Metrics and sampling designs for detecting trends in the distribution of spawning Pacific salmon (*Oncorhynchus* spp.)

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Abstract: The distribution of individuals among populations and in space may contribute to their resilience under environmental variability. Changes in distribution may indicate the loss of genetically distinct subpopulations, the deterioration of habitat capacity, or both. The distribution of Pacific salmon (*Oncorhynchus* spp.) among spawning locations has recently been recognized as an important component of status assessment by USA and Canadian management agencies, but metrics of spawning distribution have not been rigorously evaluated. We evaluated three metrics of spawning distribution and four sampling designs for their ability to detect simulated contractions in the production of coho salmon (*Oncorhynchus kisutch*). We simulated population dynamics at 100 sites using a spawner–recruit model that incorporated natural variability in recruitment, age-at-maturity, dispersal, and measurement error in observations of abundance. Sensitivity analyses revealed that high observation error and straying of spawners from their natal streams may mask changes in distribution. Furthermore, monitoring only sites with high spawner abundance, as is often practiced, failed to capture the simulated contraction of production, emphasizing the importance of matching monitoring programs with assessment objectives.

Résumé : La répartition des individus entre les populations et dans l'espace peut contribuer à leur résilience en présence de variabilité environnementale. Des changements dans la répartition peuvent indiquer la perte de sous-populations génétiquement distinctes, la détérioration de la capacité de l'habitat, ou les deux. Les agences de gestion américaines et canadiennes ont récemment reconnu la répartition des saumons du Pacifique (*Oncorhynchus* spp.) entre les sites de fraie comme une composante importante de la détermination de leur statut; les métriques de la répartition de la fraie n'ont cependant pas été évaluées de manière rigoureuse. Nous évaluons trois métriques de la répartition de la fraie et trois plans d'échantillonnage en ce qui a trait à leur capacité à déceler des contractions simulées dans la production de saumons coho (*Oncorhynchus kisutch*). Nous avons simulé la dynamique de la population à 100 sites à l'aide d'un modèle reproducteurs–recrues qui tient compte de la variabilité naturelle du recrutement, de l'âge à la maturité, de la dispersion et de l'erreur de mesure dans les observations d'abondances. Des analyses de sensibilité indiquent que de grandes erreurs d'observation et l'errance des reproducteurs loin de leurs cours d'eau de naissance peuvent masquer les changements dans la répartition. De plus, la surveillance des seuls sites à forte densité de reproducteurs, comme on le fait souvent, n'arrive pas à reconnaître la contraction simulée de la production, ce qui souligne l'importance d'adapter les programmes de surveillance aux objectifs de l'évaluation.

[Traduit par la Rédaction]

Introduction

Endangered or exploited species are commonly assigned to units of conservation (Green 2005) that reflect irreplaceable geographic and genetic diversity within that species. The distribution of individuals within these units may influence the populations' ability to tolerate disturbance (Healey 2009; Schindler et al. 2010) and may indicate population trends that are not apparent from aggregate abundance data alone. For Pacific salmon populations (*Oncorhynchus* spp.), the distribution of spawners among streams or spawning sites within evolutionary significant units (ESUs) in the USA (Waples 1991) and conservation units (CUs) in Canada (Holtby and Ciruna 2007) is of particular interest.

Metrics to quantify spawning distribution of Pacific salmon have been developed by several management agencies and assessment bodies (McElhany et al. 2000; Holt et al. 2009), but definitions of distribution vary among agencies, and metrics are often of limited applicability outside of the jurisdiction of origin. Distribution has variously been defined as the spatial arrangement of spawners on the landscape (McElhany et al. 2000), the allocation of spawners among

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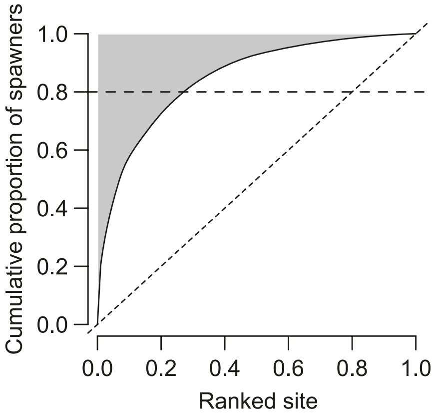
various habitat types (Sheer and Steel 2006; Cooney et al. 2007), the proportion of temporal trends in spawner abundance among sites that display declining trends (i.e., frequency distribution) (Holt et al. 2011), and (or) the distribution of spawners among sites within a unit. The metrics chosen by each agency depend on the definition of distribution used and the specific goals of the assessment, such as identifying risk of extinction (e.g., COSEWIC 2010), population viability (e.g., McElhany et al. 2000; Cooney et al. 2007; Busch et al. 2008), or response to human disturbances (e.g., Good et al. 2008). In this paper, we focus on the distribution of spawners among spawning sites as one indicator of status for CUs identified under Canada's Wild Salmon Policy (Fisheries and Oceans Canada 2005) and an indicator of viable salmonid populations for ESUs of salmon in the Pacific Northwest of the USA (Crawford and Rumsey 2011).

Units of conservation that are composed of numerous spawning groups that are genetically diverse or asynchronous in their dynamics may be more resilient to disturbance than those composed of a small number of homogeneous or synchronous groups for at least two reasons. First, a broad geographic distribution of spawners can buffer against extinction from local catastrophes, such as flooding, severe landslides, or toxic spills, by providing sources for recolonization if such an event were to occur (i.e., a rescue effect; Good et al. 2008; Healey 2009). Changes in spawning distribution may also provide information on local-scale disturbances, such as river obstructions or dewatering, which can be useful for managers seeking to reverse or mitigate those impacts. Second, genetic differences among spawning sites due to the strong homing ability of salmon and the relative reproductive isolation of those spawning groups (Quinn et al. 1999) provide the ingredients for phenotypic and life-history diversity at fine spatial scales. The resulting variability among spawning groups in a unit reduces extinction risk (Kendall and Fox 2003; Fox 2005) and contributes to a "portfolio effect" that stabilizes regional populations and the ecosystem services they provide (Hilborn et al. 2003; Schindler et al. 2010). This portfolio effect may occur among and within units of conservation and may become especially important in the face of global climate change (Crozier et al. 2008). Although dispersal among spawning groups will influence the relative magnitude of rescue and portfolio effects in opposite directions (dispersal will increase opportunities for rescue effects while reducing genetic diversity), contracted distributions (e.g., to one or a small number of spawning groups) may negatively impact both by reducing opportunities for rescue effect and diversity within units of conservation.

Sampling designs for monitoring spawning salmon have historically been developed to estimate absolute abundances and have thus focused on river systems with high returns (English et al. 2006). This strategy has often led to discontinued monitoring of sites with low or declining abundances of spawners (Price et al. 2008), which together with the coarse spatial resolution of spawner data limits the ability to detect changes in spawning distribution (Rand et al. 2007). If reducing the number of sites monitored is necessary for logistical or economic reasons, then an explicit evaluation of the trade-offs between sampling effort and the power to detect changes in status, including spawning distribution, is required to guide decisions on allocation of resources among competing assessment and management priorities (Carlson and Schmiegelow 2002; Fenichel and Hansen 2010). Although sampling designs for assessing the frequency distribution of trends have been evaluated quantitatively (Holt et al. 2011), metrics on the distribution of salmon spawners among sites have not been considered.

Fig. 1. The area over the curve (AOC) metric describes the cumulative proportion of total spawner abundances versus site ranked by spawner abundance, with both axes scaled between 0 and 1. The dotted line represents a unit in which all sites contribute equally to the total spawner abundance (AOC = 0.50), and the solid curve represents a contracted distribution of spawners among sites (grey area, AOC = 0.15). The horizontal dashed line at 80% cumulative proportion of spawners illustrates the metric $P_{80\%}$. The proportion of ranked sites at which the dashed line intersects the solid curve is $P_{80\%} = 0.27$.



Our objective was to evaluate three metrics of spawning distribution and four sampling designs by their probability of correctly detecting contractions in the distribution of production (i.e., power) and probability of correctly identifying no trend when the distribution was stable (i.e., specificity). In addition, we evaluated trade-offs between power to detect trends in distribution and both annual sampling effort and the magnitude of observation errors from enumerating spawners.

Materials and methods

Metrics for assessing spawning distribution

We selected two metrics of spawning distribution from a review of scientific and management literature, and we propose a third metric to demonstrate a range in properties of distribution among spawning sites. These metrics are calculated from data of adult spawner abundance at enumeration sites, which are typically located at the mouths of rivers or where a tributary meets the main stem.

The first metric was derived from cumulative abundance curves describing the cumulative proportion of total spawners at sites ranked from most to least abundant (Walters and Cahoon 1985). When axes are scaled between 0 and 1, the area over the curve (AOC) quantifies the relative concentration of spawners among sites (Fig. 1). When each site contributes equally to the total abundances (i.e., the spawning distribution is even), the cumulative spawner curve is a diagonal line intersecting the points (0, 0) and (1, 1) with an AOC of 0.5. When spawners are concentrated into a small number of sites, the cumulative spawner curve increases steeply to an asymptote, resulting in an AOC near zero. Declines in the AOC over time represent a shift to more unequal distribution of spawners among sites.

We propose a second metric, $P_{80\%}$, that describes the minimum number of sites (as a proportion of all sites) comprising 80% of total spawner abundance for the unit. We chose a threshold of 80% so the metric reflected changes in abundance at major spawning groups within the population aggregate and, unlike AOC, was not sensitive to changes in very small, ephemeral populations (comprising the remaining 20% of total abundance) that may not consistently contribute to total production. In addition, the interpretation of $P_{80\%}$ is more intuitive than AOC because it represents a proportion instead of the area on the cumulative spawner plot. When spawning distribution is concentrated into few sites, this proportion will be small because only these few most occupied sites will comprise 80% of total abundance. A decline in this metric over time may represent a shift of spawners to more dominant sites and loss of diversity. However, a loss of spawners in peripheral or marginal habitat that comprise only a small portion of the total may be overlooked by this metric. Further, decreases in $P_{80\%}$ due to high returns to productive sites accompanied by stable returns to other sites may be misinterpreted as contractions in spawning distribution.

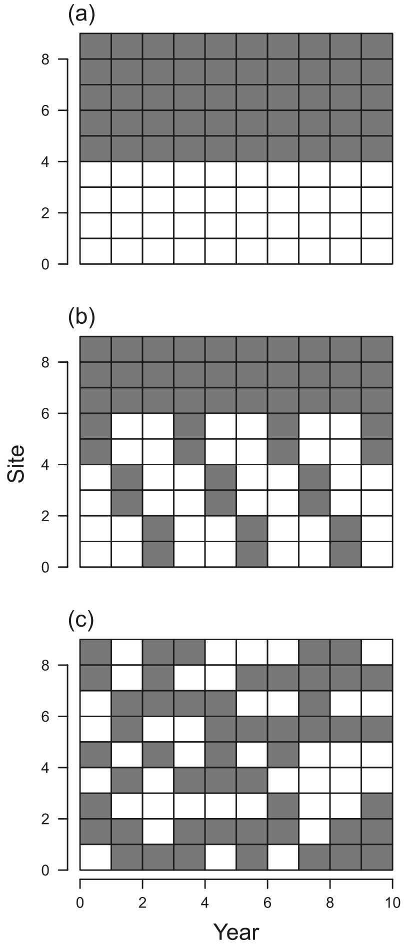
The third metric, $P_{S<100}$, is the proportion of sites with fewer than 100 spawners. Previous assessments have reported the number of sites with no spawners observed (e.g., Irvine et al. 1999), which we adapted to include a threshold of 100 to convey the consistent occupation of spawning sites that may be important for maintaining diversity and resilience of the population aggregate, and exclude peripheral sites that may only comprise a very small number of spawners and may not generate successful recruits to the adult population. This threshold can be adjusted based on previous knowledge of the system under study. For example, if the majority of sites within a unit have consistently fewer than 100 spawners, a lower threshold may be appropriate.

These three metrics represent changes in distribution among spawning sites; we did not evaluate spatially explicit metrics that capture geographic range contractions. Spatial metrics are often difficult to interpret given that most sampling designs have poor spatial coverage, spawning habitat is often patchy, and the spatial extent of spawning grounds is usually uncertain. Metrics of distribution among sites provide information on one component of stock status and can be considered in combination with other metrics to provide more complete assessments.

Sampling designs

Sampling designs describe the annual effort apportioned to sampling (e.g., 50% of sites sampled) and the distribution of that effort among sites. We considered four sampling designs in three categories. The first category consisted of a subset of indicator sites that were monitored annually, while the remaining sites were never monitored (Fig. 2*a*). We applied two variants of this design: one that reflected the historical pattern of selecting indicator sites with high spawner abundance (key indicator design) and a second where indicator sites were selected randomly from all sites (random indicator design). These designs resulted in continuous time series for indicator sites and no survey coverage at the remaining sites.

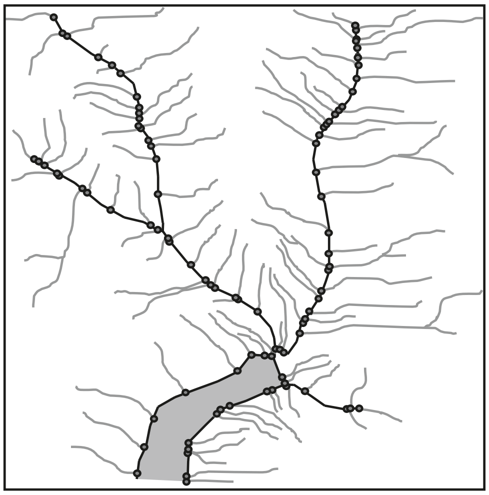
Fig. 2. A schematic of three categories of sampling designs, with an annual sampling effort of five of nine sites in all cases. Each year–site combination is either sampled (grey) or not (open). (*a*) Indicator sites are sampled every year, while other sites are not sampled at all. (*b*) Rotating panel designs in which at least two sites are sampled annually, while the remaining effort is split among several panels (three in our study). (*c*) A random subset of sites is sampled each year.



The second category combined a subset of randomly selected indicator sites that were monitored annually and several panels of sites that were monitored on a rotating basis (Fig. 2*b*, panel design) (English et al. 2006; Holt et al. 2011). Panels were sampled on a 3-year rotation to be consistent with the dominant 3-year life cycle of coho salmon (*Oncorhynchus kisutch*). Annual effort was allocated between indicator sites and rotating panels to maximize the total number of sites monitored over each 3-year rotation while maintaining at least two indicator sites and an even sampling effort among panels within years.

The third category was a random sampling design in which a subset of sites was randomly and independently selected each year and no site was consistently monitored (Fig. 2*c*, random design).

Fig. 3. Illustration of the hypothetical unit in which spawner abundances were simulated. Spawners in each stream (grey lines) were simulated separately, with some straying among streams, and enumerated at sites (black circles). Distances among sites were calculated along the mainstem river network (black lines). The map shown was scaled to be 100 km × 100 km, representing a typical coho salmon conservation unit in British Columbia.



Simulation model

We simulated a contraction in the distribution of spawning populations of coho salmon over 35 years at 100 sites on a single hypothetical river system (Fig. 3), designed with randomly selected distances among spawning locations. Contractions in spawning distribution can occur when returns to some sites are reduced compared with others, but those declines may be mitigated by the movement of spawners from populated to depleted sites. We captured these phenomena by simulating reductions in carrying capacity in a portion of sites, while allowing some spawners to return to sites other than their natal spawning ground (i.e., straying or dispersal). The simulation model included numerous biological and human components of the system that influence annual abundances (as in Holt and Peterman 2008 and Dorner et al. 2009). Specifically, it contained submodels for recruitment, harvest, dispersal, observations of abundances, and assessments of spawning distribution and a module for recording performance of metrics and sampling designs (Fig. 4).

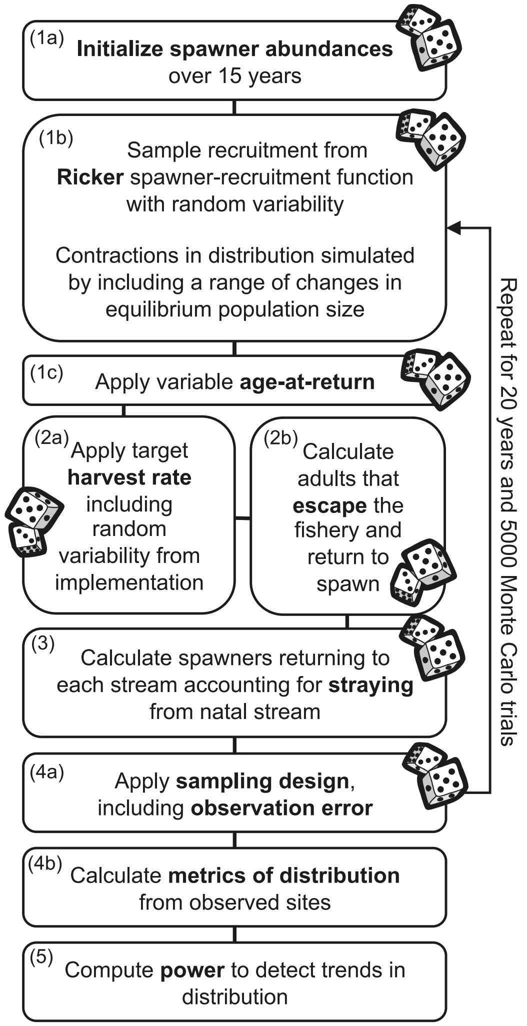
Recruitment submodel

Population dynamics were simulated separately for each site using the Ricker spawner–recruitment model (Ricker 1975):

$$R_{i,t} = S_{i,t}\exp(a_i - b_{i,t}S_{i,t} + \varepsilon_t) \tag{1}$$

where $R_{i,t}$ is the number of recruits at site i from brood year t, $S_{i,t}$ is spawner abundance at site i in year t, a_i is the productivity parameter (recruits/spawner at low spawner abundances), which is assumed to be constant over time but variable among sites, $b_{i,t}$ controls the productive capacity of the site at maximum recruitment, which varied over time and among sites, and ε_t represents stochastic variability in recruitment (see Appendix A, Table A1 for a list of parameters and values).

Fig. 4. Overview of the simulation model used to calculate power to detect contractions in production using proposed metrics of distribution and sampling designs, including submodels for (1) recruitment, (2) harvesting, (3) dispersal, (4) observation and assessment, and (5) one performance module. Each Monte Carlo trial simulated spawner abundances for 100 spawning sites over 20 years after initialization, from which metrics of spawning distribution were calculated. Dice indicate steps that involved stochastic processes. The model to calculate specificity differs from that shown here in that step 1b does not include a contraction in production, and the probability of correctly identifying no trend was computed in the performance module (step 5) instead of power.



Site-specific productivity parameters were drawn from a normal distribution with mean 1.75 and standard deviation 0.5, representing moderate productivity similar to that observed for coho salmon in British Columbia (BC) (Chen and Holtby 2002). To simulate a concentration of spawners among sites over time, we imposed a linear change in the unfished equilibrium spawner abundance ($S^*_{i,t} = a_i/b_{i,t}$) over 20 years by manipulating $b_{i,t}$. All sites started with $S^* = 1000$, and the change in equilibrium spawner abundance for each site was drawn from a uniform distribution with minimum of –1000 (representing loss of the spawning group over the simulation period) and maximum of +1000 (representing a doubling of S^* over the same period). Total spawner abundances were relatively stable over time but the distribution of spawners was less equal among sites. These changes in productive capacity represent a biologically plausible contraction in spawning distribution that may cause conservation concern. In the absence of absolute thresholds delineating unacceptable contractions in distribution, we use this (and several variants described in the sensitivity analyses) as examples for investigation. We varied capacity to simulate trends in production instead of productivity because variability in status among sites within a unit is more likely due to site-specific changes in freshwater capacity than changes in productivity, which usually covaries at larger regional scales (Peterman et al. 1998; Mueter et al. 2002).

We included temporal autocorrelation of lag 1 year in the residual error from eq. 1, ε_t, to capture the commonly observed autocorrelation in recruitment:

$$(2) \qquad \varepsilon_t = \rho\varepsilon_{t-1} + \upsilon_t, \qquad \upsilon_t \sim N\left(-\frac{\sigma_\upsilon^2}{2}, \sigma_\upsilon^2\right)$$

where $\rho = 0.3$ is the autocorrelation coefficient, within the range observed for other salmon species in BC and Alaska (Korman et al. 1995; Peterman et al. 2003), υ_t is normally distributed random variation with mean $-\sigma_\upsilon^2/2$ to ensure the arithmetic mean of the log-normal distribution is equal to one, and variance σ_υ^2. We set σ_υ^2 to 0.50, which was derived from the variance in recruitment observed for 50 coho salmon populations in BC estimated without temporal autocorrelation, $\sigma_\varepsilon^2 = 0.55$ (Chen and Holtby 2002), and accounting for the well-recognized ratio between them, $\sigma_\upsilon^2 = \sigma_\varepsilon^2(1 - \rho^2)$. We assumed annual deviations in recruitment were identical among sites because salmon within a unit share the same marine, estuarine, and similar freshwater habitats and therefore would be exposed to similar environmental conditions. Although spatial correlation among spawning groups decays with distance, empirical evidence for this phenomenon is at larger spatial scales than considered here (Peterman et al. 1998). If less than two spawners returned to a site, the recruits for that brood year were set to zero, although no spawning sites were permanently extirpated because straying allowed for future recolonization of sites with zero abundance.

We assumed the proportion of brood year recruits returning at age g, $p_{g,t}$, was constant across all sites but varied among years. This proportion was drawn from a multivariate logistic distribution (Schnute and Richards 1995):

$$(3) \qquad p_{g,t} = \frac{\exp(x_{g,t})}{\sum_{g=a_1}^{G} \exp(x_{g,t})}$$

where G is the oldest age class (4 years), and a_1 is the youngest (2 years). $x_{g,t}$ is a dummy variable:

$$(4) \qquad x_{g,t} = \log(\overline{p_g}) + \omega\xi_{g,t} - \frac{1}{(G - a_1 + 1)}\sum_{g=a_1}^{G}[\log(\overline{p_g}) + \omega\xi_{g,t}]$$

$\overline{p_g}$ are the mean proportions returning at age g, ω controls the magnitude of deviations from the mean proportions at age, and $\xi_{g,t}$ are standard normal deviates. To reflect a typical life cycle of coho salmon, the $\overline{p_g}$ parameters were set to 0.01, 0.95, and 0.04 for ages 2, 3, and 4, respectively. We chose $\omega = 0.9$, a value that results in realistic variation in age at return for coho salmon in southern BC (Irvine et al. 1999).

Spawner abundances for the first 4 years of the time series were drawn from a uniform distribution bounded between 20% and 80% of original unfished equilibrium abundance. The contraction in distribution was simulated over the subsequent 31 years, with years 16–35 used for the assessment of metrics and monitoring designs.

Harvesting submodel

The number of salmon returning in year y that hatched at site i, $R'_{i,y}$, was the sum of the recruits from brood years $y - 2$, $y - 3$, and $y - 4$ that returned at age 2, 3, and 4 years, respectively:

$$(5) \qquad R'_{i,y} = R_{i,y-2}p_{2,y-2} + R_{i,y-3}p_{3,y-3} + R_{i,y-4}p_{4,y-4}$$

Escapement of adults returning to their natal streams prior to dispersal, $E_{i,y}$, was computed as the total recruitment natal to that site minus fish harvested:

$$(6) \qquad E_{i,y} = R'_{i,y}(1 - h_y)$$

where h_y is the realized harvest rate common across sites. To incorporate random variability in outcomes of implementing target harvest rates, the h_y parameter was drawn from a beta distribution with mean equal to the target harvest rate of 0.3 and standard deviation of 0.2. Although the magnitude of outcome uncertainty has not been estimated for fisheries on coho salmon in BC, that standard deviation is in the range observed for sockeye salmon (*Oncorhynchus nerka*) fisheries on the Fraser River (Holt and Peterman 2006). While the target harvest rate may be low compared with historical catches of coho salmon on BC's south coast, fishing pressure in more recent years has declined to well below historical levels (Irvine et al. 2001).

Dispersal submodel

We modeled straying of spawners among sites with a dispersal matrix, **M**, that contained probabilities that a salmon hatched at site i returned to spawn at site j (Schick and Lindley 2007):

$$(7) \qquad \mathbf{M} = \begin{bmatrix} 1-m & m\phi_{i=1,j=2} & \cdots & m\phi_{i=1,j=N} \\ m\phi_{i=2,j=1} & 1-m & \cdots & m\phi_{i=2,j=N} \\ \vdots & \vdots & \ddots & \vdots \\ m\phi_{i=N,j=1} & m\phi_{i=N,j=2} & \cdots & 1-m \end{bmatrix}_{N\times N}$$

where N is the total number of sites, m is the stray rate, and $\phi_{i,j}$ is the probability of spawners dispersing from site i to site j. Values for $\phi_{i,j}$ were normalized so that the row sum of probabilities for all movements of salmon from site i was equal to one (i.e., no fish strayed outside the unit). Each year, the stray rate was chosen from a beta distribution with parameters β_1 and β_2. In the base-case scenario, we chose $\beta_1 = 3.9$ and $\beta_2 = 200$, corresponding to a mean stray rate equal to 2.0% based on 4 years of evidence from 14 coho salmon populations on Vancouver Island (Labelle 1992). However, because estimates of stray rates for coho salmon range from 0% to 67% (McElhany et al. 2000), we evaluated this assumption through sensitivity analyses (see below). The probability of spawners dispersing from site i to site j was dependent on the distance between sites, and was estimated as

$$\phi_{i,j} = \frac{1}{2\pi\theta^2}\exp\left[-\left|\frac{d_{i,j}}{\theta}\right|\right] \tag{8}$$

where θ is a dispersion parameter equal to the average dispersal distance, and $d_{i,j}$ is the distance between sites i and j along the river network (Clark et al. 1998). We set the average dispersal distance to 15.7 km based on empirical evidence from Labelle (1992). The distances among sites along the river network were calculated from a simulated river network in a 100 km × 100 km unit (Fig. 3). This river network was arbitrarily defined to represent a typical coho salmon CU in BC and was kept the same throughout the analysis. Distance calculations were performed using a shortest-path algorithm (Dijkstra 1959) in the RBGL package v.1.22.0 (Long et al. 2009) of the statistical program R v.2.10.1 (R Development Core Team 2010).

The number of salmon spawning at each site in return year y (equal to brood year t for the next generation) is the sum of those that returned to their natal stream and those that originated elsewhere but strayed to that site, calculated as the product of the vector of escapements to each site in return year y ($E_{1,y}\ E_{2,y}\ \ldots\ E_{N,y}$) and the dispersal matrix:

$$\begin{bmatrix} S_{1,t} \\ S_{2,t} \\ \vdots \\ S_{N,t} \end{bmatrix}_{N\times 1} = \begin{bmatrix} 1-m & m\phi_{i=1,j=2} & \cdots & m\phi_{i=1,j=N} \\ m\phi_{i=2,j=1} & 1-m & \cdots & m\phi_{i=2,j=N} \\ \vdots & \vdots & \ddots & \vdots \\ m\phi_{i=N,j=1} & m\phi_{i=N,j=2} & \cdots & 1-m \end{bmatrix}_{N\times N} \begin{bmatrix} E_{1,y} \\ E_{2,y} \\ \vdots \\ E_{N,y} \end{bmatrix}_{N\times 1} \tag{9}$$

Table 1. Power and specificity (bold) were the two performance criteria for evaluating sampling designs and metrics of spawning distribution.

	Simulated	
Observed	Trend	No trend
Trend	**True positive rate (power)**	Type I error (α)
No trend	Type II error (β)	**True negative rate (specificity)**

We initialized the recruitment, harvest, and dispersal submodels over 15 years with the contraction in spawning distribution beginning on the fifth year and computed distributional metrics over the following 20 years.

Observation and assessment submodel

To simulate monitoring, we sampled a subset of spawner abundances according to each of the four sampling designs. Spawner abundances that were not sampled under the design were treated as unknown. For the first design, key indicator sites were those that had the highest average spawner abundances over the entire time series. For example, for an annual sampling effort of 50%, sites were ranked in order of decreasing average spawner abundance over the time series, and the top 50% were selected for monitoring. Although key indicator sites may originally be chosen based on initial spawner abundances, in practice, sites with declining abundances are often dropped (Price et al. 2008), and so long-term average spawner abundance is the best criterion to select indicator sites that would likely have complete time series.

Uncertainty in the enumeration of spawners due to sampling variability and observation error was accounted for by including multiplicative log-normal variability in observed spawner abundances (Walters and Ludwig 1981):

$$S'_{i,t} = S_{i,t}\exp(\gamma_{i,t}), \qquad \gamma_{i,t} \sim N\left(-\frac{\sigma_\gamma^2}{2}, \sigma_\gamma^2\right) \tag{10}$$

where $S'_{i,t}$ are observed spawner abundances, and the mean of $\gamma_{i,t}$ was equal to $-\sigma_\gamma^2/2$ to ensure the arithmetic mean of the lognormal distribution was equal to 1.

Performance module

We considered three types of linear trends over time: (*i*) the expected trend from the simulated contraction in spawner production, (*ii*) the realized trend in the spawning distribution that includes environmental stochasticity due to recruitment variation, variability in age-at-maturity and annual harvest, and straying, and (*iii*) the observed trend that also includes variability due to incomplete sampling and observation error. The slope of the realized and observed trends in each distributional metric was estimated over 20 years using least-squares regression.

The performances of metrics of spawning distribution combined with sampling designs were evaluated on two criteria: their power to detect an expected trend in spawning distribution and their ability to correctly identify no trend when none was expected (Table 1). We based our calculation of power on expected trends rather than realized trends in distribution because we were interested in underlying change in spawning production independent of interannual variability in recruitment that may mask those trends. Power was therefore calculated as the proportion of Monte Carlo trials with a realized or observed trend in spawning distribution over the proportion of trials with an expected trend (equal to the number of Monte Carlo trials when a change in capacity was simulated). The probability of correctly finding no trend is a measure of how specific assessments of distribution are to changes in spawning distribution. This "specificity" was estimated by running the simulation without a contraction in spawning distribution and computing the proportion of Monte Carlo trials when a statistically significant trend was correctly not detected in the observed data. Performance criteria were calculated over 5000 Monte Carlo trials.

Trends were considered statistically significant when $p < 0.2$, so that under a minimum acceptable power level of 80%, the probabilities of failing to detect a realized or observed trend when a trend was expected and falsely detecting a trend when no trend was expected (types I and II statistical error, respectively) were comparable (Korman and Higgins 1997). In that way, we assumed those two types of error were of equal consequence. Although a statistically significant nonzero slope may differ from that which is biologically or ecologically important, such thresholds on these metrics have not yet been established (Holt et al. 2009).

Sensitivity analyses

We evaluated the sensitivity of metrics to changes in the annual sampling effort, observation error, magnitude of contraction, stray rates, and the length of the time series used to assess distribution. Each sampling design was evaluated over a range of annual sampling effort, between 5% and 100% of sites each year, in increments of 5% (but note that all designs converge when sampling effort is 100%). To account for variability in the accuracy of observed abundances due to, for example, differences in enumeration methods, each sampling effort was evaluated under various levels of σ_γ between 0 and 1. This range encompassed expected values of σ_γ from fence counts and mark–recapture studies with low observation errors ($\sigma_\gamma \approx 0.3$) to aerial surveys or foot counts with high observation errors ($\sigma_\gamma \approx 0.7$) (Cousens et al. 1982; Korman and Higgins 1997). We further evaluated all possible combinations of sampling effort and observation errors to identify interactions between these two components of assessment.

To assess sensitivity to smaller contractions in distribution than simulated for our base case, we calculated power of metrics for changes in capacity drawn from narrower distributions than used for the base case (ranging from no change in equilibrium spawner abundances, ΔS^*, to a change of ±1000 spawners over the simulation period, in increments of 50 spawners). To isolate the sensitivity of performance criteria to effect size, we estimated the power of metrics to detect changes in spawning distribution from all sites without observation error (i.e., assuming exact enumeration), calculated as the number of trials with a statistically significant realized trend over the total number of trials.

Although stray rates for Pacific salmon are typically low, they are highly variable and occasional high values have been observed (67%, McElhany et al. 2000). Expected changes in habitat due to anthropogenic forcing may further enhance stray rates for salmon originating from deteriorated spawning grounds seeking improved habitat. To investigate the effect of straying on changes in spawning distribution, we ran the recruitment, dispersal, and harvesting submodels with different distributions for the stray rate, under the base case assumption of 30% sampling effort and a standard deviation in observation errors of 0.3. We varied the β_2 shape parameter for the beta distribution from which the stray rate was drawn from 1 to 300, changing the mean and variance of the distribution, while keeping $\beta_1 = 3.9$ constant. We further evaluated the effects of increasing the time frame for assessments from 20 to 40 years without further contractions in distribution to investigate possible lags in observing responses.

Results

Metrics

Simulated contractions in (expected) spawning production resulted in declines in observed AOC and $P_{80\%}$ and increases in observed $P_{S<100}$ (Fig. 5). These contractions were independent of any significant decline in the realized total spawner abundances for the unit (Figs. 5*m*–5*p*) and therefore would not have been detected by examining abundance alone. The observed metrics AOC and $P_{80\%}$ tended to be negatively biased compared with realized values (by up to –9.6% of the maximum true value; Fig. 5*c*).

When evaluating metrics independent of observation error and sampling design (i.e., realized trends assuming complete and accurate sampling), AOC and $P_{80\%}$ had higher power to detect declining trends (as high as 80% power) than $P_{S<100}$ over a range in simulated contractions (Fig. 6). For AOC and $P_{80\%}$, interannual variation in recruitment was not large enough to mask underlying changes in distribution when contractions were large. When observation errors and incomplete sampling were included, AOC and $P_{80\%}$ again out-performed $P_{S<100}$ (Fig. 7). However, uncertainty in $P_{S<100}$ was larger than for other metrics (as indicated by the wider standard deviation in Figs. 5*i*–5*l*), and only severe contractions (>80% change in capacity) in spawning distribution resulted in detectable changes in $P_{S<100}$ (Fig. 6). The maximum power to detect expected contractions in spawner distribution was 0.866 (Fig. 7*g*). Metrics were generally more specific (better able to not detect contractions when they did not occur) under the key indicator design (Figs. 8*a*, 8*e*, 8*i*) than under the other designs over a range of observation error and sampling effort.

Sampling designs

The sampling design that monitored random indicator sites had the highest power to detect contractions in distribution, though the improvement over the panel and completely random designs was small, being evident only at low annual effort (Fig. 7). The design that monitored key indicator sites failed to capture the realized contraction in distribution (Figs. 5*a*, 5*e*, 5*i*). Further, over a range of annual sampling efforts and observation errors, the power to detect trends in distribution from key indicator sites was considerably lower than that for the other designs (Figs. 7*a*, 7*e*, 7*i*).

Sensitivity to magnitude of observation errors and sampling effort

Generally, the power to detect trends increased as the magnitude of observation errors declined (e.g., associated with high-quality sampling methods such as fence counts or mark–recapture experiments instead of areal surveys or stream walks) and high proportion of sites sampled annually (Fig. 7). For the design that monitored key indicator sites, annual sampling effort had more influence on power than the magnitude of observation errors, while the opposite tended to occur for other designs, especially at high annual effort (>40% sites observed annually). Below that annual effort, both factors tended to influence power.

Sensitivity to variable stray rates

We explored changing stray rates by varying the β_2 shape

Fig. 5. Observed trends (black lines) in three metrics of spawning distribution and the relative abundance of spawners (rows) calculated from observed spawner abundances at each site using one of four sampling designs (columns). The grey areas represent the realized trend, calculated as the mean ± one standard deviation among all Monte Carlo trials of the metric calculated from all sites without observation error (N = 100) and are the same across columns. Solid black lines are the mean ± one standard deviation for the metric calculated from observed sites ($n_t = 30$) with observation error $\sigma_\gamma = 0.3$. Standard deviation was calculated within each year over the 5000 Monte Carlo trials. Relative abundance is the standard deviation from the mean abundance over all years for each trial.

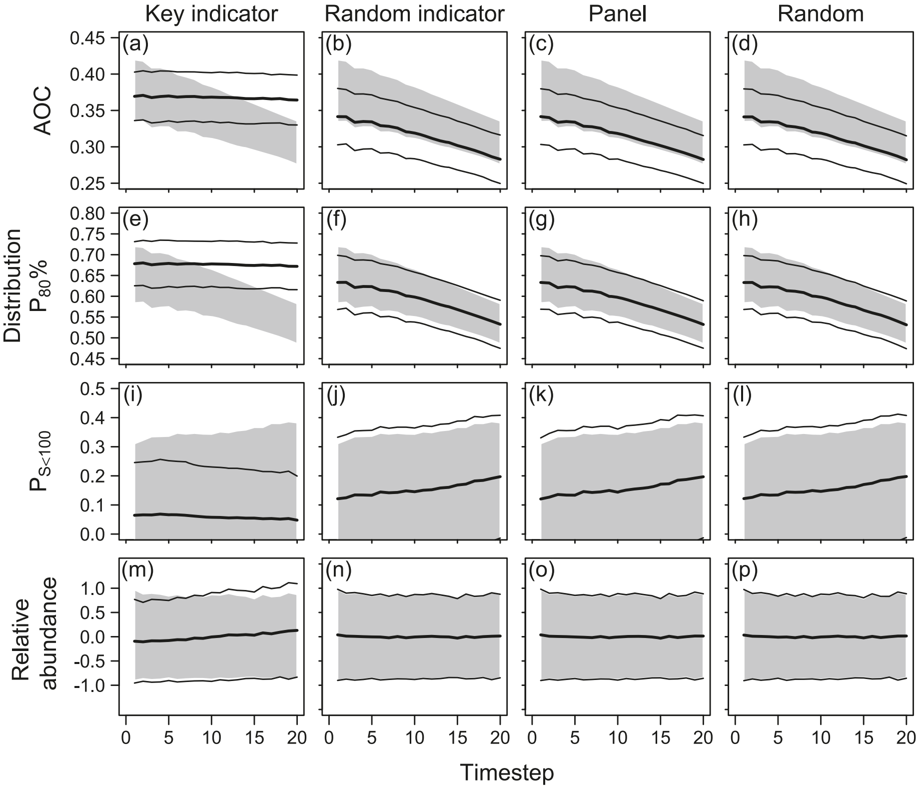
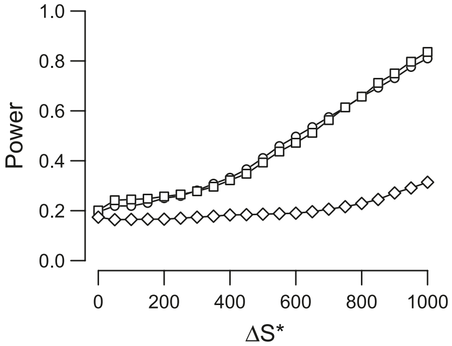


Fig. 6. Power of three metrics to detect simulated contractions in production over a range of changes in unfished equilibrium abundance, ΔS^* (capacity), where linear changes in capacity for each site were drawn from a uniform distribution bounded by $-\Delta S^*$ and $+\Delta S^*$. Circles represent AOC, squares represent $P_{80\%}$, and diamonds represent $P_{S<100}$. The base value for ΔS^* used in other simulations was 1000, representing relatively large changes in capacity resulting in collapse of some sites and doubling of capacity at others.



parameter for the beta distribution from which the stray rate was drawn (Fig. 9*a*). Low values of β_2 corresponded to higher mean stray rates. At high stray rates, the power to detect contractions declined by more than 20% for metrics AOC and $P_{80\%}$ (Fig. 9*b*).

Trade-offs between power and specificity

The relationship between the power to detect an expected trend and the specificity to detect no trend when there was none varied among metrics. In general, as power increased, specificity declined (Fig. 8), illustrating a trade-off between type I and type II statistical errors. However, the magnitude of changes in specificity over gradients in observation errors and sampling effort was relatively small compared with changes in power, and their magnitudes varied by sampling design. For example, under the key indicator design, the power of AOC ranged between 0.096 at low annual sampling effort and high observation error to 0.856 at high annual effort and low observation error (Δ power = 0.759, Fig. 7*a*), and specificity changed from 0.898 to 0.785 over the same changes in annual effort and observation error (Δ specificity = –0.113, Fig. 8*a*). For the random indicator design, the specificity was fairly uniform over the range of annual sampling efforts and observation errors (maximum Δ specificity = 0.134 for AOC), while power varied (maximum Δ power = 0.759 for AOC).

Discussion

Our results show a clear distinction between the types of metrics and sampling designs that are suitable for assessing the distribution of spawners and those that have relatively low power to detect trends even at high sampling effort and

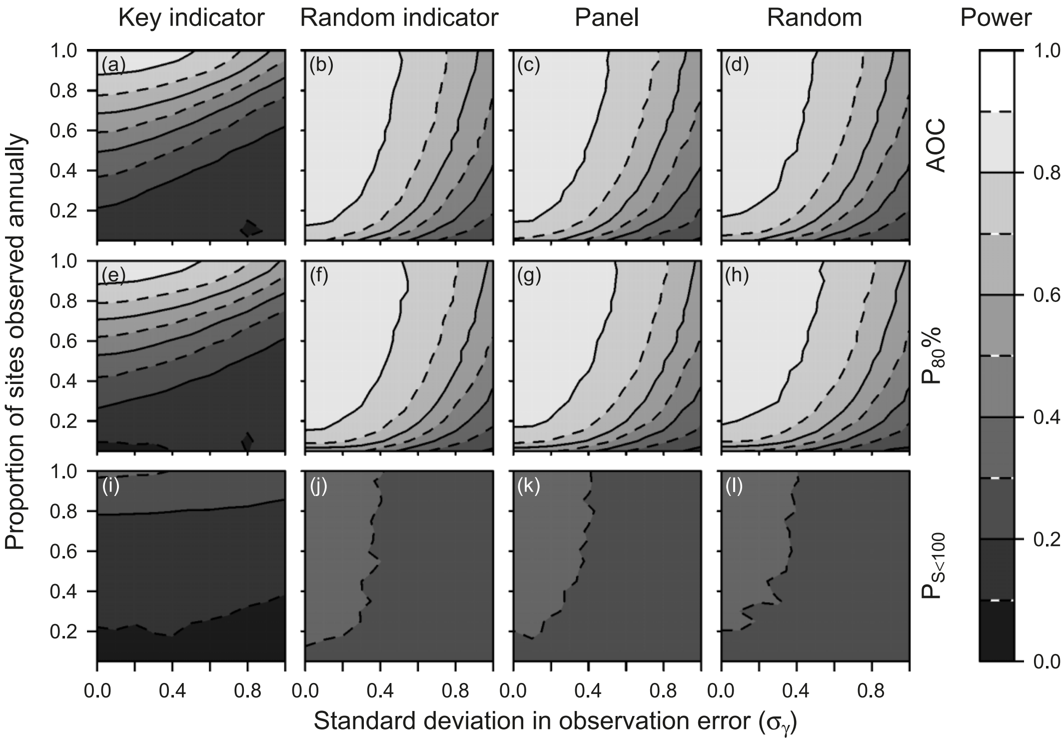


Fig. 7. Power to correctly identify distributional trends in the spawning production over different magnitudes of observation error (*x* axis of each panel) and proportion of sites sampled annually (*y* axis of each panel). Lighter shades are higher power. Power was calculated as the proportion of trials in which there was a significant ($p < 0.2$) nonzero slope in the observed value of the metric over 20 years. Each panel represents performance for one sampling design–metric combination, with designs in columns and metrics in rows.

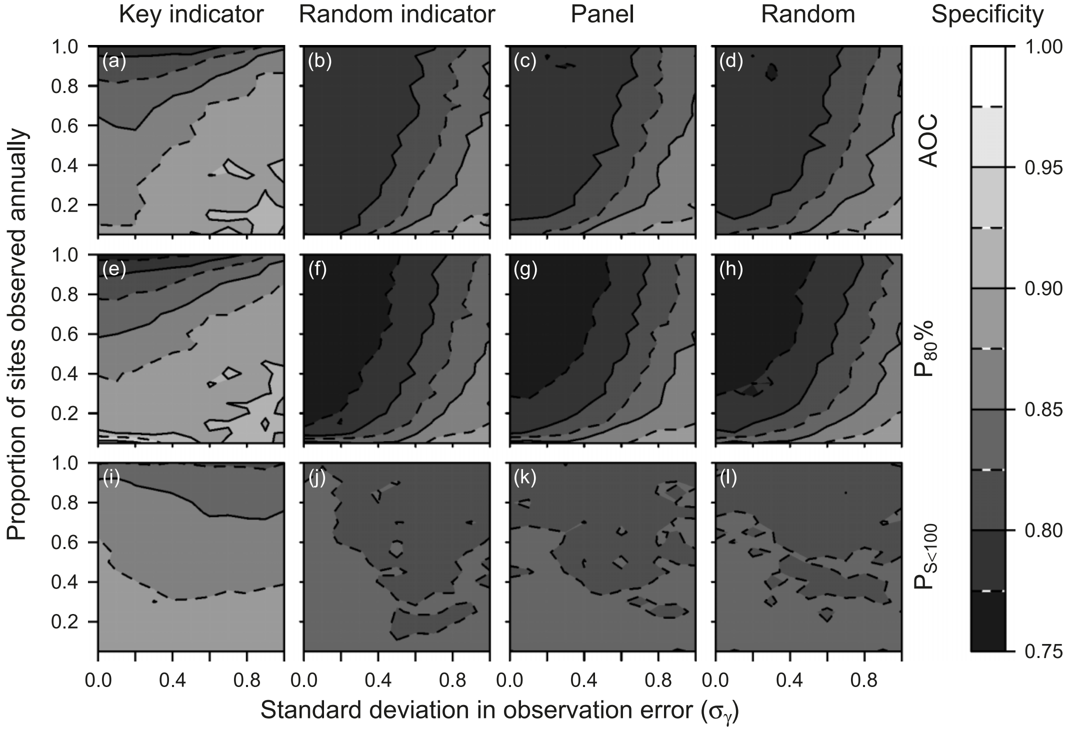
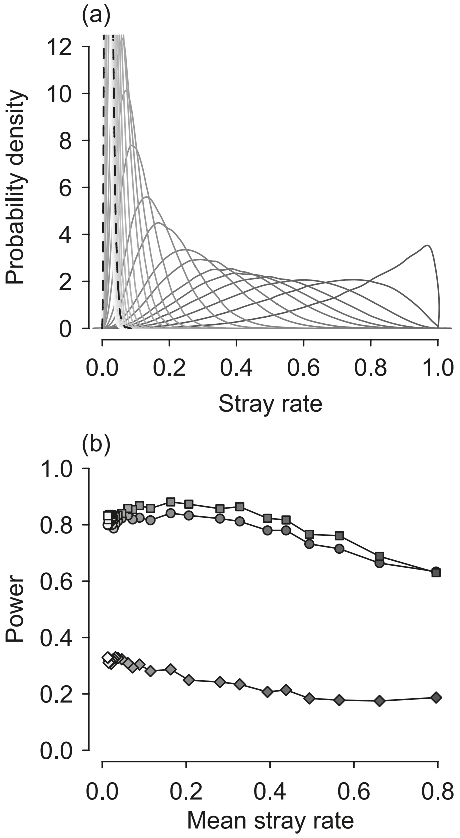


Fig. 8. The specificity of metrics and sampling to correctly identify no trend in spawning production when none was simulated over different magnitudes of observation errors (*x* axis of each panel) and proportion of sites sampled annually (*y* axis of each panel). Lighter shades are higher specificity. Specificity was calculated as the proportion of trials in which there was not a significant ($p < 0.2$) nonzero slope in the observed value of the metric over 20 years. Each panel represents performance for one sampling design–metric combination, with designs in columns and metrics in rows.

Fig. 9. (*a*) Probability density for the beta distribution of stray rates with shape parameters $\beta_1 = 3.9$ and β_2 varying between 1 (curves that peak on the right) and 300 (curves that peak on the left). The dashed line indicates $\beta_2 = 200$, corresponding to the base value stray rate of 0.02. For low stray rates, the peak of the probability density is off the plot (46.5 for the base value of β_2). (*b*) Power to detect simulated contractions in spawning production using three metrics (AOC, circles; $P_{80\%}$, squares; $P_{S<100}$, diamonds) across a range of stray rates drawn from a beta distribution for which the β_2 parameter varied.



low observation errors. The metrics AOC and $P_{80\%}$ held the most promise in combination with the random indicator, panel, and random designs, achieving >80% power of detecting a contraction. In contrast, the metric $P_{S<100}$ was unable to capture contractions, in part because of large sampling variability in this metric. $P_{S<100}$ considers sites with extremely low spawner abundances only and is less likely to detect a concentration of spawners among more abundant spawning groups.

The observed negative bias in AOC and $P_{80\%}$ compared with the realized contractions in those metrics were due to the lognormal distribution of observation errors. Occasional large positive deviations in observed abundances at some sites biased AOC and $P_{80\%}$ towards a seemingly more concentrated spawning distribution. This also highlights the danger of misinterpreting anomalously high returns to some sites as contractions in distribution, even when those increases are not accompanied by declines at other sites. For this reason, it is important that status assessments combine information from several indicators (e.g., abundance, trends in abundance, and distribution of trends among sites).

Our results suggest that improved power to detect changing spawning distribution may be better achieved by applying a sampling design that includes random selection of sites and implementing more accurate and precise enumeration methods than by increasing annual effort. However, when metrics were applied to observed data following a sampling design that monitored less than 40% of the total number of sites annually, power was reduced compared with the scenario where sampling was more complete. The key indicator design, currently applied in Canada (English et al. 2006), performed especially poorly and failed to detect contractions in spawning distribution unless survey coverage was almost complete.

Our ability to detect changes in the distribution of production was reduced by high stray rates (low β_2 values) because fish tended to stray from productive sites where capacity increased over time, mitigating declines in capacity at other sites. This result demonstrates the distinction between contractions in spawning production (the process that was simulated in our model) and the actual concentration of spawning distribution (the process that the metrics captured). Although the former more closely represents the true diversity of the population unit and is relevant to resilience, our metrics evaluate changes in spawning distribution and may therefore miss important shifts in the source populations. Thus, we must be reminded that future shifts in source–sink dynamics may confound monitoring efforts, making it difficult to detect the loss of genetically distinct spawning groups using the metrics of spawning distribution described here. Increase in stray rates similar to the ones simulated here may result from a localized disturbance (e.g., Leider 1989) and are a plausible consequence of global climate change. Under current climate change projections, stream flow regimes and river temperatures where salmon spawn are expected to become more variable among sites and over time (Nelitz and Porter 2009), which may increase the spatial and temporal variability in “attractiveness” of sites to spawners and increase stray rates (Crozier et al. 2008).

Several previous studies have examined the effect of sampling designs on the ability to detect regional trends in status, but metrics describing the distribution of spawners among sites have been notably absent from these analyses. For example, Holt et al. (2011) examined the power to detect trends in status indicators of salmon, but defined their distribution metrics as the proportion of sites where abundance indicators fell below a critical threshold. While important for detecting synchrony of trends among sites, those metrics do not capture how spawners are distributed among sites. In contrast with our results, Holt et al. (2011) found that metrics describing the frequency distribution of trends were more influenced by the level of annual effort than the magnitude of observation error. The difference between our results suggests that the best monitoring strategy depends not only on the class of indicators chosen (distribution in these cases), but also the specific metrics used (frequency distribution and distribution of spawners among sites, for Holt et al. (2011) and our study, respectively).

In studies that consider indicators of abundance, designs that include rotating panels have generally been found to be superior for detecting trends in spatially distributed resources over designs based on indicator sites or sequential sampling of all sites (Urquhart and Kincaid 1999; Urquhart et al. 1998). Given the same annual sampling effort, a larger proportion of sites are surveyed over time with rotating panels than when only indicator sites are used. Therefore, panel designs better capture region-wide status when there are diverging trends among sites within a given year. In contrast with those results and similar to ours, Holt et al. (2011) found that with the same annual sampling effort, rotating panel designs performed similarly to randomly chosen indicator designs for detecting regional-scale trends in abundance of simulated coho salmon spawners. Both Holt et al. (2011) and our study simulated spawner abundances at relatively small spatial scales, such that the interannual variability in spawner abundances was greater than the variation among sites. Thus, indicator designs that monitored sites on an annual basis were able to capture the interannual variability and performed as well or better than panel designs (Larsen et al. 2001; Urquhart and Kincaid 1999).

The interpretations of our results are limited in several ways. First, while we assessed power over a time frame appropriate for management, a longer time series of data may increase power to detect contractions in spawning distribution. In a sensitivity analysis, we evaluated trends in spawning distribution over 40 years, with the same contraction over the first 20 years followed by 20 years of constant equilibrium spawner abundances at the contracted spawning distribution. Our power to detect the same magnitude of contraction increased from a maximum of 86% to 91% with the additional 20 years of data. Thus, long-term monitoring programs are valuable for detecting trends in distribution, a conclusion widely supported for other metrics of status (Larsen et al. 2004).

Second, because biologically based thresholds of contractions in spawning distribution do not currently exist, we choose to assess probabilities of detecting a statistically significant change in spawning distribution. It is unlikely that our model failed to detect biologically important contractions in spawning distribution because we used a relatively high *p* value for statistical significance. That high *p* value allowed for increased power to detect true trends in spawning distribution at the expense of detecting trends when they did not exist.

Here, we focused on the distribution of spawners among sites, but the distribution of spawners among habitat types and the geographic range or spatial distribution of spawners may also provide information on the resilience of the population unit (McElhany et al. 2000). Spawners distributed over heterogeneous habitats may exhibit higher intersite genotypic, phenotypic, and life-history diversity than those distributed over the similar habitats (Narum et al. 2008). Spatially explicit metrics that look at contractions in the range of salmon spawners on the landscape would also be valuable for identifying shifts in spawner distribution that may be of ecological importance. In addition, distances among spawning sites influence the connectivity of the population unit by affecting two related processes: straying and reproductive isolation among sites, the relative importance of which will be scale- and context-dependent. Metrics for these two components of distribution have been suggested by management agencies (Cooney et al. 2007; Oregon Department of Fish and Wildlife 2007; Sands et al. 2009), and sampling designs have been developed (e.g., Stevens and Olsen 2004), but they are often tailored to region-specific characteristics of species and habitat (e.g., changes in occupancy across ecoregions within a unit; Cooney et al. 2007), and the data required to broadly apply these metrics (e.g., small-scale ecoregions or spatially balanced spawner surveys) are rarely available. Nevertheless, we recommend that such spatially explicit metrics be evaluated in a quantitative manner similar to the one shown here.

Our results suggest that sampling designs that include a random selection of sites (random indicators that are sampled annually, completely random, or panel designs) allow for a more accurate assessment of the distribution of production than current indicator designs (English et al. 2006; Price et al. 2008) by spreading sampling effort over sites with a range of spawner abundances and allowing a larger number of sites to be monitored over time. Such designs may be further stratified within population units by covariates such as habitat type and abundances to reduce sampling variance and ensure adequate coverage across covariates (Jacobs and Nickelson 1998; Stevens 2002). Simple random designs do not meet requirements for wide spatial coverage over short time scales because sample sites in any given year tend to cluster in space (Firman and Jacobs 2001), and the same may be true for coverage of sites of different population sizes or habitat types. Random designs could be combined with rotating panel designs, ensuring sufficient unbiased spatial coverage of sites comprising the panels and those that are consistently monitored.

For any exploited or endangered species, the monitoring strategy for units of conservation is an important part of conservation or recovery planning. In this analysis, we evaluated the power of sampling designs and metrics to detect contractions in spawning distribution of Pacific salmon, a new extension of previous evaluations of sampling designs that have considered metrics of abundance and trends in abundance. Our results suggest that metrics that use cumulative distribution of abundances among sites can better detect contractions than those that use proportion of sites with very low abundances. However, distribution reflects only one component of biological status, and multiple assessment objectives must be balanced when choosing a sampling design. Contractions in the distribution of production alone may not be of concern if, for example, causes are known and reversible, and total abundances are high and stable. Sampling designs should be quantitatively evaluated to ensure they adequately address multiple objectives. For example, obtaining reliable estimates of aggregate abundance for an entire population unit, ensuring sites of local, cultural, or commercial interest are consistently monitored, or detecting anthropogenic- or climatic-induced changes in populations may also be important. Furthermore, research into metrics and monitoring that can capture biological processes such as dispersal underlying the distribution of individuals, perhaps using modern genetic tools, is key to understanding changes. We suggest that long-term monitoring programs include the magnitude and variability of straying among sites and that research efforts focus on the impacts of straying on genetic and life-history diversity, population resilience, and the performance of alternative metrics of distribution.

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Appendix A

Table A1 appears on following page.

Table A1. List of symbols and parameter values described in text.

Eq. No.	Parameter or variable	Definition	Value or distribution (where appropriate)
1	i	Site index	
	t	Brood year	
	$S_{i,t}$	Spawner abundance	
	$R_{i,t}$	Recruits aligned by brood year	
	a_i	Productivity parameter	$\sim N(1.75, 0.5)$
	$b_{i,t}$	Capacity parameter	
	ε_t	Temporally autocorrelated deviations in recruitment	
2	ρ	Autocorrelation coefficient	0.3
	υ_t	Normally distributed random deviations	
	σ_υ^2	Variance in recruitment	0.50
3	g	Age at return	
	G	Oldest age at return	4
	a_1	Youngest age at return	2
	$p_{g,t}$	Proportion of recruits returning at age g	
	$x_{g,t}$	Dummy variable	
4	$\overline{p_g}$	Mean proportions of recruits returning at ages $g = 2, 3, 4$	0.01, 0.95, 0.04
	ω	Standard deviation in proportions at age	0.9
	$\xi_{g,t}$	Standard normal deviates	
5	y	Return year	
	$R'_{i,y}$	Abundance of returns aligned by return year	
6	$E_{i,y}$	Escapement	
	h_y	Realized harvest rate	
		Target harvest rate	0.3
		Standard deviation in realized harvest rates	0.2
	β_1	Shape parameter for beta distribution of stray rates	3.9
	β_2	Shape parameter for beta distribution of stray rates	200 (varied in a sensitivity analyses between 1 and 300)
7	$\mathbf{M}$	Matrix of dispersal probabilities	
	m	Stray rate	$\sim$Beta(β_1, β_2)
	$\phi_{i,j}$	Probability of dispersing from site i to site j	
8	θ	Dispersion parameter	15.7 km
	$d_{i,j}$	Distance from site i to site j along the river network	Derived from simulated network of spawning sites (Fig. 3)
	$S'_{i,t}$	Observed spawner abundances following a sampling design	
10	$\gamma_{i,t}$	Normally distributed random deviations	
	σ_γ	Standard deviation in observation error	0.3 (varied in a sensitivity analysis between 0 and 1)

Note: Equation numbers indicate where parameter or variable first appears.