State-Space Model to Estimate Salmon Escapement Using Multiple Data Sources

Kevin E. See[1,*], Ryan N. Kinzer[2], and Michael W. Ackerman[1]

September 23, 2020

Abstract

Accurate estimates of salmonids passing Lower Granite Dam on the Snake River, by species and origin, are a critical input to assessing the status and trends of various populations, as well as successful management of fisheries in the Snake River basin. Here we describe a state-space model that estimates such escapement past a dam by using window counts, passive integrated transponder (PIT) tag observations and data from an adult fish trap, accounting for issues such as nighttime passage, fallback and re-ascension, potential observation error at the window and uncertainty in the adult trap rate. We tested the approach using a simulation framework that mimicked several levels of observation error, differences between nighttime passage and re-ascension rates and the possibility of the adult trap being closed for some period of time. Our results demonstrate that the model produced unbiased estimates across all tested scenarios. We also applied this model to data from the Lower Granite Dam to produce estimates of wild, clipped hatchery and unclipped hatchery spring-summer run Chinook Salmon and steelhead from spawn years 2010-2019.

[1] Biomark, Inc., 705 South 8th Street, Boise, Idaho, 83702, USA

[2] Nez Perce Tribe, Department of Fisheries Resource Management, 14054 Burr Road, PO Box 1942, McCall, Idaho, 83638, USA

* Correspondence: Kevin E. See <Kevin.See@merck.com>

Introduction

Fish escapement often refers to the number of adults that survive juvenile and subadult rearing, escape harvest and return to their natal habitat to potentially spawn (e.g., Bue et al. 1998). For anadromous fishes, escapement is often estimated at a fixed location in a river system prior to fish reaching their spawning area. Escapement estimates facilitate effective fisheries management, particularly estimates of escapement for component groups (e.g., by stock, population, age, origin [wild, hatchery], Hess et al. 2014; Steinhorst et al. 2017; Camacho et al. 2018) which provide valuable information that fisheries managers use to achieve sustainable harvest, while protecting small and vulnerable populations. Accurate escapement estimates are increasingly important for depleted populations as they inform status metrics (McElhany et al. 2000) and facilitate assessments of population viability, extinction risk (Northwest Fisheries Science Center 2015; Williams et al. 2016) and climate change vulnerability (Crozier et al. 2019).

Populations of Chinook Salmon *Oncorhynchus tshawytscha* and steelhead trout *O. mykiss* in the Snake River basin of Pacific Northwest, USA, are depleted following decades of substantial harvest and anthropogenic changes to their migration corridor (e.g., construction of hydroelectric projects on the Snake and Columbia rivers) and tributary habitats (Nehlsen et al. 1991; McClure et al. 2003; Northwest Fisheries Science Center 2015). As a result, Snake River spring-summer run Chinook Salmon (hereafter Chinook Salmon) were classified as threatened in 1992 under the Endangered Species Act (ESA; Federal Registry Notice 57 FR 14653), and Snake River summer-run steelhead trout (hereafter steelhead) were listed as threatened five years later (Federal Registry Notice 62 FR 43937). Snake River Chinook Salmon and steelhead have substantial cultural, recreational, commercial and subsistence value within the Snake River basin as well as in downstream corridors (i.e., Columbia River) and ocean fisheries. The aggregate escapement of Snake River Chinook Salmon and steelhead populations, with the exception of Tucannon River, is monitored at Lower Granite

Dam located in southeast Washington; the final dam on the Snake River that returning adults must pass prior to heading to tributary spawning locations. Many fisheries management and conservation actions are made based on estimates of escapement at Lower Granite Dam parsed by species and origin (NPCC 2014; Northwest Fisheries Science Center 2015; National Marine Fisheries Service 2019). Additionally, harvest openings and closures, both upstream in Snake River fisheries and downstream in mainstem Snake and Columbia rivers fisheries, are predicated on escapements at Lower Granite Dam.

The majority of Chinook Salmon and steelhead returning to the Snake River must ascend a fish ladder on Lower Granite Dam before migrating upriver. Fish management agencies previously used counts of fish, by species, passing an observation window within the fish ladder as a census of fish escaping past the dam. For both species, total escapement was then parsed into groups (e.g., wild, hatchery) using observed marks and genetic data from a sample of fish captured at an adult trap located on the fish ladder upstream of the observation window (Steinhorst et al. 2017; Camacho et al. 2018; Steele et al. 2019). Treating window counts as a census proved beneficial as being an easy, straight-forward method ascertained in near real-time. Moreover, downriver fisheries management arenas have used window counts at lower-river dams as escapement estimates for the past several years, and consistency in methods is often desirable for management decision making (Joint Columbia River Management Staff 2019).

However, using window counts as a census of Chinook Salmon and steelhead passing Lower Granite Dam can be problematic as it fails to account for multiple sources of uncertainty and disregards known biological processes. In-person window counts, where observers look directly into the fish ladders to identify and count all passing fish, by species, occur for 50 minutes per hour, 16 hours a day from April through October (which corresponds with peak run timing for several species). Counts are then expanded to provide an estimate for the entire hour (USACE 2015). For the remainder of the year (November through March), fish passage is video-taped for 10 hours each day; fish counters then read the video tapes and submit daily fish counts. Typically, the observational error rates of live and video window counts are unknown, and sampling error rates are ignored. Hatch et al. (1994) conducted a study of the counting system at Lower Granite Dam in 1992, and found that Chinook Salmon were undercounted at the window by in-person window counters compared to video counts. There was a significant difference between daily standard counts (16 or 10 hours per day) and daily 24-hour video counts; they found a significant nighttime passage rate (crossing while the counting window was closed) with 3.5% of Chinook Salmon and 6.6% of steelhead adults passing during "nighttime" hours. They also found some species misidentification issues, which could result in either under- or over-counting of a particular species. While that study identified potential issues with the current window counting procedure, it was only conducted in a single year, nearly 30 years ago, at a time when Chinook Salmon and steelhead total returns were lower than in the past decade.

Besides potential errors in the window counts, two biological processes are unaccounted for: 1) fish that cross the dam during the 8+ hours when the window is unmonitored (i.e., nighttime passage) which may result in an underestimate of escapement, and 2) fish that migrate through the ladder and past the dam may fallback over the dam (e.g., over a spillway, through navigation locks) and later may re-ascend the fish ladder again (Boggs et al. 2004) and be double-counted at the window (re-ascension). Both fallback without and with re-ascension potentially result in an overestimate of escapement (Dauble and Mueller 2000). Previously, it was often assumed that nighttime passage rates and fallback/re-ascension rates canceled each other out resulting in window counts providing an unbiased estimate of escapement (Camacho et al. 2018).

In this study, we describe a novel method to estimate aggregate and group escapements which incorporate all sources of known uncertainty and demonstrate that the estimation method is essentially unbiased, thus better informing conservation and management decision making. We also test whether observed nighttime passage and fallback/re-ascension rates are typically equal. Our method for estimating species-specific escapement past Lower Granite Dam incorporates window counts, data from the adult fish trap, and observations of fish previously tagged with passive integrated transponder (PIT) tags in the adult ladder to explicitly model nighttime passage, re-ascension, and observation error using a state-space approach (Royle and Dorazio 2008) which separates process variance (e.g., week to week variance in true escapment) from observation error variance (e.g., observation error at the window, or sampling variance at the trap). To meet desired management and conservation objectives, modeled escapement includes estimates of uncertainty and is parsed into weekly strata. Further, total and weekly estimates are parsed into three origin groups: wild fish, hatchery fish with a clipped adipose fin, and unclipped hatchery fish. Estimates of escapement account for fish that migrate through the ladder outside of observation hours (nighttime passage) and those that ascend the ladder multiple times (re-ascension). Our model is implemented in the **ST**ate-space **A**dult **D**am **E**scapement **M**odel (STADEM) package for the statistical software R (R Core Team 2020), and is available for download or installation from https://github.com/KevinSee/STADEM. To validate the STADEM results, we simulated 12 scenarios with varying trapping rates, fallback and re-ascension rates, nighttime passage rates, and window count error rates. We then applied this model to Chinook Salmon and steelhead returns at Lower Granite Dam for spawn years 2010 - 2019. The STADEM model combines multiple imperfect sources of data to reduce bias in escapement estimates and provides improved estimates of uncertainty.

Methods

Data Requirements

We used STADEM and three sources of data to estimate Chinook Salmon and steelhead escapement at Lower Granite Dam from 2010-2019. Data sources included 1) counts of fish migrating past the observation window located on the adult fish ladder at Lower Granite, 2) information from adults captured at a fish trap located in the fish ladder, and 3) observations of fish PIT tagged prior to arriving at Lower Granite Dam and detected in the adult fish ladder. Below, we describe each of the data sources in more detail as they pertain to Lower Granite Dam; similar data could likely be obtained from other fish passage facilities.

Window Counts

Daily counts of adult Chinook Salmon and steelhead passing the observation window located on the Lower Granite Dam fish ladder were estimated and provided by the US Army Corps of Engineers. When summed, they provide an estimate of the number of fish ascending and passing Lower Granite Dam each season. Window counts were made for each species using direct in-person visual monitoring and video monitoring during daytime hours (Hatch et al. 1994). Direct visual monitoring occurred during peak run times (April 1 – October 31) for 16 hours per day (0400 – 2000 hours). Video monitoring occurred during the beginning and tail ends of the adult runs (March 1 – March 31 and November 1 – December) for 10 hours per day (0600 – 1600 hours) (USACE 2015). During direct visual monitoring, observers recorded each adult (≥ 30cm), by species, passing the window for 50 minutes of each hour of operation. The sum of the daily 50-minute counts were then multiplied by 1.2 to account for the 10 minutes when fish were not counted. Daytime window counts were not expanded for fish that may have ascended the ladder outside of operational hours (i.e., nighttime passage) (USACE 2015). Window counts were accessed through the Columbia Basin Research Data Access in Real Time (DART) website, www.cbr.washington.edu/dart/query/adult_daily, using their window count query. Counts were provided for each day the fish ladder was open to passage.

Adult Fish Trap Data

The second source of data came from a sample of fish collected in the adult trap as they migrated past Lower Granite Dam (Ogden 2016a). The trap, also located within the adult fish ladder and upstream of the observation window, provides an opportunity to collect biological data (e.g., origin [wild, hatchery], genetic stock, length, age, sex) from captured adults which allows for decomposition of the escapement into specific groups (e.g., Camacho et al. 2018; Steinhorst et al. 2017). The trap was operational for 24 hours per day and randomly sampled the run by opening four times per hour for a length of time determined by a set daily trapping rate. The trap rate was determined by a committee of collaborating management agencies with a goal of capturing a target number of wild fish while also balancing fish handling concerns. Trap sample rates were typically 10-25%, but fluctuated throughout the season due to, for example, high water temperatures, decreased flows, trap malfunctions and/or closures, fish handling logistics, in-season forecast adjustments, or adjustments due to shifting species composition throughout the year.

All captured fish were anesthetized, speciated, examined for existing marks or tags, measured for fork length and visually identified as wild or hatchery. The most widely used marking of hatchery fish is a clipped (removed) adipose fin, although coded wire tags are used in less than 10% of the hatchery releases. Some subset of hatchery fish are either intentionally or unintentionally released without a clipped adipose fin, and these are referred to as unclipped hatchery fish, or hatchery no-clips (HNC). For adults with intact adipose fins (unclipped), which includes wild and hatchery no-clip individuals, either a portion or all of fish trapped (depending on the year) had scale and genetic tissue samples taken. Scale samples were used to estimate age (Wright et al. 2015) and genetic tissue samples were used to determine sex (Campbell et al. 2012) and estimate the location of origin of wild fish using genetic stock identification (e.g., Hargrove et al. (2019)). Prior to 2013, only fish determined to be wild in origin at the trap were sampled for scale and genetics. Starting in 2013, every unclipped Chinook Salmon and steelhead trapped at Lower Granite Dam was genotyped to simplify collaborative logistics and better estimate the proportion of unclipped hatchery fish that appear phenotypically wild. Camacho et al. (2018) provide further details on trap sample rates and valid sample selection. Prior to release, all non-PIT tagged fish with an intact adipose fin (i.e., putatively wild) received a PIT tag. Final determination of wild, clipped hatchery, or unclipped hatchery origins were assigned using a post-hoc analysis of marks and tags, including parentage-based tagging (Steele et al. 2013, 2019). Data from the adult trap were collected and managed by multiple agencies and were made available by the Idaho Department of Fish and Game (Camacho et al. 2018).

PIT Tag Data

The last source of data was observations of PIT tagged adult Chinook Salmon and steelhead at detection sites located in the Lower Granite Dam fish ladder. These observations provide daily estimates of 1) a trapping rate, 2) a nighttime passage rate, and 3) a re-ascension rate. Detections used in the model include all fish that were previously PIT tagged as juveniles or adults prior to arriving at Lower Granite Dam (i.e., does not include newly tagged adults at the dam) and detected at adult detection sites in the dam passage system. PIT tag data was provided through DART and the adult ladder PIT tag query; http://www.cbr.washington.edu/dart/query/pitadult_obsyr_detail.

A trap rate estimate was derived using Lincoln-Peterson mark-recapture methods (Seber 2002) and PIT tag observations of both Chinook Salmon and steelhead at Lower Granite Dam adult detection sites. The “mark” group included all tags (both species) detected in the adult trap and the “capture” group included tags observed to cross the weir at the upstream end of the fish ladder as adults left the passage system. The proportion of tags detected leaving the passage system that were also caught in the trap each week was assumed to reflect the trap rate experienced by target species as they migrated through the ladder. The sample size of previously tagged fish detected at Lower Granite Dam influences the uncertainty in that trap rate, which is also informed by the number of adults caught in the trap and the window counts. The set trapping rate (i.e., the recorded time that the trap is open to trap adults) does not always reflect the true trapping rate or proportion of fish that are actually captured in the trap due to various issues including trap malfunctions, separation-by-code fish opening the trap more frequently than expected, and process error, among others. Therefore, we use the mark-recapture approach to estimate a “true” trapping rate.

We used PIT tag data to estimate nighttime passage and re-ascension rates, using the total number of tags passing the fish ladder for both and estimating each on a weekly basis. The nighttime passage rate was based on the count of PIT tags that migrated through the fish ladder during non-window observation hours and the total number of tags passing the fish ladder. The re-ascension rate incorporated the count of tags observed passing the upstream most detection sites in the adult fish ladder (i.e., passing the dam) and later detected re-entering the downstream end of the fish ladder at a later time and the total number of tags leaving the fish ladder. Previously, we looked for differences in nighttime passage and re-ascension rates estimated using wild fish only, versus combining hatchery and wild fish together, and found no difference. Therefore, we combine wild and hatchery PIT tagged fish observations to estimate common nighttime passage and re-ascension rates to increase sample sizes.

Model Framework

We estimated the total number of fish crossing the dam each week, based on the window counts and the total fish passing the adult trap, while also accounting for estimated nighttime passage and fallback/re-ascension rates using a state-space modeling approach (Royle and Dorazio 2008). Our model is implemented in the STADEM package for the R statistical software (R Core Team 2020). We assumed that the window counts and the estimates from the trap (fish in the trap divided by trap rate that week) were generated by processes with observation error. In the case of the trap, for example, we assumed there was sampling variation and uncertainty around our estimates of the true unknown trap rate. STADEM adjusted the window counts for the nighttime passage rate, and both window and trap estimates for the re-ascension rate to estimate the number of unique fish that crossed the dam. Finally, adult sampling data from the trap (wild, hatchery, hatchery no-clip) were used to partition the total escapement estimate by origin (Figure 1). Additional model details can be found in Appendix A. The STADEM package is available from the primary author at https://github.com/KevinSee/STADEM, and requires the use of the JAGS software (Plummer 2019) for Bayesian inference.

Simulations

We tested the STADEM model on a variety of simulated data sets. These simulated data sets contained a fixed number of unique adult fish of known origin crossing a dam, from a total of 25 fictional populations with differential run-timing (i.e., date of passage at Lower Granite Dam). Each simulated fish was given a date of ladder ascension, based on its population and the range of observed run timing for that population. Each fish was also simulated to cross the dam either while the window was open for counting, or not, and was given the chance to be "caught" in the simulated fish trap given the week when it ascended the dam, and the known trap rate that week. Fallback and re-ascension behavior was also simulated, with each fish having the possibility of falling back and re-ascending the ladder up to three times.

Our objective was to examine STADEM model estimates of origin-specific (wild, hatchery, hatchery no-clip) escapement from the combinations of two trap rate scenarios (constant and shut down for 3 weeks), two fallback/re-ascension and nighttime passage combinations, and three window count error rates; resulting in twelve different scenarios (Table 1). The simulation parameters such as proportion of origin, run-timing, nighttime passage rates, fallback and re-ascension rates and trap rates were based on observed values at Lower Granite Dam between 2010-2015. We generated 99 simulations for each scenario, and ran STADEM on each one, resulting in a total of 1,188 model runs. Further details about simulation procedures can be found in Appendix B.

We grouped the simulation results by fish origin and evaluated them by several measures. Relative bias is the difference between the simulated "truth" and the STADEM estimate, divided by the simulated "truth". We estimated the precision by examining the average coefficient of variation (CV) of the estimates. We calculated the root mean squared error (RMSE) as the square root of the mean of the squared bias in the estimate. Finally, we evaluated coverage probabilities by determining what proportion of the model results generated an estimated 95% credible interval that contained the simulated true value.

Lower Granite Application

We applied STADEM to empirical data from Lower Granite Dam for Chinook Salmon and steelhead returning to the Snake River during spawn years 2010 to 2019. Window counts for both species were accessed from DART via functions within STADEM. For Chinook Salmon, a spawn year refers to adults that migrate past the dam prior to August 17 each year and spawn that late summer and fall. For steelhead, the spawn year is defined as steelhead that migrate past Lower Granite Dam starting July 1 the previous year and prior to June 30 of the given year (e.g., spawn year 2017 steelhead migrate past Lower Granite between July 1, 2016 and June 30, 2017). Data from the adult trap was made available by Idaho Department of Fish and Game, and adult PIT tag detection data within the fish passage ladder at Lower Granite Dam was accessed from the PTAGIS regional database (https://www.ptagis.org/).

All data used in this manuscript, as well as associated code for both the simulations and the Lower Granite appllication, can be found at https://www.github.com/KevinSee/ManuscriptSTADEM.

Results

Simulations

The STADEM performance evaluation statistics were very similar for hatchery clipped (N = 70,000), hatchery no-clip (N = 5,000) and wild fish (N = 25,000). In the interest of brevity, we only present the results from wild fish, which corresponds to a medium sized escapement level.

STADEM results were very similar across all scenarios (Figure 2). Estimates of wild escapement were unbiased, with an average relative bias of 0.2–0.3%. The CV of the estimates averaged 2.0–3.0%, with higher CV's being associated with scenarios when the trap was closed for 3 weeks. The coverage probabilities always exceeded 95% across all scenarios. The RMSE was near 500 for each scenario, representing an estimate within 2% of the true value, demonstrating the accuracy of STADEM (Table 2).

Lower Granite Application

We applied STADEM to data from Lower Granite Dam for Chinook Salmon and steelhead for spawn years 2010–2019. Estimates of total escapement, as well as estimates of wild, hatchery clipped, and hatchery no-clip estimates are presented in Table 3. Estimates of total unique fish escaping past Lower Granite Dam were sometimes higher and sometimes lower than the raw window counts, indicating that the relative strength of nighttime passage and re-ascension rates differed across years. CVs ranged from 2.5-7.1% for wild fish, 2.3-5.1% for clipped hatchery fish, 3.4-8.8% for hatchery no-clip fish and 2.2-4.7% for total unique fish past Lower Granite Dam.

Weekly estimates of total escapement over Lower Granite Dam tracked the window counts and trap estimates (One example: Figure 3. Similar plots for all model runs [each species and year combination] are available on the manuscript GitHub page: https://www.github.com/KevinSee/ManuscriptSTADEM). STADEM point estimates were often between estimates based on window counts and those based on the number of fish caught in the adult trap. However, for weeks when very few fish were caught in the trap or there was more uncertainty about the trap rate, STADEM estimates tracked the window counts more closely, as seen in the second week of July 2014, in Figure 3. That year also shows the utility of STADEM in dealing with missing data, as the trap was shut down for several weeks in July and August. The model's uncertainty is always smaller than the uncertainty from the trap estimates alone, whereas the window counts alone provide no estimate of uncertainty.

Estimates of weekly nighttime passage and re-ascenstion rates did not match in most cases (Figure 4). In particular, there are several weeks when the window counts are quite large and the rates differ by as much as 10%. When nighttime passage is larger than re-ascension, the window counts will be biased low, and vice versa.

Discussion

We have presented a novel method for estimating adult salmonid escapement past a large hydroelectric facility (e.g., Lower Granite Dam) that incorporates data from window counts, a fish trap, and observations of PIT tagged fish in the adult passage ladder. Our model explicitly accounts for nighttime passage, re-ascension, and potential error in both window and trap estimates. In doing so, we demonstrated that at Lower Granite Dam, nighttime passage and re-ascension rates do not always offset each other, and assuming they do will lead to biased escapement estimates in some years. With minor adjustments this modeling framework and the STADEM package could be applied to similar migratory species at Lower Granite Dam (e.g., fall Chinook Salmon, Pacific lamprey *Lampetra tridentata*), or elsewhere, provided a fish passage barrier with a counting mechanism, a trap that can be used to sample a portion of the run and tag observation or detection infrastructure (e.g., a PIT tag detection array or similar). Our state-space model combined multiple imperfect sources of data to reduce bias in adult escapement estimates and provided quantitative estimates of uncertainty. Accurate population or group abundance estimates and uncertainty accounting for observation and process error can be particularly important when estimates are used for management and conservation decisions such as population viability analyses.

Combining data from the adult fish trap with live and video window counts provides several benefits. First, it allows us to model observer error in the window counts, which is typically unknown. If estimates rely on window counts alone, quantifying observer error is impossible. Capturing and accounting for known sources of error is prudent to minimize management decision risk. Second, by incorporating both sources of information in a state-space framework, STADEM incorporates missing data at either the observation window or adult trap seamlessly. At Lower Granite Dam, the adult trap has been closed for brief or extended periods of time (i.e., days, weeks) intermittently in five of the last ten years, often during peak run times (USACE 2010, 2011, 2012, 2013, 2015, 2016, 2017, 2018, 2019; Ogden 2016b). Trap closures are typically associated with elevated water temperatures resulting in potential fish handling stress and/or trap malfunctions (Ogden 2016a). Given predicted Pacific Northwest climate change scenarios (Zhang et al. 2019) trap closures from high water temperatures may become more commonplace in the future, amplifying the need for a modeling framework that accounts for periods of missing data while still capturing estimate uncertainty. Additionally, having a framework in place that accounts for missing periods of data will allow for increased logistic flexibility if, for example, maintenance or construction is needed at the observational window or adult trap.

STADEM could be modified and run on a weekly basis or in near real-time to provide better in-season estimates for fisheries managers. Currently, the only roadblock to this at Lower Granite Dam is the identification of hatchery no-clip fish using genetic tissue samples (Steele et al. 2013, 2019) collected at the adult trap, which currently is completed post-hoc after the trapping season. The inclusion of genetic information typically results in a reduction in wild escapement estimates and an associated increase in hatchery no-clip escapement (Hargrove et al. n.d.). However, if in-season management decisions do not require this correction or could accept the potential bias, origin calls at the trap could be used in-season as a first approximation to escapement. Final post-hoc estimates parsed by origin could then be finalized at season's end. All other data included in this model (e.g., window counts and PIT observations) are otherwise provided in near real-time by DART. Provided the Lower Granite Dam adult fish trap database was updated and available in near real-time, there are minimal obstacles for adapting the STADEM framework to provide in-season estimates of escapement.

Recently, co-managers in the Snake River basin have adopted the STADEM framework to estimate escapement of spring-summer run Chinook Salmon and steelhead past Lower Granite Dam, and returning to tributary or population specific spawning areas (Kinzer et al. 2020a, 2020b). Estimates of species and origin-specific escapement at Lower Granite Dam, including known uncertainty, are available to further parse into sex- or age-structured escapement estimates (e.g., Camacho et al. 2018; Schrader et al. 2013) that are important for fisheries management and productivity monitoring of wild populations. As an example, STADEM is being applied at Lower Granite Dam to estimate the total unique wild fish migrating past the dam. Estimates of fish passing the dam are then combined with estimated movement or transition probabilities based on PIT tag observations at instream PIT tag detection systems throughout the Snake River basin, similar to Waterhouse et al. (2020), to estimate escapement to Snake River populations and locations throughout the basin (Orme et al. 2019). Combined, escapement estimates from STADEM and movement probability estimates provide abundance estimates to given tributaries or populations. With sex and age data collected at the adult fish trap (Hargrove et al. 2019), this approach provides necessary information to evaluate productivity and population viability for select Snake River Chinook Salmon and steelhead groups (Kinzer et al. 2020b).

Although STADEM was developed with salmonid escapement at Lower Granite Dam in mind, it could be applied to any migratory fish species at locations with similar monitoring infrastructure. Justification and infrastructure exist for applying a modified STADEM framework for fish passing Bonneville Dam, the lowest dam on the Columbia River, or Priest Rapids Dam in the upper Columbia River. Both locations currently trap a sub-sample of passing Chinook Salmon and/or steelhead for biological information and use window counts as a surrogate of true escapement. However, each has at least some similar problems to those observed at Lower Granite Dam such as unaccounted observer and sampling error, nighttime passage, and/or re-ascension. Certainly, estimating an unbiased total return to the entire Columbia River basin (i.e., Bonneville Dam) and Upper Columbia River with uncertainty would benefit managers and decision making.

Acknowledgements

Funding for this study and development of the STADEM model was partially provided by the Bonneville Power Administration under project 2003-017-00. Special thanks to Darren Ogden and staff at the Lower Granite Dam adult trap for their hard work and diligent data collection. Thank you to personnel at the Idaho Department of Fish and Game, particularly Paul Bunn, Tim Copeland, and Bill Schrader, for providing access to data from the adult fish trap and conceptualizing methods, and to Matthew Campbell and staff at the Eagle Fish Genetics Laboratory for analyzing genetic samples. Special thanks to Columbia Basin Research staff and the Columbia River Data Access in Real Time (DART) application, and Susannah Iltis in particular. And finally, thank you to Rick Orme and Brice Semmens for their contributions to the development of STADEM, and all the other people who have contributed through productive critique and conversations.

References

Boggs, C., M. L. Keefer, C. Peery, T. C. Bjornn, and L. C. Stuehrenberg. 2004. Fallback, reascension, and adjusted fishway escapement estimates for adult Chinook Salmon and steelhead at Columbia and Snake River dams. Transactions of the American Fisheries Society 133(4):932–949.

Bue, B. G., S. M. Fried, S. Sharr, D. G. Sharp, J. A. Wilcock, and H. J. Geiger. 1998. Estimating salmon escapement using area-under-the-curve, aerial observer efficiency, and stream-life estimates: The Prince William Sound pink salmon example. North Pacific Anadromous Fish Commission Bulletin 1:240–250.

Camacho, C. A., J. Powell, M. Davison, M. E. Dobos, W. C. Schrader, T. Copeland, and M. Campbell. 2018. Wild adult steelhead and Chinook Salmon abundance and composition at Lower Granite Dam, spawn year 2017. Idaho Department of Fish; Game, Annual Report 19-09.

Campbell, M. R., C. C. Kozfkay, T. Copeland, W. C. Schrader, M. W. Ackerman, and S. R. Narum. 2012. Estimating abundance and life history characteristics of threatened wild Snake River steelhead stocks by using genetic stock identification. Transactions of the American Fisheries Society 141(5):1310–1327.

Crozier, L. G., M. M. McClure, T. Beechie, S. J. Bograd, D. A. Boughton, M. Carr, T. D. Cooney, J. B. Dunham, C. M. Greene, M. A. Haltuch, and others. 2019. Climate vulnerability assessment for Pacific salmon and steelhead in the California current large marine ecosystem. PloS one 14(7):e0217711. Public Library of Science San Francisco, CA USA.

Dauble, D. D., and R. P. Mueller. 2000. Upstream passage monitoring: Difficulties in estimating survival for adult Chinook Salmon in the Columbia and Snake Rivers. Fisheries 25(8):24–34. Taylor & Francis.

Hargrove, J., C. Camacho, W. Schrader, J. Powell, T. Delomas, J. Hess, S. Narum, and M. Campbell. (n.d.). Parentage-based tagging improves escapement estimates for ESA-listed adult Chinook Salmon and steelhead in the Snake River basin.

Hargrove, J. S., T. A. Delomas, and M. Davison. 2019. Chinook and steelhead genotyping for genetic stock identification at Lower Granite Dam. Idaho Department of Fish and Game, 19-08.

Hatch, D. R., D. R. Pederson, and J. Fryer. 1994. Feasibility of documenting and estimating adult fish passage at large hydroelectric facilities in the snake river using video technology; 1993 final report. Columbia River Inter-Tribal Fish Commission.

Hess, J. E., J. M. Whiteaker, J. K. Fryer, and S. R. Narum. 2014. Monitoring stock-specific abundance, run timing, and straying of Chinook Salmon in the Columbia River using genetic stock identification (GSI). North American Journal of Fisheries Management 34(1):184–201.

Joint Columbia River Management Staff. 2019. 2019 Joint Staff Report: Stock status and fisheries for Spring Chinook, Summer Chinook, Sockeye, steelhead, and other species. Oregon Department of Fish & Wildlife; Washington Department of Fish & WIldlife.

Kinzer, R. N., H. Arnsberg Bill, A. Maxwell, R. Orme, C. Rabe, and S. Vatland. 2020a. Snake River basin adult Chinook Salmon and steelhead monitoring 2019 annual report. Nez Perce Tribe, Department of Fisheries Resources Management, Research Division, Lapwai, ID.

Kinzer, R., R. Orme, M. Campbell, J. Hargrove, and K. See. 2020b. Report to NOAA Fisheries for 5-year ESA status review: Snake River basin steelhead and Chinook salmon population abundance, life history, and diversity metrics calculated from in-stream PIT- tag observations (SY2010-SY2019). IPTDSW (In-stream PIT-tag detection systems workgroup).

McClure, M. M., E. E. Holmes, B. L. Sanderson, and C. E. Jordan. 2003. A large-scale, multi-species status assessment: Anadromous salmonids in the Columbia River basin. Ecological Applications 13(4):964–989. Wiley Online Library.

McElhany, P., M. H. Rucklelshaus, M. J. Ford, T. C. Wainwright, and E. P. Bjorkstedt. 2000. Viable salmonid populations and the recovery of evolutionarily significant units. U.S. Dept. Commer., NOAA Tech. Memo. NMFS-NWFSC-42.

National Marine Fisheries Service. 2019. Endangered Species Act (ESA) Section 7(a)(2) Biological Opinion and Magnuson-Stevens Fishery Conservation and Management Act Essential Fish Habitat Response. Continued Operation and Maintenance of the Columbia River System. National Marine Fisheries Service, NMFS Consultation WCRO-2019-02395.

Nehlsen, W., J. E. Williams, and J. A. Lichatowich. 1991. Pacific salmon at the crossroads: Stocks at risk from California, Oregon, Idaho, and Washington. Fisheries 16(2):4–21. Wiley Online Library.

Northwest Fisheries Science Center. 2015. Status review update for Pacific salmon and steelhead listed under the Endangered Species Act: Pacific Northwest.

NPCC. 2014. Columbia River basin fish and wildlife program. Northwest Power; Conservation Council.

Ogden, D. A. 2014. Operation of the adult trap at Lower Granite Dam 2013. NOAA National Marine Fisheries Service.

Ogden, D. A. 2016a. Operation of the adult trap at Lower Granite Dam 2015. NOAA National Marine Fisheries Service.

Ogden, D. A. 2016b. Operation of the adult trap at Lower Granite Dam 2014. NOAA National Marine Fisheries Service.

Orme, R., R. Kinzer, and C. Albee. 2019. Population and tributary level escapement estimates of Snake River natural-origin spring/summer Chinook Salmon and steelhead from in-stream PIT tag detection systems - 2019 annual report. Nez Perce Tribe, Department of Fisheries Resources Management, Research Division, Lapwai, ID.

Plummer, M. 2019. Rjags: Bayesian graphical models using mcmc.

R Core Team. 2020. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Royle, J. A., and R. M. Dorazio. 2008. Hierarchical modeling and inference in ecology: The analysis of data from populations, metapopulations and communities. Elsevier.

Schrader, W. C., M. P. Corsi, P. Kennedy, M. W. Ackerman, M. R. Campbell, K. K. Wright, and T. Copeland. 2013. Wild adult steelhead and Chinook salmon abundance and composition at Lower Granite dam, spawn year 2011. Idaho Department of Fish; Game, Report 13-15.

Seber, G. A. F. 2002. The estimation of animal abundance and related parameters. Blackburn Press Caldwell, New Jersey.

Shumway, R. H., and D. S. Stoffer. 2010. Time series analysis and its applications: With R examples. Springer.

Steele, C. A., E. C. Anderson, M. W. Ackerman, M. A. Hess, N. R. Campbell, S. R. Narum, and M. R. Campbell. 2013. A validation of parentage-based tagging using hatchery steelhead in the Snake River basin. Canadian Journal of Fisheries and Aquatic Sciences 70(7):1046–1054. NRC Research Press.

Steele, C. A., M. Hess, S. Narum, and M. Campbell. 2019. Parentage-based tagging: Reviewing the implementation of a new tool for an old problem. Fisheries. Wiley Online Library.

Steinhorst, K., T. Copeland, M. W. Ackerman, W. C. Schrader, and E. C. Anderson. 2017. Abundance estimates and confidence intervals for the run composition of returning salmonids. Fishery Bulletin 115(1):1–12.

USACE. 2010. Annual fish passage report Columbia and Snake rivers. U.S. Army Corps of Engineers.

USACE. 2011. Annual fish passage report Columbia and Snake rivers. U.S. Army Corps of Engineers.

USACE. 2012. Annual fish passage report Columbia and Snake rivers. U.S. Army Corps of Engineers.

USACE. 2013. Annual fish passage report Columbia and Snake rivers. U.S. Army Corps of Engineers.

USACE. 2015. Annual fish passage report Columbia and Snake rivers. U.S. Army Corps of Engineers.

USACE. 2016. Annual fish passage report Columbia and Snake rivers. U.S. Army Corps of Engineers.

USACE. 2017. Annual fish passage report Columbia and Snake rivers. U.S. Army Corps of Engineers.

USACE. 2018. Annual fish passage report Columbia and Snake rivers. U.S. Army Corps of Engineers.

USACE. 2019. Annual fish passage report Columbia and Snake rivers. U.S. Army Corps of Engineers.

Waterhouse, L., J. White, K. See, A. Murdoch, and B. X. Semmens. 2020. A Bayesian nested patch occupancy model to estimate steelhead movement and abundance. Ecological Applications:e02202. Wiley Online Library.

Williams, T. H., B. C. Spence, D. A. Boughton, R. C. Johnson, E. G. R. Crozier, N. J. Mantua, M. R. O'Farrell, and S. T. Lindley. 2016. Viability assessment for Pacific salmon and steelhead listed under the Endangered Species Act: Southwest. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-SWFSC-564.

Wright, K. K., W. C. Schrader, L. Reinhardt, K. Hernandez, C. Hohman, and T. Copeland. 2015. Process and methods for assigning ages to anadromous salmonids from scale samples. Idaho Department of Fish; Game, 15-03.

Zhang, X., H.-Y. Li, Z. D. Deng, L. R. Leung, J. R. Skalski, and S. J. Cooke. 2019. On the variable effects of climate change on Pacific salmon. Ecological Modelling 397:95–106. Elsevier.

Tables

Table 1: Summary of simulation scenarios including varying adult trapping, fallback and re-ascension, nighttime passage, and window count error rates used to evaluate the performance of STADEM.

Scenario	Trap rate	Fallback & Re-ascension rate	Nighttime passage rate	Window count error
Baseline	0.15	0.06	0.06	No Error
Baseline Err L	0.15	0.06	0.06	5% Error
Baseline Err H	0.15	0.06	0.06	10% Error
N-R	0.15	0.10	0.05	No Error
N-R Err L	0.15	0.10	0.05	5% Error
N-R Err H	0.15	0.10	0.05	10% Error
N-R trap down	0.15 and 0.00 3 weeks	0.06	0.06	No Error
N-R trap down Err L	0.15 and 0.00 3 weeks	0.06	0.06	5% Error
N-R trap down Err H	0.15 and 0.00 3 weeks	0.06	0.06	10% Error
Trap down	0.15 and 0.00 3 weeks	0.10	0.05	No Error
Trap down Err L	0.15 and 0.00 3 weeks	0.10	0.05	5% Error
Trap down Err H	0.15 and 0.00 3 weeks	0.10	0.05	10% Error

Table 2: Summary statistics, including relative bias, mean coefficient of variation (CV), root mean squared error (RMSE) and 95% credible interval coverage for results from each of the twelve simulation scenarios.

Scenario	Relative bias	Mean CV	RMSE	Coverage
Baseline	0.002	0.024	495	0.978
Baseline Err L	0.002	0.024	473	0.984
Baseline Err H	0.002	0.024	502	0.978
Trap Down	0.003	0.030	495	0.996
Trap Down Err L	0.002	0.030	503	0.998
Trap Down Err H	0.003	0.030	527	0.994
N-R	-0.001	0.023	459	0.988
N-R Err L	0.002	0.024	428	0.990
N-R Err H	0.002	0.024	462	0.984
N-R Trap Down	0.002	0.030	501	0.994
N-R Trap Down Err L	0.003	0.030	515	0.996
N-R Trap Down Err H	0.003	0.030	527	0.994

Table 3: Window counts, and estimates of total, wild, hatchery and hatchery no-clip escapement, with coefficients of variation in parenthesis, for Chinook Salmon and steelhead from spawn years 2010 to 2019.

Species	Year	Window counts	Total	Wild	Hatchery	Hatchery no-clip
Chinook	2010	134,684	131,565 (0.047)	26,563 (0.054)	97,995 (0.048)	7,007 (0.078)
Chinook	2011	134,594	122,977 (0.024)	24,566 (0.029)	93,364 (0.025)	5,047 (0.046)
Chinook	2012	84,771	83,081 (0.047)	21,206 (0.043)	57,379 (0.051)	4,495 (0.065)
Chinook	2013	70,966	69,273 (0.023)	19,023 (0.032)	44,011 (0.027)	6,238 (0.047)
Chinook	2014	114,673	106,460 (0.034)	28,339 (0.036)	68,770 (0.038)	9,351 (0.048)
Chinook	2015	132,432	132,527 (0.029)	23,752 (0.043)	98,292 (0.031)	10,483 (0.059)
Chinook	2016	81,753	84,216 (0.027)	17,187 (0.029)	59,031 (0.03)	7,997 (0.035)
Chinook	2017	48,192	42,902 (0.038)	5,137 (0.045)	34,265 (0.04)	3,500 (0.049)
Chinook	2018	42,232	39,416 (0.037)	6,965 (0.044)	28,853 (0.039)	3,597 (0.052)
Chinook	2019	29,617	27,293 (0.041)	4,771 (0.045)	20,578 (0.043)	1,943 (0.06)
Steelhead	2010	323,382	347,285 (0.035)	45,240 (0.037)	265,983 (0.036)	36,063 (0.037)
Steelhead	2011	208,296	216,633 (0.036)	45,677 (0.036)	147,937 (0.037)	23,019 (0.039)
Steelhead	2012	180,320	190,171 (0.022)	40,278 (0.025)	138,918 (0.023)	10,975 (0.037)
Steelhead	2013	109,186	120,025 (0.035)	24,884 (0.039)	84,854 (0.036)	10,286 (0.057)
Steelhead	2014	108,154	116,913 (0.039)	28,043 (0.071)	80,911 (0.043)	7,959 (0.08)
Steelhead	2015	165,591	175,285 (0.032)	47,606 (0.04)	117,245 (0.032)	10,433 (0.056)
Steelhead	2016	136,126	143,646 (0.033)	35,962 (0.039)	101,446 (0.033)	6,237 (0.06)
Steelhead	2017	101,827	103,524 (0.035)	15,311 (0.038)	79,942 (0.035)	8,270 (0.062)
Steelhead	2018	74,097	69,180 (0.033)	10,043 (0.039)	56,537 (0.034)	2,601 (0.055)
Steelhead	2019	51,818	53,738 (0.036)	8,639 (0.06)	41,291 (0.033)	3,808 (0.088)

List of Figures

Figures

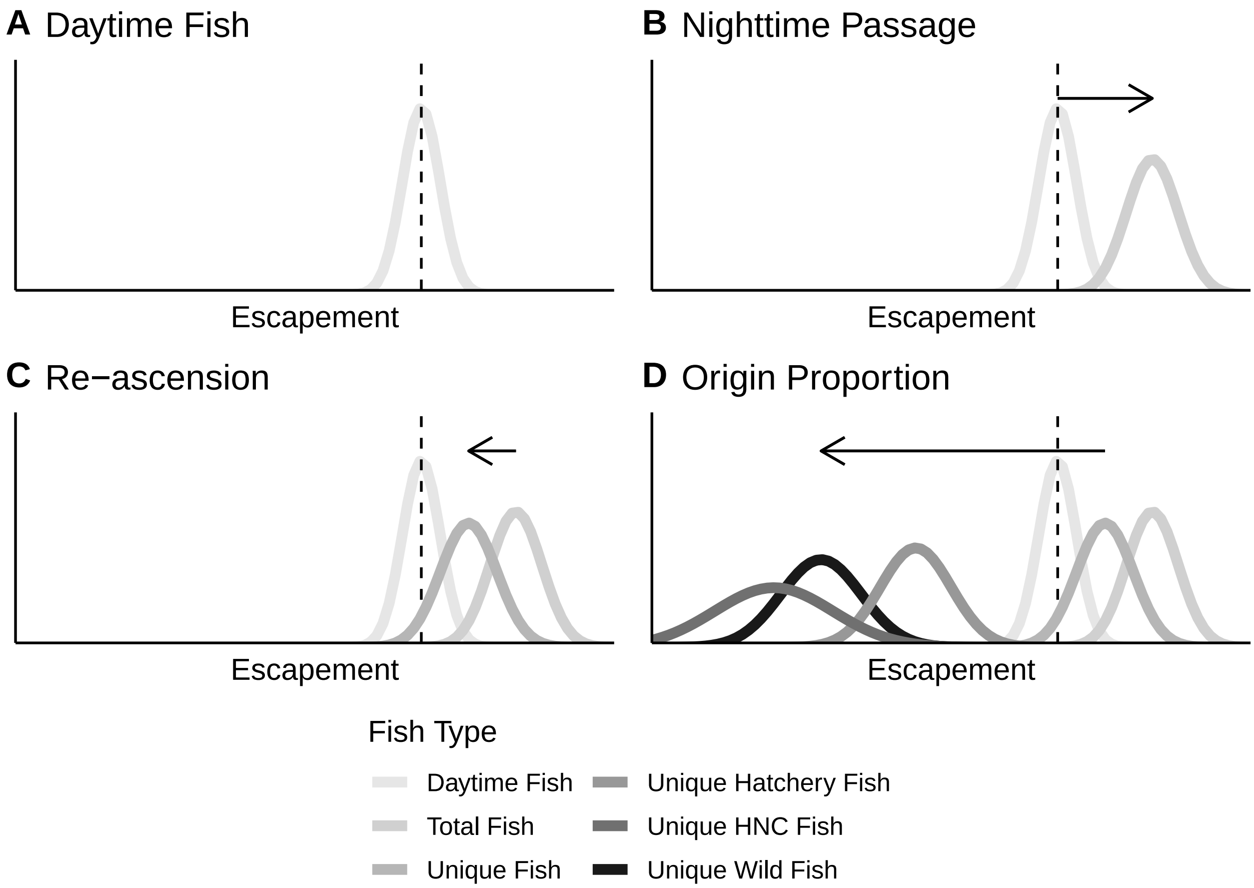

Figure 1: Schematic showing the STADEM model framework. (A) shows the posterior of the estimate of fish crossing the dam while the window is open (dashed line shows observed window counts). That estimate is divided by the nighttime passage rate (B). The total fish is then discounted by the re-ascension rate to estimate unique fish (C). Those unique fish are then multiplied by the proportions by origin (D), to estimate unique fish by origin.

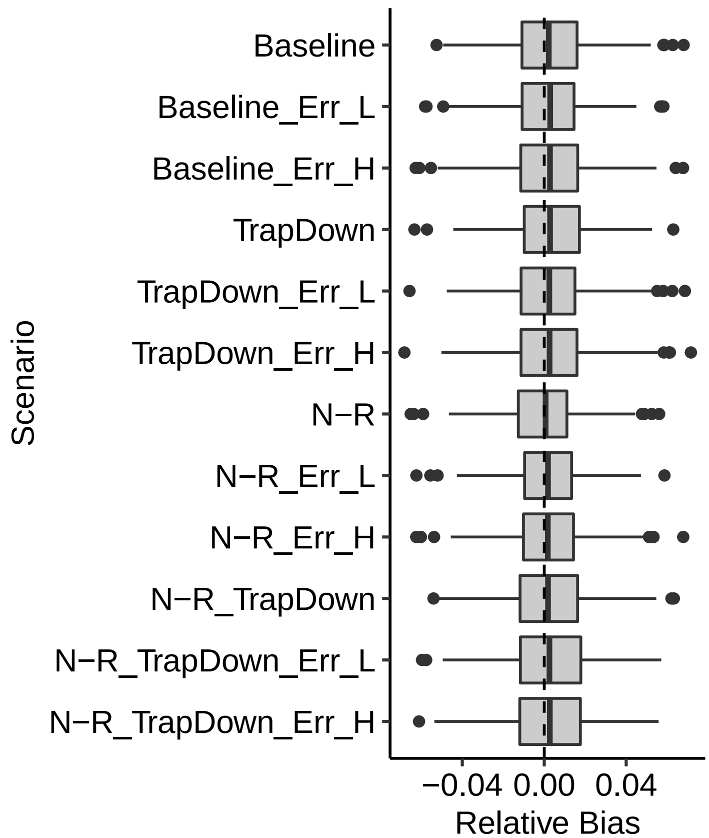

Figure 2: Boxplots of the relative bias of STADEM estimates for wild escapement across various scenarios (See Table 1).

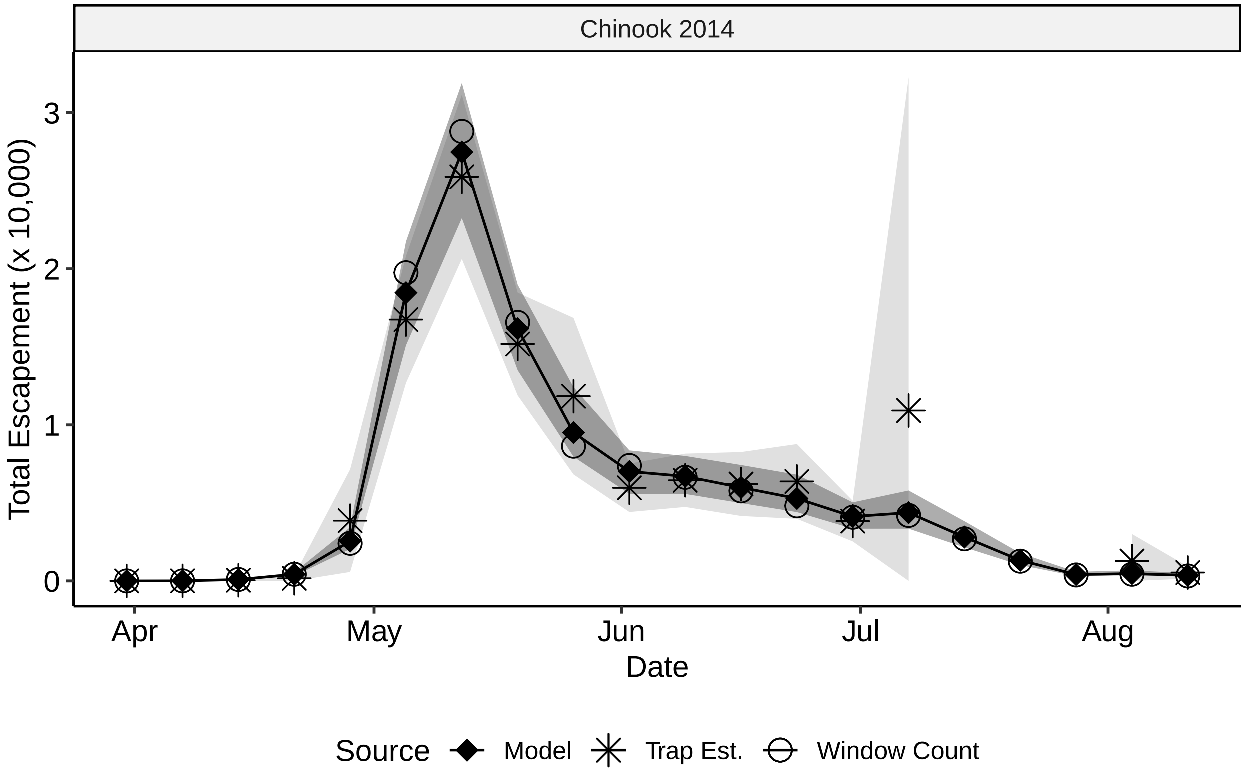

Figure 3: Time-series plot showing estimates of total escapement for Chinook Salmon in 2014, including window counts, trap estimates and STADEM estimates. The dark gray ribbon represents the 95% credible intervals for STADEM estimates, while the light gray ribbon represents the 95% confidence intervals for the trap estimates.

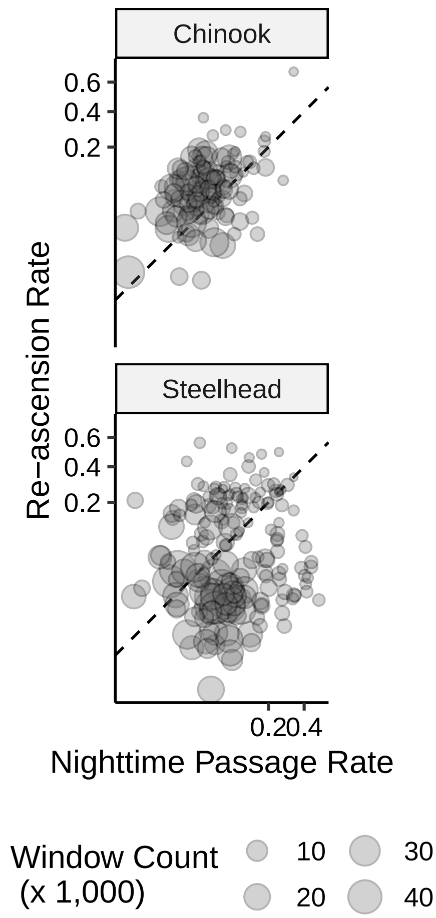

Figure 4: Nighttime passage rate plotted against re-ascension rate on the logit scale, calculated from observed PIT tags for each week of spawn years 2010-2019. The size of each point is proportional to the window count that week. The dashed line is the 1-1 line.

Appendix A - STADEM Model Description

Total and Weekly Escapement

Escapement at Lower Granite Dam (LGD) is estimated by combining two independent observations (trap catches and window counts) of the true number of fish crossing the dam in a state-space model (Royle and Dorazio 2008) with a weekly time-step. Both are assumed to be corrupted observations of the true unknown number of fish crossing LGD each week. The log of the true number of fish crossing (X_t), is modeled as a random walk process (Shumway and Stoffer 2010).

$$\ln(X_t) = \ln(X_{t-1}) + e_t$$
$$e_t \sim \mathcal{N}(0, \sigma_X^2)$$

The number of fish caught in the trap, Y_t^T, for week t is modeled as a binomial process based on the unknown true trap rate that week, ν_t, and the unknown true number of fish crossing the dam that week, X_t. The estimate of the true weekly trap rate is derived based on previously PIT-tagged spring/summer Chinook and steelhead who are crossing LGD that week, using a Lincoln-Peterson mark-recapture model (Seber 2002). The fish, from both species, caught in the trap that week are considered the "mark" group (m_t), and all the previously PIT tagged fish who are detected at the upper end of the LGD fish ladder that week are considered the second "capture" group, M_t (which includes recaptures of the the "marked" fish). The proportion of previously marked fish that are caught in the adult trap, m/M can be modeled with a binomial distribution using the same trap rate parameter, ν_t. Although the group of previously PIT tagged fish is not assumed to be representative of the overall run, the rate at which they are caught in the trap should be the same rate that the overall run experiences. The more tagged fish crossing the dam in a particular week, the more certain we can be of the true trap rate.

$$m_t \sim \text{Bin}\left(\nu_t, M_t\right)$$
$$Y_t^T \sim \text{Bin}\left(\nu_t, X_t\right)$$

The number of fish counted at the window, Y_t^W, is modeled as a (potentially) over-dispersed negative binomial process, with an expected value of X_t^{day}, the number of fish crossing the dam while the window is open. This is simply the total number of fish crossing that week, X_t, multiplied by the proportion of fish crossing while the window is open for counting, θ_t, calculated on a weekly basis. In the formula below, p_t is the proportion of fish observed at the window and r is the shape parameter. If r is estimated to be small it provides evidence for over-dispersion, and as it grows very large, the negative binomial distribution behaves like a Poisson distribution.

$$X_t^{day} = X_t * \theta_t$$
$$p_t = \frac{r}{\left(r + X_t^{day}\right)}$$
$$Y_t^W \sim \text{NegBin}\left(p_t, r\right)$$

Thus, the unknown true number of fish crossing LGD each week, X_t, is estimated from two different data source: window counts and fish sampled in the trap. The window counts provide an estimate (with some potential observer error) of the fish crossing during daytime hours, while the fish in the trap, when expanded by the estimated true trap rate, provide an estimate of the total fish crossing that week. For weeks when we have a more precise estimate of the trap rate (i.e. weeks when many previously PIT tagged fish are crossing LGD), STADEM will tend to favor the estimate of total escapement based on the trap data, whereas when that trap rate is more uncertain (e.g. fewer PIT tagged fish to use in estimating the trap rate), STADEM will rely more on the window counts to estimate total escapement. During peak run times, when many fish are crossing LGD, estimates based on trap data and trap rates will be more precise, while estimates from the window counts may have more observation error due to densely crowded (and visually obstructed) fish passing the window. For weeks when the trap is down, STADEM relies exclusively on the window counts and nighttime passage data, but there will be more uncertainty in the estimates.

Day-time Passage and Re-ascension Rates

There are two other processes that must be accounted for: first, the proportion of fish that cross the dam while the window is closed for counting (nighttime passage rate), and second, the proportion of fish that are crossing the dam multiple times (re-ascension rate) and therefore potentially double-counted. Both rates can be estimated from previously PIT tagged fish that are crossing the dam each week.

The proportion of fish passing the window during non-operational hours, nighttime passage rate, is just the complement of the rate of fish passing during the day when the window is operating. The daytime passage rate for week t, θ_t, is modeled as a random walk process and estimated from a binomial distribution based on the number of PIT tags observed to cross the dam during operational hours, y_t^{day}, and the total number of PIT tags observed to cross the dam at any point that week, N_t (Shumway and Stoffer 2010).

$$
\begin{aligned}
y_t^{day} &\sim \text{Bin}\left(\theta_t, N_t\right) \\
\text{logit}(\theta_t) &= \text{logit}\left(\theta_{t-1}\right) + g_t \\
g_t &\sim \mathcal{N}(0, \sigma_\theta^2)
\end{aligned}
$$

The number of total fish crossing Lower Granite differs from the number of unique fish crossing Lower Granite because some fish fallback and re-ascend the dam. These fish are potentially double-counted at the window, and have the potential to be caught in the fish trap more than once. The number of tags known to be re-ascending the dam each week, y_t^{reasc}, is modeled as a binomial process based on the estimated re-ascension rate, η_t, and the total number of tags crossing the dam that week, N_t. The logit of the re-ascension rate is modeled as a random walk process similar to day-time passage (Shumway and Stoffer 2010).

$$y_t^{reasc} \sim \text{Bin}\left(\eta_t, N_t\right)$$
$$\text{logit}\left(\eta_t\right) = \text{logit}\left(\eta_{t-1}\right) + f_t$$
$$f_t \sim \mathcal{N}(0, \sigma_\eta^2)$$

Origin Proportions

After estimating the total number of fish to have crossed Lower Granite each week, X_t, the total must be further refined into the number of wild fish, $X_{w,t}$, hatchery clipped fish, $X_{hc,t}$ and hatchery no-clip fish, $X_{hnc,t}$. This is done by estimating a weekly origin proportion vector, ω_t based on the random sample of fish caught in trap that week, Y_t^T. The observed number of wild, $Y_{w,t}^T$, hatchery clipped, $Y_{hc,t}^T$, and hatchery no-clip, $Y_{hnc,t}^T$, fish caught in the trap that week is assumed to come from a multinomial distribution with probability vector ω_t. The log-odds ratio of the proportions in ω_t, in relation to the proportion of clipped hatchery fish, $\omega_{hc,t}$ is modeled as a random walk, so it can change through time. This allows the proportions of wild, hatchery clipped and hatchery no-clip fish to shift throughout the season, based on the data available from the fish trap.

$$\left(Y_{w,t}^T, Y_{hc,t}^T, Y_{hnc,t}^T\right) \sim \text{Multinom}\left(\omega_t, Y_t^T\right)$$
$$\omega_t = \frac{\exp(\phi_t)}{\sum \exp(\phi_t)}$$
$$\phi_{hc,t} = 0$$
$$\phi_{w,t} = \ln\left(\frac{\omega_{w,t}}{\omega_{hc,t}}\right)$$
$$\phi_{hnc,t} = \ln\left(\frac{\omega_{hnc,t}}{\omega_{hc,t}}\right)$$
$$\phi_{w,t} = \phi_{w,t-1} + d_{w,t}$$
$$\phi_{hnc,t} = \phi_{hnc,t-1} + d_{hnc,t}$$
$$d_{w,t} \sim \mathcal{N}(0, \sigma_\omega^2)$$
$$d_{hnc,t} \sim \mathcal{N}(0, \sigma_\omega^2)$$

Finally, the number of unique fish crossing Lower Granite each week, $X_{w,t}$, is the product of the total fish crossing that week, X_t multiplied by one minus the re-ascension rate, $(1 - \eta_t)$, and the origin proportion vector, ω_t.

$$\begin{bmatrix} X_{w,t} \\ X_{hc,t} \\ X_{hnc,t} \end{bmatrix} = X_t * (1 - \eta_t) * \begin{bmatrix} \omega_{w,t} \\ \omega_{hc,t} \\ \omega_{hnc,t} \end{bmatrix}$$

Model Fitting

The model was fit using the JAGS program (Plummer 2019), run with R software (R Core Team 2020). Variance parameters $\sigma_X, \sigma_\eta, \sigma_\theta$, and σ_ω, as well as the initial abundance, X_1, and the overdispersion parameter of the negative binomial, r, were given half-Cauchy priors with mean of 0 and scale of 100. The initial day-time passage and re-ascension rates, θ_1 and η_1 were given Uniform(0,1) priors. Finally, $\phi_{w,1}$ and $\phi_{hnc,1}$ were given priors of Uniform(-3,3), in an effort to make ω_1 as uniformative as possible.

Appendix B - Simulation Details

To simulate fish passing a dam, an $\mathbb{R}$ software function was developed (R Core Team 2020). The function randomly samples observations from assumed probability distribution functions (pdf) with known parameters. Total unique fish, N, and a vector, ω, containing the proportions of wild (w), hatchery (h) and hatchery no-clip (hnc) fish passing the dam is set to establish known "truths" of escapement by origin.

$$[N_w, N_h, N_{hnc}] = N * [\omega_w, \omega_h, \omega_{hnc}]$$

Escapement of each origin is then randomly divided across a set number of populations, n, by randomly drawing proportions, $\phi_{j,p}$, of origin group j in each population p using a Dirichlet pdf. The Dirichlet function is parameterized from a vector, ζ_j, containing 1's and 0's designating populations with origin j fish returning. For each population p, $\zeta_{j,p}$ is drawn from a Bernoulli pdf using the proportion of populations that contain each origin, τ_j. Wild fish are assumed to be in all populations; $\tau_w = 1.0$. The product of sampled population proportions $\phi_{j,p}$ and fixed N_j yields a random variable of abundance for each origin in each population, $N_{j,p}$. Summing across origin abundances then gives a random total population abundance, N_p, crossing the dam.

$$\begin{aligned}
\zeta_{j,p} &\sim \text{Bernoulli}(\tau_j) \\
\left[\phi_{j,p=1}, ..., \phi_{j,p=n}\right] &\sim \text{Dir}\left(\zeta_{j,p=1}, ..., \zeta_{j,p=n}\right) \\
N_{j,p} &= N_j * \phi_{j,p} \\
N_p &= \sum_{j \in w,h,hnc} N_{j,p}
\end{aligned}$$

Mean arrival date, $\bar{a}_p$, for each population returning to the dam is drawn from a normal pdf with hyper-parameters μ_a and σ_a^2. Similarly, the variance or spread in run-timing within populations is the absolute value of random variables drawn from a normal pdf with hyper-parameters μ_s and σ_s^2.

$$\left[\bar{a}_p, ..., \bar{a}_n\right] \sim \mathcal{N}(\mu_a, \sigma_a^2)$$
$$\left[s_p, ..., s_n\right] \sim \left|\mathcal{N}(\mu_s, \sigma_s^2)\right|$$

After sampling the mean date of arrival and variances for each population, the date of arrival, $a_{i,p}$, for individual fish, i, within each population are drawn from a normal pdf with population parameters $\bar{a}_p$ and s_p^2. This simulates a random arrival day that is similar for all fish returning to the same population, regardless of origin.

$$date_{i,p} \sim \mathcal{N}(\bar{a}_p, s_p^2)$$

To model different fish behavior and dam operational scenarios, seven additional attributes are randomly assigned to each individual fish. Each attribute is randomly assigned a TRUE/FALSE using a Bernoulli pdf and a fixed probability parameter. Fish passage during the day-time (i.e., during periods of window operation) is modeled using one minus the night-time passage rate $(1-\nu)$. Window observations are conditioned on fish passing during the day and being observed at a set rate, γ. Whether fish i is sampled by the adult trap is modeled on the weekly set trap rate, δ_t. The rate of previously PIT-tagged fish is determined by λ, and their subsequent detection at the ladder PIT antenna is governed by κ. Fallback behavior is modeled with a common rate across all populations, ψ. Re-ascension occurs with probability ρ, conditioned on fish i falling back. If fish i falls back and re-ascends, the entire process described above is repeated, with some time-lag between initial ascension and re-ascension that is governed by a Poisson pdf with mean = 2 days. Fish may fallback and re-ascend up to 3 times, allowing for the possibility of the same fish being counted or trapped multiple times.

$$
\begin{aligned}
day_i &\sim \text{Bern}(1-\nu) \\
window_i &\sim \text{Bern}(\gamma \times day_i) \\
trapped_i &\sim \text{Bern}(\delta_t) \\
tagged_i &\sim \text{Bern}(\lambda) \\
ladder_i &\sim \text{Bern}(\kappa \times tagged_i) \\
fallback_i &\sim \text{Bern}(\psi) \\
re-ascend_i &\sim \text{Bern}(\rho \times fallback_i)
\end{aligned}
$$

Simulation parameters for model evaluations were set to mimic typical escapement of spring/summer Chinook Salmon to LGD with similar origin proportions, marking rates and run timing as those observed from return years 2010 - 2015. Escapement of each origin (N_j) was set at 25,000 wild, 70,000 hatchery and 5,000 hatchery no-clips spread randomly across 25 populations (n). Of the 25 populations, each had a 1.0 probability of containing wild fish, 0.50 probability of having hatchery fish and 0.15 probability of receiving hatchery no-clip (τ_j); resulting in an expected 25 wild, 12.5 hatchery and 3.75 hatchery no-clip populations. Mean arrival dates and variability were estimated from PIT-tag detection data queried from the Columbia Basin Research Data Access in Real Time (DART) website and organized by release subbasin. Mean arrival date across all subbasins and 2010 - 2015 return years was June 19th ($\mu_a = 171$) with a standard deviation of 13 days (σ_a). While the observed spread (i.e., variance) of arrival dates within subbasins was determined to have a mean (μ_s) of 22 days and a standard deviation of 7 days (σ_s).

For the specific simulated scenarios, we were interested in STADEM model estimates of origin specific escapement from the combinations of two separate trapping rates, two fallback, re-ascension and night-passage combinations and three window count error rates; resulting in twelve different scenarios. First, trapping rates were set static at 0.15 across all weeks for six scenarios to mimic an optimum trap operation for an expected return of 25,000 wild fish (i.e., trap $\approx$ 4,000 wild fish).

For the remaining six scenarios, trapping rates for weeks 30, 31 and 32 (i.e., July 22^{nd} to August 11^{th}) were changed to 0.00 to test STADEM sensitivities to potential trap shut downs similar to those observed in 2013, 2014 and 2015 (Ogden 2014, 2016b, 2016a). To simulate and control the number of re-ascending and night-time passing fish to model response, we altered fallback and night-time passage rates while holding the re-ascension rate constant at $\rho = 1.0$. Altering fallback rates and holding re-ascension constant allowed for a more simple control of the number of fish re-ascending; because the number of re-ascending fish is a function of the number of fallbacks and the re-ascension rate. Six scenarios had equal rates of fallback and night-time passage set at $\psi = \nu = 0.06$ (Boggs et al. 2004) which means other estimator assumptions (Schrader et al. 2013). The other six scenarios set fallback at $\psi = 0.10$ and night-time passage at $\nu = 0.05$ to create a 5.0% positive bias of unique fish at the window. A potential 5.0% weekly bias was determined from PIT-tag data and within the range of observed weekly difference for return years 2010 - 2015 (Figure 4). Finally, we desired to test the sensitivities of STADEM to potential rates of window count error; 0%, 5% and 10% (Hatch et al. 1994). To simulate window count error, we assumed the observed daily count was a random variable from a normal distribution with a mean equal to the true daily count, and a standard deviation equal to the applied error rate (i.e., 0%, 5%, 10%) multiplied by the true daily count. This method simulated observed counts as unbiased, and allowed for possible under and overcounts at the window.

All code for simulating data and fitting STADEM to that data can be found at https://www.github.com/KevinSee/Ma