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[Article]

A Likelihood Framework for Joint Estimation of Salmon Abundance and Migratory Timing Using Telemetric Mark–Recapture

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Abstract.—Many fisheries for Pacific salmon *Oncorhynchus* spp. are actively managed to meet escapement goal objectives. In fisheries where the demand for surplus production is high, an extensive assessment program is needed to achieve the opposing objectives of allowing adequate escapement and fully exploiting the available surplus. Knowledge of abundance is a critical element of such assessment programs. Abundance estimation using mark–recapture experiments in combination with telemetry has become common in recent years, particularly within Alaskan river systems. Fish are typically captured and marked in the lower river while migrating in aggregations of individuals from multiple populations. Recapture data are obtained using telemetry receivers that are co-located with abundance assessment projects near spawning areas, which provide large sample sizes and information on population-specific mark rates. When recapture data are obtained from multiple populations, unequal mark rates may reflect a violation of the assumption of homogeneous capture probabilities. A common analytical strategy is to test the hypothesis that mark rates are homogeneous and combine all recapture data if the test is not significant. However, mark rates are often low, and a test of homogeneity may lack sufficient power to detect meaningful differences among populations. In addition, differences among mark rates may provide information that could be exploited during parameter estimation. We present a temporally stratified mark–recapture model that permits capture probabilities and migratory timing through the capture area to vary among strata. Abundance information obtained from a subset of populations after the populations have segregated for spawning is jointly modeled with telemetry distribution data by use of a likelihood function. Maximization of the likelihood produces estimates of the abundance and timing of individual populations migrating through the capture area, thus yielding substantially more information than the total abundance estimate provided by the conventional approach. The utility of the model is illustrated with data for coho salmon *O. kisutch* from the Kasilof River in south-central Alaska.

Management of fisheries for Pacific salmon *Oncorhynchus* spp. has largely evolved from a strategy of maintaining constant effort to one of maintaining constant escapement (i.e., the number of individuals that are not harvested and that potentially reproduce; e.g., Eggers 1993). An escapement goal is usually derived from historical observations of escapements and subsequent production to either sustain annual yield at a socially acceptable level or maximize average yield (Clark et al. 2006; Shelton and Sinclair 2008). Management to achieve escapement goals is complicated by several aspects of salmon life history and harvest systems. Salmon are usually harvested from spawning migrations comprising a mixture of individuals from multiple populations, and the abundance of contributing populations can vary widely, which may lead to differential exploitation rates. Spawning migrations occur over several weeks or months, so at any one time only a proportion of the population is available for harvest and the proportion yet to come is unknown. Interannual variation in productivity, abundance, mixture composition, and migratory timing can be high (e.g., Dorner et al. 2008; Cowen et al. 2009; Doctor et al. 2010). The resulting management scenario is complex, temporally dynamic, and difficult to predict, and component fisheries may differ in their expectations of management. Salmon are highly prized, and the market for harvest product often exceeds the available surplus. Moreover, market conditions often dictate that harvests be taken early while product quality is high. In some fisheries, particularly within large river systems, this can greatly impact management outcomes as managers must make harvest

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decisions several weeks before the consequences to escapements can be observed.

In fisheries that are actively managed and where the demand for surplus production is high, a comprehensive assessment program is needed to achieve the opposing objectives of allowing adequate escapement and fully exploiting the available surplus production (e.g., Cadrin and Pastoors 2008; Price et al. 2008). Knowledge of abundance is a critical element of such assessment programs. Abundance may be (1) predicted by preseason forecasts, which can be particularly important early in the season, (2) indexed using catch per unit effort (CPUE), or (3) estimated using methods such as hydroacoustics or mark–recapture (Eggers et al. 1995; Link and Peterman 1998; Underwood et al. 2007). Mark–recapture experiments have become increasingly common in recent years, particularly within some of Alaska's larger river systems and sockeye salmon *O. nerka* lake systems (Pahlke and Bernard 1996; Cappiello and Bromaghin 1997; Cleary and Hamazaki 2007; Spencer et al. 2007; Stuby 2007; Underwood et al. 2007; Conitz and Zhang 2009).

The initial capture and marking of salmon usually occur in the downriver portion of a study area as fish are migrating in aggregations of individuals from multiple populations. Recapture sampling can assume a diversity of forms. In large river systems, recapture sampling may occur in the main stem, with the marking and recapture locations being separated by a distance deemed sufficient for marked and unmarked fish to remix. As all successful migrants must pass both locations, the migration is treated as a closed population (geographic closure), and either the Chapman abundance estimator (Seber 1982) or a temporally stratified Darroch estimator (Darroch 1961; Plante et al. 1998) is used (e.g., Cappiello and Bromaghin 1997; Underwood et al. 2007). This approach has the advantage of being capable of producing abundance estimates in near real time to be used for fishery management, but it can be expensive to implement.

If recapture sampling does not occur in the main stem, effort usually is focused in or near spawning areas. In smaller systems, such as sockeye salmon lakes that may not contain distinct spawning populations, abundance is estimated using a variety of methods depending on experimental conditions, including the temporally stratified Darroch closed-population model (Darroch 1961; Plante et al. 1998) or open-population models, such as POPAN (Schwarz et al. 1993; Arnason and Schwarz 1995) and Pollock's (1982) robust model (e.g., Conitz and Zhang 2009). Within large river systems, spawning areas may be numerous and widely dispersed in remote locations. Sampling all spawning populations is seldom feasible, and sampling efforts are often focused in locations where escapements are monitored. Telemetry is increasingly being used to take advantage of the infrastructure provided by existing networks of escapement monitoring projects, which produce counts or very precise estimates of abundance (e.g., Spencer et al. 2007). Using a primary mark that can be remotely detected with a probability approaching unity allows one to treat the entire escapement as having been examined for marks, thus maximizing recapture sample sizes and estimation precision.

When multiple populations are sampled during recapture activities, mark rates (the proportion of a population that has been marked) may vary among populations (Pahlke and Bernard 1996; Spencer et al. 2007). Unequal mark rates could be caused by a number of factors, including a lack of complete mixing at the marking site, differential migratory timing in combination with temporally variable capture probabilities, gear selectivity for features such as size or development of secondary sex characteristics that differ among populations, or differential mortality after marking (e.g., Bromaghin et al. 2007). Unequal mark rates among populations can therefore be problematic because they may reflect violations of model assumptions. Even so, a common analytical strategy is to test the hypothesis that mark rates are homogeneous, pool all recapture data if the test is not significant, and use a Chapman estimator (Seber 1982) of abundance (e.g., Pahlke and Bernard 1996; Cappiello and Bromaghin 1997; Spencer et al. 2007). This can be an effective strategy if mark rates are not too dissimilar, resulting in robust estimates of total abundance (all populations combined). However, mark rates are often low, especially when telemetry tags are used as the primary mark, and a test of homogeneity may lack sufficient power to detect meaningful differences among populations. The nonsignificance of a test with low power does not constitute strong evidence of equality, and the pooling of recapture data discards information that might otherwise be used to enhance parameter estimation.

We present a stratified mark–recapture model that permits capture probabilities and migratory timing to vary among temporal strata defined at the capture location. Mark rates are therefore allowed to vary among contributing populations as a function of migratory timing and capture probabilities, eliminating the incentive to test the homogeneity of mark rates and to pool recapture data. Abundance information from a subset of population escapements is jointly modeled with telemetry distribution data to obtain maximum likelihood estimates of abundance and migratory timing for all individual populations present in the capture area. An estimate of the total abundance of all

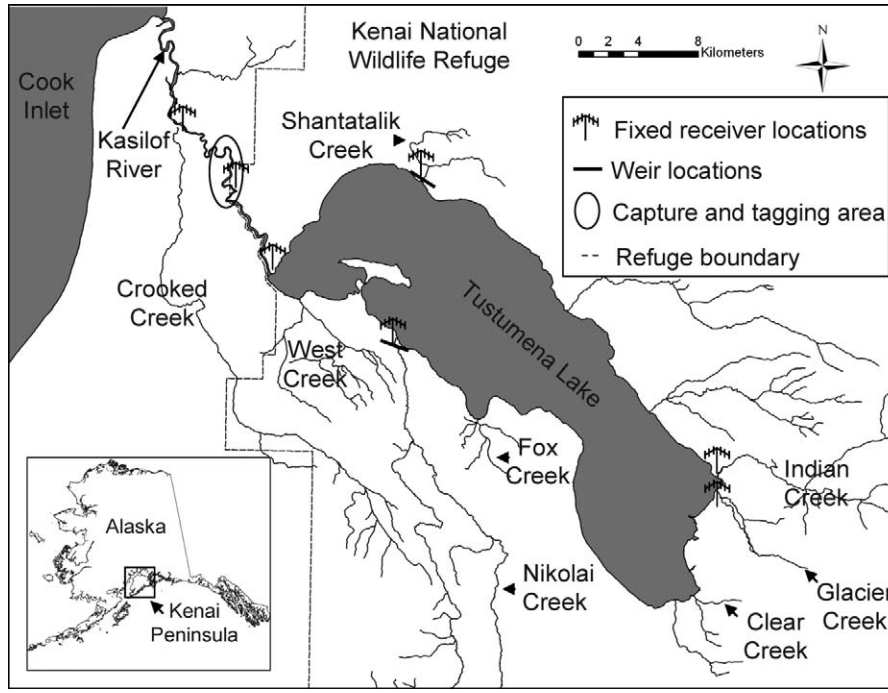

FIGURE 1.—Map of the Kasilof River watershed on the Kenai Peninsula, south-central Alaska. The study area consisted of the region upriver of the Kenai National Wildlife Refuge boundary.

contributing populations—comparable to a Chapman estimate (Seber 1982)—can be obtained by summing estimates for individual populations. The utility of the model is illustrated using data from coho salmon *O. kisutch* spawning within the Kasilof River (Figure 1), which supports popular sport and personal use fisheries in south-central Alaska (Gates et al. 2009).

Methods

The model.—Consider a riverine study area through which adult salmon from P populations are concurrently migrating upriver to their respective spawning areas. The entire migratory period is divided into S temporal strata. Fish are captured from the aggregation of multiple populations near the downriver boundary of the study area, and n_j fish are released with telemetry tags during the jth stratum. Tagged fish are monitored as they segregate into P distinct spawning populations, and n_{ij} of the n_j fish tagged during stratum j are found to be members of population i. Population membership is hereafter referred to as an individual's identity. For the ith population, the proportion that is present and available for capture in the jth stratum is denoted π_{ij}; $\Sigma_j \pi_{ij}$ equals 1.0, assuming that the entire migratory period is sampled. The total abundance of the ith population at the capture location is denoted N_i, and the abundance of F of the P populations is known from escapement monitoring at F upriver locations. The parameters of interest are the migratory timing parameters π_{ij} and the abundance of the $(P - F)$ populations that are not monitored.

For the simplistic case in which all captured fish are released with tags, the identity of every tagged fish is determined, and capture probabilities are homogeneous within each stratum, populations are tagged in proportion to their abundance during the jth stratum $(N_i \pi_{ij})$. Therefore, conditioning on the number of tags released in each stratum n_j leads to a likelihood function that is the product of a multinomial distribution for each of S strata:

$$L_{\text{naïve}} = \prod_{j=1}^{S} \left\{ n_j! \prod_{i=1}^{P} \left[\left(\frac{1}{n_{ij}!} \right) \left(\frac{N_i \pi_{ij}}{\sum_{k=1}^{P} N_k \pi_{kj}} \right)^{n_{ij}} \right] \right\} ? .$$

Unfortunately, not only is this model overparameterized if S is greater than F, with $(SP - F)$ parameters and only $(SP - S)$ degrees of freedom (assuming that all $n_{ij} > 0$), but the parameters are also not separable and only the relative magnitudes of the products $N_i \pi_{ij}$ can be estimated. We constrain this model by assuming that

CPUE is proportional to abundance, and we generalize it by relaxing the assumptions that all captured fish are tagged and that the identity of each tagged fish is determined.

Expanding the notation introduced earlier, let C_j be the number of fish captured in stratum j and let E_j be a measure of the effort required to catch them. Assuming that the CPUE is proportional to the total abundance of fish present, capture probabilities are proportional to the product of effort and abundance. Conditioning on the total number of fish captured during the experiment ($C = \Sigma_j C_j$), the likelihood function for the distribution of catches among strata is given by the multinomial distribution:

$$L_1 = C! \prod_{j=1}^{S} \left\{ \left[\frac{1}{C_j!}\right] \left[\frac{E_j \sum_{i=1}^{P} N_i \pi_{ij}}{\sum_{k=1}^{S} \left(E_k \sum_{i=1}^{P} N_i \pi_{ik} \right)} \right]^{C_j} \right\}.$$

Of the C_j fish captured during stratum j, n_j fish are tagged and released. Each tagged fish is either (1) successfully tracked and its identity is determined or (2) not successfully tracked and its identity is not determined (due to tag failure, tag loss, mortality, etc.). Let t_j be the number of the n_j fish that are successfully tracked to one of the P spawning populations (i.e., the identity of $[n_j - t_j]$ fish released in the jth stratum cannot be determined). Conditioning on the n_j, the likelihood function corresponding to the number of fish whose identity is determined is the product of S binomial distributions:

$$L_2 = \prod_{j=1}^{S} \left[\binom{n_j}{t_j} \theta_j^{t_j} (1 - \theta_j)^{n_j - t_j} \right],$$

where θ_j is the probability that the identity of a fish tagged in stratum j can be determined.

Finally, conditioning on the t_j fish in stratum j whose identity is determined, the likelihood function for the distribution of these fish among the P populations is the product of S multinomial distributions:

$$L_3 = \prod_{j=1}^{S} \left\{ t_j! \prod_{i=1}^{P} \left[\frac{1}{t_{ij}!} \left(\frac{N_i \pi_{ij}}{\sum_{k=1}^{P} N_k \pi_{kj}} \right)^{t_{ij}} \right] \right\},$$

where t_{ij} is the number of t_j fish that are found to belong to population i. The likelihood function for the entire experiment is then given by

$$L = L_1 L_2 L_3.$$

This likelihood is not overparameterized. There are $(P - F)$ abundance parameters, S probabilities of successfully determining fish identity, and $P(S - 1)$ migratory timing parameters due to the constraint that $\Sigma_j \pi_{ij}$ must be equal to 1.0; this results in a total of $[S(P + 1) - F]$ parameters. There are $(S - 1)$ degrees of freedom in L_1, S degrees of freedom in L_2, and $S(P - 1)$ degrees of freedom in L_3, totaling $[S(P + 1) - 1]$ degrees of freedom, which exceeds the number of parameters by $(F - 1)$.

In most cases, the parameters of interest will be the N_i and π_{ij}, with the θ_j being nuisance parameters. Maximum likelihood estimates of the N_i and π_{ij} parameters must be obtained by numerically maximizing the likelihood function while constraining the abundance of the F populations whose abundance is known (see below). Closed-form maximum likelihood estimators of the parameters θ_j are the binomial probability estimators t_j/n_j. However, these parameters could also be modeled as functions of covariates, perhaps using link functions that bound the probabilities between 0 and 1 (White and Burnham 1999), in which case the estimates of these parameters would also have to be obtained numerically. Variance estimates can be obtained by bootstrap techniques (Chernick 1999) or via the Rao–Cramér information limit (Rao 1973).

Although the abundance of F populations is assumed known after the populations have segregated, some number of the $(n_j - t_j)$ fish whose identities are not determined may have been members of those populations. The first component of the likelihood function, L_1, involves abundance at the capture location. Abundance at the capture and spawning locations differs by the number of fish that are not successfully tracked, so some number of the unidentified fish must be added to the assessed abundance of the F populations to estimate abundance at the capture location. If $N_{i,0}$ is the assessed abundance at the spawning locations ($i = 1, 2, \ldots, F$), unidentified fish are apportioned to the abundance of the F populations at the capture site using the recursion

$$N_{i,t} = N_{i,0} + \sum_{j=1}^{S} (n_j - t_j) \frac{N_{i,t-1} \pi_{ij}}{\sum_{k=1}^{P} N_{k,t-1} \pi_{kj}},$$

for t equal to 1, 2, ..., continuing until the total abundance values $N_{i,t}$ stabilize. Note that the abundance parameters of the $(P - F)$ populations without abundance information are not changed by the iterations. Unidentified fish must be apportioned at the beginning of each step in the numerical maximization of the likelihood function. In effect, the total

abundances of the F populations are derived parameters, being determined from a combination of known constants (assessed abundance) and model parameters (apportioned untracked fish).

Kasilof River example.—Gates et al. (2009) summarized a 2008 radiotelemetry investigation of the spawning distribution of Kasilof River coho salmon within the Kenai National Wildlife Refuge (KNWR) in south-central Alaska (Figure 1). Fish were captured in drift gill nets within a 9-km reach of the main stem that included the downriver boundary of KNWR. The spawning migration was divided into four temporal strata, and effort was measured as the number of gillnet drifts required to deploy the tags allocated to each stratum.

The identities of individual fish were determined using a combination of fixed receivers and aerial and boat surveys; all portions of the drainage were surveyed (Gates et al. 2009). Identities were summarized into nine location categories within the KNWR study area (Figure 1): KNWR main stem (designated by subscript M), West Creek (W), Shantatalik Creek (S), Nikolai Creek (N), Fox Creek (F), Indian Creek (I), Glacier Creek (G), Clear Creek (C), and Lake (L). All of these categories represented spawning locations within the Kasilof River main stem or tributaries of Tustumena Lake, except the Lake category, which contained fish that entered Tustumena Lake but were not observed to select a spawning tributary. These individuals were placed in their own category because they were suspected to originate from one of the lake tributaries, and placing them in the Unknown group (i.e., with fish that were not successfully tracked) would have biased estimates of tributary abundance. The abundance of coho salmon was monitored in Shantatalik and Nikolai creeks using video-equipped weirs ($F = 2$). There was an additional spawning location downriver of the study area, termed the Outside area, for which the parameters were not of direct interest. Parameter estimates for this category were thought to be biased by a lower capture probability than other populations; these fish were placed in their own group because their locations were known and they could be excluded from the Unknown group, thereby eliminating bias and increasing estimation precision.

The likelihood function was maximized using a custom computer program written in Fortran (Metcalf et al. 2008). The probabilities of determining the identities of tagged fish (θ_j) were viewed as nuisance parameters, and maximum likelihood estimates were the observed binomial proportions t_j/n_j. Estimation of the migratory timing parameters of the likelihood function, like the movement parameters of the Darroch model (Darroch 1961; Plante et al. 1998), expends a large proportion of the available degrees of freedom. For that reason, models implementing various constraints on the migratory timing parameters π_{ij} were constructed to reduce dimensionality and increase estimation precision. Lake tributaries were ordered based on their distance from the lake outlet along the primary axis of Tustumena Lake (Figure 1). Migratory timing models for these spawning locations, termed "base" models, were constructed by constraining the parameters of adjacent populations, excluding Glacier Creek, to be equal (Table 1). A greater proportion of the flow in Glacier Creek originates from groundwater input and the creek freezes later in the year than other lake tributaries, as does the Kasilof River main stem; thus, the migratory timing in Glacier Creek and the main stem was expected to differ from that in other locations. Therefore, each of the base models (Table 1) had five variants (denoted a–e; e.g., model 14e represents base model 14 and variant e) based on treatment of Glacier Creek and the KNWR main stem: (a) no constraints (π_{Mj}, π_{Gj}); (b) migratory timing of KNWR main stem and West Creek constrained to be equal ($\pi_{Mj} = \pi_{Wj}$; π_{Gj}); (c) migratory timing of Indian and Glacier creeks constrained to be equal (π_{Mj}; $\pi_{Ij} = \pi_{Gj}$); (d) a combination of variants b and c ($\pi_{Mj} = \pi_{Wj}$; $\pi_{Ij} = \pi_{Gj}$); and (e) the migratory timing of KNWR main stem and Glacier Creek constrained to be equal ($\pi_{Mj} = \pi_{Gj}$). Fish within the Kasilof River watershed downriver of the KNWR boundary were outside of the study area and were not of direct interest, so no constraints were placed on their (nuisance) parameters. For similar reasons, no constraints were placed on the migratory timing parameters of fish that entered Tustumena Lake but were not observed to select a spawning location (i.e., Lake category). Model suitability was evaluated using Akaike's information criterion corrected for small-sample bias (AIC_c; Burnham and Anderson 2002).

Estimation precision was estimated by drawing 10,000 bootstrap samples. To construct each bootstrap sample, records were randomly selected with replacement from among the data observed within each of the four strata, including fish in the Outside and Unknown categories. Bootstrap sample sizes equaled observed sample sizes within each stratum. Total catch and effort in each stratum were held fixed at the observed levels. Maximum likelihood parameter estimates were obtained with each bootstrap data set. Efron's (1987) bias-corrected accelerated (BCa) method was used to estimate 90% confidence limits from the bootstrapped parameter estimates. Abundance estimates for individual locations were summed to estimate the abundance of fish spawning within tributaries of Tustumena Lake

TABLE 1.—Base models of the migratory timing of coho salmon in Tustumena Lake tributaries. Tributaries are listed in order of increasing distance from the outlet of Tustumena Lake (Figure 1). Each base model had five variations: (e.g., model 14e; terms are defined in Methods) (a) π_{Mj}, π_{Gj}; (b) $\pi_{Mj} = \pi_{Wj}$, π_{Gj}; (c) π_{Mj}, $\pi_{Ij} = \pi_{Gj}$; (d) $\pi_{Mj} = \pi_{Wj}$, $\pi_{Ij} = \pi_{Gj}$; and (e) $\pi_{Mj} = \pi_{Gj}$. No constraints were placed on migratory timing parameters of the outside study area or lake locations (see Methods).

Base model	Migratory timing parameters
1	π_{Wj}, π_{Sj}, π_{Nj}, π_{Fj}, π_{Ij}, π_{Cj}
2	$\pi_{Wj} = \pi_{Sj}$; π_{Nj}; π_{Fj}; π_{Ij}; π_{Cj}
3	π_{Wj}; $\pi_{Sjj} = \pi_{Nj}$; π_{Fj}; π_{Ij}; π_{Cj}
4	π_{Wj}; π_{Sj}; $\pi_{Nj} = \pi_{Fj}$; π_{Ij}; π_{Cj}
5	π_{Wj}; π_{Sj}; π_{Nj}; $\pi_{Fj} = \pi_{Ij}$; π_{Cj}
6	π_{Wj}; π_{Sj}; π_{Nj}; π_{Fj}; $\pi_{Ij} = \pi_{Cj}$
7	$\pi_{Wj} = \pi_{Sj} = \pi_{Nj}$; π_{Fj}; π_{Ij}; π_{Cj}
8	$\pi_{Wj} = \pi_{Sj}$; $\pi_{Nj} = \pi_{Fj}$; π_{Ij}; π_{Cj}
9	$\pi_{Wj} = \pi_{Sj}$; π_{Nj}; $\pi_{Fj} = \pi_{Ij}$; π_{Cj}
10	$\pi_{Wj} = \pi_{Sj}$; π_{Nj}; π_{Fj}; $\pi_{Ij} = \pi_{Cj}$
11	π_{Wj}; $\pi_{Sj} = \pi_{Nj} = \pi_{Fj}$; π_{Ij}; π_{Cj}
12	π_{Wj}; $\pi_{Sj} = \pi_{Nj}$; $\pi_{Fj} = \pi_{Ij}$; π_{Cj}
13	π_{Wj}; $\pi_{Sj} = \pi_{Nj}$; π_{Fj}; $\pi_{Ij} = \pi_{Cj}$
14	π_{Wj}; π_{Sj}; $\pi_{Nj} = \pi_{Fj} = \pi_{Ij}$; π_{Cj}
15	π_{Wj}; π_{Sj}; $\pi_{Nj} = \pi_{Fj}$; $\pi_{Ij} = \pi_{Cj}$
16	π_{Wj}; π_{Sj}; π_{Nj}; $\pi_{Fj} = \pi_{Ij} = \pi_{Cj}$
17	$\pi_{Wj} = \pi_{Sj} = \pi_{Nj} = \pi_{Fj}$; π_{Ij}; π_{Cj}
18	$\pi_{Wj} = \pi_{Sj} = \pi_{Nj}$; $\pi_{Fj} = \pi_{Ij}$; π_{Cj}
19	$\pi_{Wj} = \pi_{Sj} = \pi_{Nj}$; π_{Fj}; $\pi_{Ij} = \pi_{Cj}$
20	$\pi_{Wj} = \pi_{Sj}$; $\pi_{Nj} = \pi_{Fj} = \pi_{Ij}$; π_{Cj}
21	$\pi_{Wj} = \pi_{Sj}$; $\pi_{Nj} = \pi_{Fj}$; $\pi_{Ij} = \pi_{Cj}$
22	$\pi_{Wj} = \pi_{Sj}$; π_{Nj}; $\pi_{Fj} = \pi_{Ij} = \pi_{Cj}$
23	π_{Wj}; $\pi_{Sj} = \pi_{Nj} = \pi_{Fj} = \pi_{Ij}$; π_{Cj}
24	π_{Wj}; $\pi_{Sj} = \pi_{Nj} = \pi_{Fj}$; $\pi_{Ij} = \pi_{Cj}$
25	π_{Wj}; $\pi_{Sj} = \pi_{Nj}$; $\pi_{Fj} = \pi_{Ij} = \pi_{Cj}$
26	π_{Wj}; π_{Sj}; $\pi_{Nj} = \pi_{Fj} = \pi_{Ij} = \pi_{Cj}$
27	$\pi_{Wj} = \pi_{Sj} = \pi_{Nj} = \pi_{Fj} = \pi_{Ij}$; π_{Cj}
28	$\pi_{Wj} = \pi_{Sj} = \pi_{Nj} = \pi_{Fj}$; $\pi_{Ij} = \pi_{Cj}$
29	$\pi_{Wj} = \pi_{Sj} = \pi_{Nj}$; $\pi_{Fj} = \pi_{Ij} = \pi_{Cj}$
30	$\pi_{Wj} = \pi_{Sj}$; $\pi_{Nj} = \pi_{Fj} = \pi_{Ij} = \pi_{Cj}$
31	π_{Wj}; $\pi_{Sj} = \pi_{Nj} = \pi_{Fj} = \pi_{Ij} = \pi_{Cj}$
32	$\pi_{Wj} = \pi_{Sj} = \pi_{Nj} = \pi_{Fj} = \pi_{Ij} = \pi_{Cj}$

and the abundance of all fish within the KNWR study area. The acceleration constants for constructing BCa confidence limits for these summed estimates were computed as the average acceleration constant among locations contributing to the sums.

The estimate of total abundance with the study area obtained via the preferred likelihood model was contrasted with a comparable estimate obtained via the typical analytical strategy (i.e., basing abundance estimation on the Chapman estimator after pooling multiple sources of recapture data). The collection of tagged fish was limited to those fish that were tracked to a location within the study area. The "chisq.test" function of R version 2.9.2 (RDCT 2009), with 100,000 replications to estimate the *P*-value, was used to test the hypothesis that the mark rates of Shantatalik Creek and Nikolai Creek fish were equal, which would justify pooling of the two data sources. Confidence limits for the Chapman estimate were obtained using the Poisson approximation of the distribution of the number of recaptures (Seber 1982). Exact confidence limits for the expected number of recaptures (Poisson parameter) were obtained using the poisson.exact function of the R package "exactci" (RDCT 2009). These limits were used in place of the number of recaptures in the Chapman estimator to obtain confidence limits for the abundance estimate.

Results

Sixty tagged coho salmon were released in each of four temporal tagging strata. Statistics regarding the total number of fish captured, the effort (number of gill-net drifts) expended to catch fish, the number of fish successfully tracked, and the distribution of tracked fish among locations are presented in Table 2. Over the course of the entire experiment, a high proportion of tagged coho salmon (204 of 240, or 85%) were successfully tracked and identified with 1 of the 10 defined locations. The observed abundances of coho salmon were 596 in Shantatalik Creek and 721 in Nikolai Creek.

Among the candidate models considered, models 23e and 31e (Table 1) were strongly preferred, each accounting for 26% of the standardized Akaike weight, whereas the third-ranked model had a weight of only 5% (Table 3), translating to an evidence ratio of 5.2. The only difference between the two preferred models involved the migratory timing of Clear Creek (Table 1). Because these models were essentially tied and only one tagged fish returned to Clear Creek, we selected the more parsimonious model, 31e, as the preferred

TABLE 2.—Number of coho salmon tracked to specific locations by stratum (t_{ij}), with catch and effort summary statistics on which the likelihood function is conditioned. Locations are listed in order of increasing distance from the outlet of Tustumena Lake (see Figure 1).

	Stratum				
Location or statistic	1	2	3	4	Total
Outside study area	9	7	18	22	56
Refuge main stem	5	31	30	28	94
West Creek	8	0	0	1	9
Shantatalik Creek	5	1	0	0	6
Nikolai Creek	3	1	0	0	4
Fox Creek	1	0	0	0	1
Indian Creek	13	7	0	0	20
Glacier Creek	2	3	2	2	9
Clear Creek	0	1	0	0	1
Lake	3	1	0	0	4
Unknown	11	8	10	7	36
Effort (*E*)	246	348	340	347	1,281
Catch (*C*)	112	147	104	101	464
Number tagged (*n*)	60	60	60	60	240
Number tracked (*t*)	49	52	50	53	204

TABLE 3.—Statistics summarizing the relative suitability of abundance and migratory timing models (Table 1) for Kasilof River coho salmon in 2008 (AIC_c = Akaike's information criterion corrected for small-sample bias; ΔAIC_c = difference in AIC_c between the best-performing model and the given model). Models with a standardized Akaike weight of less than 0.01 are excluded.

Model	Number of parameters	Log likelihood	AIC_c	ΔAIC_c	Akaike weight
23e	17	−48.55	134.35	0.00	0.26
31e	16	−49.75	134.37	0.02	0.26
24e	18	−49.04	137.74	3.39	0.05
11e	19	−48.04	138.16	3.81	0.04
25e	18	−49.30	138.25	3.90	0.04
26e	18	−49.38	138.42	4.07	0.03
12e	19	−48.24	138.57	4.22	0.03
14e	19	−48.28	138.64	4.29	0.03
30e	17	−50.79	138.84	4.49	0.03
20e	18	−49.69	139.03	4.68	0.03
28e	17	−51.05	139.36	5.01	0.02
13e	19	−48.83	139.75	5.40	0.02
17e	18	−50.04	139.75	5.40	0.02
27e	16	−52.48	139.83	5.48	0.02
29e	17	−51.35	139.95	5.60	0.02
3e	20	−47.82	140.19	5.84	0.01
32e	15	−53.93	140.38	6.03	0.01
31a	20	−48.38	141.29	6.94	0.01
23a	21	−47.18	141.38	7.03	0.01
19e	18	−50.88	141.42	7.07	0.01
7e	19	−49.88	141.84	7.49	0.01
18e	19	−49.88	141.84	7.49	0.01

model. This model has distinct migratory timing parameters for four groups of populations within the study area: (1) West Creek, (2) the Lake category, (3) all lake tributaries except Glacier Creek, and (4) Glacier Creek and the KNWR main stem. The ratio of degrees of freedom (27) to parameters (16) for model 31e is approximately 1.7. Since AIC_c provides only a relative assessment of model fit among candidate models, an absolute assessment of model fit was obtained by plotting the observed counts t_{ij} against the counts expected under model 31e (Figure 2). The model approximates the observed data well, and no systematic patterns are apparent.

Parameter estimation failed with 166 of the 10,000 bootstrap samples, so precision was estimated using 9,834 bootstrap estimates. We did not explore the reason for this small number of failures, but we suspect that they were instances in which no fish from Shantatalik or Nikolai Creek were included in the bootstrap sample. Maximum likelihood point estimates and 90% bootstrap confidence limits for the N_i and π_{ij} parameters are presented in Table 4. The corresponding abundance estimate for all coho salmon within Tustumena Lake and its tributaries is 6,839 (BCa confidence interval = 5,297–10,417), and the abundance estimate for all fish in the Kasilof River drainage upriver of the KNWR boundary is 16,302 (BCa confidence interval = 12,395–25,036).

We contrast these results with those obtained using the Chapman estimator (Seber 1982). For the Shantatalik Creek escapement, 6 of 596 fish were marked (mark rate = 1.01%); in Nikolai Creek, 4 of 721 fish were marked (mark rate = 0.55%). An exact chi-square test of independence was not significant ($P = 0.5272$). Using only the information for fish that were tracked to one of the nine locations within the KNWR, the total number of fish tagged n_1 was equal to 148 (Table 2). Assuming that the nonsignificant test indicates that capture probabilities were homogeneous among all populations, the recapture data from the two escapement monitoring projects were pooled into a single sample consisting of 1,317 fish (n_2), of which 10 fish were marked (m_2). The resulting Chapman estimate (Seber 1982) of the abundance of all coho salmon upriver of the KNWR boundary is 17,852, with a 90% Poisson approximation confidence interval of 10,932–30,562. The Chapman abundance estimate is 10% greater and its estimated confidence interval is 55% wider than the estimates obtained with the new model. Note that this analytical approach does not provide information about the abundance or migratory timing of the individual component populations.

Discussion

We present a modeling approach and analytical framework that are applicable to riverine mark–

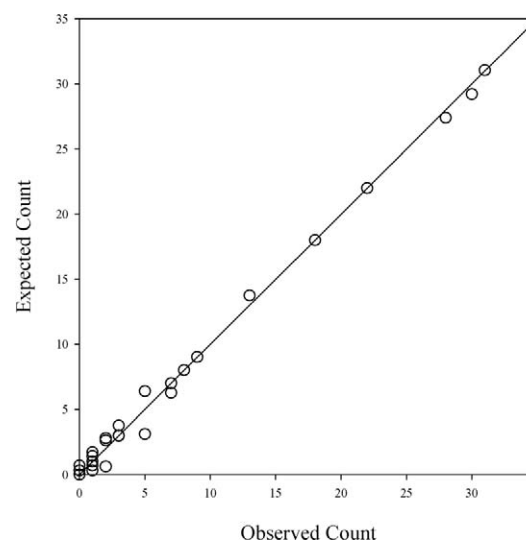

FIGURE 2.—Comparison of observed counts of Kasilof River coho salmon by population and stratum with expected counts computed using parameter estimates obtained from the preferred model 31e (defined in Table 1).

TABLE 4.—Maximum likelihood point estimates and bias-corrected accelerated (BCa) bootstrap 90% confidence limits for the abundance and migratory timing parameters (expressed as percentages) of Kasilof River coho salmon in 2008. Location groups are listed in order of their relative abundance in stratum 1. Estimates for the outside location are thought to be biased.

		Migratory timing by stratum			
Location	Abundance	1	2	3	4
West Creek	1,180 (674–2,096)	93 (78–100)	0 (0–0)	0 (0–0)	7 (0–22)
Lake	532 (238–1,030)	77 (34–100)	23 (0–66)	0 (0–0)	0 (0–0)
Shantatalik Creek	597 (596–597)	72 (60–82)	28 (18–40)	0 (0–0)	0 (0–0)
Nikolai Creek	722 (722–723)	72 (60–82)	28 (18–40)	0 (0–0)	0 (0–0)
Fox Creek	132 (0–429)	72 (60–82)	28 (18–40)	0 (0–0)	0 (0–0)
Indian Creek	2,638 (1,725–4,333)	72 (60–82)	28 (18–40)	0 (0–0)	0 (0–0)
Clear Creek	132 (0–433)	72 (60–82)	28 (18–40)	0 (0–0)	0 (0–0)
Outside study area	5,488 (3,931–8,666)	23 (13–32)	15 (7–24)	30 (22–38)	33 (24–41)
Refuge main stem	9,463 (6,976–14,622)	9 (5–14)	39 (34–45)	28 (23–32)	23 (19–28)
Glacier Creek	906 (517–1,563)				

recapture investigations of migrating salmon based on radiotelemetry. The primary advantage of the approach is that all data typically available in such investigations are incorporated into a single modeling and estimation framework. Statistical estimates of both abundance and migratory timing parameters for each population in the study area are produced concurrently—substantially more information than is obtained from the typical analytical approach. Simultaneous use of all observations should tend to increase the precision of abundance estimates, as appeared to be the case in the example. The modeling approach we present is flexible, and the likelihood function can readily be generalized to accommodate routine deviations from the experimental conditions we have considered.

The example illustrates some important considerations regarding the design of experiments employing this model. If the abundance of only one contributing population is monitored, then the number of parameters equals the number of degrees of freedom and the parameters are estimable. However, monitoring the abundance of more than one population will reduce the number of parameters to be estimated and can be expected to increase estimation robustness and precision. Experiments should be designed so that the probability of observing multiple tagged individuals in each monitored population is high; obviously, some tagged individuals must be observed among the collection of all monitored populations for the model to be viable. If only small populations can be effectively monitored, then increasing the number of populations monitored, deploying more tags, and placing reasonable constraints upon migratory timing parameters can partially compensate. In addition, it would be advantageous for at least one individual from a monitored population to be tagged in each stratum. If migratory timing differs substantially among contributing populations, the monitoring of populations with different timing can be expected to increase estimation robustness.

The version of the likelihood function we present assumes that catch rates are proportional to abundance within strata. Even though this assumption is common in fishery models, it is a strong assumption that is difficult to validate and it should not be made unless rigid sampling protocols are implemented. Even then, this assumption could be violated by factors beyond the control of researchers. We note, however, that the corresponding component of the likelihood function, L_1, could be generalized to incorporate other assumptions regarding capture probabilities. For example, capture probabilities could be modeled as a function of water velocity, water clarity, or other covariates that might reasonably be expected to influence capture probabilities in a particular experiment. Gear saturation might require nonlinear models of capture probabilities (e.g., White and Burnham 1999) in some situations. We encourage investigators to evaluate the biological and physical characteristics of their experimental conditions and to construct and compare models that are both meaningful and plausible in individual circumstances.

This modeling approach could be extended or generalized in a number of other ways. The nonparametric migratory timing parameters π_{ij} could be replaced with a parametric timing model (e.g., Schnute and Sibert 1983), which could reduce the number of parameters and might permit relaxation of the assumption that tagging occurs throughout the migratory period. The likelihood function incorporates an assumption that each fish in the escapements of monitored populations is effectively examined for a tag, which is a reasonable assumption if radio tags or other remotely detectable tags are used as the primary mark. We suspect that this assumption could be relaxed by generalizing the second and third components of the

likelihood function (i.e., L_2 and L_3) to incorporate sampling at escapement monitoring projects. The model could also be modified to exploit information on population composition obtained from sources other than telemetry, such as genetic mixture analysis (e.g., Beacham et al. 2008). One characteristic of the model is that harvests of untagged fish between the capture and recapture locations are not explicitly incorporated, although tagged fish that are harvested should be treated as unidentified individuals and are thereby incorporated in estimation. Like other models, harvests that are unbiased with respect to the population identity of individuals harvested within a stratum should not introduce bias (Seber 1982). Because postharvest abundance information from tributary locations is used to scale abundance estimates, the estimates represent postharvest abundance. These and perhaps other aspects of the model warrant exploration in future work.

The estimate of total abundance obtained with the new model was only compared with the Chapman estimate (Seber 1982); however, in some cases one might also wish to make comparisons with Darroch estimates (Darroch 1961; Plante et al. 1998). Using the Darroch model, temporally stratifying the capture effort and using spawning location to stratify the recapture effort would produce comparable estimates of population-specific abundance. However, this would require all contributing populations to be sampled, and the capture probabilities of censused populations should be constrained to unity. If capture effort and recapture effort were temporally stratified, recapture data could be pooled and stratum-specific estimates of total abundance would result. A combination of the two strategies for stratifying the recapture effort is also possible. In the Kasilof River coho salmon example, mark rate data were only obtained from two of the contributing populations, and the lack of tags released in strata 3 and 4 in the escapements to Shantatalik and Nikolai creeks (Table 2) precluded the use of a temporally stratified Darroch model.

This investigation produced the first estimate of the abundance of Kasilof River coho salmon within the KNWR. Abundance information should prove useful to fishery managers, especially if expanding fisheries lead to increased harvest levels. Substantial spawning in the main stem was expected based on telemetry conducted during 2007 (Palmer et al. 2008). Perhaps more consequential are the apparent differences in migratory timing between most populations spawning in Tustumena Lake tributaries and the Kasilof River main stem. Several of the lake tributary populations appear to be comparatively small, but they comprise the majority of the early portion of the run. These populations may therefore be susceptible to overexploitation in fisheries that target the early component of the run. However, as our results are based on observations from a single year, additional investigation is required to determine whether these patterns in relative abundance and migratory timing are typical for these populations.

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