Evaluation of visual survey methods for monitoring Pacific salmon (*Oncorhynchus* spp.) escapement in relation to conservation guidelines

Kendra R. Holt and Sean P. Cox

Abstract: Canada's Wild Salmon Policy requires that biological status of conservation units of Pacific salmon (*Oncorhynchus* spp.) be assessed regularly in relation to abundance-based benchmarks. Visual survey methods, in which periodic counts of spawning fish are made throughout a season, will likely be used for this purpose because they provide a cost-effective means of monitoring interannual trends in escapement. Trend detection performance for visual survey methods depends mainly upon consistency in (*i*) the ability of observers to detect fish and (*ii*) the annual timing of fish presence in the survey area. We developed a Monte Carlo simulation procedure to evaluate the ability of four visual survey methods (peak count, mean count, trapezoidal area-under-the-curve (AUC), and likelihood AUC) to detect 30% declines in coho salmon (*Oncorhynchus kisutch*) escapement over 10 years (i.e., the magnitude of trend that would warrant listing a coho population as threatened using the listing criteria of the Committee on the Status of Endangered Wildlife in Canada (COSEWIC)) given realistic levels of variability in these two factors. The mean count outperformed all other approaches across a wide range of scenarios about true population dynamics and survey designs, suggesting that a simple mean count method is suitable for monitoring coho escapements in relation to COSEWIC guidelines.

Résumé : La politique canadienne concernant le saumon sauvage exige que le statut des unités de conservation des saumons du Pacifique (*Oncorhynchus* spp.) soit évalué à intervalles réguliers par rapport à des niveaux d'abondance de référence. Pour réaliser cet objectif, on utilisera vraisemblablement des méthodes visuelles d'inventaire (dénombrements périodiques des poissons en fraie au cours d'une saison) parce qu'elles procurent un moyen avec un rapport rendement/coût intéressant pour suivre les tendances de l'échappement d'une année à l'autre. L'efficacité de la détection des tendances dans les méthodes visuelles d'inventaire dépend surtout de l'uniformité (*i*) de la capacité des observateurs à détecter les poissons et (*ii*) du calendrier de la présence des poissons dans la zone d'inventaire. Nous avons mis au point une procédure de simulation de Monte Carlo pour évaluer la capacité de quatre méthodes visuelles d'inventaire (dénombrement maximal, dénombrement moyen, surface trapézoïdale sous la courbe (AUC) et vraisemblance de AUC) à détecter des déclins de 30 % dans l'échappement de saumons coho (*Oncorhynchus kisutch*) sur 10 ans (soit une tendance suffisamment importante pour considérer la population de saumons coho comme menacée selon les critères du Comité sur la situation des espèces en péril au Canada (COSEPAC – COSEWIC)) avec des niveaux de variabilité réalistes de ces deux facteurs. Le dénombrement moyen fonctionne mieux que toutes les autres méthodes dans une gamme étendue de scénarios concernant la dynamique réelle de la population et les plans d'inventaire; cela indique qu'une méthodologie de dénombrement moyen est adéquate pour suivre les échappements de saumons coho selon les directives du COSEWIC.

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Introduction

Visual survey methods, in which observers periodically count fish throughout the spawning season, provide a cost-effective means of assessing interannual trends in Pacific salmon (*Oncorhynchus* spp.) escapement. Extensive survey programs that utilize visual survey methods allow a wide range of populations to be monitored; however, annual escapement estimates are generally assumed to be less certain than those obtained using more effort-intensive methods, such as enumeration fences or mark–recapture programs. Under Canada's new Wild Salmon Policy (WSP), genetically and geographically similar spawning aggregations of Pacific salmon will be grouped into conservation units (CUs), and for each CU, a monitoring plan will be developed to assess interannual trends in spawning escapement

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and the distribution of fish within the CU (DFO 2005). Extensive survey programs will likely be an important component of WSP monitoring plans.

Visual surveys have been used since the 1950s; however, the estimation methods applied to visual survey data have become increasingly complex. The peak count method, in which the highest count value observed in a spawning season is used to index escapement, was one of the earliest indices used (Bevan 1961) and is still widely used among management agencies (e.g., Geiger and McPherson 2004). Development of the trapezoidal area-under-the-curve (T-AUC) method (Ames and Phinney 1977; English et al. 1992) provided a means to estimate absolute escapement by incorporating information on survey life (the length of time fish remain alive in the survey area) and observer efficiency (the proportion of fish seen by observers) into the estimation procedure. Evaluations of the T-AUC method have shown that the accuracy of escapement estimates is highly dependent on year- and stream-specific estimates of survey life and observer efficiency (English et al. 1992; Irvine et al. 1992; Bue et al. 1998), which in themselves can be costly to obtain. More recently, a likelihood approach to AUC escapement estimation (L-AUC) has been proposed that allows uncertainty in survey life, observer efficiency, and the arrival timing of fish into the survey area to be incorporated into escapement estimates (Hilborn et al. 1999; Su et al. 2001; Korman et al. 2002).

Sources of uncertainty in escapement estimates vary with estimation method; however, all methods require that assumptions be made about (*i*) observer efficiency and (*ii*) the shape of the curve describing daily fish abundance in the survey area, which is itself dependent on arrival timing and survey life (English et al. 1992; Irvine et al. 1992; Bue et al. 1998). Unfortunately, observer efficiency, arrival timing, and survey life can be highly variable both among years and among streams within a given year. Factors influencing observer efficiency include observer experience, weather conditions, fish behaviour, and physical stream characteristics (Bevan 1961; Shardlow et al. 1987; Jones et al. 1998), while factors influencing survey life include individual body size, spawning density, arrival timing, and physical stream characteristics (Neilson and Geen 1981; Van den Berghe and Gross 1986; Fukushima and Smoker 1997). Arrival timing has a strong heritable genetic component (Smoker et al. 1998; Hodgson and Quinn 2002; Stewart et al. 2002); however, it can also vary among years and streams because of environmental conditions during migration, such as flow and temperature (Hodgson and Quinn 2002; Keefer et al. 2004).

Although the above uncertainties are relevant to escapement monitoring of all Pacific salmon species, we have chosen to focus on coho salmon (*Oncorhynchus kisutch*) populations in our study. Visual surveys of coho salmon populations are especially problematic because of high variability in both observer efficiency and daily abundance patterns. Coho salmon can be difficult to detect because of their colouration and their naturally low spawning abundances, and observer efficiency can be highly variable among surveys (e.g., Hetrick and Nemeth 2003). In addition, several observational studies suggest that the influence of environmental factors on arrival timing is particularly important for coho salmon populations, which frequently display pulsed and bimodal abundance curves and often enter spawning streams during periods of increased flow (Fraser et al. 1983; Holtby et al. 1984; Sandercock 1991).

We developed a Monte Carlo simulation procedure to evaluate the ability of four estimation methods (peak count, T-AUC, L-AUC with a beta-distributed arrival timing model, and an alternative mean count method) to detect 30% declines in coho salmon escapement over 10 years, which is one of several quantitative benchmarks that would warrant listing a coho population as threatened under the listing criteria used by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC). The specific objectives of our study were threefold: (*i*) to compare the ability of the alternative estimation methods to correctly detect declines in coho salmon escapement, (*ii*) to examine the effect of survey frequency (i.e., the number of surveys per year) on the ability to detect trends, and (*iii*) to test the sensitivity of our results to a wide range of scenarios about "true" population parameters and survey designs.

The usefulness of employing a simulation modelling approach to evaluate visual survey designs and estimation methods has been demonstrated for monitoring programs for migratory birds (Thomas 1996) and marine mammals (Adkison et al. 2003). To the best of our knowledge, however, our study of coho salmon visual programs is the first to use simulation modelling to examine how survey design and interannual variability in daily abundance patterns affect the accuracy and precision of trend detection for alternative escapement estimation methods.

Materials and methods

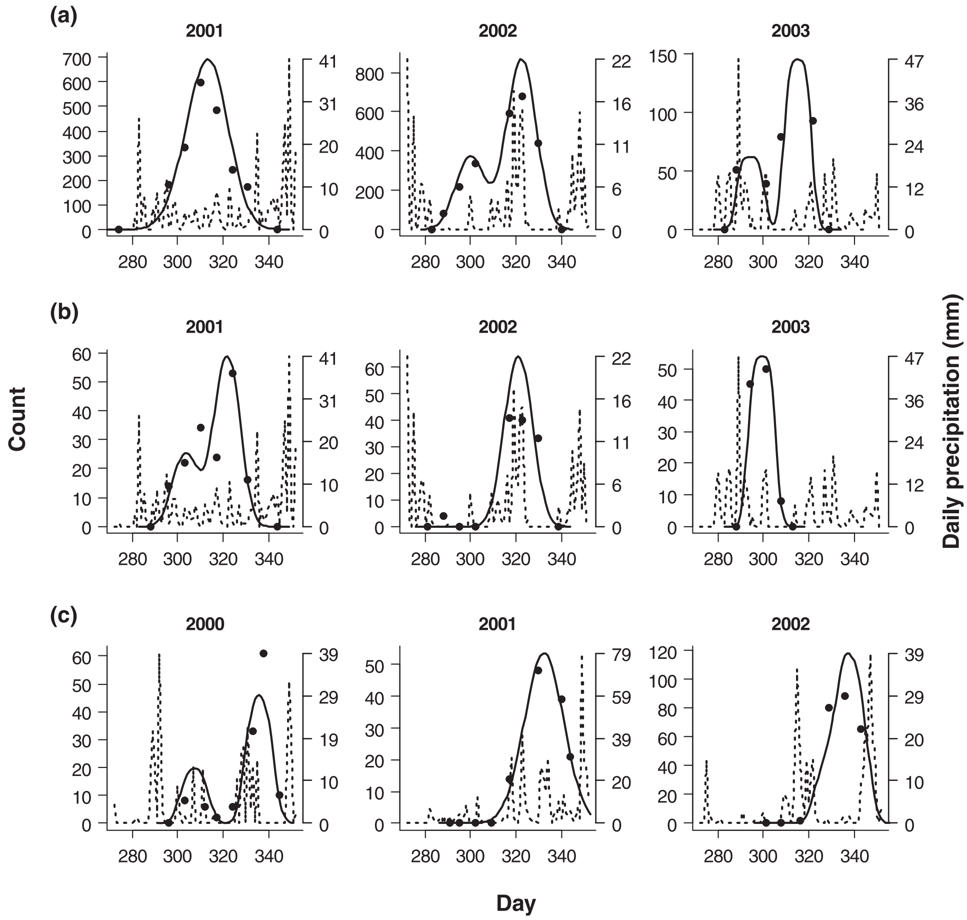
We developed a Monte Carlo simulation procedure consisting of four major components: (*i*) a model of true coho population dynamics, including annual escapement and daily abundance dynamics in a hypothetical survey area, (*ii*) a visual survey model to generate survey count data with observation error, (*iii*) calculation of alternative visual survey indices from those simulated survey count data using four different estimation methods, and (*iv*) evaluation of monitoring performance for each visual survey estimation method. To generate realistic count data for coho visual surveys, we used existing data sets to estimate interannual variability in daily abundance patterns and between-survey variability in observer efficiency. In the first half of our Methods section, we describe the data sets and analyses used to parameterize daily abundance dynamics and observer efficiency, while in the second half of the section we describe the simulation procedure. Model parameters are denoted using italicized lowercase letters (e.g., m), state variables are denoted using italicized uppercase letters (e.g., A), and functions are denoted using bold uppercase letters (e.g., $\mathbf{F}$).

Data analysis

Daily abundance patterns

We used 33 existing coho salmon visual foot survey data sets provided by Fisheries and Oceans Canada (DFO) stock assessment personnel to select an appropriate model to describe daily abundance patterns (referred to as daily abun-

Fig. 1. Daily precipitation levels (broken lines) plus observed (solid circles) and predicted (solid lines) spawner abundances from visual survey counts for coho salmon (*Oncorhynchus kisutch*) visual survey data sets from (*a*) Blue River and (*b*) Cook Creek in the North Thompson Watershed, British Columbia, and from (*c*) Bonnell Creek on Vancouver Island, British Columbia.



dance model) and estimate interannual variability in model parameter values (e.g., Fig. 1, Appendix A). Data sets were collected from 11 streams over a period of 3 years. Nine of the streams were tributaries to the North Thompson River in the Fraser River system, British Columbia (BC; data provided by R. Bailey, DFO, BC Interior Region Stock Assessment, 985 McGill Place, Kamloops, BC V2C 6X6, personal communication), and the other two streams were located on the east coast of Vancouver Island, BC (data provided by K. Simpson, DFO, BC South Coast Stock Assessment, 3225 Stephenson Point Road, Nanaimo, BC V9T 1K3, personal communication). All data sets had a minimum of five survey counts per year. Based on the results of model selection analysis, we selected a mixture model that was able to generate both unimodal and bimodal abundance curves (Appendix A). The selected mixture model required four parameters to be estimated from visual survey data sets (m, k, σ'^1, and σ'^2 in Table 1 and Appendix A). While the use of the mixture model may seem unwarranted given the small number of data points and the possibility of over-fitting, its use is justified by the high interannual variability in coho abundance curves arising from infrequent precipitation events (Fig. 1). It is apparent that coho salmon are more likely to enter streams during or immediately after several days of high-intensity precipitation and that bimodal abundance curves are common in years when dry periods are interspersed with periods of high precipitation. This level of variability cannot be produced using simpler models that restrict daily abundance dynamics to a single mode.

Among-year variation for each of the four mixture model parameters was calculated assuming that each stream i had a set of stream-specific mean parameter values from which daily abundance patterns deviated each year. For a given mixture model parameter θ, the actual parameter value observed for stream i in year t was a function of the stream-specific mean $\bar{\theta}_i$ and a stock- and year-specific deviation $\varepsilon_{i,t}$, e.g.,

$$(1) \qquad \theta_{i,t} = \bar{\theta}_i + \varepsilon_{i,t}$$

Mean parameter values reflect effects of stream-specific factors influencing arrival timing, such as local adaptation and migration distance (e.g., Smoker et al. 1998; Hodgson and Quinn 2002; Keefer et al. 2004). The methods used to estimate $\varepsilon_{i,t}$ for each of the four mixture model parameters are described in Appendix A.

Observer efficiency

Data on observer efficiency for adult coho salmon foot surveys were obtained from previous studies conducted on Black Creek, Vancouver Island, BC (J. Irvine, DFO, 3190 Hammond Bay Road, Nanaimo, BC V9T 6N7, unpublished data). The study design, in which observers visually inspected

Table 1. Simulation parameters for the baseline scenario.

Parameter	Value	Description
True population parameters		
E_0	500	Initial escapement in year 0
Decline	40%$^{++}$	Percent decline in escapement over 10 years
r	–0.057^{++}	Annual rate of population growth associated with decline
m	301.8	Stream-specific mean date of arrival (annual days)
k	12.4	Stream-specific distance parameter
σ'^1	4.7	Stream-specific standard deviation of arrival timing for first curve in mixture model
σ'^2	5.7	Stream-specific standard deviation of arrival timing for second curve in mixture model
τ_m	7.1^{++}	Standard deviation of year-specific random effect for m
τ_k	8.1^{++}	Standard deviation of year-specific random effect for k
τ_{σ_1}	2.3^{++}	Standard deviation of year-specific random effect for σ'^1
τ_{σ_2}	3.0^{++}	Standard deviation of year-specific random effect for σ'^2
s	12.8	Survey life for fish arriving on the median arrival date
z	0.3	Proportion parameter for the mixture run timing model
v	0.865^{++}	Average true observer efficiency
Survey parameters		
$f_{\max}$	(1, 2, 3,…,8)$^{++}$	Number of surveys per year
$\hat{v}$	0.865	Estimated observer efficiency
CV($\hat{s}$)	0.2^{++}	Coefficient of variation of survey life estimate
μ_s	12.8	Mean of prior distribution on s
Trend detection parameters		
Decline*	30%	Critical percent decline in escapement over 10 years
r^*	–0.04	Critical annual rate of population growth associated with decline*

Note: The symbol ++ indicates that sensitivity analyses were conducted on the parameter value (see Table 2). A detailed description of the mixture model used to describe daily abundance dynamics is given in Appendix A.

fenced off segments of stream prior to electrofishing, was repeated for 50 surveys occurring over 7 years. A more detailed description of the study design and an analysis of the first 3 years of data are available in Irvine et al. (1992). Analysis of the Black Creek observer efficiency data showed that the relationship between true abundance estimated from electrofishing, N, and survey counts, C, was linear, and that the intercept of the linear best-fit line did not differ significantly from zero ($C = a + bN$; null hypothesis (H_0): $a = 0$; $p = 0.412$, $R^2 = 0.92$). There was no significant difference in the slope of the regression among years (analysis of covariance; $F = 2.09$, $p = 0.155$). We therefore estimated the average observer efficiency over all surveys as the slope of the zero-intercept linear regression between N and C. The estimated slope was 0.865 ($R^2 = 0.95$; standard error = 0.03), indicating that on average, 86.5% of fish were detected.

Simulation procedure

We first created a baseline scenario to be used in the simulation procedure, which, based on our analyses, provided the most realistic representation of population and survey dynamics. Parameter values used in the baseline scenario were the maximum likelihood estimates obtained from fitting the daily abundance and observation models described in the previous two sections to empirical data (a summary of parameter values used in the baseline scenario is provided in Table 1). We then used sensitivity analyses to examine how deviations from parameter values used in the baseline scenario affected the performance of each estimation method. The basic steps in the simulation procedure are as follows: (*i*) Generate a true 10-year escapement time series with a rate of decline (40% decline) greater than the critical rate of decline that would result in a population being assessed as threatened under COSEWIC listing criteria (30% decline). (*ii*) Generate true daily abundances with random variation for each year t in the escapement time series. (*iii*) Generate count data with observation error for each survey frequency considered ($f_{\max} = 1,2,\ldots,8$ surveys per year) within year t. (*iv*) Calculate an estimated index of escapement for year t for each of the four estimation methods using the count data from $f_{\max}$ surveys. (*v*) Using the 10 years of observed index values, calculate probability associated with H_0: stock is not threatened. (*vi*) If the probability of H_0 is less than a prespecified confidence level (20%), reject H_0 and designate stock as threatened. (*vii*) Repeat steps (*i*) to (*vi*) for 1000 simulation trials. (*viii*) Calculate the probability of detecting a threatened population as the proportion of trials that correctly assess stock status as threatened for each combination of estimation method and survey frequency considered.

Annual escapement trends

We used an exponential growth model to generate a declining time series of true escapement values

$$E_t = E_0 e^{rt} \quad (2)$$

where E is true escapement, t is time in years, and r is the intrinsic rate of population growth (i.e., for a declining population, $r < 0$). For the baseline scenario, in which the true percent decline in escapement was 40% over 10 years, the value of r was –0.057. In comparison, the critical COSEWIC rate of decline used to designate a population as threatened is a 30% decline over 10 years ($r^* = -0.04$).

Daily abundance dynamics

The mixture model used to estimate among-year variability in daily abundance patterns was used to simulate true daily abundances for each year t in the escapement time series (Appendix A). The total duration of simulated fish presence in the survey area ranged from 17 to 91 days (mean = 51.5 days, n = 1000), which was realistic compared with the range of 19 to 82 days (mean = 47.3 days, n = 33) observed for the visual survey data sets used to parameterize daily abundance models. Interannual variability in daily abundance patterns was incorporated into simulated true data using the following variation of eq. 1 to describe a given abundance model parameter θ:

$$(3) \qquad \theta_{i,t} = \bar{\theta}_i + \Upsilon_t$$

where Υ_t is a year-specific random effect. For each parameter θ, Υ was assumed to be a normally distributed random variable with a mean of zero and standard deviation of τ,

$$(4) \qquad \Upsilon = \mathbf{N}(0, \tau)$$

where the value of τ was specific to each parameter (denoted as τ_m, τ_k, τ_{σ_1}, and τ_{σ_2} in Table 1). In the baseline scenario, values of τ were set equal to the mean values estimated from visual survey data sets (see Appendix A for description).

Visual survey model

The mean count, T-AUC, and L-AUC methods required a minimum of two, three, and five surveys per year, respectively. Survey dates were selected based on the assumption that observers would have some knowledge of historic daily abundance curves within a study stream. On average, survey dates were centred on the historic peak day of spawning abundance for the stream, d_{PK}. We developed a simple algorithm in which survey events were clustered near d_{PK} when survey frequency was low. The single survey for the one-survey case of the peak count method was conducted on d_{PK}, while the surveys for the two-survey case were conducted 1 week before and 1 week after d_{PK}. For the three- to eight-survey cases, the total number of days over which counts were conducted (l) was dependent on survey frequency ($f_{\max}$) as follows:

$$(5) \qquad l = \begin{cases} 42 \text{ days} & f_{\max} = 3 \\ 56 \text{ days} & f_{\max} = 4 \\ 70 \text{ days} & f_{\max} = 5 \\ 84 \text{ days} & f_{\max} \geq 6 \end{cases}$$

The first survey date was randomly selected from a 7-day period that occurred $0.5l$ days before d_{PK} using a uniform distribution, and subsequent surveys were evenly spaced over the next l days. Simulated survey counts were generated randomly from a Poisson distribution with a rate parameter $\lambda = vN_d$, where v is the average observer efficiency estimated from Black Creek observer efficiency studies (above).

Alternative escapement index methods

The maximum count value over surveys conducted in a given year was used as an index of annual escapement for the peak count method:

$$(6) \qquad I_{\text{PK}} = \max(C_1, C_2, \ldots, C_{f_{\max}})$$

while the mean of count values was used as an index of annual escapement for the mean count method:

$$(7) \qquad I_{\text{MN}} = \frac{1}{f_{\max}} \sum_{d=1}^{d=f_{\max}} C_d$$

The T-AUC method employs a simple trapezoidal approximation to calculate the area under the observed abundance curve for each year:

$$(8) \qquad \text{AUC} = \sum_{d=2}^{f_{\max}+1} (u_d - u_{d-1}) \frac{(C_d + C_{d-1})}{2}$$

where u_d is the day on which the dth survey was conducted. We used Bue et al.'s (1998) approximation:

$$(9) \qquad \text{AUC}_{\text{first}} = \frac{C_1 \hat{s}_t}{2}$$

$$(10) \qquad \text{AUC}_{\text{last}} = \frac{C_{\text{last}} \hat{s}_t}{2}$$

where $\hat{s}_t$ is an estimate of survey life for year t. When year- and stream-specific estimates of survey life are not available, as would be expected for extensive survey programs, survey life estimates must be extrapolated between years and (or) streams. In the baseline scenario, we model a monitoring program in which a year-specific survey life value is estimated for a single stream and then applied to multiple streams within that year. An escapement estimate is derived from eq. 8 as

$$(11) \qquad \hat{E} = \frac{\text{AUC}}{\hat{s}_t \hat{v}}$$

where $\hat{v}$ is an estimate of average observer efficiency. The selection of $\hat{v}$ and $\hat{s}_t$ values for each simulation trial was based on the assumption that stock assessment analysts had some knowledge of the true underlying parameter distributions, which is reasonable given the numerous studies that have been conducted on these parameters. The value of $\hat{v}$ was held constant at 0.865, which was the average observer efficiency value used to generate true count data. Observation error in $\hat{s}_t$ was incorporated into the simulation procedure by assuming that $\hat{s}_t$ was a random normal variable with a mean, μ_s, equal to s and a coefficient of variation, CV($\hat{s}$), of 0.2. While the selection of CV($\hat{s}$) = 0.2 for survey life estimates in the baseline scenario was somewhat arbitrary, studies of the length of time coho salmon spend on their redds (redd residence time) in two coastal streams suggest that this value is reasonable for monitoring programs that estimate survey life for a single stream each year and then extrapolate that value to other streams. Over a period of 4 years, the redd residence time estimates for French Creek and Black Creek on eastern Vancouver Island, BC, differed from each other by an average of 4.5 days (range of difference = 0.5–8.7 days; English et al. 1992; Irvine et al. 1992).

The L-AUC method (Hilborn et al. 1999) estimates escapement by treating it as an unknown parameter in a maximum likelihood estimation (MLE) procedure. The L-AUC method consists of three components. First, a daily abundance model is used to predict daily fish abundance in the survey area, $\hat{N}_d$. We used a beta distribution model to describe daily abundance dynamics in the L-AUC method (Appendix A). Second, an observation model is used to predict the number of fish counted, $\hat{C}_d$, as a function of $\hat{N}_d$ and an estimate of observer efficiency $\hat{v}$

$$(12) \qquad \hat{C}_d = \hat{v}\hat{N}_d$$

Third, a statistical model with a goodness of fit criterion measures the agreement between predicted and observed count values. For this last component, MLE was used to fit predicted counts from eq. 12 to observed counts by estimating total escapement ($\hat{E}$), survey life ($\hat{s}$), and the two shape parameters of the beta distribution ($\hat{\alpha}$ and $\hat{\beta}$). These four parameters were estimated using a penalized likelihood function that assumed a Poisson error distribution for the count data (eq. A3 in Appendix A) and a normal prior distribution on the parameter s, with a mean of μ_s and a standard deviation of σ_s. The total negative log-likelihood was thus

$$(13) \qquad \ell(C_1, C_2, \ldots, C_{f_{\max}} | v, \alpha, \beta, s) = \frac{(s-\mu_s)^2}{2\sigma_s^2} + \sum_{d=1}^{d=f_{\max}} \hat{C}_d(v, \alpha, \beta, s) - C_d \log[\hat{C}_d(v, \alpha, \beta, s)]$$

where C_d and $\hat{C}_d$ are the observed and predicted count values, respectively, for day d. The L-AUC method was only applicable to survey frequencies of five per year or greater to prevent model overparameterization. The value of μ_s was set equal to the true value of s used to generate the data, and the value of $\hat{v}$ was held constant at 0.865. Including a prior distribution on s was necessary to ensure parameter stability in the estimation procedure. In some cases, v can be treated as a free parameter in the MLE procedure (Hilborn et al. 1999); however, parameter estimates of α, β, and s were highly correlated at all survey frequencies examined when v was estimated rather than assumed.

Evaluation of monitoring performance

An observed escapement index, I_t (t = 1,2,…,10), was generated for each combination of estimation method and survey frequency considered (hereafter referred to as monitoring designs). We used a simple linear regression of log-transformed index data on year, i.e.,

$$(14) \qquad \log_e(I_t) = \log_e(\hat{I}_0) + \hat{r}t$$

to estimate the rate of population growth $\hat{r}$. A one-tailed t test was used to designate population status as threatened using the COSEWIC assessment criteria of $r \le -0.04$ over 10 years (H_0 (decline < 30%): $r > -0.04$; H_1 (decline ≥30%): $r \le -0.04$). We placed equal weight on the type I and type II error probabilities for detecting significant declines in escapement ($\alpha = \beta = 0.2$). Thus, H_0 was rejected and the population was assessed as threatened when $p \le 0.2$ for the t test. Because the true r value used to generate annual escapement followed H_1, trend detection was considered successful when this null hypothesis was rejected. The entire simulation procedure was repeated for 1000 Monte Carlo trials, and monitoring performance was measured by the following three criteria: (*i*) the proportion of trials in which a threatened population was correctly detected; (*ii*) the minimum number of years required to correctly detect a threatened population in at least 80% of Monte Carlo trials, and (*iii*) how the probability of detecting a threatened population changed in response to different levels of true population decline. For this final criterion, we examined a range of alternative rates of decline (0%, 2%, 4%,…,60%) over 10 years by changing the true value of r in eq. 2.

Sensitivity analysis

We used sensitivity analyses to examine how deviations from assumptions about interannual variability in daily abundance patterns and among-survey variability in observer efficiency affected the probability of detecting a threatened population for each monitoring design. For the first analysis, three additional levels of variability in daily abundance patterns were examined (none, low, and high) by changing the values of τ in eq. 4. To cover the range of interannual variability observed among the 11 streams analyzed, the value of τ in the low and high variability scenarios was set equal to the highest and lowest τ_i values estimated from the 11 streams (Table 2). In the second sensitivity analysis, three alternative levels of variability in observer efficiency were examined (none, low, and high; Table 2). Because the variance of a Poisson distribution is equal to the mean, variability in observer efficiency was altered by changing v. For a given level of N, the variance of C was increased when v was increased. In the no-variability scenario, the number of fish observed was nonrandom ($C_d = N_d$ for all surveys).

Survey design scenarios

To determine how the design of visual survey monitoring programs could affect the probability of detecting a threatened population, we examined a range of alternative scenarios on (*i*) the level of error in estimates of survey life, CV($\hat{s}$), (*ii*) survey spacing, and (*iii*) variation in survey frequency among years. In the first of these analyses, we examined the sensitivity of T-AUC performance to three alternative scenarios for CV($\hat{s}$) (none, low, high; Table 2). Only the T-AUC method was considered in the analysis because it is the only method that requires an annual estimate of survey life. In comparison, the L-AUC method treats survey life as an unknown parameter that is estimated annually from the count data. We examined how the spacing of survey events within a year affected monitoring performance by considering two alternatives to the baseline scenario shown in eq. 5. In the first of these, surveys were evenly spaced over l = 77 days. The second was a random spacing scenario in which the survey period of l = 77 days was stratified into $f_{\max}$ intervals of even size, and one survey date was randomly sampled from a uniform distribution within each interval. To examine how among-year variation in survey frequency affected monitoring performance, we considered three alternative scenarios. For each scenario, the survey frequency for a given year was

Table 2. Alternative scenarios about true population dynamics and survey design tested in sensitivity analyses and a subset of results for designs with three and six surveys per year.

			Probability of detecting a threatened population for three/six surveys per year			
Variable (baseline values)	Scenario	Values	Peak	Mean	T-AUC	L-AUC
Baseline			0.36 / 0.41	0.44 / 0.84	0.39 / 0.45	NA / 0.79
True population parameters						
Variability in daily abundances	None	τ = (0, 0, 0, 0)	0.87 / 0.75	0.85 / 0.92	0.44 / 0.44	NA / 0.94
$\tau = \{\tau_m, \tau_k, \tau_{\sigma_1}, \tau_{\sigma_2}\}$	Low	τ = (2.5, 1.4, 2.6, 2.9)	0.41 / 0.47	0.55 / 0.91	0.39 / 0.43	NA / 0.92
= (6.7, 5.6, 2.9, 2.4)	High	τ = (9.4, 8.9, 4.0, 1.0)	0.30 / 0.34	0.28 / 0.55	0.27 / 0.38	NA / 0.38
Variability in observer efficiency	None	See text	0.35 / 0.41	0.48 / 0.95	0.38 / 0.44	NA / 0.89
(v = 0.86)	Low	v = 0.76	0.35 / 0.41	0.46 / 0.81	0.39 / 0.46	NA / 0.78
	High	v = 0.96	0.36 / 0.41	0.44 / 0.74	0.37 / 0.42	NA / 0.71
Survey designs						
Error in survey life estimate	None	CV($\hat{s}$) = 0	NA	NA	0.65 / 0.96	NA
(CV($\hat{s}$) = 0.2)	Low	CV($\hat{s}$) = 0.1	NA	NA	0.54 / 0.66	NA
	High	CV($\hat{s}$) = 0.3	NA	NA	0.33 / 0.33	NA
Survey spacing	Even	See text	0.28 / 0.39	0.26 / 0.83	0.28 / 0.43	NA / 0.80
	Random	See text	0.27 / 0.36	0.28 / 0.51	0.28 / 0.40	NA / 0.55
Variation in survey frequency	High	f_{max} = **U**(3, 8)	0.38	0.55	0.42	NA
	Medium	f_{max} = **U**(4, 7)	0.39	0.59	0.42	NA
	Low	f_{max} = **U**(5, 6)	0.39	0.73	0.43	0.68

Note: The function **U**(g, h) denotes a uniform random number with lower bound g and upper bound h. T-AUC, trapezoidal area-under-the-curve method; L-AUC, likelihood approach to area-under-the-curve escapement estimation.

selected from a random uniform distribution (Table 2). Because of the requirement for a minimum of five surveys per year for the L-AUC method, only one of the three alternative scenarios (low variability) was applicable.

Results

Baseline scenario

In the baseline scenario, which, based on our analysis, provided the closest representation of survey dynamics for a population experiencing a 40% decline in escapement over 10 years, all of the monitoring designs we considered produced relatively unbiased estimates of r when averaged across 1000 simulations (±3%). The probability of detecting a threatened population increased with increasing survey frequency for all four estimation methods; however, the mean count and L-AUC methods were able to achieve greater gains in the probability of detecting a threatened population than other two methods (Fig. 2). The L-AUC method achieved only slightly lower probability than the mean count method at all survey frequencies examined. The rank order of the four estimation methods remained the same as in Fig. 2 when performance was measured by the minimum number of years required to achieve an 80% probability of detecting a threatened population (Table 3); however, only the mean count and L-AUC methods met this criterion within the required 10-year period.

The effect of survey frequency on the probability of detecting a threatened population depended on the true population decline relative to the null hypothesis (H_0 (de-

Fig. 2. Probability of detecting a threatened population (>30% decline in escapement over 10 years) as a function of survey frequency for mean count (triangles), likelihood approach to area-under-the-curve (L-AUC, diamonds), trapezoidal area-under-the-curve (T-AUC, squares), and peak count (circles) estimation methods in the baseline scenario, in which the actual rate of decline is 40% over 10 years. The mean count, T-AUC, and L-AUC methods require minimum survey frequencies of two, three, and five surveys per year, respectively.

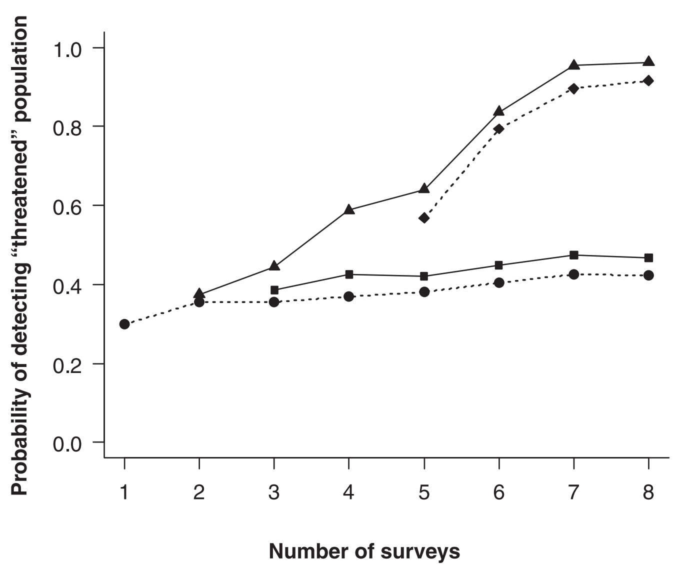


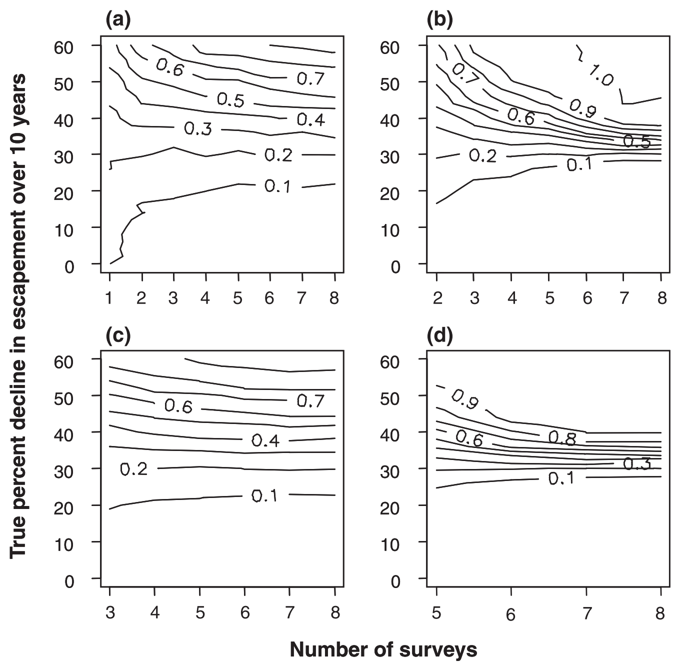
Table 3. Minimum number of years required to achieve 80% probability of detecting a threatened population (decline > 30% over 10 years) in the baseline scenario in which the actual rate of decline is 40% over 10 years.

	Survey frequency							
	1	2	3	4	5	6	7	8
Peak	>20	>20	>20	>20	>20	>20	20	20
Mean	—	>20	19	15	13	10	8	8
T-AUC	—	—	>20	>20	>20	19	19	19
L-AUC	—	—	—	—	15	10	9	8

Note: T-AUC, trapezoidal area-under-the-curve method; L-AUC, likelihood approach to area-under-the-curve escapement estimation.

cline ≤ 30%): $r \geq -0.04$) used in trend detection analysis (Fig. 3). When H_0 was actually wrong and population declines were large (i.e., decline > 30%; $r \leq -0.04$), the probability of detecting a threatened population increased with increasing survey frequency for all four estimation methods. Conversely, when H_0 was true and population declines were small or nonexistent (i.e., decline ≤ 30%; $r > -0.04$), the probability of detecting a threatened population decreased with increasing survey frequency. We use the term responsive to describe a monitoring program in which the probability of detecting a threatened population changes quickly in response to changes in the actual percent decline. The mean count and L-AUC methods became increasingly responsive to changes in the true percent decline as survey frequency increased (as shown by the narrowing of contour lines in Fig. 3). The high responsiveness of the mean count and L-AUC methods increased the probability of correctly assessing a population as threatened when it really was threatened and reduced the probability of incorrectly assessing a population as threatened when it was not. As an example of the latter case, when the true percent decline was only 20% over 10 years (i.e., not threatened), the mean count method had a less than 10% probability of incorrectly assessing the population as threatened at five or more survey counts per year, while the peak count and T-AUC method had greater than 10% probability.

Fig. 3. Sensitivity of the probability (contour lines) of detecting the rate of decline associated with a threatened population (>30% decline in escapement over 10 years) to the true percent decline in escapement and survey frequency for (*a*) peak count, (*b*) mean count, (*c*) trapezoidal area-under-the-curve (T-AUC), and (*d*) likelihood approach to area-under-the-curve (L-AUC) methods. Note that *x* axes have different scales for each estimation method.



Sensitivity analysis

The probability of detecting a threatened population was dependent on the level of interannual variability in daily abundance curves (τ in eq. 4 and Table 2) for all four monitoring methods; however, the mean count method maintained the highest level of performance at all levels of variability examined (Table 2). The peak count method required perfectly consistent daily abundance patterns over all years ($\tau = 0$) to achieve levels of performance comparable with those achieved by the mean count method in the baseline scenario. In contrast, the T-AUC method was unable to achieve greater than a 55% probability of detecting a threatened population, even when daily abundance patterns were held perfectly constant.

The range of among-survey variability in observer efficiency examined, from v known exactly to $v = 0.96$, had a relatively small effect on the probability of detecting a threatened population for all estimation methods (Table 2). Losses in performance associated with increased variability above the baseline scenario and gains in performance associated with decreased variability below the baseline scenario were greater for the mean count and L-AUC methods; however, the deviations remained less than 10% in probability. The mean count method still achieved higher levels of performance than the other three methods at all levels of among-survey variability examined.

Survey design scenarios

The performance of the T-AUC method was highly sensitive to the level of error in estimates of survey life (Table 2). Perfect information about survey life, $CV(\hat{s}) = 0$, was needed to obtain the level of performance achieved by the mean count method in the baseline scenario. The probability of detecting a threatened population for all four monitoring methods was dependent on the spacing of survey events within a year, although this was particularly true for the mean count and L-AUC methods (Table 2). For most monitoring designs considered, performance was greatest when surveys were spaced according to the baseline algorithm that increasingly clustered surveys around the historic peak date of spawning abundance when survey frequency was low (eq. 5). The random spacing scenario resulted in the lowest performance for all methods; however, the loss of probability of detecting a threatened population under the random spacing scenario was especially large for the mean count and L-AUC methods.

Examination of alternative scenarios regarding among-year variability in survey frequency revealed that when survey frequency varied between years, monitoring performance tended to be limited by the lowest survey frequency in the time series (Table 2). While this effect was observed for all estimation methods, it was particularly notable for the mean count and L-AUC methods, which achieved the greatest gains in performance with increased survey frequency. For example, when survey frequency varied between three and five counts per year, the probability of detecting a threatened population for each method was similar to that achieved with a constant survey frequency of three. Additionally, when survey frequency varied between three and eight, the level of probability was similar to that achieved with a constant survey frequency of four.

Discussion

The results of our simulation analysis suggest that a simple mean count method is more suitable than commonly used visual survey estimation methods for monitoring salmon escapement for several reasons (Table 4). While all four methods that we examined estimated the "true" rate of population decline with relatively low bias, the mean count and L-AUC methods consistently achieved higher levels of precision (as reflected by greater probability of detecting a threatened population) than peak count and T-AUC methods over a wide range of scenarios about true population parameters and survey design. High precision is a desirable property for monitoring programs because it increases the probability of correctly estimating the true status of a population. In addition to higher levels of precision, the mean count and T-AUC methods required fewer years to detect the rate of decline associated with a threatened population, which is a desirable property for a monitoring program because it provides an early warning that recovery actions are likely necessary. While escapement monitoring programs should be able to reliably detect situations of concern, such as a rate of population decline that would result in a stock being assessed as threatened under COSEWIC, they should also minimize the probability of falsely detecting these situations. By examining the response of monitoring performance to varying levels of actual population decline, we have shown that the mean count and L-AUC methods perform better than the other two methods using both of these criteria.

The performance of the L-AUC method was comparable with that of the mean count method, which may lead one to conclude that the L-AUC method is more useful for escapement monitoring given that it provides an absolute estimate of escapement instead of only a relative index. The performance of the L-AUC method in our study is likely optimistic, however, because of our treatment of the observer efficiency parameter estimate in the MLE procedure. By treating observer efficiency as a fixed parameter and assuming that the underlying mean parameter value was known without error, we allowed the estimation procedure to underestimate the level of uncertainty in L-AUC escapement estimates. As discussed in the Alternative escapement index methods section of the Materials and methods, this assumption was necessary to prevent model overparameterization. Three additional disadvantages of the L-AUC method are that its estimation procedure is more complicated than that of the mean count method, it requires prior knowledge of stream-specific survey life, and it is limited to survey designs with five or more survey counts per year, which is not always possible for extensive survey programs (D. Peacock, DFO, 202-417 Second Avenue West, Prince Rupert, BC V8J 1G8, personal communication). We therefore conclude that the mean count method is better suited than the L-AUC method for extensive monitoring of coho salmon escapements.

The success of the mean count method can be attributed to its simple, data-based estimation procedure that requires no assumptions to be made about the shape of the daily abundance curve or the length of time fish remain in the survey area. In contrast, both the peak count and T-AUC methods require strong assumptions about at least one of these factors, which limits the monitoring performance of these two methods. For example, the peak count method relies on the assumption that the ratio of the peak count to total escapement is constant among years. Our results show that this assumption is weakly supported for coho salmon stocks. Visual survey data used to parameterize daily abundances showed high interannual variability in both the timing of fish presence and the shape of the observed abundance pattern. In utilizing information from only one survey event each year (i.e., the survey in which the highest count value was obtained), the peak count method fails to incorporate information about the shape of the abundance curve into annual escapement indices. In contrast, the mean count method incorporates all available information on the shape of the abundance curve into the escapement index by using data from all surveys conducted in a year and is thus able to achieve large gains in monitoring performance with increased survey frequency.

The T-AUC method also uses information from all survey events conducted in a year; however, error in survey life estimates limited the gains in monitoring performance associated with increased survey frequency that were observed for the mean count method. Only when error in survey life estimates was low ($CV(\hat{s}) = 0.10$) or absent ($CV(\hat{s}) = 0$) was the performance of the T-AUC method comparable with that of the mean count method in the baseline scenario. Hill (1997) also found that when errors in survey life were relatively low (i.e., survey life treated as a random normal variable with mean = 10 days, standard error = 0.5 days, and $CV(\hat{s})$ = 0.13), the reliability of annual escapement estimates derived using the T-AUC method increased with increasing survey frequency. The lower level of error assumed by Hill (1997), compared with our baseline scenario, was because he simulated a monitoring program that obtained year- and stream-specific estimates of survey life.

The requirement for highly precise estimates of survey life in order for the T-AUC method to achieve high probability of detecting a threatened population is consistent with other research showing that the accuracy of annual T-AUC escapement estimates is highly dependent on both year- and stream-specific estimates of survey life (English et al. 1992; Irvine et al. 1992; Bue et al. 1998). Unfortunately, the cost and effort required to estimate this parameter can be high. Such intensive methods for estimating survey life for Pacific salmon include tagging programs and enumeration fences (English et al. 1992; Bue et al. 1998), capture–recapture studies (Manske and Schwarz 2000), and daily observations

Table 4. Summary of monitoring performance, data requirements, and recommended features for each estimation method.

Method	Maximum probability to detect $r \leq -0.04$*	Absolute or relative escapement estimates	Min. no. of surveys per year	Annual estimates of OE and SL	Measure of uncertainty in estimated escapement	Recommended features
Peak count	48%	Relative	1	Not required	No (unless replicate surveys conducted)	Not suitable for stocks with high interannual variability in daily abundance patterns Maintain a constant number of days between surveys each year Cluster surveys around historical peak date when ≤5 surveys per year conducted
Mean count	96%	Relative	2	Not required	No (unless replicate surveys conducted)	Maintain a constant number of days between surveys each year Cluster surveys around historical peak date when ≤5 surveys per year conducted
T-AUC	52%	Absolute	3	Required	No (unless replicate surveys conducted)	Use year- and stream-specific estimates of SL and OE Maintain a constant number of days between surveys each year Cluster surveys around historical peak date when ≤5 surveys per year conducted
L-AUC	92%	Absolute	5 (or more)	Depends on number of surveys used	Yes (but dependent on prior information about OE and SL)	Use estimates of SL for prior information Use stream- and year-specific estimates of OE Maintain a constant number of days between surveys each year Cluster surveys around historical peak date when 5 surveys per year conducted

Note: T-AUC, trapezoidal area-under-the-curve method; L-AUC, likelihood approach to area-under-the-curve escapement estimation; OE, observer efficiency; SL, survey life.
*At eight survey counts per year when the true $r = -0.057$ over 10 years.

(Van den Berghe and Gross 1986). There are two ways in which survey life estimates can be extrapolated between years and streams when year- and stream-specific estimates of survey life are not available (Perrin and Irvine 1990). The first approach is the one assumed in the baseline scenario, in which a year-specific survey life value is estimated for a single stream and then applied to multiple streams within that year. The second approach is to apply a constant survey life estimate to all years in a time series. While the second approach of a constant survey life would reduce the accuracy of annual escapement estimates by ignoring interannual variability in survey life, the high levels of monitoring performance achieved by the T-AUC method when survey life was held constant shows that this approach provides a more reliable index of escapement than the first approach. In this case, however, the T-AUC method would serve as only a relative index of escapement, providing the same level of information as the mean count method.

The low sensitivity of monitoring performance for all estimation methods to among-survey variability in observer efficiency is likely a result of the small differences in variability among the four scenarios. For each scenario, we assumed that observation error followed a Poisson distribution with a constant rate parameter set at the mean observer efficiency value estimated from Black Creek observer efficiency studies (Irvine et al. 1992). While varying the mean observer efficiency between different scenarios allowed us to affect the variance of the Poisson distribution, the overall change in the coefficient of variation decreased as daily abundances increased. The assumption of a Poisson error distribution for generating count data is highly uncertain. Unfortunately, the limited data available on among-survey variability for coho salmon and the challenge of separating observation errors from process errors when calculating observer efficiency made it necessary for us to assume an error structure. A Poisson distribution was used because it is commonly associated with count data (Hilborn and Mangel 1997). Korman et al. (2002) also assumed Poisson-distributed observation errors for visual surveys of steelhead (sea-run rainbow trout, *Oncorhynchus mykiss*).

It should be noted that while we did not find a significant difference in mean observer efficiency values among the 7 years of data available for Black Creek coho, this will not necessarily be the case for all species and all streams. In some cases, observer efficiency can vary substantially among years within a single stream (e.g., Bue et al. 1998 for pink salmon, *Oncorhynchus gorbuscha*). The presence of jacks (males that return to spawn after only one summer at sea) in some coho populations could also affect among-survey variability in observer efficiency if the ratio of jack to adult salmon in a stream varies among years, which is common for some coho populations (Sandercock 1991), and if jack salmon are harder to observe, as noted by Irvine et al. (1992). We included only counts of adult salmon in our analysis of observer efficiency. For the above reasons, we recommend that observer efficiency studies be conducted independently on all streams where visual survey methods are used to gain a better understanding of among-survey variability for each stream.

Our evaluation of alternative survey design scenarios regarding the spacing of surveys within a year and variability in survey frequency across years demonstrates the importance of establishing a standardized sampling protocol that can be applied consistently over multiple years. In order for the mean count method to achieve the high levels of monitoring performance seen in the baseline scenario, both the spacing of surveys and the frequency of surveys should remain constant among years. The simple algorithm for spacing surveys used in the baseline scenario (eq. 5), in which survey dates were increasingly clustered around the historical peak date of spawning abundance at low survey frequencies (three–five surveys per year), tended to produce higher levels of monitoring performance at these frequencies than when surveys were spaced evenly over the historic spawning period. While the particular spacing design that maximizes the probability of detecting a threatened population would likely differ between streams because of varying lengths of fish presence, the advantage of clustering surveys near the historic peak date of spawning abundance is expected to apply to all streams. The decreased levels of monitoring performance for the mean count method when survey dates were spaced randomly shows that in order for this method to maximize performance, the number of days between surveys should be held constant among years. These results have implications not only for the design of visual survey programs, but also for the application of these methods to historic time series of count data that have not followed a consistent sampling protocol. When inconsistencies in survey spacing and frequency exist within a time series, the gains in monitoring performance achieved by the mean count method compared with the other methods will be reduced.

The levels of monitoring performance achieved in our simulation study are higher than would be expected in the field because our true population model did not allow for temporal variability in annual escapement trends. Escapement declined deterministically over 10 years for our true population with a constant rate of decline each year. In reality, however, annual trends in salmon escapement can vary greatly among years because of variable fishing mortality and survival rates. While incorporating temporal variability into the escapement model would be expected to decrease the probability of detecting a threatened population, the performance of the four methods relative to each other would remain unchanged.

Although our evaluation of visual survey methods focussed on coho salmon populations, our findings are relevant to the design of extensive survey programs for many salmonid species including pink salmon (Bue et al. 1998), Chinook salmon (*Oncorhynchus tshawytscha*; Parken et al. 2003), and steelhead (Korman et al. 2002). Additional research is needed to determine whether the mean count method is suitable for these species. The simulation modelling approach we used could be easily adapted for other species by re-parameterizing the models used to generate daily abundance and survey dynamics. We suggest, however, that the mean count method has the potential to outperform peak count and AUC methods for other salmon species based on the superior performance of the mean count method across a wide range of sensitivity analyses.

In this study, we focused on the ability of visual survey methods to detect changes in escapement within a single spawning stream. However, given that the primary purpose of extensive visual survey programs, as identified in the WSP, is to examine distribution and consistency in escapement trends, a useful extension of our simulation framework would be to expand the current single-stock model to a multistock model. The development of a multistock model, in which a subset of populations with co-varying escapement and daily abundance dynamics are randomly selected for monitoring, would allow for explicit consideration of the effects of different spatial and temporal allocations of survey effort on the strength of trend detection within a CU. For example, the question of “what is the optimal allocation of effort between the number of streams monitored and the frequency applied to each stream?” could be examined for individual CUs. This type of information would be useful for the development of WSP monitoring plans aimed at maximizing the strength of trend detection while minimizing survey costs. Future research is needed to develop a means of combining data from several streams into a single performance measure.

While the level of effort afforded to visual survey programs will depend on trade-offs made between program costs and the level of detail required to assess status of fish populations relative to management and conservation goals, applying a mean count method and maintaining constant survey dates among years will maximize the strength of trend detection for a given level of effort. Despite high interannual variability in coho daily abundance dynamics and variable observer efficiency, the mean count method provides higher confidence in trend detection than peak count and T-AUC methods across a wide range of scenarios about true population dynamics and survey design. The peak count method required consistent daily escapement patterns among years to achieve the level of monitoring performance seen for the mean count method in the baseline scenario, while the T-AUC method required almost perfect information about annual survey life values to achieve this level. Both of these conditions are unlikely to be met for extensive monitoring programs. The L-AUC method achieved high levels of monitoring performance in our study; however, large data requirements limit the usefulness of this method for coho salmon. The success of the mean count method can be attributed to its simple, data-based estimation procedure that requires no assumptions about the shape of the daily abundance curve or the length of time fish remain in the survey area.

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Appendix A

Selection of a daily abundance model

We considered five candidate models for describing daily abundance of coho salmon in spawning streams (a normal model, a beta model, and three mixture models). Equations describing the five models are shown in Table A1, with model notation defined in Table A2. The letter "M" placed before an equation indicates that it is a component of one of the daily abundance models in Table A1. When describing the mixture models, we use a superscript to denote which of the two component models a given parameter or state variable refers to (e.g., σ'^1 is the standard deviation of arrival for the first model, and σ'^2 is the standard deviation of arrival for the second model). Two probability density functions are used in the daily abundance models in Table A1. The first is the normal cumulative distribution function

$$\text{(A1)} \quad \mathbf{F_N}(d,m,\sigma) = \int_{i=0}^{d} \frac{1}{\sigma\sqrt{2\pi}} \exp\left[-\frac{(i-m)^2}{2\sigma^2}\right] di$$

and the second is the beta cumulative distribution function

Table A1. Alternative daily abundance models used in model selection analysis.

Normal model		
Parameters		
(M1)	$\hat{\Theta}_{\text{Normal}} = \{m, \sigma, s\}$	
Predicted states		
(M2)	$\hat{A}_d = C_T \mathbf{F_N}(d, m, \sigma)$	where $C_T = \sum_{f=1}^{f_{\max}} C_f$
(M3)	$\hat{D}_d = C_T \mathbf{F_N}(d - s, m, \sigma)$	
(M4)	$\hat{C}_d = \hat{A}_d - \hat{D}_d$	
Beta model		
Parameters		
(M5)	$\hat{\Theta}_{\text{Beta}} = \{\alpha, \beta, s\}$	
Predicted states		
(M6)	$\hat{A}_d = C_T \mathbf{F_B}\left(\frac{d}{n}, \alpha, \beta\right)$	
(M7)	$\hat{D}_d = \begin{cases} C_T \mathbf{F_B}\left(\frac{d-s}{n}, \alpha, \beta\right) & \text{for } d \geq s \\ 0 & \text{for } d < s \end{cases}$	
(M4)	$\hat{C}_d = \hat{A}_d - \hat{D}_d$	
Mixture model		
Parameters		
(M8)	$\hat{\Theta}_{\text{Mixture}} = \{m'^1, \sigma'^1, k, \sigma'^2\}$	
Predicted states		
(M9)	$\hat{A}'^1_d = zC_T \mathbf{F_N}(d, m'^1, \sigma'^1)$	$\sigma'^1 \geq 2$
(M10)	$\hat{D}'^1_d = zC_T \mathbf{F_N}(d - s, m'^1, \sigma'^1)$	
(M11)	$\hat{A}'^2_d = (1-z)C_T \mathbf{F_N}(d, m'^1 + k, \sigma'^2)$	$k \geq 0,\ \sigma'^2 \geq 2$
(M12)	$\hat{D}'^2_d = (1-z)C_T \mathbf{F_N}(d - s, m'^1 + k, \sigma'^2)$	
(M13)	$\hat{C}_d = (\hat{A}'^1_d + \hat{A}'^2_d) - (\hat{D}'^1_d + \hat{D}'^2_d)$	

Note: The functions $\mathbf{F_N}$ and $\mathbf{F_B}$ are defined in eqs. A1–A2. Symbols are defined in Table A2.

$$\text{(A2)} \quad \mathbf{F_B}(x, \alpha, \beta) = \int_{i=0}^{x} i^{\alpha-1}(1-i)^{\beta-1} di$$

Parameter vectors for each of the daily abundance models are denoted $\hat{\Theta}_{\text{model}}$.

Daily abundance for the normal (eqs. M1–M4) and beta models (eqs. M4–M7) is characterized using cumulative distributions of fish arrival and death (Hilborn et al. 1999) that are scaled by the total number of fish observed over all surveys, C_T. Application of the beta model requires that start and end dates for arrival are specified so that day can be scaled between 0 and 1. We assumed that start and end dates coincided with the first and last surveys each year, and n is the number of days between these two dates. Daily abundance for the mixture models (eqs. M8–M13) is characterized as two separate normal models. The standard deviations for both component models (σ'^1 and σ'^2) were constrained to be equal to or greater than 2 days during estimation. The number of data points for most streams limited the number of parameters that could be estimated for the mixture models to four (eq. M8), making it necessary to fix the values of s and z in eqs. M9–M12 to ensure parameter stability. The value of s was held constant at the mean of coho survey life

Table A2. Definition of symbols used to describe daily abundance models in Table A1.

Symbol	Definition
Index variables	
f	Survey index (f = 1, 2, …, f_{max} surveys)
f_{max}	Total number of surveys conducted on a given stream within a year
d	Day (from annual calendar; January 1 = day 1)
n	Total number of days of fish presence in survey area
Observed data	
C_d	Number of fish counted within a single stream on day d
C_T	Total number of fish counted within a single stream over all surveys in a year
Predicted states	
Normal and beta models	
$\hat{A}_d$	Cumulative number of fish arriving by survey day d
$\hat{D}_d$	Cumulative number of fish departing by survey day d
$\hat{C}_d$	Predicted number of fish counted on survey day d
Mixture models	
$\hat{A}'^1_d$	Cumulative number of fish from first component model arriving by d
$\hat{A}'^2_d$	Cumulative number of fish from second component model arriving by d
$\hat{D}'^1_d$	Cumulative number of fish from first component model departing by d
$\hat{D}'^2_d$	Cumulative number of fish from second component model departing by d
Daily abundance model parameters	
Normal model	
m	Mean date of arrival (from annual calendar)
σ	Standard deviation of arrival date
s	Survey life (days)
Beta model	
α	Beta shape parameter 1
β	Beta shape parameter 2
Mixture models	
m'^1	Mean date of arrival for first component model
k	Number of days that the mean date of arrival for second component model is offset from that of the first component model
σ'^1	Standard deviation of arrival for first component model
σ'^2	Standard deviation of arrival for second component model
z	Proportion of counted fish belonging to first component model

estimates obtained from empirical studies (12.8 days; Table A3), while three values of z = {0.3, 0.5, 0.7} produced the alternative mixture models. The mixture models differed from the normal and beta models in that they could display both unimodal and bimodal shapes through adjustment of the k parameter. Small k values tended to create unimodal curves, while large values tended to create bimodal curves.

Candidate models were fitted to count data sets using an MLE procedure assuming the following Poisson negative log-likelihood function for the observed counts

$$\text{(A3)}\quad \ell(C_1, C_2, \ldots, C_{f_{max}} \mid \hat{\Theta}_{model}) = \sum_{i=1}^{i=f_{max}} [\hat{C}_i - C_i \log(\hat{C}_i)]$$

where the predicted counts $\hat{C}_i$ are functions of the daily abundance model parameters $\hat{\Theta}_{model}$. The five candidate models were ranked using the following small sample version of Akaike's information criterion (AIC) (Burnham and Anderson 2002),

$$\text{(A4)}\quad \text{AIC} = -2\ell^* + 2K + \frac{2K(K+1)}{f_{max} - K - 1}$$

where ℓ^* is the maximum log-likelihood value, K is the number of parameters to be estimated and f_{max} is the number of count events. The best model for each data set given the candidate models considered was the one that produced the smallest AIC value.

The results of the AIC test showed that the mixture model with z = 0.3 was the best of the five candidate models for the largest number of data sets (mixture (z = 0.3) was best for 10 out of 33 data sets, compared with 8 out of 33 for mixture (z = 0.7), 7 out of 33 for mixture (z = 0.5), 7 out of 33 for beta, and 1 out of 33 for normal). Based on these results, we selected the mixture model (z = 0.3) to estimate interannual variability in abundance model parameters for the simulation procedure.

Estimation of interannual variability in daily abundances

Recall from eq. 1 that for each of the each of the four

Table A3. Summary of survey life estimates collected from the literature.

Stream	Location*	Year	Estimate	Source
Spring Creek	OR	1952	11.5	Perrin and Irvine 1990
Flynn Creek	OR	1966	13.1	Perrin and Irvine 1990
Oregon streams	OR	1980	11.0	Perrin and Irvine 1990
Harris Creek	WA	1980–1983	10.0	Perrin and Irvine 1990
Deer Creek	WA	1981	9.2	Perrin and Irvine 1990
Eagle River	BC	1982	12.5	Perrin and Irvine 1990
Salmon River	BC	1982	15.0	Perrin and Irvine 1990
Adams River	BC	1982	10.0	Perrin and Irvine 1990
Coldwater River	BC	1982	12.5	Perrin and Irvine 1990
Keogh River	BC	1985	13.0	Perrin and Irvine 1990
Little Qualicum	BC	1986	13.3	Perrin and Irvine 1990
French Creek	BC	1987	13.3	Irvine et al. 1992
Black Creek	BC	1987	16.6	Irvine et al. 1992; English et al. 1992
Trent River	BC	1987	7.1	Perrin and Irvine 1990
French Creek	BC	1988	16.7	Irvine et al. 1992
Black Creek	BC	1988	8.0	Irvine et al. 1992; English et al. 1992
Trent River	BC	1988	9.6	Perrin and Irvine 1990
French Creek	BC	1989	15.5	Irvine et al. 1992; English et al. 1992
Black Creek	BC	1989	15.0	Irvine et al. 1992; English et al. 1992
Chase River	BC	1989	16.3	Manske and Schwarz 2000
French Creek	BC	1990	20.3	English et al. 1992
Black Creek	BC	1990	15.0	English et al. 1992
Chase River	BC	1990	10.4	Manske and Schwarz 2000
All streams, OR	OR	—	11.3	Perrin and Irvine 1990
Clear Creek	AK	1996	13.8	Hetrick and Nemeth 2003
Mean			12.8	

*AK, Alaska; BC, British Columbia; OR, Oregon; WA, Washington State.

mixture model parameters, among-year variation was calculated assuming that each stream i had a set of stream-specific mean parameter values (m'^1, k, σ'^1, and σ'^2 in Table A2) from which daily abundance patterns deviated each year

(eq. 1 repeated)

$$\theta_{i,t} = \bar{\theta}_i + \varepsilon_{i,t}$$

where θ is any one of the four model parameters, $\bar{\theta}_i$ is the stream-specific mean parameter value, t is year, and $\varepsilon_{i,t}$ is a stock- and year-specific deviation. For each of the 33 coho salmon visual survey data sets (11 steams, each with 3 years of data) used to estimate interannual variability in daily abundance patterns, an estimate of $\varepsilon_{i,t}$ was calculated by subtracting $\bar{\theta}_i$ from $\theta_{i,t}$. The standard deviation of $\varepsilon_{i,t}$ within each stream, τ_i, was then calculated using the three estimates of $\varepsilon_{i,t}$ (t = 1, 2, 3). The 11 values of τ_i were used to develop alternative scenarios for the simulation of interannual variability in daily abundance patterns.

Simulation of true daily abundances

To simulate daily abundances for year t, the mixture model was modified slightly so that the cumulative normal distributions presented in eqs. M9–M12 were scaled by total escapement for year t, E_t, instead of total counts. This modification allowed for predictions of the total number of arrivals and deaths that actually occurred up to a given day d, as opposed to the total number of arrivals and deaths counted up to d. The difference between cumulative arrivals and cumulative deaths on day d thus determines the total abundance of fish that are alive and in the survey area on that day (N_d).

Application of daily abundance model to L-AUC method

The L-AUC method (Hilborn et al. 1999) estimates escapement by treating it as an estimated parameter in an MLE procedure. Application of the beta arrival timing model to the L-AUC method requires a slight modification from the version presented in eqs. M4–M7. The scalar C_T in eqs. M6–M7 is replaced with a total escapement parameter for year t, E_t. This modification causes eq. M4 to predict the total number of fish alive in the survey area on day d, $\hat{N}_d$.

References

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