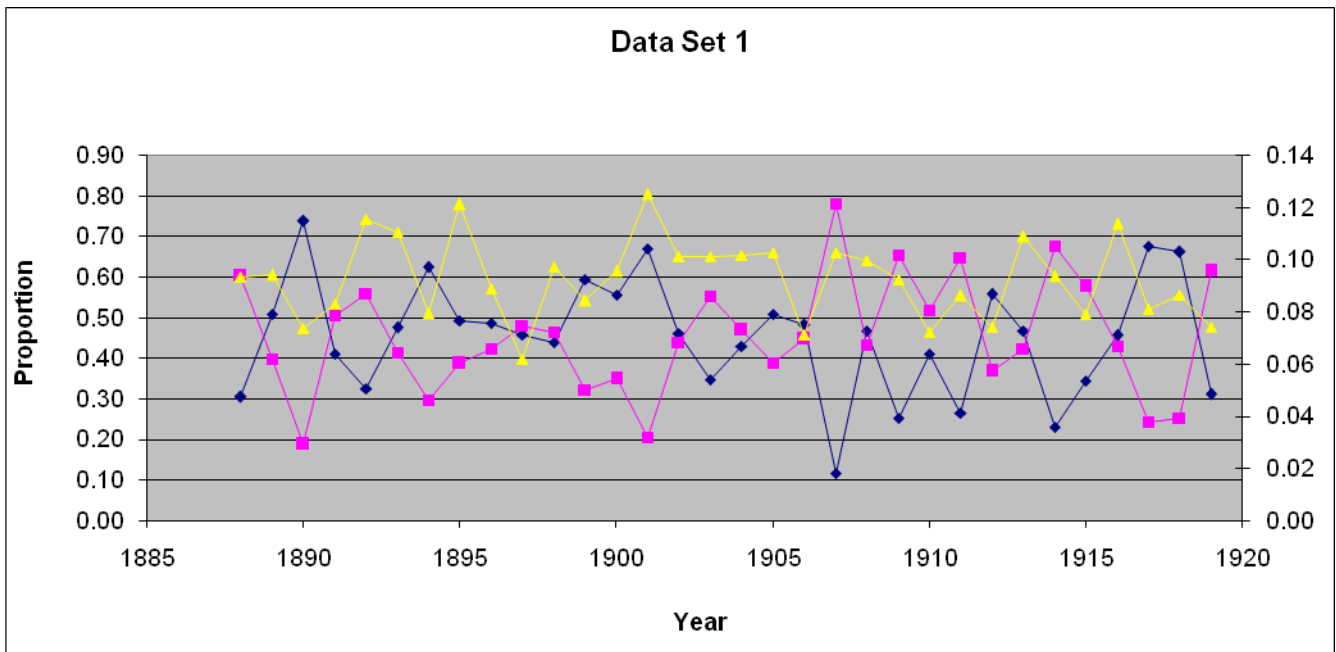


Figure 4. Proportions of 4, 5, and 6 year old sockeye in the estimated annual returns of Skeena sockeye for return years 1888 to 1919. Age 4 (blue), Age 5 (magenta), Age 6 (yellow). Age 6 proportions are on the right y axis.

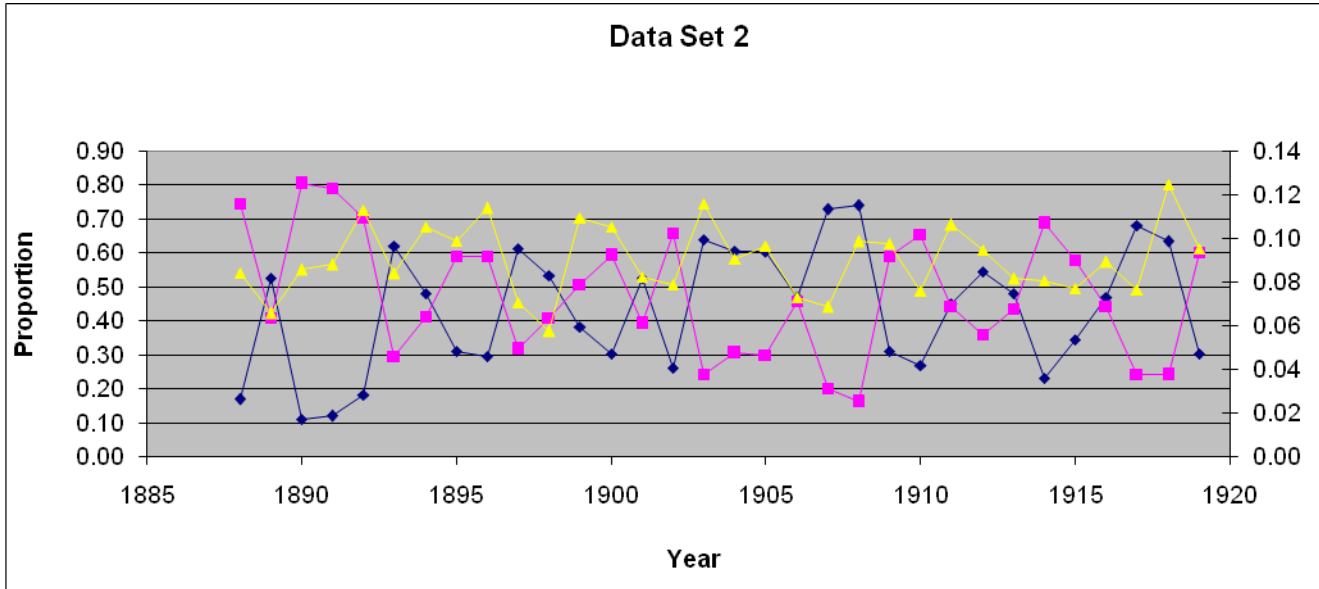
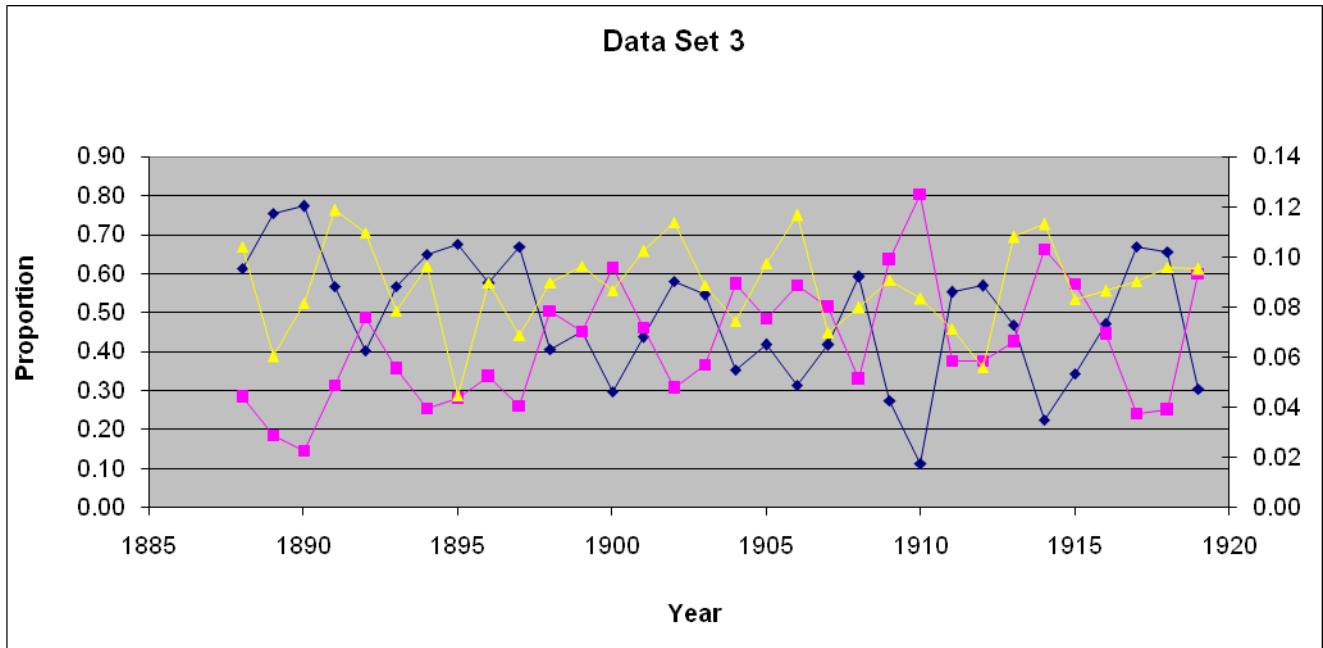


Figure 5. Proportions of 4, 5, and 6 year old sockeye in the estimated annual returns of Skeena sockeye for return years 1888 to 1919. Age 4 (blue), Age 5 (magenta), Age 6 (yellow). Age 6 proportions are on the right y axis.



01

Figure 6. Proportions of 4, 5, and 6 year old sockeye in the estimated annual returns of Skeena sockeye for return years 1888 to 1919. Age 4 (blue), Age 5 (magenta), Age 6 (yellow). Age 6 proportions are on the right y axis.

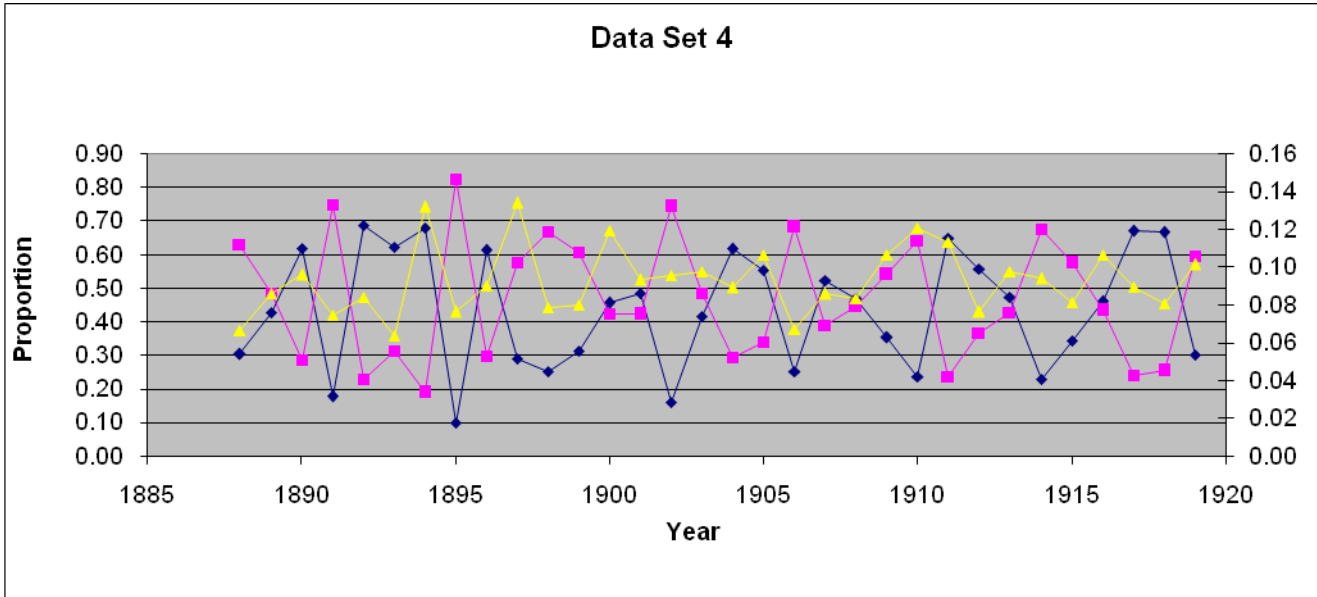


Figure 7. Proportions of 4, 5, and 6 year old sockeye in the estimated annual returns of Skeena sockeye for return years 1888 to 1919. Age 4 (blue), Age 5 (magenta), Age 6 (yellow). Age 6 proportions are on the right y axis.

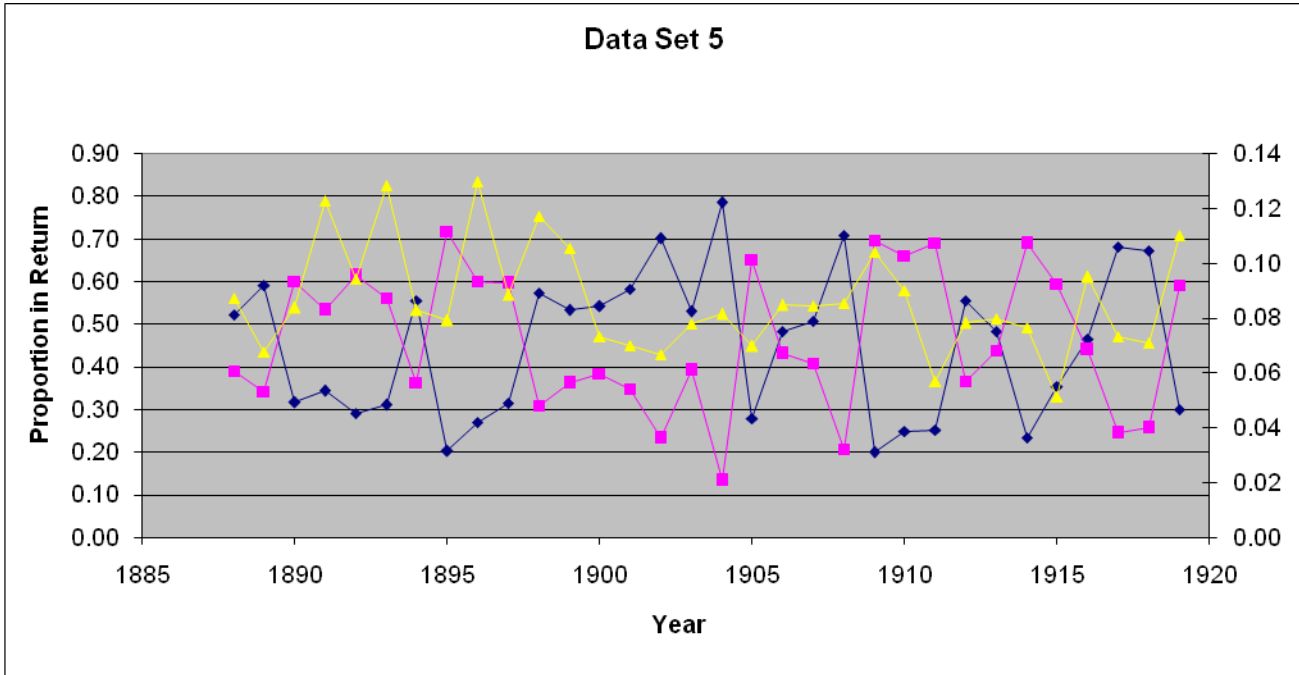


Figure 8. Proportions of 4, 5, and 6 year old sockeye in the estimated annual returns of Skeena sockeye for return years 1888 to 1919. Age 4 (blue), Age 5 (magenta), Age 6 (yellow). Age 6 proportions are on the right y axis.

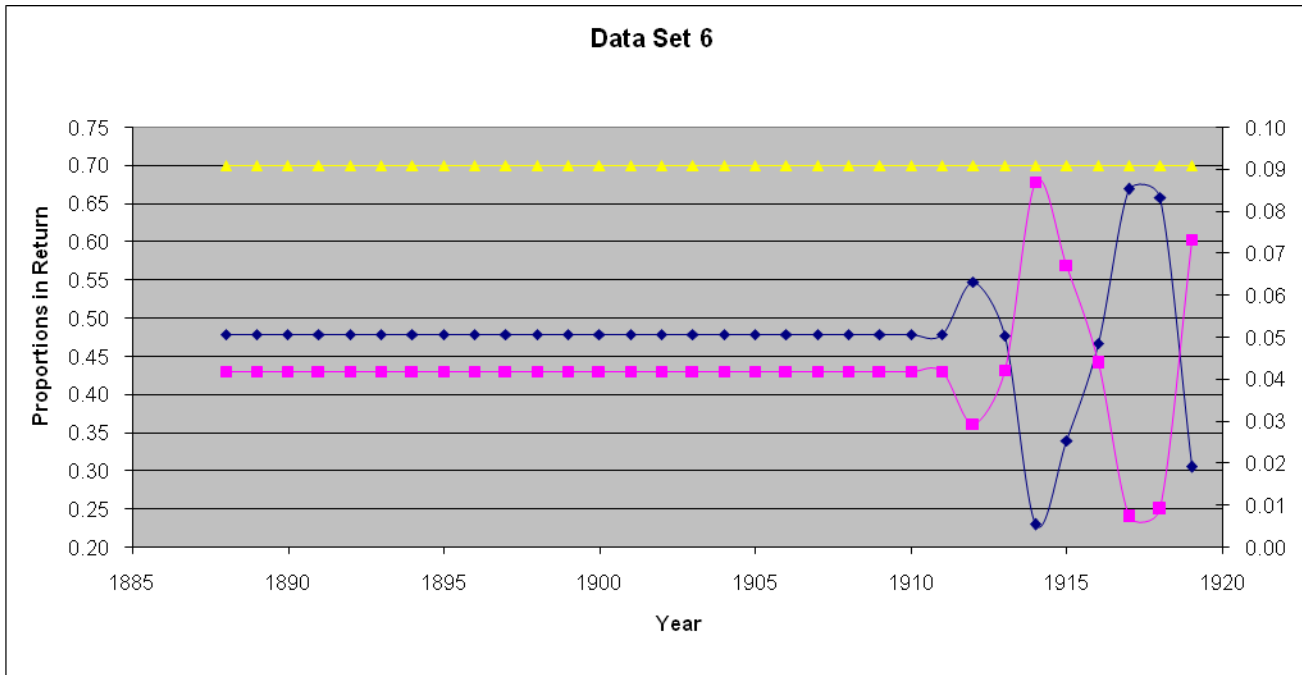


Figure 9. 1000 retained samples from the posterior marginal distribution of the Ricker model alpha (α) parameter fit to data set #2 (blue bars) with a Gamma distribution fit to the alpha values (red curve). The parameters of the Gamma are: shape = 24.1664; scale = 0.3092. The mean of the Gamma is shape*scale = 7.47. The standard deviation is square root(mean*scale) = 1.52.

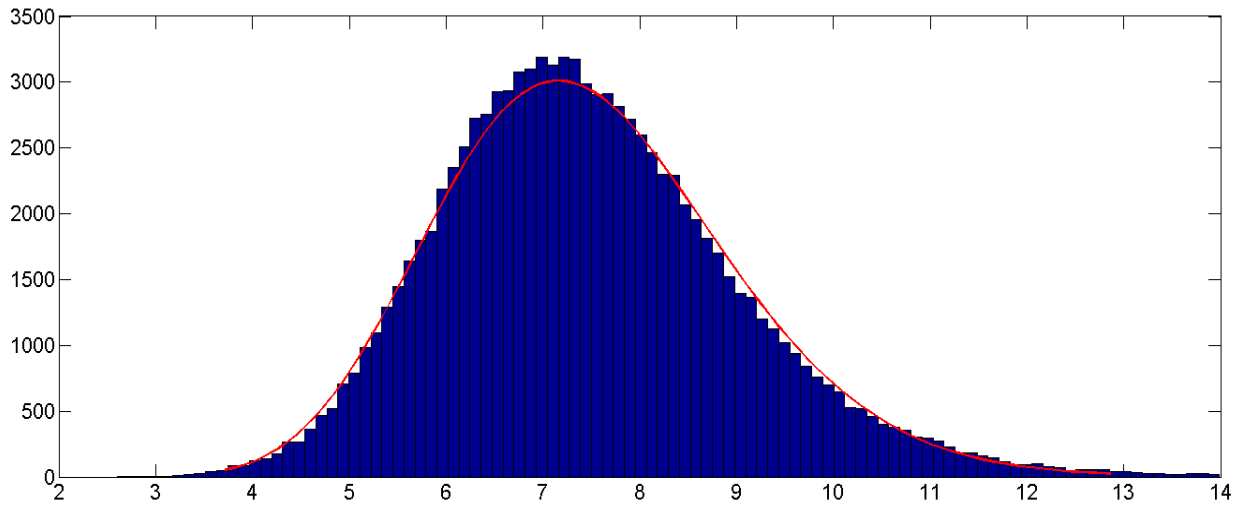


Figure 10. Posterior distribution of the Schnute-Kronlund shape parameter gamma for data set #2 (black line) overlaid on the posterior for data set #4 (grey fill).

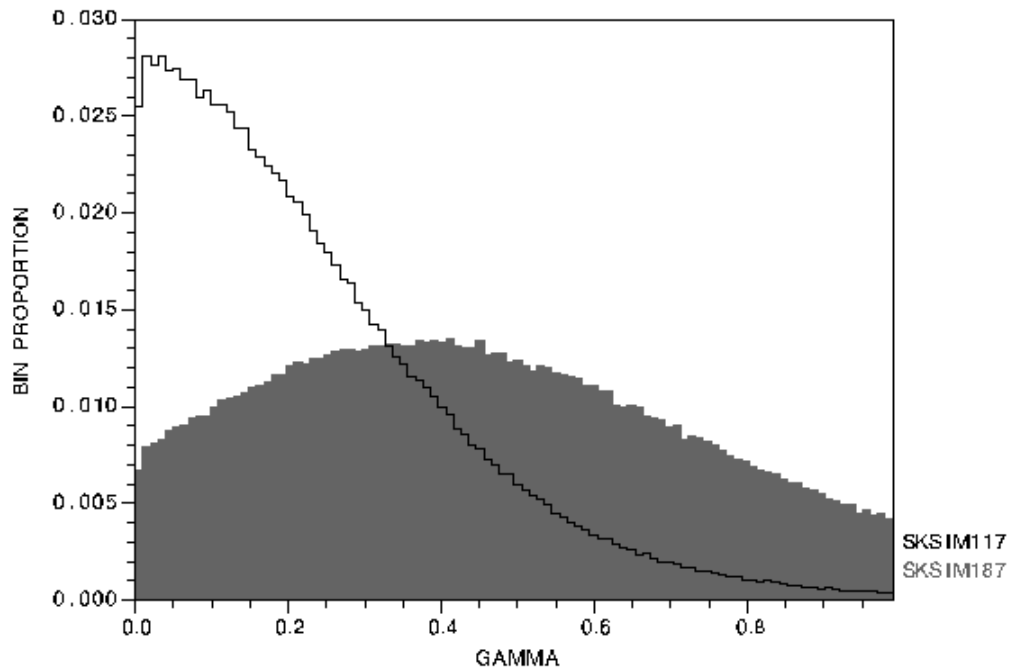


Figure 11. The posterior distribution of the productivity parameter (α) for the fit of the Ricker model to data sets #2 (black line) and #4 (grey fill).

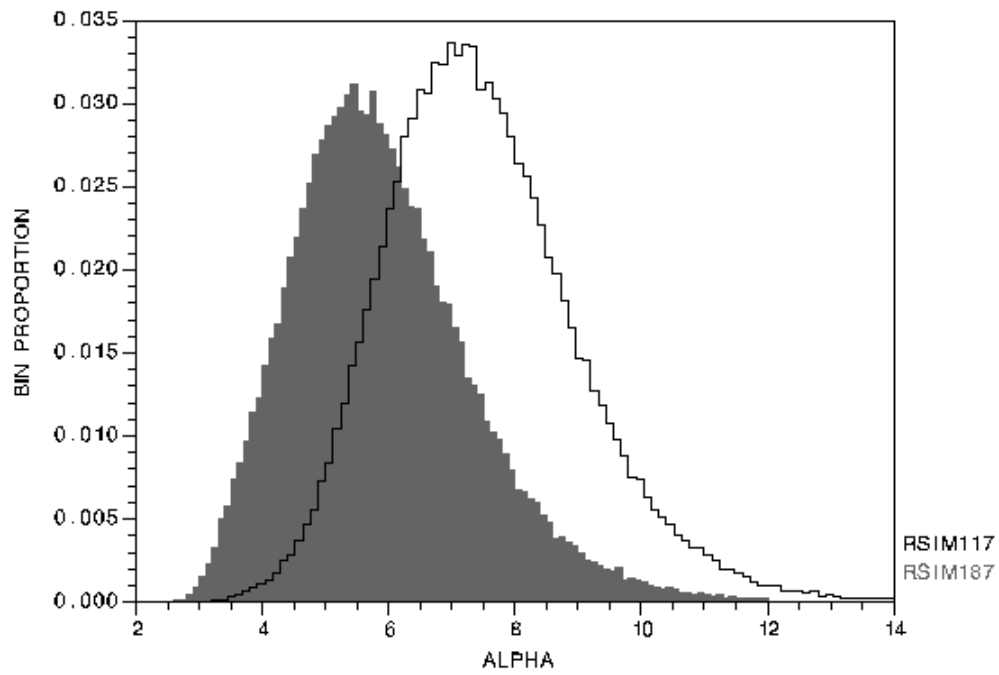


Figure 12. The posterior distribution of the capacity parameter (β) for the fit of the Ricker model to data sets #2 (black line) and #4 (grey fill). Values are in thousands.

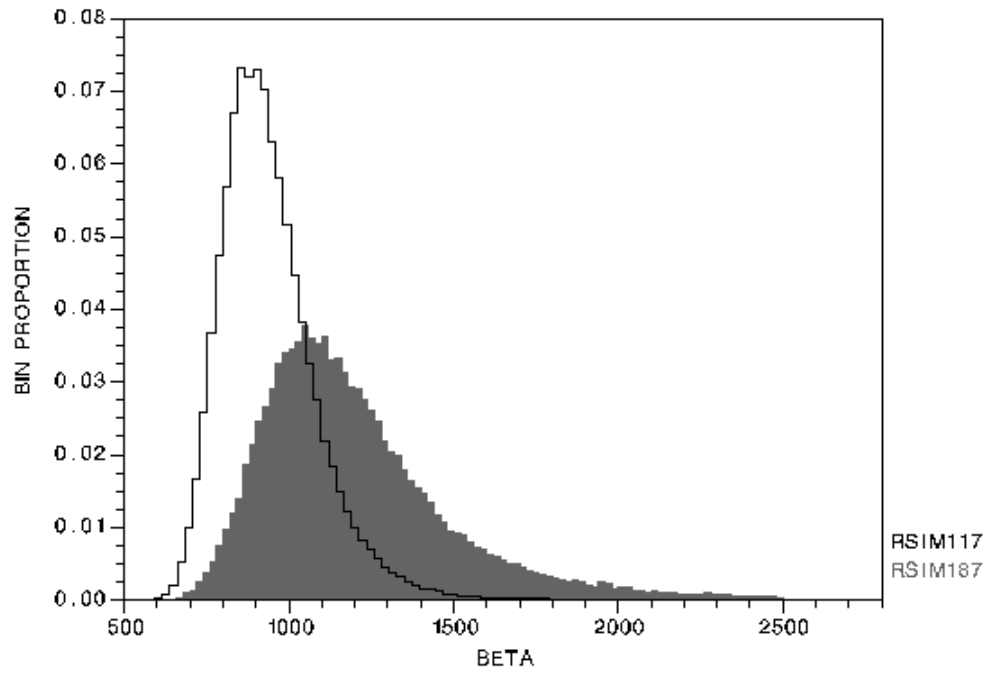


Figure 13. The posterior distribution of the equilibrium (EQ) for the fit of the Ricker model to data sets #2 (black line) and #4 (grey fill). Values are in thousands.

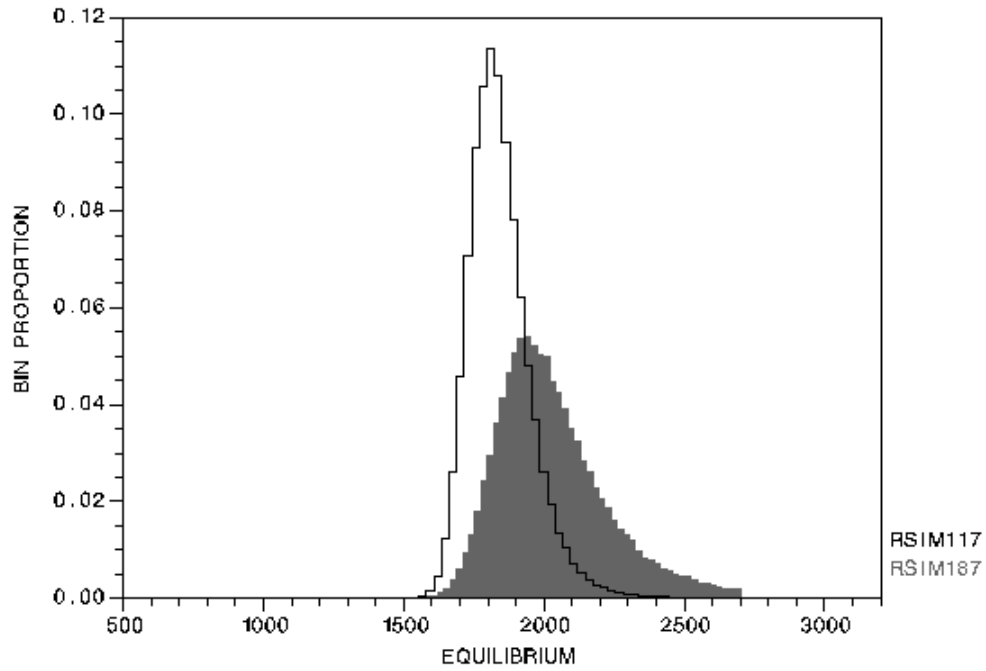


Figure 14. The posterior distribution of the productivity parameter (α) for the fit of the Schnute-Kronlund model to data sets #2 (black line) and #4 (grey fill).

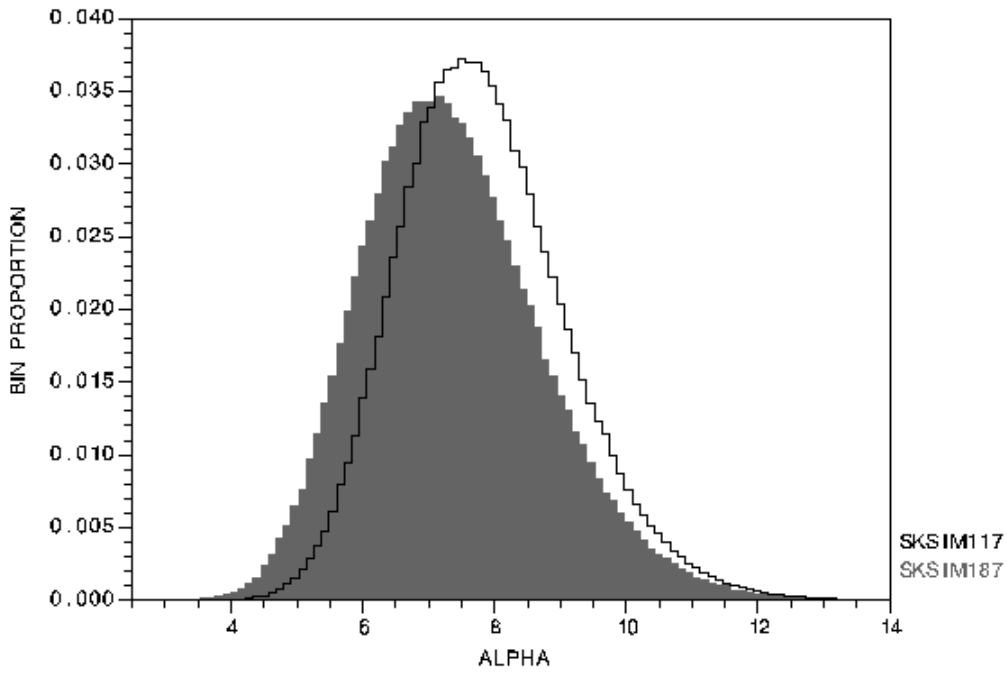


Figure 15. The posterior distribution of the capacity parameter (β) for the fit of the Schnute-Kronlund model to data sets #2 (black line) and #4 (grey fill). Values are in thousands.

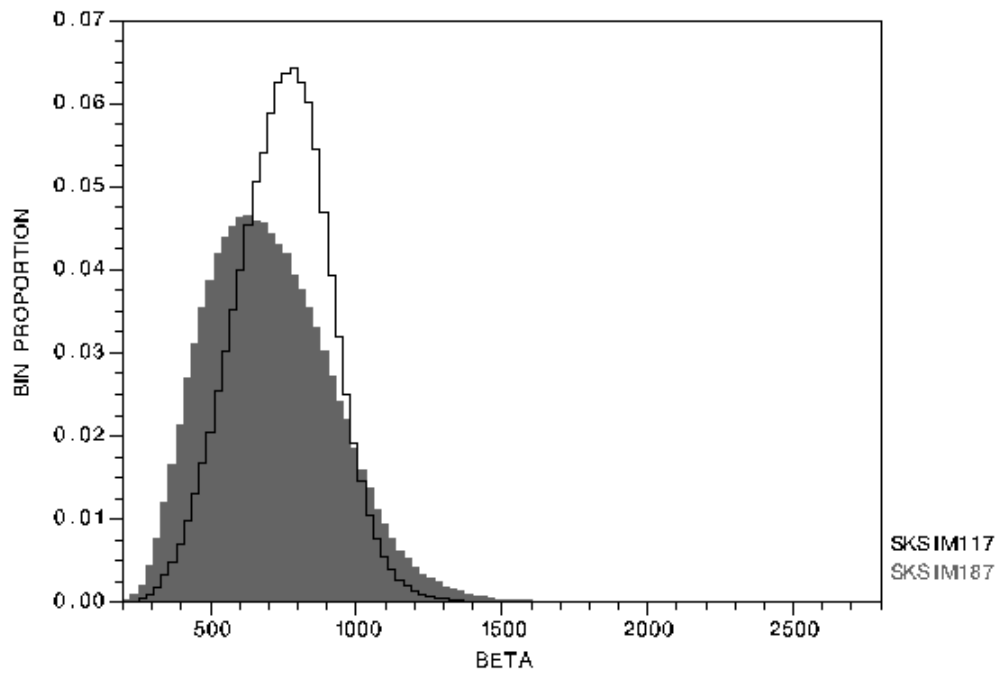


Figure 16. The posterior distribution of the equilibrium (EQ) for the fit of the Schnute-Kronlund model to data sets #2 (black line) and #4 (grey fill). Values are in thousands.

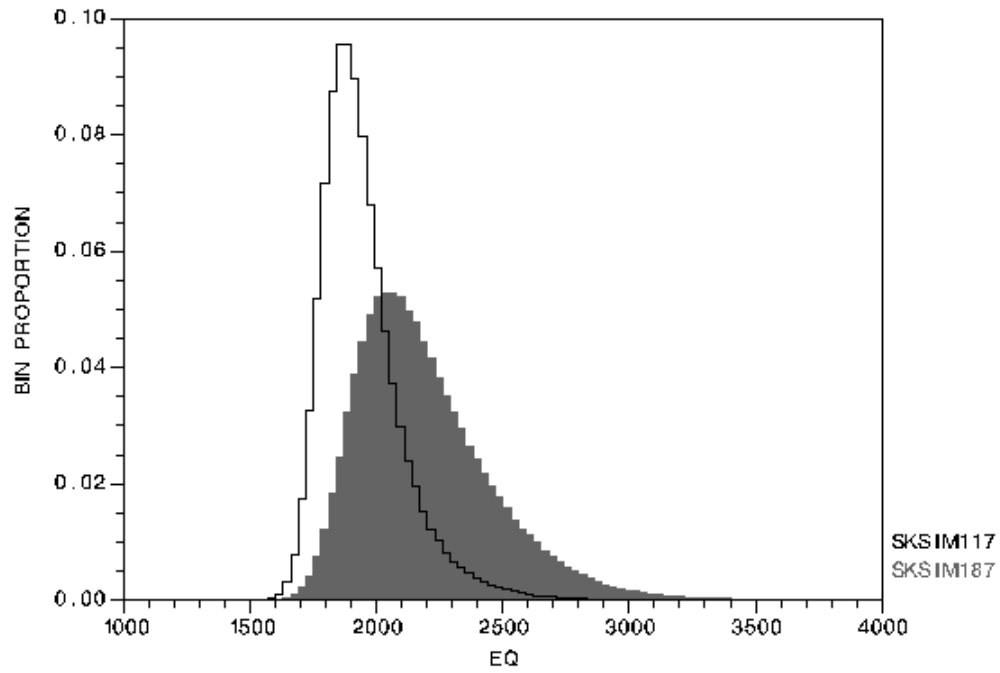


Figure 17. Posterior distribution of the S-K alpha for data set #4 overlaid on the informative $\text{Gamma}(24.1664, 0.3092)$ prior distribution.

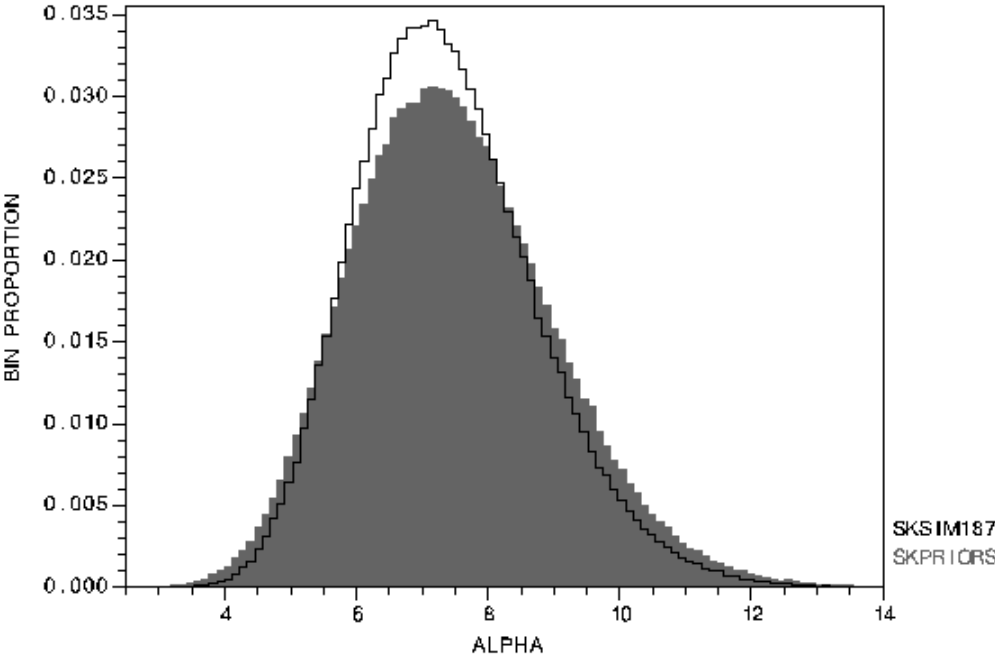


Figure 18. Posterior distribution of the S-K alpha for data set #6 overlaid on the informative $\text{Gamma}(24.1664, 0.3092)$ prior distribution.

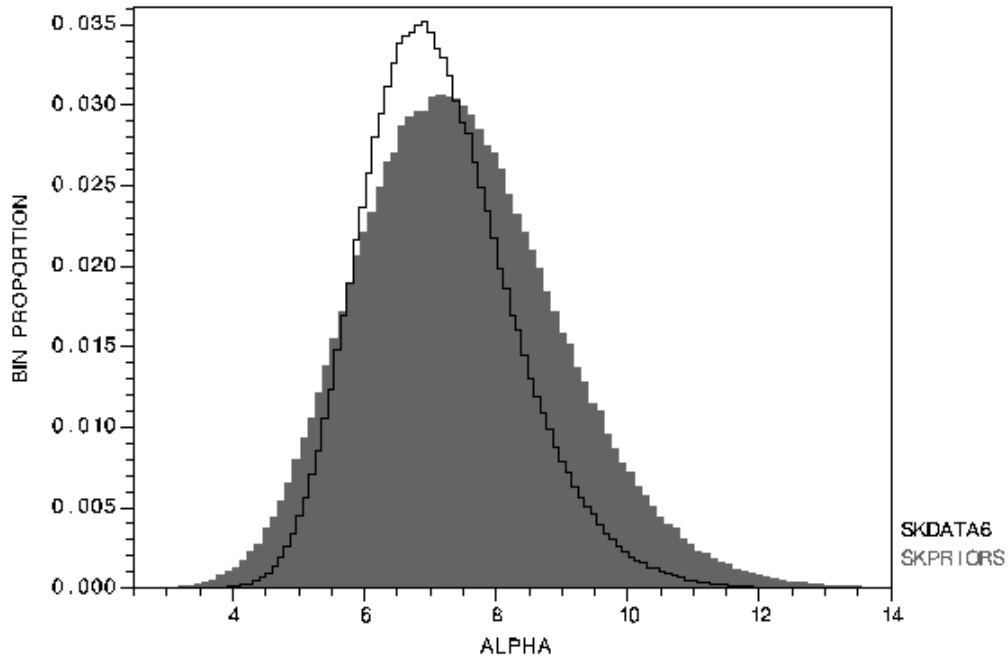


Figure 19. The posterior distribution of the equilibrium (EQ) for the fit of the Ricker model to data sets #6 (black line) and #2 (grey fill). Values are in thousands.

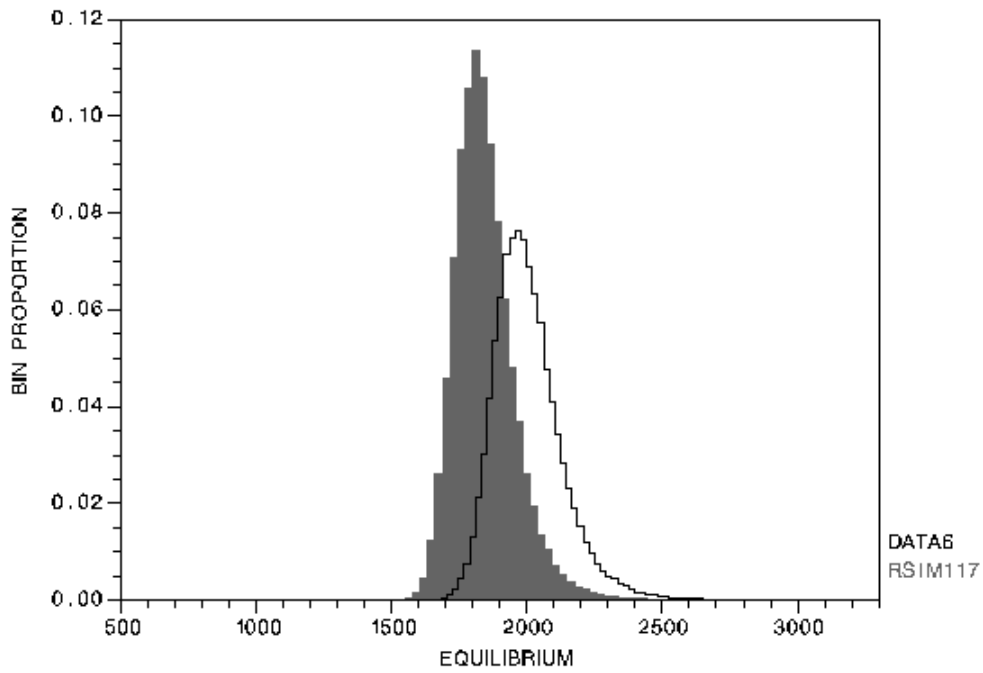
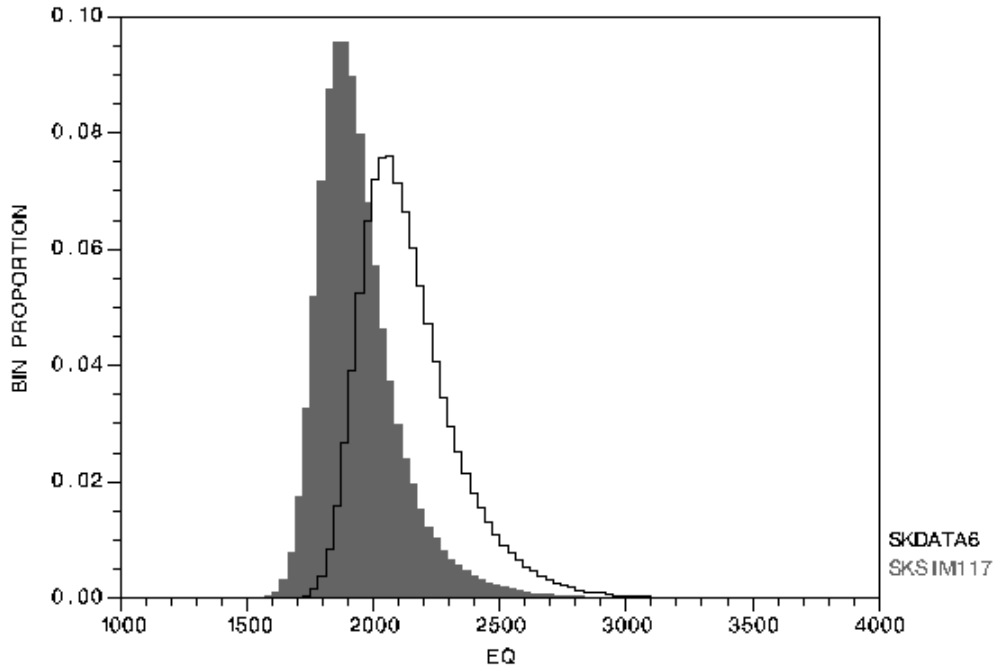


Figure 20. The posterior distribution of the equilibrium (EQ) for the fit of the Schnute-Kronlund model to data sets #6 (black line) and #2 (grey fill). Values are in thousands.



CHAPTER SIX.
Estimation of the Historical and Current Chum Salmon
Habitat Capacity of the Skeena River

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December 21, 2015

ABSTRACT

Estimating the production potential of depressed wild anadromous salmon in large river systems is challenging in the absence of extensive, costly, and long-term empirical studies; yet, a defensible estimate is critical for developing risk-averse objectives towards rebuilding diminished populations. This Chapter examines the production potential of Skeena River chum salmon (*Oncorhynchus keta*), a population currently in decline and of high conservation concern, by combining historical adult abundance estimates with remote-sensing-based estimates of freshwater habitat abundance. The link between historical adult abundance and freshwater habitat is provided by an age-structured life-cycle model parameterized by a combination of historical information and allometric modeling. The results show that only 4% of rearing habitat historically available to Skeena chum has been subsequently lost. The life-cycle model estimated that 13,300,000 juveniles were required to produce the equilibrium historical adult abundance of 312,000 in 1919, which corresponds to 0.99 juveniles/m² of floodplain habitat. If freshwater habitat is as productive as in 1919, the current annual production potential for juvenile chum of the Skeena is 12,800,000. Assuming suitable ocean rearing capacity, cohort smolt-to-adult survival of between 0.5% and 2.3% should return 64,000 to 294,000 adults annually, which is substantially different than current annual returns of less than 9,000. The disparity may be due to overfishing, loss of riverine fertility, competition with hatchery fish, depensatory effects, or reduced ocean productivity; all of which may be ameliorated by managing fisheries in relation to production potential. The results provide novel insight into the recovery potential of Skeena River chum, and add an important tool to the recovery science toolbox for wild salmon and their natal rivers worldwide.

INTRODUCTION.

As described in Chapter 1, among the critical issues in developing strategies to rebuild salmon populations is to identify the levels of abundance and life-history diversity that a population should attain in order to assure its long-term persistence. In previous chapters I noted the recent interest and efforts to estimate the historical abundance of several salmon and steelhead populations. In Chapters 3 and 4, I provided estimates of historical Skeena River chum salmon and Stillaguamish River steelhead populations and showed them to be considerably larger than their current counterparts, and I showed that the declines in these two populations are of a considerably greater magnitude than estimates of the associated extent of loss of spawning or rearing habitats. It remains to consider further of what value to conservation planning and current salmon management such estimates of historical adult abundance have. In this chapter, I address this key issue by showing how the historical estimate of the abundance of Skeena chum circa 1920 may be applied to assist in the development of benchmarks for Skeena chum conservation units (CUs).

I first develop a life-cycle model for Skeena River chum salmon in order to estimate the number of juvenile chum salmon (smolts) that would most likely have been required to produce the equilibrium abundance of adult chum salmon in 1916 – 1919 (circa 1920) as estimated in Chapter 3 and by Price et al. (2013). Next, I describe the estimation of the amount of floodplain rearing habitat area in the Skeena River that was accessible to chum salmon circa 1920 and the proportion of that habitat area remaining today. This estimation is based on remote sensing data for the Skeena from the Riverscape Analysis Project (RAP) database developed by the Flathead Lake Biological Station (available at <http://rap.ntsg.umt.edu/>). I then scale the estimated equilibrium number of chum smolts circa 1920 to the estimated floodplain rearing area accessible to chum salmon at that time to provide an index of the per-unit-rearing habitat area capacity of the Skeena for producing chum salmon. I then describe how the capacity index can be applied to the estimated amount of currently available floodplain rearing area to facilitate the development of benchmarks for Skeena chum salmon conservation units (CUs) described in Chapter 3.

The results show that only 4% of rearing habitat available to Skeena chum circa 1920 has been subsequently lost. The life-cycle model estimates that 13,300,000 juveniles were required to produce the equilibrium adult abundance circa 1920 of 312,000 produced from non-estuary spawning areas, which corresponds to 0.99 juveniles/m² of floodplain habitat. If freshwater habitat is as productive as in 1919, the current annual production potential for juvenile chum of the Skeena is 12,800,000. Assuming suitable ocean rearing capacity, cohort smolt-to-adult survival of between 0.5% and 2.3% should return 64,000 to 294,000 adults annually, which is substantially greater than current annual returns of less than 9,000.

METHODS.

Life-cycle model.

The life-cycle model is an age-structured matrix model that uses annual time steps. The model is deterministic and explores the life-history of chum salmon under an average set of environmental conditions that affect age-specific survival and fertility. I modeled females only and assumed a 1:1 sex ratio with four mature age classes (3–6), which generally reflects the life history of Skeena River chum salmon (Ricker 1980, Salo 1991). When total numbers of adults are required, I double the numbers produced by the model for the relevant age(s) or stage(s) of interest. Unlike many other historical salmon populations, there is a surprising amount of useful information available for Skeena and North Coast British Columbia chum salmon that I was able to use to develop the model. I chose to rely as much as possible on this data to parameterize the model so as to keep reliance on general life-history data to a minimum.

Fecundity (eggs/female) is treated as age-specific with values based on Beacham (1982) and length-at-age data applicable to Skeena chum salmon based on data in Ricker (1964, 1980; Table 1). I based the age composition of mature adults on historical information applicable to Skeena chum reported in Pritchard (1943). I define “smolts” as juveniles up to the time they depart the estuary to rear in the open ocean environment, at approximately one-to-two months of age (Salo 1991).

Age-specific post-smolt survival is treated as density-independent. While I include females only in the projection model, I made full use of the length-at-age data for both sexes that were available from Ricker (1980). I applied an allometric growth-mortality model to estimate the marine mortality of each sex separately for each age-at-maturity, and then averaged the annual marine mortality rates of each age-at-maturity between the two sexes to create the age-specific survival rates of adults used in the projection model.

Density-dependence is assumed to occur in freshwater between spawning/egg deposition and smolt entry to the estuary. I chose not to attempt to locate density-dependence more finely within the spawner-to-smolt life-cycle due to lack of data, nor did I attempt to estimate the actual form of density-dependence. While I believe that it is possible to estimate the form of density-dependence for chum salmon as well as for species such as stream-type Chinook and coho salmon and steelhead that are well-known to rear in freshwater for one or more years before migrating to the ocean (see, e.g. Chapter 7), there is a significant lack of data regarding the freshwater residence time of post-emergent chum salmon in large rivers. This not only makes it difficult to detect the existence of density-dependence, much less its form, but makes any attempt to model density-dependence prior to estuary residence highly controversial.

For the immediate purpose of the life-cycle modeling exercise, however, this is not necessary. Rather, I aim to achieve the more limited objective of an egg-to-smolt survival estimate that corresponds to the historical estimate of the unfished equilibrium adult abundance. This is accomplished by: i) estimating the total egg deposition from the equilibrium number, age-composition, and age-specific fecundity of female spawners, and ii) estimating the total number of smolts required to produce the equilibrium number of total returning adults (males and females). The model consisted of 13 stages, including four stages without associated transition rates that account for age-specific harvest of returning adults. All modeling was conducted in Matlab[®] 7.10 (The Mathworks 2010).

Before describing the details of the development of the model, I provide a brief description of chum salmon life history to provide context for some of the modeling choices I make.

Chum salmon life history.

Chum salmon (*Oncorhynchus keta*) spawn primarily in lower gradient reaches on main channels of large (sixth-order and larger) rivers and large (fourth-order and higher) tributaries, and in side- and off-channel floodplain habitats characterized by moderate-sized gravels and groundwater intrusion (Salo 1991, Kuzishchin et al. 2010, Mouw et al. 2013). In rivers of northern British Columbia, chum spawn in the early to late fall, and juvenile fry generally emerge in April at ~ 35 mm length (fork-length; FL), and ~ 0.35 g mass (Beacham and Murray 1985, 1987, Salo 1991). Emergent fry disperse from spawning sites and rear for a period of days to up to one month in freshwater shallow shoreline and floodplain habitats, followed by downstream migration to estuarine habitats, which they enter from May to June. Following a brief period of near-shore rearing, fingerling chum smolts (~ 65 mm FL or longer) migrate to open marine waters by July, where they grow rapidly; the bulk of their first year growth increment is attained by November. Most adults mature at the beginning of their third, fourth, or fifth year, though a small percentage may mature at the beginning of their sixth year, and ocean growth is complete by the late spring of their final year (Salo 1991). In the Skeena River, adult chum return to freshwater from mid-July through September, and spawn from September to November (Gottesfeld and Rabnett 2008). Early-run chum preferentially spawn in shallow shoreline habitat and deeper areas of the main channel with suitable current velocities and substrate size at locations, such as riffle crests, that are characterized by strong downwelling; late-run spawners prefer floodplain springbrook channels characterized by strong upwelling (Kuzishchin et al. 2010, Mouw et al. 2013).

Skeena chum life-cycle model

Skeena chum salmon mature at ages 3 to 6 (Ricker 1980). I followed the nomenclature adopted by Ricker (1964, 1976, 1980), whereby the age-designation refers to the age a fish would be if it survives to complete its current year of life. For example, a spawning adult of age-5 would have

experienced four ocean winters and be approximately halfway through its fifth year of life. For parent spawning year 2000, the fish would have emerged from the gravel by April 2001 and returned as a mature adult of age-5 in the fall of 2005. Smolts are therefore treated in the model as age-1: the age that surviving smolts will attain in the spring of the year following their entry into saltwater, and their first summer and fall of marine growth. The projection matrix contained 13 stages: two juvenile stages (smolts of age 1 and juveniles of age 2), three stages for adult ages 3 to 5 to account for immature fish (I), matures that survive to spawn (S), matures that are harvested during spawning migration but before they are able to spawn (H), and two stages for adults age-6, which is the maximum age of maturation (S and H; Table 1).

Age-specific fecundity and all post-smolt life-stage transitions were treated as density-independent constants. I determined age-specific density-independent mortality from sex-specific growth and length-at-age data, as described in section iv below. I assumed that density-dependence occurred in the stage between egg deposition and near-shore (smolt) emigration. Further description of the form or location of density-dependence within the egg-to-smolt stage was deemed unnecessary because the analysis was confined to conditions of equilibrium abundance. Thus, the equilibrium density-dependent egg-to-smolt survival rate was simply estimated from the estimates of equilibrium egg deposition and smolt abundance. Age-specific fertility (F_x) is treated as the number of female age-1 juveniles produced by each female of age x , where x equals 3 to 6. Therefore, density-dependent survival was incorporated into age-specific fertility values, which is the product of fecundity (number of eggs per age x female), the density-dependent egg-to-smolt survival rate, sex-ratio, and density-independent smolt-to-age-1 juvenile survival rate. Age-specific fecundity values, age-specific proportions in the adult return and parameter values for all life-stage transitions are shown in Table 2.

Determination of smolt size and emergent fry-to-smolt growth rate.

Based on length-weight regressions reported in Ricker (1980), I used the following equation to estimate weights for both sexes:

$$\text{Ln}(W) = 3.2 * \text{Ln}(\text{FL}) - 12.5, \tag{1}$$

where W is weight in grams, FL is fork-length in millimeters, and Ln is the natural logarithm. Transformed from log space,

$$W = 0.000003727 * FL^{3.2}. \quad (2)$$

I used an average weight for newly emerged chum salmon fry of 0.35 g based on data from Beacham and Murray (1985, 1987), which corresponds to a fork-length of 36 mm based on the allometry of equation [1]. I used an average smolt weight of 2.4 g based on a mean smolt length of 65mm and equation [1], which I determined to be a reasonable mean length based on data from Salo (1991). To check the appropriateness of the estimate of smolt weight, I determined the length of time in days required to reach the target smolt weight from a starting weight of 0.35 g. by applying the time integrated growth-in-weight equation described by McGurk (1996), explained in section vi below (equation [6]) with the parameters ($a = 0.05$, $b = 0.33$) estimated for the life-cycle model). A weight of 1 g is attained in 18 days, and the weight of 2.4 g is attained in the following 20 days. Thus, a total of 38 days is required to attain the target smolt size from the emergence of fry from spawning gravel, consistent with the data for the early life history of chum salmon in northern British Columbia (Salo 1991, Pauley et al 1988, Martin et al 1986).

Determination of marine size and growth rates.

A single sex-averaged length and weight for each post-smolt age was estimated from available historical data on sex-specific size-at-age and age-specific annual growth rates for the life-cycle projection model. I relied on two primary data sources to estimate growth in length: i) historical data from Skeena River chum reported by Ricker (1980), and ii) annual growth-in-length data from coastal British Columbia chum reported by Ricker (1964). Lengths-at-age for each sex were based largely on the average length data for mature Skeena chum ages 3 to 5 for the years 1957–1972 reported in Ricker (1980). The data reported by Ricker (1964, 1976) showed that chum salmon have different marine growth trajectories depending on sex and age-at-maturation, which is reflective of the strong sexual dimorphism typical of the species. Younger-maturing fish

grow faster in their first two years in the ocean, and annual growth (increase-in-length) rates decrease as fish age, though at different rates depending on the age-at-maturity.

Given four ages of maturity, eight growth trajectories (four per sex) had to be averaged so as to estimate average model lengths for the two post-smolt juvenile ages: one, and two (Table 2). Once the first age-at-maturity (age 3) is reached, the model sizes-at-age are the sex-averaged sizes of each age-at-maturity. These lengths are the final column entries in the last four rows under the heading “Combined” in Table 3, indicated with the superscript “c”. These lengths were then used to calculate the average weight of the modeled adult population during the historical period of interest (1916–1919) from equation [1], as described below.

Ricker (1964) noted that the instantaneous rate of growth in weight g_i for a fish of age i can be calculated from the annual increase in length, and the length exponent of weight b (3.2 for chum), as $g_i = b \cdot \ln(L_i/L_{i-1})$, where L_i is the fork length at age i . The sex-specific and sex-averaged (combined) lengths-at-age of chum and the associated instantaneous rates of increase in weight (g_i) are listed in Table 3. The combined lengths for the mature ages (3 to 6) were used to calculate the weights-at-age in the life cycle model shown in Table 1. The average of these weights when weighted by the age-specific proportions of age-at-maturity is identical to the target average weight of 14.0 pounds noted in Chapter 3.

To estimate the lengths-at-age of the two immature ages of the model, the combined lengths of each age-at-maturity were first averaged by weighting the age- x ($x= 1$ or 2) lengths of each age-at-maturity in proportion to its maturation rate. For example, the combined (sex-averaged) age-1 lengths (L_1) for fish maturing at ages 3 to 6 are 265 mm, 255 mm, 240 mm, and 220 mm, respectively (Table 3). Weighting each length by the respective maturation proportions from Table 1 we obtain $L_1 = (265 \cdot 0.215 + 255 \cdot 0.433 + 240 \cdot 0.317 + 220 \cdot 0.035) = 251$ mm. Similar calculations applied to the length of age-2 yield a model average length-at-age-2, $L_2 = 465$ mm. The average length for age 2 (465 mm) yielded values of g_3 for $L_3 = 709$ mm (Table 3), which is significantly greater than g_3 values for British Columbia chum reported in Ricker (1964). To achieve a value of g_3 between L_2 and L_3 (i.e., closer to the values in Ricker (1964)), L_2 was adjusted upward to 490 mm. Because this produced a value of g_2 that was slightly higher than in

Ricker (1964), L_1 was increased to 260 mm. Ultimately, a reasonable set of annual weight increments, g , was obtained across all model ages, so that the sex-averaged model lengths-at-age are a reasonable average of the sex- and age-specific differences in size and growth rate.

Determination of fecundity.

I used the following formula estimated by Beacham (1982) for samples of Skeena chum collected from 1974-1976 to calculate the age-specific fecundity of females:

$$\text{Egg\#} = 7.38 * \text{length} - 1032, \quad (3)$$

where length is postorbital-hypural (POH) length in millimeters. The above equation was applied to the modeled length of mature females in Table 3 to determine the age-specific fecundity in the model after first transforming fork-lengths to POH lengths using the formula: $\text{POH (mm)} = \text{FL(mm)}/1.25$ (Ricker 1980). The age composition of the terminal run of Skeena chum during the historical period of interest (1916–1919) was based on data for British Columbia chum salmon for the years 1916–1942 from Pritchard (1943; Table 1). The weight of mature fish (L_3 to L_6) used in the model was calculated by applying equation [2] to the sex-averaged (combined) lengths reported in Table 3.

Estimation of age-specific density-independent marine survival rates.

I applied the allometric marine growth and survival model of McGurk (1996) to the length data in Table 3 to estimate age-specific annual density-independent marine survival rates for the life-cycle model. McGurk (1996) developed an equation (equation [6] in McGurk (1996), equation [8] below) to estimate marine mortality of salmon based on the allometries of growth and size-specific mortality. Given information on size-at-age and estimates of parameters governing the allometries of growth and size-specific mortality, instantaneous mortality and survival (and thus mortality and survival over a finite interval of time) can be estimated.

Let the mortality rate M , and the growth rate G , both be described by power functions of body weight, as follows:

$$M = cW^{-x}, \quad (4)$$

$$G = aW^b. \quad (5)$$

Equation [5] can be integrated with respect to time t , to yield:

$$W_t = (W_0^b + abt)^{1/b}, \quad (6)$$

where W_0 is initial weight. Equation [6] can then be combined with equation [4] to yield McGurk's (1996) equation [5]:

$$\text{Ln}(s) = \text{Ln}(W_{t+1}/W_t) = -(c/(a(b-x)))(W_{t+1}^{b-x} - W_t^{b-x}), \quad (7)$$

where $\text{Ln}(s)$ is the log annual survival rate. The coefficients a and c are the instantaneous daily growth and mortality rates, respectively, at a weight of 1 g, and b and x are the weight exponents of growth and mortality, respectively.

Equation [7] can then be rearranged to yield McGurk's (1996) equation [6]:

$$\text{Ln}(s) = -(\alpha/\beta)(W_{t+1}^\beta - W_t^\beta), \quad (8)$$

where $\alpha = c/a$ and $\beta = b-x$.

McGurk (1996) hypothesized that the weight exponents b and x are likely to have values that are very close to one another, with b ranging from 0.25 to 0.45. If true, then the coefficient of mortality c must be smaller in absolute value than the growth coefficient a if the biomass of a cohort is to increase with age. McGurk (1996) further hypothesized that within species and populations, c is a constant proportion, α (alpha), of a , greater than 0 and less than 1; $c = \alpha a$.

McGurk (1996) then fit equation [8] to smolt weight and smolt-to-adult survival data for a combination of data from several species of salmonids, including chum, and obtained estimates of $\alpha = 0.528 \pm$ one standard deviation (sd) of 0.490, and $\beta = -0.053 \pm$ one sd of 0.221.

McGurk (1996) had three data points for chum salmon, all from southern British Columbia populations, and all included smolt size measured as size-at-emergence (average weight = 0.36 g). I modeled Skeena chum salmon smolts at 1 to 2 months of age, 65 mm, and 2.4 g. I chose parameter values that were close to those estimated by McGurk (1996) by assuming a value of the growth exponent, $b = 0.33$, and mortality exponent, $x = 0.38$, which results in a value of the derived parameter $\beta = -0.05$. Rather than use the point estimate of McGurk (1996) for growth coefficient parameter α , I estimated the growth and mortality rate coefficients, a and c , separately by first choosing a value of a that would achieve growth of a post-emergent chum fry from a weight of 1 g to 2.4 g in $t = 20$ days as described above. Given the value of $b = 0.33$, this was achieved by a value of $a = 0.05$. I then evaluated a conservative value of $c = 0.03$, which is equivalent to a value of McGurk (1996)'s $\alpha = 0.6$, slightly larger than the point estimate of 0.528 but well within the range of variability for the parameter reported by McGurk (1996). These parameter values produce reasonable results for the estimates of age- and size-sex-specific annual marine survival rates.

The parameterization of the McGurk (1996) model was then used to calculate age-specific survival rates separately for each sex and sex-specific growth trajectory of each age-at-maturity shown in Table 3. Results of these calculations are shown in Table 4.

Average age- and sex-specific survival rates were calculated by weighting each age-at-maturation trajectory by its proportion in the terminal run (Table 2). For example, survival from age-1 to age-2 of all males was averaged from the survivals of males maturing at age-3 (65 mm to 265 mm), males maturing at age-4 (65 mm to 255 mm), males maturing at age-5 (65 mm to 240 mm), and males maturing at age-6 (65 mm to 220 mm). To calculate the annual survival rate of males maturing later than age-3, the earlier ages-at-maturity were removed from the calculation of these averages, and the weighting was adjusted by rescaling the remaining age-specific maturation proportions in the terminal run to sum to one. Finally, Each of the sex-

specific weighted average marine survival rates of each age were averaged together, weighting each sex equally given the 1:1 sex ratio, to produce the age-specific survival rates used in the life-cycle model (Table 5).

Modeled historical scenarios.

To encompass the range of uncertainty in the estimate of the historical abundance of Skeena chum salmon, I estimated the smolt production corresponding to the posterior mode, and the posterior fifth- and ninety-fifth percentiles of the estimated terminal run of Skeena chum for the period 1916–1919. The posterior mode was 325,000 based on the geometric mean annual catch of 154,000 (Argue and Shepard 2005), the posterior fifth and ninety-fifth percentiles were 297,000 and 408,000, respectively. These numbers included chum produced by small streams that emptied directly into the Skeena estuary. Because habitat data required to estimate juvenile production in the estuarine segment is not available, I used a revised average catch and historical abundance estimate specific to the Skeena River and associated tributaries exclusive of the Skeena estuary. I estimated this by subtracting from the posterior mode of the run estimated run (325,000) the 13,000 estimated to have been the proportion produced by estuary tributary production (Chapter 3, Table 3) and adjusting the catch and the other posterior quantities accordingly. This resulted in an estimated catch of 147,840, and total returns of 312,000, 285,000 and 392,000 for the mode, fifth, and ninety-fifth percentiles, respectively. The smolt production required to achieve each of these revised historical numbers was then estimated from the life-cycle model, under the conservative assumption (Chapter 3, Price et al. 2013) that the catch was obtained from a population at or near its unfished equilibrium abundance, which may or may not have been sustainable on a long-term basis.

Modeling juvenile rearing habitat.

To estimate main channel and floodplain rearing habitat areas of the Skeena currently accessible to, and historically utilized by, chum salmon I used data from the RAP project database (Whited

et al. 2012, 2013) provided to me for this project by Diane Whited at the Flathead Lake Biological Station. The RAP database is derived from a regional classification and analysis of riverine floodplain physical features that represent key attributes of salmon rearing habitats. Riverine habitat classifications, including floodplain area and river channel complexity, were derived at moderate (30 m) spatial resolution using multispectral Landsat imagery and global terrain data (90 m) encompassing over 3,400,000 km² and most NPR salmon rivers. Similar classifications were derived using finer scale (i.e., ≤ 2.4 m resolution) remote sensing data over a smaller set of 31 regionally representative flood plains that included the Skeena. A suite of physical habitat metrics (e.g., channel sinuosity, nodes, floodplain width) were derived from each data set and used to assess the congruence between similar habitat features at the different spatial scales, and to evaluate the utility of moderate-scale geospatial data for determining abundance of selected juvenile salmon habitats relative to fine-scale remote sensing measurements. The resulting habitat metrics corresponded favorably ($R^2 > 0.5$, $p < 0.0001$) between the moderate-scale and the fine-scale floodplain classifications (Whited et al. 2013). The strong correlation of moderate-scale remotely-sensed habitat metrics to fine-scale classifications enable the abundance and distribution of three critical shallow water floodplain habitats (parafluvial springbrooks, orthofluvial springbrooks, and shallow shoreline; sensu Stanford et al. 2005), to be estimated across the entire NPR domain (Whited et al. 2013). Both moderate- and fine-scale measurements of Skeena floodplain habitat from the RAP database were used.

Main channel segments and major tributaries of the Skeena River were identified following Gottesfeld and Rabnett (2008). The total area (m²) for each main channel segment and major tributary was calculated for the following categories: total floodplain, floodplain water inundation, main channel, shallow shoreline (SS), parafluvial springbrook (PF), and orthofluvial springbrook (OF); all areas of which were calculated at base-flow discharge. Shallow shoreline, PF, and OF habitats were defined following Stanford et al. (2005): SS is the area of the main river channel adjacent to the bank and extending out to a depth of 0.5 m with current velocities equal to or less than 0.5 m/s, PF is the area of the floodplain that is annually scoured by flooding and inundated frequently by bankfull or higher flows, and OF is the older, more stable, and primarily depositional area of the floodplain that is inundated infrequently by large floods with

long (multidecadal) recurrence intervals. These habitats provide the majority of the riverine rearing habitat for juvenile salmonids, such as chum, that migrate to sea soon after emergence from redds, and serve as a surrogate measure of finer scale freshwater habitats (Whited et al. 2003, 2013). Accordingly, the amount of this area that is available to, and useable by, juveniles for freshwater rearing will constitute a key control on the total capacity of the river system to produce chum.

The Skeena River basin and component subbasins as delineated by Gottesfeld & Rabnett (2008) are shown in Figure 1. To simplify the presentation of the rearing habitat data, historical and current chum production regions of the Skeena were aggregated into the following 3 segments: lower Skeena (subbasins 1–5, including the Skeena River main channel downstream of the confluence of Lakelse River); middle Skeena (sub-basins 6–9, 11, and 13, including the Skeena River main channel from Babine River confluence to the confluence of Lakelse River); and upper Skeena (sub-basins 12, 14, and 15, including the Skeena River main channel from the confluence of Sustut River to the confluence of Babine River).

Loss of historical rearing habitat

Two major periods of infrastructure development resulted in loss of floodplain rearing habitat for chum along the lower and middle reaches of the mainstem of the Skeena River's. Railroad construction along the Skeena from the confluence with the Bulkley River downstream to Prince Rupert at the Skeena estuary occurred between 1910 and 1914, approximately one generation prior to the period for which Price et al. (2013) estimated adult chum abundance. Highway development along this same corridor occurred post-1920. Consequently, we assume that the loss of habitat affecting chum salmon today relative to the amount of habitat available in 1920 is the loss due to post-1920 highway development only. To provide a complete perspective on the loss of floodplain habitat in the Skeena, both the loss due to railroad development from 1910 to 1914, and the additional loss due to highway development post-1920 were estimated. This loss was confined entirely to the main channel reaches of the lower Skeena (from Terrace to Prince Rupert), and middle Skeena south (from the mouth of the Bulkley River to Terrace). Floodplain

rearing area in these two reaches today constitutes 59% of the total floodplain area available in all reaches accessible to chum circa 1920.

To estimate the amount of rearing habitat that was accessible in the two main channel reaches pre-1910 and ~1920 (RAh1910 and RAh1920; the periods before and immediately the 1916–1919 historical period of interest, respectively), I assumed that the total amount of floodplain rearing habitat (RA) in each reach bears a constant proportion to the total amount of floodplain area (FA) in each reach. Whited estimated the total amount of floodplain area in the lower Skeena and middle Skeena south main channel reaches prior to railway (FAh1910), or impermeable roads (FAh1920) which eliminated some habitat during 1910–1914 and post-1920, and compared that to the total area in the two reaches present today (FAc). Then, based on data provided by Whited, I calculated the ratio of the total rearing area in the two mainstem reaches available today ($RAc = SS + PF + OF$) to total floodplain area in those reaches available today (RAc/FAc), and expanded RAc by the ratios $FAh1910/FAc$ and $FAh1920/FAc$ to obtain an estimate of RAh separately for pre- and post-railway development (RAh1910 and RAh1920, respectively), which is the total amount of floodplain rearing area available historically in the lower Skeena and middle Skeena south: $RAh1910 = RAc*(FAh1910/FAc)$ (and similarly for RAh1920).

RESULTS.

Life-cycle model

The life-cycle model was parameterized so as to reproduce the estimated historical age composition of the adult return and the corresponding average weight of 14.0 pounds. The modeled cohort smolt-to-adult survival rate that achieved this was 0.0234. This is the smolt-to-adult survival rate averaged over each of the four ages of maturity, which takes into account the age-specific maturation rates required to yield the estimated historical age composition of the adult return (Table 2, columns 6 and 7). At the posterior modal estimate of equilibrium adult abundance of 312,000, the geometric mean catch of 1916–1919 of 147,840 was achieved at a

harvest rate of 47%, which is the posterior mode of the historical harvest rate estimated in Chapter 3 and by Price et al. (2013). At an equilibrium abundance equal to the 5th percentile of the posterior distribution (285,000), the harvest rate would have been 52%. Finally, at the posterior 95th percentile abundance (392,000), the harvest rate would have been 38%. In all three cases, the equilibrium egg-to-smolt survival rate is 0.0247. The estimated equilibrium number of smolts corresponding to the posterior 5th percentile, mode, and 95th percentile, rounded to the nearest hundred thousand, is 12,200,000, 13,300,000, and 16,700,000, respectively.

Floodplain habitat loss

Analyses of the RAP data suggest that the loss of floodplain area in the lower and middle Skeena main channel downstream of the Bulkley River confluence was 27% and 19%, respectively, due to railway development between 1910 and 1914. Of what remained after railway intrusion (FAh1920), impermeable road development post-1920 resulted in an additional loss of floodplain area in these two segments of 3% and 33%, respectively. Combined, the total loss of floodplain area to the lower and middle Skeena due to transportation infrastructure is 29% and 45%, respectively, which equates to a total reduction in historical floodplain area in these two main channel segments from 322,000,000 m² pre-1914 to 217,000,000 m² post-1920.

The amount of productive floodplain rearing habitat for juvenile chum in the Skeena is roughly 3.2% of the total floodplain area, averaged over the lower, middle, and upper chum production segments. The total area of actual floodplain rearing habitat accessible to chum in the entire Skeena was reduced from RAh1910 = 16,436,352 m² to RAh1920 = 13,494,112 m² due to railway development during 1910-1914, and was further reduced to RAc = 12,970,697 m² post-1920 due to impermeable road development. The estimated rearing habitat currently accessible to chum in the Skeena for the lower, middle, and upper segments are: 9,383,346 m², 2,998,113 m², and 589,238 m², respectively (Figure 1). Significantly, 96% of the floodplain rearing habitat area of the lower and middle-south main channel segments of the Skeena accessible to chum during the period of Price et al. (2013)'s estimate of abundance (RAh1920) remains accessible today (12,970,697/13,492,112).

Habitat production.

Based on the available rearing habitat of the Skeena circa 1920 (RAh1920), the smolt production corresponding to the posterior 5th percentile, modal, and 95th percentile estimates of chum salmon equilibrium adult abundance equate to 0.90, 0.99, and 1.24 smolts/m² of accessible floodplain rearing habitat, respectively. The corresponding current annual smolt production potential of the Skeena based on the estimates of rearing habitat are 11,700,000, 12,800,000, and 16,100,000, respectively (Table 6).

Based on the age-structure and fecundity data used in the model, the egg-to-smolt (freshwater) survival rate is approximately 2.5% under equilibrium conditions. Combined with the cohort (marine) survival rate of 2.3%, the total cohort life-cycle (egg-to-adult) survival rate is 0.06%. Assuming the current cohort smolt-to-adult survival rate is within the range 0.5% to 2.3% (approximately 20% to 100% of the model-estimated rate of the circa 1920 equilibrium), and assuming that freshwater density-dependence is perfectly compensatory within this range so as to maintain the cohort egg-to-adult survival rate near 0.06%, the results suggest that the Skeena River catchment has the potential to produce a total annual return of chum salmon between 58,000 and 370,000 (Table 7). Based on the most probable value of 0.99 smolts/m² of baseflow rearing habitat and the posterior modal abundance estimate of 12,800,000 smolts under current habitat conditions, and given a range of cohort smolt-to-adult survival rates of 0.05% and 2.3%, current annual adult returns would be expected to be between 64,000 and 294,000 (Table 7).

DISCUSSION.

This study integrates estimation of historical salmon abundance with a state-of-the-art remote sensing-based quantification of rearing habitat area so as to estimate current adult chum production potential in a large river system. Separate estimates were obtained for freshwater (smolt) and ocean (returning adult) production potential, which permits managers and researchers to focus on possible limitations in freshwater production independent of the confounding effects of marine survival. Although some floodplain area was lost from the lower and middle Skeena during the early 1900s, the RAP analyses show that significant rearing

habitat remains in segments of the Skeena historically important for chum. These results provide novel insight into the recovery potential of Skeena River chum salmon—a species of high conservation concern—and underscores the value of the approach to salmon recovery plans.

The study illustrates the ability of the model-based approach to address the data shortcomings that are inherent in most contexts involving estimates of past abundance and salmon life-stage survival rates. Historical data pertaining to juvenile and adult survival rates for chum salmon are scarce; in fact, there are none for Skeena chum. Nor are there any estimates of total fry or smolt production that could be associated with returning adult cohort numbers to produce estimates of chum smolt-to-adult survival. But data deficiencies aside, the values used to parameterize the life-cycle model did not produce unrealistically large juvenile or adult survival rates. Regarding survival specifically, the model-estimated cohort smolt-to-adult survival rate of 2.3% is similar to values for other highly exploited Pacific salmon populations (Bradford 1995, McGurk 1996, Quinn 2005). Additionally, the model yielded annual adult survival rates that ranged from 75% to 90% (Table 2), which is consistent and generally equivalent to previous studies (e.g., Parker 1962, Ricker 1964, 1976), and typical of highly fecund fishes and other species with type III survival curves (Waples 2004).

However, rather than rely on these broad estimates, I estimated survival by applying a partially validated allometric model of salmon marine survival to available historical data on the size-at-age, age-at-maturation, and ocean growth of chum salmon along the north and central British Columbia coast. The fact that the model-estimated annual adult marine survival rates agreed well with the available literature values is support for the credibility of the McGurk model and the parameterization of the model that I employed. The availability of age-specific size and fecundity data, adult age-composition data, and average weight data of the commercial catch of Skeena chum salmon (Argue & Shepard 2005) supplied independent constraints on the parameterization of the life-cycle model that further constrained the parameterization of the McGurk model, but resulted in the selection of parameter values that were close to the mean values identified by McGurk(1996), further validating the appropriateness of the McGurk model for this kind of context.

Despite these strengths, questions may nonetheless be raised as to the appropriateness of measuring the production potential of chum salmon by floodplain rearing habitat area, given the fact that juvenile chum salmon spend very little time in freshwater following emergence from the gravel, and generally migrate to the estuary or nearshore marine environment within days of emergence. However, most of the data concerning post-emergence behavior of chum salmon in the available literature is from studies of small coastal streams a mile or two in length that enter directly into an estuary or the ocean (Salo 1991, Quinn 2005). Yet, many significant large populations of chum salmon are from large river systems, the most noteworthy being the Yukon River in Alaska/British Columbia and the Amur River in southeastern Russia/northeastern China, both over 2000 kilometers in length with chum salmon spawning populations present nearly their full lengths (Salo 1991, Quinn 2005). Chum salmon fry from most populations in these large rivers must have to spend some time rearing in shallow shoreline and floodplain habitats as they migrate downstream to the ocean if they are to survive. This is also likely to be the case to some extent over distances of 100 or more kilometers, such as in the Skeena which is greater than 500 km. long, and perhaps over even shorter distances.

Chum salmon have a relatively complex life history as revealed in part by multiple ages at maturity within populations. With regard to post-emergence freshwater residency the juvenile life history of chum appears to be intermediate between pink salmon (*Oncorhynchus gorbuscha*) and ocean-type Chinook salmon (*Oncorhynchus tshawytscha*). Pink salmon fry migrate downstream to saltwater within days or hours of emergence (Salo 1991, Quinn 2005). Ocean-type Chinook salmon fry exhibit up to four juvenile life histories (Reimers, 1973 (cited in Greene and Beechie, 2004), Salo 1991, Quinn 2005). Three of the four are likely to have counterparts in chum salmon: parr migrants that rear in freshwater shallow shoreline and floodplain habitats for one or more months before initiating downstream migration, slow fry migrants that rear for a period of one to several weeks as they migrate downstream, and fast fry migrants that migrate seaward within days of emergence and do little if any rearing as they migrate.

Skepticism regarding the significance of shallow shoreline and floodplain rearing habitat for chum may be warranted in the case of rapid fry migration, similar to pink salmon. It is less convincing if chum fry exhibit either of the other two behaviors, which does not appear unlikely

for populations in large rivers having to migrate distances of several tens or hundreds of kilometers or more. In a modeling study of the relative importance to juvenile ocean-type Chinook salmon of density-dependent mechanisms in freshwater and estuary/nearshore rearing habitats, Greene and Beechie (2004) showed that both the quantity and the quality of stream rearing habitats could be significant for the recruitment of ocean-type Chinook, depending on the mechanism of density-dependence (whether it caused a decrease in *in situ* survival or an increase in the rate of migration to downstream habitats) and the quantity and quality of downstream habitats. In particular, if density-dependent survival was weak or non-existent in the estuary/nearshore the quantity of stream rearing habitat could significantly restrict recruitment even if the time spent in stream rearing habitats was a relatively small proportion of the total time juveniles spent rearing prior to migrating to offshore marine habitats. So, it is not out of the question that the amount and quality of shallow shoreline and floodplain rearing habitat could cause density-dependent mortality in juvenile chum salmon.

It is also thought that density-dependence in chum salmon occurs during spawning and results from scramble competition for limited spawning habitat. This would produce Ricker-like stock recruit relationships. If data were available on the quantity of chum-suitable spawning habitat in the Skeena, it would have been important to have designed the life-cycle model to include Ricker-like density dependence in the egg-to-emergent fry transition. This would have permitted a more direct evaluation of whether or not the historical equilibrium abundance estimated in chapter 3 and by Price et al. (2013) was reasonable. However, as yet RAP is not capable of measuring spawning habitat area, which in any case is particularly challenging for chum salmon given their propensity for homing in on downwelling areas within areas of suitable spawning gravel in mainstem channels and upwelling areas in off-channel floodplain habitats (Kuszischin et al. 2010, Muow et al. 2013).

Valuable as this would undoubtedly be, in the case of the Skeena I hypothesize that density-dependent spawning is not likely to be significant because of the extensive amount of high-quality spawning habitat throughout the catchment, including accessible off-channel habitats. To evaluate this I scaled the estimated adult production from the historical abundance estimate to the

lengths of main channel associated with each floodplain rearing area of mainstem river segments of the RAP analysis.

The results support the hypothesis that spawning habitat is not likely to be limiting chum production in the Skeena. For example, the estimate of smolt production potential of $0.99/\text{m}^2$ based on the posterior mode of the estimate of Skeena chum abundance circa 1920 (Chapter 3, Price et al. 2013) produced estimates of the number of chum spawners (both sexes combined) per floodplain-associated-main-channel length that ranged from 170/km to 1,206/km and averaged 688/km for the chum production areas of the entire Skeena. For the high productivity estimate of $1.24 \text{ smolts}/\text{m}^2$, values ranged from 213/km to 1,510/km, and averaged 861 chum per kilometer. The low productivity estimate of $0.90/\text{m}^2$ yielded values from 155/km to 1,096/km with a mean of 625/km. These are comparable to values for chum salmon in rivers in Puget Sound, Hood Canal, and the coast of Washington State. Index counts for the period 1986 to 2003 in the Satsop River, a tributary to the Chehalis River, averaged 3,560/km; counts for the same period in Stevens Creek, a tributary to the Humptulips River, averaged 310/km (SASSI 2002). Minimum estimates based on total escapement data for 1986 to 2003, combined with estimates of the maximum lengths of total river channel available to chum spawners for the Skagit River and Skykomish River in Washington State, averaged 621/km and 713/km, respectively (SASSI 2002).

The Skeena catchment has experienced some habitat loss over the last century. The period from 1916 to 1919 occurs shortly after the building of the Grand Trunk Pacific Railway (1910–1914) on the north bank of the lower Skeena River, and on the south bank of the middle Skeena (Gottesfeld and Rabnett 2008). The historical period also occurs well before the development of an impermeable highway, which spans the Skeena valley in length from the mouth of the Skeena River to the confluence of the Bulkley River, and extends the entire length of the Bulkley. Both developments have effectively cut-off or impeded habitat suitable for chum, restricted or eliminated channel migration, and likely impaired floodplain function to some degree. Prior to 1910, there was an estimated 18% more floodplain rearing habitat in the lower and middle-south main channel segments than during the years immediately after; impermeable road development post-1920 has resulted in an additional 4% loss. Chum-accessible tributaries to the lower and

middle Skeena have also been affected by transportation infrastructure. The Zymoetz River is the most notable example where considerable floodplain area in the lower river was destroyed due to channelization and highway bridge repositioning in the 1970s and early 1980s, which is postulated to have had a negative effect on chum (Gottesfeld and Rabnett 2008).

Notwithstanding, the amount of rearing habitat loss to chum-accessible tributaries in the lower and middle Skeena due to transportation infrastructure is estimated to have been less than 2% of all floodplain chum-rearing habitat in the Skeena, and chum habitat in the upper Skeena has remained relatively unchanged. Transportation infrastructure in river valleys is known to disrupt the natural connectivity between main channel, floodplain, and surrounding landscape, and diminish the “shifting habitat mosaic” (Stanford et al. 2005) that creates and maintains the rich diversity of shallow water habitat important for salmon (Eberle and Stanford 2010). Specifically, transportation-impacted channels tend to be straighter, narrower, and contain fewer active depositional surfaces (such as bars, and islands), and railway and road structures disconnect floodplain habitat from water and nutrient supply (Blanton and Marcus 2013). While transportation developments have likely had the largest impact on salmon habitat in the Skeena, the analysis presented here indicates that roughly 78% of the historical (i.e., predevelopment) floodplain rearing habitat accessible to chum in the lower and middle main channel segments of the Skeena River (i.e., RAh1910) remains today. Importantly, 96% of the chum rearing habitat that was present in these main channel segments during the period of historical Skeena chum abundance estimated in Chapter 3 (RAh1920) is currently accessible, arguably more than sufficient for the recovery of currently diminished chum salmon.

The estimates of current freshwater rearing habitat available to Skeena chum are conservative. The amount of floodplain habitat area estimated from the RAP data is predicated on base-flow conditions, which occur in late summer. Chum fry emerge, rear briefly in freshwater, and migrate to the estuary by late spring when discharge and hence, floodplain habitat area, is much larger than during base-flow. Additionally, the focus of the habitat assessment is on the three regions of the Skeena that most likely accounted for chum production circa 1920. Because the historical estimate is based on chum abundance after 18% of main channel floodplain rearing

habitat had been lost, the true historical abundance may have been much greater. Chum also may have historically utilized areas of the Skeena that were omitted from the analyses.

Furthermore, the assessment does not include the Bulkley River (number 10 on Fig. 1), a major Skeena River tributary that was largely inaccessible to chum salmon in 1920. Anthropogenic alterations to natural passage obstructions at Hagwilget and Moricetown canyons in the Bulkley River during the 1920s and 1950s have recently opened access to species such as chum and pink salmon. Thus theoretically, there may be more rearing habitat available to chum than we have quantified. But whether chum can and will traverse the difficult canyon sections in the Bulkley remains to be seen.

Given the amount of accessible rearing habitat currently available for Skeena chum, it is evident that other factors beyond habitat area are limiting production. The estimate of current habitat combined with the estimates of per-unit-habitat area smolt production based on the analysis of Chapter 3 (also, Price et al. 2013) indicates that the three regions of the Skeena that most likely accounted for chum production circa 1920 have the potential to produce between 12 and 16 million out-migrant juvenile chum annually. If the cohort-to-adult survival rate is equal to the rate estimated by the life-cycle model for Skeena chum circa 1920 (i.e., 2.3%), 12 to 16 million smolts would produce between 269,000 and 370,000 adults annually (Table 3). Even under very poor ocean conditions (i.e., cohort smolt-to-adult = 0.5%), annual returns would range 58,000–80,000 (Table 3). These results are contingent, of course, on habitat productivity being similar to what existed historically (1916–1919). Despite a total adult recruitment of 353,000 chum in 1988 (English 2013), including an estimate of 166,000 spawners (Connors et al. 2013), Skeena chum have declined considerably over the last century. On average ~ 40,000 chum returned to the catchment annually during the contemporary period of 1980–2010, and <9,000 chum returned annually during the most recent period of 2007–2010 (English 2013, Chapter 3).

One explanation for the decline in Skeena chum over the last century may be the deterioration of habitat quality, which RAP cannot quantify. Human activities beyond floodplain transportation infrastructure, such as intense clear-cut logging and associated roads, mining, and urban development, have occurred throughout the Skeena, and have been particularly intense in the

lower and middle Skeena where chum spawning and rearing habitat is most plentiful (Gottesfeld and Rabnett 2008). However, based on a global assessment of relative impact from human populations derived from Sanderson et al. (2002), the influence of humans on habitat in the Skeena has been relatively low (Figure. 2). And compared to other salmon producing catchments of the North Pacific Rim, the current riverine habitat quality of the Skeena is considered moderately high (Whited et al. 2012).

One among several other plausible reasons for a recent reduction in Skeena chum productivity may be the loss of marine-derived nutrient inputs (i.e., salmon subsidies) due to fewer returning salmon. The fertility of the Skeena River and estuary has likely declined considerably owing to the more than 100 years of intense exploitation of most Skeena salmonids, and the subsequent reduction in nutrients that spawning salmon provide. The abundance and availability of freshwater invertebrate prey of juvenile salmonids have been shown to be strongly dependent on salmon subsidies (Kiffney et al. 2014); thus, a large reduction in returning spawners may diminish the production potential of rearing habitat otherwise endowed with large floodplain area and complexity. Estuaries in particular receive a large proportion of post-spawning salmon nutrients (Cak et al. 2008), and are important rearing areas for chum salmon during an assumed critical period in their life-history (Quinn 2005). Whether or not prey species of chum are of critically low abundance in the Skeena estuary due to fewer salmon subsidies remains an important research question.

Another possibility is that chum may be particularly susceptible to compensatory effects at low spawner densities, due perhaps to the occurrence of a predation trap sensu Peterman (1977) or other mechanisms that may operate in freshwater during spawning or early juvenile rearing as suggested by Parkinson (1990) for sockeye salmon, and reviewed more generally by Liermann and Hilborn (2001). Overcoming such an effect would require that the population attain some as yet unknown threshold population size and sustain it for some period of time. This effect is likely to be synergistic with the loss of marine-derived nutrients that would additionally impair juvenile survival.

Alternatively or synergistically, competitive effects from the increased abundance of hatchery fish rearing in the north Pacific may be negatively impacting Skeena chum (Price et al. 2013). There are assertions that hatchery chum rearing in the north Pacific are competing with, and have caused declines in, wild chum from Russia (Klovatch 2000, Zaporozhets and Zaporozhets 2004) and western Alaska (Ruggerone et al. 2010, 2012). The annual release of hatchery-produced chum from North America, Russia, and Asia could affect wild chum from the Skeena because salmon commonly share finite resources in the north Pacific.

The successful recovery of wild Skeena chum salmon will require an assessment of the primary factors currently limiting productivity and abundance, followed by the initiation of conservation measures aimed at reducing such factors. Rearing habitat area, at least in the Skeena River and its major tributaries, is not a limiting factor; floodplain habitat is sufficiently abundant to support near historical numbers of chum. Though as stated above, greatly reduced salmon subsidies may have diminished the production potential of this otherwise large and complex rearing habitat.

The results of this modeling effort suggests two important themes for investigation, the utilization of floodplain rearing habitats by juvenile chum salmon and the distribution of primary spawning areas in both the main channel and off-channel habitats. The first theme will need to be addressed by field studies of selected rearing habitats in the lower Skeena, first to verify presence of juvenile chum following emergence and second to determine rearing densities and the residence time. Initial results will need to be interpreted cautiously given the evidence that the Skeena is currently considerably under seeded. Further, the historic and current diversity of juvenile chum life histories is unknown as is the relative magnitude of each basic life history type if there are two or more types still present in the Skeena.

The second theme will need to be addressed by extensive field sampling of main channel and floodplain spawning habitats. Main channel habitats will likely require sampling by remote sensing technology such as Didson sonar that can identify numbers and body size of adult salmon in turbid water condition that are typical of the Skeena during late summer and early fall chum spawning.

Regardless of the investigation of these two themes, the results of the exercise of scaling estimated historical abundance of adult chum salmon returns to main channel segment lengths demonstrates that low to moderate spawner densities, measured as number of spawners per main channel segment length, would support a spawning population of more than 100,000. For example, the total length of the Lower and Middle Skeena combined (from the mouth to the confluence of the Babine River) including major tributaries used by chum salmon for spawning is 313 kilometers. At a spawner density of 600 adults/kilometer, which is lower than the estimated density associated with the posterior 5th percentile of the estimated historical abundance, the Lower and Middle Skeena would support 188,000 chum salmon spawners. The length of the Lower Skeena mainstem and tributaries alone is 268 kilometers, which would support 160,000 spawners at a mean density of 600/kilometer. These data alone might reasonably support interim target benchmark spawner numbers for the entire Skeena of 80,000 to 100,000.

Identification of these kinds of management targets for population benchmarks is one of the benefits of the kind of modeling effort undertaken in this Chapter. Identification of key themes for investigation regarding juvenile rearing habitat use and spawning location and distribution is another. These results show that it is possible to achieve a plausible integration of credible estimates of historical adult salmon abundance and life-cycle modeling that can be employed to provide direction for contemporary conservation management efforts. By grounding current conservation efforts in expectations shaped by historical population abundance conservation management will be more likely to insure against under-estimating the recovery potential of current populations, better identify the minimum levels of population abundance and life history diversity necessary to assure long-term persistence of recovered populations, and thereby guard against a myopic perspective of population abundance that results in management from a shifting baseline.

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TABLES.

Table 1. Model projection matrix used in the chum salmon life-cycle model.

<i>Stage_a</i>	<i>J1</i>	<i>J2</i>	<i>3S</i>	<i>3H</i>	<i>3I</i>	<i>4S</i>	<i>4H</i>	<i>4I</i>	<i>5S</i>	<i>5H</i>	<i>5I</i>	<i>6S</i>	<i>6H</i>
<i>J1</i>	-	-	F3	-	-	F4	-	-	F5	-	-	F6	-
<i>J2</i>	<i>s1^b</i>	-	-	-	-	-	-	-	-	-	-	-	-
<i>3S</i>	-	<i>s2*Pmat3*(1-H)</i>	-	-	-	-	-	-	-	-	-	-	-
<i>3H</i>	-	<i>s2*Pmat3*H</i>	-	-	-	-	-	-	-	-	-	-	-
<i>3I</i>	-	<i>s2*(1-Pmat3)</i>	-	-	-	-	-	-	-	-	-	-	-
<i>4S</i>	-	-	-	-	<i>s3*Pmat4*(1-H)</i>	-	-	-	-	-	-	-	-
<i>4H</i>	-	-	-	-	<i>s3*Pmat4*H</i>	-	-	-	-	-	-	-	-
<i>4I</i>	-	-	-	-	<i>s3*(1-Pmat4)</i>	-	-	-	-	-	-	-	-
<i>5S</i>	-	-	-	-	-	-	-	<i>s4*Pmat5*(1-H)</i>	-	-	-	-	-
<i>5H</i>	-	-	-	-	-	-	-	<i>s4*Pmat5*H</i>	-	-	-	-	-
<i>5I</i>	-	-	-	-	-	-	-	<i>s4*(1-Pmat5)</i>	-	-	-	-	-
<i>6S</i>	-	-	-	-	-	-	-	-	-	-	<i>s5*(1-H)</i>	-	-
<i>6H</i>	-	-	-	-	-	-	-	-	-	-	<i>s5*H</i>	-	-

^aStages: *Jx* = juvenile at age *x*, *xS* = mature age *x* surviving to spawn, *xH* = mature age *x* harvested, and *Ix* = immature age *x* remaining in the ocean and not subject to harvest. *Fx* = number of surviving age-1 offspring produced by a female age *x* spawner, *H* = harvest rate, *sx* = survival rate from age *x* to age *x+1*, and *Pmatx* = probability of an age *x-1* that survives to age *x* maturing.

^bTransitions are from the stage in the column of the transition rate entry to the stage in the row of the entry.

Table 2. Skeena River chum model life-stages, and size-at-age during density-independent rearing in the marine environment. Length is fork-length in millimeters; Survival Rate is the rate of survival from age x to age x+1; Proportion is the proportion of age at maturity.

<i>Stage</i>	<i>Stage name</i>	<i>Age</i>	<i>Length (mm)</i>	<i>Weight (g)</i>	<i>Survival Rate</i>	<i>Fecundity</i>	<i>Proportion</i>
0	Emerged smolt *	0	65	2.3	0.11		
1	Smolt	1	260	199	0.42		
2	Juvenile	2	490	1,513	0.67		
3	Mature spawner	3			0.79		
			709	4,936		3,121	0.215
4	Mature harvested	3	-	-	-		
5	Immature	3	-	-	-		
6	Mature spawner	4			0.87		
			767	6,348		3,483	0.433
7	Mature harvested	4	-	-	-		
8	Immature	4	-	-	-		
9	Mature spawner	5			0.88		
			797	7,178		3,630	0.317
10	Mature harvested	5	-	-	-		
11	Immature	5	-	-	-		
12	Mature spawner	6					
			814	7,679		3,674	0.035
13	Mature harvested	6	-	-			

* Stage, size, and weight at the end of the density-dependent rearing period in the estuary.

Table 3. Sex-specific, and averaged (Combined), model lengths-at-age of chum salmon maturing at ages 3 to 6.

<i>Age</i>	<i>L1^a</i>	<i>g2^b</i>	<i>L2</i>	<i>g3</i>	<i>L3</i>	<i>g4</i>	<i>L4</i>	<i>g5</i>	<i>L5</i>	<i>g6</i>	<i>L6</i>
Males											
3	265	2.10	511	1.10	720 ^c	-	-	-	-	-	-
4	255	2.05	484	0.95	651	0.55	773 ^c	-	-	-	-
5	240	2.00	448	0.95	603	0.60	728	0.33	807 ^c	-	-
6	220	1.90	398	0.98	541	0.65	663	0.40	751	0.33	833 ^c
Females											
3	265	2.05	503	1.05	698 ^c	-	-	-	-	-	-
4	255	1.90	462	1.00	631	0.60	761 ^c	-	-	-	-
5	240	1.80	421	1.00	576	0.65	705	0.35	787 ^c	-	-
6	220	1.75	380	0.95	512	0.70	637	0.38	717	0.33	795 ^c
Combined											
3	265	2.08	507	1.08	709 ^c	-	-	-	-	-	-
4	255	1.98	473	0.98	641	0.58	767 ^c	-	-	-	-
5	240	1.90	435	0.98	590	0.63	717	0.34	797 ^c	-	-
6	220	1.83	389	0.97	526	0.68	650	0.39	734	0.33	814 ^c

^a Lengths (*L1–L6*) are fork-lengths in millimeters.

^b Growth rates (*g2–g6*) are the instantaneous rates of weight increases.

^c Length-at-maturity.

Table 4. Sex-specific marine survival rates from length-at-aget-1 to aget (years) of model males and females maturing at ages 3 (L3) to 6 (L6).

<i>Model age</i>	<i>Male fork-length (mm)</i>	<i>Male survival rate</i>	<i>Female fork-length (mm)</i>	<i>Female survival rate</i>
L3				
0	65	-	65	-
1	265	0.0988	265	0.0988
2	511	0.4003	503	0.4087
3	720	0.6432	698	0.6550
L4				
0	65	-	65	-
1	255	0.1045	255	0.1045
2	484	0.4065	462	0.4326
3	651	0.6796	631	0.6645
4	773	0.8061	761	0.7898
L5				
0	65	-	65	-
1	240	0.1144	240	0.1144
2	448	0.4121	421	0.4484
3	603	0.6758	576	0.6590
4	728	0.7874	705	0.7726
5	807	0.8801	787	0.8720
L6				
0	65	-	65	-
1	220	0.1304	220	0.1304
2	398	0.4249	380	0.4529
3	541	0.6621	512	0.6678
4	663	0.7694	637	0.7529
5	751	0.8551	717	0.8610
6	833	0.8800	795	0.8796

Table 5. Sex-averaged marine survival rates from length-at-*aget* to *aget*+1 (years) of model chum salmon maturing at ages 3 to 6.

<i>Model age</i>	<i>Fork-length (mm)</i>	<i>P(L_{x-1} to L_x)^a</i>	<i>Survival rate abbreviation^b</i>
0	65	-	-
1	260	0.1073	s0
2	490	0.4204	s1
3	709 ^c	0.6654	s2
4	767 ^c	0.7891	s3
5	797 ^c	0.8743	s4
6	814 ^c	0.8798	s5

^a *P(L_{x-1} to L_x)* is the survival rate from length at stage *x-1* to length at age *x*.

^b Survival rate is from length at stage *x* to length at stage *x+1*.

^c Length-at-maturity.

Table 6. Estimated Skeena chum salmon smolt production circa 1920, and currently corresponding to the posterior mode and posterior 5th and 95th percentile equilibrium adult abundance estimated by Price et al. (2013).

<i>Posterior</i>	<i>Run/Spawners</i>	<i>Smolts 1920</i>	<i>Smolts/m^{2a}</i>	<i>Smolts Current^b</i>
5%	285,000	12,200,000	0.90	11,700,000
Mode	312,000	13,300,000	0.99	12,800,000
95%	392,000	16,700,000	1.24	16,100,000

^aSmolts/m² based on total floodplain rearing habitat accessible to chum circa 1920 of 13,494,000 m².

^bSmolts current is the number of smolts given the estimate of the total amount of floodplain habitat accessible to chum circa 1920 that is still available today of 12,971,000 m².

Table 7. Potential Skeena chum salmon adult returns based on estimated smolt production under current habitat conditions, and a range of cohort smolt-to-adult survival rates between a low of 0.5% and the life-cycle model-derived estimate of 2.3%. Smolt production numbers correspond to the posterior mode, 5th, and 95th percentile circa 1920 adult abundance estimates of Price et al. (2013) scaled to the proportion of total rearing habitat circa 1920 currently remaining.

<i>Cohort Smolt-to-Adult Survival Rate</i>	<i>Posterior 5th %-ile Smolt Production</i>	<i>Posterior Mode Smolt Production</i>	<i>Posterior 95th %-ile Smolt Production</i>
	11,700,000	12,800,000	16,100,000
0.005	58,500	64,000	80,500
0.01	117,000	128,000	161,000
0.015	175,500	192,000	241,500
0.02	234,000	256,000	322,000
0.023	269,100	294,400	370,300

FIGURES.

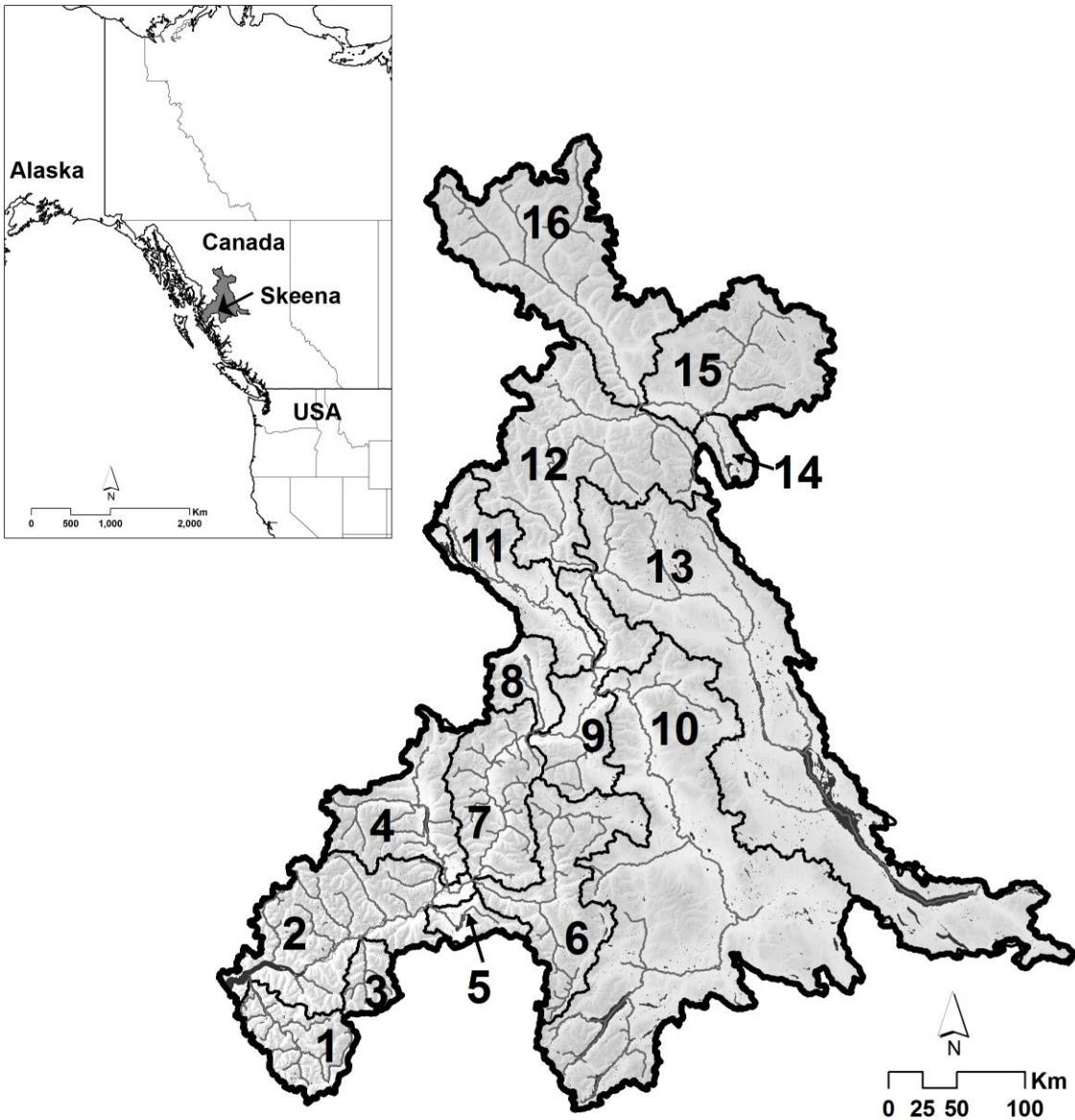


Figure 1. Map of Skeena River catchment and sections of river accessible to chum; numbers correspond to river reaches and subbasins used in the analysis and reported in the text. The following chum accessible reaches and tributaries were included in our analyses: Khyex, Kasiks, Exchamsiks, Exstew, Shames, and Zymagotitz Rivers (2), Gitnadoix River (3), Kitsumkalum River (4), Lakelse River (5), Zymoetz River downstream of the confluence of the Clore River (6), Kitwanga River (8), Kispiox River (11), Babine River downstream of the confluence of Nilkitkwa River (13), and Sustut River downstream of Bear River (14–15).

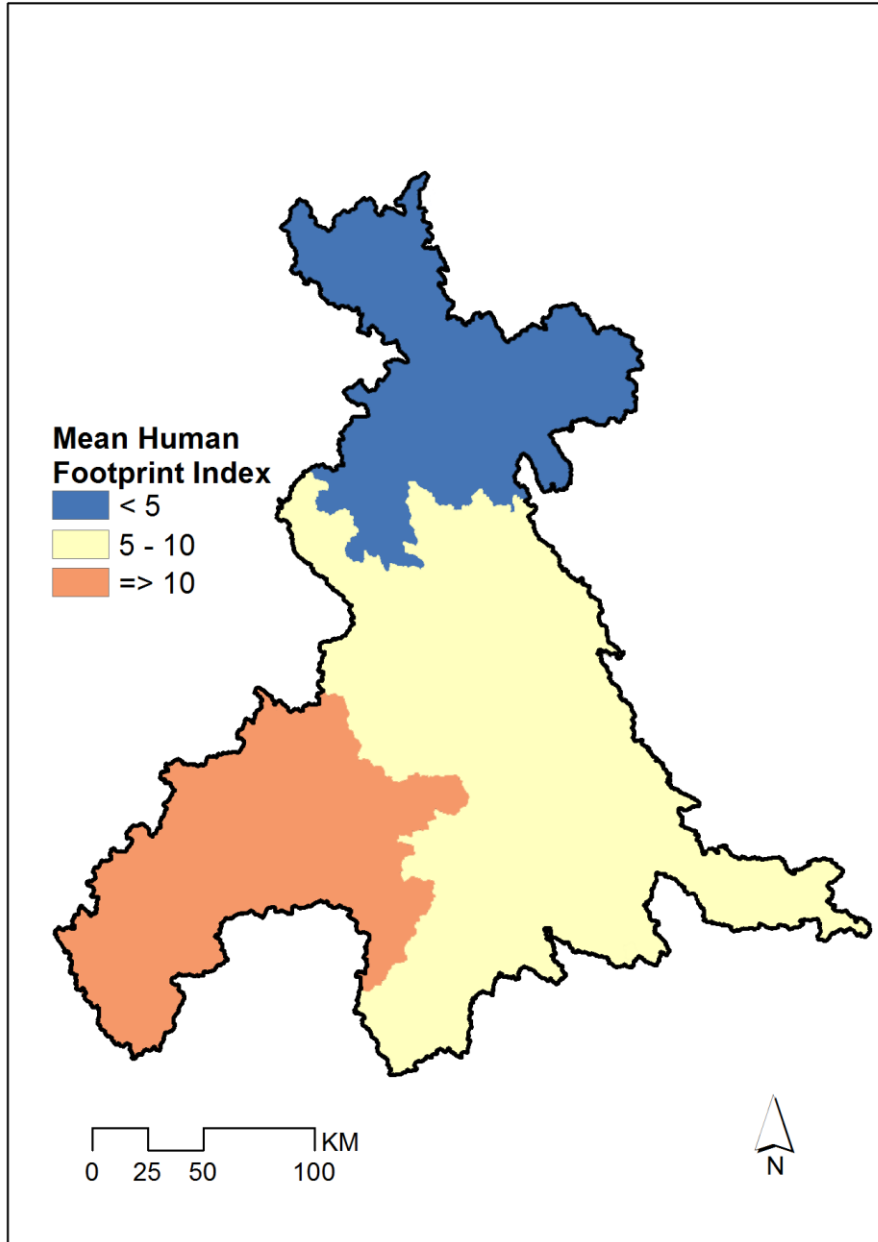


Figure 2. Mean relative human footprint for each Skeena chum salmon conservation unit, derived from Sanderson et al. (2002). The human footprint index represents the percentage of relative human influence within this region; low percentages denote relatively low human impact.

CHAPTER SEVEN

A Life-Table Model Estimation of the Parr Capacity of a Late-Nineteenth Century

Puget Sound Steelhead Population

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Abstract

An age-structured life-cycle model for Stillaguamish River steelhead was employed to estimate the number of age-one steelhead parr that could have produced the estimated adult return of 69 000 in 1895. We then divided the estimated parr numbers by the estimated area of steelhead rearing habitat in the Stillaguamish River basin in 1895 and under current conditions to estimate density of rearing steelhead then and now. Scaled to total wetted area of mainstem habitat, our historic estimates range from $0.08 \text{ parr}\cdot\text{m}^{-2}$ to $0.19 \text{ parr}\cdot\text{m}^{-2}$. Values for smaller tributary habitats range from $0.24 \text{ parr}\cdot\text{m}^{-2}$ to $0.7 \text{ parr}/\text{m}^2$. These values are significantly greater than current densities in the Stillaguamish (mainstem: $0.04 \text{ parr}\cdot\text{m}^{-2}$, tributaries: $0.07 \text{ parr}\cdot\text{m}^{-2}$), but well within the range of recent estimates of steelhead parr rearing densities in high quality habitats. Our results indicate that modest improvement in the capacity of mainstem and tributary rearing habitat in Puget Sound rivers will yield large recovery benefits if realized in a large proportion of the area of river basins currently accessible to steelhead.

Introduction

Setting endangered species recovery goals and objectives requires a systematic and scientifically rigorous assessment of population needs and the ability of the environment to support those needs (Tear et al. 2005, Beechie et al. 2010). This is especially true when habitat loss is a significant contributor to species declines, and recovery plans emphasize habitat restoration as a means to achieving recovery goals (e.g., Beechie et al. 2003). Within a recovery plan, recovery goals may be narrative statements, but habitat restoration objectives must be specific and measureable actions and targets for improving habitat quantity and quality (Tear et al. 2005, Skidmore et al. 2013). One example of this type of recovery plan is for the threatened Puget Sound steelhead (*Oncorhynchus mykiss*), which declined at least in part due to loss and impairment of freshwater spawning and rearing habitats (Hard et al. 2007, PSSTRT 2013).

Recovery of Puget Sound steelhead to a condition of de-listing will require, among other objectives, identifying threshold levels of freshwater juvenile rearing capacity necessary to sustain robust population numbers over multiple generations. However, identifying appropriate thresholds for the production of juvenile steelhead in freshwater will be hampered by lack of information about the capacity of freshwater rearing habitat that supported a much larger adult run size than exists today. Based on the available record of commercial catches for 1895, Gayeski et al. (2011) estimated the total adult run size for each of four large rivers in north Puget Sound, including the Stillaguamish, plus the aggregate of the remaining rivers in Puget Sound. The estimated run size in the Stillaguamish River in 1895 ranged from 52 000 to 100 000 (5th and 95th percentiles of the posterior, respectively) (Gayeski et al. 2011), whereas a recent five-year geometric mean number of natural-origin spawners was 327 (Ford et al. 2011, Table 74,

page 237) This 100-fold decline far exceeds what might be expected in response to the loss of only 33% of stream habitat accessible to adult steelhead since 1895 (Gayeski et al. 2011). Hence, it appears that the productivity of the freshwater rearing environment has experienced a decline since 1895 that is considerably out of proportion to the loss of accessible stream habitat area.

The main objective of this paper is to estimate this loss of productivity by estimating the steelhead parr rearing capacity of the Stillaguamish River in 1895 and comparing it to the current productivity. We used an age-structured life-cycle model to estimate the number of age-1 steelhead parr that could produce an adult run size of 69 200 (the posterior modal estimate from Gayeski et al. 2011) over a range of plausible parameter values for both freshwater production and marine (smolt-to-adult return) survival. We then divided the number of parr by estimates of the area of steelhead parr rearing habitat available in 1895 to derive estimates of historical steelhead parr rearing densities ($\text{parr}\cdot\text{m}^{-2}$). The life-cycle model incorporates density dependence and a realistic, complex adult age structure that is likely to well approximate the complex spawning structure of steelhead under minimally-disturbed conditions. We conclude with a discussion of the applicability of our estimates to the development of recovery goals for Puget Sound steelhead and associated research and monitoring.

Materials and methods

Life cycle model

We modeled a steelhead population consisting of a total of six age-classes, with four adult ages (3 – 6) (Table 1). We modeled females only and assumed a 1:1 sex ratio (Withler 1966, Ward & Slaney 1988, Seamons et al. 2004). The model includes repeat spawning at ages four, five and six because repeat spawning is believed to have been an important characteristic of steelhead life history prior to the major reductions in winter-run steelhead population sizes during the past forty years (PSSTRT 2013). Fecundity (# eggs·female⁻¹) is treated as age- and type-specific (maiden or repeat spawner) based on weight-at-age (Table 2). The model includes a single smolt age-class (age two), which is the most common smolt age for most coastal and Puget Sound steelhead populations (Quinn 2005, Withler 1966). Population projections of the model were conducted at annual time steps.

Density-dependence is incorporated during the period of freshwater residence prior to smolting in the transition from emergent fry-to-age-1 (parr). Accordingly, the model includes two sub-age-one life stages: eggs and fry. Fry-to-parr survival (fp) is modeled as a type II (Beverton-Holt) function with fixed parameters α and β :

$$(1) \quad fp = \alpha / (1 + n_{fry} * \beta)$$

where α is the inherent maximum fry-to-parr survival rate at low density under optimal conditions, β is the inverse of the number of fry at which fry-to-adult survival = $\alpha/2$, and n_{fry} is the number of fry. The number of fry is:

$$(2) \quad n_{fry} = n_{eggs} * sr * ef,$$

where n_{eggs} is total egg deposition, sr is the sex ratio, ef is the deterministic egg-to-fry survival rate. Consequently, fp will vary non-linearly with the number of fry produced by each year's total spawner abundance as will the number of parr produced the following year by each age and type spawner. All other life stage transitions are considered deterministic and density independent. The model tracks all life stages from egg deposition to adult return by age and stage class, so that production by each spawner type (age and repeat-spawning status) could be accounted separately.

For modeling convenience, we assume that repeat spawners attempt to repeat spawn the year after their maiden spawning and that there are no third-time spawners. Repeat spawning in only the one year after maiden spawning was found to be the most common pattern in steelhead in western Kamchatka as determined by scale analysis of several hundred samples collected by a joint US-Russian conservation research program between 1996 and 2005 (Pavlov et al. 2001, Gayeski, unpublished data). Repeat spawning was modeled for each maiden spawner in age-classes three to five by simply assigning an age-specific probability of surviving spawning to re-enter the ocean. We assumed that there was no difference in reproductive effort between maiden spawners in a given age-class that succeeded in repeat spawning and those that did not. The maximum adult age was set at six and the maturation rate of six-year old fish was set implicitly to 1.

Puget Sound steelhead in the late 19th century were harvested exclusively in terminal area and in-river fisheries (Wilcox 1898). Thus only mature fish, both maiden and potential repeat spawners

were harvested. Gayeski et al. (2011) argued that given that the peak commercial harvest of steelhead in Puget Sound occurred in 1895, six years after statehood and the initiation of large-scale commercial fishing for steelhead, the total adult return (harvest plus spawning escapement) was likely recruited from a population at or very near its unfished equilibrium abundance. The posterior mode of the estimated total adult return in 1895 of 69 200 corresponded to an estimate of 34 600 adult females assuming a sex ratio of 1:1. Gayeski et al. (2011) estimated that this return was most likely harvested at a rate of nearly 55%, yielding a total harvest of females of nearly 18 900 and a spawning escapement of approximately 15 700. We assume that this was the case and employ the life-cycle model to estimate the numbers of age-1 individuals that must have been produced in order to recruit a female population of 34 600. We did this by running the model for 25 time steps (years) starting with 10 years of no harvest and adding harvest at time step 11 that built up steadily to a maximum rate of 0.545 at time step 16 equal to the harvest rate on the 1895 population estimated by Gayeski et al. (2011). The model was run for an additional 9 time steps to verify that the year 16 total catch was a maximum, reflecting the historical harvest record (Figure 1). The density-dependence capacity parameter was adjusted to achieve the estimated 1895 total catch and total spawner abundance, as described below. The model was then run with the harvest rate set to zero to determine the total unfished equilibrium abundance of all ages at the stable age distribution. We refer to this henceforth as *the 1895 equilibrium*.

Figure 1 here.

We tracked the annual abundance of harvested and un-harvested maiden and repeat spawners separately in order to evaluate the impact of harvest on age-classes and on maiden and repeat

spawners. The model has 19 stages, including 17 stages for the four oldest age-classes, of which 14 stages are matures. These enable the model to keep track of all spawner life histories and the life histories of all harvested matures.

Fertilities, also referred to as “effective fecundities”, are measured as the number of age-1 progeny (parr) produced by each spawner of a particular age and type, x ; that is, the number of offspring surviving to year $t + 1$ produced by each age- x spawner in year t . These numbers occupy the first row of the square population projection matrix. Thus, the model assumes a pre-breeding census, whereby parents are counted each year prior to spawning and their offspring are counted prior to spawning the following year. Fertilities are therefore matrix elements generated by underlying vital rates. The vital rates are fecundity (eggs/age and type female), sex ratio, egg-to-emergent fry survival, and density-dependent fry-to-parr survival (Table 2). Fecundity was treated as age- and size (weight)-specific for both maiden and repeat spawners in each mature age-class. Since repeat spawners must recover body condition upon re-entering marine waters before they invest energy in gonad production and because they have less time to feed in marine waters before returning to freshwater to spawn than maiden fish of the same age, we assigned repeat spawners a fecundity value slightly greater than maiden spawners in the previous age-class (to account for some body size increase) but less than the value assigned to maiden spawners in the same age-class.

Age-specific weights and fecundities are based on length, weight, and fecundity data collected from steelhead in western Kamchatka in 2001 – 2004 (Gayeski, unpublished data), and scale analyses of the same individuals made by Dr. Kiril Kuzhichin at the Department of Ichthyology,

Moscow (Russia) State University. We selected representative lengths-at-age for 3-, 4-, 5-, and 6-year old maiden and repeat-spawning females that provided representative weights and fecundities when compared to the estimated range of the average weight of steelhead in the 1895 commercial catch as reported in Gayeski et al. 2011. This yielded average fecundities of 4900, nearly identical to the average value for steelhead reported by Quinn (2005, Table 15-1). Length-weight and length-fecundity equations are provided in Appendix A. Age-specific fecundities are listed in Table 2.

Modeling was conducted in MATLAB 7.10. The age-stage structured model for the population consists of 19 stages (Table 1). Transition rates and fecundities used in the projection matrix and their abbreviations are listed in Table 2.

Table 1 here.

Table 2 here.

Modeling the Stillaguamish circa 1895 steelhead population

Estimating the number of parr produced at the 1895 equilibrium requires that we appropriately partition the recruitment process between the freshwater and marine (post-smolt) periods.

Because there is scant empirical data for annual survival rates of smolts and post-smolt age-classes of Pacific salmon and steelhead we chose two marine survival scenarios, one low and one

high, that we believe bracket the likely true values of age-specific post-smolt marine survival of steelhead during the late 1800s.

Modeled marine survival

We started from an estimate of average smolt weight of 54 grams which is equivalent to a smolt fork length of 175 millimeters and Fulton Condition Factor (K) of 1.0, and assumed a smolt-to-age-three survival rate of 0.20 (Quinn 2005, Ward & Slaney 1993). Age three is the earliest age of maturation and age six the oldest. We estimated the survival rate from age-three to age-six for fish that first mature at age 3 to be 0.40 for the low marine survival scenario and 0.80 for the high survival scenario. The value of 0.40 corresponds to an average annual survival rate of 0.74; the value of 0.80 to an average annual rate of 0.93. We assume that annual marine survival increases with size, and therefore with age. To determine age-specific annual marine survival values for ages 3, 4, and 5 that reflect this assumption while meeting the cumulative survival constraints of the two survival scenarios, we applied the allometric growth-survival model of McGurk (1996) to the length- and weight-at-age data we chose for the model. The weights-at-age for ages 3 to 6 were independently constrained by having to achieve an average fish weight of 8.25 pounds, the mean of the weight range estimated by Gayeski et al. 2011, and the total weight of the catch estimated for the Stillaguamish by Gayeski et al. (2011). Having chosen the weights of each spawner age and type (maiden or repeat spawner), we applied the McGurk model to the average weight of smolts and each post-smolt maiden spawner age-class and estimated annual age-specific survivals using parameter values from within the range estimated for steelhead by McGurk (1996). This resulted in values of 0.73, 0.74, and 0.75 for the annual

rates of age 3, 4, and 5 immatures, respectively. Values for the high survival scenario were 0.92, 0.93, and 0.94, respectively.

Modeled maturation and repeat spawning rates

To determine the proportions of spawners of each age and type (maiden and repeat) in the total return, we estimated age-specific maturation rates of ages three to five and post-spawning survival rates of maiden spawners ages three to five that would result in repeat spawner proportions of returning adults between 20 and 30 percent (Withler 1966, Pavlov et al. 2001) and would achieve the target average weight of returning adults of 8.25 pounds, assuming that all adult ages and types were equally susceptible to harvest and thus were represented in the total catch in direct proportion to their relative abundance in the total return. We assumed that post-spawning survival increased with the size and age of maiden spawning fish. These values (Sp3S, Sp4S, Sp5S, Table 2) represent the proportions of maiden spawners at each age that survive to re-enter the ocean at a point in the year at which their survival from that point to the next spawning year is equal to the annual survival rate of immatures of the same age (S34, S45, S56, Table 2), so that the total survival of repeat spawners to repeat spawning the following year is equal to the product of the two rates (e.g., Sp3S*S34, Table 2).

Modeled freshwater survival.

Given the model values for age-specific fecundity, maturation rates, probabilities of repeat spawning, and marine survival rates, it remained to determine the density-dependent parameters alpha (α) and beta (β) and values for egg-to-fry (ef) and parr-to-smolt (ps) survival. We chose a value of 0.2 for egg-to-fry survival based on a range of literature values (Ward & Slaney 1993,

Quinn 2005), taking into consideration that this is an average value for the entire Stillaguamish watershed that spans a range of mainstem and tributary spawning geologies and habitat conditions.

We considered two different values for the density-dependence alpha parameter and for ps , the density-independent parr-to-smolt survival parameter. The alpha parameter is the value for the survival rate of fry to age 1 (parr) when fry densities are very low. We chose values of 0.20 and 0.40. For parr-to-smolt survival, we chose a value of 0.3, the value used by the Puget Sound Steelhead Technical Recovery Team for current optimal conditions (Quinn 2005, PSSTRT 2013 (Appendix C)), and a value of 0.4 as a conservative estimate for the near-pristine habitat conditions that likely existed throughout the Stillaguamish basin in the late nineteenth century. The value of 0.4 is similar to several (Oosterhout et al. 2005, Pess et al. 2011) contemporary estimates of over-winter survival of pre-smolt coho salmon in high quality habitats. Pre-smolt coho are smaller in body size than steelhead parr and can be expected to survive at lower rates than steelhead parr in similar quality habitats. Given values for all parameters, the total equilibrium abundance is determined by the beta parameter of the density-dependence function, which is in effect the fry capacity parameter.

Thus we evaluated juvenile production under four variants of the freshwater component of the life cycle model corresponding to all combinations of the two parameters governing freshwater survival: α (0.2 or 0.4) and ps (parr-to-smolt, 0.3 or 0.4), for each of the two sets of post-smolt marine survival parameterizations, a total of eight parameterizations of the model. For each of the eight parameterizations we ran simulations for a period of 25 years under a no harvest and a

harvest scenario starting at the unfished equilibrium abundance and stable age distribution (Figure 1). For the harvest scenario we set the base harvest rate to 0.545, the posterior mode of the estimate in Gayeski et al. (2011).

We recorded summary data for equilibrium conditions for each of the eight parameterizations of the model. The value of the density dependence capacity parameter, β , under equilibrium conditions was determined by trial and error by first identifying the stable age distribution of the model and then running the harvest scenario as described above and tuning the beta parameter and the initial population abundance until the total female harvest and spawner escapement corresponded closely to the values estimated by Gayeski et al. (2011) (female spawners = 15 743, total female harvest = 18 857, total female return = 34 600, at simulation year 16 with the harvest rate = 0.545). Equilibrium values of the quantities of interest were then determined by setting the harvest rate to zero.

Results

The results for each of the eight models are listed in Table 3.

Table 3 here.

Models 1 to 4 are the four parameterizations of the free freshwater transition parameters (α and ps) for the low post-smolt marine survival scenario; models 5 to 8 are the corresponding models for the high marine survival scenario. The strongest contrast in the outputs is between the two

marine survival scenarios. Density-dependent fry-to-parr survival at the unfished equilibrium is significantly lower under high post-smolt survival (0.021 to 0.029) than under low post-smolt survival (0.037 to 0.049). This results from higher values for the fry capacity parameter beta (lower fry capacities) under the high marine survival scenarios (Table 3).

The same number of total fry are produced at equilibrium under all eight models. The mean number of fry (males and females) across all eight models is 39 000 000 with a coefficient of variation (c.v., standard deviation/mean) of 0.006. Parr and smolt production are more variable. Parr production ranges from a low of 826 000 under model 8 to a high of 1 926 000 under model 1. Smolt production ranges from a low of 330 000 under model 8 to a high of 578 000 under model 1. Mean parr production over all eight models is 1 320 000 with a c.v. of 0.33. Mean smolt production is 452 000 with a c.v. of 0.28.

The proportions of repeat spawners are noticeably greater than for any current Puget Sound steelhead population for which there is data (PSSTRT 2013): 0.235 for the low post-smolt survival scenarios and 0.286 for the high ones. Calculation of cohort smolt-to-adult return and female spawner-to-total adult (males plus females) return values reveals the importance of repeat spawning in the life-cycle model. Calculated only for first-time spawners for the low marine survival scenario, the cohort smolt-to-total adult rate is 0.105 and the female spawner-to-total adult return rate is 1.54 (calculated from mean fecundity and the mean egg-to-adult survival of 0.0003); for the high survival scenario, the cohort smolt-to-adult rate is 0.172 and the female spawner-to-total adult return rate is 1.46. In other words, the population cannot replace itself at equilibrium (which would require 2 adults returning for each female spawner).

When cohort and egg-to-adult survival is calculated by including repeat spawners the cohort smolt-to-total adult return rate for the low post-smolt survival scenario is 0.138 and for the high survival scenario is 0.237. Egg-to-adult survival under both scenarios is 0.0004, an increase of over 30% from the calculation based only on maiden spawners. These raise the female spawner-to-total adult return rate to just over 2.0, assuring replacement at equilibrium.

Juvenile production scaled to historical rearing habitat

The production of parr of both sexes from the eight models ranged from 826 000 to 1 926 000 (Table 3) and averaged 1 320 000. Gayeski et al. (2011) estimated that 668 linear kilometers of mainstem and tributary stream habitat was accessible to winter-run steelhead in the Stillaguamish River in 1895. We updated this estimate using data for historical mainstem and tributary rearing habitat in the Stillaguamish (Pess et al. 1999, Pollock et al. 2004). We estimate that there were a total of 706 kilometers of tributary habitat available for juvenile steelhead rearing, and 160 kilometers of mainstem. For tributaries, we estimated the average channel width available to steelhead rearing during near baseflow conditions during the summer and fall growing season to be 3 meters. This resulted in an estimated total tributary rearing area of 2 118 000 square meters ($706 \times 1000 \times 3$). For mainstem rearing habitats we used a range of estimates of the average width (each bank) of total mainstem length available for juvenile steelhead rearing during the summer and fall growing season of 2, 3, and 4 meters (4, 6, and 8 meters both banks combined) this results in a range of total mainstem rearing habitat area of 640 000 to 1 280 000 square meters ($160 \times 1000 \times 4$ to $160 \times 1000 \times 8$). These estimates yield an estimate of total historically available juvenile parr rearing area of 2 780 000, 3 078 000, and 3 398 000 square meters (Table 4).

Dividing each of the eight estimates of 1895 equilibrium parr production by the three estimates of total rearing area yields estimates of parr densities in juvenile rearing habitats of 0.24 to 0.70 parr·m⁻². For the average total parr production of 1 320 000 (averaged across all eight model runs), rearing densities range from 0.39 to 0.48 parr·m⁻². The average across the four low marine survival scenarios is 0.49 to 0.61 parr·m⁻². The average across the four high marine survival scenarios is 0.29 to 0.35 parr·m⁻² (Table 5).

Parr capacity in the Stillaguamish River under current conditions

Roni et al. (2010) estimated steelhead parr production in a modeled Puget Sound watershed the size of the Stillaguamish before restoration, which is to say, under current conditions. They estimated the lengths of three types of stream habitats, small, medium, and large and the current number of parr produced by each. Small and medium streams correspond to tributaries in our analysis; large streams to mainstems. The total length of large streams is 117 751 meters (118 km.). Steelhead parr production in large streams was estimated to be 99 238. Using our estimates of mainstem rearing habitat area as equal to stream length x 4, 6, and 8 meters, the estimated rearing area of large streams is 471,000; 707 000; and 942 000 square meters. This would yield parr densities of 0.21, 0.14, and 0.11 parr·m⁻². These densities are lower than the mean values of our historic estimate of 0.48, 0.43, and 0.39 parr·m⁻², respectively (Table 5).

Discussion

We provide the first model-based estimate of steelhead parr rearing capacities and associated densities for a representative Puget Sound river basin under the near-pristine conditions that existed in the late nineteenth century. We employed an age-structured life-cycle model to generate the number of steelhead parr (age-1) produced under equilibrium conditions by a population of female spawners in a representative river basin in Puget Sound under the more pristine environmental conditions that existed at the end of the nineteenth century. The modeled spawning populations consisted of an array of sizes, ages, and spawning types (maiden and repeat) in proportions that are likely to have obtained at that time given available historical information (as summarized, for example, in Withler 1966) and data from populations in western Kamchatka that still exhibit the complex life histories that likely characterized Puget Sound steelhead populations under the more pristine conditions of the late nineteenth century (Pavlov 2001).

Age- and stage-structured life-cycle models are appropriate to contexts such as ours where the aim is to examine the relationships between population numbers at different life stages and/or between one or more critical life stages and candidate environmental covariates affecting growth and survival. Our approach is consistent with other uses of age and stage structured life-cycle models employed in various conservation and management contexts involving salmon (Greene and Beechie 2004, Oosterhout et al. 2005, Schuerell et al. 2006) and marine mammals (Brault and Caswell 1993, Olesiuk 2005). In our case, we sought to improve our understanding of how the complex adult spawning life histories and population abundance that characterized Puget Sound steelhead populations at the end of the nineteenth century were maintained across generations by modeling the life cycle of a representative Puget Sound steelhead population, the

Stillaguamish River population. Specifically, we were interested in characterizing the parr production and associated adult life history required to sustain the 1895 equilibrium abundance, and then comparing that historical parr capacity to potential parr production under current habitat conditions. By modeling the entire life-cycle and making judicious use of available data pertaining to steelhead life history, we were able to achieve those aims.

A comparison of parr densities

Gayeski et al. (2011) estimated a 100-fold decline in the abundance of adult Stillaguamish River steelhead between 1895 and the first decade of the twenty-first century. This decline far exceeds what might be expected in response to the estimated loss of only 33% of stream habitat accessible to adult steelhead since 1895. This implies that the productivity of the freshwater rearing environment has experienced a decline since 1895 that is considerably out of proportion to the loss of accessible stream habitat area. Consistent with the estimate of adult steelhead abundance at the end of the nineteenth century, our results show that parr abundance and densities were significantly greater than estimates for high quality habitats under current conditions. Our results suggest that currently reduced steelhead abundance is the product of both loss of the quantity of suitable juvenile rearing habitat and loss of quality of extant rearing habitats expressed as a reduction in the densities of parr that habitat of a given area can support.

Our model estimates of parr densities are averages over all stream types, tributary and mainstem. These estimates were made by assuming that all tributary and mainstem rearing habitats were equal in quality. We therefore simply assigned the total numbers of parr to mainstem and tributary habitat in direct proportion to the respective total lengths of each stream type (160 and

706 kilometers, respectively. Table 4). We did this for lack of any historical or current information on the distribution of total steelhead parr across stream types, which is largely a result of the absence of parr estimates at the whole basin scale. This probably results in somewhat under-estimating the rearing capacity of tributaries and over-estimating that of the mainstem river. However, we minimized this potential bias by estimating rearing habitat area for each stream type by assuming a maximum width of stream within which most rearing during the summer-fall growing season occurred. This approach treats mainstem river rearing habitats more like that in tributaries with respect to the key features of depth and velocity. Consequently, we expect that our densities should be reasonably accurate as average values for both tributary and mainstem rearing habitats combined.

Our estimates of the numbers of steelhead parr produced under the conditions of the 1895 equilibrium are considerably larger than any credible estimate of annual numbers of parr under current conditions for larger river basins in Puget Sound (e.g., Roni et al. 2010), which is what we expected given the estimated 1895 equilibrium adult population. Nonetheless, our estimates of the per-unit-area capacity of tributary and mainstem rearing habitats in the Stillaguamish River in the late nineteenth century are comparable in magnitude to or smaller than several recent estimates of densities of rearing juvenile steelhead in small tributary streams.

McCarthy et al. (2009) reported rearing densities of age 0 to age 2 rainbow/steelhead for nine small (approximately third order) tributary stream of the South Fork of the Trinity River in northern California. Age 0 fish sampled at the end of the growing season in October weighed approximately 3 grams. Age 1 and 2 fish weighted between 8 and 37 grams which correspond to

fork lengths between 94 and 155 mm at a Fulton condition factor, K, of 1.0, which is within the size range for steelhead parr. Densities ranged from 0.16 parr·m⁻² to 0.89 parr·m⁻². Harvey et al. (2005) reported densities for steelhead/rainbow parr (less than 130 mm fork length) in 59 small habitat units in a small coastal stream in northern California (average width 4 meters) and reported a maximum density of 0.9·m⁻². Harston & Kennedy (2014) reported densities of rearing steelhead yearlings (parr) in several small tributaries to the Clearwater River in Idaho. Mean parr densities at the least hydrologically altered sites estimated from their figure 3 ranged from 0.2 parr·m⁻² to 0.35 parr·m⁻² at the beginning of the growing season in July to 0.1 parr·m⁻² at the end of the season in September.

There are few published estimates of rearing densities of larger mainstem rivers, fifth order or higher. The best available recent information on the density of steelhead parr in Puget Sound and coastal Washington rivers under fully-seeded conditions is that provided by two reports from the 1980s, Chapman (1981) and Gibbons et al. (1985) (see also, PSSTRT 2013, Appendix C). The maximum estimated parr densities from these two reports ranged from 0.05 parr·m⁻² to 0.12 parr·m⁻². These are considerably lower densities than those we report in Table 5 (0.243 to 0.698), but comparable to densities measured in edge habitats of the Skagit River (0.05 to 0.10 parr·m⁻²; Beechie et al. 2005). It is important to note, however, that our density estimates apply to estimates of suitable rearing habitat only, which is most often a small proportion of total stream area, and not to the entire area of sampled stream reaches as in Gibbons et al. (1985). To facilitate a more accurate comparison to Gibbons et al. (1985) which contains the more extensive analysis of the two reports, we re-analyzed the Gibbons et al. (1985) data for mainstem river

reaches, and re-scaled our rearing area-based density estimates to estimates of total mainstem area. Details are provided in Appendix B.

Our adjusted parr density estimates range from 0.050 for the most productive high marine survival scenario (model 8, Table 3) to 0.187 for the least productive low marine survival scenario (model 1, Table 3). The average density over all eight models ranges from 0.079 to 0.128. The mean over the four low marine survival scenarios ranges from 0.10 to 0.163, and for the four high marine survival scenarios ranges from 0.058 to 0.094 (Table AII-1). Notably, the average adjusted parr densities over all eight models and the average of the four high marine survival scenarios are consistent with the estimates based on Gibbons et al. (1985) (0.05 to 0.12 parr·m⁻²) and with estimates based on Beechie et al. (2005) (0.05 to 0.10 parr·m⁻²). The low marine survival scenarios produce adjusted densities that are within the range of Gibbons et al. (1985) to as much as 56% higher than their highest density (0.12).

A second estimate of rearing densities of juvenile steelhead/rainbow in a large, fifth order stream is available to us from unpublished data from a study conducted by one of us (Gayeski). Gayeski conducted a mark-recapture/sight-resight snorkel survey of rainbow trout abundance in a 55 meter long by 24 meter wide reach of upper Icicle Creek, a high-gradient fifth-order tributary of the Wenatchee River in the Columbia River basin in eastern Washington State, USA. Abundance was estimated using several Bayesian models for multiple mark-resight periods based on binomial and trinomial likelihoods that produced concurrent results. The rainbow trout in the site ranged from 100 to 280 mm fork length and so included both steelhead parr- and smolt-sized individuals. Estimated densities ranged from 0.14 parr·m⁻² to 0.25 parr·m⁻² for the central 99% of

the posterior distribution of estimated abundance. These values are higher than those of Gibbons et al. 1985 and our estimates for the 1895 Stillaguamish equilibrium re-scaled to estimated total mainstem area (though not for our estimates of mainstem densities as originally scaled to estimated rearing habitat area). Therefore, we conclude that our model-based estimates of total parr production required to produce the Stillaguamish River 1895 equilibrium are not unrealistically high.

This suggests that there is value in estimating rearing habitat area of large (fifth-order and larger) tributaries and mainstem rivers by multiplying channel length by estimates of maximum rearing width adjacent to the shoreline and calculating rearing densities with respect to these areas (as $\text{parr} \cdot \text{m}^{-2}$) rather than calculating based on the entire area where measures of total stream width may be available. At least where data is reported as number of fish per linear length of stream channel this approach would enable such measurements to be compared to our historic estimates. At a minimum future studies and field monitoring reports should state the area of stream channel in which fish surveys were conducted and report whether or not channel width was measured or estimated.

Application to recovery planning for Puget Sound steelhead

Though of comparable magnitude, our model-based densities are slightly higher overall than those of Gibbons et al. (1985) measured in tributary and mainstem river reaches considered to be fully seeded. Independent of such comparison, it is reasonable to expect that rearing habitats under current best conditions may have lower capacities than under more pristine conditions for at least three reasons. First, stream rearing habitats may have become less complex resulting in a

reduction in the number of suitable microhabitat sites per unit length that are energetically suitable for rearing steelhead parr. This would result in stream reaches of a given length that are fully seeded under current conditions having a lower parr capacity than under more pristine conditions. Second, the throughput of diet items available to drift feeding parr per unit area and time may be lower under current conditions as a result of reduced stream habitat complexity and/or reduction of marine-derived nutrients due to reduced abundance of salmon carcasses. This would result in individuals having to spend more time foraging during the day and to expend more energy per day to acquire the food intake needed to sustain minimum growth trajectories. Third, as a result of the reduction in throughput of energetic resources and/or loss of habitat complexity, juvenile steelhead may need to defend larger rearing spaces to obtain sufficient food, which results in decreased density. All three of these phenomena would, of course, be synergistic with one another.

A fourth reason likely to become increasingly important in the face of rapid climate change (Wade et al. 2014) should also be considered: increasing stream temperatures during the summer-fall growing season. Increasing stream temperatures can be expected to increase metabolic rates and foraging costs resulting in reduced growth rates per calorie consumed. This will also require larger foraging areas for fish of given sizes to obtain the requisite food intake required to sustain growth (Rosenfeld 2003, McCarthy et al. 2009, Weber et al. 2014).

Each of these possible explanations provide themes for investigation. The second mechanism (reduced food resources) is probably the highest priority because it influences both the first and third mechanisms as well (i.e., they are both partly dependent on the throughput of food

resources, primarily invertebrate drift (e.g., McCarthy et al. 2009, Rosenfeld et al. 2014, Weber et al. 2014). Evaluation of this mechanism would require *in situ* evaluation of juvenile rearing in stream habitats following the approach described in Weber et al. (2014), evaluating the daily flux of invertebrate drift and terrestrial invertebrate fall, daily consumption of rearing parr and associated territory size, and growth rate over the course of the summer/fall growing season. The data obtained would help understand whether current rearing densities are limited by the daily or seasonal energy flux. If, as does not seem at all unlikely, the daily flux appears to exceed the daily consumption demands of rearing juveniles this may indicate that habitat complexity (mechanism 1) and/or temperature is limiting capacity and recruitment. If current rearing density appears closely matched to resource flux, this might indicate that mechanism 2 (loss of marine-derived nutrients) and/or temperature is limiting.

We hypothesize that rearing habitats which appear to be fully seeded under current conditions suggest lower capacities relative to similar habitats in Puget Sound rivers at the end of the nineteenth century. Reduced habitat capacity can result from loss at coarser and finer extents. Obvious loss of stream habitat complexity in the form of reduced numbers of main stem stream channels, or reduced habitat quality due to simplification of habitat from a reduction in in-channel structural habitats (i.e. wood) can result in fewer areas of habitat that are energetically suitable for juvenile rearing (Beechie et al. 1994, Rosenfeld and Taylor 2009, Rosenfeld et al. 2011). This is something which has been quantified. A reduction in extent of suitable habitat area also occurs with the potential reduction of the daily flux of energetically suitable diet items which can result in micro-habitat units of a given area supporting fewer individuals. Conversely, reduction in the flux of diet items will result in individual juveniles also requiring larger micro-

habitat areas to obtain the minimum required daily food intake. Both components of capacity reduction result from the three suggested mechanisms and all three can potentially contribute to a reduced current parr capacity in Puget Sound steelhead streams relative to the late 1800s. And all three will interact negatively with increasing stream temperatures during the summer-fall growing season. Therefore a critical question is how close may we expect to come to attaining the parr densities estimated by the models? Focused studies to evaluate the three mechanisms described above would provide much of the data required to answer this question.

While there are data showing that declines in the productivity of the marine environment in recent decades that have impaired the recruitment of steelhead on a regional basis (Friedland et al. 2014, Welch et al. 2000, Ward et al. 2000, Smith et al. 2000, Ward and Slaney 1988, 1993), considerably less is known about how alterations of freshwater habitats have affected juvenile production. Partitioning the life history between the freshwater and marine phases of the life cycle in our model facilitates the identification of conditions that can result in positive population growth ($\lambda > 1$). In particular, it should facilitate the identification of minimum spawner-to-smolt survival rates necessary to achieve positive population growth under varying marine survival scenarios. This is well-illustrated by the contrast in equilibrium fry-to-parr survival rates between our low and high marine survival scenarios (Table 3), where lower marine survival requires higher fry-to-parr survival rates (weaker density dependent fry mortality/greater total fry capacity) than when marine survival rates are higher.

The marine survival scenarios used in our modeling were intended to bracket the likely range within which annual post-smolt survival rates lie. By widely bracketing average survival rates to

reflect the uncertainty surrounding adult marine survival we were able to identify a broad but reasonable range of parr capacities for the 1895 equilibrium population. The majority of remedial actions directed at recovering Puget Sound steelhead are most likely to be directed at freshwater habitat conditions. The results from our modeling effort suggest that measuring and monitoring the parr capacity of rearing habitats by measuring parr density provides an integrative metric of population performance within the entire freshwater life cycle. Consequently, quantifying parr capacities and parr-to-smolt survival rates are key information needs for recovery planning.

1) Changes in the adult steelhead population since 1895

Our model of the 1895 steelhead population assumed a more complex age-structure than exists today in the Stillaguamish River, particularly with respect to the degree of repeat spawning. The model also assumed four mature ages, 3 to 6, with the proportions at equilibrium dominated by the two older age classes which combined accounted for 70% of annual returns at equilibrium. These assumptions resulted in an average fecundity (eggs/female) of the modeled populations of 4800 and 4900 for the two marine survival scenarios (Table 3), which are essentially identical to the average value for steelhead generally noted by Quinn (2005). The contemporary population has a much lower, perhaps negligible, percentage of repeat spawners (PSSTRT 2013), and is dominated by age 3 and age 4 year old individuals (Hard et al. 2007). This undoubtedly has reduced the average fecundity of the population and thus the total potential egg deposition.

These changes in the age- and life-history structure of the contemporary population, however, do not affect the validity of our results nor their applicability to contemporary recovery planning, since the purpose of the modeling is to provide estimates of the abundance of parr and the

associated rearing densities that were most likely responsible for the level of adult equilibrium abundance in 1895 estimated by Gayeski et al. (2011). These estimates are directly relevant to conservation planning for Stillaguamish and other Puget Sound steelhead populations. As discussed in the previous subsection, there are several reasons why current parr rearing densities are lower in the Stillaguamish than they were near the turn of the twentieth century as estimated by our models. Attaining higher rearing densities in the Stillaguamish River is directly relevant to the recovery of the steelhead population. This will require both improvements to habitat quality and quantity (physical structure and complexity, and food web) and synergistic increases in the numbers of returning adult spawners. The structure (ages, proportion of repeat spawners) of the recovering adult population that may also be required to achieve recovery under the ESA for example is a separate, if related, matter that it was not our purpose to address in this paper.

2) *Rainbow trout in the Stillaguamish*

Our model also did not attempt to include resident rainbow trout that can play a significant role in the population dynamics of steelhead (see Kendall et al. 2014 for a thorough contemporary review). There are two reasons for not doing so. First, there is no historical data regarding the size of resident rainbow trout populations in Puget Sound rivers either at the turn of the twentieth century or currently, but what is known suggests that populations are very small, unlike conditions in many rivers tributary to the Columbia River (PSSTRT 2013, Kendall et al. 2014 and references therein). Second, incorporating a resident rainbow population would significantly increase the complexity of the model as it would require modeling two populations, including both sexes, and modeling their interactions. In particular, it would require making assumptions about the controls governing the development of smoltification in the two life histories, which is

known to differ between the sexes (Kendall et al. 2014), and there is no real data to support any particular parameterization of this.

More importantly, with regard to the main objectives of this paper, accounting for the contribution of a resident population to the steelhead population is not required in order to estimate the parr production and capacity that was associated with the estimated abundance of adult steelhead. We assumed that all production of anadromous parr was, and could be, accounted for by the spawning of anadromous females. Given the large differences in fecundity between resident and anadromous females based on body size differences alone (Kendall et al. 2014), it would require several resident females to produce the same number of parr as one anadromous female. Thus, if the contribution of resident females to the production of anadromous parr were significant in 1895, the total population would have been even larger than estimated by Gayeski et al. 2011, but still would have produced the total adult equilibrium anadromous population. Consequently, accounting for the abundance of a resident population and its contribution to anadromy, even were the necessary data to do so available, would not affect the estimated number of anadromous parr at equilibrium, however otherwise valuable such an exercise would be to understanding the structure of the presumed resident/anadromous population complex.

It is possible, however, that the changes in the abundance and age/life-history complexity of the Stillaguamish River steelhead population that have occurred since 1895 may have resulted in a shift in the proportions and abundance of resident rainbow and steelhead in the population. This is certainly a relevant contemporary research topic relevant for the conservation of Stillaguamish

River steelhead. But it is unlikely to affect the implications of our results for habitat-based recovery measures directed at increasing the complexity and abundance of rearing habitat and the associated aquatic food web. In the context of the general reduction in the abundance of all salmon species in the Stillaguamish River in addition to steelhead since the turn of the twentieth century (Myers et al. 1998, Ford et al. 2011), we believe it most likely that the resident rainbow population in the river was larger in 1895 than it is now. Consequently total juvenile *O. mykiss* rearing densities would have been somewhat greater than we estimate. Current rearing densities, as noted in Results (*Parr capacity in the Stillaguamish River under current conditions*) are much lower, than our historic estimate and include resident rainbow trout.

It is possible that the costs to anadromy have changed between 1895 and the late twentieth/early twenty-first centuries. Specifically, marine survival of steelhead has declined significantly during the past three decades or more (Ward & Slaney 1993, Welch et al. 2000, PSSTRT 2013). The extent to which this has caused a reduction in the proportion of anadromy and a corresponding increase in residency in rivers in the Puget Sound such as the Stillaguamish, if any, is an important research question. But we believe that it is unlikely to be the primary cause of the reduction in the abundance of the current steelhead population. We think it much more likely that the loss of the quantity and quality of juvenile rearing habitat discussed above (*Application to recovery planning for Puget Sound steelhead*) is responsible for the majority of the recent reduction in steelhead abundance compared to either competition with resident rainbow or changes in the costs of anadromy.

Conclusion.

We re-iterate that the majority of efforts directed toward the recovery of Stillaguamish steelhead and other Puget Sound steelhead populations will focus on improving the conditions of freshwater juvenile rearing habitats as described above. The primary outcome of successful efforts of this kind will best be measured by increases in the rearing densities of habitats at the reach and finer spatial scales (reflecting an increase in habitat quality) and by increasing the total abundance and spatial distribution of such higher quality habitats at the scale of entire river basins, as previously recommended by Roni et al. (2010). Our results provide realistic numbers for target steelhead parr densities that should be of value to guiding such habitat-based recovery efforts.

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Tables

Table 1. Stage numbers, names, ages, and descriptions.

Stage Number	Age	Stage Name	Description
1	1	Parr	
2	2	Smolt	
3	3	Age 3 Maiden S	Maiden that spawns
4	3	Age 3 Maiden H	Maiden harvested
5	3	Age 3 Immature	Remaining in ocean
6	4	Age 4 Maiden S	Maiden that spawns
7	4	Age 4 Maiden H	Maiden harvested
8	4	Age 4 Repeat S	Repeat that spawns
9	4	Age 4 Repeat H	Repeat harvested
10	4	Age 4 Immature	Remaining in ocean
11	5	Age 5 Maiden S	Maiden that spawns
12	5	Age 5 Maiden H	Maiden harvested
13	5	Age 5 Repeat S	Repeat that spawns
14	5	Age 5 Repeat H	Repeat harvested
15	5	Age 5 Immature	Remaining in ocean
16	6	Age 6 Maiden S	Maiden that spawns
17	6	Age 6 Maiden H	Maiden harvested
18	6	Age 6 Repeat S	Repeat that spawns
19	6	Age 6 Repeat H	Repeat harvested

Table 2. Transition rates, abbreviations and fecundities used in the projection matrices.

Parameter	Values
Eggs/Age 3 Female	3200
Eggs/Age 4 Maiden Female	4000
Eggs/Age 4 Repeat Spawning Female	3400
Eggs/Age 5 Maiden Female	5000
Eggs/Age 5 Repeat Spawning Female	4300
Eggs/Age 6 Maiden Female	6000
Eggs/Age 6 Repeat Spawning Female	5400
sr (Proportion females)	0.5
ef (Egg-fry survival)	0.2
α (Fry-parr maximum survival rate)	0.2, 0.4
β (Fry capacity parameter)	Variable
fp (Fry-parr survival rate)	$\alpha/(1 + \text{fry}/\beta)$
ps (Parr to smolt survival)	0.3, 0.4
S23 (Smolt-Age 3 survival)	0.2
Mat3 (proportion of ocean age 3 that mature)	0.0278, 0.0422
Mat4 (proportion of ocean age 4 that mature)	0.2227, 0.3564
Mat5 (proportion of ocean age 5 that mature)	0.3884, 0.4366
Sp3S (proportion of age 3 maiden spawners that survive to re-enter the ocean)	0.5
Sp4S (proportion of age 4 maiden spawners that survive to re-enter the ocean)	0.6
Sp5S (proportion of age 5 maiden spawners that survive to re-enter the ocean)	0.7
S34 (Ocean survival age 3 to age 4)	0.73, 0.92
S45 (Ocean survival age 4 to age 5)	0.74, 0.93
S56 (Ocean survival age 5- age 6)	0.75, 0.94

Table 3. Summary of model results for 25 year simulations of each of the eight parameterizations of the steelhead life-cycle model under equilibrium (no harvest) conditions. *: cohort smolt-to-adult, egg-to-smolt, and spawner-to-spawner measured for maiden (first-time) spawners only. **: cohort smolt-to-adult, egg-to-smolt, and spawner-to-spawner measurements including separate accounting of repeat spawners.

Parameters/Model Number	1	2	3	4	5	6	7	8
Mean Fecundity at stable age	4924	4924	4924	4924	4832	4832	4832	4832
Egg-to-Fry	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2
Alpha	0.2	0.2	0.4	0.4	0.2	0.2	0.4	0.4
Beta	1/6383700	1/4399000	1/2708000	1/1955700	1/3245000	1/2326800	1/1485200	1/1090700
Parr-Smolt	0.3	0.4	0.3	0.4	0.3	0.4	0.3	0.4
Smolt-Ocean Age 3	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2
pMat4	0.2636	0.2636	0.2636	0.2636	0.3306	0.3306	0.3306	0.3306
pMat5	0.3648	0.3648	0.3648	0.3648	0.3974	0.3974	0.3974	0.3974
Ocean Age 3-to-Ocean Age 4	0.73	0.73	0.73	0.73	0.92	0.92	0.92	0.92
Ocean Age 4-to-Ocean Age 5	0.74	0.74	0.74	0.74	0.93	0.93	0.93	0.93
Ocean Age 5-to-Ocean Age 6	0.75	0.75	0.75	0.75	0.94	0.94	0.94	0.94
Female Spawners at EQ.	39,817	39,560	39,282	39,150	40,469	40,300	40,117	40,038
Proportion Repeat Spawners	0.235	0.235	0.235	0.235	0.286	0.286	0.286	0.286
Fry-Parr at Equilibrium	0.049	0.037	0.049	0.037	0.029	0.021	0.029	0.021
Total Fry	39 188 957	38 936 845	38 662 997	38 532 736	39 110 847	38 946 025	38 771 453	38 693 191
Total Parr	1 926 005	1 435 288	1 900 214	1 420 379	1 113 266	831 380	1 103 609	825 993
Total Smolt	577 802	574 115	570 064	568 152	333 980	332 552	331 083	330 397
Fry-to-Smolt	0.0148	0.0148	0.0148	0.0148	0.0086	0.0086	0.0086	0.0086
Egg-to-Smolt	0.0030	0.0030	0.0030	0.0030	0.0017	0.0017	0.0017	0.0017
Cohort Smolt-to-Adult*	0.105	0.105	0.105	0.105	0.172	0.172	0.172	0.172
Egg-to-Adult*	0.000311	0.000311	0.000311	0.000311	0.000295	0.000295	0.000295	0.000295
Spawner-to-Spawner*	1.54	1.54	1.54	1.54	1.46	1.46	1.46	1.46
Cohort Smolt-to-Adult**	0.138	0.138	0.138	0.138	0.237	0.237	0.237	0.237
Egg-to-Adult**	0.000408	0.000408	0.000408	0.000408	0.000406	0.000406	0.000406	0.000406
Spawner-to-Spawner**	2.02	2.02	2.02	2.02	2.02	2.02	2.02	2.02

Table 4. Estimated total steelhead rearing habitat area of mainstem plus tributaries of the Stillaguamish River circa 1895. *: tributary width is total width; mainstem width is the total for both banks combined.

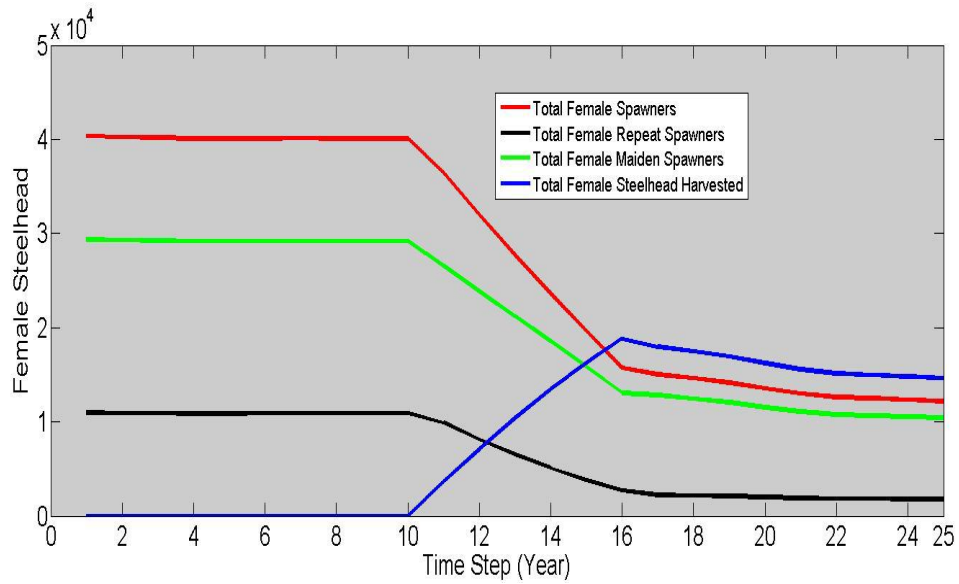
Habitat Type	Length (km)	Length (m)	Width (m)*	Area (m ²)
Tributaries	706	706 000	3	2 118 000
Mainstem 1	160	160 000	4	640 000
Mainstem 2	160	160 000	6	960 000
Mainstem 3	160	160 000	8	1 280 000
Tribs+Mainstem1				2 758 000
Tribs+Mainstem2				3 078 000
Tribs+Mainstem3				3 398 000

Table 5. Modeled Parr Densities (parr·m⁻²) for the eight models and 3 estimates of total rearing area.

Model	Total Parr	Estimated rearing area (m ²)		
		2 758 000	3 078 000	3 398 000
L1	1 926 005	0.698	0.626	0.567
L2	1 435 288	0.520	0.466	0.422
L3	1 900 214	0.689	0.617	0.559
L4	1 420 379	0.515	0.461	0.418
H1	1 113 266	0.404	0.362	0.328
H2	831 380	0.301	0.270	0.245
H3	1 103 609	0.400	0.359	0.325
H4	825 993	0.299	0.268	0.243
Average of All Eight Models	1 319 517	0.478	0.429	0.388
Average of L1:L4	1 670 472	0.606	0.543	0.492
Average of H1:H4	968 562	0.351	0.315	0.285

Figures

Figure 1. Time trajectory of the modeled late nineteenth century Stillaguamish adult female steelhead population starting at the unfished equilibrium in year 0, with harvest starting in year 11 and building to a constant maximum rate of 0.545 in year 16.



Appendix A

Equations used to estimate age/length-specific fecundities used in the model.

$$(A1) \quad \text{Egg\#} = \text{Exp}[(2.9 * \text{Ln}(\text{fork length}(\text{mm})) - 10.8 + (0.137^2/2)]$$

$$(A2) \quad \text{Wt}(\text{g}) = \text{Exp}[2.9 * \text{Ln}(\text{fork length}(\text{mm})) - 11.0 + (0.0733^2/2)]$$

Fork lengths (mm) and weights-at-age (g, lbs.):

Age 3: 670 mm, 2628 g, 5.79 lbs.

Age 4: 720 mm, 3237g, 7.14 lbs.

Age 5: 780 mm. 4083g, 9.0 lbs.

Age 6: 830 mm, 4889g, 10.78 lbs.

Appendix B

Gibbons et al. surveyed tributary streams of several Puget Sound and Olympic Peninsula steelhead rivers and estimated parr numbers by conducting electrofishing removals in selected stream reaches. Data for sampled tributaries was reported only as parr per square meter (Gibbons et al. 1985, Table 1) so we were not able to further compare Gibbons et al.'s rearing density estimates for tributaries to ours. Several large rivers were sampled and parr counted by snorkeling. The snorkel count data was reported in Table 3 of Gibbons et al. 1985 and included the lengths, widths, and total area of sampled reaches in addition to the total number of steelhead parr counted. The total length of rivers reaches sampled ranged from 400 to 1100 meters. Parr densities were determined by dividing the total parr counts by the calculated total area of the sampled reaches.

We used the following approach to compare our model-based estimates of parr densities to Gibbons et al.'s estimates for mainstem river reaches. We first apportioned our model-based estimates of total parr to mainstem reaches in direct proportion to the ratio of the estimated total area of mainstem rearing to total (mainstem plus tributary) rearing area (Table 4). From table 4, these proportions are 0.232, 0.312, and 0.377 for estimated total mainstem rearing habitat widths of 4, 6, and 8 meters, respectively. Each of the eight model estimates of total parr production were multiplied by these proportions to produce model-based estimates of parr production for the mainstem only (Table 5). Next, from the data in Gibbons et al.'s table 3 (excluding two river reaches discarded by Gibbons et al. as being from under-seeded habitats) we calculated adjusted total rearing areas of each reach from total reach lengths of the 16 remaining river reaches by multiplying total length by 4, 6, and 8 meters as we did for our estimates of historically available mainstem rearing habitat area. These adjusted areas represent the rearing habitat area that would

have been estimated by Gibbons et al. if the only habitat information they had were the reach lengths and they estimated rearing habitat area from these lengths following the approach we used to estimate historical rearing habitat area.

We then divided each of the three adjusted areas by the total measured areas of each of the 16 reaches reported in Gibbons et al.'s table 3, and calculated the average ratio of adjusted to total area of each area adjustments (reach widths of 4, 6, or 8 meters). The average ratios were 0.165, 0.248, and 0.331, respectively. These ratios estimate the amount by which our estimates of historical mainstem rearing habitat area would under-estimate the total area of the Stillaguamish river mainstem historically available to steelhead parr, if the average width of the Stillaguamish mainstem segments (North Fork, South Fork, and main river below the two forks) bore the same relationship to our three estimates of the width of mainstem rearing habitat as the widths of the reaches in Gibbons et al. table 3 bear to these estimates. We then expanded our estimates of historical mainstem rearing area by dividing each of our three estimates of the total rearing habitat area of the Stillaguamish mainstem (Table 4) by the appropriate corresponding ratio of adjusted-to-total area. Since total mainstem lengths are multiplied by the same estimated channel width to estimate both historical mainstem rearing area and the Gibbons et al. adjusted areas, each of the three expanded historical mainstem channel areas is the same: 3 782 000 m².

Our model-derived estimates of total parr rearing in the Stillaguamish river mainstem were then divided by the adjusted estimate of total mainstem habitat area (3,780,000 m²) to produce adjusted model-derived parr density estimates to compare to the estimates in table 3 of Gibbons et al. (B1). Our adjusted parr density estimates range from 0.050 for the most productive high

marine survival scenario to 0.187 for the least productive low marine survival scenario. The average density over all eight models ranges from 0.079 to 0.128. The mean over the four low marine survival scenarios ranges from 0.10 to 0.163, and for the four high marine survival scenarios ranges from 0.058 to 0.094 (Table B1).

Table B1. Modeled mainstem parr densities (parr/m²) for the eight models and 3 estimates of total mainstem rearing habitat area adjusted to total main channel area using data for mainstem snorkel reaches from Gibbons et al. 1985 Table3. The total adjusted mainstem channel area is the same for all three estimates of mainstem channel rearing habitat widths: 3,872,000 square meters. MS1, MS2, and MS3 are estimated mainstem rearing habitat areas for total channel widths of 4, 6, and 8 meters, respectively from Table 4. MS__T Area are the ratios of each estimated mainstem rearing area to the corresponding total mainstem-plus-tributary rearing area from Table 4. The ratios are 0.232, 0.317, and 0.377, respectively. Numbers in the columns MS_ Parr are the model-estimated numbers of total parr in the mainstem rearing area, the result of multiplying the number of total parr in each row by the appropriate MS__T Area ratio. MS_ Density is the parr density calculated dividing the corresponding total number of parr by the total adjusted mainstem channel area of 3,782,000 m².

Model	Total Parr	MS1 Parr	MS1 Density	MS2 Parr	MS2 Density	MS3 Parr	MS3 Density
L1	1,926,005	446,934	0.115	600,703	0.155	725,511	0.187
L2	1,435,288	333,062	0.086	447,653	0.116	540,662	0.140
L3	1,900,214	440,949	0.114	592,659	0.153	715,796	0.185
L4	1,420,379	329,602	0.085	443,003	0.114	535,046	0.138
H1	1,113,266	258,336	0.067	347,217	0.090	419,359	0.108
H2	831,380	192,924	0.050	259,300	0.067	313,174	0.081
H3	1,103,609	256,095	0.066	344,206	0.089	415,721	0.107
H4	825,993	191,674	0.050	257,620	0.067	311,145	0.080
Mean:	1,319,517	306,197	0.079	411,545	0.106	497,052	0.128
MeanLs	1,670,472	387,637	0.100	521,005	0.135	629,254	0.163
MeanHs	968,562	224,757	0.058	302,086	0.078	364,850	0.094

CHAPTER EIGHT

Synthesis of Results

The conservation value of integrating estimates of historical adult and juvenile salmon abundance with estimates of contemporary habitat quantity and quality.

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ABSTRACT.

The approach to estimating historic salmon and steelhead populations near the turn of the twentieth century is reviewed together with the use of life cycle modeling to estimate the juvenile (parr, smolt) production that achieved large unfished equilibrium adult abundance. The scaling of historic estimates of juvenile production to historic and current available freshwater rearing habitat is also reviewed together with estimates of historic juvenile capacity for the two case studies of Chapter 6 and 7. Several ways in which the estimates of juvenile rearing capacity from the two case studies can be employed under current conditions to develop management thresholds for rebuilding populations and to identify research that addresses critical uncertainties regarding the identification of management thresholds are presented and discussed to illustrate the value of the entire project. The results from Chapters 2 – 7 are shown to provide a robust approach for integrating estimates of historic salmon and steelhead abundance to contemporary conservation issues, particularly the development of recovery-based targets for rebuilding the juvenile production capacity of freshwater rearing habitats.

INTRODUCTION.

Populations of wild salmon and steelhead in what I have referred to as the historic period, that encompasses the late nineteenth and early twentieth centuries from approximately 1890 to 1930, several decades prior to the majority of the recent population declines, were considerably larger than their current levels (Chapter 1, Myers et al. 1998, Yoshiyama et al. 1998, Lichatowich 1999, Meengs and Lackey 2005, Gayeski et al. 2011, Price et al. 2013). This period is also the period during which freshwater spawning and rearing habitat began to be degraded through development of transportation infrastructure, urbanization, floodplain settlement and agricultural development, and timber extraction (Gayeski et al. 2011, Gottesfeld & Rabnett 2008). Many of these populations were subject to intense commercial fisheries at this time.

Compared to the ending decades of the twentieth and the first two decades of the twenty-first centuries, however, most freshwater salmon habitats in the historic period were relatively intact and healthy, if not totally pristine. Salmon populations in this historic period can provide useful benchmarks for the abundance and diversity of which minimally disturbed wild salmon and steelhead populations are capable. The key to obtaining the benchmarks from historic abundance is the availability of historic in-river commercial catch data, which may make it possible to achieve credible estimates of the abundance of the populations from which the catches were obtained. Such benchmarks may be relevant to contemporary salmon conservation by helping to identify the conditions that permitted populations to attain and maintain levels of abundance that were considerably larger than today. This, in turn, may be relevant to conservation in one of two ways. It may help conservation planners and managers to temper rebuilding objectives by recognizing what is not attainable as a result of the loss of conditions that are unlikely, and perhaps impossible, to re-establish in the near future. Alternatively, such benchmarks can lead to a better understanding of how salmon populations operate which can, in turn, lead to the recognition that levels of abundance and diversity that are close to the levels that existed during the historic period may still be attained, and to the development of conservation actions that have a high probability of achieving such levels in the not too distant future. It is the objective of Chapters 2 – 7 to show how this latter alternative may be attained.

SUMMARY OF METHODS and RESULTS.

In this concluding chapter I first review the salient results of chapters 2 – 7, and then briefly synthesize how the results can support specific conservation research and monitoring objectives for the two cases described in chapters 3, 4, 6, and 7.

The first step, noted in chapters 1 and 2, is to obtain commercial catch data for the population of interest from a period early in the development of the commercial fishery that targeted the population of interest, so that the population was unlikely to have had time to experience changes in life history characteristics such as the distribution of mature ages and size-at-maturation in response to the sudden imposition of harvest-induced mortality on top of pre-existing levels of natural mortality. It is also important that the commercial catch occur during the period before motorized fishing vessels enable commercial fisheries to fish far from river mouths and estuaries where they would be likely to encounter multiple conspecific salmon populations, an unknown proportion of which would be from rivers of origin other than that of the population of interest. If this can be achieved, the resulting estimate of population abundance will have a high probability of being very close to the unfished, or equilibrium abundance of the population immediately prior to the beginning of intense commercial fisheries.

Chapter 2 evaluated the appropriateness of two probability distributions (likelihoods) that appear to be reasonable to employ to estimate the total returning adult salmon (or steelhead) populations subject to commercial harvest. The results from a variety of simulated salmon run and catch data showed that both the binomial and negative binomial (parameterized as a Gamma-Poisson) achieve comparable results for the total catch for an entire season if employed in a Bayesian estimation framework, provided that a modestly informative prior probability distribution for the harvest rate can be provided. Where this is not possible and a broad uniform prior distribution for the harvest rate must be adopted, the negative binomial may provide more conservative estimates of total abundance than the binomial, though the difference is unlikely to be very great.

Chapter 3 described in detail the application of the negative binomial likelihood to estimate the historic abundance of Skeena River chum salmon circa 1920, using the geometric mean of the commercial catches for the four-year period (corresponding to the average generation time of Skeena chum salmon) 1916 to 1919. This case study showed how a moderately informative prior on the harvest rate of Skeena chum salmon was obtained from the combination of several prior distributions on elements of the commercial harvest in the lower Skeena targeting sockeye and coho salmon in addition to chum salmon. This illustrated how historic information on the conduct of the fishery could be combined to informatively delimit the range of the harvest rate that most likely was applied to chum salmon during this period. The results yielded an estimate of the Skeena chum population for the period, in the form of a posterior probability distribution of the size of the run, that was well-estimated with a coefficient of variation (posterior standard deviation/posterior mean) of 10% (0.10) and a well-defined posterior mode (most probable value) of 325,000 from the geometric mean catch of 154,000.

Chapter 4 described the approach taken by Gayeski et al. (2011) to estimating the total abundance of Stillaguamish River, Puget Sound, steelhead in 1895 from a single year's commercial catch using the binomial likelihood, and compared the estimation of the prior distribution on the harvest rate in that case to the estimation in the case of Skeena chum from chapter 3. This illustrated the diversity in data quantity and quality that may be available for parameterizing a prior probability distribution for the harvest rate in such historic cases. The analysis by Gayeski et al. (2011) also illustrated the flexibility provided by a Bayesian approach by describing how qualitative and quantitative historic information concerning the development of European settlement in the Stillaguamish basin at the time could be incorporated to estimate a significant level of non-commercial in-river harvest of steelhead by Indian tribes and settlers on the floodplain, which added to the commercial harvest data and enabled a more precise estimate of the possible range of the harvest rate to be obtained for the prior distribution. This increased the precision of the posterior distribution of the total steelhead population for 1895.

The two estimates of the adult populations (Stillaguamish steelhead and Skeena chum) were compared to show the increased precision of the estimate of Skeena chum that was attained due to the greater amount of information that was available for parameterizing the prior distribution

of the harvest rate. The posterior distribution of the Stillaguamish steelhead population had a coefficient of variation of 20% (0.20) compared to 10% for Skeena chum salmon. Despite the greater uncertainty of the steelhead estimate, the estimate was still highly informative, with the 95th percentile of the posterior distribution of the total population only 1.93 times greater than the posterior 5th percentile compared to 1.37 for the Skeena chum estimate, and a well-defined posterior mode of 69,200. The estimate of Stillaguamish river steelhead abundance in 1895 was sufficiently narrow to demonstrate a large and significant decline in total adult abundance by the last two decades of the twentieth century that was considerably greater than the estimated amount of rearing and spawning habitat accessible to steelhead that had been lost during this period. Together, the estimates of historic adult abundance for the two case studies provide benchmarks for comparing the levels of abundance that have been lost since those periods in the not-too-distant past, approximately one century ago.

Chapter 3 and 4 left unanswered whether either estimate of historic abundance has more relevance to current conservation issues pertaining to the two populations than scaling the loss of total abundance. This issue is addressed in part in chapters 6 and 7.

Chapter 5 provided another detailed case study, Skeena River sockeye salmon in which a more traditional stock-recruit analysis was applied to estimate the unfished equilibrium abundance of a historic salmon population subjected to an intense commercial fishery for several generations and for which life-history information was available. The availability of estimates of the proportion of adult age at return from samples of the commercial catch and research on the age distribution of component populations of the aggregate Skeena sockeye population harvested in the lower river commercial fishery enabled several hypothetical annual runs and associated brood year spawner and recruit data sets to be estimated for brood (spawning) years 1888 to 1913 and subjected to a Bayesian stock-recruit analysis.

The parameters estimated from the stock-recruit analyses were employed to estimate the levels of the unfished equilibrium abundance associated with each data set. These were then compared to simple non-Bayesian applications of Method I that applied the binomial likelihood to geometric mean commercial catches for five-year periods corresponding to well-defined point

estimates of the harvest rate from previous published studies. The abundance estimates from the simple application of Method I were several hundred thousand greater than those from the stock-recruit analyses, all of which were close to a value of 2,000,000. However, the posterior distributions of the stock-recruit analyses all encompassed the simple point estimates within the central 90%-iles of each.

As in the cases of Stillaguamish steelhead and Skeena chum salmon the Bayesian analysis provided generally well-defined estimates of both the most probable value of the equilibrium abundance of Skeena sockeye during the historic period, but properly represented the uncertainty of the estimate. However, due to the greater amount of information available, including life-history information that is generally rare for historic commercial fishery data, the posterior distributions of the stock-recruit analyses of Skeena sockeye were more precise than that for Stillaguamish steelhead, and of similar precision to that for Skeena chum. The most precise estimate for Skeena sockeye was for data set #2 (coefficient of variation, c.v., = 0.084). The c.v. of the estimate for the average data set (data set #6) was 0.091. The data set with the least precise estimate, data set #4, had a c.v. of 0.123.

Chapter 6 extended the results for Skeena chum from Chapter 2 to the estimation of juvenile production associated with the estimated adult return based on the geometric mean catch of 154,000 for 1916-1919 of 325,000 of which 312,000 were estimated to have been produced by non-estuary tributaries. The estimated juvenile production was based on an age-structured life-cycle model of Skeena chum salmon that made use of available historic data for the adult age-structure, data for the fecundity of Skeena chum based on length, and allometric modeling of age-specific mortality based on size-at-age and annual growth increments. The juvenile production estimated to have produced the posterior mode of the adult return of 312,000 and the posterior 5th and 95th percentiles of abundance (297,000 and 408,000, respectively), was measured as number of smolts of an average length of 65 millimeters in the estuary and nearshore of the Skeena at the time of migration to open ocean rearing areas in July. After obtaining an estimate of the total number of smolts, the amount of mainstem and tributary juvenile chum rearing habitat during the historic period and under current conditions was estimated using data from the Riverscape Analysis Project (RAP) database. The estimate of

available juvenile rearing habitat and total historic smolt numbers were then used to estimate the rearing densities of juvenile chum associated with the estimated historic adult abundance. The results yielded estimates of total smolt production that ranged from 12,200,000 to 16,700,000, with a mode of 13,300,000 which corresponded to freshwater rearing densities of 0.90 to 1.24 smolts/m², with a mode of 0.99/m² (Chapter 6, Table 5).

Chapter 6 noted that there is some controversy regarding the extent to which juvenile, post-emergent chum salmon rear in freshwater as opposed to rapid migration to estuarine or nearshore marine habitats as pink salmon (*Oncorhynchus gorbuscha*) do. To address this I also provided estimates of the numbers of adult chum spawners per kilometer of length of the Skeena River mainstem at equilibrium for several segments of the Skeena available to Skeena chum in the historic period and showed that these numbers were comparable to those available for several contemporary chum populations in Washington State, whose numbers are reduced relative to historic conditions. This provides collateral information supporting the inference that the numbers of chum estimated in Chapter 3 for the historic period are not unrealistically large.

Chapter 7 described the development of an age-structure model for the Stillaguamish River steelhead population in 1895 whose total adult abundance was estimated from the 1895 commercial catch by Gayeski et al. (2011) and summarized in chapter 4. The model incorporates a realistic, complex adult age structure with four mature age classes (ages 3 to 6) including three repeat-spawner age classes (ages 4 to 6). The proportions of mature ages and repeat spawners at each age present in the average annual return at the unfished equilibrium of the 1895 population were based on comparable data from steelhead populations in western Kamchatka and the total weight in pounds of the estimated commercial and non-commercial harvest of Stillaguamish steelhead in 1895. The total weight of the catch provided a constraint to the adult age distribution, since the modeled population had to achieve the estimated total weight of the 1895 catch when harvest of the modeled population was simulated at the estimated average harvest rate (Chapter 7, Figure 1).

The estimation of the total numbers of juvenile parr (age 1) that produced the estimated total adult return in 1895 required estimates of both freshwater density-dependent survival (from

emergent fry to parr) and density-independent marine (post-smolt) survival to each mature and immature age for all ages 3 to the maximum age (6). The McGurk (1996) integrated annual growth-mortality allometric model, described in Chapter 6, was parameterized to achieve annual age-specific survival rates for two different marine survival scenarios, one “low” and one “high. The two marine survival scenarios spanned a broad range of total adult cohort lifetime survival rates (0.4 and 0.8) that span the range of values that are likely to have been experienced by Puget Sound steelhead during the historic period based on the available literature (Chapter 7). A set of parameter values for freshwater density dependent fry survival and density independent parr-to-smolt (age 2) survival were also chosen on similar grounds to bracket a reasonable range of post-emergence survival during the period of freshwater rearing. This resulted in a total of eight population models, four for each of the two marine survival scenarios.

The primary purpose of parameterizing a broad range of marine and freshwater survival values was to evaluate the full range of potential parr production values that may have produced the 1895 equilibrium. These values represent the capacity of the freshwater environment for producing parr, and thus smolts (modeled as age 2). The resulting parr capacity values were then translated into parr densities (#parr/m²) using recent estimates from NOAA Fisheries of the length and area of mainstem and tributary rearing habitats in the Stillaguamish River for the historic period and under current conditions (Chapter 7). The parr densities for the mainstem habitat of the Stillaguamish River were estimated by scaling mainstem habitat area to the width of the shallow shoreline (defined in Chapter 6) by multiplying the estimated main channel length in meters by 4, 6, and 8 meter widths. The results (Chapter 7, Table 5) showed that parr rearing densities estimated for the historic period were comparable to several recent estimates of steelhead and rainbow trout rearing densities in tributary streams up to fourth stream order in California, Idaho, and Washington States. The estimated densities were re-scaled to estimated total main channel rearing area in order to compare the model-derived densities to estimates of current steelhead parr rearing densities under fully seeded conditions made in the mid-1980s by Washington Department of Fish and Wildlife (Gibbons et al. 1985; Chapter 7, Appendix B).

The average parr rearing densities estimated for the historic period over the range of estimates of total rearing area ranged from 0.49/m² to 0.61/m² for the low marine survival scenarios and from

0.29/m² to 0.35/m² for the high marine survival scenarios (Table 5). The average over all low and high marine survival scenarios ranged from 0.39/m² to 0.48/m². The estimates of mainstem rearing densities alone re-scaled to total mainstem area ranged from 0.10/m² to 0.16/m² for the average of the low marine survival scenarios to 0.06/m² to 0.09/m² for the average of the high survival scenarios, and averaged from 0.08/m² to 0.13/m² across all low and high scenarios (Chapter 7, Appendix Table B1). The average across all low and high marine survival scenarios (0.08/m² to 0.13/m²) is only slightly greater than the average range from Gibbons et al. 1985 (0.05/m² to 0.12/m²).

DISCUSSION.

Applying the results of Chapter 6 and 7 to contemporary salmon and steelhead conservation and management.

The life cycle modeling undertaken in chapters 6 and 7 facilitates the separation of the total life cycle from spawning and egg deposition to adult return the following generation into freshwater and marine periods, linked to one another by the migration of smolts from freshwater to ocean entry. Managers have little, if any, practical control over natural marine mortality rates, but considerable control to undertake measures that may improve survival during the freshwater part of the life cycle. The modeling in chapters 6 and 7 can inform expectations regarding actions undertaken to improve freshwater survival and suggest research and monitoring topics that can help to track progress of such actions.

Skeena chum.

Chapter 6 provides two different measures of juvenile chum capacity estimated for the historic period that can be employed to derive near-term benchmarks for population rebuilding. The first measure is provided by the estimates of total smolt production at the circa 1920 equilibrium from the 5th, modal, and 95th percentiles of the posterior distribution of the adult abundance scaled to the remaining amount of historic rearing habitat currently remaining (96%). The second measure is provided by the scaling of total smolt numbers to the estimated total remaining freshwater rearing habitat area to yield estimates of rearing densities as #smolts/m².

The current realized capacity of the Skeena River basin for chum salmon may therefore be measured either as total numbers of juveniles (smolts) produced or by the densities of juveniles rearing in an appropriate suite of rearing off-channel floodplain and shallow shoreline rearing habitats. It is this latter that is currently controversial, based on uncertainty regarding the extent if any to which Skeena chum salmon rear in freshwater habitats prior to and/or during migration to the Skeena estuary. This uncertainty could be addressed by appropriate pilot research to evaluate the feasibility of monitoring post-emergence floodplain rearing of chum. If validated, a statistically valid suite of monitoring sites could then be established and monitored. Here the principal response variable would be juvenile chum densities. A complementary (or alternative) approach that may be more logistically feasible is to estimate the total production of smolts, either by the use of smolt traps near the Skeena estuary or sampling of selected sites in the estuary using beach seines.

Once an appropriate and feasible method of estimating the production of juvenile chum is established, benchmarks or target levels of juvenile abundance can be chosen based on target levels of adult recruitment chosen for the four Skeena chum conservation units (CUs, Chapter 1). Estimation of the total annual production of smolts is essential for estimating the marine survival of Skeena chum salmon cohorts. The life cycle model (Chapter 6) estimated the average cohort smolt-to-adult return (SAR) survival rate at the circa 1920 equilibrium as 2.3% (0.0234). It is known that SARs of most salmon and steelhead populations from the eastern Pacific rim are lower than they were several decades ago, including perhaps during the historic period (Quinn 2005). In chapter 6 it was noted that if the current SAR of Skeena chum salmon were as low as 0.5% (0.005), 12,200,000 smolts, the posterior 5th percentile of the current smolt capacity estimate, would recruit at least 60,000 adult chum (30,000 females), which is considerably greater than the recent five-year average of 9,000 or fewer. Chapter 6 also noted that there is extensive chum salmon spawning habitat in the Skeena that is well in excess of the amount needed by 30,000 female chum salmon. If the SAR were actually greater, say 1.5% (0.015), only 4,000,000 smolts would be required to return 60,000 spawners.

A figure such as 60,000 adult spawners and/or 12,000,000 smolts, fewer if the SAR is greater than 0.005, might thus serve as an initial benchmark for the total for all four Skeena chum CUs. It is also advisable that any such figure be subjected to a quantitative population viability analysis (PVA) to estimate the viability of such a relatively small chum salmon population in a catchment as large and generally healthy as the Skeena. But the present discussion is sufficient to provide a clear idea of how the estimates of adult and juvenile abundance from the life cycle model in Chapter 6 may be applied to help identify key contemporary research and monitoring tasks to conserve and rebuild Skeena chum salmon.

Stillaguamish steelhead.

Chapter 7 also provides estimates of potential total steelhead parr production in the Stillaguamish River based on the 1895 equilibrium. Estimates are provided for both a low and high marine survival scenario for four different parameterizations of freshwater emergent fry-to-smolt survival. It was shown that under the high marine survival scenario, fewer parr are required to achieve the equilibrium adult return of approximately 40,000 females than under the low marine survival scenario (969,000 vs. 1,670,000 (Chapter 7, Table 5). The cohort smolt-to-adult survival of Puget Sound steelhead under current conditions is closer to the low marine survival scenario than to the high survival scenario (PSSTRT 2013, Ward & Slaney 1993, Welch et al. 2000). Consequently, parr rearing density estimates derived from the low marine survival scenario are more appropriate for determining rebuilding targets for Stillaguamish River steelhead for the foreseeable future.

Rearing densities for the Stillaguamish were estimated by assuming functional shallow shoreline rearing habitat widths of 4, 6, and 8 meters (both banks) for main channel habitat. Under the low marine survival scenario, the estimated average densities for the 1895 equilibrium ranged from 0.49 to 0.61 parr-per-square meter of mainstem rearing habitat. Extended to the total width of the main channel, these estimates are equivalent to 0.10 to 0.163 parr-per-square meter (Chapter 7, Table B1). Under current conditions, the estimates of steelhead parr densities in main channel habitats of the Stillaguamish River estimated by Roni et al. (2010, Chapter 7) are 0.035 parr-per-square meter. Accordingly, the range of densities for the four freshwater survival models under

the low marine survival scenario provide a reasonable set of target recovery densities, starting with the lowest value (0.10) which is nearly three times as large as current densities.

A target interim recovery objective for the Stillaguamish River of 0.10 age-1 parr-per-square meter of total main channel habitat provides a value around which habitat monitoring and research can be developed. Chapter 7 discussed several hypotheses about the causes of the reduction in rearing densities of Stillaguamish steelhead evidenced by Roni et al (2010)'s data: loss of channel complexity, reduction in the flux of diet items available to drift feeding juveniles, increase in territory defended by individual juveniles, and increased metabolic costs of foraging due to rising summer/fall stream temperatures.

These four hypotheses suggest several critical field-based research topics that all can be addressed simultaneously by selecting an appropriate suite of micro- and reach-scale main channel and tributary rearing habitat units for focused study of diet flux, consumption, individual foraging territory, and individual condition and growth. Such research would help to estimate the current maximum parr density of the highest quality habitats and would permit a more robust evaluation of reach-scale habitat improvement actions by focusing evaluation on the issue of the extent to which the actions increase local densities and achieve appropriate individual fish condition and growth trajectories.

Chapter 7 noted that an important feature of the loss of rearing habitat since the historic period is due to the simplification of channel structure (loss of complexity), particularly the loss of in-channel woody debris and the loss of process that form and maintain channel braiding and island formation. These features of channel complexity result in an increase in the number and area of micro-habitat units of high quality that can support high target rearing densities. Channel simplification results in considerably fewer such areas per length of main channel than when channels are more complex. If monitoring of parr rearing densities in studied main channel habitats reveals densities near or at target densities, but total parr numbers per kilometer of mainstem habitat remain low, this will reveal that lack of channel complexity is a primary limiting condition, requiring directed corrective action.

In addition to informing directed field research, the results of the modeling in Chapter 7 show the importance of estimating parr numbers in addition to smolt numbers to estimate post-parr freshwater survival as well as to estimate adult-to-parr survival or egg-to-parr survival (the latter from estimates of spawner age composition and age-specific fecundity).

These are, of course, highlights of but a few research and monitoring topics that the results of the life cycle model of Chapter 7 can identify. Prioritizing which, if any, to undertake can, of course, only be determined in the context of a total steelhead recovery planning effort. Be this as it may, the results from the model indicate that field-based research topics such as the ones described are likely to provide critical data that will help to effectively and efficiently direct freshwater steelhead recovery planning.

Conclusions.

The overview of the Dissertation project provided in this chapter serves to unify the elements of the six main chapters. Chapter 2 to 5 show the several principal approaches available for estimating the abundance of historic salmon and steelhead populations subject to large commercial catches early in the period of development of large commercial fisheries. Chapter 6 and 7 illustrate how estimates of historic abundance can be informatively connected to contemporary conservation of at-risk salmon and steelhead populations by employing age structured life cycle models together with measurements and estimates of historic and current freshwater juvenile rearing habitats. The total approach is capable of addressing many of the uncertainties that attend the estimation of the several key quantities of interest.

Given an estimate of the size of an historical population of interest and a life-cycle model appropriate to that population, parameter values can be identified that will reproduce the estimated historic run size (total adult return), numbers harvested, and (if available) the average weight and age of the catch. The immediate value of this kind of exercise is an estimate of the numbers of spawners, eggs deposited and/or juveniles that would be required in order for a population exhibiting the life history depicted by the life-cycle model to have produced the historic catch and total estimated adult return. The number of juveniles required during the freshwater rearing portion of the life-cycle of the species provides the critical measure, albeit an

estimate, of the capacity of the freshwater habitat extant at the time of the historical harvest. If data regarding the amount of juvenile rearing habitat for the population exists for the historical period of interest, or can be estimated, the estimated total numbers of juveniles can be scaled to provide an estimate of the historical per-unit-area productivity of juvenile rearing habitats. This can then be employed to derive an index of the potential productivity of current habitat for the species as total numbers of parr or smolts or as mean numbers per square meter of freshwater rearing habitat.

Viewing the productive potential of contemporary salmon populations from the perspective of freshwater juvenile production potential derived from such historical estimates has several potential benefits for managing for population recovery and resilience over the common alternative of estimating adult spawner and adult recruitment relationships or population growth rates based on annual measures (estimates) of adult population sizes. First it circumvents the need to consider and estimate the marine survival of a salmon population when monitoring the effect of population recovery action directed at freshwater habitat. This makes it possible for a clear partition of indices of salmon population performance between factors affecting survival in freshwater and saltwater environments. Second, it gives a clear quantitative expectation for the productive potential of freshwater spawning and rearing habitats thus making it easier to identify the impacts of salmon harvest and marine survival on recruitment dynamics and population rebuilding.

Salmon conservation and sustainable management requires focussed research to resolve identified critical uncertainties and to help to identify robust targets thresholds for management. The approach described and carried out up to the point of directed field research in chapters 2 – 7 provides a way of linking robust estimates of historic salmon abundance and juvenile production to contemporary population conservation and rebuilding. It is hoped that this contribution will help make past levels of salmon abundance more relevant to the current and future management of these icons of healthy aquatic/terrestrial ecosystems.

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