

Assessing seasonal and biological indices of juvenile Chinook Salmon for freshwater decision triggers that increase ocean survival

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Abstract: Decision triggers, used in adaptive management frameworks to decide when a specific management action will be implemented, are often informed by monitoring data. The identification and application of decision triggers is highly relevant to endangered fishes migrating through regulated rivers, as examined in the current study. The main goal was to determine whether seasonal patterns of behavioral, physical, and physiological indices of juveniles were related to subsequent smolt-to-adult return (SAR) survival and, if so, to determine whether these indices could be used to guide decisions related to the mitigation strategy of the juvenile fish transportation program in the Federal Columbia River Power System (Pacific Northwest, USA). Hatchery yearling Chinook Salmon (*Oncorhynchus tshawytscha* Walbaum in Artedi, 1792) were collected over the migration season at 3 dams in the hydrosystem and measured for fork length, wet mass, Fulton's K (or condition factor), Na^+/K^+ -ATPase (NKA) activity (or smoltification index), and % dry mass (or index of energetic reserves and smoltification). We estimated SAR survival from passive integrated transponder-tagged fish representative of our field samples and assessed its relationship to our fish indices, as well as indices of transported vs run-of-river passage and distance of sampling site to ocean. SAR survival was associated to interaction effects between juvenile fish transportation and % dry mass or NKA activity. Transported hatchery Chinook Salmon with dry mass <23% of whole fish wet mass and NKA activity >7 $\mu\text{mol ADP mg protein}^{-1} \text{ h}^{-1}$ showed greater SAR survival than their run-of-river counterparts. Fish with the highest predicted SAR survival had been transported and had fish indices consistent with smolts that were more developed (i.e., lower % dry mass and higher NKA activity). Furthermore, our results on % dry mass provided support for the hypothesis that greater lipid content increases fish buoyancy leading to greater susceptibility to predation. The buoyancy effect is expected to be greatest in hatchery fish. Overall, this study shows that decision triggers based on biological indices of migrating fish are potentially useful tools for in-season management.

Key words: anadromous salmon, carryover effects, decision trigger, life-history stages, hydroelectric power dams, management, river and ocean, survival, threshold, translocation

Natural resource managers are often required to make rapid decisions that potentially affect the survival of the resources they are charged to protect. This process can be described

with a framework of decision triggers, which are predefined guidelines for a critical threshold that can trigger a management action to achieve a favorable ecological outcome (Cook

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et al. 2016). Some examples of triggered actions include setting harvest quotas, translocating threatened populations in the wild, and limiting recreational activities that influence biodiversity (see references in Addison et al. 2016). Guidelines for this type of decision making require a good understanding of biological and ecosystem processes. There can be challenges in identifying threshold values for triggers of management actions or for triggers that result in detectable effects (e.g., increased survival estimates with minimal error) with existing monitoring programs. Triggers based solely on historically observed environmental patterns may become unreliable under a changing climate, through continued land-use modifications to habitat, and with alternative hydrosystem operations, which may consequently change the ecological mechanisms associated with the triggers (Allan 2004, Lynch et al. 2016). As such, it is becoming increasingly relevant and vital to develop new decision triggers that integrate an understanding of ecological mechanisms. Triggers tied to simple correlative patterns will eventually become less effective (Addison et al. 2016, Cook et al. 2016, de Bie et al. 2018).

Real-time decision making for migratory organisms can be especially complex when actions triggered in one habitat (or life stage) affect future life stages. Such cross-life-stage effects, in which the conditions experienced in one life stage carryover to affect an organism's performance and survival in subsequent life stages (termed carryover effects), are im-

portant indirect pathways to consider (Gosselin et al. 2021). Thus, to the degree possible, the design and application of decision triggers that act across the life cycle should be based on an understanding of carryover effects.

A prime example of a triggered action with carryover effects is the Juvenile Fish Transportation Program (JFTP) for juvenile Pacific salmon (*Oncorhynchus* spp.; subyearling or yearling) from the Snake River in the Pacific Northwest, USA (Fig. 1; USACE 2015, 2020), many of which receive protection under the United States Endangered Species Act (NMFS 2017). This program collects juvenile salmon and steelhead, both hatchery and wild, passing through dams on the Snake River, transports them in barges, and releases them below Bonneville Dam, the last dam in the river system, to help increase survival in downstream and ocean life stages. Transported fish have nearly 100% survival in the barges (McMichael et al. 2011). In comparison, juvenile survival through the same hydrosystem for the run-of-river yearling Chinook Salmon (*Oncorhynchus tshawytscha* Walbaum in Artedi, 1792) is ~40 to 60%. However, transportation can cause Chinook Salmon to enter the ocean environment too early, resulting in low smolt-to-adult return (SAR) survival compared with the fish entering the ocean later in the season (Gosselin et al. 2018b), possibly because of a mismatch of their evolved timing with food resources (Cushing 1990). This mismatch can be particularly evident in

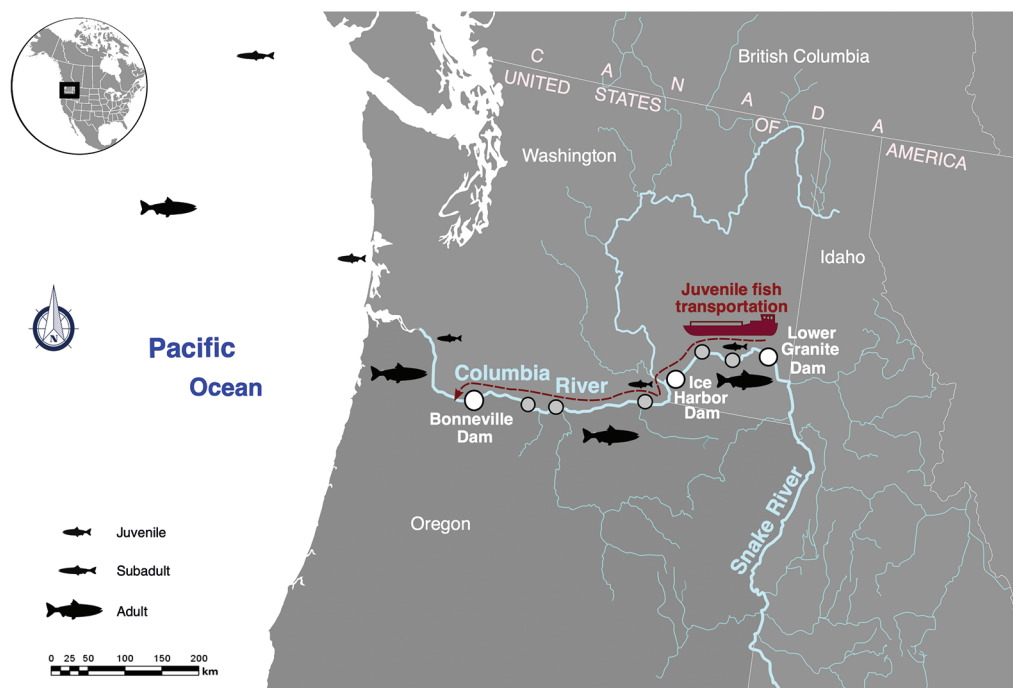


Figure 1. Map of study system: Federal Columbia River Power System of the Snake and Columbia rivers, Washington and Oregon, USA. We collected fish samples at 3 locations (Lower Granite, Ice Harbor, and Bonneville dams; white dots), but not at the 5 other dams (gray dots). In the spring, the Juvenile Fish Transportation Program collects juveniles at the 3 most upstream dams, transports them in barges through the hydropower system, and releases them below Bonneville Dam for their continued migration through the estuary and to the Pacific Ocean. For spring/summer Chinook Salmon, adults generally return to the river to spawn after being in the ocean for 1 to 5 (mostly 2) y.

early-season fish, which take ~3 to 4 wk to pass through the hydrosystem, compared with their transported counterparts, which pass the same distance in a barge for a ~2-d trip.

To balance the benefits from both run-of-river and transported passage experiences, the JFTP has been initiated (i.e., triggered) around 1 May each year for the last couple of decades with some early-season barge transportation scheduled in late April to help provide data for research (USACE 2015). This date was determined from retrospective analyses (Anderson et al. 2005) and has provided for relative success, likely because of the brief historical stability in river and marine conditions and resulting migratory behaviors and biological conditions of the fish (Scheuerell et al. 2009, Gosselin and Anderson 2017). Of these factors, only migration timing has demonstrable relationships with SAR survival, with seasonal patterns of declining SAR survival in wild Chinook Salmon, and a bell-shaped relationship in hatchery Chinook Salmon (i.e., fish spawned, hatched, and reared at a hatchery then released as juveniles). River and marine indices may help to improve SAR survival predictions by capturing complexities in effects from the physical environment (Gosselin et al. 2018b) but may also generate greater uncertainty than triggers based on migration timing. Furthermore, as climate patterns become more variable and modifications to habitat and hydrosystem operations continue to occur, the seasonal correlations between environmental and fish conditions are likely to weaken. Thus, a more reliable trigger for transportation might need to be based on indices more closely related to biological mechanisms underlying the carryover effect of passage experience to ocean survival.

It is generally believed that marine survival of anadromous fishes is regulated by their physiological adaptation to seawater (i.e., smoltification; Wedemeyer et al. 1980, Bassett et al. 2018), and incomplete smoltification can be a consequential obstacle for anadromous fishes transitioning to the marine environment (Houde et al. 2019). However, smoltification is a complex process and cannot be easily characterized by a single index. The smoltification process involves many physiological and metabolic changes, such as a reduction in total body lipids, increased moisture content, reduced liver glycogen, accelerated protein and lipid catabolism, and elevated blood glucose levels (Wedemeyer et al. 1980, Beckman et al. 2000). Studies on Chinook Salmon (Spangenberg et al. 2015, Beckman et al. 2017), Sockeye Salmon (*Oncorhynchus nerka* Walbaum in Artedi, 1792; Bassett et al. 2018), and Atlantic Salmon (*Salmo salar* Linnaeus, 1758; Chaput et al. 2018) show that differential changes through the season and across years in juvenile fish lipid content, osmoregulation through the gills, growth hormone, growth rate, and fork length have important effects on early ocean survival.

Some studies have focused on the osmoregulatory aspect of smoltification in relation to behavior and survival

in the early ocean environment. In the Columbia River Basin, transit time through the plume is related to survival and varies from a few days to a few weeks (Brosnan et al. 2014). The success of evading predators during this transit time can depend on the fish's smoltification level (Wedemeyer et al. 1980, Schreck et al. 2006, Kennedy et al. 2007). Juveniles not fully smolted are thought to be confined to the freshwater lens of the estuary and river plume environment (i.e., upper water column caused by lower density of freshwater relative to seawater) making them more susceptible to avian predators than the more smolted juveniles, which tend to swim deeper in the seawater (Schreck et al. 2006, Stich et al. 2016). Indices of low Na^+/K^+ -ATPase (NKA) activity have been associated with decreased marine survival in salmon and steelhead (Stich et al. 2015, Healy et al. 2018), but what is unknown is the importance of osmoregulatory processes on early marine survival in a system with a juvenile fish transportation mitigation strategy. The earlier arrival of transported fish to the estuary may disrupt timing of the smoltification process relative to timing of ocean entry.

Independent of the smoltification stage, the level of fish energetic reserves at marine entrance could affect marine survival (Post and Parkinson 2001) through increased risk of starvation, disease, and predation (Finstad et al. 2004, Biro et al. 2005, Mathes et al. 2010). Although energetic density naturally declines as length increases during smoltification (Wedemeyer et al. 1980, Beckman et al. 2000), critically low energetic reserves can decrease survival (Gosselin and Anderson 2020). However, it is possible that high energetic reserves in fish, resulting from high lipid levels, could decrease survival if the lipids increase buoyancy, thereby making the fish more susceptible to predators, especially after they enter dense seawater (Weitkamp 2008). Relating survival directly to biological indices such as these would help generate and provide support for hypotheses of different mechanistic processes, thereby alleviating a gap in understanding imposed by studies that use environmental indices to represent assumed biological processes.

We addressed 2 objectives in this study: 1) assess whether various fish indices of hatchery-born yearling Chinook Salmon are associated with SAR survival and 2) determine if these indices could be useful as decision triggers for initiating or pausing the JFTP, given their associated carryover effects to SAR survival. In particular, we aimed to examine the relationships between survival and smoltification, critically low levels of energy, and increased susceptibility to predation through buoyancy. What is novel in this study is the examination of mechanism-based biological indices for decision triggers for the JFTP. Assessing environmental and fish indices together in the same study will also help evaluate the contribution of each type of index to SAR survival for in-season decisions. Our research contributes to the knowledge and evaluation of fish condition monitoring and its importance in helping guide fish species recovery.

METHODS

To examine how biological mechanisms could be relevant to decision triggers of the JFTP, we collected fish samples ($n = 889$) at 3 dams and throughout the fish's migration season (~weekly) in 2016 to determine physical and biological indices measured at the dams and processed in the laboratory. We used these indices to examine SAR survival of representative tagged fish ($n = 100,013$) through fixed, random, and interaction effects in generalized linear mixed effects models (GLMM).

Study system

The Snake and Columbia rivers are in the Columbia River Basin, which is one of the largest watersheds in the USA at ~650,000 km², spanning Washington, Oregon, and Idaho, USA, as well as parts of other surrounding states and Canada (NRC 2004; Fig. 1). Historically, 75% of annual flows were in late spring through summer, with snowmelt flows peaking in May and June. When multiple dams were constructed from the 1930s through the 1970s, large reaches of the rivers became reservoirs, and the river hydrograph was largely flattened. The various hydrologic regimes in this region support several species and runs of salmon and steelhead.

The focus species in this study was yearlings of spring/summer Chinook Salmon from the Snake River and spring Chinook Salmon from the Columbia River. Generally, the adults return in the spring and summer seasons to spawn in August and September. The eggs incubate through the winter and hatch in the spring, followed by fry emergence. The fish continue to rear in the headwater streams through the next year; the parr overwinter and the yearlings migrate downstream in the spring to enter the ocean. After 1 to 5 (mostly 2) y in the ocean, they complete their life cycle by returning to their spawning grounds to lay their eggs and die.

Salmon and steelhead adult abundance in the region is a small fraction (~1–2 million) of what it was in the 1860s, as inferred by commercial landings of salmon and steelhead in the Columbia River (WDFW and ODFW 2002, Williams et al. 2006) and with estimated historical adult returns as high as 16 million/y (NRC 2004). There have been many stressors over the past ~200 y with legacy and current effects, including commercial fishing, logging, construction of hydroelectric power dams, large hatchery productions, farming, water diversions for irrigated agriculture, human population growth, urbanization, and climate change impacts (Lichatowich 1999, Williams et al. 2006, Crozier et al. 2019). In addition to the JFTP, another major mitigative strategy is hatchery production, which in recent decades contributes ~60 to 80% of the Chinook Salmon in the region (USACE et al. 2020, NPCC 2021). It is important to keep in mind that these are technological fixes, embedded in complex processes across freshwater and marine ecosystems.

Fish sampling

Untagged yearling Chinook Salmon of hatchery origin were collected weekly in 2016 throughout their downstream migration at Lower Granite Dam (LGR; river km [rkm] 695), Ice Harbor Dam (ICH; rkm 538), and Bonneville Dam (BON; rkm 234; see Table S1 for sample sizes). We subsampled fish that had been diverted through the bypass systems at the dams for other research and monitoring programs (the Smolt Monitoring Program at ICH and BON; NWFSC 2022). Biologists from these programs identified the yearling spring/summer Chinook Salmon by morphological characteristics and fish length. From their samples, we collected only untagged fish as required by our sampling permits to help minimize impact on other research studies that had tagged their fish with passive integrated transponder (PIT) tags or coded wire tags. We examined and scanned all fish with a PIT-tag detector and a Blue Handheld Wand Detector (Northwest Marine Technology, Tumwater, Washington) to ensure the fish collected had no tags. We identified hatchery fish by their distinctive clipped adipose fin, and we avoided sampling yearling fall-run Chinook Salmon by collecting fish with fork lengths <155 mm. We then euthanized the fish by immersing them in 250 mg/L tricaine methanesulfonate (MS-222; Tricaine-S; Thermo Fisher Scientific, Waltham, Massachusetts) buffered with NaCO₃ to a pH of 7, as directed in animal care protocol #3382-05, approved by the University of Washington Institutional Animal Care and Use Committee, for further fish processing and measurements of physical and physiological indices.

Indices of fish condition and passage experience

We recorded 3 physical indices of fish condition related to length and mass. At the dams, we measured fork length (distance from the tip of a fish's nose to the middle caudal fin rays) to the nearest 1 mm with a measuring board (EZ ID, clear plastic 20-cm, embedded in a board with a 90° bend; Northwest Fisheries Science Center, Pasco, Washington) and wet mass to the nearest 0.01 g with an Ohaus® Adventure Pro electronic balance (model AV612N; Parsippany, New Jersey; Table 1). From these measurements, we calculated Fulton's K ($K = 100 \times \frac{W}{L^3}$) where W is wet mass and L is fork length.

We measured NKA activity in the gills as an index of smoltification. Specifically, after fish were euthanized in the field, we immediately collected gills, including supporting arches, and fully immersed them in cold sucrose–EDTA–imidazole buffer (250 mM sucrose, 10 mM Na₂EDTA, and 50 mM imidazole; Zaugg 1982) to help preserve tissue samples prior to freezing. While in the field, gill samples (see Table S1 for sample sizes) were stored on dry ice until they were moved to –80°C freezers, whereas whole-body fish samples were stored on ice until they were moved to –20°C freezers. In the laboratory, gill NKA activity (μmol ADP mg

Table 1. Covariates examined against smolt-to-adult return survival of hatchery yearling Chinook Salmon from Bonneville (BON), Ice Harbor (ICH), and Lower Granite (LGR) dams in Washington and Oregon, USA. For sampling dates, locations, and sample sizes, see Table S1. NKA = Na^+/K^+ -ATPase, – = not applicable.

Covariate	Covariate symbol in Eq. 1	Covariate symbol in Eq. 2	Description
Migration timing	x_1	m_1	Day of year of passage and sampling at LGR, ICH, or BON dam
Fork length	x_2	–	Mean fork length (mm) for each sample
Wet mass	x_3	–	Mean wet mass (g) for each sample
Fulton's K	x_4	–	Mean Fulton's condition factor ($K = 100 \times \frac{W}{L^3}$, where W is wet mass and L is fork length) for each sample
% dry mass	x_5	m_2	Mean % dry mass by wet mass (%) for each sample
NKA activity	x_6	m_3	Mean NKA activity ($\mu\text{mol ADP mg protein}^{-1} \text{ h}^{-1}$) for each sample; smoltification index
Juvenile transportation	x_7	m_4	Presence or absence of juvenile fish transportation passage through hydrosystem
Distance to ocean	x_8	m_5	Location of dam by river distance (rkm) to ocean

protein⁻¹ h⁻¹) was measured according to the method of McCormick (1993). The assays were performed on a SpectraMax[®] 190 plate reader (Molecular Devices, San Jose, California) with SoftMax[®] Pro software (version 5.4; Molecular Devices).

We also determined % dry mass from whole-body fish samples to represent an index related to energetic reserves. We cut fish, dried them in ovens at 60°C for 2 to 3 d, and then weighed their dry mass to determine % dry mass by wet mass. To verify % dry mass as an index of energetic reserves, we measured % lipid content by wet mass with a Soxhlet fat extraction system (model 810; BÜCHI, New Castle, Delaware) with CH₂Cl (stabilized/certified ACS; Fisher Chemical™, Thermo Fisher Scientific) as a solvent. Percent dry mass explained a large percentage of variance in the % lipid content (% lipid content = $-14.3 + 0.8$ (% dry mass); $r^2 = 0.91$, $p < 0.01$, $n = 136$) and, thus, served as an appropriate index of energetic reserves (see Fig. S1). This linear regression was conducted in R statistical software (version 4.0.5; R Project for Statistical Computing, Vienna, Austria) with the function `lm` in the `stats` package. Other studies on Chinook and Coho Salmon (*Oncorhynchus kisutch* Walbaum, 1792) have found measurements of % moisture (i.e., the complement of % solids) to explain much of the variation in whole-body lipids ($r^2 = 0.88$; Shearer 1994) and, likewise, with % solids for energy density ($r^2 = 0.92$; Trudel et al. 2005). Using % dry mass allowed us to quantify an index of energetic reserves more quickly than was possible with other methods, such as extraction of lipids.

To determine the indices for juvenile transport vs run-of-river hydrosystem passage and for migration timing in tagged fish representative of our fish samples, we used a data set of PIT tags (PIT Tag Information System [PTAGIS], Pacific States Marine Fisheries Commission; <https://ptagis.org/>), which provided observations on dates of detections

at LGR, ICH, and BON dams; species; run; rear-type; and fork length at time of tagging, release, and recapture, if available. We also used the Columbia Basin Research transport filter criteria (<http://www.cbr.washington.edu/dart/metadata/pit#transport>) that identifies whether each PIT-tagged fish had a transported or run-of-river passage experience based on their detection histories.

For run-of-river fish, because mortality can occur as they migrate through the river and the distance between sampling sites are hundreds of km, we included the distance between the sampling site and ocean entrance as another index (Table 1). This distance index could also serve as an index of other differences in populations originating upstream of each sampling site.

Our indices of fish condition and passage type were the best estimates we could determine from our samples and PTAGIS data. The spatiotemporal resolution of the SAR survival estimates of interest was relatively fine scale (i.e., weekly SAR survival from each of 3 dams and based on individually PIT-tagged fish) and would require thousands of fish for sufficient numbers of adult returns. Given these large sample sizes and our sample collection permits, sampling the same tagged individuals for biological indices and for estimating SAR survival was not possible. We think that it was still reasonable to associate the biological indices from our untagged fish samples to SAR survival of PIT-tagged fish under 3 considerations related to sampling selectivity, tagging effects, and representativeness of biological indices. First, because the untagged fish were sampled at the same collection sites (through bypass systems at LGR, ICH, and BON dams) as fish sampled or detected for SAR survival estimates, we believe our comparison between the untagged and tagged fish data sets is supported. Second, to eliminate any potential negative effects from tag burden on their condition and survival, we excluded PIT-tagged fish

that were too small at time of tagging (Vollset et al. 2020). We provide more details on the criteria of PIT-tagged fish for representativeness of the untagged fish samples collected in the next section. Third, other studies have often relied on the best estimates from data available on environmental conditions (e.g., river temperature, flow, ocean, and climate indices; e.g., Smith et al. 2003, Williams et al. 2014), which is similar to the current study with our best available measures of biological indices.

Survival model

A large number of tagged fish are required to estimate survival of Chinook Salmon from the Snake and Columbia rivers, which generally have low SAR survival (Quinn 2018). We relied on public data from PIT tags generated by many agencies and biologists in the region and made available through PTAGIS. Thus, the detections from all PIT-tagged hatchery Chinook Salmon are data from normal operations at the dams and were not altered for our study. To make use of observed SAR survival from PIT-tagged fish in a manner that best aligned with our field samples of run-at-large hatchery Chinook Salmon, we queried all PIT-tagged hatchery yearling Chinook Salmon passing through the juvenile fish facilities and other routes at LGR, ICH, and BON dams relevant to our sampling dates in 2016 (i.e., weekly and centered on the dates we collected samples at the dams). We excluded any tagged fish with a fork length <65 mm, which is considered too small for tagging, to guard against any possible tagging effects (Peterson et al. 1994, Vollset et al. 2020). Detections of adult returns and survival estimates are through 2021 (i.e., up to 5-y-old fish, no 6-y-old fish were observed; Table S2). We applied these criteria to help better match our fish samples to the PIT-tagged fish data available in PTAGIS used to estimate survival for run-of-river juveniles at LGR to returning adults at BON, run-of-river juveniles at ICH to adults at BON, and run-of-river juveniles at BON to adults at BON. We also estimated survival for juvenile fish transported from LGR and released below BON to adults returning to BON. We assumed that fish collected at LGR for transportation had fish condition metrics equivalent to those of our LGR-sampled juveniles and, hence, used these metrics for the transported fish survival estimates.

The PIT-tag data were binned weekly and centered to the dates we measured fish indices (i.e., 4th d of the weekly bins matched our fish sampling dates) to observe sufficient adult returns for an estimate of SAR survival. The covariates measured in the fish samples at the dams were associated with each PIT-tagged individual and used to estimate SAR survival: day of year of dam passage, mean fork length, mean wet mass, mean Fulton's K , mean % dry mass, mean NKA activity, presence or absence of juvenile fish transportation (hereafter, passage type), and distance of sampling site to ocean entrance (Table 1). We scaled all covariates

to a mean of 0 and 1 SD except for the binary passage-type index. We checked for correlations (Pearson's r -values) among covariates in 2 datasets: a dataset associated with covariates available for all fish samples and a sub-dataset of fish samples that had NKA activity data (Fig. 2). The correlations with all samples help provide an understanding of the extent to which the covariates could be correlated, and the correlations with the sub-dataset are representative of the covariate data we used to model survival.

We modeled survival based on these PIT-tag data and covariates as a probability of a PIT-tagged juvenile sampled at 1 of the 3 dams returning as an adult to BON (i.e., LGR-BON, ICH-BON, or BON-BON survival). This model is essentially a Bernoulli trial: $y_{ij} \sim \text{Bernoulli}(p_{ij})$, where y_{ij} indicates whether individual i ($i = 1, \dots, n$) at site j returns as an adult, with probability p_{ij} in a Bernoulli distribution. The covariates were related to survival through a logit-link function in a GLMM (Zuur et al. 2009). The GLMM includes fixed effects from explanatory variables of interest and random effects that explain additional variation through random deviations, modeled as normally distributed with a mean of 0 and SD s . The GLMM we examined was:

$$\text{logit}(p_i) = b_0 + (b_1 + \phi_1)x_{1i} + \sum_{k=2}^{k=8} b_k x_{ki}, \quad (\text{Eq. 1})$$

$$\phi_1 \sim N(0, s),$$

with a fixed effect intercept b_0 for the whole model, a fixed slope b_1 and random slope ϕ_1 for migration timing covariate x_1 (which, respectively, would determine seasonal effects and additional random effects for each sample), and fixed slope b_k for covariate k , in which x_k is the mean value of covariate k associated with individual i through its equivalent observed time. Therefore, the median day of the weekly bin of PIT-tagged fish is the same as the day of fish sample collections for biological indices. Some of the NKA activity estimates were not usable because of accidental improper preservation of gill samples and substandard laboratory processing; therefore, we had to exclude the corresponding PIT-tagged data. The number of PIT-tagged fish used to estimate SAR survival were adjusted accordingly (see Table S3 for weekly sample sizes; run-of-river juveniles at LGR to returning adults at BON: $n = 35,587$ juveniles, 129 adults; run-of-river juveniles at ICH to adults at BON: $n = 6,300$ juveniles, 34 adults; run-of-river juveniles at BON to adults at BON: $n = 34,749$ juveniles, 483 adults; and juvenile fish transported from LGR, released below BON, and adults returning to BON: $n = 23,377$ juveniles, 213 adults).

We considered 64 submodels using model averaging ranked by the corrected Akaike Information Criterion (AICc; Burnham and Anderson 2002). Because of high correlations between the indices of Fulton's K , % dry mass, and NKA activity (Fig. 2), we did not examine combinations of 2 or all 3 of these covariates in the same submodel but examined them in separate submodels. We therefore reported

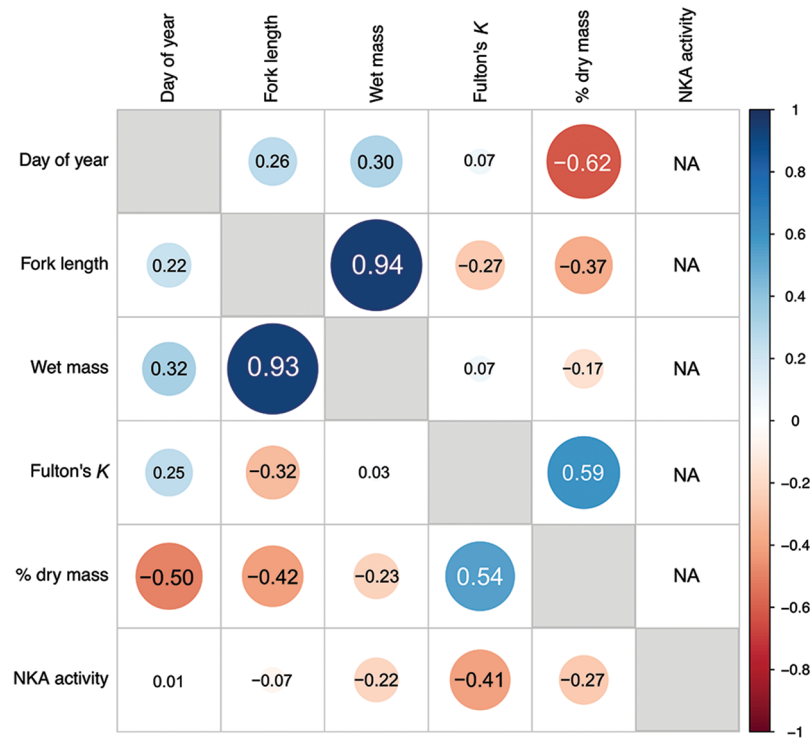


Figure 2. Pearson's r -values between covariates for all hatchery yearling Chinook Salmon samples from Bonneville, Ice Harbor, and Lower Granite dams in Washington, USA (upper triangle of matrix, i.e., above gray-colored diagonal; $n = 23$ samples; Table S1), that excluded Na^+/K^+ -ATPase (NKA) activity data and for a subset of fish samples (lower triangle of matrix, i.e., below gray-colored diagonal; $n = 16$ samples) that only included fish samples that had NKA activity data (Table S1) and that aligned with dates of passive integrated transponder tag data (Table S3). The strength of each correlation is represented by both the size and depth of color of the corresponding circle. NA = not applicable.

in model averaging the conditionally averaged parameters (i.e., averaged over the submodels where the parameter appears). The analyses were conducted in R statistical software with the function `glmer` in the `lme4` package (version 1.1–23; Bates et al. 2015, 2020) and the function `model.avg` in the `MuMIn` package (version 1.43.17; Bartoń 2020).

In a 2nd model, we reduced the 1st model to include a smaller subset of covariates and to allow for interaction effects. We examined interaction effects between the transport index and % dry mass or NKA activity:

$$\text{logit}(P_i) = \beta_0 + (\beta_1 + \psi_1)m_{1i} + \sum_{q=2}^{q=5} \beta_q m_{qi} + \beta_6 m_{2i} m_{4i} + \beta_7 m_{3i} m_{4i}, \psi_1 \sim N(0, \sigma) \quad (\text{Eq. 2})$$

with a fixed effect intercept β_0 for the whole model, a fixed slope β_1 and random slope ψ_1 for migration timing covariate m_1 , and fixed slope β_q for covariate q , in which m_q is the mean value of covariate q associated with individual i through its equivalent observed time (Table 1). When a covariate in Eq. 1 did not have a $p < 0.05$ in any of the submodels of the model-averaged confidence set, we excluded it in Eq. 2. We had to make decisions about which covariates to exclude because there were insufficient data to

examine Eq. 1 with interaction effects and yield model convergence. To inform values for decision triggers, we included interaction effects of the juvenile fish transportation index with other included covariates. To identify potential trigger decision points, from the model-averaged results of Eq. 2, we compared the biological indices related with % dry mass and NKA activity further through partial regression plots across ranges of the covariates we observed in our individual fish samples, which include ranges previously observed (Beckman et al. 2000, Trudel et al. 2005, Weitkamp 2008). We also produced a partial regression plot of SAR survival associated with migration timing in a model that included an interaction effect between the juvenile fish transportation index and migration timing to compare with the partial regressions associated with % dry mass and NKA activity.

RESULTS

Fish condition indices

The seasonal patterns of fish condition indices showed visually similar trends across LGR, ICH, and BON dams for % dry mass, but there were dam-specific patterns within fork length, wet mass, and NKA activity (Fig. 3A–C). Fork

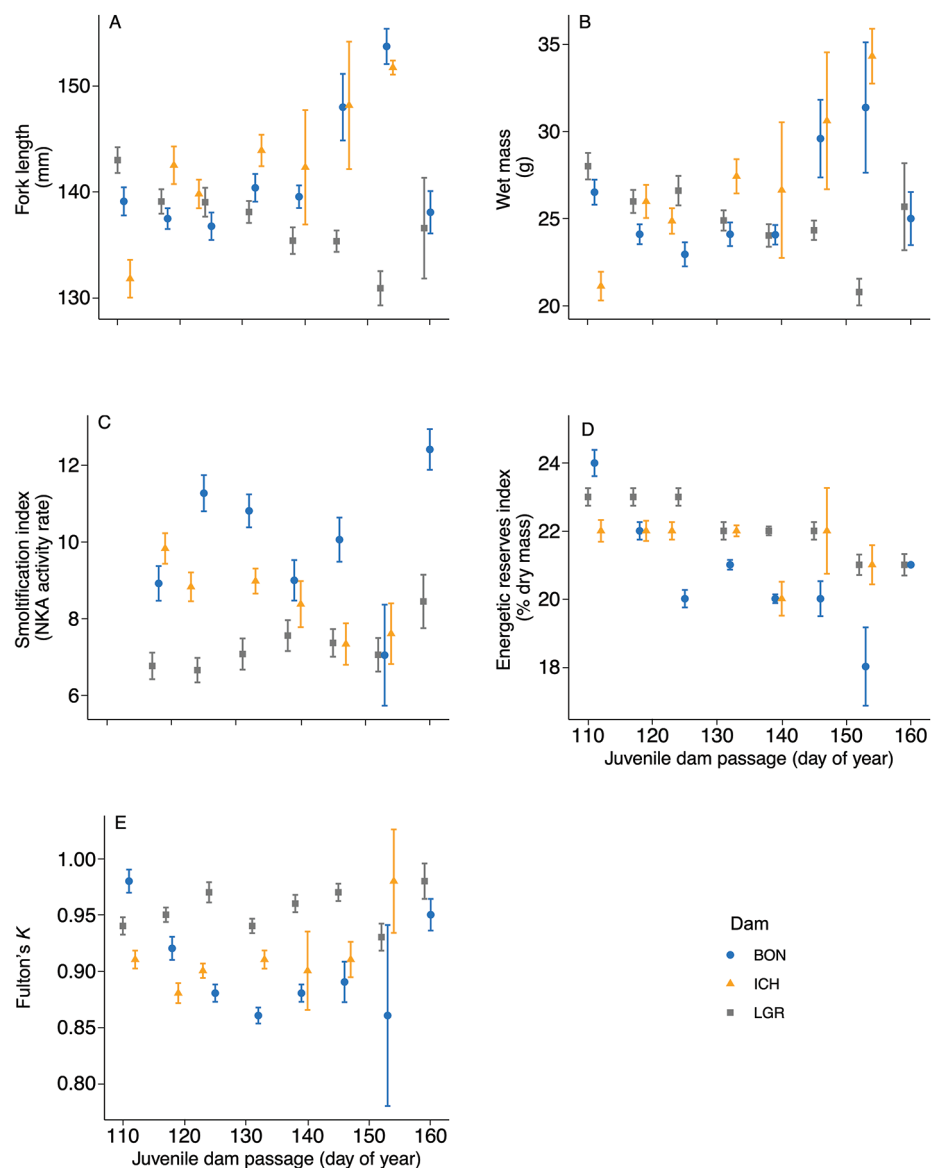


Figure 3. Mean values of fish indices for hatchery yearling Chinook Salmon observed in 2016 at Bonneville (BON), Ice Harbor (ICH), and Lower Granite (LGR) dams in Washington, USA. A.—Fork length (mm), the length of a fish from the tip of its nose to the middle caudal fin rays. B.—Wet mass (g). C.—Smoltification index (Na^+/K^+ -ATPase [NKA] activity in $\mu\text{mol ADP mg protein}^{-1} \text{h}^{-1}$). D.—Energetic reserves index (% dry mass by wet mass). E.—Fulton's K (or condition factor). Bars represent SD. For sample sizes, see Table S1. See Fig. S2 for boxplots of panels A through E and of energetic reserves index of % lipid.

length for fish at LGR generally declined through the season from a mean \pm SD of 143 ± 9 to 131 ± 5 mm, whereas those at ICH and BON generally increased through the season, with means of 132 ± 11 to 152 ± 1 and 139 ± 10 to 154 ± 3 mm, respectively (Fig. 3A). Seasonal patterns of wet mass by sampling location followed patterns similar to those of fork length (Fig. 3A, B). In contrast, seasonal patterns of NKA activity measured at LGR, ICH, and BON were different: respectively increasing (6.76 ± 1.73 – 8.44 ± 2.20 $\mu\text{mol ADP mg protein}^{-1} \text{h}^{-1}$), decreasing (9.82 ± 1.78 – 7.60 ± 1.37 $\mu\text{mol ADP mg protein}^{-1} \text{h}^{-1}$), and variable (Fig. 3C). The % dry

mass index of fish samples declined through the season from a mean of $\sim 24\%$ and was lowest for the last fish sample at BON ($18 \pm 2\%$ dry mass; Fig. 3D). Fulton's K were generally highest upstream (i.e., LGR; range of 0.93 ± 0.04 – 0.98 ± 0.05) and lowest downstream (i.e., BON; range of 0.86 ± 0.14 – 0.98 ± 0.08 ; Fig. 3E).

The seasonally variable and sometimes nonlinear patterns of many indices highlight the existence of unique sample differences and support our decision to include a random effect for each sample indexed by day of year. Many of the indices were correlated, specifically fork length with

mass and Fulton's K with both % dry mass and NKA activity indices (see Fig. 2 for Pearson's r -values).

Relating survival to fish condition indices

The SAR survival of PIT-tagged juvenile fish from LGR, ICH, and BON with adult returns to BON differed in their seasonal patterns (Fig. 4A–D). The survival of run-of-river fish sampled at LGR and ICH declined over the season from ~ 0.01 to 0, whereas survival of fish transported from LGR increased from 0 early in the season to ~ 0.02 at around 24 May (or day of year 145), after which it decreased to 0. The survival of run-of-river fish sampled at BON decreased from ~ 0.03 early in the season to ~ 0.01 at around 24 May and then was variable in the last week of the season because of the small sample size (Table S3).

The results from submodels examined in Eq. 1 indicated negative effects on survival from migration timing, % dry mass, and distance to the ocean and positive effects from NKA activity and juvenile fish transportation (Tables S4, S5). Fork length, mass, and Fulton's K did not explain the majority of the variation in SAR survival in Eq. 1 submodels, did not have parameters with $p < 0.05$ and were therefore excluded from Eq. 2.

The results from Eq. 2 also indicated that fish migrating later in the season tended to have lower survival and trans-

ported fish had higher survival than run-of-river fish, as demonstrated by the strong positive parameter effect of 1.42 ± 0.45 SE for transported fish (Table 2). Fish with lower % dry mass and higher NKA activity were associated with higher survival but with noticeably high SE in their main effects. Percent dry mass showed greater importance than NKA activity by $\Delta AICc$ weight across all the submodels in the model-averaging confidence set (Table 3). Furthermore, distance to the ocean was negatively associated with survival (Table 2).

More importantly, the interaction effects between juvenile fish transportation and % dry mass or NKA activity had notable weights by $\Delta AICc$ in the model-averaging confidence set (Table 3). Partial regression plots revealed that SAR survival was greater in transported hatchery Chinook Salmon when dry mass was $< 23\%$, where the confidence intervals do not overlap (Fig. 5A), and NKA activity was $> 7 \mu\text{mol ADP mg protein}^{-1} \text{ h}^{-1}$ (Fig. 5B). In comparison, a model with migration timing and its interaction with juvenile fish transportation could only demonstrate that transportation was always beneficial to SAR survival (Fig. 5C). Furthermore, the upper range of SAR survival in transported fish has the potential of reaching higher levels at the lower ranges of % dry mass and higher ranges of NKA activity than higher ranges of migration timing.

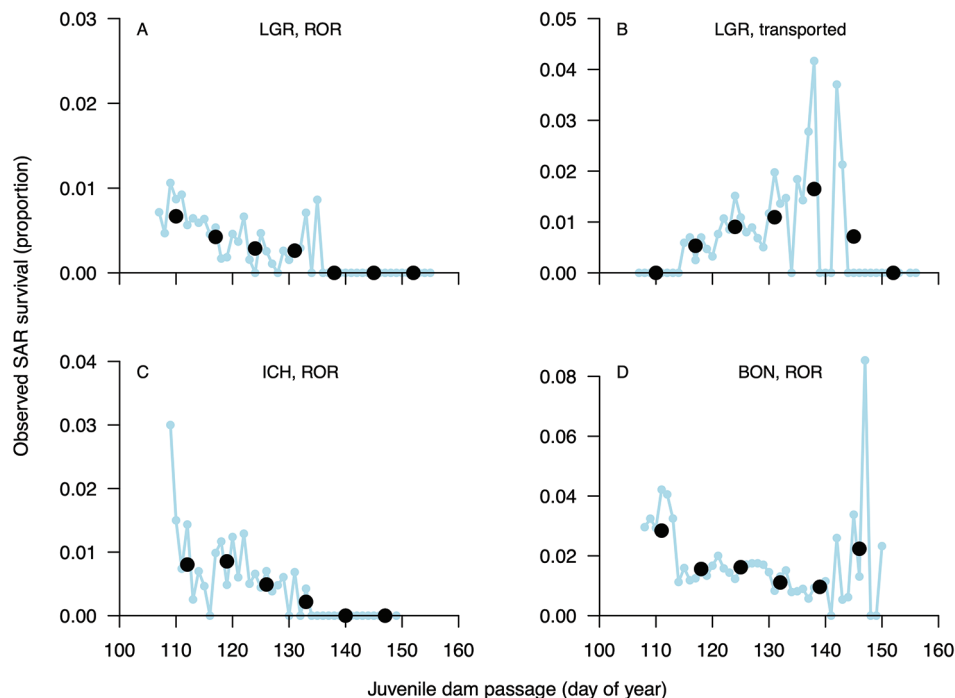


Figure 4. Smolt-to-adult return (SAR) survival observed from passive integrated transponder-tagged hatchery yearling Chinook Salmon detected in Bonneville (BON), Ice Harbor (ICH), and Lower Granite (LGR) dams in Washington and Oregon, USA. A.—LGR as run-of-river fish. B.—LGR as transported fish. C.—ICH as run-of-river fish. D.—BON as run-of-river fish. Survival estimates are from observed juvenile passage site to BON as adults. Weekly binned estimates are black points, and daily estimates are light blue points and solid light blue line. ROR = run-of-river fish.

Table 2. Eq. 2 generalized linear mixed-effects model of smolt-to-adult return survival with model averaging and conditional averaged parameters reported. $NKA = Na^+/K^+-ATPase$.

Intercept and covariates	Parameter	Estimate	SE	<i>p</i> -value
Intercept	β_0	-5.15	0.06	<0.001
m_1 : Migration timing	β_1	-0.15	0.05	0.003
m_2 : % dry mass	β_2	-0.13	0.07	0.084
m_3 : NKA activity	β_3	0.10	0.08	0.205
m_4 : Distance to ocean (i.e., from dam)	β_4	-0.60	0.08	<0.001
m_5 : Juvenile transportation (run-of-river = 0, transported = 1)	β_5	1.42	0.45	0.002
$m_2 \times m_4$: Interaction between % dry mass and juvenile transportation	β_6	-0.46	0.18	0.009
$m_3 \times m_4$: Interaction between NKA activity and juvenile transportation	β_7	1.57	0.61	0.010

The observed SAR survival from PIT-tag data correlated with our predicted SAR survival based on the median values generated by the fixed effects from the model-averaged parameters of Eq. 2 (Fig. 6). Looking at these predictions by sampling site showed that SAR survival of run-of-river fish from ICH and LGR was generally underpredicted, and the predicted SAR survival for transported juveniles from LGR was poor. However, across sampling sites and passage-types, observed and predicted SAR survival were correlated (Pearson's $r = 0.86$, $p < 0.01$).

DISCUSSION

Identifying mechanistic processes underlying decision triggers is important for pre-season and in-season management of natural resources in a highly regulated system. Currently, the JFTP in the Snake and Columbia river systems is operated on a calendar schedule and is not based on clear biological mechanisms, such as smoltification for increased preparedness to enter marine waters, or lipid-related buoyancy and predation risk. Because the decisions can only be as good as available knowledge of the system, and the costs of underinformed decisions can be as high as losses of populations and genetic diversity, it seems logical to invest proactively in more long-term, evidence-based biological monitoring programs. To help advance this knowledge, we collected hatchery yearling Chinook Salmon during their migration season at the hydrosystem and examined several indices (fork length, wet mass, Fulton's K , NKA activity, % dry mass, transported vs run-of-river passage, migration timing, and distance of sampling site to ocean) in association with SAR survival. We found that transported hatchery Chinook Salmon with dry mass <23% and NKA activity >7 $\mu\text{mol ADP mg protein}^{-1} \text{h}^{-1}$ displayed greater SAR survival than their run-of-river counterparts. In the rest of our discussion, we further address these findings in context of biological process-based predictors of SAR survival, discuss how predictors may incorporate specific or representative mechanisms, and consider study limitations and future studies.

Biological processed-based predictors of SAR survival

Our finding that % dry mass was more important than NKA activity in explaining variation in SAR survival (Table 3) supports our hypothesis that % dry mass may represent more than just the smoltification process, thus, offering further insights into lipid content and buoyancy. The negative relationship between SAR survival and % dry mass supports the hypothesis that increased buoyancy from high lipids lowers survival by increasing vulnerability to avian predators (Weitkamp 2008). Additionally, the relationship does not support the hypothesis that greater energetic reserves for health and growth increase survival. Lipid-related buoyancy may be a mechanism in all fish, but it is more pronounced in hatchery fish because of the differences in how hatchery and wild salmon rear in their early life stages and their resulting length, mass, body composition, and behavior (Beckman et al. 2000, Larsen et al. 2006).

Percent lipid may be an important difference between hatchery and wild salmon to consider in association with their survival. In wild salmon, lipid content by wet mass can average ~1% in the spring (Beckman et al. 2000, Weitkamp 2008). In our study, we predicted SAR survival to a low range of 19% dry mass (i.e., the lowest % dry mass we observed in a fish in the current study at LGR), which is equivalent to 0.9% lipid content by wet mass (see Fig. S1). This low lipid level was associated with predicted SAR survival of 0.08% (Fig. 5A). Hatchery salmon generally have much higher lipid content than wild fish and can reach an upper range of about 29% dry mass (or 9.1% lipid; Weitkamp 2008). We observed comparably high levels of dry mass (up to 32%) in our hatchery fish samples. These levels of % dry mass in hatchery fish appear to be too high because improvements to SAR survival of transported fish began at a moderately low dry mass of ~23% and progressively increased in leaner fish. The current study did not find evidence supporting the hypothesis that greater energetic reserves increase SAR survival. Overall, our study found that % dry mass index, depending on the range, may indicate benefits to SAR survival from smoltification, increased

Table 3. Eq. 2 covariate parameters (\pm SE) in generalized linear mixed-effects submodels of smolt-to-adult return survival in the 99% confidence set of model averaging. NKA = Na^+/K^+ -ATPase, AICc = corrected Akaike Information Criterion, - = not applicable.

Submodel	Covariate parameters (\pm SE) in submodels										Cumulative weight
	Migration timing, β_1	% dry mass, β_2	NKA activity, β_3	Distance to ocean, β_4	Juvenile transportation, β_5	% dry mass \times juvenile transportation, β_6	NKA activity \times juvenile transportation, β_7	Δ AICc	Weight		
1	-0.16 \pm 0.05	-0.12 \pm 0.07	-	-0.60 \pm 0.07	1.29 \pm 0.15	-0.46 \pm 0.18	-	0.00	0.71	0.71	
2	-0.12 \pm 0.04	-	-0.10 \pm 0.08	-0.60 \pm 0.08	2.22 \pm 0.48	-	1.57 \pm 0.61	2.86	0.17	0.88	
3	-0.14 \pm 0.04	-0.16 \pm 0.07	-	-0.56 \pm 0.07	1.01 \pm 0.11	-	-	4.67	0.07	0.95	
4	-0.07 \pm 0.05	-	-	-0.66 \pm 0.06	0.97 \pm 0.12	-	-	6.40	0.03	0.98	
5	-0.08 \pm 0.05	-	0.11 \pm 0.09	-0.57 \pm 0.09	0.99 \pm 0.12	-	-	7.23	0.02	1.00	

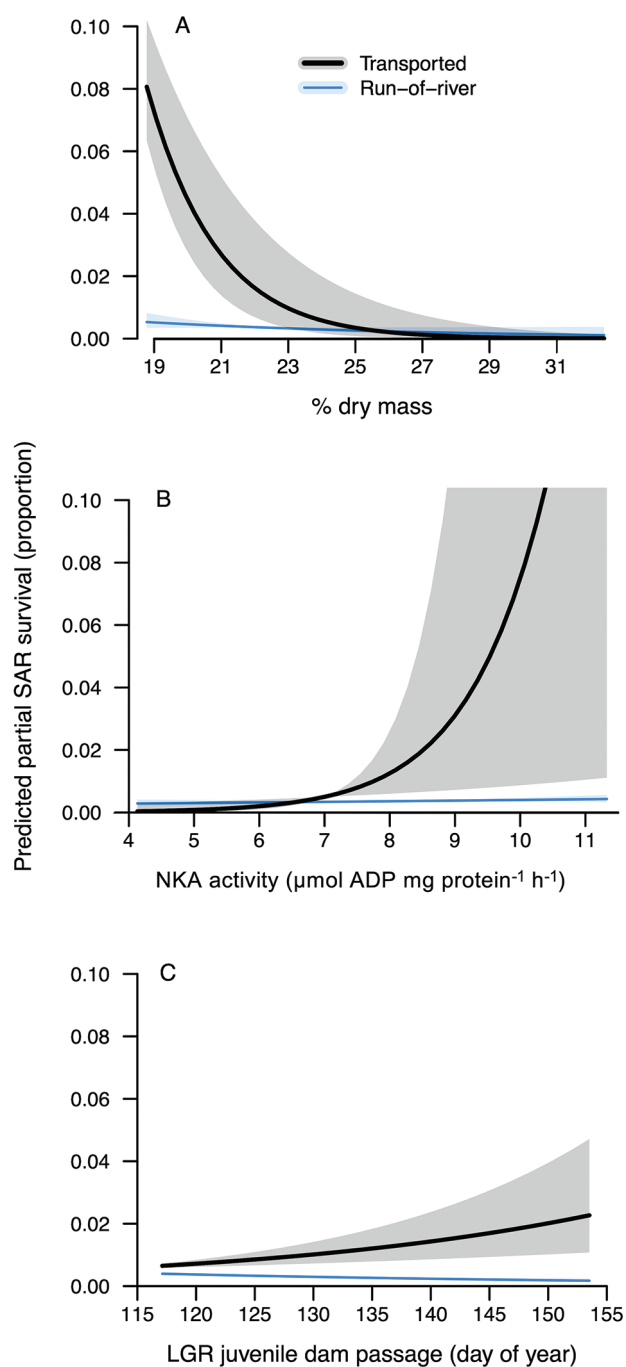


Figure 5. Fitted smolt-to-adult return (SAR) survival from Lower Granite (LGR) to Bonneville dams, Washington and Oregon, USA, for hatchery yearling Chinook Salmon plotted as partial regressions of biological or date-based fixed effects with model-averaged parameters (Table 2). A.—% dry mass. B.— Na^+/K^+ -ATPase (NKA) activity ($\mu\text{mol ADP mg protein}^{-1} \text{h}^{-1}$). C.—LGR juvenile dam passage (day of year). Shaded areas around each line represent 95% CIs.

preparedness to enter marine waters, decreased buoyancy, and reduced predation risk.

We note that levels of smoltification within and between cohorts, hatcheries/stocks, and species can show considerable variation, and may be a reason for why our index of NKA activity was not one of the more important covariates in our study. For example, Spangenberg et al. (2015) found that Chinook Salmon from Parkdale Hatchery on the Hood River, Oregon, USA, showed high variation in springtime NKA activity across years, but those from the nearby Carson National Fish Hatchery on the Wind River, Washington, USA, did not. In another study, stocks with low but variable NKA activity had lower SAR survival than those with high and less variable NKA activity (Beckman et al. 2017). It is well established that smoltification status varies by stock, temporally through the season, spatially as juveniles migrate downstream, and through other factors (Bassett et al. 2018, Houde et al. 2019), highlighting the dynamic nature of the smoltification process. Furthermore, species differ in their migration rate (or time spent in each habitat or reach) through the estuary and early-ocean environment, possibly, at least in part, because of differences in their smoltification levels. In general, Chinook Salmon have more variable migration rates and smoltification levels (NKA activity) than those of Sockeye Salmon and steelhead (Moore et al. 2016, Bassett et al. 2018). The NKA activity we observed in

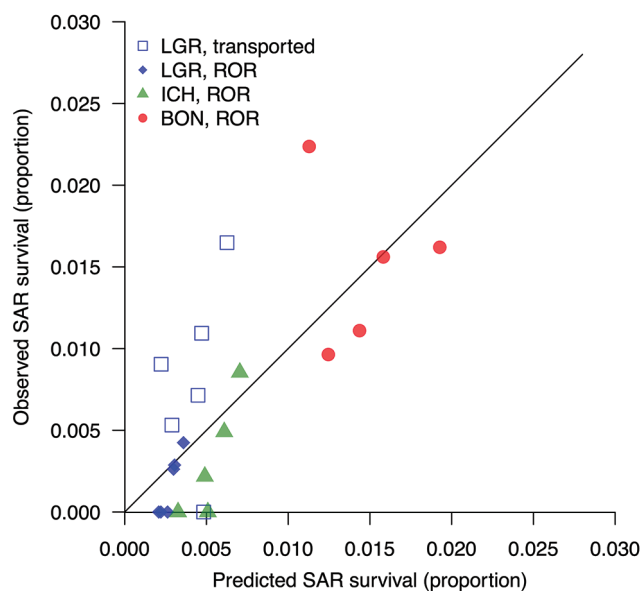


Figure 6. Observed compared with predicted smolt-to-adult return (SAR) survival from weekly samples (centered around field sampling dates) of passive integrated transponder-tagged hatchery yearling Chinook Salmon from Bonneville (BON), Ice Harbor (ICH), and Lower Granite (LGR) dams in Washington and Oregon, USA. See model-averaged parameters used to predict SAR survival in Table 2. ROR = run-of-river. Pearson's $r = 0.86$. The diagonal line represents the 1:1 line.

Chinook Salmon was more variable at the 3 dams through the outmigration season compared with the variability of % dry mass (Fig. 3C, D) and may be a reason for its less certain effects on SAR survival than the effects of % dry mass.

Specific vs representative predictors

Many changes in physiological indices occur through the parr–smolt development stages (Houde et al. 2019), and, thus, multiple decision triggers derived from biological mechanisms might further improve the fish transportation program. Different types of smoltification indices have provided some support for the hypothesis that smolted fish migrate quickly through high-predation-risk areas (e.g., estuary and early ocean environments) and, consequently, experience low mortality (Schreck et al. 2006, Houde et al. 2019). Alternatively, a general index representing multiple processes could be more convenient than one representing a specific biological mechanism. For example, the migration timing index (i.e., day of year of dam passage) can correlate with multiple mechanistic processes, such as smoltification status, growth, travel rate, and pre-hydrosystem and river conditions experienced. Alternatively, Fulton's *K*, an easy-to-measure index, may be a suitable biological index because it was correlated with both % dry mass and NKA activity indices. Overall, it is still uncertain whether a small number of key mechanistic indices (e.g., % dry mass and NKA activity) or a general index correlated with a multitude of processes (e.g., day of year of dam passage and Fulton's *K*) would be more promising for decision triggers to optimize SAR survival.

It is noteworthy that migration timing and its interaction with juvenile fish transportation did not provide a clear indication for a trigger associated with substantially improved SAR survival. A date-based trigger for the onset of barging of Snake River fish is a relatively simple trigger to apply, and it may correlate with multiple seasonal processes (e.g., temperature effects, coastal ocean conditions including prey and predators) that promote higher SAR survival (McCullough et al. 2009, Holsman et al. 2012). However, transportation date is not always a dependable index. The correlation between calendar dates and ecological conditions may break down from time to time, and potentially increasingly so into the future. Furthermore, transportation may be beneficial to SAR survival in most, but not all, years for hatchery Chinook Salmon, and less so for wild than hatchery Chinook Salmon (Gosselin et al. 2018b). Thus, a date-based trigger may not be as germane as a biologically mechanistic index such as % dry mass. Given the convenience of a date-based trigger, it may be most suitable to continue its use but to consider a biological index as additional information in anticipation of seasons when calendar dates and ecological conditions may be uncorrelated.

Fish transportation can be an advantageous mitigation strategy for yearling Chinook Salmon as exemplified in the

current study and other studies (Gosselin et al. 2021) likely because of near 100% survival during barging (McMichael et al. 2011). However, there is still room for improvement because transportation does not yield improved SAR survival every year and for every species and rear type (Gosselin et al. 2018a) because of negative carryover effects to post-transport survival that outweigh the benefit of near-perfect survival downstream in barges. It is, thus, important to understand the specific mechanisms underlying these negative carryover effects, which may be missed when applying a date-based trigger to every species and every year.

Moreover, managing conditions in hatcheries and tributaries to optimize smoltification and lipid levels at estuarine and marine entrance could also improve SAR survival. These conditions may relate to how the fish are reared, food availability, and growth rates achieved, on a case-by-case basis, given the variation among populations and hatcheries (Beckman et al. 1999, Björnsson et al. 2011). Managing conditions in hatcheries and tributaries is no small feat, but even recognizing when smolt development is advanced and fish physical condition is conducive to lower predation risk could help with management decisions. Information on fish condition indices could be useful for refining the date of juvenile transportation to when it is likely advantageous to SAR survival.

Study limitations and future studies

It is important to interpret our findings while acknowledging our limited sample sizes and other types of data that could be useful to examine in association with SAR survival. Our field sampling of yearling Chinook Salmon was all conducted within 1 y and, thus, may reflect unique conditions in that year. For example, fish likely experienced relatively warm and low-flow conditions during their 1st y of life in 2015 and a yearling life stage in warm temperatures and average flow in 2016 (see river temperature and flow data at <http://cbr.washington.edu/dart>), but exact conditions experienced could also depend on their specific hatchery rearing conditions. Thus, generalizing the findings and hypotheses of this study would require additional years of research. Adding another covariate to the model to account for genetic identification may also help to explain differences by stock origin as fish migrate through the system by pulses of releases (Appendix S1). Furthermore, including wild Chinook Salmon and other species, such as steelhead and Sockeye Salmon, would provide more information on how to define decision triggers that optimize juvenile transportation for all species and rearing types. For example, differences in the relationships between SAR survival and % dry mass likely occur between hatchery and wild salmon because of differences in their rearing conditions and consequent body composition and behaviors (Beckman et al. 2000, Larsen et al. 2006).

We found that fork length was one of the least important predictors of SAR survival, whereas other studies using the same stocks found this relationship to be one of the most important among the predictors examined (Faulkner et al. 2019, Gosselin et al. 2021). It is possible that our fork length index, observed from our field samples, was not representative of fork length of the PIT-tagged fish. This discrepancy in findings related to SAR survival and fork length is especially relevant to fish at BON, in which PIT-tagged fish are mostly from the Snake River, whereas untagged fish are mostly from other rivers and streams (R. Absolon and B. Sandford, Northwest Fisheries Science Center, National Oceanic and Atmospheric Administration Fisheries, Pasco, Washington, personal communication). Unfortunately, few PIT-tagged, hatchery Chinook Salmon were measured at the dams, precluding a comparison with our field collected samples. In the PIT-tagged data set, only 3 fish were measured at LGR, 1 fish was measured at BON, and no fish were measured at ICH. More years of sampling would be needed to resolve the importance of fork length to survival in comparison with other biological indices. It is still noteworthy that other indices may be better predictors than fork length and that differences may exist between tagged and untagged fish. If physiological indices, such as % dry mass, are indeed better predictors than fork length, the ability to measure such fish condition indices in a timely and non-lethal manner in the field is critical to developing in-season decision triggers (e.g., pilot study on Quantitative Magnetic Resonance Imaging, see Appendix S2, Fig. S3).

It is important to determine and periodically re-evaluate suitable seasonal indices because decision triggers (or thresholds) are essential to both evidence-based management and applied sciences (Addison et al. 2016, Larned and Schallenberg 2019, Munsch et al. 2020). The best decision triggers require a good understanding of ecosystem processes and how those processes change (e.g., by relying primarily on a date-based trigger and incorporating additional biological indices, such as % dry mass). By design, these triggers should offer decision makers a way to assess the conditions of a system and gain greater clarity about when, where, and under what conditions a management action is beneficial. Accordingly, decision triggers increase transparency around the reasons for management interventions or why there was deliberate inaction. With more real-time monitoring, along with data and evidence to support management decisions, the need for guess work and any inaction due to uncertainty can both be minimized. In the long run, the cost-effectiveness of proactive decisions outweighs those of reactive decisions, thereby eliciting better conservation and management outcomes.

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Author contributions: JLG and JJA conceived and designed the research study. JLG, BLS, MAM, BPS, and LAW collected

the data. JLG analyzed the data, and JLG and BPS interpreted the data. JLG, JJA, BLS, MAM, BPS, and LAW wrote the paper.

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