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#### Abstract

Coho salmon populations of the Thompson River drainage have been declining at a rate of $50-70 \%$ per generation since 1988. Of a sample of 34 extant populations in 1988, no fish were observed in 11 of them ( $32 \%$ ) in 1997. To identify the causes of these declines, freshwater production was modelled using reconstructed smolt abundances. The results of this analysis showed that: (1) interior populations are likely less productive than coastal populations, (2) Thompson coho populations are currently in the linear portions of their smolt-spawner relations, (3) populations are well below levels required to fully seed freshwater habitats. Simulations showed that the declines in Thompson coho are due to a roughly equal effect of declining marine survivals and fishing at inappropriately high rates in recent years. Under current ocean conditions Thompson coho will continue to decline in the absence of fishing and the rate of decline will increase with fishing. Because of the current poor population status, and because the risk of extinction increases exponentially with decreasing population size, it is recommended that no fishing mortality be imposed on these populations.


## Résumé

Les populations de saumon coho du bassin de la Thompson baissent au rythme de 50-70 \% par génération depuis 1988. Sur un échantillon de 34 populations qui existaient en 1988, aucun poisson n'a été observé dans 11 d'entre elles ( $32 \%$ ) en 1997. Pour trouver la cause de ce déclin, nous avons modélisé la production en eau douce par reconstitution de l'abondance des saumonneaux. Les résultats de cette analyse ont montré : 1) que les populations de l'intérieur sont vraisemblablement moins productives que les populations côtières; 2) que les populations de coho de la Thompson se situent actuellement dans les portions linéaires de leurs relations saumonneaux géniteurs; 3) que les populations se situent nettement au-dessous des niveaux nécessaires pour repeupler entièrement les habitats d'eau douce. Les simulations ont montré que les déclins du coho de la Thompson sont dus aux effets globalement égaux de la baisse de la survie en mer et du taux de capture excessivement élevé de ces dernières années. Dans les conditions océaniques actuelles, le coho de la Thompson va continuer à décliner même en l'absence de pêche, et le rythme de ce déclin va s'accroître avec la pêche. Étant donné le faible état actuel de la population, et du fait que le risque d'extinction augmente de façon exponentielle en fonction de la baisse de la taille de la population, il est recommandé de n'imposer aucune mortalité par pêche à ces populations.

## Introduction

Coho salmon of the Thompson River basin have declined in the last 10-15 years (Irvine et al. 1998). Similar declines in the whole Georgia Strait/Fraser River aggregate have prompted the implementation of a number of fishery management measures, and in 1998, the formation of a large DFO task force to deal with conservation concerns.

The investigation of declining or diminished populations falls into the realm of conservation biology. Caughley (1994) argues that there has been two main avenues of investigation of threatened or endangered species in conservation biology: the largely empirical search for the causes of population declines, and the more theoretical 'small population paradigm' of population viability analysis (PVA). While the latter has a more attractive scientific appeal because of the generalizations that can result from modelling and analysis, Caughley argues that the former activity has had a more lasting impact in the efforts to conserve species (but see Hedrick et al. 1996).

Following Caughley's advice, I first attempt to reconstruct the recent population dynamics of 4 Thompson 'stocks' with the goals of (1) identifying the causes of the major declines that have occurred in the last decade, and (2) estimating some important population parameters. I then describe some preliminary projections for Thompson coho under different harvest and marine survival scenarios.

## Description of Trends

I divided the Thompson coho data into 4 groups that I call stocks for this analysis; some of the groupings were based on the data in Irvine et al. (1998). Data were considered for 1984-1997 only, because exploitation and marine survival rate data were not available for earlier years. The groups were North Thompson ( 8 streams), South Thompson (19 unenhanced streams), the Salmon and the Eagle. The North Thompson is the same as Irvine et al's 10 stream index, except Blue River and Lion Creek have been removed. Blue River has been devoid of coho in the last few years because of the blockage at the North Thompson river, and Lion Creek coho appear to have been supplemented by upper North Thompson coho that fell back from the blockage to spawn. I examined the Eagle and Salmon separately because they were the 2 largest coho populations in the area in the 1980's, however, they have also been the site of major hatchery activities. A number of adjustments were made to these data to account for hatchery effects- these are listed in Appendix 1.

For each of the 4 stocks the rates of decline in the populations were calculated from the slopes of the regressions of $\ln (S p a w n e r s)$ vs. year (19881997). These slopes are estimates of the annual intrinsic rates of increase of the population, $r_{a}$. The finite rate of increase (or decrease) per year is $1-\mathrm{e}^{r_{a}}$; the per generational rate is $1-e^{3_{5}}$ (assuming a 1.1 or $3_{2}$ life history). The results are
summarized in Table 1, and show that populations have been declining at rates of 54-71 \% per generation since 1988.

Table 1. Annual rates of population change, $r_{9}$, and the finite rates ( $=1-\mathrm{e}^{r_{1}}$ ) for 4 stocks of the Thomson River watershed, for years 1988-1997.

|  |  | Finite Rate of Increase |  |
| :--- | :---: | :---: | :---: |
|  | r (annual) | Per year | Per generation |
| North Thompson | -0.27 | -0.23 | -0.55 |
| South Thompson | -0.26 | -0.23 | -0.54 |
| Salmon | -0.41 | -0.34 | -0.71 |
| Eagle | -0.41 | -0.34 | -0.71 |

## Local 'Extinctions'

While the proceeding analysis provides information on the overall declines of 2 large aggregates, it does not illustrate the fate of many of the small populations that comprise these aggregates. To show this, I assembled all available North and South Thompson populations for which there were data in both 1988 and 1997. I then tallied the number of streams that had 'noneobserved' status in 1997 (those above Little Hell's Gate were not included). While it is not clear if 'none-observed' is zero or a very small population; to assume that they are real zeros is the risk-adverse approach. These data illustrate that within an overall decline rate of greater than $50 \%$ per generation (Table 1), some populations go to 'none-observed' status, which might be called a 'local extinction' of a brood line, in 3 generations (Table 2). Further, 'extinction' is a real possibility for initial populations as large as 500-1000 fish (Figure 1).

Table 2. Proportion of North and South Thompson coho populations extant in 1988 that had 'none-observed' status in 1997, sorted by abundance in 1988.

| 1988 abundance class | Extant in 1988 | 0 in 1997 | $\% 0$ |
| :--- | :---: | :---: | :---: |
| $1-100$ | 15 | 6 | 40 |
| $101-1000$ | 15 | 5 | 33 |
| $1000+$ | 4 | 0 | 0 |

## A Model for Coho Salmon Dynamics

To project the effects of different marine survival rates and fishing scenarios, a model for coho production is needed. For simplicity I assume all fish have the age $1.1\left(3_{2}\right)$ life history type. I represented the dynamics of coho salmon by partitioning the life cycle into 2 phases, the freshwater and marine environment. Freshwater production was modelled with one of 2 functions:

$$
\begin{align*}
& S_{t+2}=\min \left(\alpha^{*} N_{t}^{*} p_{t}, K\right)  \tag{1}\\
& S_{t+2}=a * N_{t}^{*} p_{t}\left[1+a / b N_{t}^{*} p_{t}\right]^{-1} \tag{2}
\end{align*}
$$

where $\mathrm{N}_{\mathrm{i}}$ is the abundance of spawners in the stream in year $\mathrm{i}, \mathrm{S}_{\mathrm{i}}$ is the abundance of smolts, and $p_{f}$ is the proportion of females among the spawners. I assumed $p_{f}=0.45$, based on recent data (Irvine et al. 1998). Equation (1) is the broken stick model for smolt production that has proven useful in the analysis of a much larger database of coho salmon streams (Bradford and Myers unpubl. data). There are 2 parameters: $\alpha$, the productivity (smolts/female), and K, the stream carrying capacity. From the broken stick model the number of spawners needed to fully seed the habitat is $N^{*}=K /\left(\alpha^{*} p_{t}\right)$.

The second equation is the Beverton-Holt model, with parameters $a$, the slope at the origin, and $b$, the asymptotic smolt production at very large spawning populations. There is no simple parameter analogous for $\mathrm{N}^{*}$ for this model, however, a biological reference point could be some fraction of $b$.

In the marine environment, survival from smolt to spawner is given as:

$$
N_{t+3}=S_{t+2} * M S *(1-h),
$$

where MS is the 'marine' survival rate (which includes mortality during migration from the natal rearing area to the sea), and h , the total exploitation rate.

## Reconstruction of Smolt Production

The steep rate of decline observed in Thompson River coho populations has lead to speculation that these stocks are inherently less productive that coastal streams, and are less able to sustain the effects of high harvest rates and decreasing marine survival rates. However, a long time series of smolt abundances and CWT data similar to the Black Creek program are needed to directly contrast the productivity of coastal and interior populations. Because these data are lacking, I attempted to reconstruct smolt production for the 4 Thompson stocks from the adult data in obtain crude estimates for parameters of the 2 freshwater production models.

In theory, the number of smolts emigrating from a stream in year $t$ can be backcalculated from the resulting escapement as:
$S_{t}=N_{t+1}{ }^{*}[M S *(1-h)]^{-1}$
with symbols as before.
I used (3) and the 4 escapement time series to reconstruct the abundances of smolts. For the Eagle and Salmon some adjustments were made because of the hatcheries; details are in Appendix 1. To apply equation 3, 1 required time series of marine survival and exploitation rates. I used exploitation rate data from Thompson CWT data (Appendix 2). For the marine survival series I used the average of the Black Creek and Salmon River (Langley) wild indicator
populations (Appendix 3). No wild smolt survival rates are available for Thompson coho.

I then plotted the smolts produced against the in-river spawner escapement in order to estimate freshwater production parameters. Either the broken-stick or Beverton-Holt model was fit to the data. I used a non-linear searching procedure to find the maximum likelihood parameter estimates (including $\sigma$ ) by minimizing the -log likelihood (see Hilborn and Mangel 1996, p. 150). A log-normal error term was assumed. Confidence limits for a or $\alpha$ were calculated from the likelihood profile (Hilborn and Mangel 1997, p. 162).

Results
The resulting relation between reconstructed smolts and parent spawners were highly variable, but there appeared to be a relation between smolt production and spawners at low spawner abundances, that suggests that escapements have been limiting in recent years (Figure 2). The residual variation was higher than the average for datasets where smolts are estimated directly ( $0.37-0.77$ vs. 0.31 , the average for 14 coastal streams, Bradford and Myers, unpublished data). For the broken stick model the estimated values of $\alpha$ for the 4 Thompson stocks were all lower than the mean for the meta-analysis of coastal populations (the mean of coastal populations was $88, \mathrm{SD}=24$ ).

Table 3. Summary statistics from the maximum likelihood fit of the broken stick model to reconstructed smolt estimates. With $\alpha$ are the $90 \%$ confidence intervals. $\mathrm{N}^{*}$ is the escapement estimated to fully seed the habitat, $\mathrm{N}_{97}$ is the current population estimate for each stock.

| Stock | $\alpha$ | $\mathrm{K}(1000 ' \mathrm{~s})$ | $\sigma$ | $\mathrm{N}^{*}$ | $\mathrm{~N}_{97}$ |
| :--- | :---: | :---: | :---: | :---: | :---: |
| North Thompson | $48(39,62)$ | 42 | 0.39 | 1900 | 295 |
| South Thompson | $48(41,68)$ | 88 | 0.37 | 4000 | 500 |
| Salmon | $47(39,57)$ | 48 | 0.65 | 2300 | 50 |
| Eagle | $63(44,88)$ | 123 | 0.62 | 4300 | 150 |

The predicted asymptotic smolt production (b) for the Beverton-Holt model was much higher than for the broken stick model because the reconstructed smolt data were very variable at higher spawner levels (Table 4), which did cause inflection in the fitted curve (Figure 2). Based on the $\sigma$ values, the broken stick model fit the data slightly better than the Beverton-Holt form; this is consistent with the results from the analysis of the 14 coastal streams. The productivity parameter (a) for the Beverton-Holt model is the predicted smolts/female at the origin, and is expected to be higher than $\alpha$ of the broken stick model, which is constant across all $N<N^{*}$. To make the predicted productivities more comparable between models, I defined $a^{\star}$ as the productivity (smolts/female) from the Beverton-Holt model for the 1995 escapement (1998 returns) for each stock. $a^{*}$ values were similar to $\alpha$ 's, and suggest the average productivity for the Thompson complex is in the range of 50-60 smolts/female for underseeded populations.

Table 4. Summary statistics from the maximum likelihood fit of the Beverton-Holt model to reconstructed smolt estimates. $90 \%$ confidence limits indicated for $a ; a$ is the productivity (smolts/female) predicted for the 1995 escapement (i.e. for the 1998 returns).

| Stock | $a$ | $b(1000 ' s)$ | $\sigma$ | $a^{*}$ |
| :--- | :---: | :---: | :---: | :---: |
| North Thompson | $61(45,83)$ | 103 | 0.44 | 56 |
| South Thompson | $73(56,97)$ | 164 | 0.37 | 62 |
| Salmon | $39(26,60)$ | 177 | 0.74 | 36 |
| Eagle | $54(25,55)$ | 2838 | 0.73 | 53 |

## The role of fishing in the historical decline

With the population parameters estimated above it is possible to determine the role that fishing has had on changes in abundance. In this analysis I used the 3 peak years (1984-1987) of escapement data as a starting point, and simulated forward to 1997. I used the either the broken stick or Beverton-Holt model to forecast smolt production. For each population, the residuals from the fit of the models to the historical data were used to simulate variability in the freshwater environment. Adults were calculated as the product of the smolts produced and the annual estimates of marine survival. I used 2 different fishing scenarios to calculate the spawning escapement for the next generation: (1) fishing at a rate lower than the historical series, approximating the results of recent analyses (see Appendix 3), and (2) no fishing. I then calculated $r_{a}$ from each of the time series, for years 1988-1997 (Figure 3, Tables $5 \& 6$ ).

Table 5. Observed and simulated annual rates of decline, $r_{\mathrm{a}}$ for 4 Thompson stocks based on the broken stick model for 3 different fishing scenarios.

| Stock | Observed | Moderated | No fishing |
| :--- | :---: | :---: | :---: |
| North Thompson | -0.27 | -0.13 | -0.13 |
| South Thompson | -0.26 | -0.11 | -0.07 |
| Salmon | -0.43 | -0.27 | -0.19 |
| Eagle | -0.41 | -0.19 | -0.16 |

Table 6. Observed and simulated annual rates of decline, $r_{a}$ for 4 Thompson stocks based on the Beverton-Holt model for 3 different fishing scenarios.

| Stock | Observed | Moderated | No fishing |
| :--- | :---: | :---: | :---: |
| North Thompson | -0.27 | -0.15 | -0.08 |
| South Thompson | -0.26 | -0.14 | -0.08 |
| Salmon | -0.43 | -0.34 | -0.19 |
| Eagle | -0.41 | -0.19 | 0.02 |

The results from this analysis suggest that even without fishing, the populations would have declined from the peak levels. For the more productive North and South Thompson aggregates, fishing at the moderated rate would have had only a small effect on the overall rate of decline compared to the no fishing scenario. For the Eagle and the Salmon, fishing at the reduced rate would have still caused major declines. There was little difference in the results from
the 2 models for freshwater production. From this analysis, I conclude that fishing was responsible for approximately $50-70 \%$ of the average rate of decline in abundance of Thompson River coho stocks.

## The productivity of the populations

The implications of the parameter estimates obtained in this analysis are clear when the intrinsic rates of growth are calculated. For underseeded populations ( $\mathrm{N}<\mathrm{N}^{*}$ ) the broken stick model predicts that smolt production and spawner abundance are linearly related. Thus the intergenerational value for $r$ can be calculated as:
$r=\ln \left(\alpha^{*} M S^{*}(1-h)^{*} p_{f}\right) ;$
note that I define $r$ as the per generation growth rate, in contrast to $r_{\mathrm{a}}$, the annual rate of change used earlier. Populations will decline when $r<0$; the per generation proportional change in the population is ( $1-e^{r}$ ). Equation 4 is approximately correct for the Beverton-Holt model for small populations (substitute $a^{*}$ for $\alpha$ ), where the function is nearly linear (see Figure 2). For the 4 Thompson stocks the minimum marine survival rate to achieve population stability $(r=0)$ is $>4 \%$ with no fishing. The effects of different marine survival rates and exploitation rates for $\alpha=60$ are plotted in Figure 2. Under the current forecasts of $2-3 \%$ marine survival rates populations are predicted to decline at $h$ $=0$. Only if marine survival rates exceed the forecasts, or if my analysis has greatly underestimated $\alpha$, are populations likely to increase above brood levels. These predictions are for the median or most likely rates of change; the actual trajectory for any single population is highly uncertain because of populationspecific differences in productivity, and chance events and variability in the environment.

I also plotted the observed combinations of marine survival and exploitation rates used in the current analysis, to illustrate that these populations have probably been overharvested in most years since 1990 (Figure 4).

## Risk Assessment

Risk is the probability or chance of loss. To conduct a risk assessment the loss function must be clearly specified; for the current discussion I loosely define loss as continued population declines and local extinctions. As well, there are 2 forms of risk- the risk to fish populations, and the risk to us. For the fish, risk can be calculated from population parameters, and demographic and environmental variability. This is the biological risk, and it is fairly straightforward to build a simulation model that captures these elements for a theoretical population. Or it can be examined retrospectively, as I have done in an earlier section.

However, to estimate risk to humans of coho extinctions, we must also include our uncertainty about the true population parameters, model form and the sources of variability, all of which are estimated from noisy data, uncertain forecasts or expert elicitation. This uncertainty must be added to the real biological variability that exists for each population. Adding our uncertainty increases the risk, sometimes quite substantially (Ludwig 1996). Models for the incorporation of uncertainty in a Bayesian framework for coho salmon are currently under development. Such a risk assessment is not possible in the current time frame.

Because equation (4) for underseeded coho populations is a simple exponential growth model, we can rely on existing theory to make some generalizations about trends without proceeding to a full risk assessment. Lande (1993) has analyzed the exponential model and has a useful approximation for the average time to extinction (in generations) of a population $\mathrm{T}(\mathrm{N})$ with a negative growth rate, which includes the effects of environmental variation:

$$
\mathrm{T}(\mathrm{~N})=(-\ln \mathrm{N}-1 / \mathrm{c}) / r
$$

where $N$ is the number of females, $r$ is the estimated rate of population growth, $\mathrm{V}_{\mathrm{e}}$ is the environmental variance ( 0.18 is used here) and $\mathrm{c}=\left(2 N_{e}\right) r$. Demographic variation is ignored here. Plotting this function (Figure 5) illustrates an important point: if we equate decreasing time to extinction with increasing risk, then risk increases exponentially with decreasing population size.

Equation (4) can be used to predict the average effect of fishing on the abundance of underseeded coho populations. From equation 4, the effects of fishing on $r$ is proportional to the harvest rate, i.e., a $20 \%$ harvest rate will increase the rate of decline of the Thompson populations by $20 \%$ per generation. The effects of fishing are cumulative; harvesting at $20 \%$ for 3 generations will reduce populations to one-half the level if they had not been fished. Other scenarios involving different marine survival and harvest rates are given in Table 7 ; it is clear from the table that the status of a population in 3 generations is critically dependent on the marine survival rate over the 9 year period.

Although population declines dominate the values in the table, it should be noted that in reality we do not know with precision $\alpha$ for these populations, or the marine survival rates in the coming years. There is some probability that some populations are more productive than the $\alpha$ values used, and that marine survival rates may rise above 3-4\%. In these cases coho populations will grow. The effects of fishing on that growth are similar to the declines: the reductions in productivity caused by fishing will accumulate over time and will delay population recoveries significantly.

Table 7: Percentage of starting population after 1 and 3 generations, under different fishing and marine survival rates for 3 different rates of stream productivity ( $\alpha$ ). The proportion of females is assumed to be 0.45 .

| $\alpha=40$ | Generation <br> Exploitation Rate |  |  |  |  | 3 |  |  |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | Generations <br> Exploitation Rate |  |  |  |  |  |  |  |
| MS | $0 \%$ | $10 \%$ | $20 \%$ | MS | $0 \%$ | $10 \%$ | $20 \%$ |  |
| 0.01 | 18 | 16 | 14 | 0.01 | 1 | 0 | 0 |  |
| 0.02 | 36 | 32 | 29 | 0.02 | 5 | 3 | 2 |  |
| 0.03 | 54 | 49 | 43 | 0.03 | 16 | 11 | 8 |  |
| 0.04 | 72 | 65 | 58 | 0.04 | 37 | 27 | 19 |  |

$\alpha=60$

| MS | $0 \%$ | $10 \%$ | $20 \%$ | MS | $0 \%$ | $10 \%$ | $20 \%$ |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 0.01 | 27 | 24 | 22 | 0.01 | 2 | 1 | 1 |
| 0.02 | 54 | 49 | 43 | 0.02 | 16 | 11 | 8 |
| 0.03 | 81 | 73 | 65 | 0.03 | 53 | 39 | 27 |
| 0.04 | 108 | 97 | 86 | 0.04 | 126 | 92 | 64 |

$\alpha=80$

| MS | $0 \%$ | $10 \%$ | $20 \%$ | MS | $0 \%$ | $10 \%$ | $20 \%$ |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 0.01 | 36 | 32 | 29 | 0.01 | 5 | 3 | 2 |
| 0.02 | 72 | 65 | 58 | 0.02 | 37 | 27 | 19 |
| 0.03 | 108 | 97 | 86 | 0.03 | 126 | 92 | 64 |
| 0.04 | 144 | 130 | 115 | 0.04 | 299 | 218 | 153 |

## The Short-Term Prognosis for Thompson Coho

The 1997 escapements were $28 \%$ of the brood year abundance; even after accounting for an estimated fishery removal of $35 \%$, total recruitment in 1997 was still only $43 \%$ of the parent population size. Over all 4 Thompson stocks the summed brood year escapement for 1998 returns are $12 \%$ less than the parent population of the 1997 return. The marine survival forecast is for similar or perhaps worse conditions than faced the 1997 returns. Therefore the most likely scenario is that recruitment of Thompson River coho in 1998 will be less than we observed in 1997. However, there is considerable, and as yet unquantified, uncertainty in this forecast. Returns could be much better or worse than this. The prognosis for the 1999 and 2000 returns are bleaker because both (1996 and 1997) parent escapements are less than a third of the 1995 brood.

An ominous signal that will make the recalculation of population growth rates and persistence necessary is the observation that the fecundity of some interior coho salmon populations has dropped in 1996 and 1997. For the Salmon River, fecundity in these years was only 66\% of the 1987-1995 average, and all other things being equal, that implies that $\alpha$ for the Salmon will drop
correspondingly. Further, there are indications that the proportion of females in the spawning populations is declining. Decreases in productivity will increase the rate of population decline in the short term, as will any other changes (i.e. smaller body size, decreased fertility) that might be associated with poor ocean conditions.

## Discussion

By any metric the declines in Thomson coho are sufficient for the populations to be considered to be at considerable risk unless the causes of the declines can be identified and altered or mitigated. On average, all stocks I considered are projected to continue to decline in the absence of fishing unless marine survival rates improve to $>4 \%$. If marine survival rates fall in the $1-2 \%$ range the rate of decline could be the order of $40-70 \%$ per generation. Fishing these populations will increase the rate of decline, and correspondingly there will be exponential decrease the projected average time to extinction. However, it must be recognized that because of random demographic and environmental events and our lack of information, predicting the future of any one population involves considerable uncertainty, which has not been accounted for here.

Are the catastrophic declines in the Salmon and Eagle rivers related to, or are only coincident with the extensive hatchery operations on both of these systems? In both cases large numbers of fed fry were released at rates up to 10,000 fish $/ \mathrm{km}$ during years when the streams were likely to have been fully seeded by the progeny of wild spawners (Pitre and Cross 1992). Hatchery fry have been found to replace smaller wild fish when planted in this manner, and a number of studies have shown that the productivity of populations can be reduced after 1-2 generations of this practice (Nickelson et al. 1986; Reisenbichler 1996). Further investigation is needed to resolve this issue, but experience elsewhere suggests that hatcheries can be considered a factor in population declines, and their role in conservation activites must be considered carefully.

My estimates of the $\alpha$ parameter for the 4 stocks (Table 3 ) are somewhat lower than the average estimated by hierarchical Bayesian methods for 14 coastal streams (Bradford and RA Myers, Dalhousie University, unpublished data). The lower productivity can be largely explained by the difference in fecundity between interior and coastal streams: for Thompson streams fecundity averages $1200-1800$ eggs, $25-50 \%$ lower than coastal streams that have fecundities ranging from 2000-3000 (Irvine 1998, Beacham 1982). There are likely other, as yet unidentified, causes for the difference in productivity between regions.

The analysis cannot powerfully detect whether the recent declines are related to freshwater habitat change. The lower reconstructed smolt abundances
in recent years are well correlated with parent spawner abundance, suggesting underseeding has occurred in recent years. In the case of the Eagle and Salmon systems, both have about 85 km of main river rearing habitat, however, the capacity of the two systems to produce smolts is quite different. According to the broken stick model $\mathrm{K}_{\text {eage }}$ is about 1450 smolts $/ \mathrm{km}$, and for the Salmon K is much lower at 560 smolts/km. I am ignoring non-natal rearing in these approximations. Both of these values are well within the range observed in a large survey of coho smolt production (Bradford et al. 1997). The difference between the 2 systems is consistent with regional staff's opinions of the quality of the habitat; the Salmon has had a long standing problem with agricultural development and flows, whereas the Eagle is seen as better habitat, although logging impacts are a concern.

Fishing mortality has played a significant role in the current status of these populations. A useful reference point for coho salmon management is the point at which spawner populations fall below $\mathrm{N}^{*}$, the full seeding level, and it seems reasonable that fishing mortality should be adjusted to try to maintain full seeding in freshwater. This will maximize the population's capacity to withstand changes in the ocean environment. In retrospect, reduction in fishing should have taken place beginning in the early 1990's. In the absence of fishing, the current populations might be 2-10 times their current levels. These higher abundances provide a necessary reserve of production that the species has undoubtedly used historically to survive periods of unfavourable environmental conditions. This buffer has been eliminated by fishing, making persistence somewhat less likely if marine conditions do not improve in the next few years.

The effects of fishing mortality on these populations has probably been underestimated because the exploitation rates used are based on CWT's that have been recorded as caught in the various fisheries. Other fishing-related sources of mortality (i.e., illegal fishing, misreporting, fisheries not sampled for CWT's, hooking mortality of legal and undersized fish) are currently included in natural mortality. Thus the true marine survival rates may be higher than the estimates from CWT data. Closures of fisheries will reduce the negative bias in the marine survival rates, and may cause them to artificially increase relative to the years when all fisheries were operating.

I have ignored the meta-populational structure of coho salmon of large watersheds such as the Thompson River. Rather, I have treated the 2 population aggregates as single populations in much of the analysis. Yet under the current conditions of average negative growth rates, local extinctions in individual streams may be common. We do not know what the likelihood is that these streams will be recolonized by nearby populations. If there is a constant extinction-recolonization process in small streams of large watersheds, it seems that rebuilding the extinguished sub-populations will be enhanced by maintaining as large an extant population base in the watershed as possible. Thus a full evaluation of the risks of fishing should not only focus on maintaining the
remnant populations currently in the Thompson basin, but should also include the role that rebuilding these populations will play in the potential recovery of the many streams from which coho appear to have disappeared from.

## CONCLUSIONS

1. Thompson River coho salmon have declined since 1988 at rates of 50-70\% per generation, and the Eagle and Salmon populations are currently 1-2\% of recent peak levels. Many streams have decreased to 'none-observed' status in 3 generations.
2. The cause of the decline of the Thompson coho populations appears to be a combination of declining marine survival and recruitment overfishing.
3. Under current marine survival forecasts, Thompson coho salmon are likely to continue to decline, even in the absence of fishing. Fishing mortality will increase the rates of declines in these populations.
4. The risk of extinction increases with decreasing population size at an accelerating rate.
5. Unless there is a reversal in ocean conditions, the risks and conservation concerns for Thompson coho will be even higher in 1999 and 2000 because of smaller brood populations.

## RECOMMENDATION

1. There is no fishing mortality that is consistent with the goals of conserving Thompson River coho salmon under a precautionary approach to fisheries management. Fishing will increase the risk of extinction of these populations.

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## Appendix 1. The Salmon and Eagle River data

Escapement data for the Eagle and Salmon Rivers were adjusted to account for the effects of the hatchery operations on these systems. Estimates of the number of fish spawning, and those taken for hatchery operations were taken from SEP records and Irvine et al. (1998). There is some uncertainty surrounding the 1997 Eagle estimate as the fence was not operated. About 40 live and dead fish were counted in 2 floats -1 exanded this to a guess of 150 for the actual escapement for this year.

In order to reconstruct smolt production from fish spawning in each system I had to estimate the number of returning adults from the hatchery. This can be complicated because hatchery fry can compete and replace wild fish in the stream, and then should probably be considered part of the natural production.

In the case of yearling smolts that were released in both systems, I assumed there was no interaction between these fish and wild smolts. Therefore I subtracted the number of adults produced from smolts from the total adult return to the river the following year. Estimates of adults from smolt releases were from spawners examined at the counting fences. Corrections were made for fish not inspected for tags.

Estimates of the adults produced from the extensive fry releases in both system were available from the CWT database. For the fry releases I assumed hatchery fish competed with smaller wild fish and there would be no overall improvement in smolt production from either stream (Nickelson et al. 1986, Pitre and Cross 1992), and made no adjustments for these fish.

Alternatively, one could assume that in years when there were few wild spawners, there would have been little competition between hatchery and wild fish. In this case the adults produced from the fry releases would be subtracted from the total adult return, to obtain an estimate of adults produced from wild juveniles. For the years having spawners above some threshold level, competition occurred, and there would be no incremental increase in adult production from these broods. I recalculated the wild smolt production for different thresholds and found that it made little difference to the results, largely because in recent years of small spawning populations there were no hatchery fry releases.

## Appendix Table 1: Coho salmon data used in the analysis

| Brood Year | Total Escapement | Hatchery Take | Natural Spawning | Hatchery Releases(1000's) |  | Hatchery Contribution to $\mathrm{Esc}_{t+3}$ |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  |  |  | Fry | Smolts | From Fry | From Smolts |
| Salmon |  |  |  |  |  |  |  |
| 1984 | 1550 | 620 | 930 | 462 | 0 | 1555 | 0 |
| 1985 | 3800 | 356 | 3444 | 284 | 0 | 2192 | 0 |
| 1986 | 2700 | 574 | 2126 | 446 | 0 | 2387 | 0 |
| 1987 | 2479 | 519 | 1960 | 453 | 0 | 767 | 0 |
| 1988 | 4405 | 636 | 3769 | 428 | 0 | 169 | 0 |
| 1989 | 3800 | 591 | 3209 | 530 | 0 | 967 | 0 |
| 1990 | 1216 | 302 | 914 | 298 | 0 | 263 | 0 |
| 1991 | 308 | 30 | 278 | 0 | 10 | 0 | 27 |
| 1992 | 2250 | 260 | 1990 | 137 | 21 | 284 | 114 |
| 1993 | 518 | 91 | 427 | 45 | 0 | 27 | 0 |
| 1994 | 376 | 32 | 344 | 8 | 0 | 0 | 0 |
| 1995 | 900 | 149 | 751 | 130 | 0 | 0 |  |
| 1996 | 170 | 64 | 106 | 15 | 0 | 0 |  |
| 1997 | 50 | 17 | 33 |  |  |  |  |
| Eagle |  |  |  |  |  |  |  |
| 1984 | 7100 | 776 | 6324 | 691 | 27 | 4112 | 524 |
| 1985 | 4500 | 590 | 3910 | 537 | 30 | 1897 | 356 |
| 1986 | 3500 | 484 | 3016 | 423 | 32 | 1200 | 927 |
| 1987 | 11005 | 431 | 10574 | 450 | 65 | 541 | 498 |
| 1988 | 10052 | 744 | 9308 | 413 | 65 | 348 | 98 |
| 1989 | 5856 | 742 | 5114 | 541 | 57 | 618 | 169 |
| 1990 | 4396 | 511 | 3885 | 604 | 58 | 329 | 15 |
| 1991 | 1943 | 583 | 1360 | 546 | 0 | 75 | 0 |
| 1992 | 3352 | 320 | 3032 | 261 | 37 | 73 | 34 |
| 1993 | 876 | 116 | 760 | 109 | 0 | 26 | 0 |
| 1994 | 1438 | 0 | 1438 |  |  |  |  |
| 1995 | 800 | 0 | 800 |  |  |  |  |
| 1996 | 241 | 0 | 241 |  |  |  |  |
| 1997 | 150 | 0 | 150 |  |  |  |  |

Appendix 2. Thompson River exploitation rates calculated from CWT data. Data are for hatchery fish only, combined over all tag groups for each year. Also shown are the average and standard error. In the smolt reconstructions, the Eagle and Salmon data were used for those 2 streams, with the average value used in 1997. For North and South Thompson aggregates the average series was used.

| Return <br> Year | Eagle | Salmon | Lemieux | Louis | Average | SE |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- |
| 1987 | 0.51 | 0.62 |  |  | 0.57 | 0.05 |
| 1988 | 0.76 | 0.63 |  |  | 0.69 | 0.06 |
| 1989 | 0.66 | 0.63 |  |  | 0.64 | 0.01 |
| 1990 | 0.74 | 0.69 |  |  | 0.72 | 0.03 |
| 1991 | 0.64 | 0.79 |  |  | 0.72 | 0.07 |
| 1992 | 0.84 | 0.76 |  |  | 0.80 | 0.04 |
| 1993 | 0.91 | 0.79 |  |  | 0.43 | 0.06 |
| 1994 | 0.44 | 0.43 |  | 0.00 |  |  |
| 1995 | 0.85 | 0.46 | 0.44 | 0.47 | 0.55 | 0.09 |
| 1996 | 0.90 | 0.52 | 0.83 | 0.82 | 0.77 | 0.07 |
| 1997 |  |  | 0.22 | 0.49 | 0.36 | 0.10 |

Appendix 3. Other data used in this paper. Moderated harvest rates are a hypothetical intermediate level of fishing based on the lower range of suggested rates in Stocker et al. (1989, p.208) and Rice et al. (1994, p. 363); these rates were used in the development of scenarios for each aggregate. Last 2 columns are listed by brood year.

|  |  | Escapement |  |  |
| :--- | :---: | :---: | :---: | :---: |
| Brood <br> Year | North <br> Thompson | South <br> Thompson | Marine <br> Survival | Moderated <br> Harvest |
| 1984 | 3210 | 3367 | 0.13 | 0.65 |
| 1985 | 2020 | 4750 | 0.17 | 0.65 |
| 1986 | 343 | 4300 | 0.12 | 0.65 |
| 1987 | 2280 | 3452 | 0.13 | 0.65 |
| 1988 | 2915 | 5190 | 0.08 | 0.65 |
| 1989 | 1362 | 4205 | 0.11 | 0.65 |
| 1990 | 1518 | 2105 | 0.07 | 0.65 |
| 1991 | 106 | 1005 | 0.07 | 0.45 |
| 1992 | 1200 | 2985 | 0.06 | 0.45 |
| 1993 | 692 | 925 | 0.07 | 0.45 |
| 1994 | 803 | 1145 | 0.03 | 0.0 |
| 1995 | 327 | 905 |  |  |
| 1996 | 179 | 391 |  |  |
| 1997 | 295 | 507 |  |  |



Figure 1. Fate of 34 spawning populations from the North and South Thompson watersheds between 1988 and 1997 showing the variation in the rate of decline among populations. Many streams have declined to 'none-observed' status for this broodline in 3 generations.


Figure 2. Reconstructed smolt abundances for 4 Thompson stocks. Solid line is the fit of broken stick model, dashed line is the BevertonHolt model. Triangles are the predicted smolt yields (broken-stick model) for the 1995-1997 broods, illustrating the poor smolt production expected in the next few years.


Figure 3. Trends in actual (solid lines) and simulated (dotted: moderated harvest rates [see Appendix 3], dashed: no fishing) escapements for 4 Thompson coho stocks. Simulations began with the actual 1986-1988 escapements.


Figure 4. Predicted rates of increase, $\mathbf{r}$, for different combinations of marine survival and harvest mortality for an underseeded population if productivity $\alpha=60$. The solid isopleth ( $\mathrm{r}=0$ ) indicates the conditions of no population change. Dotted lines connect the actual data used in this paper (Appendices 2 and 3); shown are return years. Data illustrates how in most years since 1990 combination of fishing and ocean mortality has caused population declines ( $r<0$ ), however, only in 1997 was the ocean mortality so high that declines would have occurred in the absence of fishing. It should be noted that in any aggregate there will be populations more or less productive than the average.


Figure 5. Example of Lande's (1993) equation for predicting the average time to extinction of population under negative growth rates, illustrating how risk increases exponentially with smaller initial populations. Here $r=-0.50$.

