

Differentiating mortality from delayed migration in subyearling fall Chinook salmon (*Oncorhynchus tshawytscha*)

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Abstract: A total of 1154 acoustic-tagged subyearling fall Chinook salmon (*Oncorhynchus tshawytscha*) were monitored during their movement through Lower Monumental Reservoir, Snake River, Washington, USA. A release–recapture design was developed to partition their fates into migration, delayed migration (i.e., holdover or temporary residualization), and mortality using a series of standard detection arrays augmented with individual intrareach autonomous receivers. The standard detection arrays were used in conjunction with traditional release–recapture models to estimate the joint probabilities of migrating and surviving through the reservoir. Closed population estimators were used to estimate the abundance of tagged fish still alive in the river reaches and to differentiate mortality from delayed migration. Over the course of the study from 15 August to 14 November 2007, delayed migration rates increased and mortality rates generally declined. A minimum of 10.6% of the fish were estimated to have delayed migration in the reservoir during the study period.

Résumé : Nous avons suivi un ensemble de 1 154 saumons chinook (*Oncorhynchus tshawytscha*) d'automne âgés de moins d'un an et porteurs d'une étiquette acoustique au cours de leurs déplacements à travers le réservoir Lower Monumental, sur la rivière Snake, Washington, É.-U. Nous avons mis au point un plan de libération–recapture afin de répartir leur sort en migration, migration retardée (c'est-à-dire arrêé ou résidence temporaire) et mortalité à l'aide de réseaux standards de détection avec en plus des récepteurs autonomes individuels dans les différentes sections de rivière. Les réseaux standards de détection ont été utilisés conjointement avec des modèles traditionnels de libération–recapture afin d'estimer les probabilités conjointes de migrer et de survivre à travers le réservoir. Des estimateurs de population fermée ont servi à déterminer l'abondance des poissons marqués encore vivants dans les sections de rivière et de distinguer la mortalité de la migration retardée. Au cours de l'étude, du 15 août au 14 novembre 2007, les taux de migration retardée ont augmenté et les taux de mortalité ont en général décliné. Nous estimons qu'un minimum de 10,6% des poissons ont retardé leur migration dans le réservoir durant la période d'étude.

[Traduit par la Rédaction]

Introduction

The coexistence of different life history strategies within a species or population complicates the nature of scientific inquiry and the specification of management plans to accommodate the alternative life histories. Multiple life histories also complicate analysis of release–recapture data used to estimate survival and mortality. Species with multiple life histories that are listed under the Endangered Species Act (16 USC 1531–1544) pose special challenges because managers need information on the proportion of individuals adopting the alternative life history strategies, the factors that influence the choice of strategy, and the survival rates of the alternative strategies.

An example of such a species is fall Chinook salmon (*Oncorhynchus tshawytscha*). Healy (1991) documented two juvenile life histories among fall Chinook salmon. Juveniles with the “ocean-type” life history migrate from spawning

areas to the ocean as subyearlings, spending their first winter in the ocean. Juveniles with the “stream-type” life history rear through the winter in freshwater prior to seaward migration. Connor et al. (2002, 2005) observed further flexibility in the life history of juvenile fall Chinook salmon from the Snake River basin in the Pacific Northwest of the United States, with some juveniles migrating partway to the ocean as subyearlings, spending either part or all of their first winter within the river or reservoirs along the migration route and continuing their migration seaward as yearlings the following spring. Connor et al. (2005) used the term “reservoir-type” to describe these juveniles that delayed migration in reservoirs in the Snake River basin.

The Snake River evolutionarily significant unit of fall Chinook salmon is listed as threatened under the Endangered Species Act. Thus, fishery managers need to know what fractions of the population exhibit the different life histories and how to manage the river system to maximize the

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benefit to the species. For example, managers need to know how spill operations at hydroelectric dams or changes to dam passage technology affect either the proportion or the survival of fish adopting the reservoir-type life history. Distinguishing between mortality and migratory delay is necessary to design management strategies that accommodate the reservoir-type life history. Similar questions may arise for other populations of fall Chinook salmon (e.g., in the Fraser River, Sacramento River, New Zealand rivers, and South American rivers) or for other migratory species that exhibit migratory delay (e.g., adult steelhead (*Oncorhynchus mykiss*)).

Until recently, the survival of migrating salmonids within the Snake River has been estimated primarily using detection data from passive integrated transponder (PIT) tags. PIT-tagged juvenile salmonids in the Snake and Columbia rivers are typically detected only as they pass through fish bypass systems at the hydroelectric dams. Thus, PIT tag data provide estimates of survival on the project scale (dam and reservoir combined) but not on smaller spatial scales. Furthermore, because the bypass systems at the dams are dewatered in winter, PIT tag data provide only minimal information about winter migration and survival.

The miniaturization of acoustic tags has greatly expanded the ability to investigate survival and migratory processes of fish (Clements et al. 2005). Unlike PIT tag detectors, acoustic telemetry arrays can be deployed in a myriad of configurations that are tailored to the life history of the tagged species. Depending on the deployment layout of the receivers, acoustic tags may be used to estimate survival through subreaches of a reservoir rather than only on the project level as is the case with PIT tags. Additionally, acoustic receivers may be deployed year-round, and thus, acoustic tags have the potential to provide information on winter migration and survival. The flexibility of the receiver deployment scenarios coupled with high detection probabilities enable acoustic telemetry tags to extract detailed information on migrating salmonids and especially on populations with flexible life histories such as fall Chinook salmon.

The detailed detection data provided by acoustic tags for juvenile fall Chinook salmon require more sophisticated analysis methods than those used for simpler life histories. For species that migrate fairly quickly through the river and exhibit a single juvenile life history, downstream survival from one dam to the next is usually estimated using the single release–recapture model (Skalski et al. 1998). This model, along with the traditional Cormack–Jolly–Seber (Cormack 1964; Jolly 1965; Seber 1965) model and the paired release–recapture models of Burnham et al. (1987), assumes unidirectional movement and equal detection probabilities among individuals and equates lack of movement with mortality. These models may yield biased estimates of mortality when used with the flexible life history of fall Chinook salmon, particularly later in their emigration season. Lowther and Skalski (1998) were the first to develop a release–recapture model expressly for juvenile fall Chinook salmon that separately estimated delayed migration and survival probabilities. Their model was designed for PIT tag detections at the dams and assumed that all migration, in-

cluding any delay, was completed by the end of the study, with no migration occurring during the winter when the PIT tag detectors were shut down. Thus, the Lowther–Skalski model is inappropriate either for exploring short-term (e.g., within-season) delay or for cases where tagged individuals migrate past dams in winter.

In this paper, we present a novel deployment of acoustic receiver arrays along with a statistical model that provides a robust approach to differentiating mortality and delayed migration processes among subyearling fall Chinook salmon during the latter portion of the emigration season. The receiver deployment includes both primary arrays that separate reaches within the reservoir and within-reach receivers that provide information on migratory delay. The statistical model is built on the robust design of Pollock (1982) in which secondary sampling within the primary sampling periods is used to estimate abundance of tagged individuals. Pollock's (1982) model was designed to account for unequal detection probabilities in estimating abundance and survival through time. We extend it here to distinguish between delay and mortality on a spatial scale. The approach applied here to Snake River fall Chinook salmon may be used in other well-defined riverine environments where the goal is to provide unbiased survival or mortality estimates corrected for the probability of delayed migration.

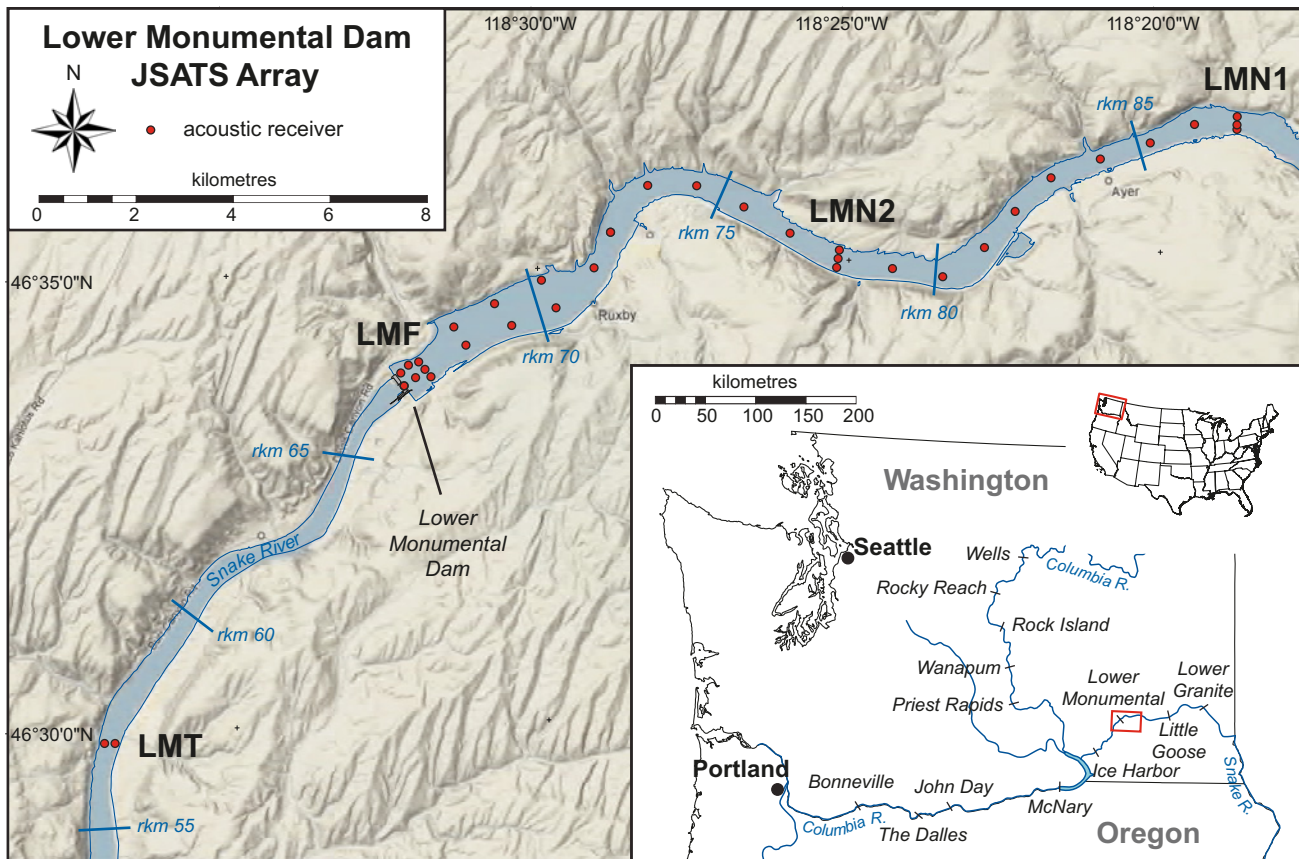
Materials and methods

Study area

Fall Chinook salmon within the Snake River basin reproduce naturally in isolated mainstem areas downstream of hydroelectric dams and in the Clearwater River and the Hells Canyon area on the Snake River upstream of Lower Granite Dam (Groves and Chandler 1999; Dauble et al. 2003). However, most juvenile fall Chinook salmon in the Snake River basin are released from hatchery facilities in the Snake and Clearwater rivers (Garcia et al. 2004). The acoustic tag telemetry study was conducted in the Snake River in Washington State (Fig. 1) downstream of Little Goose Dam (river kilometre (rkm) 113 from the mouth of the Snake River) through the tailrace of Lower Monumental Dam (rkm 57). The Lower Monumental Reservoir was subdivided into three reaches by cross-river acoustic receiver arrays at rkm 86 (labeled LMN1), rkm 78 (LMN2), and the forebay of the dam (rkm 67) at the boat restricted zone (LMF, 500 m upstream of the dam). There was also a terminal array downstream of Lower Monumental Dam at rkm 57 (LMT) (Fig. 1). These cross-river arrays, composed of two or three receivers, were used to gather detection histories to estimate the joint probabilities of subyearling fall Chinook salmon surviving and migrating through each reach.

Between the cross-river arrays, an additional 20 autonomous receivers were placed at 1 km intervals centered in the middle of the river channel. These intrareach receivers were used to periodically estimate the abundance of acoustic-tagged subyearling fall Chinook salmon still alive within the various reaches. Analyses were performed within the separate reaches, reach 1 = LMN1–LMN2, reach 2 = LMN2–LMF, and reach 3 = LMF–LMT, and collectively, LMN1–LMT, at the reservoir scale (Fig. 1).

Fig. 1. Map of the fall Chinook salmon study area in the lower 20 km of Lower Monumental Reservoir on the Snake River. River kilometres are measured from the mouth of the Snake River.



Fish tagging

Juvenile fall Chinook salmon were obtained from the juvenile fish bypass facility at Little Goose Dam on the Snake River between 30 July and 12 October 2007. Study fish were a mix of naturally produced and hatchery-reared sub-yearlings. Previously tagged fish were excluded. Natural and hatchery-origin fish were not visually distinguishable. Fish were held without food for 24–48 h prior to surgery in two 84 L tanks with freshly circulating ambient temperature river water. Fish were anesthetized in 80–100 mg·L⁻¹ tri-caine methanesulfonate (MS-222) prior to surgery for 3–4 min until equilibrium was lost (i.e., fish could no longer hold themselves upright). One PIT tag (Destron-Fearing, model TX1411ST, 12.5 mm × 2 mm) and one Juvenile Salmon Acoustic Telemetry System acoustic tag (model E101, Sonic Concepts, Inc., Bothell, Washington; 16 mm (SD = 0.2, *N* = 100), weighing 0.585 g in air) were surgically implanted into the peritoneal cavity through a 1 cm incision parallel to and 2–4 mm lateral to the ventral midline between the pectoral and pelvic girdles of the fish. Both tags were positioned parallel to the long axis of the fish. The incision was closed with two simple interrupted sutures using 5-0 Monocryl (monofilament manufactured by Ethicon). Acoustic microtransmitters were programmed to emit an individually encoded signal every 10 s, with an expected battery life of 60 days.

After surgery, tagged fish were held until the following evening in 120 L recovery buckets with flow-through river

water. Salmon were transferred from the recovery buckets to a 600 L release tank on a boat (supplied with supplemental oxygen) for release. All fish were released in the center of the Snake River 5 km downstream of Little Goose Dam (rkm 108). Before 4 October, releases occurred at 2000 Pacific Daylight Time; releases thereafter occurred at 1900 Pacific Daylight Time.

Receiver system

Autonomous acoustic receivers (model N201, Sonic Concepts) were placed at the detection arrays and intrareach positions (every 1 km). Each autonomous receiver consisted of receiver electronics and data storage on CompactFlash media, a hydrophone, battery component, acoustic beacon, buoy line, acoustic release (model 111, InterOcean Systems Inc., San Diego, California), anchor line, and anchor. The beacons emitted a signal every 15 s, which was used as confirmation that receivers were working properly. Each acoustic receiver was attached to an acoustic release by a 0.9 m bridle made of 12.7 mm braided nylon rope. Three yellow buoys (Baolong BL-6, 16.5 × 12.4 cm, 1.45 kg buoyancy each) were threaded on the bridle. Depending on water depth, each acoustic receiver was shackled to a 35 kg anchor with either a 1.5 or a 3.6 m long shock-corded mooring made from 12.7 mm braided nylon rope. Receivers were monitored from 26 July to 12 December 2007. The receivers were recovered, serviced, and redeployed every 2 weeks throughout the study period to download detection information.

Table 1. Release groups of acoustic-tagged subyearling fall Chinook salmon and detection periods used in the Lower Monumental Reservoir study.

Release group	LMN1 arrival: start date (2007)	LMN1 arrival: end date (2007)	Duration of release period (weeks)	Number of fish
1	1 August	8 August	1	241
2	8 August	15 August	1	282
3	15 August	22 August	1	131
4	22 August	29 August	1	135
5	29 August	5 September	1	155
6	5 September	19 September	2	109
7	19 September	24 October	5	101

Note: Release groups were defined based on arrival date at the LMN1 acoustic detection array.

Release schedule

Acoustic-tagged fish used in this analysis were those known to have arrived at LMN1, 22 km downstream from the release location. This procedure allowed initial post-release handling mortality to be controlled for before the fish entered the study area. Conceptual release groups at LMN1 were assigned based on arrival date there for a total of seven release groups (Table 1). Average travel times (harmonic mean) from initial release to arrival at LMN1 ranged from 1.27 days for the first release group to 2.96 days for the last release group. Detection data corresponding to the first 8 weeks (i.e., the minimal tag life) after a release group was formed at LMN1 were processed. For each release group, data analysis was performed on a biweekly time scale and separately on an 8 week (studywide) time scale.

Statistical methods

Our approach was a derivative of the Pollock (1982) robust method of estimating survival and abundance. Pollock (1982) used release–recapture methods to estimate survival probabilities over time punctuated by intense sampling to estimate population abundance in a study area closed to migration. Instead, we used release–recapture methods to estimate the joint probabilities of migration and survival through river reaches based on the cross-river arrays and then used the intense sampling at the intrareach receivers to estimate how many tagged fish remained alive and residing within a reach. The mortality probability was then easily extracted.

To understand the temporal and spatial dynamics of fall Chinook salmon migration and delay processes, survival and movement parameters were estimated by time period, reach, and release group over the course of the study. In addition, separate survival and migration parameters were estimated for fish originating in separate reaches for all time periods after the first. The underlying survival and movement parameter estimated was ϕ_{gij} , the joint probability of survival and (downstream) migration for fish from initial LMN1 release group g ($g = 1, \dots, G$) through reach i ($i = 1, \dots, K$) in time period t ($t = 1, \dots, T$) for fish that began time period t in reach j ($j \leq i$). For our study, $G = 7$, $K = 3$, and $T = 4$. All fish began the first time period in reach 1, so ϕ_{g1j} was estimated only for $j = 1$. Live fish may have begun later time periods in any reach, so for periods $t > 1$, parameters ϕ_{gij} were estimated for all reaches $j \leq i$.

Estimation in period $t = 1$ was based on the single release–recapture (SR) model (Skalski et al. 1998). The den-

sity of the detection arrays permitted setting the detection probabilities in the release–recapture model to 1 as confirmed by the capture histories. By the end of the study, only one fish was detected downstream that was not also detected upstream. An implicit assumption of the SR model is that all fish movement is directed downstream. If fish also moved upstream, estimates of ϕ_{g11} represent only the extent of downstream movement through the study area in the first time period.

For time periods $t > 1$, estimation of the survival and movement parameters was complicated by the fact that at the beginning of such periods, live tagged fish may have been distributed throughout the study area. Consequently, virtual release groups for each reach were constructed of fish known to be alive. This was made feasible by near-perfect detection rates at the cross-river arrays for most release groups (Table 2) and additional detections at the intrareach receivers, which allowed for tracking fish from reach to reach. Although battery failure at two receivers in the LMF array resulted in a lower detection probability for the first release group (Table 2), the high density of intrareach receivers in the forebay compensated for the missing detections. Live fish assigned to reach j ($j = 1, \dots, K$) at the beginning of time period t ($t = 2, \dots, T$) comprised the virtual release group for that reach and period of size $R_{(gjt)}$ for fish from initial LMN1 release group g . The SR model was used with each virtual release group independently to estimate the ϕ_{gij} for reaches $i = j, \dots, K$.

In forming the virtual release groups of size $R_{(gjt)}$, live tagged fish needed to be distinguished from dead fish with an active tag. Typically, this requires a quantitative decision rule, the details of which will depend on the species under investigation. For the fall Chinook salmon study, a decision rule was developed based on the distribution of movement behaviors of fish known to be alive as judged by subsequent detection events. Two criteria were used to distinguish dead fish from live fish at the final detection location: elapsed time between detection events (i.e., “gap”) and the length of time the tag was detected at a given location (i.e., “duration”). Fish known to be alive (i.e., those that were subsequently detected at a different location) were characterized by relatively frequent movements of short durations between detection nodes. We used the 95th percentiles from the distributions of gaps (6.4 h) and durations (9.4 h) from known live fish to identify dead fish with active tags. Tags that had not moved recently between locations (i.e., gap > 6.4 h) and lingered more than 9.4 h at their final detection location

Table 2. Point estimates and standard errors of detection probability at the LMN2 and LMF arrays for each release group during the 8 weeks of detection after release at LMN1.

Release group	LMN2		LMF	
	Estimate	SE	Estimate	SE
1	1.0000	0	0.7051	0.0516
2	0.9944	0.0056	1.0000	0
3	1.0000	0	1.0000	0
4	1.0000	0	1.0000	0
5	1.0000	0	1.0000	0
6	1.0000	0	1.0000	0
7	0.9512	0.0238	1.0000	0

Note: Estimates are based on the Manly–Parr model (Seber 1982, pp. 233–234).

were classified as belonging to dead fish. Out of the 1154 acoustic-tagged fish analyzed in this study, there was only one fish (0.09%) with a discrepancy between a visual inspection of the entire fish tracks and the mortality classification algorithm implemented.

For each initial release group g , ϕ_{git} was defined to be the joint probability of migrating and surviving through reach i in time period t , conditional on either beginning period t in reach i or else entering reach i from upstream in period t . The parameter ϕ_{git} was defined analytically in terms of the underlying ϕ_{gij} parameters. For the first time period, $\phi_{gi1} = \phi_{gi11}$ because all fish originated in the first reach. For later time periods, ϕ_{git} was estimated as a weighted average of the ϕ_{gij} parameters across the virtual release groups for period t from reaches $j \leq i$:

$$\hat{\phi}_{git} = \frac{\sum_{j=1}^i \left(R_{(gjt)} \prod_{k=j}^i \hat{\phi}_{gktj} \right)}{\sum_{j=1}^i \left(R_{(gjt)} \prod_{k=j}^{i-1} \hat{\phi}_{gktj} \right)}$$

for $i = 1, \dots, K$ and $t = 2, \dots, T$. We interpreted $\prod_{k=i}^{i-1} \hat{\phi}_{gktj} = 1$.

Variance estimators were derived using the delta method (Seber 1982, pp. 7–9; Appendix A).

Two additional parameters were used to represent delayed migration and mortality. We defined ψ_{git} to be the joint conditional probability of delaying migration and surviving within reach i throughout period t for the g th release group. The parameter μ_{git} is the conditional probability of dying in reach i during time period t for the g th release group. Both ψ_{git} and μ_{git} were defined conditionally on either beginning period t in reach i or else arriving in reach i from upstream in period t . For each reach and time period, $\phi_{git} + \psi_{git} + \mu_{git} = 1$.

The parameter ψ_{git} was estimated as the ratio of the estimated abundance of live fish in reach i at the end of period t to the estimated number of fish that were either present in reach i at the beginning of period t or entered reach i during period t . For $t = 1$, all fish present in reach i began the time period in reach 1 in the initial LMN1 release group, so ψ_{gi1} was estimated as

$$\hat{\psi}_{gi1} = \frac{\hat{N}_{gi1}}{R_g \prod_{k=1}^{i-1} \hat{\phi}_{gk1}}$$

where R_g is the size of initial LMN1 release group g and \hat{N}_{gi1} is the estimated number of live tagged fish present in reach i at the end of the first period. For $t > 1$, fish present in reach i began the time period either in reach i or upstream, so the denominator of $\hat{\psi}_{git}$ depended on the size of the virtual release groups ($R_{(gjt)}$ for $j \leq i$) and the transition parameters ϕ_{gktj} for reaches $j \leq i$ and $k = j, \dots, i - 1$:

$$\hat{\psi}_{git} = \frac{\hat{N}_{git}}{\sum_{j=1}^i \left(R_{(gjt)} \prod_{k=j}^{i-1} \hat{\phi}_{gktj} \right)}$$

where $\prod_{k=i}^{i-1} \phi_{gktj} = 1$. The probability of mortality (μ_{git}) was

estimated by $\hat{\mu}_{git} = 1 - \hat{\phi}_{git} - \hat{\psi}_{git}$. Variance estimators for $\hat{\psi}_{git}$ and $\hat{\mu}_{git}$ were based on the delta method (Appendix A).

To estimate N_{git} , two temporal sampling periods were used at the intrareach receivers to collect detections in reach i near the end of period t for the g th LMN1 release group. Detections were restricted to those fish that were classified as “alive” based on the mortality decision rule described earlier. The abundance of live tagged fish (N_{git}) was estimated using the Chapman (1951) bias-corrected Lincoln–Petersen estimator with associated variance (Seber 1982, p. 60). This is a closed population abundance estimator; if mortality is operating, \hat{N}_{git} estimates the abundance at the time of the first sampling period. To fulfill the assumptions of closure and random mixing, we used the telemetry data from 0600 to 1200 h on each of the last 2 days of a study period.

Parameter estimates $\hat{\phi}_{git}$, $\hat{\psi}_{git}$, and $\hat{\mu}_{git}$ for the biweekly time periods ($t = 1, \dots, T$) give information on a detailed spatial and temporal scale for each release group. To investigate studywide dynamics for each reach i and release group g , we also estimated $\hat{\phi}_{git}$, $\hat{\psi}_{git}$, and $\hat{\mu}_{git}$ using a single time period of 8 weeks, equivalent to the minimal tag life. This approach to estimating long-term dynamics is both simpler and more robust to errors in the mortality decision rule than the alternative approach of integrating the individual biweekly parameter estimates over the shorter time periods.

The studywide (i.e., 8 week) reach- and release-specific parameter estimates were integrated over all reaches to summarize migration performance through the entire study area for each release group, yielding estimates $\hat{\phi}_g$, $\hat{\psi}_g$, and $\hat{\mu}_g$. Furthermore, these release-specific results were combined to estimate seasonwide results using a weighted average with weights based on a smolt passage index (I_g , $g = 1, \dots, G$) at Little Goose Dam obtained from the Fish Passage Center (www.fpc.org/). The smolt passage index is an index of daily passage abundance of juvenile fall Chinook salmon at Little Goose Dam. The release-specific estimates $\hat{\phi}_g$ were weighted by the proportions of emigrating smolts entering the Lower Monumental Reservoir associated with each release group according to the formula

$$\hat{\phi} = \frac{\sum_{g=1}^G I_g \phi_g}{\sum_{g=1}^G I_g}$$

with associated variance estimator

$$\widehat{\text{Var}}(\hat{\phi}) = \frac{\sum_{g=1}^G I_g (\hat{\phi}_g - \hat{\phi})^2}{(G-1) \sum_{g=1}^G I_g}$$

Analogous calculations were performed for $\hat{\psi}$ and $\hat{\mu}$.

The major modeling assumptions used here are that all fish present in a given reach had common probabilities of migration and survival (ϕ), migratory delay and survival (ψ), and mortality (μ) through the reach. Seasonal variations in these probabilities were accommodated by analyzing LMN1 release groups separately and by partitioning the study period into biweekly time periods. An additional assumption is that all fish from a given release group that were present at a receiver and had a working tag were equally detectable. This assumption could have been violated if some fish traveled primarily in the shallows near the shoreline where the range of the acoustic telemetry system was reduced. However, there is no indication that juvenile fall Chinook salmon exhibited this type of behavior. Furthermore, the very high detection probabilities estimated for the cross-river arrays were consistent with equal detection probabilities (i.e., 100% at most arrays). Other implicit assumptions are that acoustic tags neither failed nor were expelled before the end of the study. A tag-life study indicated 98% survival of tags through day 60, justifying our choice of a 56 day study period. Tag expulsion rates were unobservable from the data collected but were expected to be low based on the low observed tag burden (tag weight divided by fish weight, mean = 1.3%). In addition, laboratory studies with these small tags and large juvenile Chinook salmon have reported low tag expulsion rates (Brown et al. 2008). Additional assumptions follow those of the SR model (Skalski et al. 1998).

Results

A total of 1154 subyearling fall Chinook salmon comprised the seven release groups at LMN1 from 1 August through 24 October 2007 (Table 1). Median fish fork length was 156 mm with a range of 118–230 mm. Of the 1154 fish detected at LMN1, 510 were later detected on the Lower Monumental tailrace array or on other receivers downstream of the study area.

The biweekly analyses allowed examination of the temporal trends in survival and migration for each release group and reach i ($i = 1, 2, 3$) through time (Figs. 2, 3, and 4). Biweekly fates within a reach are conditional on the fish entering (from upstream) or being alive in the reach during the 2-week period. Hence, the probabilities of the three fates (migration, delay, and mortality) sum to 1 for each reach, time period, and release group, but represent fewer and fewer fish over time.

Most fish that arrived at reach 1 (LMN1–LMN2) by early September (i.e., releases 1–5, Table 1) migrated downstream within the first 2 weeks (Fig. 2). Those fish that delayed migration beyond 2 weeks experienced high mortality. Fish that arrived at LMN1 in mid-September (i.e., release 6) experienced little or no mortality, with fish either migrating successfully through the reach or else remaining alive (delaying migration) within that area. Fish that arrived at LMN1 from mid-September through mid-October (i.e., release 7) had high mortality in reach 1 initially, with surviving fish showing considerable delay in later time periods (Fig. 2). In general, the probability of delaying migration in reach 1 increased over the course of the study (Fig. 2). Similar results were seen for reach 2 (LMN2–LMF) (Fig. 3), with the exception of release 7, which showed high migration and high delay probabilities in that reach throughout the study. Delayed migration in the Lower Monumental Dam forebay (i.e., reach 3, LMF–LMT) became evident only for the last two release groups (6 and 7) in late September and early October.

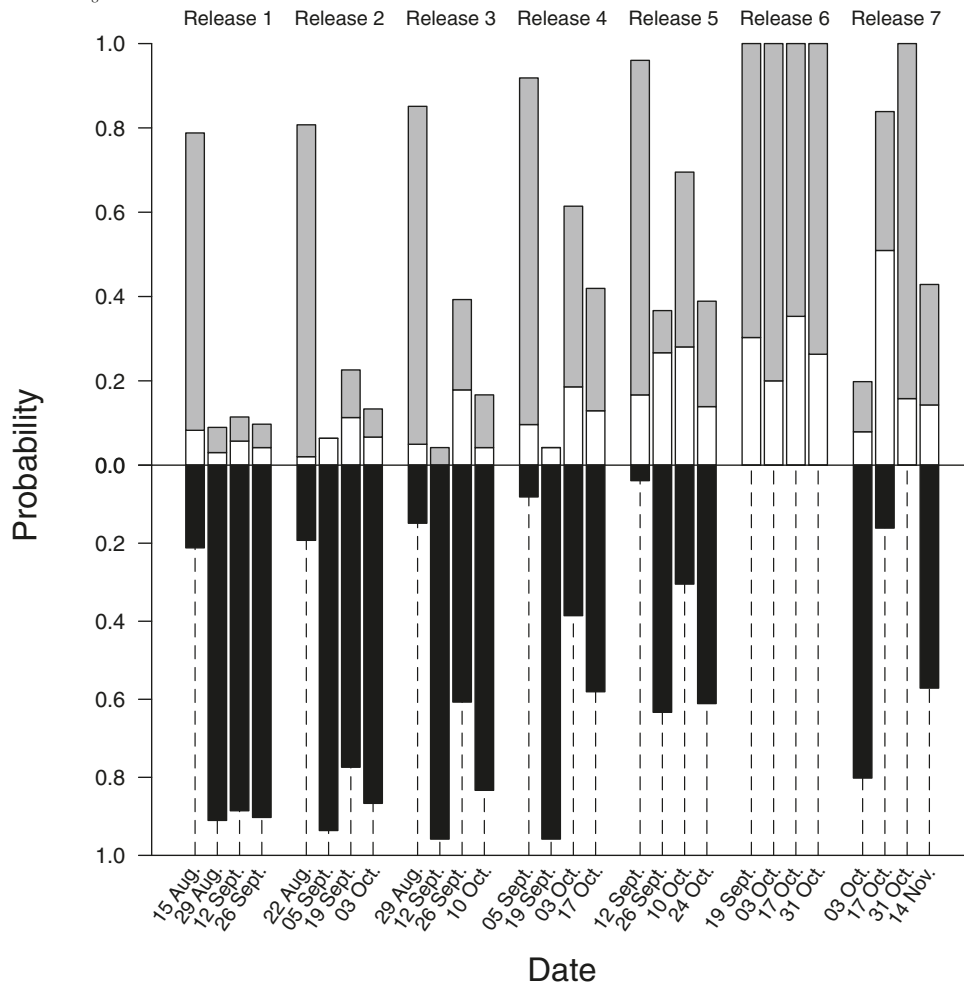
For each release group, the 12 reach-specific biweekly estimates of conditional fate (Figs. 2, 3, and 4) were collapsed over time and space to provide estimates of fate over the course of the study (i.e., 8 weeks) (Table 3; Fig. 5). Over the course of the first 6 release groups, the proportion that migrated remained relatively constant, ranging from 34% to 44% (Fig. 5). However, mortality declined over time, being replaced by delays in migration. The exception to this trend was release 7, with both lower migration and higher mortality than the previous release group. By the end of the study, approximately a third of the fish delayed their migration within the lower 19 km of Lower Monumental Reservoir (releases 5–7, Fig. 5).

The fate results by release group were further combined to provide an overall study result. The studywide weighted average estimated the probability of successful migration out of the study area to be $\hat{\phi} = 0.361$ ($\widehat{\text{SE}} = 0.022$), the probability of delayed migration to the end of the study (i.e., 8 weeks) to be $\hat{\psi} = 0.106$ ($\widehat{\text{SE}} = 0.035$), and the mortality probability to be $\hat{\mu} = 0.533$ ($\widehat{\text{SE}} = 0.030$). Had a traditional release–recapture analysis been performed, the 0.106 probability of delayed migration would have been incorrectly included in the perceived mortality probability.

Discussion

The detection system we used, composed of cross-river arrays augmented by intrareach receivers, appears to provide a robust framework for investigating subyearling fall Chinook salmon migration dynamics. The cross-river arrays provide estimates of the joint probability of surviving and migrating (ϕ). Intense sampling at the intrareach receivers analyzed with closed population models such as the Lincoln–Petersen and Schnable estimators (Seber 1982, pp. 130–140) can then assess how many live tagged fish are still residing within the reaches at the conclusion of each study period. The combined result is unbiased estimates of survival and mortality in the presence of migratory delay. While the overall pattern of the results presented here may be generally applicable to other reservoir areas within the Snake River basin and for different years, we nevertheless

Fig. 2. Estimated biweekly conditional probabilities of migrating and surviving ($\hat{\phi}_{g1t}$, gray bars), delaying migration and surviving ($\hat{\psi}_{g1t}$, white bars), and mortality ($\hat{\mu}_{g1t}$, black bars) for each of the seven release groups in the reach LMN1–LMN2 in 2007.



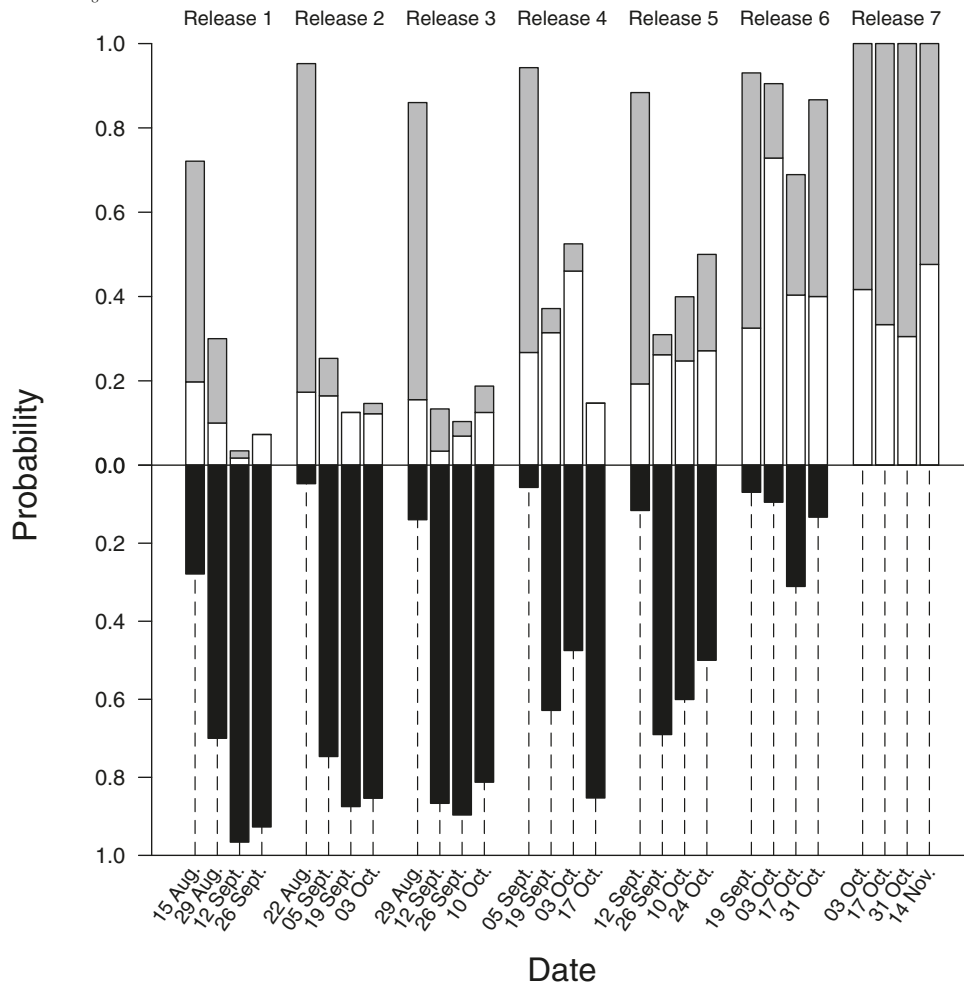
caution against the broad application of our exact estimates to other locations or time periods because we present data for only one location and year of study.

Other studies have estimated the joint probability of migration and survival of subyearling fall Chinook salmon farther upstream in the Snake River or earlier in the season using either the Cormack–Jolly–Seber model (e.g., Connor et al. 2003; Smith et al. 2003) or an alternative model (e.g., Lowther and Skalski 1998). However, in no case did the study area and season coincide with those studied here, and in most cases, migratory delay was not estimated. Connor et al. (2003) studied migration upstream of Lower Granite Dam for wild fish released in spring and early summer. Smith et al. (2003) studied migration both farther upriver (i.e., from Lower Granite to the Lower Monumental tailrace) and for fish migrating later in the season. For fish leaving Lower Granite from mid-August through mid-September, they found an average migration and survival estimate of 0.35 from Lower Granite through the Lower Monumental tailrace. Assuming equal probabilities through both the intervening projects, this implies a joint probability of migration and survival of about 0.59 from Little Goose Dam to the Lower Monumental tailrace. This is considerably higher than our studywide estimate of approximately 0.36, which

refers to a smaller study area (i.e., LMN1 through the Lower Monumental tailrace). However, our release groups included fish migrating somewhat later in the year than those in Smith et al. (2003). As noted both here and in that study, later fish tend to have lower estimates of migration and survival. It is likely that interannual variability is high, so comparisons across years, release groups, and release locations must be made with caution.

Lowther and Skalski (1998) estimated both the joint probability of migration and survival and the total probability of survival from release to the tailrace of Lower Granite Dam for hatchery subyearling fall Chinook salmon released upstream in 1996. They found little evidence of overwintering within the 62 km between their release site and Lower Granite Dam. However, direct comparisons between their results and ours are inappropriate because their estimates of migration and mortality covered both a different stretch of river and a different time scale. Their estimates referred to nearly the entire period of juvenile emigration of fall Chinook salmon, including summer and fall of their first year after emergence and spring of their second year, excluding their first winter. Our estimates of migration and mortality refer only to the late summer and fall of the first year after emergence. We believe that both local environmental conditions and seasonal

Fig. 3. Estimated biweekly conditional probabilities of migrating and surviving ($\hat{\phi}_{g2t}$, gray bars), delaying migration and surviving ($\hat{\psi}_{g2t}$, white bars), and mortality ($\hat{\mu}_{g2t}$, black bars) for each of the seven release groups in the reach LMN2–LMF in 2007.



timing may influence the onset of migratory delay, which may explain the increased evidence of delay found here.

Our analysis focused on the acoustic tag detections generated by the subyearling fall Chinook salmon study during the first 8 weeks (56 days) after tagging and release based on an expected 60 day tag life. However, each fish was also given a PIT tag, which provided detections at dams on the Snake and Columbia rivers as tagged fish passed through the bypass systems into November and December of 2007 and again in the spring of 2008. The bypass systems are typically closed during winter months and have much lower detection probabilities than the acoustic telemetry system even when they are operational, so the resulting sparse PIT tag data can provide only qualitative information. Nevertheless, 66 of the 1154 juvenile fall Chinook salmon tagged in summer and fall 2007 and analyzed here were detected in PIT tag detection systems at mainstem Snake or Columbia River dams in spring 2008. This amounts to 54% of the fish estimated to have remained alive in the reservoir at the end of their 8 week acoustic tag life. The trend in PIT tag detections supports the conclusions of the fate analyses within this paper: a larger proportion of the fish tagged later in the summer and early fall were detected migrating seaward the following spring than those fish tagged earlier in the

summer. Up to 30% of the individuals in later release groups were detected migrating seaward in spring 2008. If PIT tag detection probabilities were 30% during the spring emigration period, that would indicate that the majority of individuals in later releases delayed migration and survived through the winter to emigrate the following spring. Connor et al. (2005) found that these “reservoir-type” fish had higher ocean survival than their summer- or fall-emigrating “ocean-type” counterparts and provided a disproportionately higher contribution to adult returns.

The release–recapture model we used considered only net downstream fish movements. Actual tracks of individual fish, however, showed much more complex behavior. Many fish tagged for this study exhibited movement behaviors indicating that they were not directed in their seaward migration. These fish often moved fairly rapidly (within a few days) from the release site (rkm 108) to the immediate forebay of Lower Monumental Dam (rkm 67), then turned around and swam back upstream, and then changed direction again and swam all or part of the way back toward the dam. Our analysis accommodated this behavior by including these fish in the virtual release groups for time periods after the first. However, our fate estimates may be biased by fish that arrived at the top of our study area (i.e., LMN1) and

Fig. 4. Estimated biweekly conditional probabilities of migrating and surviving ($\hat{\phi}_{g3t}$, gray bars), delaying migration and surviving ($\hat{\psi}_{g3t}$, white bars), and mortality ($\hat{\mu}_{g3t}$, black bars) for each of the seven release groups in the reach LMF–LMT in 2007.

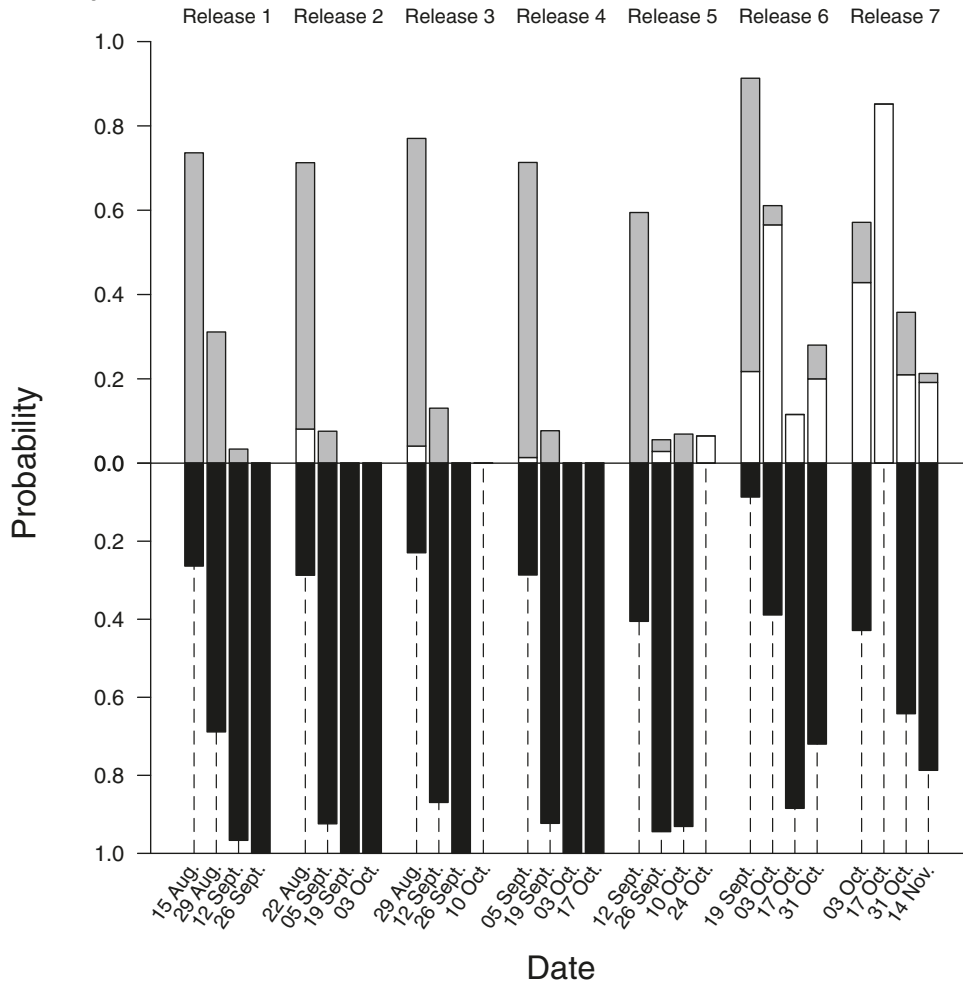


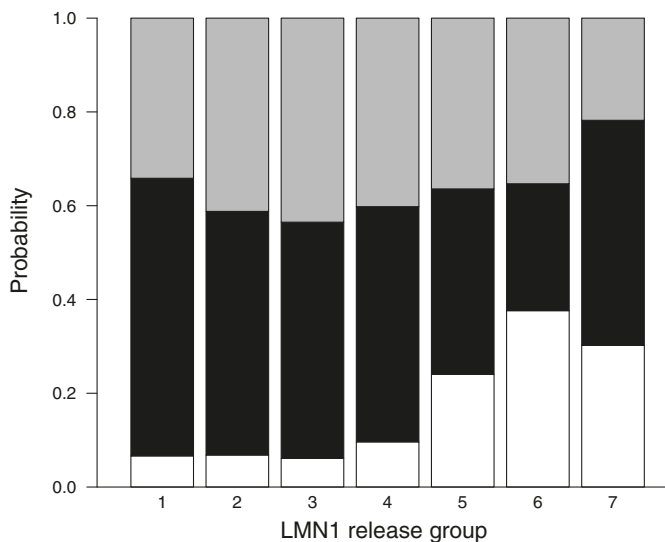
Table 3. Estimates and standard errors of ϕ_g (joint probability of migration and survival), ψ_g (joint probability of delay and survival), and μ_g (probability of mortality) within the study area (i.e., between the arrays at LMN1 and LMT) during the 8 weeks of detection after release for release groups $g = 1-7$.

Release group	Migration and survival		Delay and survival		Mortality	
	$\hat{\phi}_g$	SE($\hat{\phi}_g$)	$\hat{\psi}_g$	SE($\hat{\psi}_g$)	$\hat{\mu}_g$	SE($\hat{\mu}_g$)
1	0.3415	0.0325	0.0664	<0.0001	0.5921	0.0325
2	0.4122	0.0294	0.0683	0.0020	0.5195	0.0294
3	0.4352	0.0433	0.0611	<0.0001	0.5038	0.0433
4	0.4021	0.0435	0.0963	<0.0001	0.5016	0.0435
5	0.3642	0.0399	0.2405	0.0320	0.3953	0.0512
6	0.3533	0.0484	0.3761	0.0697	0.2706	0.0736
7	0.2179	0.0739	0.3020	0.0579	0.4801	0.0895

then returned upstream to delay their migration out of the study area. Our fate analysis would classify such fish as mortalities. Based on the number of fish determined to have ended their 8 week tracking period upstream of LMN1, we may have misspecified mortality by as much as 0.045. Adjusted mortality would therefore be 0.488 (i.e., $\hat{\mu} - 0.045$) over the course of the study. Locating intrareach receivers in the reach between the release site and LMN1 would eliminate this source of bias in future studies.

This study found a general trend of increasing migratory delay and decreasing mortality through the late emigration season. This trend was associated with decreases in the amount of temperature stratification in the lower reservoir (McMichael et al. 2008). An untested hypothesis is that sub-yearling Chinook salmon migrating late in the emigration season may encounter a high density of prey resources that prompts them to remain in freshwater rather than continue seaward. It would be illuminating to compare seasonal

Fig. 5. Estimated proportions of fall Chinook salmon smolts that migrated successfully (gray bars), delayed migration and survived (white bars), and died (black bars) within the Lower Monumental Reservoir (rkm 67–87) by release group over the 8 week course of the study in 2007.



changes in the prey base with patterns of delay and mortality in the Lower Monumental Reservoir and elsewhere in the Snake River.

The novel deployment of acoustic technology and the statistical analysis used in this study produced initial estimates of the prevalence of migratory delay in the Lower Monumental Reservoir and demonstrated that operations at Lower Monumental Dam must accommodate juvenile fall Chinook salmon even in the winter. This finding is a step forward in untangling the complex juvenile life history of Snake River fall Chinook salmon. However, designing appropriate management strategies requires even more information, particularly on the proportion of these fish that delay migration through either part or all of the winter, and their subsequent survival to the ocean and then back to Lower Granite Dam as adults (i.e., the smolt–adult return rate). Such data will provide feedback on management strategies such as spill operations and smolt transportation, which are currently difficult to assess for fall Chinook salmon. Observing these expanded data would require acoustic transmitters with lifetimes of 280 days or more. Larger, longer-lived tags than those used here are currently undergoing tag-life and bioeffects testing at the Pacific Northwest National Laboratory in Richland, Washington, for the purpose of studying overwinter survival of juvenile fall Chinook salmon that adopt the reservoir-type or extended rearing strategy within the Columbia River basin. The basic study design described in this paper may be used with these larger tags to develop a much better understanding of smolt–adult survival and therefore the impacts of hydroelectric system management on the protection or recovery of these populations.

Modeling problems caused by alternative life histories, such as that described here for juvenile fall Chinook salmon, are likely to be encountered for other migratory species and study areas. This study indicates that feasible methods using active tag systems can be developed to study and quantify

the complex life histories of subyearling fall Chinook salmon. The further development of tagging technology, combined with creative study designs and analysis methods, has great potential to increase understanding of species with variable life histories.

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Appendix A. Variance estimators

Migration and survival probability (ϕ_{git})

For time period $t = 1$, initial release group g , and reach i , ϕ_{gi1} (equivalent to ϕ_{gi11}) is estimated from the single release–recapture model, and variances and covariances come directly from the matrix of partial second derivatives in the numerical fitting routine. For time period $t > 1$, the variance estimator of $\hat{\phi}_{git}$ is based on the delta method (Seber 1982, pp. 7–9) and depends on the partial derivatives of ϕ_{git} with respect to each of the ϕ_{gktj} parameters:

$$\widehat{\text{Var}}(\hat{\phi}_{git}) = \sum_{j=1}^i \sum_{n=1}^i \sum_{k=j}^i \sum_{m=n}^i \left(\frac{\partial \phi_{git}}{\partial \phi_{gktj}} \right) \bigg|_{\hat{\phi}} \left(\frac{\partial \phi_{git}}{\partial \phi_{gmtn}} \right) \bigg|_{\hat{\phi}} \widehat{\text{Cov}}(\hat{\phi}_{gktj}, \hat{\phi}_{gmtn})$$

where

$$\frac{\partial \phi_{git}}{\partial \phi_{gmtj}} = \frac{R_{(git)}(\phi_{git} - \phi_{git}) \prod_{k=j}^{i-1} \phi_{gktj}}{\phi_{gmtj} \sum_{n=1}^i \left(R_{(gnt)} \prod_{k=n}^{i-1} \phi_{gktn} \right)} \quad \text{for } j = 1, \dots, i; \quad m = j, \dots, i - 1$$

$$\frac{\partial \phi_{git}}{\partial \phi_{git}} = \frac{R_{(git)} \prod_{k=j}^{i-1} \phi_{gktj}}{\sum_{n=1}^i \left(R_{(gnt)} \prod_{k=n}^{i-1} \phi_{gktn} \right)} \quad \text{for } j = 1, \dots, i$$

Delayed migration probability (ψ_{git})

The joint probability of remaining in reach i and surviving there through the end of period t for fish in release group g , conditional on either beginning period t in reach i or else entering that reach from upstream during period t , is ψ_{git} . The variance estimator for $\hat{\psi}_{git}$ is based on the delta method:

$$\widehat{\text{Var}}(\hat{\psi}_{git}) = \hat{\psi}_{git}^2 \left[\frac{\widehat{\text{Var}}(\hat{N}_{git})}{\hat{N}_{git}^2} + \sum_{k=1}^{i-1} \frac{\widehat{\text{Var}}(\hat{\phi}_{gkt})}{\hat{\phi}_{gkt}^2} + 2 \sum_{k=1}^{i-1} \sum_{m=k+1}^{i-1} \frac{\widehat{\text{Cov}}(\hat{\phi}_{gkt}, \hat{\phi}_{gmt})}{\hat{\phi}_{gkt} \hat{\phi}_{gmt}} \right]$$

for $t = 1$. For $t > 1$, the variance estimator for $\hat{\psi}_{git}$ is

$$\widehat{\text{Var}}(\widehat{\psi}_{git}) = \frac{\widehat{\psi}_{git}^2}{\widehat{N}_{git}^2} \widehat{\text{Var}}(\widehat{N}_{git}) + \frac{\widehat{\psi}_{git}^4}{\widehat{N}_{git}^2} \left\{ \sum_{j=1}^i \left[R_{(git)}^2 \widehat{\text{Var}} \left(\prod_{k=j}^{i-1} \widehat{\phi}_{gktj} \right) \right] + 2 \sum_{j=1}^i \sum_{k=j+1}^i \widehat{\text{Cov}} \left(R_{(git)} \prod_{m=j}^{i-1} \widehat{\phi}_{gmtj}, R_{(gkt)} \prod_{n=k}^{i-1} \widehat{\phi}_{gntk} \right) \right\}$$

where

$$\widehat{\text{Var}} \left(\prod_{k=j}^{i-1} \widehat{\phi}_{gktj} \right) = \left(\prod_{k=j}^{i-1} \widehat{\phi}_{gktj} \right) \left[\sum_{k=j}^{i-1} \frac{\widehat{\text{Var}}(\widehat{\phi}_{gktj})}{\widehat{\phi}_{gktj}} + 2 \left(\prod_{k=j}^{i-1} \widehat{\phi}_{gktj} \right) \sum_{k=j}^{i-1} \sum_{m=k+1}^{i-1} \frac{\widehat{\text{Cov}}(\widehat{\phi}_{gktj}, \widehat{\phi}_{gmtj})}{\widehat{\phi}_{gktj} \widehat{\phi}_{gmtj}} \right]$$

and

$$\widehat{\text{Cov}} \left(R_{(gjt)} \prod_{m=j}^{i-1} \widehat{\phi}_{gmtj}, R_{(gkt)} \prod_{n=k}^{i-1} \widehat{\phi}_{gntk} \right) = R_{(gjt)} R_{(gkt)} \left(\prod_{m=j}^{i-1} \widehat{\phi}_{gmtj} \right) \left(\prod_{n=k}^{i-1} \widehat{\phi}_{gntk} \right) \sum_{m=j}^{i-1} \sum_{n=k}^{i-1} \frac{\widehat{\text{Cov}}(\widehat{\phi}_{gmtj}, \widehat{\phi}_{gntk})}{\widehat{\phi}_{gmtj} \widehat{\phi}_{gntk}}$$

Estimates of $\widehat{\text{Cov}}(\widehat{\phi}_{gmtj}, \widehat{\phi}_{gntk})$, for $m = j, \dots, i - 1$ and $n = k, \dots, i - 1$, are available from the matrix of second partial derivatives estimated in the numerical optimization routine used to estimate the ϕ parameters.

Other variance estimators depend on the covariance between the migration and survival parameter estimates ($\widehat{\phi}_{git}$) and the delayed migration parameter estimates ($\widehat{\psi}_{git}$). This covariance is estimated with the delta method. For $t = 1$:

$$(A1) \quad \widehat{\text{Cov}}(\widehat{\phi}_{git}, \widehat{\psi}_{git}) = -\widehat{\psi}_{git} \sum_{k=1}^{i-1} \frac{\widehat{\text{Cov}}(\widehat{\phi}_{git}, \widehat{\phi}_{gkt})}{\widehat{\phi}_{gkt}}$$

For $t > 1$:

$$(A2) \quad \widehat{\text{Cov}}(\widehat{\phi}_{git}, \widehat{\psi}_{git}) = \sum_{j=1}^i \sum_{n=1}^i \sum_{k=j}^i \sum_{m=n}^{i-1} \left[\left(\frac{\partial \phi_{git}}{\partial \phi_{gktj}} \right) \Big|_{\widehat{\phi}} \left(\frac{\partial \psi_{git}}{\partial \phi_{gmtn}} \right) \Big|_{\widehat{\phi}} \widehat{\text{Cov}}(\widehat{\phi}_{gktj}, \widehat{\phi}_{gmtn}) \right]$$

$$\frac{\partial \phi_{git}}{\partial \phi_{gktj}} = \frac{R_{(gjt)}(\phi_{gitj} - \phi_{git}) \prod_{m=j}^{i-1} \phi_{gmtj}}{\phi_{gktj} \sum_{n=1}^i \left(R_{(gnt)} \prod_{m=n}^{i-1} \phi_{gmtn} \right)} \quad \text{for } k = j, \dots, i - 1$$

$$\frac{\partial \phi_{git}}{\partial \phi_{gktj}} = \frac{R_{(gjt)} \prod_{m=j}^{i-1} \phi_{gmtj}}{\sum_{n=1}^i \left(R_{(gnt)} \prod_{m=n}^{i-1} \phi_{gmtn} \right)} \quad \text{for } k = i$$

$$\frac{\partial \psi_{git}}{\partial \phi_{gktj}} = \frac{-\psi_{git}^2 R_{(gjt)} \prod_{m=j}^{i-1} \phi_{gmtj}}{N_{git} \phi_{gktj}} \quad \text{for } k = j, \dots, i - 1$$

Mortality probability (μ_{git})

The probability of dying in reach i and period t for fish in release group g , conditional on starting period t in reach i or arriving there from upstream during period t , is μ_{git} . The variance estimator for $\widehat{\mu}_{git}$ is derived from the delta method. For $t = 1$:

$$\widehat{\text{Var}}(\widehat{\mu}_{git}) = \widehat{\text{Var}}(\widehat{\phi}_{git}) + \widehat{\text{Var}}(\widehat{\psi}_{git}) - 2\widehat{\psi}_{git} \sum_{k=1}^{i-1} \frac{\widehat{\text{Cov}}(\widehat{\phi}_{gkt}, \widehat{\phi}_{git})}{\widehat{\phi}_{gkt}}$$

For $t > 1$, the variance estimator for $\widehat{\mu}_{git}$ is

$$\widehat{\text{Var}}(\widehat{\mu}_{git}) = \widehat{\text{Var}}(\widehat{\phi}_{git}) + \widehat{\text{Var}}(\widehat{\psi}_{git}) + 2\widehat{\text{Cov}}(\widehat{\phi}_{git}, \widehat{\psi}_{git})$$

where $\widehat{\text{Cov}}(\widehat{\phi}_{git}, \widehat{\psi}_{git})$ is estimated as in eq. A2.

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