

Reference points for coho salmon (*Oncorhynchus kisutch*) harvest rates and escapement goals based on freshwater production

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Abstract: We describe a simple scheme for the management of coho salmon (*Oncorhynchus kisutch*) population aggregates that uses reference points derived from an empirical analysis of freshwater production data. We fit a rectilinear "hockey stick" model to 14 historical data sets of female spawner abundance and resulting smolt production and found that at low spawner abundance, the average productivity was about 85 smolts per female spawner. Variation in productivity among streams may be related to the quality of the stream habitat. We show how freshwater productivity can be combined with forecasts of marine survival to provide a limit reference point harvest rate. Our method will permit harvest rates to track changes in ocean productivity. We also used the historical data to estimate that, on average, a density of 19 female spawners·km⁻¹ is required to fully seed freshwater habitats with juveniles. However, there was considerable variation among the streams that might limit the utility of this measure as a reference point. Uncertainty in the forecasts of marine survival and other parameters needs to be incorporated into our scheme before it can be considered a precautionary approach.

Résumé : Nous décrivons un système simple de gestion de groupes de populations de saumon coho (*Oncorhynchus kisutch*) qui utilise des valeurs de référence établies à partir d'une analyse empirique des données de production en eau douce. Nous avons ajusté un modèle rectilinéaire en « bâton de hockey » à 14 ensembles de données historiques sur l'abondance des génitrices et la production connexe de smolts, modèle qui a montré que lorsque l'abondance de génitrices est faible, la productivité moyenne était d'environ 85 smolts par génitrice. La variation de la productivité d'un cours d'eau à l'autre pourrait être liée à la qualité des habitats fluviaux. Nous montrons comment la productivité en eau douce peut être combinée avec les prévisions de la survie en mer pour produire un taux de récolte correspondant à une valeur de référence limite. Notre méthode permettra de faire en sorte que les taux de récolte reflètent les changements dans la productivité océanique. Au moyen des données historiques, nous avons aussi estimé qu'en moyenne il faut une densité de 19 génitrices·km⁻¹ pour faire le plein de juvéniles dans les habitats dulcicoles. Cependant, une variation considérable entre les cours d'eau pourrait limiter l'utilité de cette mesure comme valeur de référence. L'incertitude des prévisions de la survie en mer et d'autres paramètres doit être intégrée à notre système avant qu'il puisse être considéré comme obéissant au principe de précaution.

[Traduit par la Rédaction]

Introduction

The management of coho salmon (*Oncorhynchus kisutch*) is extremely difficult because the species tends to be found in many streams and rivers (e.g., Slaney et al. (1996) identified nearly 2600 spawning populations in British Columbia alone), and adults are mainly harvested by mixed-stock marine hook-and-line fisheries. Populations are usually aggre-

gated into management or conservation units that may consist of hundreds of populations to which blanket fishing regulations are applied. Populations within these aggregations will differ in productivity, and their response to management actions will vary. Unfortunately, assessing the status of individual spawning populations within the aggregate is logistically difficult because of the large numbers of small populations and difficulties in estimating spawner abundance (Irvine et al. 1992).

Faced with these problems, biologists sometimes rely on a small number of well-studied index streams to manage coho salmon. The key assumption of index streams is that population parameters estimated from them are representative of other populations in the region (Symons and Waldichuk 1984). The assumption is reasonable for marine survival rates (Coronado and Hilborn 1998), marine harvest rates, and ocean catch distributions, but it may be less appropriate for the freshwater segment of the life cycle because there can be considerable stream-specific variation in productivity and survival (Bradford et al. 1997; Bradford 1999).

In this paper, we present a simple model for the dynamics of coho salmon. We then parametrize the model with an

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analysis of existing data on the productivity of coho salmon in freshwater. We propose that the model can be used to establish general conservation goals for coho salmon in the form of harvest rates and spawning populations; these goals are akin to "limit reference points" that are often part of precautionary approaches to fisheries management (Richards and Maguire 1998).

Model for the coho salmon life cycle

Mature coho salmon usually spawn in the fall and early winter in both small streams and larger rivers. Fry emerge from spawning gravels in the spring, and a large portion of the emergent population migrates immediately downstream. The remainder establish rearing locations within the stream, or sometimes a nearby lake, where they spend a year before migrating to sea as smolts. Most fish return as adults to the spawning streams after 18 months in the ocean and therefore have a 3-year life cycle. There are variations on this basic life history, including older smolts in northern streams and the presence of precocious males that only spend 6 months in the ocean (Sandercock 1991), but we ignore them in this paper. Population data for a particularly well-studied stream are shown in Fig. 1.

The production of smolts from freshwater habitats appears strongly limited by the availability of suitable physical habitat (Chapman 1965; Bradford et al. 1997), and streams can become fully "seeded" with juveniles at relatively low spawner abundances. Thus, we define the following simple model for the production of smolts from a stream:

$$(1) \quad S_{t+2} = \min(\alpha N_t, K)$$

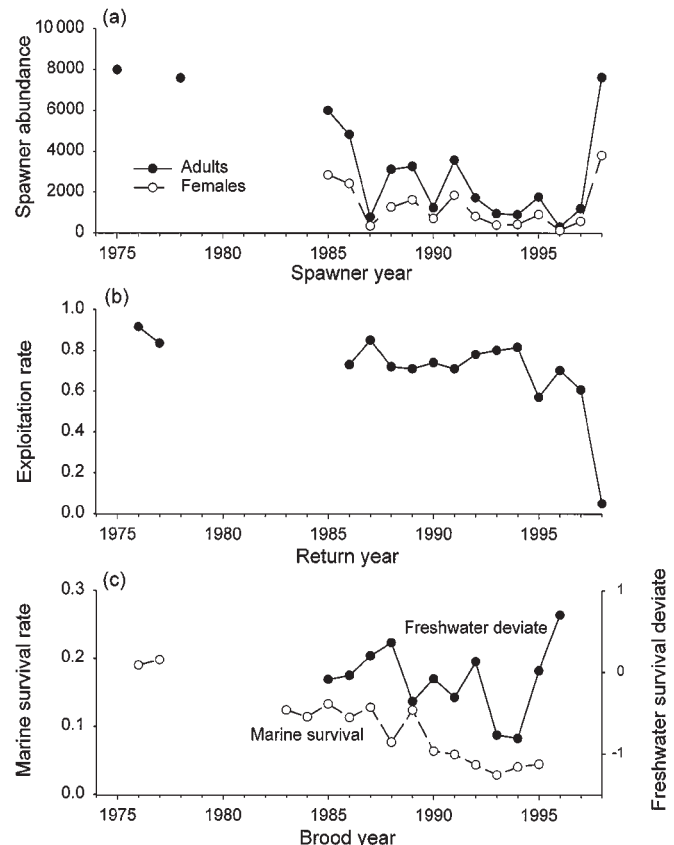
where S_{t+2} is the abundance of age-1 smolts migrating to the sea in year $t + 2$, α is the productivity parameter (smolts per female) for low spawner abundance, N_t is the number of female spawners in year t , and K is the carrying capacity of the stream for smolts. This is a piecewise linear model that we call the "hockey stick" model, and it assumes that survival is independent of density up to a critical spawner level N^* ($= K/\alpha$), at which point the habitat becomes fully seeded (Fig. 2). While the abrupt transition at N^* may be biologically unrealistic, this model does have readily interpretable parameters that are largely independent of each other. Although the units of K are smolts or smolts per kilometre, it is unlikely that the abundance of smolts (strictly defined as the seaward migrating stage) is limited by stream habitat. Rather, the carrying capacity is probably determined in the juvenile or presmolt stages, possibly during the overwintering period (Nickelson 1998).

The full life cycle for female fish is

$$(2) \quad N_{t+3} = \min(\alpha N_t, K)MS(1 - h)p_f$$

Here, the abundance of female spawners in year $t + 3$ is the product of the number of smolts, the marine survival rate (MS), the exploitation rate (h), and the proportion of smolts that return as adult females (p_f). The latter parameter accounts for sex-specific differences in survival in the ocean (Spidle et al. 1998). We assume that the survival of a population in the ocean is independent of its density.

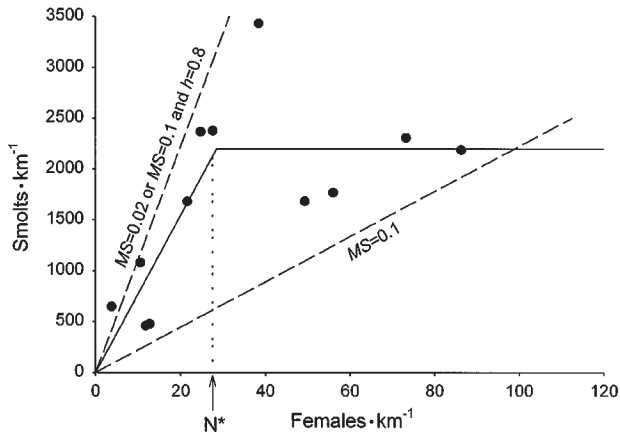
Fig. 1. Summary of population data for Black Creek coho salmon. (a) Total adult spawner and female spawner abundances by spawning year. Abundances were estimated by the methods of Irvine et al. (1992). (b) Total exploitation rate by marine fisheries on Black Creek coho salmon, based on coded wire tag returns, by return (fishing) year. Note that stringent harvest measures enacted in Canadian waters in 1998 to conserve British Columbia coho salmon populations have resulted in an apparent recovery of the Black Creek population. (c) Marine survival rate estimated from coded wire tag returns (open circles) and annual deviations from the fit of the hockey stick model (Fig. 2), calculated as $\ln(\text{data}/\text{model})$ (solid circles).



Empirical review of freshwater production

We obtained estimates of the parameters of eq. 1 by summarizing existing information on smolt production. We used 14 data sets collated from the literature and unpublished sources that contained annual estimates of female spawners and the number of smolts that they produced. In most cases, the estimates were made from fences or weirs installed near the mouth of the stream. All of the data sets were from coastal streams located along the western slope of North America from Oregon to central British Columbia. Estimated abundances of adults or juveniles were standardized by dividing them by the length of the stream. Stream lengths were usually obtained from the source reports, but in a few cases, they were measured from topographic maps, usually at 1 : 50 000 or 1 : 63 360 scale (Bradford et al. 1997). Measured stream lengths will underestimate the true length of the watercourse, resulting in an upward bias in K (α is unaf-

Fig. 2. Freshwater production data for Black Creek with the fitted hockey stick model. Dashed lines illustrate the outcomes of different combinations of marine survival and harvest rates on this population; the intersections of the coho salmon smolt model and the dashed lines are the equilibrium points. The sex ratio of returning fish is assumed to be 45% female. The model predicts that this population will not sustain itself when the marine survival is less than 2.9%.



fected). In one stream, Minter Creek, newly emerged fry migrants were collected at the counting fence and were returned to the headwaters of the creek (Salo and Bayliff 1958). Because this will affect the production of smolts at low spawner abundances, we did not include this population in the calculation of the average smolt production parameters.

The hockey stick model was fit by maximum likelihood methods. The variability around the model was described by a lognormal distribution. To characterize the uncertainty in α , a key parameter in our analysis, we calculated likelihood profiles for this parameter (Davison and Hinkley 1997; Barrowman and Myers 2000).

Seven of the smolt data sets also contained estimates of the number of newly emerged fry that migrated past the counting facility during the spring months. The downstream migration of fry from natal streams in the spring months is thought to be due to the effects of high and variable freshet flows or to competitive interactions among fish for space (Chapman 1962; Mason 1975; Hartman et al. 1982). We analysed these data to see if variation in the rate of fry outmigration among streams might yield insight into why streams different in their smolt production parameters. Standard linear models were used to describe the relationship between the abundance of outmigrating fry and female parents.

Results

Likelihood profiles for α of the hockey stick model for smolt production usually took on one of two forms depending on how informative the data were. For smolt series that included some data on the ascending part of the relationship, profiles were peaked, although the location and shape of the peak varied among streams (Fig. 3). Data on the ascending limb of the hockey stick were generally scarce, and the profiles were broad when there were only one or two points that determined the model fit. For data sets that lacked any data at low spawner densities, the profiles were flat for larger val-

ues of α because the available data made it impossible to determine how steep the smolt-spawner relationship might be. The exception was Flynn Creek, where one data point at very low spawner abundance caused the profile to be irregularly shaped, with maxima at both 80 and about 300 smolts per female. We thought that the higher mode was an unlikely representation of the underlying model and considered the data point an outlier. We used the lower mode in the calculation of the summary statistics.

In spite of the diversity of streams in our database, there was some coherence in the estimates of α , and the average, excluding Minter Creek, was 85 smolts per female (Table 1). There were five data sets that did not have strongly peaked profiles, and for some of these, the true values of α might be higher than listed in Table 1. The average of α for the eight populations that had peaked posteriors (again excluding Minter Creek) was 84 smolts per female.

Our estimates for N^* , the estimated density of spawners that results in full smolt recruitment, ranged from 4 to 44 females · km⁻¹, with an average of about 19 (Table 1). The estimates of N^* were positively correlated with their corresponding stream lengths ($r = 0.56$, $P = 0.04$) because there was a correlation between estimates of K and stream length ($r = 0.58$, $P = 0.04$) (recall that $N^* = K/\alpha$). Stream length and estimates of α were not correlated ($r = -0.24$, $P = 0.4$), nor were α and K ($r = 0.19$, $P = 0.5$) ($N = 13$ in all cases, as Minter Creek data were excluded).

The number of outmigrating fry captured in the downstream traps was linearly related to the density of female spawners (Fig. 4). A linear model, which estimated a common slope and stream-specific intercepts, yielded an overall estimate of 413 outmigrant fry per female spawner (SE = 23). A second model, which estimated stream-specific slopes, was also fit to the fry data (Fig. 4; model parameters are listed in Table 1).

We found that estimates of α and K of the smolt production model were both correlated with the corresponding slopes of the regressions of outmigrant fry abundance on spawners (Fig. 5). These relationships suggest that streams in which high fry outmigration rates are observed are likely to be less productive (lower α) and have a lower K .

Discussion

Our summary of existing data suggests that, on average, about 85 smolts per female spawner will be produced in coastal coho salmon streams that are not fully seeded. This estimate appears reasonable because it implies that under good ocean conditions (>10% marine survival, Nickelson 1998), greater than eight recruits per female spawner will be produced. It is this high rate of productivity that has allowed intense fisheries to operate during periods of favourable ocean conditions.

Our estimates for N^* , the minimum spawner density that results in maximum smolt production, were quite variable (Table 1). The positive correlation between N^* or K and stream length was unexpected because in an analysis of coho salmon production from 83 streams, Bradford et al. (1997) found the smolt production rate (smolts per kilometre) was independent of stream size. In our database, four of the smaller streams, which were part of intensive research pro-

Fig. 3. Female spawner–smolt data for 14 coastal coho salmon populations showing the maximum likelihood fit of the hockey stick model to each. To the right of each data panel is the profile log-likelihood for α ; for each, the maximum log likelihood has been subtracted, so the maximum values shown are all zero. The horizontal line is at -1.35 , and its intersection with the profiles approximates the 90% confidence bounds for α . In some cases, the data are not informative about the upper bounds on α . Parameter estimates are given in Table 1.

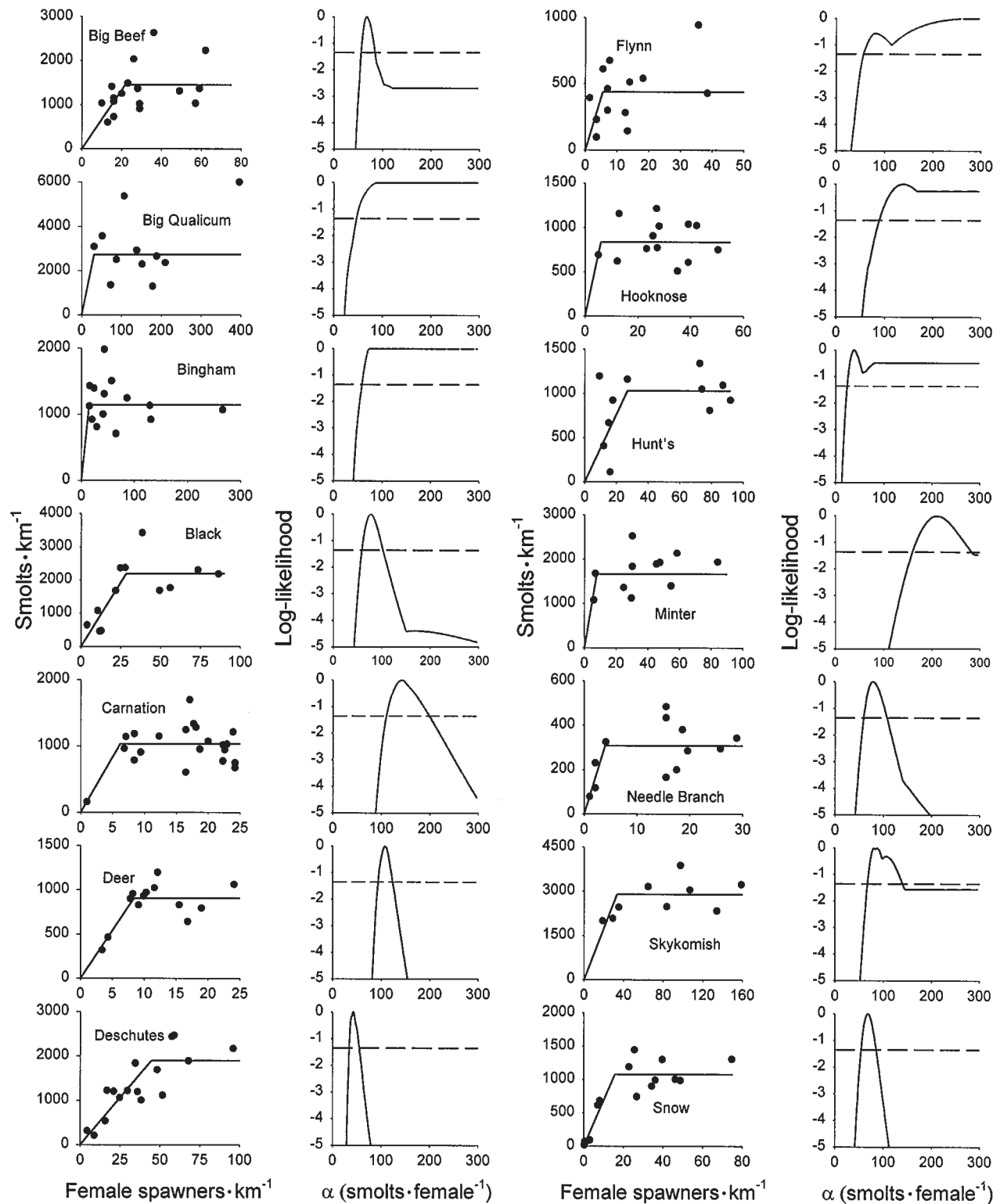


Table 1. Parameter estimates resulting from the fitting the hockey stick model (Fig. 3) to 14 coho salmon smolt-spawner data sets.

Stream	Len	<i>n</i>	α	<i>K</i>	σ	<i>N</i> *	β_0	β_1	
Big Beef	18	17	67 (55, 83)	1589	0.31	24			Sharma 1998
Big Qualicum	9.8	11	88 (46, ∞)	2740	0.46	31	-25 694	442	Fraser et al. 1983
Bingham	22	10	80 (58, ∞)	1154	0.26	14			Sharma 1998
Black	33	12	77 (58, 101)	2182	0.42	28			J.R. Irvine and K. Simpson, unpublished data
Carnation	3.1	24	144 (109, 197)	1033	0.26	7.2	192	193	Andersen and Scrivener 1993; P. Tschaplinski, B.C. Ministry of Forests, unpublished data
Deer	2.3	13	108 (93, 122)	907	0.16	8.4	-290	232	Knight 1980
Deschutes	54	16	43 (34, 55)	1902	0.34	44			Sharma 1998
Flynn	1.4	13	80 (56, ∞)	440	0.61	5.5	-1701	575	Knight 1980
Hooknose	5.8	13	140 (89, ∞)	842	0.25	6.0	557	98	Hunter 1959
Hunt's	5.4	11	38 (24, ∞)	1036	0.65	27	1739	146	Fraser et al. 1983
Minter	16	11	212 (159, 282)	1743	0.22	8.2			Salo and Bayliff 1958
Needle Branch	1.0	12	79 (59, 107)	309	0.32	3.9	897	590	Knight 1980
Skykomish	92	9	87 (67, 138)	2895	0.18	33			Sharma 1998
Snow	7	15	68 (54, 85)	1049	0.32	15			Johnson and Cooper 1995
Average			85	1390	0.35	19			
SD			31	819	0.15	13			

Note: Len, stream length (km); *n*, the number of years of data; α , *K*, and σ , maximum likelihood estimates for the model parameters; *N**, estimated minimum female spawner density that maximizes smolt production ($=K/\alpha$). For streams where the likelihood profile for α is not peaked, the entries in this table are the minimum values that maximize the likelihood. For Flynn Creek, the α shown is the lower mode of the profile in Fig. 3. In parentheses are 90% confidence intervals for α derived from the likelihood profiles (Fig. 3). In some cases, the upper bound is undefined because of a lack of information in the data. Minter Creek is not included in the averages. The last two columns are estimated parameters (β_0 , intercept; β_1 , slope) for linear regressions of migrant fry on female spawner abundance.

grams, produced less than 1000 smolts-km⁻¹, fewer than the average found in Bradford et al. (1997). Estimates of *K* may also be biased upwards for large rivers because it is difficult to inventory from maps all the small tributaries, side-channels, and other watercourses that coho salmon might use, which will cause stream lengths to be underestimated. Our findings highlight the need to proceed cautiously with metaanalysis when the number of data sets is small and their representativeness is in question (Hilborn and Liermann 1998).

Our analyses of the outmigrant fry data suggest that most fry leave the natal stream soon after emergence from spawning areas. Coho salmon egg-to-fry survival has been estimated to range from about 20 to 30% (Sandercock 1991; Bradford 1995); based on a mean fecundity of 2000–2500 eggs, the average rate of fry outmigration that we observed (413 fry per spawner) means that 60 to >90% of the emergent fry could leave the stream in their first spring (Mason 1975). In the Big Qualicum River, no fry migrated out of the stream at low spawner abundances (Fig. 4), perhaps because displaced fry are more likely to find suitable habitat in this stream, which is flow controlled for salmon production.

The approximately linear relationships between the abundance of outmigrating fry and female spawners suggest that density-dependent mortality in the egg-fry stage does not occur, at least in the range of spawner densities in the available data. Coho salmon spawning is usually scattered in the natal stream, and limits to coho salmon production imposed by the physical habitat for rearing juveniles means that subsequent spawner abundances are not likely to reach the densities observed in some pink (*O. gorbuscha*), chum (*O. keta*), and sockeye salmon (*O. nerka*) streams. High densities of spawners of these species can reduce egg-to-fry survival (e.g., sockeye salmon, West and Mason 1987).

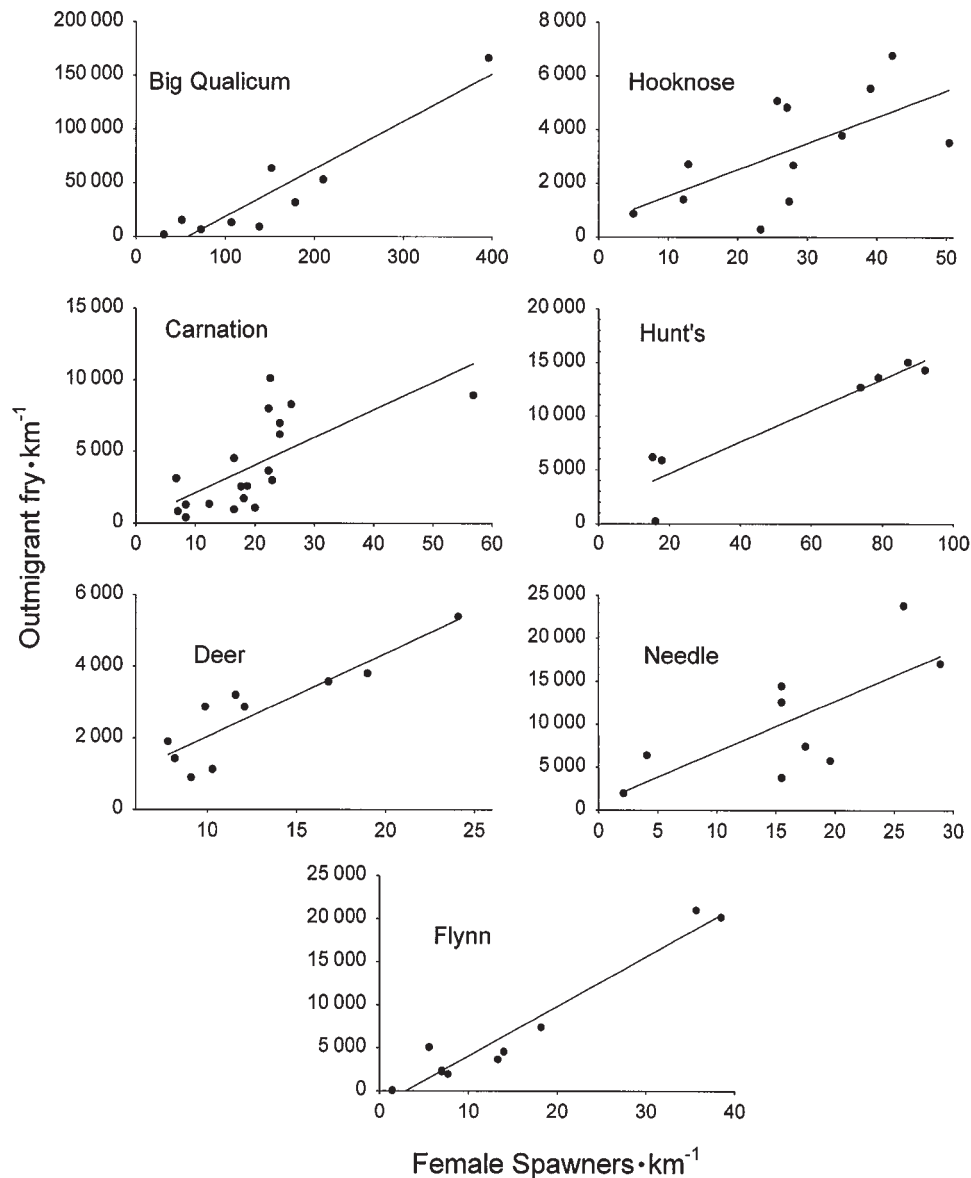
For streams that drain directly into the ocean, many newly emerged fry are thought to perish and not contribute signifi-

cantly to adult production (Mason 1975; Crone and Bond 1976) unless there is a brackish water estuary in which fry can acclimate to saline conditions (Tschaplinski 1987). In the case of natal streams that are tributary to larger rivers and lakes, fry that move to downstream and upstream habitats can make a significant contribution to smolt production (Irvine and Johnston 1992). Since fry production from natal streams appears to increase linearly with spawner abundance up to at least 50 females-km⁻¹ (Fig. 4), watersheds with good rearing habitat in nonnatal areas up or downstream could have their natal areas seeded with more spawners than would be suggested by smolt-spawner data for the natal stream alone. Indeed, if spring fry-to-smolt survival rates are on the order of 10–30% (Chapman 1965; Bradford 1995; Nickelson 1998), fry migrants could contribute significant numbers of smolts (possibly 40–120 per female spawner) to the brood. Thus, while smolt production estimates in Table 1 are appropriate for each natal stream, they may underestimate total smolt production for a population if there are significant amounts of suitable habitat in nonnatal areas.

The fry data also provide some insight into why streams vary in their rates of smolt production. Variation in α (smolts per female) among streams could result from differences in the rate of production of emergent fry and (or) differences in the survival of juvenile fish to the smolt stage. If variation in α was largely due to differences in the production of emergent fry, we might expect to find the slope of the outmigrating fry-spawner relationship to be positively correlated with estimates of α . This is because streams producing more newly emergent fry per female might be likely to have greater rates of outmigration as well produce more smolts per female. However, we found the opposite, as streams that were more productive for smolts (higher α) produced fewer fry migrants per spawner (Fig. 5a).

We hypothesize that when streams are not fully seeded,

Fig. 4. Numbers of newly emerged coho salmon fry migrating downstream from seven study streams as a function of the density of spawners. Linear regressions for each are also shown with model parameters listed in Table 1.



differences in productivity (α) might be partly due to differences in the stream's capacity to retain fry in the spring and early summer months. Factors such as instream habitat complexity, flow stability, and stream morphology will help to reduce fry outmigration rates, which might result in increased smolt production. This hypothesis is supported by the Minter Creek data, where the return of all downstream fry migrants to the headwaters of the stream resulted in the highest estimates of α in our database (Table 1). The exception was Hunt's Creek, which is a small flashy stream, so much so that a flood channel was built to divert high flows away from the Big Qualicum River that it drains into (Fraser et al. 1983). The estimates of both α and the fry production rate were low for Hunt's Creek, suggesting that egg-to-fry survival for this creek may be much lower than for the other streams.

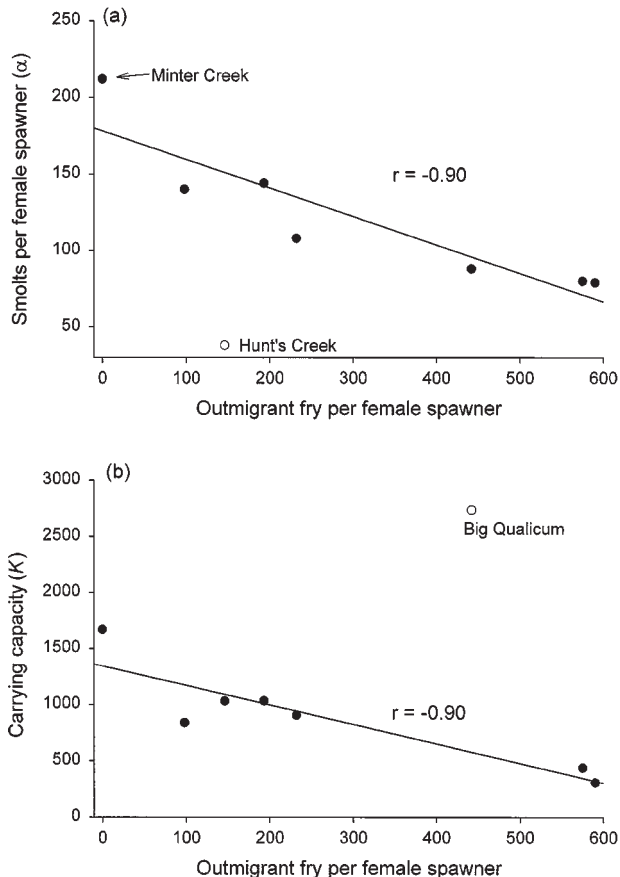
We surmise that the negative correlation between estimates of the fry outmigration rates and K (Fig. 5b) is proba-

bly not the result of a direct causative process but may result from a similar effect of habitat quality on both the fry outmigration rate and the stream carrying capacity. That is, the qualities of the habitat that lead to low rates of fry outmigration in the spring months noted above may be those that increase the K of the stream for smolts. The exception was the Big Qualicum River, which is flow regulated for fisheries production and has a very high K .

Reference points for coho salmon

Our simple smolt production model and the synthesis of existing smolt data provide enough information to devise some provisional reference points for the management of coho salmon aggregates. We follow Caddy and McGarvey (1996) and define the limit reference point (LRP) as a threshold (defined in terms of fishing mortality rates or

Fig. 5. (a) Relationship between α (smolts per female at low spawner abundance) and the slope of the corresponding outmigrant fry – female spawner regression for the coho salmon populations in Fig. 4 (data in Table 1). For Minter Creek, there were no fry migrants, as all fry collected at the fence were returned to the stream. The Hunt's Creek point was not included in the regression. (b) Relationship between K and the slope of the fry – female spawner regression. The Big Qualicum River datum was not included in the regression.



spawning stock size) that should not be crossed for any length of time.

Our approach is based on a variety of assumptions. First, we assume that within a coho salmon management aggregate, smolt production from freshwater can be reasonably approximated as a collection of independent, randomly varying lakes, rivers, and streams (Bradford 1999), each following the dynamics of the hockey stick model. The distribution of productivities is assumed to be approximated by our empirical results. We assume that all smolts from a management unit will be exposed to similar conditions once they reach the ocean (Coronado and Hilborn 1998) and that annual variation in survival rates in the freshwater and the marine segments of the life cycle is independent (e.g., Fig. 1c). The latter assumption is supported by the Black Creek data (Fig. 1c), which show a strong trend in the marine survival rate but random variation in freshwater productivity. While one might expect large-scale climatic influences to affect both marine and freshwater habitats and that might cause covariation in survival among life stages (Kope and Botsford

1990), evidence for this is lacking. Further, the nearly independent variation in annual smolt abundances from neighbouring streams (Bradford 1999) argues against regional effects of climate in freshwater survival.

Harvest rate based reference points

Advice on harvest rates can be derived from the hockey stick model when it is coupled with a forecast of the marine survival rate. At low population size ($N < N^*$), populations will be sustained or will increase when the replacement rate (N_{t+3}/N) is greater than 1. Rearranging eqs. 1 and 2 when $N < N^*$ yields the condition for sustainability as

$$(3) \quad \alpha MS(1 - h)p_f \geq 1$$

We then define a critical harvest rate that, if exceeded, will cause populations to decline to eventual extinction:

$$(4) \quad h^* = 1 - 1/(\alpha MS p_f)$$

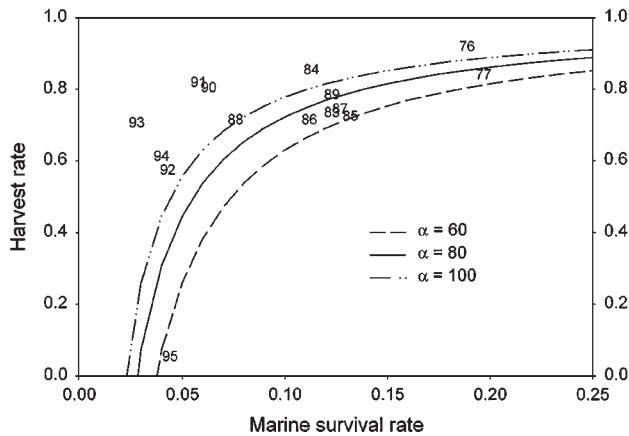
which holds when $\alpha MS p_f \geq 1$. Otherwise, populations will decline in the absence of harvest. Thus, h^* can be considered an LRP and is analogous to the extinction fishing mortality (F_e) of Mace (1994). The implications of harvest rates less than or greater than h^* are illustrated by dashed lines in Fig. 2.

Most investigations of reference points have been for large stocks or populations and have not considered variability in the subcomponents *within* a stock. Management units for coho salmon will contain spawning populations that will differ in productivity, and a reference point designed for the “average” will not be appropriate for the less productive populations and could lead to their eventual extirpation. Conversely, conservative reference points based on the least productive components of the management unit may be deemed overly restrictive for the unit as a whole. Our database provides a preliminary estimate of the variability in α among a collection of streams, and the LRP could be based on a specific percentile of the distribution of the estimates of α to permit the protection of less productive populations. For example, setting h^* based on $\alpha = 60$ would be conservative for 11 of 13 data sets in Table 1.

Realistic values for α were inserted into eq. 4 to illustrate the dependency of the LRP harvest rate, h^* , on the marine survival rate and α (Fig. 6). When $h > h^*$, populations will decline, so in Fig. 6, the area below and to the right of the h^* isocline is considered the region of sustainable exploitation. Figure 6 also illustrates how the exact value of α chosen to calculate h^* is less critical when marine survival rates are high but has a much larger effect when ocean conditions are poor (compare the vertical difference among isoclines).

We caution, however, that the distribution of estimated α values in Table 1 may not be an accurate representation of the true variability in a collection of coho salmon populations. Our analysis is based on relatively few data sets, and the sampling variability of a variance based on few data is always large. As well, each estimate of α contains uncertainty due to process and measurement error, which will tend to inflate the overall variability in the set of maximum likelihood estimates. We are also concerned that unproductive populations that may be reduced to very low levels or have

Fig. 6. Plot of h^* , the LRP harvest rate, calculated from eq. 4. The three contours are based on α values of 60, 80, and 100 coho salmon smolts per female. The proportion of females in returning fish was set at 0.45. Combinations of harvest rate and marine survival that lie above and to the left of the contours are unsustainable. Also shown are the Black Creek data (return year indicated) from Fig. 1.



been extirpated by continuous exploitation may be under-represented in our data.

Abundance-based reference points

A reference point for population status that is immediately apparent from the hockey stick model is N^* , the inflection point for the hockey stick model ($N^* = K/\alpha$). This reference point is the minimum escapement that will maximize smolt production. Our estimates for N^* are similar to those made by Beidler et al. (1980) for a smaller subset of data and are comparable with the range (11–31 females·km⁻¹, depending on marine survival rates) estimated to be required by a habitat-based model for Oregon coho salmon by Nickelson (1998). The wide range of variation in the empirical data (Table 1) suggests that without detailed knowledge of the productivity of each watershed in the management unit (e.g., Nickelson 1998), it will be difficult to establish all but the most general of escapement goals.

Reference points could also be designed to minimize the risk of extirpation of coho salmon populations. For example, a conservation “floor” spawner density of 3 females·km⁻¹ has been proposed for Canadian coastal coho salmon populations (Stocker and Peacock 1998). LRPs based on spawner densities may have to be adjusted upward for short streams, as the potentially small total number of spawners may expose the population to increased demographic risks (Routledge and Irvine 1999).

Chaput et al. (1998) and Nickelson (1998) have also proposed that salmon can be managed on the basis of freshwater habitat characteristics. In both their models, target spawner densities were linked to marine survival rates, so that in years of poor survival, the escapement goals would be reduced from average conditions. Chaput et al. (1998) used either a Beverton–Holt or a power model for smolt production and based their reference points on spawner levels that resulted in the maximum sustainable yield of adults, or variations thereof. When marine survival rates are low, the greatest yields come from smaller escapements, on the more

steeply ascending part of the smolt–spawner function. For the rectilinear hockey stick model that we used, the maximum yield in adults is always N^* , so spawner goals remain constant, regardless of the marine survival rates.

The model of Nickelson (1998) and Nickelson and Lawson (1998) is based on detailed knowledge of the habitat quality of the rearing environments and assumptions about the metapopulation dynamics of coho salmon in relatively large drainage basins. In times of poor marine survival, they suggested that only coho salmon rearing in the best habitats are able to sustain themselves. Target escapements are then adjusted downward to provide escapement to the most productive areas, resulting in a positive correlation between marine survival and the escapement goals. Our approach does not consider variations in habitat quality within larger drainage basins and also ignores “source-sink” interactions between neighbouring populations of differing productivity. The lack of metapopulation detail in our model means that it is probably more conservative in providing management advice than Nickelson’s approach.

British Columbia example

Southern British Columbia coho salmon catches and escapements have declined in the last 20 years, and there has been a lively debate about the causes of this decline (Walters and Ward 1998; Beamish et al. 1999). As an example of the use of our LRP approach, we plotted marine survival and harvest rate data for Black Creek coho salmon (estimated $\alpha = 70$, Table 1) on Fig. 6 to show that in many years, the harvest rate – marine survival trace was in the region of $h > h^*$. Marine survival rates declined through this period, and harvest rates remained high, except in recent years. As a result, the spawning population has declined over the past 20 years. Of course, the exact trajectory of Black Creek spawner abundance or any other single population will partly depend on density-independent variation in freshwater survival, which has a coefficient of variation typically of about 30% (Table 1), and population-specific variation in marine and harvest mortality.

Conclusions

Our analysis of the freshwater productivity of coho salmon suggests that there might be a reasonably well-defined range for the productivities of populations at low spawner abundances. The results indicate that the average coastal coho salmon population will be unable to sustain itself when marine survival rates fall below about 3%. We hypothesize that variation in productivities among populations might be caused by factors in the stream environment that affect the retention of newly emerged fry in the spring months.

We have proposed some general “rules” for the management of coho salmon stocks that result from the disaggregation of the marine and freshwater components of the life cycle. Management advice on maximum harvest rates can be formulated from knowledge of the density-dependent relationships in freshwater and a forecast of the marine survival rate. The LRP harvest rate, based on a predetermined percentile of the probability distribution of α , sets an upper

limit for the harvest rate. In practice, a harvest rate somewhat less than h^* is probably desirable to allow populations to exist somewhat above N^* , thus allowing a margin for "safety." Routledge and Irvine (1999) found that even small increases in the amount of chance variation in recruitment could result in significant reductions in population persistence.

Our approach is based on the premise of short-term stationarity of freshwater production parameters and forecastable marine survival rates (Fig. 1c). Our approach is therefore flexible to changes in ocean productivity and avoids the messy problems associated with traditional stock-recruit analysis when survival rates are trending (Walters and Parma 1996). However, the performance of our approach when marine survival forecasts and other parameters are uncertain needs to be evaluated.

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