Fisheries and Oceans Canada
Science

Pêches et Océans Canada
Sciences

Canadian Science Advisory Secretariat (CSAS)

Research Document 2014/089

Pacific Region

Estimating Regional Distributions of Freshwater Stock Productivity, Carrying Capacity, and Sustainable Harvest Rates for Coho Salmon Using a Hierarchical Bayesian Modelling Approach

Josh Korman[1] and Arlene Tompkins[2]

[1]Ecometric Research Inc. and Department of Zoology
University of British Columbia
3560 W 22nd Avenue
Vancouver, BC V6S 1J3

[2]Fisheries and Oceans Canada
3190 Hammond Bay Road
Nanaimo, BC V9T 6N7

November 2014

Foreword

This series documents the scientific basis for the evaluation of aquatic resources and ecosystems in Canada. As such, it addresses the issues of the day in the time frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

Research documents are produced in the official language in which they are provided to the Secretariat.

Published by:

Fisheries and Oceans Canada
Canadian Science Advisory Secretariat
200 Kent Street
Ottawa ON K1A 0E6

http://www.dfo-mpo.gc.ca/csas-sccs/
csas-sccs@dfo-mpo.gc.ca

ISSN 1919-5044

Correct citation for this publication:

Korman, J. & A. Tompkins. 2014. Estimating Regional Distributions of Freshwater Stock Productivity, Carrying Capacity, and Sustainable Harvest Rates for Coho Salmon Using a Hierarchical Bayesian Modelling. DFO Can. Sci. Advis. Sec. Res. Doc. 2014/089. vii + 53 p.

TABLE OF CONTENTS

ABSTRACT

We estimated regional distributions of freshwater stock productivity (smolts/spawner at low spawning stock size) and carrying capacity (smolts/km when spawners are not limiting) for Coho salmon to support a simulation analysis intended to describe the tradeoff between harvest and conservation in mixed-stock fisheries. The objectives of this analysis are to: determine the most suitable form of a freshwater stock-recruitment model using information theoretic and other criteria; estimate and compare regional distributions of freshwater stock-recruitment parameters from alternate models; estimate regional distributions of sustainable harvest rates under different marine survival regimes; and to determine the validity of applying the estimated regional stock-recruitment distributions to streams in the Georgia Basin West (GBW) management unit and the Thompson River drainage.

We compiled spawner-to-smolt data from 16 coastal streams supporting Coho salmon in Oregon, Washington, and BC (n=251)**.** We used a hierarchical Bayesian modeling approach because it correctly weighs the contribution of each stream to the regional distribution based on its information content. Hierarchical Beverton-Holt (BH), Ricker (RI), and Logistic Hockey Stick (LHS) models fit the data well and were consistent with the assumed lognormal error structure. There was considerable shrinkage in all hierarchical models, as evidenced by the relatively low number of effective parameters (pD= 17-23) relative to the total number of parameters that were estimated (K=37 and 55 for standard and depensatory models, respectively). Although an additional 18 parameters were estimated for the depensatory BH model, the effective number of parameters was similar to values for non-depensatory models. This indicated little evidence for depensation in the data. Estimates of the depensation parameter were largely determined by the prior distribution. The Beverton-Holt model had a substantially lower deviance information criteria (DIC) statistic than the Ricker (ΔDIC=43.2) and Logistic Hockey Stick (ΔDIC=70.6) models, indicating that the former model had the best out-of-sample predictive power. The mean and standard deviation of the lognormal regional distributions for stock productivity for the BH model was 71 smolts/spawner (σ_α=0.49) and 1564 smolts/km (σ_α=0.67), respectively. The form of the stock-recruitment function had a significant influence on the regional distributions of stock productivity, but little effect on distributions for carrying capacity. Regional distributions of stock productivity based on LHS and RI models had lower means (31 and 49 smolts/spawner, respectively) and lower variability (σ_α = 0.32 and 0.38, respectively) compared to the distribution based on the BH model.

Regional distributions of harvest rate (Umsy) that resulted in maximum sustainable yields were computed based on samples from the marginal predictive distributions of stock productivity and carrying capacity from the Beverton-Holt model. As expected, Umsy declined considerably at lower marine survival rates (ms). In the worst scenario (ms=0.025), 15% of the streams represented in the regional distributions could not sustain a viable population, even in the absence of harvest. Modal Umsy values at ms=0.025, 0.05, and 0.10 were 0.25, 0.45, and 0.65, respectively.

The product of mean smolt capacity per km of stream from the predictive regional distribution (2052 smolts/km) and total accessible stream length (1335 and 2268 km for GBW and Thompson, respectively) under predicted adult recruitment at full seeding by about 2-fold for GBW and overestimated recruitment by a similar magnitude for the Thompson River drainage. In the case of the Thompson, it is possible that the total amount of stream length used for rearing was overestimated because larger mainstem reaches comprised about 50% of the total. There was good agreement between predicted and escapement-based estimates of adult recruitment when 6th and 7th order reaches were removed (total length after removal = 1105 km). In the case of GBW, where recruitment at full seeding was underestimated, accessible stream length could have been underestimated, as many productive side-channel habitats

would not be shown on a 1-50,000 map-scale. Comparison of map- and field-based estimates of habitat for Black Creek however suggests the latter method underestimates habitat by only about 15%. Thus, other factors must have contributed to the discrepancy between escapement- and habitat-based carrying capacity estimates. We suspect that the historical escapement data overestimates wild stock capacity because it includes an unknown, but potentially large component of hatchery-origin fish. In the absence of reliable estimates of naturally produced escapement, the comparison of predicted and observed carrying capacities for GBW remains inconclusive.

Simulated aggregate escapement trends, driven by historical exploitation and marine survival rates and random draws from the marginal distributions of spawner-to-smolt stock-recruitment parameters, agreed well with the observed aggregate trend for the Thompson drainage. Simulations also matched the observed decline in escapement in GBW until the late 1980s, but substantially under predicted escapement from 1990 to the present. As marine survival for wild stocks for this latter period in GBW is likely reasonably well defined by index stocks and has a declining trend, and there is no indication from the stock-recruitment analysis that freshwater productivity has declined, it seems likely that the aggregate escapement trend for GBW does not represent the trend for wild stocks, or is at least inconsistent over the time series. Further analysis would benefit from a rigorous review of GBW escapement data that would include removing the hatchery component. In general, the simulations tended to over predict the extent of declines in abundance relative to what has been observed, even in the case of the Thompson drainage, where hatchery returns are removed from escapement estimates. Thus, there was no indication from the simulation analysis that the regional distribution of freshwater productivity estimated from the hierarchical stock-recruitment analysis over-represents more productive stocks in GBW or the Thompson drainage.

Estimation des répartitions régionales de la productivité des stocks en eau douce, de la capacité de charge et des taux de prélèvement durables du saumon coho en fonction d'une méthode de modélisation bayésienne hiérarchique

RÉSUMÉ

Nous avons estimé les répartitions régionales de la productivité des stocks en eau douce (ratio saumoneau/géniteur lorsque la taille du stock des géniteurs était faible), ainsi que la capacité de charge (ratio saumoneau/km lorsque les géniteurs ne sont pas un facteur limitant) du saumon coho afin de soutenir une analyse par simulation visant à décrire le compromis entre la récolte et la conservation dans les pêches d'espèces multiples. Les objectifs de cette analyse sont les suivants : déterminer la forme la plus appropriée d’un modèle stock-recrutement en eau douce en fonction de l'information théorique et d'autres critères; estimer et comparer les répartitions régionales des paramètres stock-recrutement en eau douce en fonction d'autres modèles; estimer les répartitions régionales des taux de prélèvement durables dans le contexte de différents taux de survie en mer; déterminer la validité de l'application des répartitions régionales de stock-recrutement estimées dans les cours d'eau de la zone de gestion du bassin de Géorgie – Ouest (BGO) et du bassin de la rivière Thompson.

Nous avons compilé les données « du géniteur au saumoneau » de 16 cours d'eau côtiers qui comptent des saumons coho en Oregon, dans l'État de Washington et en Colombie-Britannique (n = 251)**.** Nous avons utilisé une méthode de modélisation bayésienne hiérarchique parce qu'elle effectue correctement la pondération de la contribution de chaque cours d'eau à la répartition régionale à partir du contenu d’information. Les modèles hiérarchiques de Beverton-Holt (BH), de Ricker (RI) et logistiques de « bâton de hockey » [Logistic Hockey Stick – LHS] s’ajustent bien aux données et étaient conformes à la structure d'erreur lognormale présumée. Il y a eu un rétrécissement considérable dans tous les modèles hiérarchiques, comme le montre le nombre relativement faible de paramètres efficaces (pD = 17-23) par rapport au nombre total de paramètres qui ont été estimés (K = 37 et 55 pour les modèles standards et anticompensatoires, respectivement). Même si 18 paramètres supplémentaires ont été estimés pour le modèle anticompensatoire de BH, le nombre effectif de paramètres était semblable aux valeurs des modèles non anticompensatoires. Cela indique qu'il y a peu d'éléments de preuve à l’appui d’un effet anticompensatoire dans les données. Les estimations du paramètre de l'effet anticompensatoire ont été établies en grande partie selon la distribution préalable. Le modèle de BH présentait des statistiques relatives au critère d'information de déviance (DIC) considérablement plus faibles que le modèle de RI (ΔDIC = 43,2) et de LHS (ΔDIC = 70,6), ce qui indique que le modèle de BH a eu la meilleure pouvoir explicatif hors échantillon. La moyenne et l'écart-type des répartitions régionales lognormales de la productivité du stock du modèle de BH étaient de 71 saumoneaux/géniteur (σ_α = 0,49) et de 1 564 saumoneaux/km (σ_α = 0,67), respectivement. La forme de la fonction de stock-recrutement a eu une incidence significative sur les répartitions régionales de la productivité du stock, mais peu d'incidence sur les répartitions de la capacité de charge. Les répartitions régionales de la productivité du stock dérivées des modèles LHS et de RI ont eu des moyennes plus faibles (31 et 49 saumoneaux/géniteur, respectivement) et une variabilité plus faible (σ_α = 0,32 et 0,38, respectivement) par rapport à la distribution fondée sur le modèle de BH.

Les répartitions régionales du taux de prélèvements (Urms) qui ont donné lieu à des rendements maximaux soutenus ont été calculées d'après des échantillons des répartitions prédictives marginales de la productivité du stock et de la capacité de charge provenant du modèle de BH. Comme prévu, Urms a diminué considérablement à des taux de survie en mer (sm) plus faibles. Dans le pire des scénarios (sm = 0,025), 15 % des cours d'eau représentés

dans les répartitions régionales ne pouvaient soutenir une population viable, et ce, même à l'absence des récoltes. Les valeurs Urms modales à des taux de sm de 0,025, 0,05 et 0,10 étaient de 0,25, 0,45 et 0,65, respectivement.

Le produit de la capacité moyenne en saumoneaux par km de cours d'eau dérivé de la répartition régionale prédictive (2 052 saumoneaux/km) et de la longueur totale des cours d'eau accessibles (1 335 et 2 268 km pour le BGO et le bassin de la rivière Thompson, respectivement) selon un recrutement adulte prévu en ensemencement complet était environ deux fois plus élevé pour le BGO et a surestimé le recrutement pour le bassin de la rivière Thompson par un ampleur semblable. Dans le cas du bassin de la rivière Thompson, il est possible que la longueur totale de cours d'eau utilisé pour l'élevage ait été surestimée parce que des tronçons principaux plus grands constituaient environ 50 % du total. Les estimations de recrutement d'adultes prévues et en fonction des échappées concordaient bien lorsque les tronçons du 6^{e} et 7^{e} ordre ont été retirés (longueur totale après le retrait = 1 105 km). Dans le cas du BGO, lorsque le recrutement en ensemencement complet était sous-estimé, la longueur des cours d'eau accessibles aurait pu être sous-estimée aussi, étant donné que de nombreux habitats productifs des chenaux latéraux n'apparaissent pas sur une carte à l'échelle 1 : 50 000. La comparaison entre les estimations de l'habitat du ruisseau Black basées sur les cartes et sur les observations sur le terrain suggère toutefois que la seconde méthode sous-estime l'habitat de seulement 15 %, environ. Par conséquent, d'autres facteurs ont contribué à l'écart entre les estimations de capacité de charge basées sur les échappées et celles basées sur l'habitat. Il est possible que les données historiques sur les échappées surestiment la capacité des stocks sauvages parce qu'elles comprennent une composante inconnue, et possiblement importante, de poissons d'élevage. En l'absence d'estimations fiables des échappées naturelles, la comparaison des capacités de charge prévue et observée pour le BGO demeure peu concluante.

Les tendances simulées des échappées totales des populations comigratoires, dictées par les taux historiques d'exploitation et de survie en mer et les tirages aléatoires parmi les répartitions marginales des paramètres stock-recrutement et géniteur-saumoneau conviennent bien à la tendance globale des populations comigratiores observée dans le bassin de la rivière Thompson. Les simulations correspondaient également au déclin observé des échappées dans le BGO jusqu'à la fin des années 1980, mais elles ont considérablement sous-estimé les échappées des années 1990 à aujourd'hui. Puisque la survie en mer des stocks sauvages pour cette dernière période dans le BGO est vraisemblablement assez bien définie par les stocks indicateurs, qu'elle affiche une tendance à la baisse et que l'analyse du stock-recrutement n'indique pas que la productivité en eau douce a diminué, il semble probable que la tendance pour le BGO des échappées totales des populations en comigration ne représente pas la tendance pour les stocks sauvages ou, du moins, qu'elle ne soit pas uniforme au cours de la série chronologique. Un examen rigoureux des données sur les échappées du BGO, qui comprendrait la suppression de la composante provenant d'écloseries, pourrait contribuer à une analyse approfondie. En règle général, les simulations avaient tendance à surestimer l'ampleur des déclins de l'abondance par rapport à ce qui a été observé, et ce, même dans le cas du bassin de la rivière Thompson, où les montaisons de saumons d'élevage ne font pas partie des estimations des échappées. Par conséquent, l'analyse de simulation n'indique pas que la répartition régionale de la productivité en eau douce estimée à partir de l'analyse du stock-recrutement hiérarchique surreprésente les stocks plus productifs dans le BGO ou dans le bassin de la rivière Thompson.

1. INTRODUCTION

A group of populations with different productivities will exhibit highly divergent responses to a common harvest regime (Ricker 1958). At an intermediate harvest rate, weak or unproductive populations will be depleted and possibly extirpated, while highly productive ones will be under-exploited. Under fixed escapement or abundance-based harvest rate policies, the carrying capacity of individual populations must also be considered. Conservation concerns for Coho salmon in southern British Columbia require that harvest regimes be evaluated based on the response of multiple populations in a management unit, rather than on the aggregate response. Evaluation of harvest regimes in this setting therefore requires estimation of distributions that reflect the variation in carrying capacity and stock productivity among populations. The objective of this analysis is to define regional distributions of freshwater productivity and carrying capacity for Coho salmon in southern BC to evaluate the efficacy of a range of fixed harvest rate and abundance-based harvest rate policies.

In this analysis, carrying capacity is defined, as the number of smolts produced per length of accessible stream when spawning stock size is not limiting. Capacity will be determined by the amount of habitat and the magnitude of compensatory mortality. Stock productivity is defined as the slope at the origin of the spawner-to-smolt relationship and depends on fecundity and maximum (density-independent) incubation and juvenile survival rates. The product of freshwater stock productivity and marine survival rate will determine the maximum sustainable harvest rate and the rate at which populations recover from overharvesting or extended periods of low marine survival. Since the relationship between smolt and adult production is commonly thought to be density independent, estimating stock-recruitment parameters for the freshwater stage of the Coho salmon life cycle has the advantage of providing reference points for a range of marine survival scenarios. The use of an abundance-based harvest rate rule as recommended by the Pacific Salmon Commission (PSC 2004) requires an estimate of the carrying capacity for each management unit to define status. This can be calculated by multiplying a length-standardized carrying capacity estimate by the total productive stream length in the management unit. The product of total smolt production for a management unit and marine survival determines adult recruitment at full seeding, that in turn can be used as a reference point to define specific harvest rate thresholds according to abundance-based harvest rules.

Dramatic declines in Coho salmon escapements (Simpson et al. 2004) over the last two decades have motivated much analysis of existing stock-recruitment data, and some of these analyses have focused on estimating regional distributions of stock productivity and capacity. In this analysis we improve on past efforts using extended datasets and a hierarchical Bayesian approach. Bayesian hierarchical stock-recruitment models have been applied to Atlantic salmon spawner-to-smolt data (Michielsens and McAllister 2004, Prevost et al. 2001), but not to any Pacific salmon data to date. Bradford et al. (2000) developed regional distributions of freshwater productivity and capacity for Coho salmon by computing the mean and variance of stock-recruitment parameters estimated individually for 13 streams. Barrowman et al. (2003) and Chen and Holtby (2002) show that such an approach can lead to overestimates of the mean and variance of regional distributions, leading in turn to overestimates of the sustainable harvest rate. The form of the stock-recruitment model has been shown to have a large influence on stock productivity and carrying capacity estimates (Barrowman and Myers, 2000). The use of hockey stick and Ricker stock-recruitment models in the analyses of Bradford et al.

(2000) and Chen and Holtby (2002) to estimate regional distributions of stock productivity were not rigorously supported. The hockey stick model, with its abrupt transition, is poorly suited for estimating uncertainty in stock-recruitment parameters, an essential element for determining regional distributions (Barrowman et al. 2003). The Ricker, and especially the Beverton-Holt model, potentially overestimate stock productivity in cases where there is little information about recruitment at low stock size (Barrowman and Myers 2000). Chen and Holtby (2002) concurred with this assessment of the Beverton-Holt model for Coho salmon, but concluded that the Ricker model could provide reasonable estimates of stock productivity for management purposes. They used the Ricker model because it produced lower estimates of stock productivity leading to more conservative harvest rates. Model selection should be based on objective statistical criteria (e.g., out-of-sample predictive power sensu Burnham and Anderson 2002) or policy performance (Walters and Martell 2004) where trade-offs between conservation and harvest are transparent to decision makers.

The objectives of this analysis are to:

1) determine the most suitable form of a stock-recruitment model for the freshwater phase of Coho salmon based on a rigorous assessment of fit, bias, and information loss associated with alternate models;
2) to estimate and compare regional distributions of stock productivity and smolt carrying capacity based on alternate stock-recruitment models in a Bayesian hierarchical modeling framework;
3) to estimate regional distributions of sustainable harvest rates under different marine survival regimes; and to
4) determine the validity of applying the regional stock-recruitment distributions to represent populations in the Georgia Basin West management unit and the Thompson River drainage.

The main advantage of a hierarchical model is that it correctly weighs the contribution of each stream or population to the regional distribution based on its information content. For example, stock productivity estimates will be highly uncertain for streams where there is little information about smolt production at low escapement. It makes little sense that parameter estimates in these cases should contribute equally to the regional distribution relative to other streams where stock productivity is better determined from the data. This is why hierarchical models tend to produce regional parameter distributions that often have less variance (sometimes referred to as 'shrinkage'), and lower means than those developed by estimating parameters individually for each stream (e.g. Chen and Holtby 2002), and why estimates of independently-derived regional distributions, such as those in Bradford et al. (2000), have been criticized. By using a Bayesian hierarchical model to objectively assess alternate stock-recruitment models, this analysis addresses limitations of the previously published estimates of regional distributions of stock-recruitment parameters for Coho salmon (Chen and Holtby 2002, Chen et al. 2002, Bradford et al. 2000).

2. METHODS

We use a hierarchical Bayesian model to jointly estimate stream-specific spawner-to-smolt stock-recruitment parameters as well as hyper-parameters that define their regional distributions. The regional distributions of productivity and carrying capacity are of direct interest in this analysis. Stream-specific estimates are considered nuisance parameters but need to be estimated to determine regional distributions. The data (section 2.1), model structure (2.2), methods for model estimation (2.3), model comparison (2.4), and evaluation of the applicability of regional distributions for populations in the Georgia Basin West (GBW) management unit (MU) and the Thompson River drainage (2.5) are described below.

2.1. DATA

We compiled spawner-to-smolt data from 16 coastal streams in Oregon, Washington, and BC (Tables 1 and A1). The majority of this information was originally compiled and analyzed by Bradford et al. (2000). In this analysis, we have updated data sets from Big Beef, Black, Carnation, and Snow Creeks and included data from two new systems (Queets and Skagit Rivers). The meta-analysis assumes that each dataset used in the analysis represents a single and entire population. This is unlikely the situation for all 16 streams because some likely represent only a component of the total population. We therefore refer to individual datasets as ‘streams’ rather than populations, and make the assumption in the meta-analysis that the stock-recruitment parameters for these streams are representative of the dynamics for the wider population. Further, while the abundance of spawners and smolts are relatively well determined in these streams, they may not provide a representative sample of all streams in southern BC because: 1) the sample may over-represent streams with higher productivity and/or carrying capacity (Bradford et al. 2000); and 2) the majority of streams in the dataset are coastal systems in Washington and Oregon and may therefore not be representative of coastal and especially interior streams in British Columbia.

The alternate dataset to estimate regional distributions of stock productivity and carrying capacity is the DFO salmon escapement data (SEDS), which includes information for tens to hundreds of streams within each management unit. Due to its extensive coverage, the SEDS data in theory would allow better definition of regional distributions (e.g., Chen and Holtby 2002, Walters 2009). However, distributions developed from the SEDS data will be highly uncertain because of methodological problems and inconsistencies in escapement estimates within and among streams over time. In addition, to back-calculate smolt recruitment from escapement requires application of uncertain exploitation and marine survival rates (e.g., Folkes et al. 2005). Such estimates are available for only a few stocks and typically for shorter time periods than the period over which escapement data is available.

In this analysis we estimate regional distributions of stock productivity and carrying capacity using spawner-to-smolt data only. These data have considerably less observation error than SEDS data and are therefore more useful for determining the best form of the stock-recruitment relationship and the regional distribution of stock-recruitment parameters. However, we use SEDS data from streams in the GBW management unit and the Thompson River drainage to evaluate whether regional distributions of stock-recruitment parameters developed from the spawner-to-smolt data can reproduce trends in the aggregate escapement in these areas.

2.2. MODEL STRUCTURE

We evaluated fits of hierarchical Beverton-Holt (BH), Ricker (RI), and Logistic Hockey Stick (LHS) stock-recruitment models to spawner-to-smolt data from multiple streams. The form of the Beverton-Holt applied here (following Sharma and Hilborn 2001) is:

$$R_{i,t+x} = \frac{S_{i,t}}{\frac{1}{\alpha_i} + \frac{S_{i,t}}{\beta_i}} \tag{1}$$

where, $R_{i,t+x}$ is the number of smolts from stream ‘i’ in year ‘t+x’ (x=2 and 3 for age-1 and -2 yr. smolts, respectively), $S_{i,t}$ are the number of spawners for the same stream that produced those smolts, α_i is the initial slope of the line and is equivalent to the number of smolts produced per spawner at low density (freshwater stock productivity), and β_i is the maximum number of smolts that can be produced per km of stream when stock size is not limiting (freshwater carrying capacity). The form of the Ricker model used here is:

$$R_{i,t+x} = \alpha_i S_{i,t} e^{-\delta_i S_{i,t}} \tag{2}$$

where, δi is the reduction in survival due to increasing density. In this analysis, estimation of βi (maximum number of smolts) is of interest and is calculated from $\frac{\alpha_i}{\delta_i} e^{-1}$ (Hilborn and Walters 1992). This parameterization is convenient because the interpretation of the estimated parameters αi and βi is consistent across stock-recruitment models.

The form of the Logistic Hockey Stick model (Barrowman and Myers 2000) is:

$$R_{i,t+x} = \alpha_i C\delta_i (1+e^{\frac{-1}{C}}) \left[\frac{S_{i,t}}{C\delta_i} - \log(\frac{1+e^{(S_{i,t}-\delta_i)/(C\delta_i)}}{1+e^{\frac{-1}{C}}}) \right] \tag{3}$$

where,

$$\delta_i = \frac{\beta_i}{\alpha_i} \left[C(1+e^{\frac{-1}{C}}) \left(\frac{1}{C} + \log(1+e^{\frac{-1}{C}}) \right) \right]^{-1} \tag{4}$$

As for the previous stock-recruitment models α_i and β_i are estimated. C is a tuning parameter that determines the smoothness at the transition between the initial slope at low stock size and the asymptote at higher stock size. The logistic hockey stick model approaches the hockey stick model as C→0. In this analysis the tuning parameter was held constant at C=1 as in Barrowman and Myers (2000).

We evaluated depensatory versions of the Beverton-Holt, Ricker, and logistic hockey stick models. Following the approached used in Chen et al. (2002), we define a new parameter γ_i to represent the minimum spawning stock size where recruitment can be greater than zero (termed S_{offset} in Chen et al. 2002). For depensatory models, the ‘$S_{i,t}$’ term in the stock-recruitment equations (eqn.’s 1, 2, and 3) is replaced with the term ‘$S_{i,t} – \gamma_I$’.

2.3. ESTIMATION

Parameters of the hierarchical stock-recruitment models developed here include stock-specific values of productivity and carrying capacity, an estimate of the variance around each streams stock-recruitment curve, and hyper-parameters which describe the mean and extent of variation in productivity and carrying capacity values across streams. Estimated were derived using a Bayesian analysis, where the probability of model parameters depends on the likelihood of the data given the parameters as well as prior probabilities on model parameters.

We used a lognormal likelihood function to describe the form of error between predicted and observed smolt numbers. For the non-depensatory models, the log-likelihood function is,

$$L(R_{i,t} \mid \alpha_i, \beta_i, \sigma) = \frac{1}{\sqrt{2\pi\sigma^2}} e\left[-\frac{[\log(R_{i,t} - \hat{R}_{i,t})]^2}{2\sigma^2} \right] \tag{5}$$

where, $\hat{R}_{i,t}$ is the predicted number of smolts from eqn.'s 1, 2, or 3, and σ is the estimated standard deviation of the residuals around the stock-recruitment relationship which is assumed to be common among streams. σ represents variation in freshwater survival rate (i.e., process error) as we assume there is essentially no observation error in the data.

Stream-specific estimates of stock productivity and carrying capacity are assumed to belong to lognormal (*LN*) hyper-distributions:

$$\begin{aligned} P(\alpha_i) &\sim LN(\mu_\alpha, \sigma_\alpha) \\ P(\beta_i) &\sim LN(\mu_\beta, \sigma_\beta) \end{aligned} \tag{6}$$

Hyper-parameter means μ_α and μ_β, and standard deviations σ_α and σ_β define the regional (i.e., hyper) distributions for stock productivity and carrying capacity, respectively. Note that unlike Chen and Holby (2002), the model structure does not assume that there is a correlation between stock productivity and carrying capacity across streams. In empirical Bayes' methods, hyper-parameters would be estimated from related streams, but then treated as fixed and known in subsequent estimation of stream-specific parameters (e.g., Chen and Holtby 2002). In this analysis, which uses a Bayesian approach, hyper-parameters and nuisance stock-specific parameters are jointly estimated. Priors for the hyper-distribution parameters, or hyper-priors, denoted as $P(\mu_\alpha)$, $P(\sigma_\alpha)$, $P(\mu_\beta)$, and $P(\sigma_\beta)$, must therefore be specified. Lognormal and inverse gamma distributions were used for the hyper-priors for the means and standard deviations of the hyper-distributions, respectively. Prior distributions for all hyper-parameters (μ_α, μ_β, σ_α, σ_β) were very uninformative (Table 2).

For depensatory models, we include the extra parameter γ_i i in eqn. 5, as well as additional hyper-parameters μ_γ and σ_γ in eqn. 6. The mean of the prior distribution for the mean of the lognormal hyper-distribution for the depensation parameter was set at 1.9, which is equivalent to 6.6 spawners/km in linear space. This value was chosen based on the Soffset estimate for North Thompson River Coho salmon of 5,211 spawners from Chen et al. (2002) standardized by the estimated accessible habitat for the North Thompson of 790.7 km (Interior Fraser Coho Recovery Team 2006). There was little information about depensation in the 16 spawner-to-smolt datasets. We therefore needed to increase the extent of information in the prior distribution for μ_γ in order to get the hierarchical model to achieve reasonable convergence of posterior distributions. We set the standard deviation of the prior for the regional mean for μ_γ to 1 (Table 2).

The total probability of parameter values given the data is the product of the prior probabilities for the hyper-parameters, the probability of the stream-specific parameter estimates given the hyper-parameter estimates, and the likelihood of the data given the stream-specific parameters. For non-depensatory and depensatory models the total probabilities are, respectively:

$$\begin{aligned} &P(\alpha_i, \beta_i, \sigma, \mu_\alpha, \sigma_\alpha, \mu_\beta, \sigma_\beta \mid R_{i,t}) = \\ &P(\mu_\alpha)P(\sigma_\alpha)P(\mu_\beta)P(\sigma_\beta)\prod_i P(\alpha_i \mid \mu_\alpha, \sigma_\alpha)\prod_i P(\beta_i \mid \mu_\beta, \sigma_\beta)\prod_{i,t} L(R_{i,t|} \mid \alpha_i, \beta_i, \sigma) \end{aligned} \tag{7}$$

and,

$$\begin{aligned} &P(\alpha_i, \beta_i, \gamma_i, \sigma, \mu_\alpha, \sigma_\alpha, \mu_\beta, \sigma_\beta, \mu_\gamma, \sigma_\gamma \mid R_{i,t}) = \\ &P(\mu_\alpha)P(\sigma_\alpha)P(\mu_\beta)P(\sigma_\beta)P(\mu_\gamma)P(\sigma_\gamma)\prod_i P(\alpha_i \mid \mu_\alpha, \sigma_\alpha)\prod_i P(\beta_i \mid \mu_\beta, \sigma_\beta)\prod_i P(\beta_i \mid \mu_\gamma, \sigma_\gamma)\prod_{i,t} L(R_{i,t|} \mid \alpha_i, \beta_i, \gamma_i, \sigma) \end{aligned} \tag{8}$$

Posterior probability distributions were estimated using the WinBUGS software (version 1.4). A total of 37 parameters were estimated for non-depensatory models: 2 parameters per stream ($\alpha_i + \beta_i$) * 16 streams+ 1 common variance parameter (σ) + 4 regional parameters defining hyper distributions (μ_α, μ_β, σ_α, σ_β). In the case of depensatory models, an additional 16 stream-specific parameters (□) and 2 additional hyper-parameters (μ_γ and σ_γ) were estimated, for a total of 55 parameters. Posterior distributions were estimated based on a total sample of 3000 parameters from each of 3 chains that were initialized at divergent starting values. The first 1000 simulations were discarded (burn-in), and every second simulation value was taken from the remaining 2000 samples of each chain for the posterior sample. Thus, the final posterior samples were determined from 1000 simulated values from each of the 3 chains. Gelman et al's potential scale reduction factor was used to evaluate convergence of posterior distributions (Gelman et al. 2003). The scale reduction factor compares the difference in the variation of parameter values within chains to the variation among chains. When these two types of variation reach similar values, that is, when the scale reduction factor is close to one, the posterior distributions are considered to have converged.

The ultimate objective of the hierarchical analysis is to develop regional distributions of stock productivity and carrying capacity to drive a simulation model that evaluates the trade-off between conservation and fishery objectives in a setting where populations with varying productivity experience a common harvest regime. Generating these regional distributions using the expected values defining the hyper-distributions (μ_α, μ_β, σ_α, σ_β) can underestimate the true uncertainty in stock-specific values because there is also uncertainty in hyper-distribution estimates. Thus, to compute the predictive regional distributions for productivity and capacity to drive the simulation study, 10,000 sets of hyper-parameter values were randomly drawn from the joint posterior distribution of hyper-parameters with each pair defining a regional distribution of stock productivity and carrying capacity. A single random draw from each of these 10,000 distributions was then taken to define stream-specific productivity and carrying capacity. These values were aggregated over all draws to generate marginal predictive posterior distributions for productivity and capacity. The same general approach was used to develop the marginal predictive posterior distribution of variation around the spawner-to-smolt stock-recruitment curve (σ). However, in this case, we took random draws from the posterior distribution of σ. We also derived regional distributions of harvest rate and spawning stock size that resulted in maximum sustained yields. For each randomly drawn value of productivity and capacity, we computed adult recruitment as the product of the predicted smolt production given a spawning stock size, and an assumed marine survival rate. Yield was then computed as the difference between total adult recruitment and recruitment required for replacement. A nonlinear iterative search procedure was used to identify the spawning stock size that maximized yield (MSY). The harvest rate that produced MSY (Umsy) was calculated by dividing MSY by the predicted recruitment at MSY. The analysis was conducted using marine survival rates of 2.5, 5.0, and 10.0%.

2.4. MODEL-FIT AND COMPARISONS

Model-fit was evaluated by examining plots of predicted and observed spawner-to-smolt relationships and analysis of residuals. Pearson residuals (PR), which express the deviation relative to the predicted variability, were computed from:

(9)
$$PR_{i,t} = \frac{\log(\hat{R}_{i,t}) - \log(R_{i,t})}{\sigma}$$

Residuals were plotted as a function of spawning stock size and brood year to evaluate whether the functional form of the model was adequate and whether there was evidence for non-stationarity, respectively. The standard deviation (SDR) and median of the absolute residuals (MAR) were computed for each stream. SDR and MAR should have respective expected values of 1 and 0.67 if residuals are normally distributed. The χ^2 goodness of fit test statistic was used to test the null hypothesis that the models fit the data. The discrepancy between predicted and observed values was computed as:

(10)
$$X^2 = \sum_{i,t} \frac{(\log(R_{i,t}) - \log(\hat{R}_{i,t}))^2}{\log(\hat{R}_{i,t})}.$$

X^2 approximates the χ^2 distribution with degrees of freedom = n-1 (Sokal and Rolf 1981). Given n=251 smolt-spawner observations across 16 streams, there is not sufficient evidence to reject the null hypothesis, that is, model fit can be considered adequate, if $X^2 < \chi^2_{.05[250]}$ where $\chi^2_{.05[250]}=214.4$.

Hierarchical models were compared using the Deviance Information Criteria (DIC, Gelman et al. 2003). DIC quantifies the tradeoff between model fit and complexity for hierarchical models and is computed as:

(11)
$$DIC = 2\hat{D}_{avg} - D_{\hat{\theta}}$$

where, $\hat{D}_{avg}$ is the average deviance (-2* P() as defined in eqn.s 7 or 8) across the posterior sample, and $D_{\hat{\theta}}$ is the expected deviance computed by 'plugging-in' the expected values for each parameter from their posterior distributions into eqn.'s 7 or 8.

The difference between $\hat{D}_{avg}$ and $D_{\hat{\theta}}$ is termed the effective number of parameters (pD). pD approximates the number of 'unconstrained' parameters in the model, where a parameter counts as: 1 if it is estimated with no constraints or prior information; 0 if it is fully constrained or all the information about the parameter comes from the prior distribution; or an intermediate value if both the data and prior distributions are informative (Gelmen et al. 2003). In the hierarchical models developed here, stream-specific parameters are treated as random-effects as they are assumed to originate from lognormal hyper-distributions. When there is insufficient information to estimate stream-specific parameters based on data from each stream alone, the number of effective parameters will be considerably less than the total number of parameters. This situation is often referred to as ‘shrinkage’. Extensive shrinkage indicates that the hyper-distributions have a substantive influence on stream-specific estimates. Alternate models were compared based on differences between model-specific DIC values (DIC_i) and the model with the lowest DIC (DIC_{min} , $\Delta_i = DIC_i - DIC_{min}$). Δ_i values represent the level of empirical support for each model. We used the levels suggested by Burnham and Anderson (2002) for the Akaike information criteria, the maximum likelihood equivalent of DIC, to classify the amount of support for each model ($\Delta_i < 2$ = strong; $2 < \Delta_i < 10$ = considerably less; $\Delta_i > 10$ essentially no support).

2.5. EVALUATION OF REGIONAL DISTRIBUTIONS OF STOCK-RECRUITMENT PARAMETERS FOR SIMULATING COHO POPULATION DYNAMICS IN GEORGIA BASIN WEST AND THE THOMPSON RIVER

We evaluated whether regional distributions of stock-recruitment parameters developed from the hierarchical model would generate trends in aggregate escapements in the Georgia Basin West management unit and the Thompson River drainage that were consistent with historical observations. This required a synthesis of GIS data to estimate freshwater habitat capacity in these regions (2.5.1), compilation of historical harvest rate, marine survival rate, and escapement data (2.5.2), and simulation of historical aggregate escapement trends (2.5.3).

2.5.1 Freshwater Habitat

The BC Watershed Atlas (WA) provides a digital inventory of all blue lines that are drawn on NTS 1:50,000 scale maps. The WA contains a “Historical Fish Distribution” layer that defines the upstream limit for anadromous salmonids. These limits were determined based on observed fish presence and known barriers as recorded in the FISS database updated to the year 2000. We extracted all stream reaches from the fish distribution layer that were accessible to anadromous salmonids within Georgian Basin West and Interior Fraser management units. Streams outside of the Thompson River drainage were excluded because the abundance of mid- and upper-Fraser Coho salmon populations is very likely not limited by habitat (J. Irvine and M. Bradford, Fisheries and Oceans Canada, pers. comm.). Thus, application of a simple habitat-based model in this case would substantially overestimate the true capacity of these streams. As well, the status of populations in the Thompson drainage is the most important conservation issue for south coast Coho salmon and it is therefore reasonable to focus the analysis in this area. The sum of accessible stream length from the Watershed Atlas was used to determine the number of km of freshwater rearing habitat for Coho salmon in GBW and the Thompson River drainage.

2.5.2 Escapement, Harvest Rate, and Marine Survival Trends

The sum of annual escapements from all streams that are surveyed in GBW and the Thompson River drainage was computed from SEDS records to produce aggregate escapement trends. SEDS contained escapement data from 97 streams in GBW and 87 streams in the Thompson River drainage. For the Thompson, we used the same escapement data compiled in Folkes et al. (2005), while data from GBW was obtained directly from the SEDS database. The Thompson escapement time series excludes hatchery contributions but data were not available to do this for GBW streams.

We used annual marine survival rates determined from CWT returns from wild and hatchery indicator stocks to develop historical time series (return years 1975-2005) of marine survival rates for wild stocks in the GBW MU and the Thompson drainage (Table A2). An aggregate marine survival rate for GBW streams for return years 1986-2005 was computed by averaging the rates from Black Creek and Salmon River wild index stocks. To estimate marine survival rates from 1975-1985 for GBW wild stocks (a period when marine survival rates for wild stocks is not available), we multiplied the average annual survival rates from GBW and the Lower Fraser River (LFR) hatchery stocks (Big Qualicum, Chilliwack, and Inch) for this period by the ratio of wild-to-hatchery survival rates during the 1980s (1.5). The Quinsum River hatchery stock was not included in the analysis because its northern location might result in an overestimate of typical hatchery survival for stocks using the Strait of Georgia.

Data on marine survival for wild smolts originating from the Thompson River is not available to directly calculate the historic trend. We assumed that the trend in the average marine survival rates for Thompson River hatchery stocks (Eagle and Salmon Rivers, and Louis, Lemieux, and Spius Creeks, Irvine et al. 2001) for brood years 1987 to 2001 represented the trend for wild stocks, and that the ratio of survival rates of wild and hatchery fish for GBW stocks is the same as the ratio for hatchery and wild Thompson stocks. To estimate the aggregate marine survival rate for wild Thompson stocks, the marine survival rates form Thompson River hatchery stocks (available for return years 1990-2005) were increased by multiplying their values by the ratio of annual wild-to-hatchery survival rates for GBW stocks over this time period (range of 1.7 to 3-fold). For the period prior to availability of marine survival rates for Thompson hatchery stocks (return years 1975-1989), we calculated values by multiplying the wild GBW estimate for each year by the average ratio of the estimates for wild Thompson and wild GBW survival rates (0.79) during the period of overlap. We also considered using the wild marine survival trend from the Salmon River (LF) to represent survival rates for Thompson stocks rather than using the approach just described. However, such an assumption would provide a relatively optimistic view of historical wild survival rates for Thompson stocks, as the average marine survival for comparable periods (1987-2001) for the Salmon River (0.069) was 50% higher than the estimate for the Thompson composite index (0.046).

Historical exploitation rates for the Thompson and GBW aggregates were also required to evaluate regional distributions of capacity and productivity. The exploitation trend for GBW was based on the average exploitation rates for Goldstream, Black, Big Qualicum, Chilliwack, Inch, and Salmon Rivers (Table A3). The Quinsum hatchery stock was not included in the analysis because its northern position could result in substantially different harvest rates compared to more southern stocks that spend more time in the Strait of Georgia. We used harvest rates reported in Table 3 of Folkes et al. (2005) for the Thompson River aggregate.

2.5.3 Simulation of Aggregate Escapement Trend

The trend in the aggregate escapement for GBW and the Thompson River drainage between 1975 and 2004 was simulated as follows:

1) A random draw from the predictive marginal distributions of stock productivity and carrying capacity were used to determine stock-recruitment parameters for each simulated stream in the GBW or the Thompson drainage. The number of independent populations is uncertain, so both low (10) and high (90) values were simulated.

2) The mean number of smolts produced for each stream per unit stream length was calculated based on parameters sampled from the predictive marginal distributions of Beverton-Holt stock productivity and carrying capacity parameters. Smolts were predicted for each timestep based on the escapement 2 years earlier. The mean smolt number was multiplied by a lognormal random deviate to simulate variation in freshwater survival rate (σ=0.42 determined from stock-recruitment analysis).
3) The number of returning spawners per unit stream length was computed based on the product of the smolt production from the previous year, and the historical marine survival rate and the proportion of fish surviving harvest (1-historical harvest rate) for the return year.
4) The escapement in each year for GBW or the Thompson drainage was computed as the sum of the product of stream-specific escapements and the number of km of stream length per stream. The latter values were simply the ratio of the total number of km of accessible habitat (Section 2.5.1) divided by the number of streams that were simulated.

The average observed escapement over the first 3 years, divided by the number of streams, was used to initialize the simulations. The procedure was repeated 500 times, and the distribution of aggregate annual escapements across trials was plotted over time and compared to the observed aggregate escapement trend.

3. RESULTS

3.1. MODEL FIT AND COMPARISON

Hierarchical Beverton-Holt (BH), Ricker (RI), Logistic Hockey Stick (LHS), and depensatory Beverton-Holt spawner-to-smolt stock-recruitment models all fit the data well (Figures 1-4). The extent of uncertainty in stock productivity and carrying capacity varied across streams and depended on the amount of information on smolt production at low and high spawning stock size, respectively. The Ricker model predicted strong overcompensation for many of the streams even though there was little evidence of declining smolt production at higher escapements (Fig. 2). This behaviour was most apparent for streams where there was little information about stock productivity because there were few or no observations at low spawning stock size. It was very difficult to achieve convergence for depensatory stock-recruitment models because there was little indication in the data of depensatory smolt production (Fig. 4). In spite of using a moderately informative prior on the depensation parameter relative to other parameters (Table 2), it was not possible to get depensatory stock-recruitment models to achieve reasonable convergence. The depensatory Beverton-Holt model was the most stable of the three, but still had scale reduction values for depensation parameters ranging from 1.1-1.4, as opposed to other models, where all parameters had reduction factors very close to 1.0. As seen by the fits of the expected model and a random sample from the posterior distributions, most estimates of the depensation parameters were near zero (Fig. 4).

Expected values for stock productivity varied considerably among model types, but estimates of carrying capacity were very similar (Table 3). The Beverton-Holt model had higher stock-productivity values relative to RI and LHS models, a result consistent with other analyses (e.g., Barrowman et al. 2003). There was considerable shrinkage in all hierarchical models, as seen by the relatively low number of effective parameters (pD= 17-23) compared to the total number of parameters that were estimated (K=37 and 55 for standard and depensatory models, respectively). Although an additional 18 parameters were estimated for the depensatory BH model, the effective number of parameters was similar to values from non-depensatory models. This indicates little evidence for depensation in the data, which was also supported by depensation parameter estimates tending to be very close to those determined from prior probabilities. The Beverton-Holt model had substantially lower DIC values than the Ricker (ΔDIC=43.2) and Logistic Hockey Stick (ΔDIC=70.6) models, indicating that the former model had the best out-of-sample predictive power. The DIC for the depensatory BH model was similar to the standard BH model (ΔDIC=3.3). However, considering the poor convergence of this model its DIC value and parameter estimates are not reliable.

The fit of all spawner-to-smolt models that were evaluated was adequate (Table 4). On average, the models explained 37-38% of the variation in smolt numbers. The X^2 statistics ranged from 6.3-7.9, well below the $\chi^2_{.05[250]}$ threshold of 214.4. Thus, there was not sufficient evidence to reject the null hypothesis that the models fit the data. The structural forms of all stock-recruitment models were consistent with the assumption that residuals are log normally distributed. The standard deviation of Pearson residuals for most streams was close to 1 and the median absolute values of residuals were near the expected value of 0.67. Residual patterns were very similar for all hierarchical models so results for only the Beverton-Holt model are shown. Most streams did not show any temporal trend in residuals with the exception of Carnation Creek and Skagit River, where the model under predicted smolt production since the mid 1990's (Fig. 5). There was a positive trend in residuals for Flynn Creek. There was no apparent trend of higher positive residuals (over-predictions of smolt numbers) at low stock size that would be indicative of depensatory mortality (Fig. 6).

3.2. REGIONAL DISTRIBUTIONS OF STOCK-RECRUITMENT PARAMETERS AND SUSTAINABLE HARVEST RATES

The underlying stock-recruitment function had a significant influence on the regional distributions of stock productivity, but little effect on distributions for carrying capacity (Fig. 7). The means of the regional distributions of stock productivity were lowest for LHS and RI models and highest for the BH model. Differences between expected and predictive regional distributions were minor because expected estimates of σ_α and σ_β were already quite high. The marginal predictive distribution for carrying capacity was similar to the distribution from Bradford (1999), although his analysis showed a higher proportion of streams with very low carrying capacity. This difference could be caused by his larger sample of streams or because he assumed that stock size was not limiting in all cases. There was little effect of hyper-prior distributions on posterior distributions of regional parameters with the exception of the depensation parameter for the depensatory Beverton-Holt model (Fig. 8). In this case, the mean of the posterior distribution was largely determined by the mean of the hyper-prior. However, the variance in the mean of the regional depensation posterior is considerably less the variance of the hyper-prior. Thus, the data suggest less evidence for large values of depensation than implied by the hyper-distribution.

The predictive regional distribution of stock productivity estimated in this analysis based on the best stock-recruitment model (Beverton-Holt) was similar to distributions determined in other analysis (Fig. 9). Differences between our distribution and Bradford et al.'s (2000) were caused by small differences in data, but mostly due to their choice of the stock-recruitment function (hockey stick). The Barrowmen et al. (2003) distribution was determined using a Beverton-Holt mixed-effects model and the same data used in

Bradford et al. (2000). Their regional distribution was very close to ours. Distributions from Chen and Holtby (2002, southern BC) and Walters (2009) were based on a hierarchical Ricker model applied to SEDS data from the Thompson River and its tributaries (1975-1999, 60 streams), and southern BC (statistical areas 11-29, 1953-1986, 487 streams), respectively. To convert their estimates of stock productivity (adult recruits/spawner) into the units estimated here (smolts/spawner), we assumed that marine survival over the period of their analyses was 10%. The regional distribution from Chen and Holtby (2002) was similar to the distribution presented here, while the mean of the distribution from Walters (2009) was lower.

Distributions of harvest rate (Umsy) and spawner densities (Smsy) that result in maximum sustainable yields based on samples from the marginal predictive distributions for stock productivity and carrying capacity (Beverton-Holt model) and alternate marine survival scenarios are shown in Figure 10. Umsy declined considerably at lower marine survival. In the worst scenario (marine survival = 0.025), approximately 15% of the streams are unsustainable even in the absence of harvest. Modal Umsy values at ms=0.025, 0.05, and 0.10 were 0.25, 0.45, and 0.65, respectively. Escapement to achieve MSY increased at higher marine survival rates.

3.3. EVALUATION OF REGIONAL DISTRIBUTIONS FOR GEORGIA BASIN WEST AND THOMPSON RIVER COHO AGGREGATES

There were a total of 1,335 and 2,268 km of accessible stream length distributed over 245 and 118 streams in the Georgia Basin West management unit and the Thompson River, respectively (Table 5, Fig. 11). The estimate for the Thompson drainage is almost identical to the estimate of 2,239 km provided in the Interior Fraser Coho Conservation strategy (see Table 1 of IFCRT 2006). The carrying capacity for GBW and the Thompson River drainage to produce smolts, computed as the product of total stream length and the mean of the predictive marginal distribution for carrying capacity (Fig. 7, 2052 smolts/km), was 2.7 and 4.7 million smolts, respectively (Table 6). The expected adult recruitment when spawning stock is not limiting (i.e., at full 'seeding') for GBW and the Thompson River could be as low as 68,000 and 116,000 at a marine survival rate of 2.5%, and as high as 274,000 and 465,000 at a marine survival rate of 10%, respectively. We backcalculated historical adult recruitments based on annual escapements and exploitation rates (recruitment=escapement/(1-harvest rate)). Historical GBW and Thompson River recruitments were 334,000 and 95,000 between 1975 and 2004. The GBW recruitment, which occurred over a period when marine survival rate averaged about 8% (based on wild index stocks), was considerably higher than the predicted recruitment at full seeding of 274,000 spawners at a similar marine survival rate (10%). In contrast, the Thompson River historical recruitment of 95,000 (average wild marine survival =4.7%) was approximately ½ the recruitment estimate of 233,000 at a marine survival of 5%. In the case of the Thompson, we suspect we have overestimated the amount of stream length that contributes to Coho salmon production by including higher order mainstem reaches in the total. Removing 6th and 7th order systems (mainstem Lower Thompson, North Thompson, and Adams) reduced accessible stream length to 1105 km, and lead to good agreement between predicted (113,000) and backcalculated (95,000) recruitments (Table 6).

Marine survival rates for both GBW and Thompson populations have declined substantially over the period of record, reaching minimum values of 1.4% and 0.5% in return year 2005 and 1996, respectively (Fig. 12). Historical exploitation rates for GBW and Thompson populations were very similar and averaged about 70% prior to the fisheries closure in 1995. The Thompson River aggregate escapement trend was relatively constant at a average of 45,000 spawners between 1975 and 1988, after which it dropped substantially, reaching a minimum of about 6,000 spawners in 1996 (Fig. 13). The aggregate escapement trend for GBW has been relatively stable and did not show a decline in abundance that is expected based on the declining trend in wild marine survival. Reductions in harvest beginning in the 1995 would have partially offset the effects of reduced marine survival, but it was surprising that escapements did not decline in the 1980's when marine survival declined and exploitation rates remained high. We suspect that the GBW escapement data may not accurately reflect the escapement of wild populations because it includes hatchery contributions, which substantially increased over this period. Inconsistencies in monitoring effort over the time series could also have masked declines in wild populations.

The trend in across-trial medians of simulated escapement provided a reasonable match to the observed escapement trend for the Thompson aggregate (Fig. 13). In early years (1975-1980), the model substantially over predicted escapements, either because the extrapolated marine survival rates were overestimated, or because the stock was already well below carrying capacity as assumed at the start of the simulations. The model tended to accurately reflect escapement trends from the 1985-2005, capturing both the large decrease in escapement from 1987-1995 and the sustained low escapement from 1995-2000. There was no indication from the comparison that the regional distribution of freshwater productivity that drives the simulations over-represents productive stocks. If this were the case, the model would tend to under predict the extent of the decline in the 1990s. There was less agreement between predicted and observed aggregate escapement for Georgia Basin West. The model predicted a substantial decline in escapement beginning in the late 1980s due to reduced marine survival (Fig. 12), but the escapement data indicate that abundance has remained high. Given the consistent declining trend in marine survival over this period across wild indicator stocks, it is likely that the discrepancy is due to unaccounted increases in hatchery contributions to the aggregate escapement index or inconsistencies in monitoring effort.

The extent of variation around predicted annual aggregate escapements depended on the number of streams that were simulated. When only 10 streams were simulated (Fig. 13a) there was considerably more inter-trial variance because the probability of randomly selecting an unrepresentative sample of high or low stock productivities and carrying capacities from the regional distributions increased. Simulating more streams (e.g. 90 in Fig. 13b) provided a more representative sample from the marginal distributions of stock-recruitment parameters, resulting in simulated aggregate trends that were less variable among trials.

4. DISCUSSION

The hierarchical non-depensatory Beverton-Holt model had the best predictive power (Table 3) and provided the best fit (Table 4) to the coho salmon spawner-to-smolt data. All models that were evaluated fit the data relatively well (Fig.'s 1-4), however there was little evidence of overcompensation (Ricker) or depensation in smolt production (depensatory Beverton-Holt) in the data. There was considerable shrinkage in all the hierarchical models, indicating that the regional distributions had a substantive effect on stream-specific estimates. The mean of the regional distribution for stock productivity from the Beverton-Holt model was 71 smolts/spawer. The distribution determined in this analysis is likely the most robust estimate provided to date given the expanded data set, the use of a Bayesian hierarchical model, and the application of objective model selection criteria (Fig. 9).

Predicted regional distributions of stock productivity were used to define distributions of harvest rates that attain maximum sustainable yields (Umsy). At marine survival rates of 2.5%, typical of more recent values for south coast Coho salmon indicator populations, harvest rates as low as 20% are not sustainable for about half the streams modeled by the regional distribution (Fig. 10). Much higher harvest rates could be supported under improved marine survival, but only for a fraction of the streams. For example, at an improved survival rate of 5%, about 1/3rd of the streams could sustain a harvest rate of 60%, but this rate would not be sustainable for the majority of streams. In the 1970s and 1980s, when marine survival rates were likely 10% or greater (Fig. 12), historical harvest rates of 65% were sustainable for about 50% of the streams modeled by the regional distribution (Fig. 10). Thus, there was considerable overexploitation of lower productivity streams at this time even though marine survival rates were much higher than today. Over the 1990s, marine survival dropped substantially. Average marine survival and exploitation rates were 5% and 55%, respectively, resulting in overexploitation of about 75% of the streams in the regional distribution.

The predicted adult recruitment at full seeding, calculated as the product of the mean of the marginal distribution of smolt capacity, accessible stream length, and marine survival, was different than estimates derived from historical escapements and harvest rates. The model under predicted recruitment by about 2-fold for GBW and overestimated recruitment by a similar magnitude for the Thompson River drainage. In the case of the Thompson, it is possible that the total amount of stream length used for rearing was overestimated because larger mainstem reaches, which may only be used as migratory pathways, comprised about 50% of the total. There was good agreement between predicted and backcalculated recruitment when these reaches were removed from the analysis. There are two possible reasons why the recruitment to GBW determined from escapement and harvest rate data appears to be so much higher than the habitat-based estimate. First, accessible stream length could be underestimated as many productive side-channel habitats would not be shown on a 1-50,000 map-scale. Second, the GBW escapement includes hatchery-produced fish, while our approach for estimating adult recruitment at full seeding is only based on wild production. Brown et al. (1999) found that the linear stream length of Coho salmon habitat was underestimated by only 12% for Black Creek based on 1:20,000 TRIM maps. The estimate of anadromous habitat for Black Creek based on the 1:50,000 maps used in this analysis was 28 km, 16% lower than the field based estimate of 33 km. If this single comparison is representative of the underestimation of habitat from map-based methods, the majority of discrepancy between predicted and observed adult recruitment at full seeding must be due not excluding the hatchery component of adult recruitment to GBW, or due to temporal inconsistencies in escapement estimation methodologies.

Simulated aggregate wild escapements, driven by historical exploitation and marine survival rates and random draws from the marginal distributions of spawner-to-smolt stock-recruitment parameters, agreed well with the observed aggregate trend for the Thompson drainage (Fig. 13). Simulations also matched the observed decline in escapement in GBW until the late 1980s, but then substantially under predicted escapement after that. As marine survival for wild stocks for this latter period in GBW is likely reasonably well defined by index stocks and has a declining trend (Fig. 12), and there is no indication from the stock-recruitment analysis that freshwater productivity has declined (Fig. 5), it seems likely that the escapement trend for wild GBW populations is incorrect, or at least inconsistent over the entire time series. Further analysis would benefit from a rigorous review of GBW escapement data that includes the removal of the hatchery component of returns and corrections for changes in methodology over time. In general, the simulations tended to over predict the extent of population decline due to the combination of overexploitation and reduced marine survival. The datasets used to develop the marginal distributions of stock-recruitment parameters were from index streams that were not a random selection from all Coho salmon streams. It has been suggested that index streams may be more productive than the average stream, as unproductive systems with few or erratic numbers of fish are difficult to justify monitoring (Bradford et al. 2000). Our analysis suggests that this is not the case with respect to streams in the GBW management unit or the Thompson River drainage. The distributions of stock-recruitment parameters generated from the index stream data tended to predict a decline in population size that was more severe than what the escapement data suggests. This conclusion should be considered preliminary as marine survival and exploitation rates for Thompson populations are highly uncertain, and the GBW escapement data likely contains temporally varying and large hatchery contributions. However, taking the data at face value, it seems reasonable to use the regional distributions of freshwater carrying capacity and stock productivity developed from this hierarchical meta-analysis to represent the population dynamics for GBW and Thompson River stocks in a forthcoming simulation analysis that examines trade-offs between harvest and conservation in mixed-stock coho salmon fisheries.

5. ACKNOWLEDGEMENTS

Thanks to Blair Holtby, Mike Bradford, Michael Folkes, Jim Irvine, Michael Chamberlain, Kent Simpson, Eric Parkinson, Joseph Tadey, Gary Morishima, and Bob Hayman for providing data or useful commentary on this analysis.

6. REFERENCES

Barrowman, N.J., and R.A. Myers. 2000. Still more spawner-recruitment curves: the hockey stick and its generalizations. Can. J. Fish. Aquat. Sci. 57:665-676.

Barrowman, N.J., Myers, R.A., Hilborn, R., Kehler, D.G., and C.A. Field. 2003. The variability among populations of coho salmon in the maximum reproductive rate and depensation. Ecological Applications 13(3):784-793.

Bradford, M.J. 1999. Temporal and spatial trends in the abundance of coho salmon smolts from western North America. Trans. Am. Fish. Soc. 128:840-846.

Bradford, M.J., Myers, R.A., and J.R. Irvine. 2000. Reference points for coho salmon(*Oncorhynchus kisutch*) harvest rates and escapement goals based on freshwater production. Can. J. Fish. Aquat. Sci. 57: 677-686.

Brown, T.G., Barton, L., and G. Langford. 1999. Coho salmon habitat within Black Creek, Vancouver Island. Canadian Technical Report of Fisheries and Aquatic Sciences 117:546-551

Burnham, K.P., and D.R. Anderson. 2002. Model Selection and Multimodel Inference, 2nd ed. (Springer).

Chen, D.G., Irvine, J.R., and A.J. Cass. 2002. Incorporating Allee effects in fish stock-recruitment models and applications for determining reference points. Can. J. Fish. Aquat. Sci. 59:242-249.

Chen, D.G., and L.B. Holtby. 2002. A regional meta-model for stock-recruitment analysis using an empirical Bayesian approach. Can. J. Fish. Aquat. Sci.. 59: 1503-1514.

Folkes, M., Ionson, B., and J.R. Irvine. 2005. Scientific advice for input to the Allowable Harm Assessment for Interior Fraser Coho Salmon. DFO Can. Sci. Advis. Sec. Res. Doc. 2005/093. iv + 45 p.

Gelman, A., Carlin, J.B. Stern, H.S., and D.B. Rubin. 2003. Bayesian data analysis. Chapman and Hall/CRC. 668 pp.

Hilborn, R. and C.J. Walters. 1992. Quantitative fisheries stock assessment. Chapman and Hall, New York, NY.

Interior Fraser Coho Recovery Team. 2006. Conservation strategy for coho salmon (*Oncorhynchus kisutch*), interior Fraser River populations. Fisheries and Oceans Canada.

Irvine, J.R., C.K. Parken, D.G. Chen, J. Candy, T. Ming, J. Supernault, W. Shaw, and R.E. Bailey. 2001. Stock Assessment of Coho Salmon from the Interior Fraser River. DFO Can. Sci. Advis. Sec. Res. Doc. 2001/083. 67 p.

Michielsens C.G.J. and M.K. McAllister. 2004. Bayesian hierarchical analysis of stock-recruit data: quantifying structural and parameter uncertainties. Can. J. Fish. Aquat. Sci 61:1032-1047.

Prevost, E., Chaput, G., and E.M.P. Chadwick. 2001. Transport of stock-recruitment reference points for Altantic salmon. In stock, recruitment, and reference points: assessment and management of Altantic salmon. E. Prevost and G. Chaput (eds.). INRA, Paris.

Pacific Salmon Commission. 2008. Pacific Salmon Treaty, March 2004. 116 pp.

Ricker, W.E. 1958. Maximum sustained yields from fluctuating environments and mixed stocks. J. Fish. Res. Bd. Can. 15:991-1006.

Sharma, R., and R. Hilborn. 2001. Empirical relationships between watershed characteristics and coho salmon (*Oncorhynchus kisutch*) smolt abundance in 14 western Washing streams. Can. J. Fish. Aquat. Sci. 58:1453-1463.

Simpson, K., Chamberlain, M., Fagan, J., Tanasichuk, R.W., and D. Dobson. 2004. Forecast for southern and central British Columbia coho salmon in 2004. DFO Can. Sci. Advis. Sec. Res. Doc. 2001/083. viii + 69 p.

Sokal, R.R., and F.J. Rohlf. 1981. Biometry 2nd Edition. W.H. Freeman and Company. New York. 859 pp.

Walters, C.J. 2009. Variation in productivity of Southern British Columbia coho salmon (*Oncorhynchus kisutch*) stocks and implications for mixed-stock management. Univ. British Columbia Fisheries Centre, Working Paper Series 2009-02.

7. TABLES

Table 1. Sample size (N= number of years) for the 16 spawner-to-smolt datasets used in this analysis, the first and last year of data available for each time series, and the length of accessible Coho salmon rearing habitat used to standardize the data (km).

		Brood Yr		
Stream	**N**	**First**	**Last**	**km**
Big Beef	29	1976	2004	18
Big Qualicum	11	1961	1972	10
Bingham	10	1980	1989	22
Black	20	1985	2004	33
Carnation	34	1971	2004	3
Deschutes	17	1977	1996	54
Deer	13	1959	1971	2
Flynn	13	1959	1971	1
Hooknose	13	1947	1959	6
Hunts	11	1961	1971	5
Needle	12	1960	1971	17
Nile	5	1945	1951	1
Queets	20	1979	1998	6
Skagit	14	1989	2002	357
Skykomish	11	1968	1984	542
Snow	18	1976	1996	92
Total	251			

Table 2. Description of hierarchical stock-recruitment model parameters and priors. Values in parentheses represent the mean and standard deviation (SD) for lognormal distributions, and the shape and scale parameters for inverse gamma distributions.

Parameter	Description	Prior Distribution (type/value)
α_i	Stock productivity (by population)	Hyper Lognormal (μ_{α}, σ_{α})
β_i	Carrying capacity (by population)	Hyper Lognormal (μ_{β}, σ_{β})
γ_i	Depensatory stock size (by population)	Hyper Lognormal (μ_{γ}, σ_{γ})
σ	SD of stock-recruitment relationships	Inverse-gamma (0.001, 0.001)
μ_{α}	Mean of stock productivity hyper-distribution	Lognormal (4.7, 1000)
μ_{β}	Mean of carrying capacity hyper-distribution	Lognormal (7.3, 1000)
μ_{γ}	Mean of depensation hyper-distribution	Lognormal (1.9, 1)
σ_{α}	SD of stock productivity hyper-distribution	Inverse-gamma (0.001, 0.001)
σ_{β}	SD of carrying capacity hyper-distribution	Inverse-gamma (0.001, 0.001)
σ_{γ}	SD of depensation hyper-distribution	Inverse-gamma (0.001, 0.001)

*Table 3**.** Expected spawner-to-smolt stock-recruitment parameter estimates based on four hierarchical models. Expected values are the average from posterior distributions. See Table 2 for definition of model parameters. pD and DIC denote the effective number of parameters and deviance information criteria, respectively. ∆DIC is the difference in DIC values relative to the model with the lowest DIC.*

	Beverton-Holt		**Ricker**		**Logistic Hockey Stick**		**Depensatory Beverton-Holt**		
	α	β	α	β	α	β	α	β	γ
μ_x	4.25	7.34	3.82	7.30	3.42	7.32	4.40	7.28	0.74
σ_x	0.49	0.67	0.38	0.67	0.32	0.66	23.22	2.53	0.44
$\exp(\mu_x)$	71	1564	49	1499	31	1533	84	1473	4.62
σ	0.42		0.45		0.48		0.42		
Big Beef	73	2094	47	1974	30	1936	83	2014	1.51
Big Qualicum	106	3181	55	3485	24	2971	127	3136	2.89
Bingham	107	1469	56	1706	18	2347	130	1447	1.81
Black	74	3081	52	2968	36	3195	80	2997	0.77
Carnation	97	1536	67	1388	40	1493	116	1476	0.57
Deschutes	35	3267	30	2653	26	2391	43	2929	1.90
Deer	87	1812	64	1730	47	1860	109	1649	0.96
Flynn	88	617	56	652	32	715	110	583	0.31
Hooknose	107	1087	68	1014	35	1010	126	1059	0.92
Hunts	65	1134	41	1164	24	1215	77	1105	1.49
Needle	67	415	51	405	30	424	84	399	0.43
Nile	88	1171	62	1118	29	1196	91	1082	2.54
Queets	84	1280	64	1233	47	1328	103	1134	0.47

	Beverton-Holt		**Ricker**		**Logistic Hockey Stick**		**Depensatory Beverton-Holt**		
	α	β	α	β	α	β	α	β	γ
Skagit	82	2222	49	2146	29	2176	94	2197	2.88
Skykomish	103	3502	68	3385	41	3305	116	3444	1.20
Snow	36	1555	31	1344	27	1252	40	1438	0.11
pD	17.6		20.2		22.9		19.1		
DIC	3721.1		3764.3		3791.7		3724.4		
ΔDIC	0.0		43.2		70.6		3.3		

Table 4. Statistics describing the fit of hierarchical spawner-to-smolt stock-recruitment models. Parameter estimates used to compute statistics were values from the posterior distributions with the lowest deviance. MAR, SDR, and r^2 denote the median of absolute values of residuals, the standard deviation of residuals, and the square of the Pearson correlation coefficient. X^2 denotes the chi-square statistic.

	Beverton-Holt			**Ricker**			**Logistic Hockey Stick**			**Depensatory Beverton-Holt**		
Population	MAR	SDR	r^2	MAR	SDR	r^2	MAR	SDR	r^2	MAR	SDR	r^2
Big Beef	0.43	0.71	0.35	0.63	0.73	0.33	0.63	0.69	0.35	0.53	0.74	0.32
Big Qualicum	0.54	1.16	0.00	1.31	1.48	0.10	1.08	1.19	0.01	0.78	1.22	0.00
Bingham	0.39	0.67	0.12	0.64	1.11	0.06	1.17	1.39	0.14	0.43	0.71	0.12
Black	1.05	1.20	0.44	0.89	1.22	0.42	0.85	1.16	0.45	0.89	1.25	0.44
Carnation	0.63	0.76	0.50	0.59	0.78	0.49	0.76	0.81	0.45	0.57	0.81	0.51
Deschutes	0.81	0.84	0.85	0.77	0.81	0.85	0.52	0.80	0.84	0.70	0.88	0.84
Deer	0.53	0.60	0.56	0.40	0.50	0.72	0.33	0.47	0.65	0.58	0.68	0.53
Flynn	0.86	1.48	0.09	1.18	1.63	0.05	1.12	1.51	0.09	1.13	1.60	0.10
Hooknose	0.52	0.70	0.02	0.53	0.69	0.06	0.49	0.70	0.03	0.37	0.69	0.02
Hunts	0.69	1.61	0.14	0.76	1.58	0.11	0.56	1.47	0.12	0.80	1.69	0.13
Needle	0.62	0.88	0.57	0.43	0.93	0.47	0.64	0.98	0.56	0.74	0.94	0.56
Nile	0.57	0.66	0.22	0.52	0.78	0.24	0.53	0.60	0.22	0.46	0.61	0.23
Queets	0.70	0.82	0.39	0.70	0.75	0.46	0.57	0.72	0.42	0.79	0.86	0.39
Skagit	0.40	0.83	0.16	0.46	0.85	0.06	0.48	0.77	0.14	0.45	0.86	0.16
Skykomish	0.25	0.39	0.85	0.38	0.48	0.74	0.29	0.53	0.85	0.29	0.44	0.84
Snow	0.90	1.60	0.77	0.79	1.60	0.75	0.58	1.48	0.77	0.98	1.67	0.77
Average	0.62	0.93	0.38	0.69	1.00	0.37	0.66	0.95	0.38	0.66	0.98	0.37
X^2	6.34			7.29			7.92			6.3		

Table 5. Number and length of streams that contain Coho salmon in the Georgia Basin West management unit and in the Thompson drainage by maximum stream order estimated from a summary of the BC Watershed Atlas. The number of streams with escapement records (SEDS) is also shown.

Maximum	**Georgia Basin West**		**Thompson River**	
Stream Order	**# Streams**	**km**	**# Streams**	**km**
1	73	93	9	5
2	87	218	20	28
3	62	404	26	72
4	15	295	34	236
5	6	291	21	764
6	2	34	5	597
7			3	566
Total	245	1,335	118	2,268
SEDS	97		87	

Table 6. Estimates of freshwater (smolts in millions of fish) and total (adult recruits) carrying capacity of the Georgia Basin West (GBW) management unit and the Thompson River drainage based on the mean smolt carrying capacity from the predictive marginal distribution (2052 smolts/km). Thompson capacities were computed using all accessible stream length and a subset that excluded large mainstems (6th and 7th order streams). Adult recruitment was calculated as the product of smolt capacity and marine survival rates at 2.5%, 5.0%, and 10.0%. For reference, the average historical adult recruitment is shown, which was calculated based on historical estimates of escapements and harvest rates. The marine survival rates from index stocks over this period are also shown.

	Georgia Basin West	**Thompson (all)**	**Thompson (<=5)**
Habitat (km)	1335	2268	1105
Smolts (million)	2.74	4.65	2.27
Marine Survival (%)		Adult Recruits	
2.5%	68,000	116,000	57,000
5.0%	137,000	233,000	113,000
10.0%	274,000	465,000	227,000
Avg. Recruits (75-04)	334,000	95,000	
(75-04) Marine Survival	8.2%	4.7%	

8. FIGURES

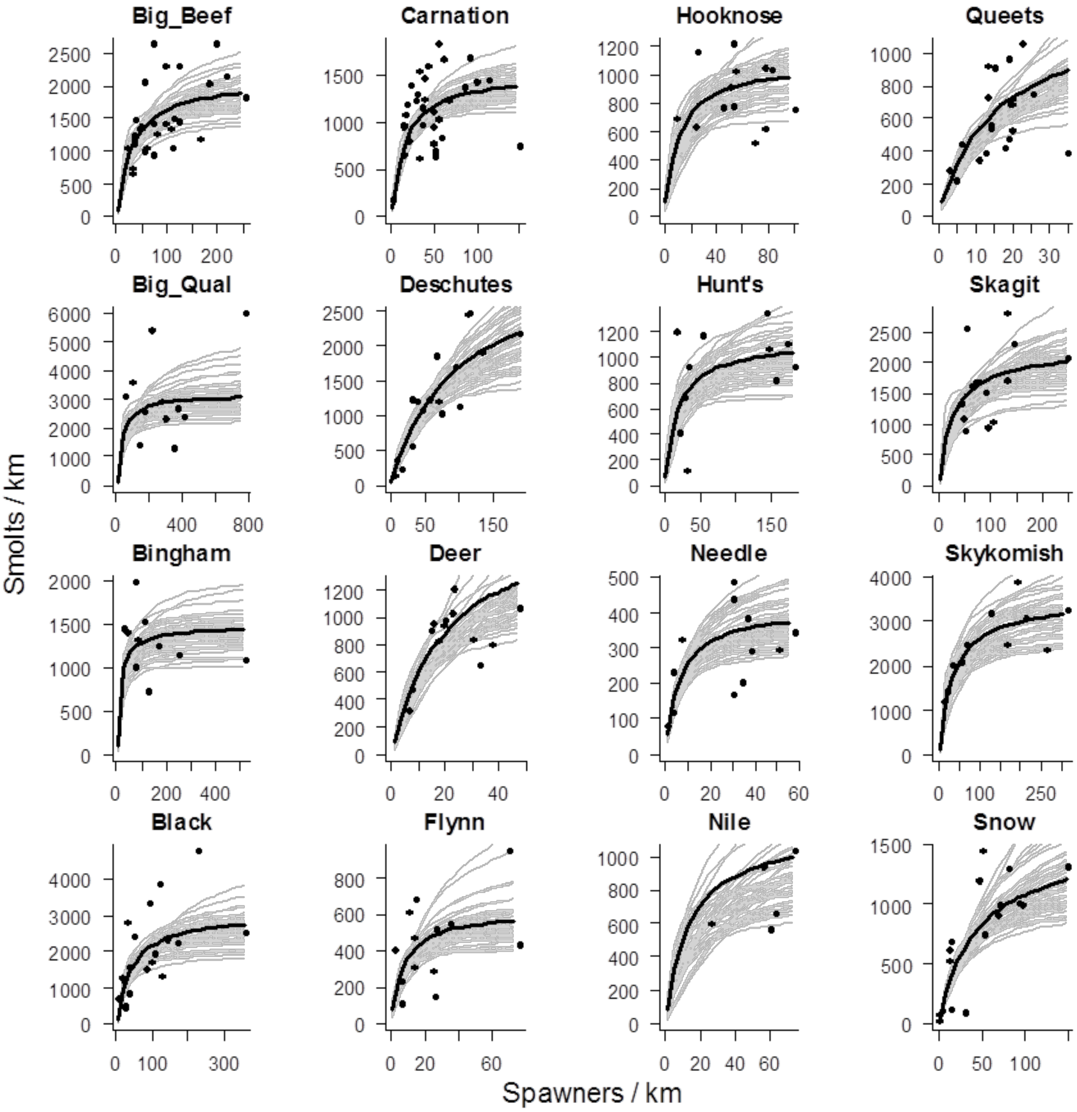

Figure 1. Expected spawner-to-smolt stock recruitment curves (thick lines) for 16 streams based on the Beverton-Holt hierarchical model. The expected curve is based on the average estimates of stock productivity and carrying capacity from their posterior distributions. The light-gray curves represent the extent of uncertainty in stock-recruitment relationships, and are a random sample of 50 parameter sets from the posterior distributions.

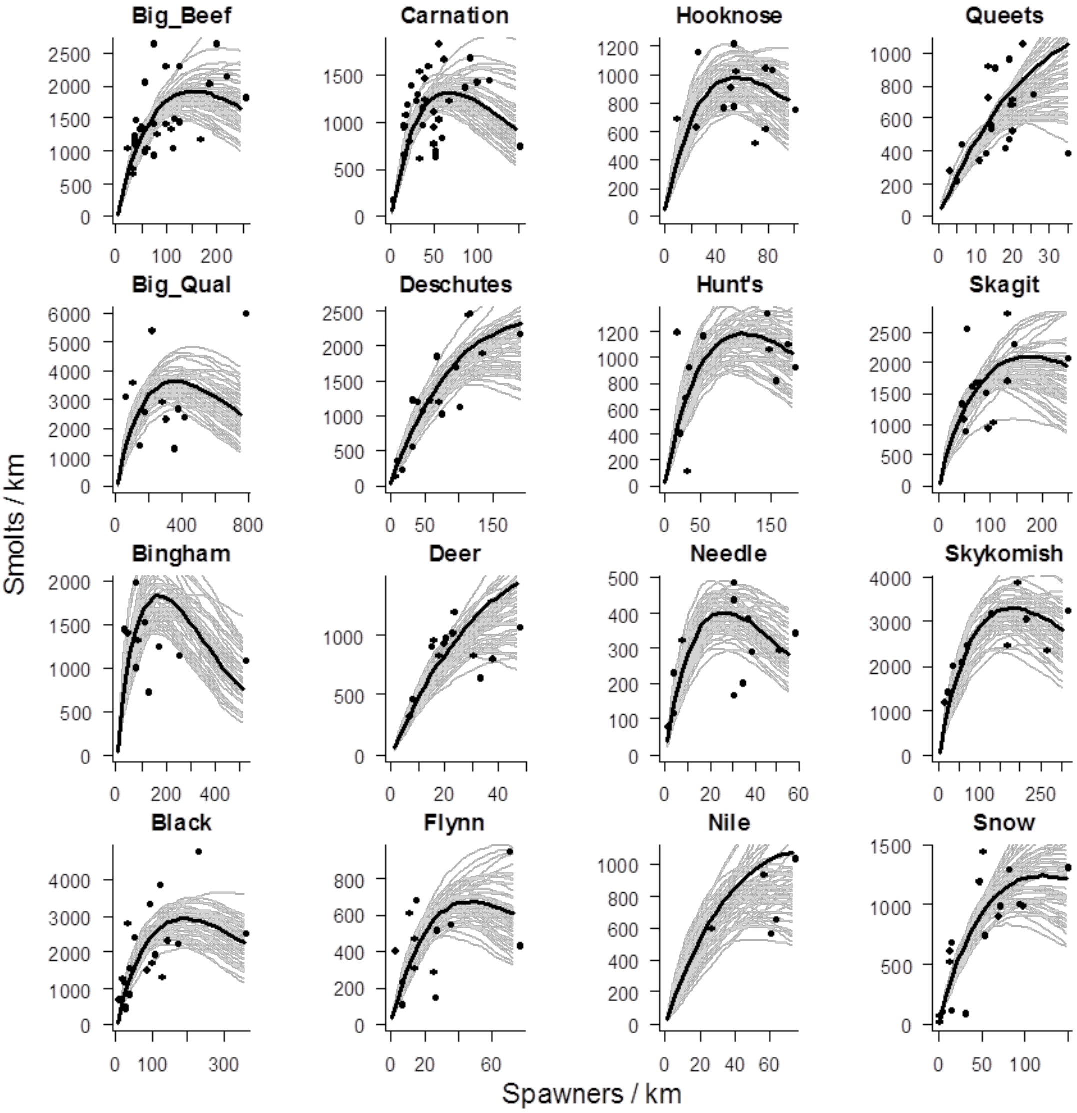

Figure 2. Expected spawner-to-smolt stock recruitment curves (thick lines) for 16 streams based on the Ricker hierarchical model. See caption for Fig. 1 for details.

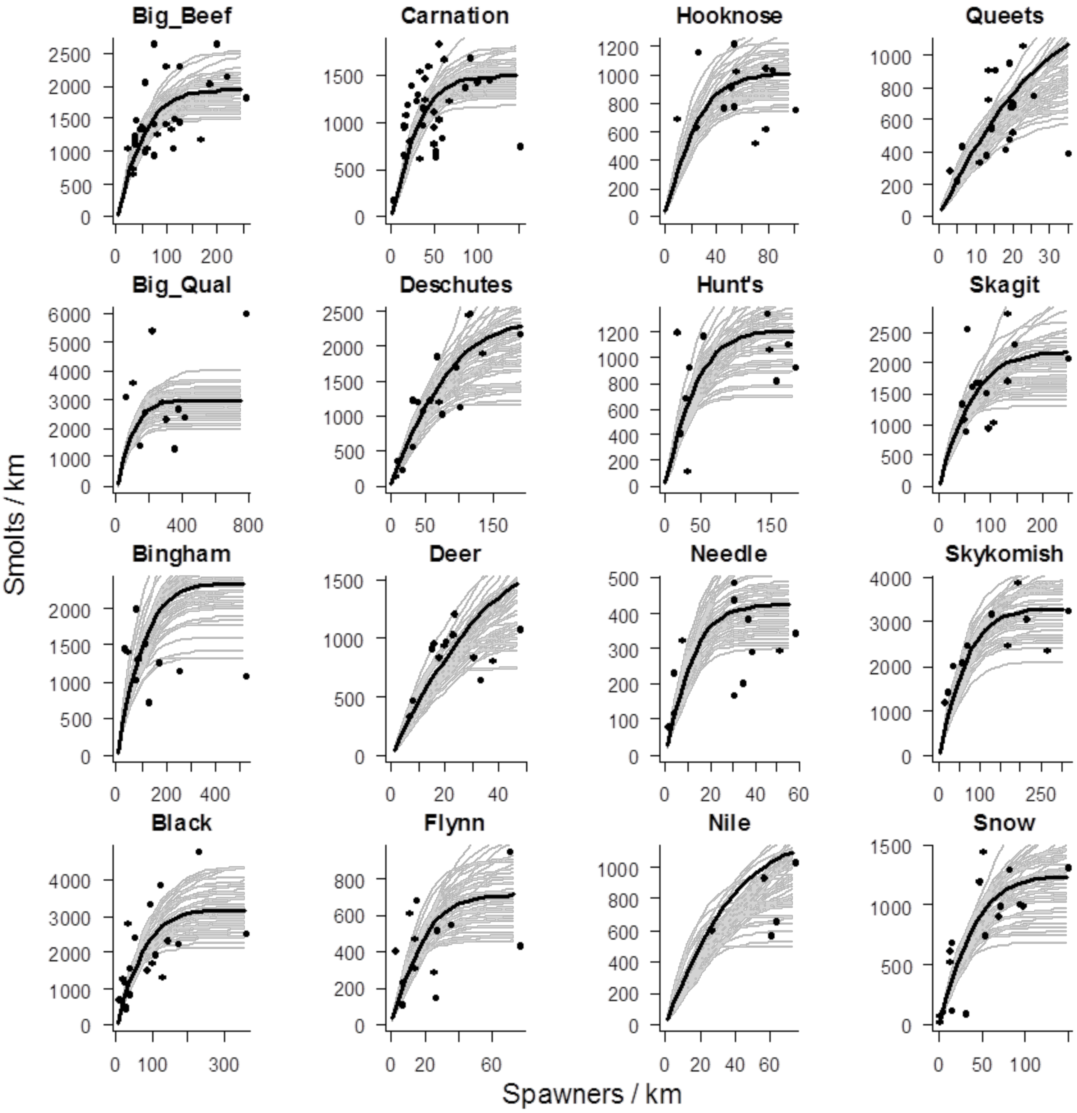

Figure 3. Expected spawner-to-smolt stock recruitment curves (thick lines) for 16 streams based on the logistic hockey stick hierarchical model. See caption for Fig. 1 for details.

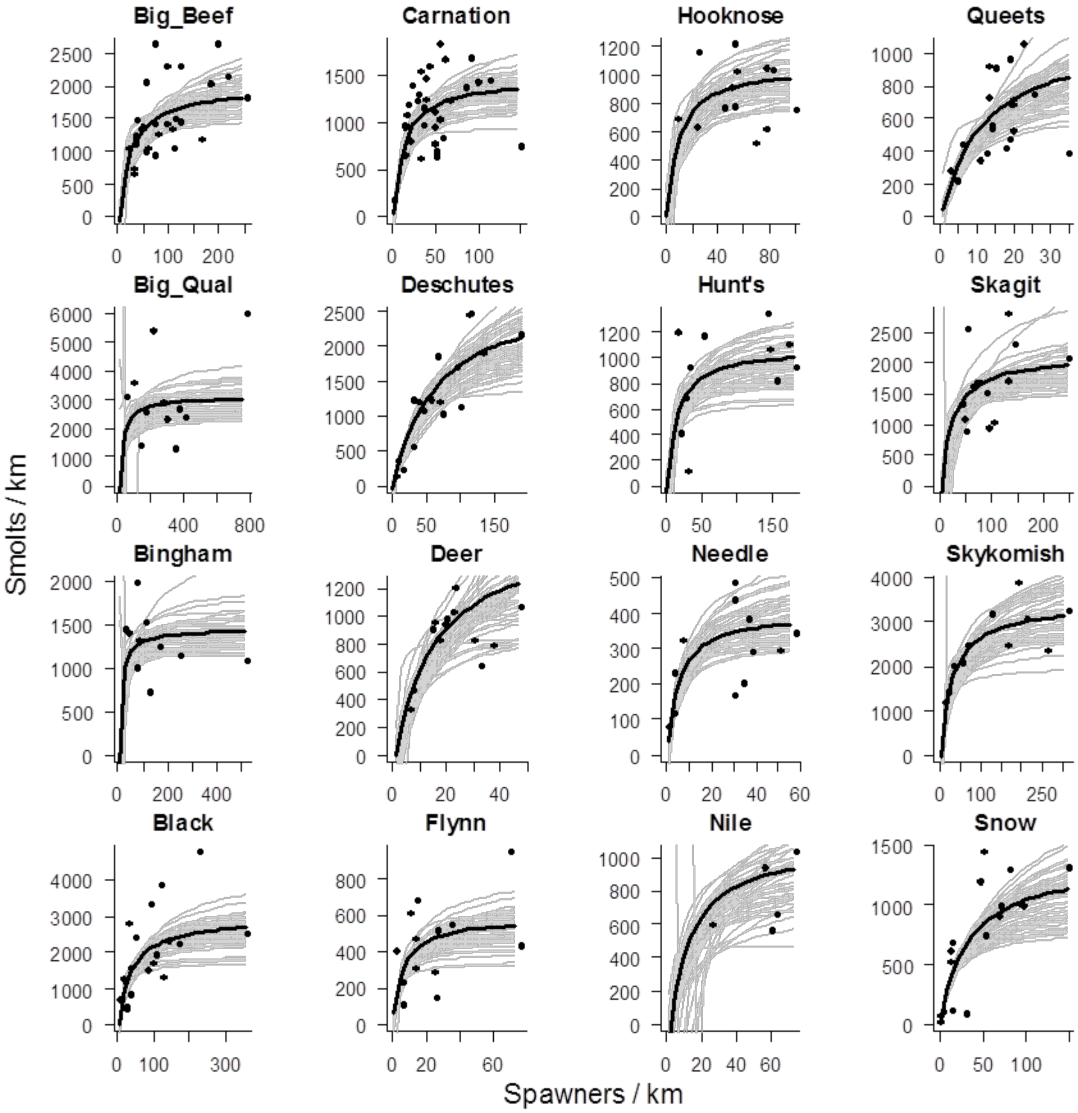

Figure 4. Expected spawner-to-smolt stock recruitment curves (thick lines) for 16 streams based on the depensatory Beverton-Holt hierarchical model. See caption for Fig. 1 for details.

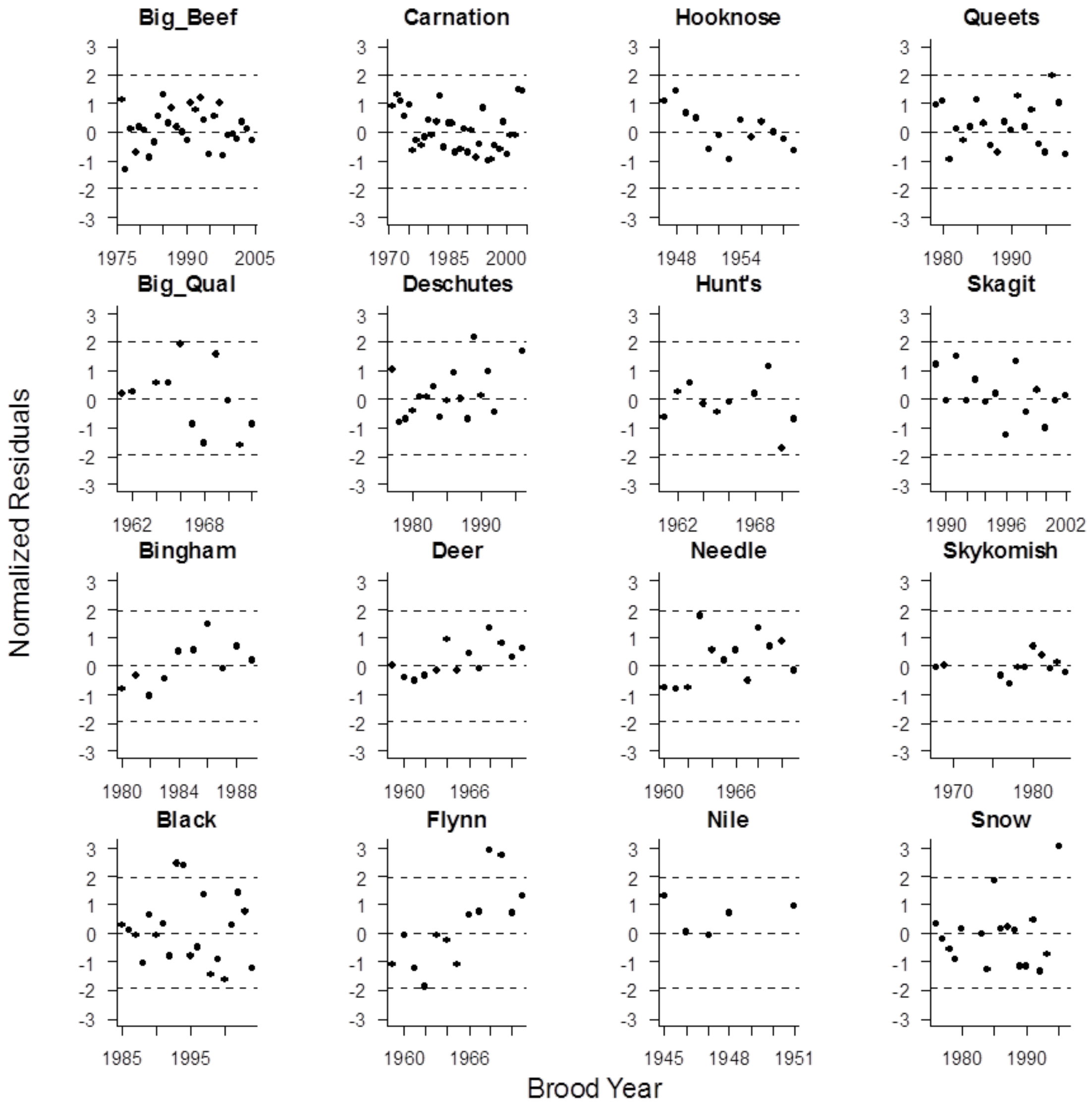

Figure 5. Pearson-residuals from the hierarchical Beverton-Holt model as a function of brood year. The horizontal lines show the median (y=0), and 95% confidence intervals (y=± 1.96). A positive residual indicates that the model overestimates the number of smolts.

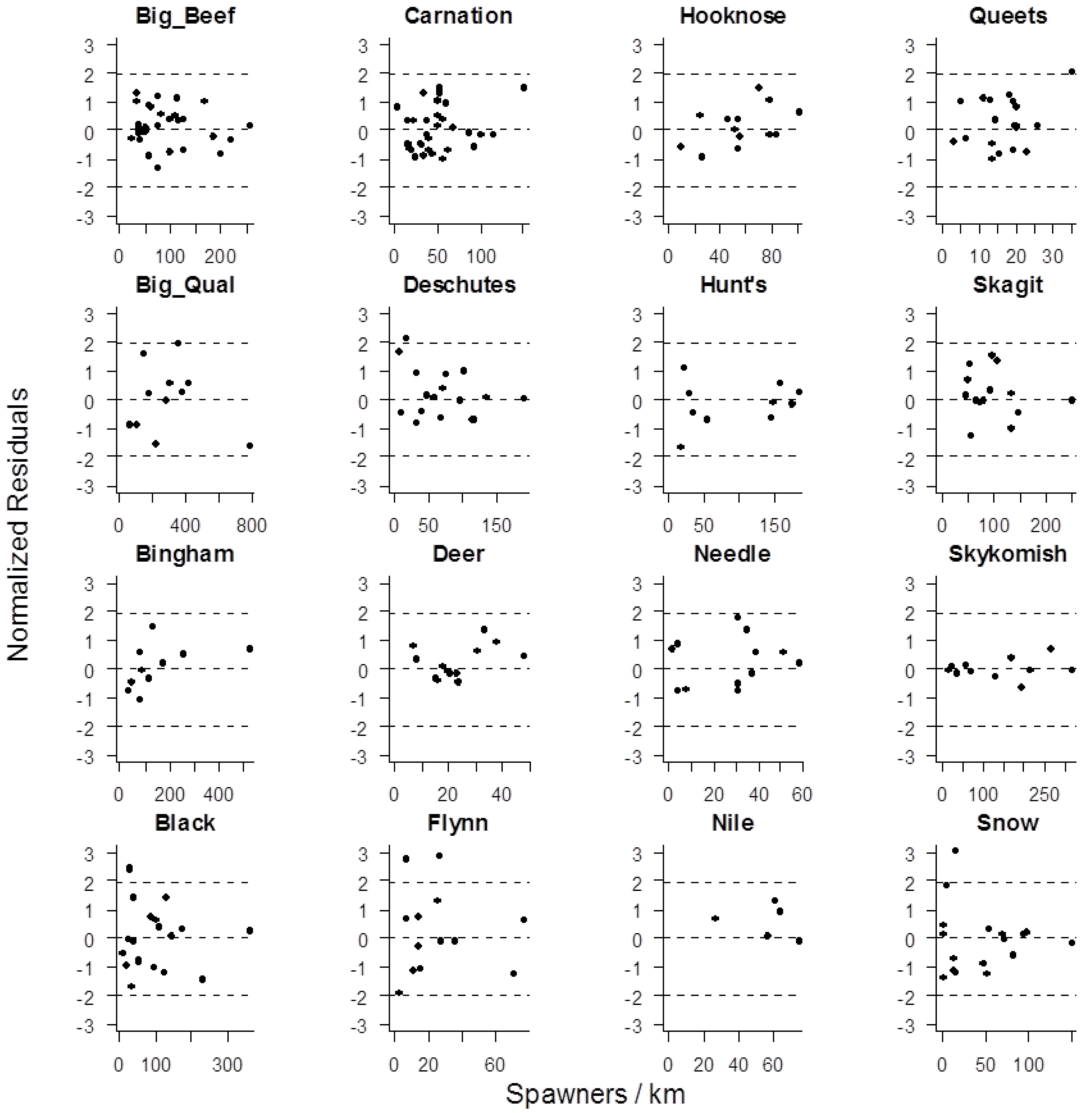

Figure 6. Pearson-residuals from the hierarchical Beverton-Holt model as a function of spawning stock. The horizontal lines show the median (y=0), and 95% confidence intervals (y=± 1.96). A positive residual indicates that the model overestimates the number of smolts.

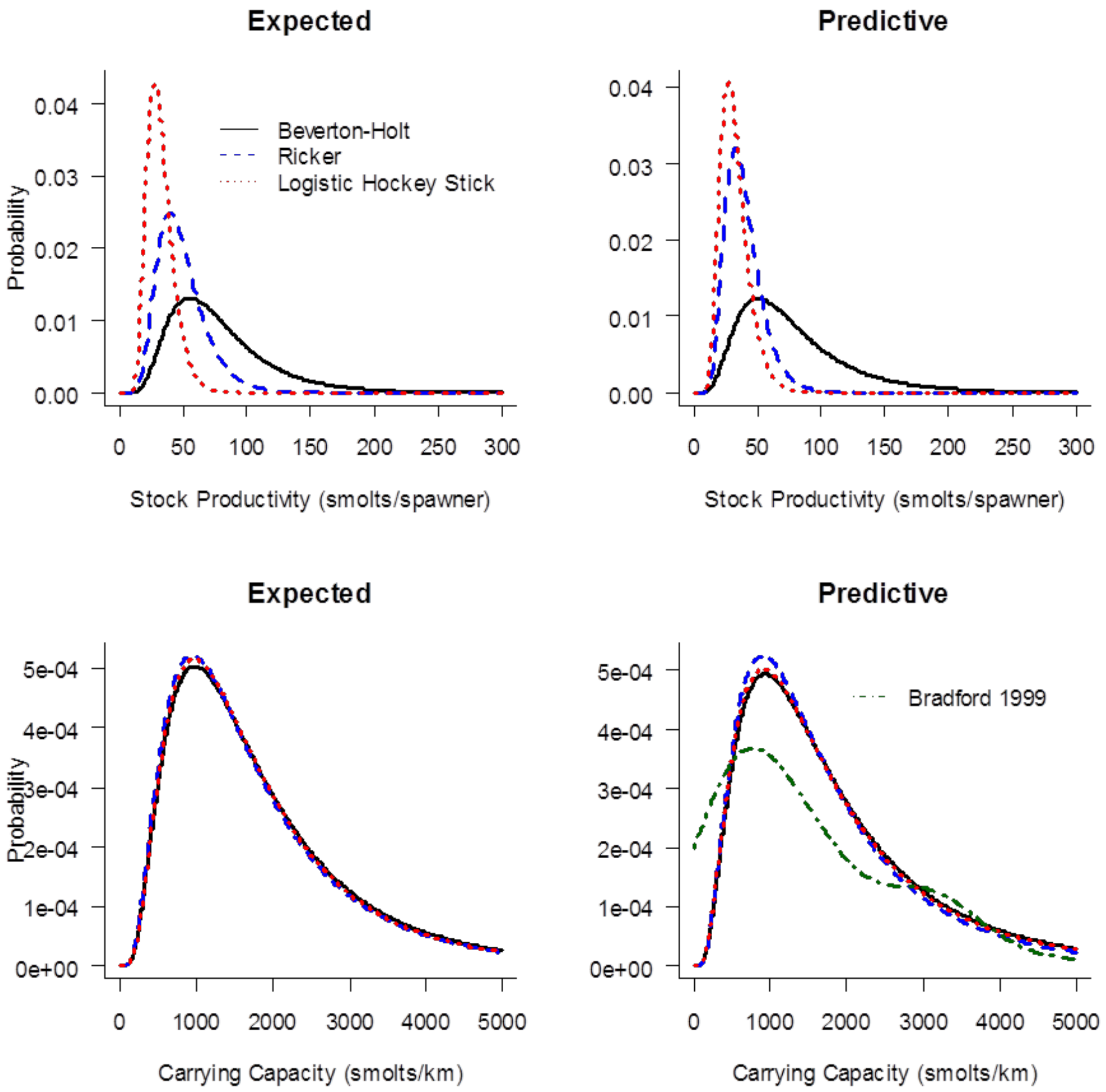

Figure 7. Regional distributions of stock productivity and carrying capacity for 3 spawner-to-smolt stock-recruitment models. The expected relationships are based on the average regional parameter estimates for stock productivity (μ_α and σ_α), and carrying capacity (μ_β and σ_β, see Table 3) from their posterior distributions. The predictive distributions are determined by sampling from these posteriors and therefore account for uncertainty in the estimates of the mean and standard deviation of the regional distributions. For reference the distribution of carrying capacity estimates from Bradford (1999) is shown.

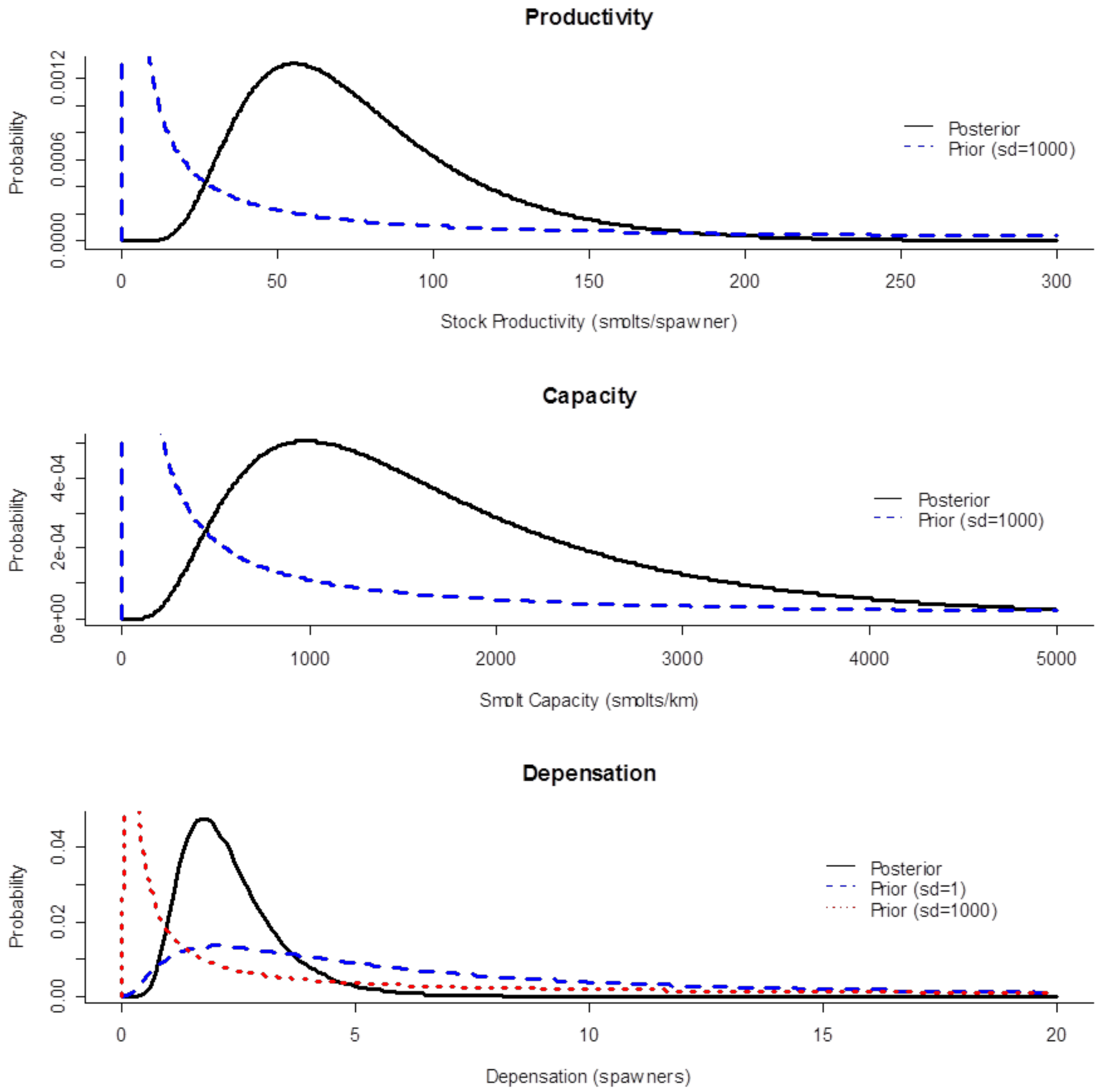

Figure 8. Comparison of the prior distributions and posterior distributions of the mean of regional distributions for stock productivity (μ_α) and carrying capacity (μ_β) for the Beverton-Holt model, and the depensation parameter for the depensatory Beverton-Holt model (μ_γ). The standard deviation for the prior distribution for the depensatory term was set at 1. For reference the shape of the prior distribution at an SD of 1000 is also shown.

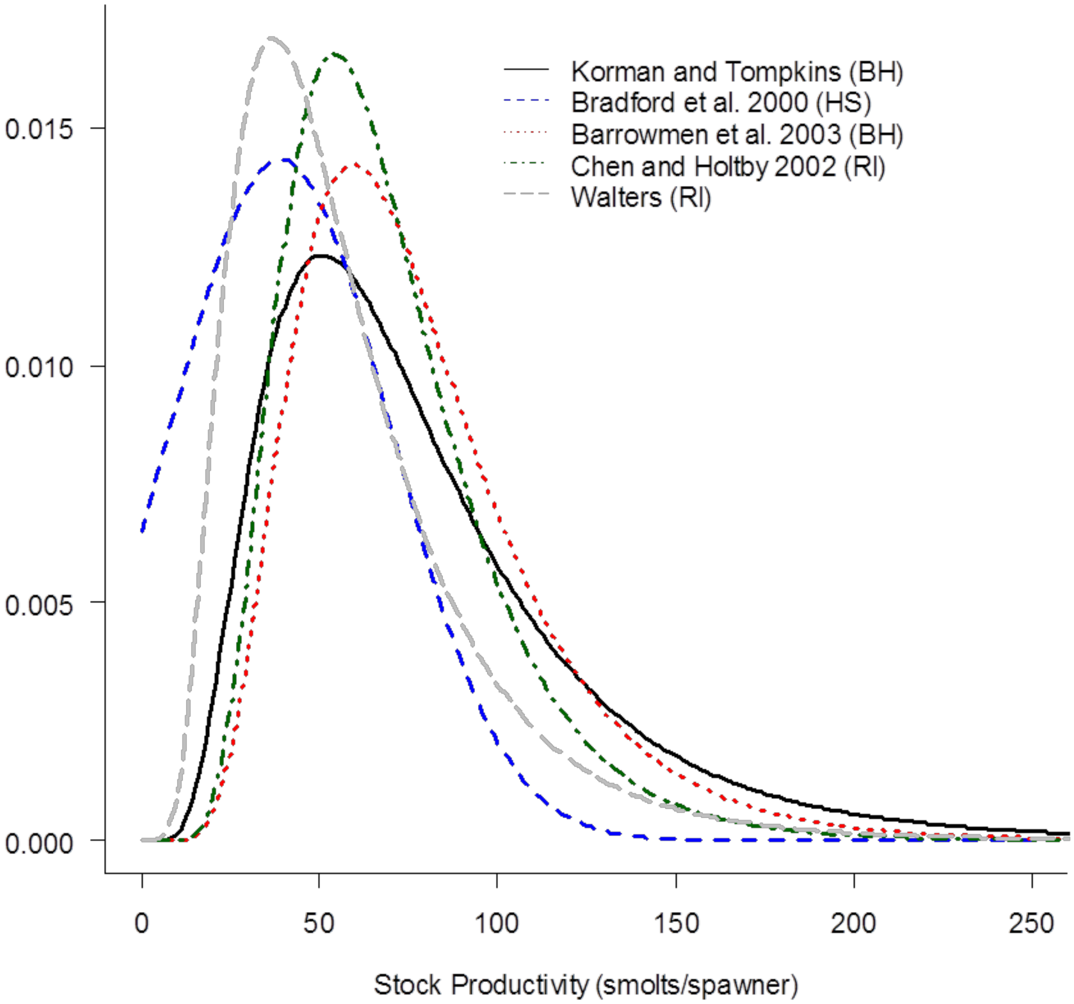

Figure 9. Comparison of regional distributions of stock productivity. BH, HS, and RI refer to Beverton-Holt, Hockey Stick, and Ricker stock-recruitment models respectively. See text for details.

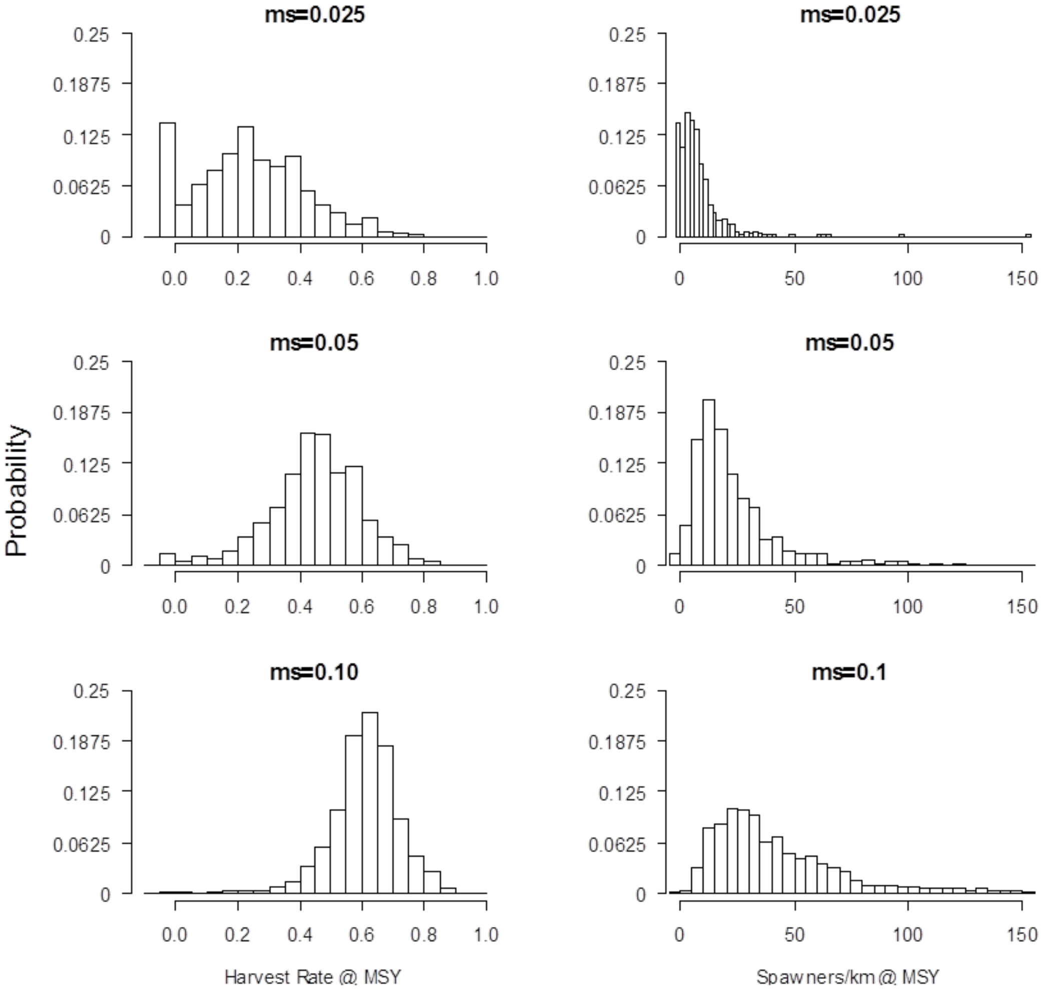

*Figure 10. Marginal probabilities for harvest rates and escapements to produce maximum sustainable yield (MSY) at different marine survival rates (ms).Values <0 represent populations that are not sustainable even without harvest (α*ms<1). Results were computed from predictive marginal distributions of stock productivity and carrying capacity based on the hierarchical Beverton-Holt model (Fig. 7).*

a)

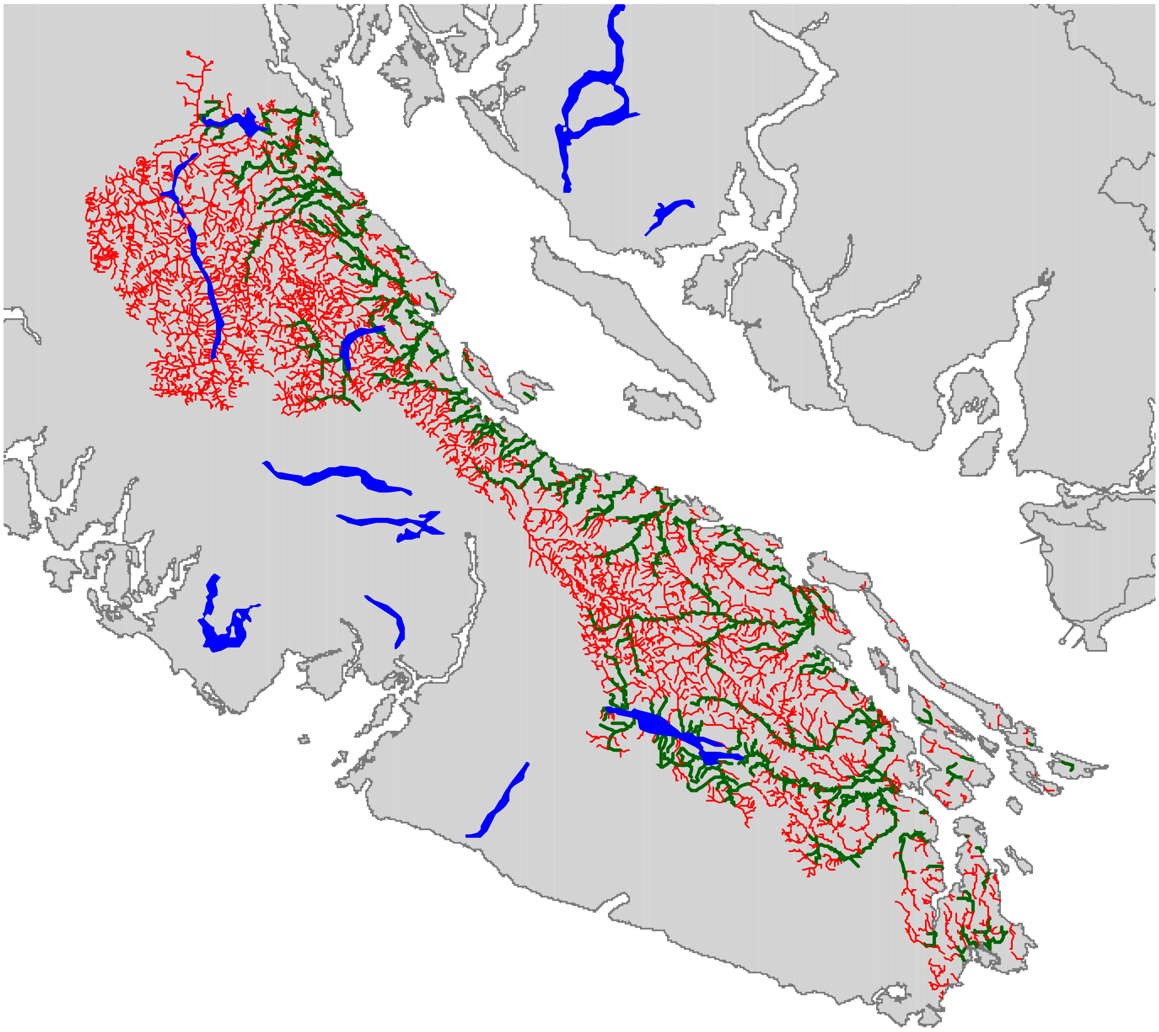

Figure 11. 1-50,000 Watershed Atlas showing the distribution of accessible (green) and unaccessible (red) coho habitat in the Georgia Basin West management unit (a) and the Thompson River drainage (b).

b)

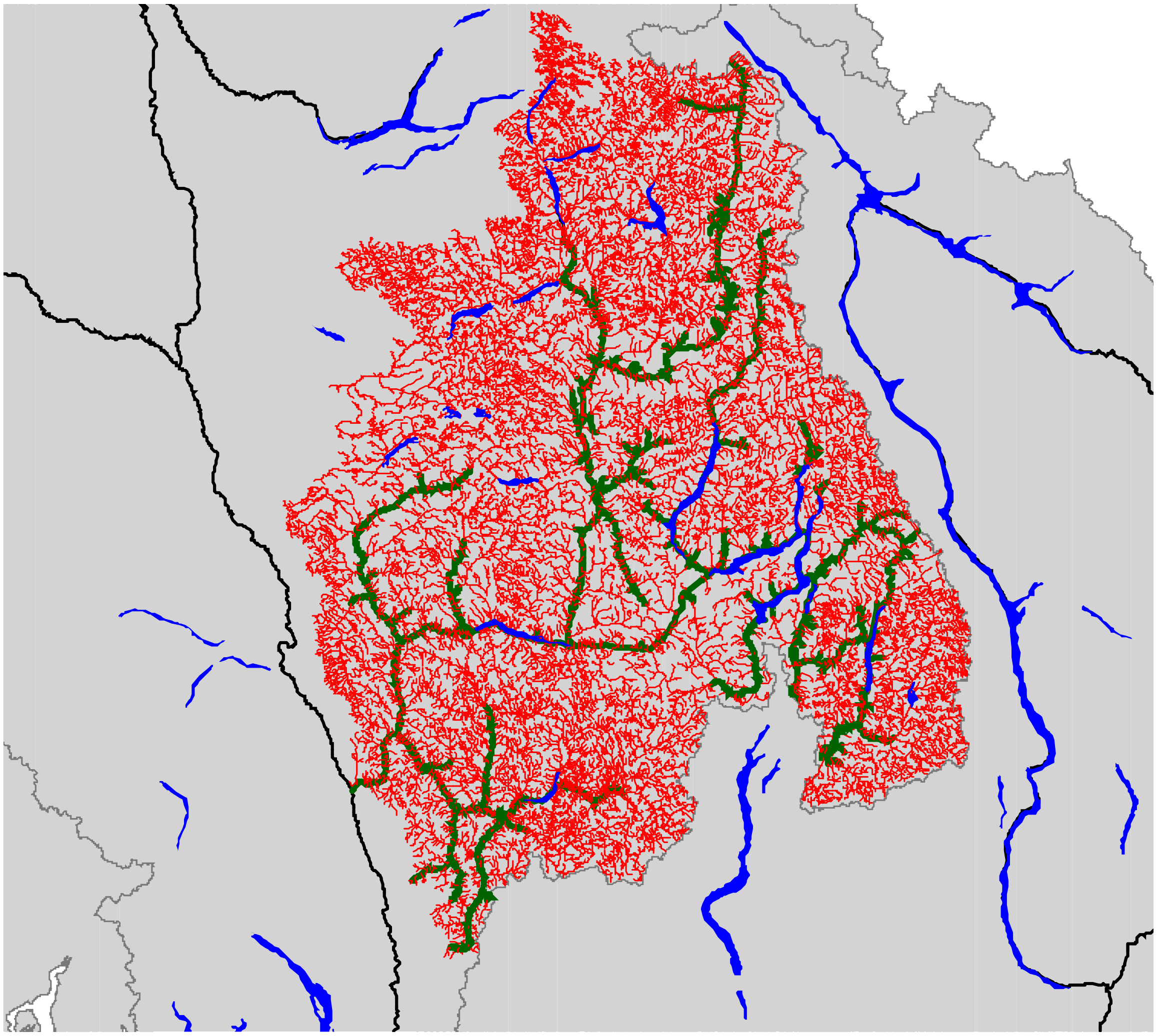

Figure 11. Con't.

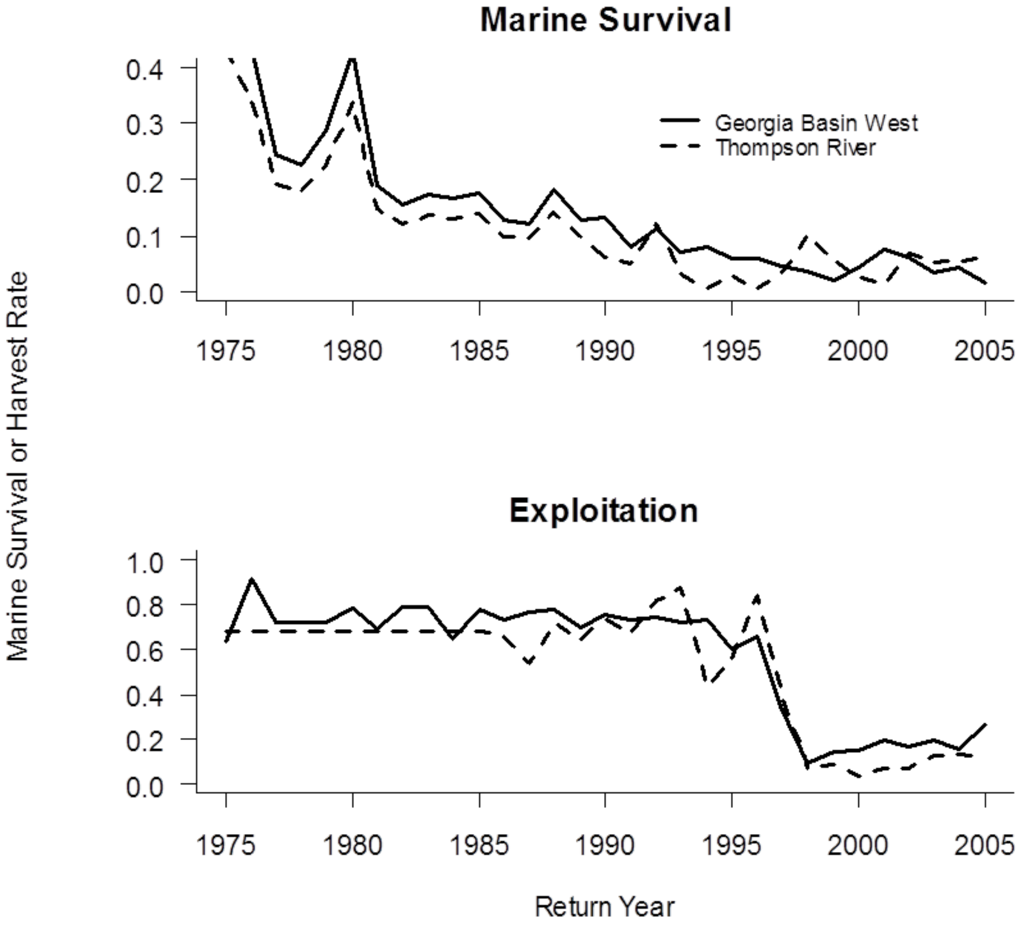

Figure 12. Estimated aggregate marine survival (wild stocks only) and exploitation rates for populations in the Georgia Basin West management unit and the Thompson River drainage.

a)

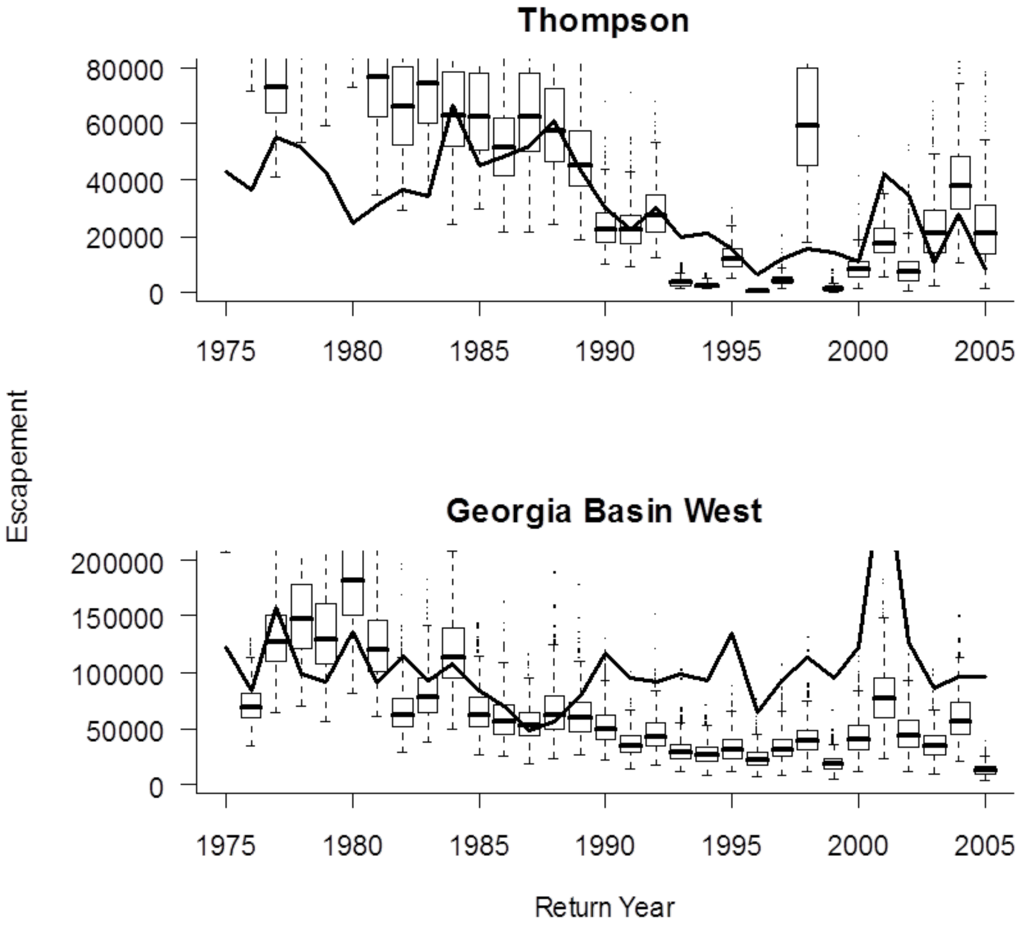

Figure 13. Simulated (box plots) and observed (lines) aggregate escapement trends in the Thompson River drainage and the Georgia Basin West management unit assuming 10 (a) and 90 (b) populations. Simulation results show the distribution of annual escapement over 500 trails.

b)

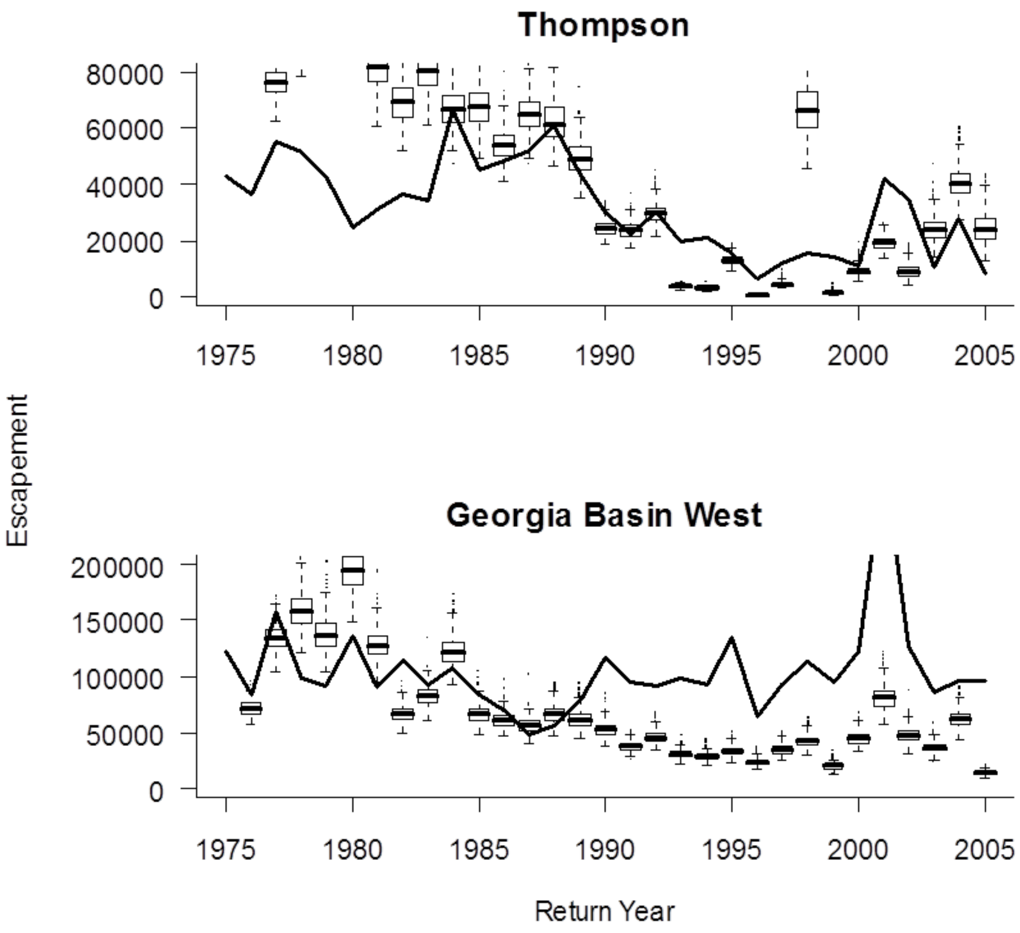

Figure 13. Con’t.

9. APPENDIX A. SUMMARY OF SPAWNER-TO-SMOLT, MARINE SURVIVAL, AND EXPLOITATION RATE DATA

Table A1. Spawner-to-Smolt data by brood year for 16 populations used in the hierarchical meta-analysis.

Big Beef			**Big Qualicum**			**Bingham**		
Year	Spawners	Smolts	Year	Spawners	Smolts	Year	Spawners	Smolts
1976	2036	18600	1961	1706	24500	1980	710	31806
1977	1308	47300	1962	3668	25900	1981	2536	33464
1978	675	20493	1964	4094	23000	1982	1892	43945
1979	2249	41056	1965	2962	22400	1983	1086	30939
1980	1308	25217	1966	3480	12600	1984	5738	25205
1981	922	23620	1967	1002	34800	1985	1828	22233
1982	1047	36564	1968	2086	52400	1986	2890	15742
1983	745	26062	1969	1422	13200	1987	1926	29041
1984	1948	23994	1970	2692	28400	1988	11790	23712
1985	589	11510	1971	7716	58500	1989	3810	27639
1986	2085	26534	1972	606	30100			
1987	1028	17594						
1988	675	19740						
1989	850	23646						
1990	395	18677						
1991	579	13071						
1992	1101	18431						
1993	1339	16574						
1994	2276	25820						
1995	1795	40828						

Big Beef			Big Qualicum			Bingham		
Year	Spawners	Smolts	Year	Spawners	Smolts	Year	Spawners	Smolts
1996	1478	22222						
1997	2994	20967						
1998	3570	47087						
1999	628	21803						
2000	895	24352						
2001	3318	36060						
2002	1789	25062						
2003	4647	32222						
2004	3973	38083						

Year	Spawners	Smolts	Year	Spawners	Smolts	Year	Spawners	Smolts
1985	5696	72157	1971	189	2559	1977	5568	60275
1986	4840	76123	1972	162	2088	1978	1810	65776
1987	785	38043	1973	156	2315	1979	6208	131261
1988	3122	109629	1974	158	2929	1980	2270	64757
1989	3273	54957	1975	158	2403	1981	3198	65518
1990	1237	50309	1976	123	4536	1982	7338	101901
1991	3574	63095	1977	127	3853	1983	3892	64452
1992	1722	79411	1978	102	3972	1984	3742	99241
1993	959	14962	1979	312	4390	1985	5218	91057
1994	900	14681	1980	175	3153	1986	4138	54397
1995	1760	79366	1981	119	3559	1987	10370	117087
1996	284	21490	1982	174	3184	1988	6376	133066

Year	Spawners	Smolts	Year	Spawners	Smolts	Year	Spawners	Smolts
1997	1200	26387	1983	103	1876	1989	946	11248
1998	7616	157952	1984	49	2985	1990	2680	57204
1999	515	40831	1985	69	2436	1991	1720	30000
2000	1114	91360	1986	119	2964	1992	480	18750
2001	12100	81829	1987	64	3672	1996	376	6000
2002	4322	42621	1988	57	3332			
2003	2781	49132	1989	156	3410			
2004	4065	126893	1990	195	5143			
			1991	211	3759			
			1992	107	4714			
			1993	95	3772			
			1994	9	518			
			1995	175	5663			
			1996	74	4257			
			1997	49	2882			
			1998	285	5182			
			1999	47	2014			
			2000	136	4913			
			2001	269	4203			
			2002	357	4440			
			2003	468	2286.3			
			2004	160	1961			

Table A1. Con't.

Deer			**Flynn**			**Hooknose**		
Year	Spawners	Smolts	Year	Spawners	Smolts	Year	Spawners	Smolts
1959	42	1917	1959	16	875	1947	456	3551
1960	38	2210	1960	52	776	1948	408	2982
1961	56	2775	1961	102	1354	1949	588	4389
1962	36	2082	1962	4	565	1950	142	3621
1963	54	2368	1963	40	736	1951	58	4037
1964	88	1836	1964	20	663	1952	492	5987
1965	48	2245	1965	22	968	1953	150	6756
1966	112	2461	1966	110	616	1954	320	4513
1967	46	2160	1967	20	430	1955	456	6074
1968	78	1484	1968	38	207	1956	272	4452
1969	16	738	1969	10	140	1957	300	5291
1970	20	1072	1970	10	330	1958	326	5945
1971	72	1923	1971	36	404	1959	316	7094

Hunts			**Needle**			**Nile**		
Year	Spawners	Smolts	Year	Spawners	Smolts	Year	Spawners	Smolts
1961	784	7260	1960	4	223	1945	370	3388
1962	994	5010	1961	30	470	1946	344	5626
1963	852	4380	1962	8	314	1947	448	6227
1964	942	5930	1963	30	160	1948	162	3577
1965	192	4990	1964	50	286	1951	384	3946

Hunts			**Needle**			**Nile**		
Year	Spawners	Smolts	Year	Spawners	Smolts	Year	Spawners	Smolts
1966	798	5690	1965	56	333			
1967	174	600	1966	38	277			
1968	164	3620	1967	30	421			
1969	130	2200	1968	34	194			
1970	100	6470	1969	2	76			
1971	290	6270	1970	4	113			
			1971	36	369			

Queets			**Skagit**			**Skyhomish**		
Year	Spawners	Smolts	Year	Spawners	Smolts	Year	Spawners	Smolts
1979	6800	168300	1989	28126	473357	1968	1500	107000
1980	4700	135500	1990	35768.5	865428	1969	2200	130000
1981	4800	324272	1991	53113	499862	1976	12000	291991
1982	7000	243031	1992	42977	910426	1977	18000	358104
1983	2282	153741	1993	26947.5	580608	1978	19774	281624
1984	9200	266935	1994	38999	907200	1979	29342	298736
1985	4001	120650	1995	72738.5	916287	1980	24778	215788
1986	5160	195795	1996	29699	1E+06	1981	15450	228603
1987	4747	258711	1997	58100	546561	1982	6510	226633
1988	8185	375977	1998	80442	1E+06	1983	5376	191692
1989	5194	190703	1999	50774	817305	1984	3494	184584
1990	7215	252158	2000	71856	2E+06			
1991	6525	146315	2001	136240	1E+06			

Queets			**Skagit**			**Skyhomish**		
Year	Spawners	Smolts	Year	Spawners	Smolts	Year	Spawners	Smolts
1992	7188	243826	2002	25000	713730			
1993	7228	185600						
1994	1200	98742						
1995	6773	339787						
1996	12567	136754						
1997	1851	76077						
1998	5515	322395						
1989	28126	473357						
1990	35768.5	865428						
1991	53113	499862						
1992	42977	910426						
1993	26947.5	580608						
1994	38999	907200						
1995	72738.5	916287						
1996	29699	1377029						
1997	58100	546561						
1998	80442	1242332						
1999	50774	817305						
2000	71856	1519880						
2001	136240	1114831						
2002	25000	713730						

Table A1. Con't.

	Snow	
Year	Spawners	Smolts
1976	374	5201
1977	1046	9156
1978	576	9090
1979	332	8344
1980	656	7048
1983	505	6947
1984	358	10113
1985	44	641
1986	481	6296
1987	681	6915
1988	14	448
1989	98	4300
1990	112	4787
1991	4	117
1992	8	495
1993	100	3657
1994	0	3
1995	106	783
1996	224	632
1998	6	0
1999	12	0
2000	2	143.02
2001	308	25947

Snow		
Year	Spawners	Smolts
2002	486	11954
2003	348	10287
2004	1494	18924

Table A2. Marine survival data by brood year, stock type (wild or hatchery), management unit (MU), and population.

Type	Wild	Wild	Hatchery	Hatchery	Hatchery	Hatchery
MU	GBW	LF	GBW	GBW	LF	LF
Brood Year	Black	Salmon	Big Qualicum	Goldstream	Chilliwack	Inch
1972			0.366			
1973			0.290			
1974			0.164			
1975			0.152			
1976			0.193			
1977			0.287			
1978			0.127			
1979			0.103			
1980			0.112		0.120	
1981			0.079		0.144	
1982			0.050		0.188	
1983	0.125		0.009		0.131	0.067
1984	0.115	0.124	0.006		0.174	0.089
1985	0.134	0.229	0.015		0.181	0.204
1986	0.115	0.136	0.013		0.126	0.109
1987	0.129	0.136	0.043		0.106	0.080
1988	0.080	0.081	0.062		0.090	0.071
1989	0.125	0.098	0.059		0.057	0.097
1990	0.054	0.088	0.067		0.059	0.083
1991	0.059	0.100	0.069		0.064	0.060
1992	0.045	0.071	0.029		0.037	0.055

Type	Wild	Wild	Hatchery	Hatchery	Hatchery	Hatchery
MU	GBW	LF	GBW	GBW	LF	LF
Brood Year	Black	Salmon	Big Qualicum	Goldstream	Chilliwack	Inch
1993	0.034	0.082	0.016		0.040	0.039
1994	0.048	0.045	0.014		0.025	0.011
1995	0.045	0.028	0.004		0.013	0.005
1996	0.017	0.028	0.013	0.005	0.013	0.019
1997	0.022	0.062	0.013	0.010	0.034	0.011
1998	0.074	0.073	0.012	0.025	0.047	0.058
1999	0.049	0.071	0.010	0.004	0.032	0.018
2000	0.030	0.036	0.006	0.023	0.025	0.007
2001	0.04	0.04	0.01	0.018	0.02	0.02
2002	0.01		0.00	0.004	0.01	0.02
2003	0.02		0.00			0.01
2004	0.03		0.00	0.007		0.01

Table A2. Con't.

Type	Hatchery	Hatchery	Wild	Hatchery	Hatchery	Hatchery
MU	GBW	WCVI	WCVI		Interior Fraser	
Brood Year	Quinsam	Robertson	Carnation	Lower Thompson	South Thompson	North Thompson
1972		0.067	0.167			
1973	0.065	0.077	0.196			
1974	0.097	0.072	0.122			
1975	0.074	0.049	0.111			
1976	0.101	0.088	0.179			
1977	0.071	0.047	0.108			
1978	0.048	0.022	0.068			
1979	0.070	0.020	0.162			
1980	0.054	0.057	0.086			
1981	0.076	0.069	0.048			
1982	0.092	0.021	0.057			
1983	0.078	0.039	0.153			
1984	0.079	0.029	0.050			
1985	0.106	0.018	0.073			
1986	0.078	0.049	0.188			
1987	0.042	0.090	0.155		0.036	
1988	0.059	0.059	0.152		0.046	
1989	0.035	0.046	0.124		0.076	
1990	0.023	0.024	0.075		0.028	
1991	0.025	0.000	0.006		0.004	
1992	0.014	0.013	0.091		0.019	

Type	Hatchery	Hatchery	Wild	Hatchery	Hatchery	Hatchery
MU	GBW	WCVI	WCVI	Interior Fraser		
Brood Year	Quinsam	Robertson	Carnation	Lower Thompson	South Thompson	North Thompson
1993	0.012	0.018	0.047		0.003	
1994	0.010	0.030	0.082		0.011	
1995	0.007	0.035	0.059		0.010	0.03
1996	0.012	0.020	0.010			0.04
1997	0.016	0.103	0.050			0.01
1998	0.014	0.076	0.059	0.009		0.01
1999	0.010	0.043	0.175	0.020		0.02
2000	0.01	0.097	0.105	0.019		0.02
2001	0.00	0.04	0.03	0.023		0.02
2002	0.00	0.03	0.03	0.032		0.04
2003	0.01	0.01	0.00			
2004		0.02	0.02			

Table A3. Exploitation rates by brood year, type (wild or hatchery), management unit (MU), and population.

Type	Wild	Wild	Hatchery	Hatchery	Hatchery
MU	GBW	LF	GBW	GBW	LF
Brood Yr	Black	Salmon	Big Qualicum	Goldstream	Chilliwack
1972			0.636		
1973			0.916		
1974			0.722		
1975			0.722		
1976			0.726		

Type	Wild	Wild	Hatchery	Hatchery	Hatchery
MU	GBW	LF	GBW	GBW	LF
Brood Yr	Black	Salmon	Big Qualicum	Goldstream	Chilliwack
1977			0.784		
1978			0.694		
1979			0.791		
1980			0.810		0.771
1981			0.683		0.610
1982			0.840		0.719
1983	0.728		0.666		0.741
1984	0.847	0.674	0.734		0.763
1985	0.677	0.713	0.793		0.828
1986	0.698	0.724	0.611		0.775
1987	0.713	0.735	0.683		0.770
1988	0.677	0.729	0.693		0.726
1989	0.767	0.734	0.760		0.715
1990	0.739	0.523	0.740		0.822
1991	0.790	0.640	0.682		0.760
1992	0.570	0.476	0.555		0.629
1993	0.703	0.568	0.590		0.617
1994	0.550	0.117	0.349		0.324
1995	0.030	0.070	0.143		0.090
1996	0.030	0.090	0.182	0.23	0.153
1997	0.030	0.037	0.089	0.21	0.424
1998	0.046	0.078	0.102	0.35	0.376
1999	0.059	0.105	0.113	0.17	0.235

Type	Wild	Wild	Hatchery	Hatchery	Hatchery
MU	GBW	LF	GBW	GBW	LF
Brood Yr	Black	Salmon	Big Qualicum	Goldstream	Chilliwack
2000	0.043	0.080	0.080	0.40	0.312
2001	0.043	0.062	0.101	0.16	0.422
2002	0.04		0.08	0.74	0.40
2003	0.04		0.11		
2004	0.04		0.05	0.80	

Type	Hatchery	Hatchery	Hatchery	Wild	Hatchery
MU	LF	GBW	WCVI	WCVI	IF
Brood Yr	Inch	Quinsam	Robertson	Carnation	Interior Fraser
1972			0.646	0.644	0.681
1973			0.703	0.703	0.681
1974		0.835	0.661	0.661	0.681
1975		0.796	0.642	0.640	0.681
1976		0.711	0.625	0.625	0.681
1977		0.821	0.542	0.542	0.681
1978		0.772	0.628	0.619	0.681
1979		0.718	0.744	0.742	0.681
1980		0.773	0.659	0.656	0.681
1981		0.694	0.733	0.728	0.681
1982		0.797	0.618	0.614	0.681
1983	0.801	0.730	0.632	0.608	0.657
1984	0.840	0.820	0.567	0.550	0.537

Type	Hatchery	Hatchery	Hatchery	Wild	Hatchery
MU	LF	GBW	WCVI	WCVI	IF
Brood Yr	Inch	Quinsam	Robertson	Carnation	Interior Fraser
1985	0.887	0.780	0.721	0.706	0.712
1986	0.680	0.690	0.705	0.694	0.645
1987	0.861	0.833	0.682	0.674	0.737
1988	0.809	0.669	0.645	0.568	0.677
1989	0.757	0.790	0.725	0.722	0.815
1990	0.792	0.757	0.772	0.758	0.876
1991	0.798	0.735	0.621	0.621	0.433
1992	0.773	0.619	0.594	0.594	0.562
1993	0.821	0.410	0.553	0.548	0.835
1994	0.347	0.391	0.353	0.329	0.405
95	0.127	0.050	0.034	0.030	0.070
1996	0.173	0.050	0.040	0.040	0.090
1997	0.102	0.050	0.229	0.050	0.034
1998	0.245	0.065	0.216	0.050	0.070
1999	0.289	0.164	0.163	0.030	0.071
2000	0.244	0.065	0.249	0.050	0.126
2001	0.157	0.089	0.262	0.040	0.135
2002	0.05	0.03	0.31	0.04	
2003	0.05	0.05	0.18	0.20	
2004	0.04	0.02	0.27	0.07	