Quantitative Assessment of Salmonid Escapement Techniques in the Pacific Northwest

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Abstract. Most reviews of salmonid escapement estimation techniques have been based on logistical considerations or site-specific applications and not on statistical first principles. We reviewed six categories of salmon escapement techniques: area-under-the-curve, carcass abundance, mark-recapture, passage count, peak count, and redd count methods, based on statistical accuracy (i.e., unbiasedness), precision, and the ability to meet model assumptions. Within each of these categories of escapement techniques, we make recommendations on the best approaches to use for valid estimates and suggest five considerations when selecting an escapement estimation method. Currently in the Pacific Northwest, peak spawner counts are the most commonly employed technique and least defensible on a statistical basis than other methods. We recommend statistical accuracy and precision be given higher consideration when monitoring often increasingly scarce salmon resources.

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INTRODUCTION

Reliable estimates of salmonid escapement are required to establish sustainable harvest limits, forecast future run sizes, assess the impacts of management decisions and evaluate the success (or failure) of conservation efforts (Manske and Schwarz, 2000; Perrin and Irvine, 1990; Ames et al., 1974; Beidler and Nickelson, 1980; Bue et al., 1998). A reliable estimate must be both accurate and precise (Paulik and Robson, 1969; Rose et al., 2000). If an estimate is inaccurate, i.e., biased, it does not measure the desired quantity and is therefore deceptive. If an estimate is accurate but brings with it great uncertainty, i.e., is highly variable, it is similarly useless for management purposes. Thus, knowing the bias and variance of an estimate provide managers the "basic tools for determining the trustworthiness of an estimate" (Paulik and Robson, 1969).

Previous reviews of salmon escapement estimation techniques do not address the statistical bias or variance of the reviewed techniques. The two most prominent comprehensive reviews, written by Cousens et al. (1982) and Schubert (1998), focused on logistic procedures, locations of use, best and worst situations for use, comparative empirical accuracy and suggestions for improvement of operational techniques. Neither included thorough analyses of the statistical bias or variance associated with any method.

There have been numerous reviews comparing empirical estimates of escapement for a single system using multiple techniques (Schubert, 2000; Johnston et al., 1986; Irvine et al., 1992; Miyakoshi et al., 2003) or using one technique across multiple years or systems (Perrin and Irvine, 1990; Hilborn et al., 1999). In these reviews the performances of the estimators are judged relative to each other, rather than to known escapement, and statistical behavior is ignored.

The purpose of this paper is to offer a statistically based review of methods currently employed to estimate salmon escapement in the Pacific Northwest. This paper is a synopsis of a much larger and statistically detailed review of salmon escapement techniques by Parsons and Skalski (2009) [http://pisces.bpa.gov/release/documents/documentviewer.aspx?doc=P112130]. Readers wanting more information on the construction of escapement estimators and their variances should refer to this publically available document. Out of this review, a suite of methods emerged as being statistically accurate and precise (i.e., reliable). We hope that with this review managers will be equipped to select escapement estimation methods that are statistically reliable as well as logistically practical.

REVIEW METHODS

Literature Search and Brief Description of Escapement Categories

We conducted a database review of escapement results for the Pacific Northwest (http://www.streamnet.org/) and an extensive literature search to identify escapement techniques used in Washington, Oregon, California, Alaska, and British Columbia between 1997 and 2007. We chose methods to review based on (1) StreamNet queries, (2) recent salmon management book reviews, (3) almost 300 peer-reviewed journal articles and management agency publications, and (4) personal communication with the Washington Department of Fish and Wildlife (WDFW). All of the reviewed methods fell into one of the following six categories of escapement estimation summarized below.

1. *Area-Under-the-Curve Methods*

The numbers of fish present in the survey area each day are summed over the course of the spawning seasons to determine the total number of fish-days for that survey area (and season). Total fish-days are typically estimated from periodic foot surveys (Perrin and Irvine, 1990; Irvine et al., 1992; Lady and Skalski, 1998), boat or snorkel surveys (Cousens et al., 1982; Bocking et al., 1988), or aerial surveys (Hill, 1997; Bue et al., 1998; Neilson and Geen, 1981). Total fish-days is divided by an estimate of the amount of time, on average, the adult salmon spend in the survey area. This quantity is most often referred to as “stream residence time” (Irvine et al., 1992; Hill, 1997; Lady and Skalski, 1998; Manske and Schwarz, 2000) but is also called “survey life” (Ames, 1984; Perrin and Irvine, 1990) or “stream life” (Bue et al., 1998). We use the term “stream life” for simplicity with the assumption that it applies only to regions of the stream being surveyed for fish-days.

2. *Carcass Abundance Methods*

Since every spawner dies and produces exactly one carcass, an estimate of the number of carcasses produced in a stream during a run can serve as an estimate of escapement (Frith and Nelson, 1994; Bue et al., 1998).

3. *Escapement Estimation Using Mark-Recapture Methods*

Escaping salmon are captured and marked, usually with a Petersen disk tag (e.g., Rajwani and Schwarz, 1997) or a spaghetti tag (e.g., Smith et al., 2005), sometimes in conjunction with an operculum punch (e.g., Bocking, 1991). Later, more fish are captured and an estimate of escapement is made by comparing ratios of marked and unmarked fish. Variations of the method exist for cases in which the population can be assumed closed (no arrivals or losses) versus when the population must be assumed open (arrivals and/or losses).

4. Passage Count Methods

Fish are enumerated as they migrate past a reference point. The reference point may be a tower from which an observer notes the passing salmon (e.g., Reynolds et al., 2007), an acoustic transducer (SONAR), a viewing station (e.g., Hatch et al., 1998), or a weir (e.g., Ripley, 1949; Bocking et al., 1988).

5. Peak Count Methods

Periodic counts are made of live spawners (e.g., McPherson et al., 1999), of live plus dead fish (e.g., Parken et al., 2003) or of live plus cumulative dead (e.g., Schubert, 1998) until the number of live fish detected starts to decline. The count with the largest number of fish is reported as the peak count. The peak count can be calibrated to total escapement via standard regression (Beidler et al., 1980), means-of-ratios (McPherson et al., 1999), ratio-of-means (Cochran, 1977), and errors-in-variable-regression (Fuller, 2006).

6. Redd Count Methods

Salmonid nests, called ``redds," are often distinguishable from the surrounding substrate as lighter circular or ovoid patches on the stream bed (Chapman, 1943; Dauble and Watson, 1990). Surveys that count salmon redds are conducted aerially from fixed-wing aircraft (Meekin, 1967; Ames and Phinney, 1977; Dauble and Watson, 1997), from the ground (e.g., Meekin, 1967), by boat (e.g., Gallagher and Gallagher, 2005), with snorkels (e.g., Al-Chokhachy et al., 2005), or using SCUBA equipment (e.g., Swan, 1989). The number of redds detected is assumed to be proportional to the total number of female salmon, which is extrapolated to a total escapement estimate using an estimated male-to-female ratio.

Review Criteria and Ratings

For each method and its variations we derived a mathematical expression for the escapement estimator. For the interest of space, the derivations and expressions are not given here (see instead Parsons and Skalski, 2009). We evaluated the direction and magnitude of any statistical bias in each estimator and rated the bias of the estimator under ideal circumstances, which included adjustments to reduce statistical bias. The estimator was deemed “Poor” if it was inherently biased even with adjustments. The estimator was deemed “Fair” if it was statistically unbiased to the first order Taylor series expansion, but has been shown to be unreliable in empirical studies. For example, the ratio estimator $\bar{y}/\bar{x}$ is an unbiased estimator of μ_y/μ_x only to the first order of a Taylor series; to the third order, it has expected value $\left(\mu_y/\mu_x\right)\left(1+\mathrm{CV}\left(\bar{x}\right)^2\right)$. The estimator was “Good” if it was statistically unbiased to the first-order Taylor series expansion and has performed well empirically.

For each estimator, we determined if a variance estimator exists, and if not, derived an estimator for the variance, where possible. We rated each method's variance as “None,” “Poor,” “Good,” or “N/A.” A “None” indicates that either there was no variance estimate provided or it could not be derived. The variance was deemed ``Poor'' if it failed to incorporate all sources of error or was poorly derived. The variance was deemed “Good” if all sources of error were incorporated correctly into the estimator. When an escapement estimate was based on an exact count, the sampling variance was zero and a variance estimator was no longer applicable, “N/A.”

We rated each of the estimators based on the ease of ensuring their required assumptions. A “Reasonable” rating implied that the assumptions could generally be ensured in well-designed studies. An “Unreasonable” rating indicates that the assumptions were often biologically or logistically unreasonable. A method with “Conflictual” assumptions was one for which fulfilling one assumption precluded either the fulfillment of another or the rationale for using that particular method.

We also rated each estimator's performance with respect to empirical studies. The best rating was “Feasible” if the method could be readily implemented in appropriate statistical simulations. The rating “Inapplicable” implies that the method does not actually measure the desired quantity. “Index only” is assigned to methods that do not provide an actual estimate of abundance, only an index proportional to abundance. “Not much testing” indicates that a method is uncommon or relatively new and has not been subject to many performance tests in the field.

Finally, we gave each estimator an overall recommendation based on the method's bias, variance, assumptions, and empirical performance. A method was given a “Do Not Use” if the estimator was inherently biased or failed to estimate its desired end. A method was given a “Cautionary” if the estimator was statistically unbiased but the empirical evidence suggests that either experimental bias or the variance is so large that the estimator is rendered practically useless. A method was given a “Good Alternative” if the estimator was theoretically unbiased, but the assumptions required may be difficult to attain. A method was only recommended as a “Best Choice” if both the estimator and variance were unbiased and the supporting assumptions were reasonably attainable. It is possible that an escapement category of methods may have multiple or zero “Best Choices.”

RESULTS

A survey of the escapement methods used in the Pacific Northwest (i.e., Washington, Oregon, Idaho, California, and Alaska), 1997–2007, indicates the survey approaches differ generally by salmonid species (Fig. 1). Nevertheless, the peak count method constituted 41.6% of all survey effort, followed by “spawning ground” techniques that included mark-recapture, area-under-the-curve, or carcass counts, accounting for another 39.6%. Redd count methods were another 17.0%, with dam and weir counts making up the remaining 1.8% of escapement survey efforts.

Area under the Curve

Of the methods used to estimate fish-days, the Ames method (Ames, 1984) served as the conceptual framework upon which the rest of the AUC methods were built, but should not be used in salmon fisheries management. The AUC was calculated from a hand-drawn curve that produced an estimator of unknown bias and with no variance estimator (Table 1).

The trapezoidal method of AUC is widely used because of its simplicity in both comprehension and computation (e.g., Bocking et al., 1988). Intermittent estimates of abundance are plotted against days in a run. Values for unsampled days are extrapolated linearly between sampled days and the area under the resulting ``curve'' (trapezoid) is calculated as the total fish-days for the run. Unfortunately, the trapezoidal estimator and estimate of variance are unbiased only if the stream is surveyed every day of the run (Liao, 1994). The trapezoidal method is typically used when a nonprobabilistic sample of spawning days is surveyed. In which case, the estimate of total fish-days will be biased with no variance estimate possible. Better options exist such as the average spawner method (Liao, 1994) described below when a probabilistic sample is drawn (Table 1).

The Likelihood AUC method assumes a partially mathematical arrival time distribution for the escaping salmon. While mathematically elegant, the actual arrival patterns of Pacific Northwest salmon have been shown to be different from the assumed arrival patterns used in the parametric models and have been shown to be less accurate than trapezoidal-based estimates (Hilborn et al., 1999). Since the applicability of the likelihood model for a given year is not known and the estimates are less accurate than other more applicable methods, the likelihood-based parametric methods of estimating fish-days are not recommended for regular use.

The average spawner method (Liao, 1994) provides unbiased estimates of both fish-days and variance, and requires design-based assumptions that are more attainable than other methods (Table 1). Salmonid abundances are estimated using classical survey sampling methods (Cochran, 1977), such as random or stratified random sampling of the days of the escapement. By using a stratified random selection of days, strata (i.e., weeks) can be easily added or dropped depending on run timing, while still ensuring an unbiased point estimate and variance. The average spawner method is theoretically the best method available to estimate fish-days for use in the AUC Method. The only drawback is that it is infrequently used in practice so there is little empirical evidence to evaluate its logistical efficacy.

Of the 15 different ways reviewed to estimate stream life, only 7 are capable of producing unbiased estimates of stream life. These are the Tag Depletion method (Bocking et al., 1988), the four mark-recapture methods of Lady (1996) and Lady and Skalski (1998) and the two timer tag methods of Shardlow et al. (2007).

Bocking et al.'s (1988) tag-depletion method is essentially the same as the trapezoidal area-under-the-curve method using tag-days instead of fish-days. Like the trapezoidal AUC method, the tag-depletion method only provides an unbiased estimate of residence time if the surveys are conducted daily. Under relatively strict conditions, the tag-depletion method of estimating stream life can provide an unbiased estimate. If the season is short enough for changes in stream life to be considered negligible, or if the method can be repeated over the run and a weighted average of the multiple estimates calculated (weighted by the proportion of fish entering the stream during each period), then the tag-depletion method may be considered a "good alternative" way to estimate stream life.

The Lady (1996) and Lady and Skalski (1998) methods apply only to fish arriving at the initial tagging event. Consequently, all tagged fish are expected to have the same probability of survival and stream life and the assumptions are reasonably met. To obtain season-wide estimates, the methods of Lady (1996) and Lady and Skalski (1998) must be applied multiple times throughout the course of the run, and a weighted average must be calculated. Estimates made by including carcass detections (Live and Dead) are more precise than estimates derived exclusively from live counts (Lady and Skalski, 1998). Lady (1996) recommended a parametric estimator, because it was more accurate than the non-parametric estimator, especially in cases where many of the tagged fish were still alive at the end of the study. However, if the data do not fit the assumed survival function (i.e., Weibull), then a non-parametric estimator provides more accuracy (i.e., less bias) and should be used (Lady, 1996, p. 146).

Timer-tags provide an almost exact measurement of time from tagging (i.e., arrival) to death and are among the best options for estimating stream life. The measurement error is on the order of minutes (Shardlow et al., 2007), which is negligible when stream life is reported in days. Though timer tags have only been tested on one wild population, controlled tests indicated that deaths were recorded accurately (Shardlow et al., 2007). Therefore, the validity of the timer-tag method will depend on how representative the sample of tagged salmon is to the escapement population. Provided that every fish has an equal probability of being tagged, the method gives a simple, unbiased estimate of average stream life. Timer-tags can also provide an unbiased estimate of stream life if the run is stratified by time and estimates from each stratum are weighted by the proportion of fish entering during each stratum. When the survival curve based on individual stream lives follows a parametric distribution such as the Weibull or exponential, the parametric estimator will provide a more precise estimate of stream life. When the survival curve does not fit a specified distribution, a non-parametric estimator based on the Kaplan-Meir method will be more accurate (Lady, 1996).

Carcass Abundance

The simplest carcass abundance method is an attempt to completely enumerate the population of dead spawners. This method is inherently negatively biased because of carcass losses due to predators, scavengers, floods, and decay (Schubert, 2000; Simpson, 1984; Johnston et al., 1986; Gende et al., 2001; Dunwiddie and Kuntz 2001). There is no analytical way to ascribe sampling error to this method.

To account for losses and imperfect detections, investigations have used mark-recapture methods to estimate the population of salmon carcasses. Closed population models are inappropriate because of assumption violations due to carcass loss. Both the Pooled Petersen and the Schaefer estimators overestimate escapement (Law, 1994) and, in general, closed population methods should not be used (Table 2).

The Jolly-Seber (Jolly, 1965; Seber, 1965) and Manly-Parr (Manly and Parr, 1968) mark-recapture methods are more appropriate than closed population methods when estimating salmon carcass abundance (Shardlow et al., 1986; Conrad, 2000; Fieberg, 2002). In this application, the death of a fish represents recruitment, and losses due to scavengers, etc., represent mortality in these open population models. The Jolly-Seber method allows for carcass loss but relies on the assumption that all carcasses are equally detectable, which is usually not the case (Sykes and Botsford, 1986). It may be robust to age- and size-dependent detectability if decayed carcasses are removed after second capture (Conrad, 2000), though empirical evidence is limited, and simulations provide contradictory results (Law, 1994). Great care must be taken to ensure that all carcasses are accessible to surveyors, lest significant portions of an escapement be missed and abundance be underestimated (Conrad, 2000). Salmon deaths (new carcasses) occurring after the last survey cannot be estimated, contributing negative bias to the estimate unless a study is carried out until no live salmon are present. Unaccounted-for predation of live fish and moribund drifters contribute further negative bias. The Carcass Jolly-Seber method is recommended with caution because of limited empirical evidence regarding its robustness to model violations (Table 2). The Manly-Parr method has fewer assumptions than the carcass Jolly-Seber method but does not provide variance estimates and is not recommended for this reason (Table 2).

The Daily Dead Estimator (Skalski et al., 2009) incorporates carcass loss and incomplete detection probabilities in the development of the estimator. In theory, the Daily Dead Estimator is unbiased for escapement and provides a variance estimate, though the variance estimate may be negatively biased in extreme cases. The Daily Dead Estimator remains to be tested in the field, but may prove to be a valid option for estimating escapement using carcass abundance, so it is recommended with caution (Table 2).

Escapement Estimation Using Mark-Recapture Methods

When applied to salmon escapement, most mark-recapture methods fail due to violations of model assumptions. There are cases, however, when assumptions can be met, and an unbiased estimate of escapement is possible.

The Pooled Petersen estimator, while often recommended for ease of use and robustness to assumption violations (Schubert, 2000), has been shown to be positively biased both statistically and empirically (Schubert, 2000; Simpson, 1984; Maselko et al., 2003). Corrections proposed by Chapman (1951) (cited in Seber, 1982) and Bailey (1951) provide nearly unbiased estimators, but do not address violations of assumptions in data collection. Of all the mark-recapture methods considered, the Pooled Petersen estimator has the smallest perceived variance because it is estimating the fewest parameters. However, because the Pooled Petersen estimator is biased due to violations of model assumptions, it is not recommended (Table 2). The Schaefer estimator (1951) allows different tagging and recovery probabilities for fish tagged at different times but requires assumptions that are unlikely to be fulfilled. The Schaefer (1951) estimator does not provide a variance estimate and is therefore not recommended (Table 2).

The Darroch method (Darroch, 1961) is the best mark-recapture method available to estimate salmon escapement, but not as traditionally used (Table 2). Traditionally, salmon are tagged while alive and recovered as carcasses. Since fish are continuously arriving and dying, tagging times and recovery times are often grouped into tagging and recovery strata. This method requires the assumption that bodies of all the salmon remain in the study area until the study is complete (e.g., Maselko et al., 2003). However, carcasses and moribund fish are frequently washed downstream and out of the study area (Simpson, 1984; Johnston et al., 1986; Schubert, 2000), negatively biasing escapement estimates. These losses can be mitigated by placing a downstream weir at the end of the study area to trap and count migrant carcasses (Simpson, 1984). However, weirs may be inoperable during high run-off, precisely when the rate of carcass loss is greatest (Johnston et al., 1986; Shardlow et al., 1986). Additional carcasses may be lost to scavengers, decay, and deep pools, further biasing the escapement estimator. Live fish are also subject to predation (Johnston et al., 1986), and removals are not usually accounted for in escapement counts.

Underwood et al. (2007) appropriately applied the Darroch Estimator for escapement estimation by constructing a well-defined, closed population of migrating spawners. By tagging salmon downstream and recovering them alive upstream, Underwood et al. (2007) ensured the assumptions of the Darroch Estimator were reasonably met (Table 2). The Underwood et al. (2007) study is perhaps the best example of applying the Darroch Estimator to date. Thus, when the assumptions are ensured, the Darroch Estimator is the best mark-recapture option for estimating salmon escapement.

The Jolly-Seber method (Seber, 1965; Jolly, 1965) of estimating salmon escapement is convoluted and includes biases due to assumption violations, even with adjustments suggested by Schwarz et al. (1993). The Jolly Seber method cannot account for fish present at the time of the first survey or for new arrivals after the penultimate survey period. It also requires that the probability of survival is the same for all fish. Realistically, fish that arrive early are more likely to die during a survey interval than later arriving fish. Manly (1970) showed that when mortality was dependent on arrival time, the Jolly-Seber estimate of escapement was positively biased. Additionally, the Jolly-Seber estimate is a function of numerous parameters which results in very large variance estimates (Manly et al., 2003). The Jolly-Seber method is not recommended for estimating escapement using live tagged fish (Table 2).

The Schwarz-Arnason method (Schwarz and Arnason, 1996) yields larger variance estimates than the Jolly-Seber method and requires more assumptions, although the additional assumptions are meant to ensure escapement estimates are more realistic and biologically meaningful. The model has greater realism at the expense of perhaps more assumption violations. However, the trade-offs are uncertain and the method remains untested in practice. Therefore, we do not recommend it at this time (Table 2).

The Manly-Parr method (Manly and Parr, 1968) does not require the assumption that all fish present between two survey occasions have a common survival rate. Thus, the Manly-Parr method has more reasonable assumptions than the Jolly-Seber method. However, without the assumption of common survival, those spawners that both arrive and die between consecutive surveys cannot be estimated, potentially rendering the Manly-Parr estimator negatively biased. Furthermore, the Manly-Parr method does not provide a variance estimate on total escapement. A bootstrapping procedure may provide variance estimates (Manly, personal communication), but there is little empirical testing of the Manly-Parr method with or without variance estimates. Due to the lack of empirical testing and the lack of a variance estimator, we do not recommend the Manly-Parr method for estimating salmonid escapement (Table 2).

The Robust Design method (Pollock, 1982; Pollock et al., 1990) is an alternative to traditional open population abundance estimators that can provide both abundance and survival estimates. If primary surveys are conducted over a short interval of time so that the population can be reasonably assumed to be closed, then the abundance estimates will be valid. However, as with the Jolly-Seber method, the Robust Design method requires that the probability of survival is the same for all fish between surveys. Thus, robust recruitment estimates will likely be biased in the same ways as the Jolly-Seber estimates (Table 2). The Robust Design has not been applied in practice to escapement estimation and should be applied only with careful consideration and planning.

The Change-In-Ratio method (CIR) (e.g., Paulik and Robson, 1969) is not commonly used and requires special circumstances to be applicable. A hatchery or some other demographic intervention point must be placed below wild salmon spawning grounds. The ratio of wild to hatchery fish below the intervention point (where some known quantity of hatchery fish are removed) is compared to the ratio of wild to hatchery fish above. It does provide an unbiased estimator and an estimate of variance with reasonable assumptions. An estimate of the total number of hatchery returns can also be estimated and the wild population estimated as the difference between the total escapement and the hatchery returns (Skalski and Millspaugh, 2006). If the circumstances are amenable, the CIR method can be a good choice to estimate salmon escapement, though CIR estimates typically have large variances (Seber, 1982:366-371).

Passage Counts

Passage count methods are potentially the most accurate and precise methods of estimating salmon escapement (Table 2). They are statistically simple, design-based methods that require few assumptions, but do require special circumstances. Inter-dam estimates require that there be at least two dams where fish are enumerated or estimated as they pass (Gangmark and Fulton, 1952; Beiningen, 1976; Boggs et al., 2004). Weir counts require that river flows and debris loads are low enough to keep weirs in operation through the escapement season (Bue et al., 1998; Skud, 1958; Shardlow et al., 1986; Labelle, 1994). Sonar counts require suitable streambed morphology and the run timing of the species of interest not to overlap with the migration of other species (Eggers, 1994; Ransom et al., 1998; Lilja et al., 2000; Maxwell et al., 2007). All passage count methods require probabilistic sampling during passage to provide unbiased abundance estimates and variance estimates.

Peak Counts

The maximum number of spawners present at any time during the escapement is considered the peak abundance. The peak is estimated as the largest of periodic survey counts of live spawners, live and dead spawners, or live spawners plus the cumulative dead. Peak counts are widely used, but only provide an index of salmon escapement. Equating raw peak counts to total escapement requires multiple years of abundance estimates and regression assumptions that are rarely met in practice. In most cases, there is insufficient data to calibrate peak counts to escapement abundance. Similarly, comparing peak counts between index areas from year to year (relative peak count method) can, at best, only provide estimates of relative change in escapement. None of the uncalibrated peak count methods are recommended for estimating salmon escapement (Table 3).

Both ratio and regression estimators have been used to calibrate peak counts to total escapement. The Mean-of-the-Ratios (McPherson et al., 1999) estimator requires multiple years of both peak counts and separate escapement estimates. The escapement-to-peak ratio is calculated each year and the ratios are averaged across years to estimate a conversion factor for subsequent years' peak counts. The Mean-of-the-Ratios estimator provides a biased estimate of escapement and requires no fewer assumptions than the Ratio-of-the-Means estimator. The Ratio-of-the-Means estimator (Cochran, 1977) averages the escapement estimates and peak counts before calculating the ratio to estimate a conversion factor. The Ratio-of-the-Means estimator is less biased than the Mean-of-the-Ratios estimator but can require as many as 30 years of data estimation for the bias to be considered negligible $\left(\text{i.e., } E\left(\bar{y}/\bar{x}\right) \doteq \left(\mu_y/\mu_x\right)\left(1+\text{CV}\left(\bar{x}\right)^2\right)\right)$ (Cochran, 1977). It has a large variance that is often underestimated, and assumes a straight-line relationship through the origin between escapement and peak counts. The Ratio-of-the-Means method is statistically valid despite logistical limitations and so is recommended with caution (Table 3).

The Calibration Regression method (e.g., Beidler and Nickelson, 1980) is the most direct method used to adjust peak counts to escapement. Escapement estimates are regressed against historical peak counts, and the fitted regression relationship is used to predict the current year’s escapement based on the current year’s peak counts. Unfortunately, empirical efforts to calibrate peak counts to escapement have shown to be highly variable and of little use to management

(Beidler and Nickelson, 1980). Standard regression techniques also require that the peak counts are known without error, which is unreasonable given different observer efficiencies, run timing, and sampling efforts. Consequently, statistical calibration methods should not be used to estimate salmon escapement (Table 3).

The Inverse Prediction method can allow for error in the predictor variable and is therefore more applicable for estimating salmon escapement than calibration regression. Rather than regressing the escapement against the peak count, the peak is regressed against the escapement if known without error. Once a relationship has been established, it can be solved (or inverted) for subsequent values of the peak count. The variance is larger than that of Calibration Regression because inverse prediction incorporates extra uncertainty associated with predicting (rather than estimating) an escapement. When the error of the predictor variable, here the escapement, must be estimated, the variance of the inverse prediction will underestimate the true uncertainty. The Inverse Prediction method is more appropriate than the calibration regression method, though it does not seem to be used in practice (Table 3).

A statistically valid approach to the analysis of peak count data is to use errors-in-variable regression, where both independent and dependent variables are measured with error (Fuller, 2006). Standard regression techniques will underestimate the slope of a line when independent variables are measured with error. Errors-in-variable regression will account for this statistical bias but will do little to help the inherent variability in the relationship between peak count and escapement abundance. No peak count method is therefore recommended.

Redd Counts

In theory, Redd Count methods can provide unbiased estimates of escapement. In practice, however, most Redd Count estimates are biased, largely due to the failure of one or more assumptions.

Peak Redd Count methods provide only an index of escapement (Table 3) and not an "absolute measure of the spawning population" (Dauble and Watson, 1997). Dauble and Watson (1990) compared 24 years of Chinook salmon dam counts on the Columbia River (corrected for sport and commercial harvest) with peak redd counts and found that the average adult-to-redd ratio was 16:1, which ranged from 5:1 to 39:1. Dauble and Watson (1997) continued the comparison seven years later and found that while the correlations between redd counts and escapement were good (i.e., $r = 0.70$), the "wide range of fish-to-redd ratios" prevents the Peak Redd Count from being a precise indicator of escapement. Consequently, Peak Redd Count methods, like the Peak Escapement Count, should not be used to monitor salmon escapement.

The Redd Census method is the best available method of interpreting redd counts. The method, however, is generally limited to streams where escapement is low enough to ensure that redds do not overlap and can be individually identified. Even then the method is subject to strict assumptions about the proportion of true redds built per female, the number of redds per female, and the male-to-female ratio. Of the redd count methods, it is the most accurate and precise, but should be applied with careful consideration regarding the assumptions and the need for auxiliary information (Table 3).

The Strip Transect method (Swan, 1989) can be a legitimate method for estimating the total number of true redds, but should also be applied with caution (Table 3). Strip transects are used to survey sample the redds in a stream. Underwater surveys can be used to ensure that redds are not overlooked and provide an opportunity to check the proportion of true redds. In some cases, flagging redds can be used to help avoid double counts. Sampling units other than strip transects can also be applied to survey the stream bottom, using classical finite sampling techniques (Cochran, 1977). The Strip Transect estimator, because of survey sampling error, generally has a larger variance than the Redd Census estimator.

The Welsh (1983) method was intended to alleviate difficulties in enumeration caused by redd superimposition by using redd area rather than redd count. The total stream bottom covered in redds is estimated, and that area converted to number of spawning females. To make the conversion, an independent estimate of redd area per female must be available. Because the extent of superimposition and the ratio of redd counts to redd area are usually unknown, the Welsh (1983) method can provide only an index of spawner abundance. The Welsh method should not be used to estimate salmon escapement.

The Redd Area method (Gallagher and Gallagher, 2005) is yet another approach to surveying salmon redds. The area of each redd or patch of redds is estimated, and a proportion of female spawners is assigned to each based on the area. For example, Gallagher and Gallagher (2005) assumed that redds less than 2 m^2 represent one-fourth of a female, 2.1 – 5 m^2 represent one-half of a female, and ≥5.1 m^2 represent one female spawner effort for coho salmon. On the other hand, Briggs (1953) estimated the average redd area of coho to be about 0.56 m^2. According to Gallagher and Gallagher (2005), a female coho would have to build four redds this size to be counted as a single female. There is evidence that female coho build up to four redds, but four is at the extreme high end of the range. If the average coho builds only three redds of average size, then the female-area relationship described by Gallagher and Gallagher (2005) underestimates the true number of females. The Redd Area method should not be used unless the redd area per female spawner is empirically measured and verified with each application (Table 3). The variance of the Redd Area method will be a function of survey error in estimating redd area and the area/female ratio. Conversion to total escapement would also require an independent estimate of the sex ratio.

CONCLUSION

There are numerous variations within the six categories of escapement estimators. Below we summarize the recommended methods based on statistical accuracy, precision, and ease of achieving assumptions.

Recommended Escapement Estimation Methods

Passage counts are the most accurate and precise methods of estimating salmon escapement, as they are capable of providing complete censuses of migrating salmon populations (Table 4). They are most accurate when enumerating fish 24 hours per day every day of the run, but can still provide an unbiased estimate of escapement based on probabilistic sampling of the run. Inter-dam enumeration can estimate escapement on a large-scale (i.e., watershed) level. Weirs are best used in small tributaries where the risk of weir failure due to washout or debris load is small. Sonar techniques are more resistant to flooding than weirs, but should only be used when species identification is accurate through size distribution or run timing. When species identification is necessary and detection distances are relatively short, the DIDSON is generally recommended over split-beam transducers because it provides higher resolution data (Maxwell and Smith, 2007). DIDSON sonars have a limited receiving range of about 15 meters at high frequencies (1.6 MHz) (Lilja et al., 2008). A high-resolution lens is capable of extending the range of high-frequency (1.2 MHz) DIDSON sonars to about 30 meters (Deborah Burwen, personal communication). Low-resolution DIDSON sonars (at 0.700 MHz) have a range of up to

80 meters, but can fail to detect fish (SoundMetricsCorp., 2009). Split-beam echosounders have ranges of more than 100 meters (Burwen and Fleischman, 1998; Xie et al., 2002). Both sonar techniques require suitable river bottom profiles and weir structures in order to ensure that all fish pass through the ensonified volume of water.

For streams where live salmon are visible to surveyors, Area-Under-the-Curve methods can provide unbiased estimates of escapement with reasonable assumptions (Table 4). The Average Spawner method provides the best estimate of fish-days along with an estimate of sampling variance. The Trapezoidal method of estimating fish-days does not account for day-to-day variance and is biased. The estimate from either method will be more precise as the number of surveys increases.

One of the best methods to estimate average stream life is to employ timer tags (Shardlow et al., 2007) because the tags directly measure time from tagging (i.e., stream entry) to death. A parametric tag life estimate generated from timer tag data will be more precise than a non-parametric Kaplan-Meier estimate, because it estimates fewer parameters. If the data do not conform to a parametric distribution, then the Kaplan-Meier estimate should be used, as it will likely be more accurate. Valid use of timer tags is predicated on a representative sample of fish throughout the escapement process. The tag-depletion method can also provide a valid estimate of stream life, but requires that salmon be surveyed every day.

In general, mark-recapture methods do not provide unbiased estimates of escapement due to difficulty in fulfilling model assumptions. The Darroch method as used by Underwood et al. (2007) may be one exception (Table 4). Underwood et al. (2007) met the assumption of a closed population by tagging and recapturing only live fish migrating through a geographically closed section of the river. The Change-In-Ratio method is another method that can provide an unbiased estimate of escapement. It has reasonable assumptions but is limited to streams with an intervention downriver of wild spawning grounds, so the ratios of wild-to-hatchery spawners above and below the intervention can be compared.

Not Recommended Escapement Estimation Methods

Peak Count methods, whether applied to live fish or to redds, do not provide estimates of fish abundance. Even when there is a unique peak, the relationship between peak count and escapement for a given year is unknown, and the regression relationship over years is often weak. Peak–escapement relationships are noisy from year to year due to differences in run durations, arrival distributions, and sampling frequency. Any escapement estimate generated by expanding a peak count using a conversion factor is likely to be so imprecise as to be uninformative.

For the most part, mark-recapture methods produce biased estimates of salmon escapement because of the difficulty in fulfilling assumptions. Closed-population methods such as the Pooled Petersen and the Schaefer methods fail because the models do not account for recruitment and loss of spawners over time. The open-population, Jolly-Seber method fails because (1) it does not allow for the estimation of new arrivals at the start and finish of the experiment, (2) it does not account for fish that both arrive and die within the same period, and (3) it assumes that all fish present during a sampling interval have the same probability of survival. Adjustments to the Cormack-Jolly-Seber model have been made to estimate the numbers of new arrivals at the start and end of a study, and for those fish that arrive and die between surveys. No adjustment can be made for bias caused by mortality probabilities dependent on arrival time. The Manly-Parr method requires no assumptions about common mortality and is therefore more robust than the Jolly-Seber method, but is unable to account for new arrivals that die before the next survey and unable to provide a variance estimate.

Theoretically, redd counts could provide unbiased estimates of escapement if visibility was good and enough ancillary information was available. The redds can be easily censused, though some redds may be missed if they are located in deep water. Unfortunately, the requisite ancillary information to convert redd counts to escapement is typically not available. Of the redds produced, an estimate of the proportion of true redds (i.e., the proportion of counted nests that have eggs) is required. Additional information to properly interpret redd counts includes redds/female and male/female sex ratios. In practice, redd counts perform poorly when compared to other total escapement estimates, likely due to the biases in the gender ratio. Gender ratios often change over the course of a run, and must be estimated throughout a season to provide an unbiased estimate. The male-female ratio is usually estimated using recovered carcasses, but the sex ratio of carcasses is typically lower than that of live fish (fewer males than females) because males are more likely to be washed downstream or sink into deep pools than females (Shardlow et al., 1986).

Attempts to enumerate carcasses are usually negatively biased because of imperfect detection and unaccountable losses. The Carcass Jolly-Seber method and the Daily Dead method may provide unbiased estimates of the total number of carcasses created, and the total escapement, but do not account for fish that are washed out of the system or removed by predators. If the number of moribund salmon washed downstream is negligible, predation rates are low, and all carcasses are accessible to surveyors, then the Carcass Jolly-Seber method and the Daily Dead method could theoretically be applicable. However, neither method has been rigorously tested. In addition, both methods estimate large numbers of parameters that can result in large variance estimates.

Considerations for Managers

No single method of estimating salmon escapement is the best method for all circumstances. An escapement estimation method that works well in one river system may work poorly in another. There are five issues managers should consider when selecting an escapement estimation method. The assumptions for any selected estimation method should be reviewed in conjunction with the logistical feasibility of implementing the method at a particular location.

Geographic Scale

The first consideration in study design is geographic scale of the estimate. For basin-wide estimates of escapement, the Inter-dam Enumeration method is the most practical. Facilities to count salmon passage over dams are already established in many places and provide large-scale estimates of salmon abundance. At finer geographic scales, other options for estimating escapement to specific rivers or tributaries exist.

River Dimensions

The depth and width of a river may prevent some methods that rely on visual counts from being effective. River depth and width may limit the probability of seeing spawners, so Area-Under-the-Curve methods may not be applicable. Constructing a temporary weir across a river may be impractical in many systems or ineffective if periods of high flow could wash the weir out. On narrow or shallow rivers, a weir may be the best way to estimate escapement, especially if multiple species migrate concurrently. On very large rivers, the only options for escapement estimation may be the Darroch method of mark-recapture or Sonar. The Darroch method can be used on any portion of the river where the migration route is closed, does not depend on water clarity, and can be used regardless of the number of species present, as long as release-recapture sample sizes are adequate for precise estimation. Sonar can be used in rivers of any size, as long as only one species migrates past at a time, or stocks can be differentiated by size using split-beam transducers, or independent species composition data are available.

River Characteristics

River discharge, flow changes, water clarity, degree of plant overgrowth, and presence of deep pools and other fish hiding places should all be taken into account when selecting an escapement estimation method. A river with high discharge may not be suitable for a weir, or for methods requiring the recovery of carcasses (i.e., AUC stream-life estimates). Large fluctuations in discharge may preclude certain equipment from being used, i.e., fish-wheels in a mark-recapture study. Rivers with clear water are ideal for Area-Under-the-Curve methods. Sonar may be the only means of detecting salmon in a low visibility, i.e., glacial, stream. However, sonar techniques can be affected by water turbulence and plant debris.

Overgrowth, deep pools, and other fish hiding places influence the probability of live and carcass detections (observer efficiency), which may also influence the selection of methods. Observer efficiency is crucial to visual count methods, particularly Area-Under-the-Curve methods. The classic AUC method requires the fish detection probability to be absolute. The daily dead estimator (Skalski et al., accepted) allows for imperfect detection probabilities but nevertheless assumes all fish have equal opportunity to be detected. However, it must be expected that the lower the observer efficiency, the lower the precision of the escapement estimates from the daily death estimator and mark-recapture techniques.

Species Characteristics

Life history and behavior of each estimated species must be taken into account. Chinook salmon have been shown to delay or reverse migration when tagged, making them poor candidates for mark-recapture studies which rely on the assumption that tagging has no effect on behavior and movement is unidirectional. Weirs used to count chum should be built high enough to prevent chum from jumping over uncounted (McNeil, 1966). Sockeye spawn in streams and lakes, so the study area must be clearly defined geographically, and method assumptions must be evaluated for both habitats. Coho tend to spawn in small streams with low gradients (Quinn, 2005), making them prime candidates for Area-Under-the-Curve methods. Pink and sockeye are the most abundant salmon in the Pacific Northwest (Quinn, 2005), and may migrate in such large numbers that sonar and human counters may not be able to distinguish individuals well enough to count them, although such occurrences are rare (Enzenhofer et al., 1998). In such cases, the Darroch method of mark-recapture may be an option.

Level of Precision

Some escapement estimation methods are more precise than others and the manner in which a study is conducted will influence the level of uncertainty in the resulting estimate. Passage Counts can provide a census with no variability under ideal circumstances, but when temporal and spatial sampling is introduced, so is uncertainty. Statistical uncertainty further increases as detection probabilities decline and when auxiliary information is needed to convert direct measurements into escapement estimates. Robson and Regier (1964) recommended that estimates should have a coefficient of variation (CV) of 50% for rough management, 25% for precise management and, at most, 10% for precise research. These limits are only suggested rules of thumb. Nevertheless, they indicate that as the use of the escapement estimates changes, so should the precision to meet management needs.

FINAL COMMENTS

A successful escapement survey is brought about through the interplay of salmon biology, hydrology, habitat considerations, logistics, and statistics in a well planned and implemented survey design. The preponderance of current escapement surveys—based on inadequate designs, unrealistic and unjustified assumptions, and without valid measures of survey uncertainties—indicate that more investigators need to adapt to the interdisciplinary demands of resource monitoring. Nowhere is this truer than in the Pacific Northwest, where salmon recovery is an important environmental and economic issue, and where adult returns are the paramount measure of that success.

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Table 1 Evaluation of fish-days and stream life estimation methods for use in the Area-under-the-Curve (AUC) method.

AUC methods	Estimator	Variance	Assumptions	Empirical Experience	Recommendation
Fish-days					
Ames					
Trapezoidal	Fair	Good	Reasonable	Can be accurate	Good alternative
Parametric	Unknown	Good	Unreasonable	Less accurate than trapezoidal	Do not use
Average spawner	Good	Good	Reasonable	Not widely used	Best choice
Stream Life					
Constant	Poor	N/A	Unreasonable	Inapplicable	Do not use
Time-to-tag recovery	Poor	Good	Unreasonable	Robust	Do not use
Peak-to-peak	Poor	None	Unreasonable	Inapplicable	Do not use
Median-to-median	Poor	None	Unreasonable	Inapplicable	Do not use
Expected-to-expected	Fair	Good	Conflictual	Inapplicable	Do not use
Inverted	Fair	Good	Conflictual	Inapplicable	Do not use
Tag-depletion	Fair	Good	Reasonable	Fair	Good alternative
Redd residence	Poor	None	Unreasonable	Inapplicable	Do not use
Cormack	Fair	Good	Conflictual	Not much testing	Do not use
Live nonparametric	Fair	Good	Reasonable	Not much testing	Good alternative
Live and dead nonparametric	Good	Good	Reasonable	Not much testing	Good alternative
Live parametric	Fair	Good	Reasonable	Not much testing	Good alternative
Live and dead parametric	Good	Good	Reasonable	Not much testing	Good alternative
Timer tags, nonparametric	Good	Good	Reasonable	Not much testing	Best choice
Timer tags, parametric	Good	Good	Reasonable	Not much testing	Best choice

Table 2 Evaluation of carcass count, mark-recapture, and passage count methods for estimating salmon escapement.

Methods	Estimator	Variance	Assumptions	Empirical	Recommendation
Carcass count					
Simple carcass count	Fair	Zero	Unreasonable	Negatively biased, index only	Do not use
Carcass Petersen	Fair	Good	Unreasonable	Positively biased	Do not use
Carcass Schaeffer	Fair	Good	Unreasonable	Positively biased	Do not use
Jolly-Seber	Poor	Fair	Unreasonable	Not much tested	Cautionary
Manly-Parr	Poor	Poor	Reasonable	Not much tested	Do not use
Daily Dead	Good	Fair	Unreasonable	Not much tested	Cautionary
Mark-Recapture					
Pooled Petersen	Fair	Good	Unreasonable	Biased or robust	Cautionary
Schaeffer	Fair	None	Unreasonable	Unnecessary	Do not use
Darroch	Fair	Good	Reasonable	Requires closed migration route	Best choice
Jolly-Seber	Poor	Good	Unreasonable	Imprecise	Do not use
Schwarz & Arnason	Good	Good	Unreasonable	Not much tested	Do not use
Manly-Parr	Poor	None	Reasonable	Not much tested	Do not use
Robust Design	Good	Good	Unreasonable	Not much tested	Do not use
Change in ratio	Good	Good	Reasonable	Requires intervention and partial removal	Best choice
Passage count					
Inter-dam enumeration	Good	Good	Reasonable	Requires dams	Best choice
Weir counts	Good	N/A	Reasonable	Can get washed out	Best choice
Sonar counts	Good	N/A	Reasonable	For single species only	Best choice

Table 3 Evaluation of peak count and redd count methods for estimating salmon escapement.

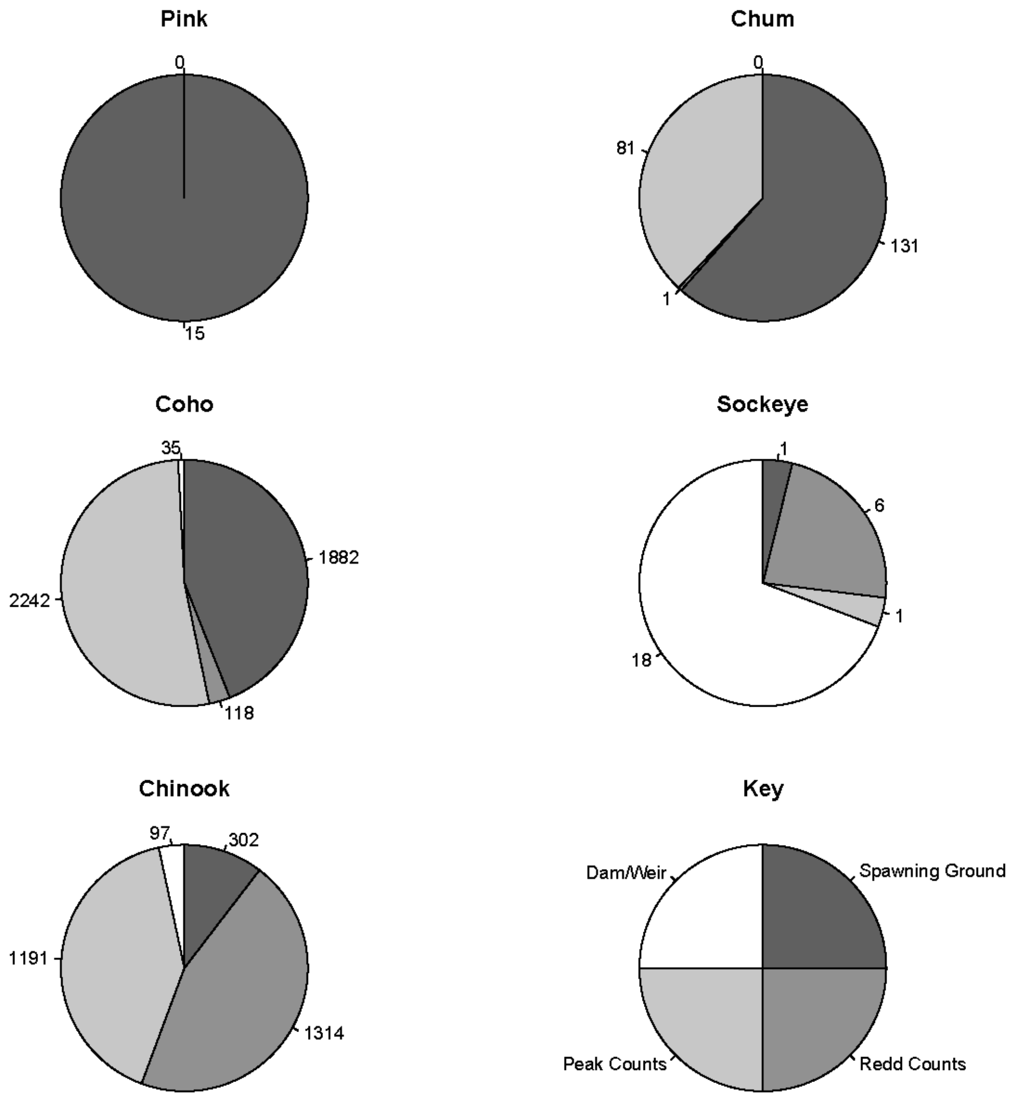
Methods	Estimator	Variance	Assumptions	Empirical	Recommendation
Peak count					
Raw count, live only	Poor	Poor	Unreasonable	Index only	Do not use
Raw count, live and dead	Poor	Poor	Unreasonable	Index only	Do not use
Raw count, live and cum. dead	Fair	Fair	Unreasonable	Index only	Do not use
Relative peak	Poor	None	Unreasonable	Index only	Do not use
Fish/mile	Poor	Poor	Unreasonable	Index only	Do not use
Means of ratios	Poor	Poor	Unreasonable	Not much testing	Do not use
Ratios of means	Fair	Poor	Unreasonable	Imprecise, data-hungry	Cautionary
Calibration regression	Good	Good	Unreasonable	Imprecise, data-hungry	Do not use
Inverse prediction	Good	Good	Reasonable	Imprecise, data-hungry, not much testing	Cautionary
Redd count					
Peak redd	Poor	None	Unreasonable	Index only	Do not use
Redd census	Fair	Good	Reasonable	Accuracy questionable	Cautionary
Welsh	Fair	Good	Conflictual	Not much testing	Do not use
Strip transect	Fair	Good	Reasonable	Not much testing	Cautionary
Redd area	Unknown	Poor	Unknown	Imprecise	Do not use

Table 4 Summary of recommended ("Good Alternative" or "Best Choice") methods of estimating salmon escapement. All recommended estimators are rater either "Fair or "Good," have variance estimators that are either "Good" or "N/A" (as in census) and have "Reasonable" assumptions. AUC = area under the curve.

Type	Name	Special implementation requirements
AUC: Fish-days	Trapezoidal	High observer efficiency
	Average spawner	High observer efficiency
AUC: Stream life	Tag-depletion	High observer efficiency
	Live nonparametric	≥10 recaptures
	Live and dead nonparametric	≥10 recaptures, access to carcasses
	Live parametric	≥10 recaptures
	Live and dead parametric	≥10 recaptures, access to carcasses
	Timer tags, nonparametric	Rivers or tributaries with access to carcasses
	Timer tags, parametric	Rivers or tributaries with access to carcasses
Mark-recapture:	Darroch	Closed migration route, ≥10 recaptures per stratum
	Change in ratio	Rivers with hatcheries that mark smolts prior to release
Passage	Inter-dam enumeration	Basin-wide estimate where dams are present
	Weir counts	Tributaries with low washout risk
	Sonar counts	Single species

LIST OF FIGURES

Figure 1 Results of www.streamnet.org search for Washington,, Oregon, Idaho, California, and Alaska salmon (*Oncorhynchus* spp.) escapement estimation efforts for 1997–2007. “Spawning ground” includes mark-recapture, area-under-the-curve, or carcass count methods. The numbers adjacent to each wedge indicate the number of records using the escapement estimation method.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Chum
0
81
131
1
Coho
35
1882
2242
118
Sockeye
1
6
1
18
Chinook
97
302
1191
1314
Key
Dam/Weir
Spawning Ground
Peak Counts
Redd Counts